THIRD
EDITION

Systematics
Taxonomy
Natural History
Conservation

VERTEBRATE
Biology

Donald W. Linzey

VERTEBRATE BIOLOGY

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Systematics, Taxonomy, Natural History, and Conservation

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To my wife, Nita, who has supported my academic and personal interests, and whose love and enduring patience have made this work possible

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PREFACE

Vertebrate biology is a vast and diverse field in which changes are constantly occurring, new research is continually being published, and new species are continually being discovered (and, unfortunately, some species are becoming extinct). As discoveries are made, old concepts fade away and new ones emerge. We are now at a point in time where acceptable solutions must be found to major environmental problems such as global warming, fragmentation of habitats, isolation of populations, and the decline in biodiversity—all of which play a role in the distribution and abundance of vertebrate populations. This is why vertebrate biology is so important: it is an opportunity for you to learn about the organisms most closely related to humans with whom we share this ever-more-crowded planet.

Vertebrate biology is a broad field: there is no reason to ignore parts that may be currently unpopular or that do not engage us personally. We will use information from physical sciences such as chemistry and geology as well as from a wide variety of biological specializations such as botany, genetics, cell biology, physiology, anatomy, and ecology. I have tried to achieve balance in terms of the whole field of vertebrate biology: systematics, paleontology, physiology, ecology, and so on. I have also tried to achieve balance both taxonomically and geographically.

Vertebrate Biology is designed to provide a firm foundation for students interested in the natural history of vertebrates. A course in vertebrate biology can be the gateway to an exciting and gratifying career. It may lead one person to specialize in a field like ichthyology, herpetology, ornithology, or mammalogy, while another may wish to work in a broader field like ecology, conservation, or wildlife management. Still others may become museum curators, writers, or videographers. As an instructor of vertebrate biology courses, I recognize the rewards and challenges in providing a strong foundation for persons with interests in each of these fields.

This third edition has been completely revised and updated to reflect the most recently published research. New illustrations have been added to complement those already in the text. A color plate section of 32 photographs and illustrations has been added. The bibliography, websites, and selected readings have all been updated and expanded.

Vertebrate Biology has provided a firm foundation for a wide array of students, teachers, and researchers in many countries for more than 20 years. It is my sincere hope that it will continue to do so for many years to come.

* * *

I wish to thank all of the many scientists, researchers, colleagues, and photographers who have graciously allowed me to use their data and/or photographs as well as those who offered beneficial comments to strengthen the third edition. Many of their contributions have been incorporated into this work.

I am also grateful to the many individuals at Johns Hopkins University Press, especially Tiffany Gasbarrini, Senior Science Editor, and Esther Rodriguez, Editorial Assistant, for their help in producing the third edition. Copyeditor Carrie Love is the most meticulous person with whom I have ever worked. Her dedicated efforts have strengthened the manuscript.

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Finally, I thank my wife, Nita, for putting up with the piles of books, correspondence, and manuscript chapters that cluttered several rooms of our home for many months. Her understanding, patience, and computer expertise, as well as assuming many of the chores around our home to allow me additional time to work on the manuscript, made the revision of this book possible.

VERTEBRATE BIOLOGY

1 | The Vertebrate Story

An Overview

Treat the earth well: it was not given to you by your parents, it was loaned to you by your children. We do not inherit the Earth from our Ancestors, we borrow it from our Children.

Native American Proverb

INTRODUCTION

Life on Earth began some 3.5 billion years ago (Bya), when a series of reactions culminated in a molecule that could reproduce itself. Although life forms may exist elsewhere in our universe or even beyond, life as we know it occurs only on the planet Earth. From this beginning has arisen all of the vast variety of living organisms—viruses, bacteria, fungi, protozoans, plants, and multicellular animals—which inhabit all parts of our planet. The diversity of life and the ability of life forms to adapt to seemingly harsh environments are astounding. Bacteria live in the hot thermal springs in Yellowstone National Park and in the deepest parts of the Pacific Ocean. Plants inhabit the oceans to the lower limit of light penetration and also cover land areas from the tropics to the icepacks in both the Northern and Southern hemispheres. Unicellular and multicellular animals are found worldwide. Life on Earth is truly amazing.

Vertebrates, which have been a part of the Earth's fauna for more than 500 million years, have evolved into many different groups, which have successfully adapted to virtually every habitat. They can swim, crawl, walk, run, climb, glide, and fly. Insects (phylum Arthropoda: class Insecta) are the only other group in the Animal Kingdom whose evolution surpasses that of the vertebrates in terms of global distribution and adaptation to such a wide variety of habitats.

Humans are vertebrates and represent one of the most recent products in the evolution of placental mammals. Although the first modern humans—*Homo sapiens sapiens* (as "Cro-Magnon" man)—appeared only about 165,000 years ago in Africa, the impact that our species has made has been greater than that of any other species in the history of the Earth. Not only have humans had a direct impact on many other species (extirpation, extinction, propagation, and dispersal), but indirect actions by humans may ultimately threaten the continued existence of vertebrates and even life as we know it. Activities that threaten biodiversity, like destruction of the rain forests, damaging of the ozone layer, global warming, production of acid rain, and pollution of waterways, are major global concerns. Humanity ultimately may determine whether *Homo sapiens* and all other organisms on Earth will continue to survive. The fate of 500 million years of vertebrate evolution seemingly rests with one species.

Our knowledge of the processes that create and sustain life has grown over the years and continues to grow steadily as new discoveries are announced by scientists. But much remains to be discovered—new species, new drugs, improved understanding of basic processes, and much more.

* * *

All forms of life are classified into five major groups known as **kingdoms**. The generally recognized kingdoms are Monera (bacteria), Fungi (fungi), Protista (single-celled organisms), Plant (plants), and Animal (multicellular animals). Within each kingdom, each group of organisms with similar characteristics is classified into a category known as a **phylum**.

Whereas many members of the Animal Kingdom possess skeletal, muscular, digestive, respiratory, nervous, and reproductive systems, there is only one group of multicellular animals that possesses the following combination of structures: (1) a dorsal, hollow nerve cord; (2) a flexible supportive rod (notochord) running longitudinally through the dorsum just ventral to the nerve cord; (3) pharyngeal slits or pharyngeal pouches;

and (4) a postanal tail. These morphological characteristics may be transitory and may be present only during a particular stage of development, or they may be present throughout the animal’s life. This group of animals forms the phylum **Chordata**. This phylum is divided into three **subphyla**: Urochordata, Cephalochordata, and Craniata. The Urochordata and Cephalochordata consist of small, nonvertebrate marine animals and are often referred to collectively as protochordates. To clearly understand and compare their evolutionary significance in relation to the vertebrates, it is necessary to briefly discuss their characteristics.

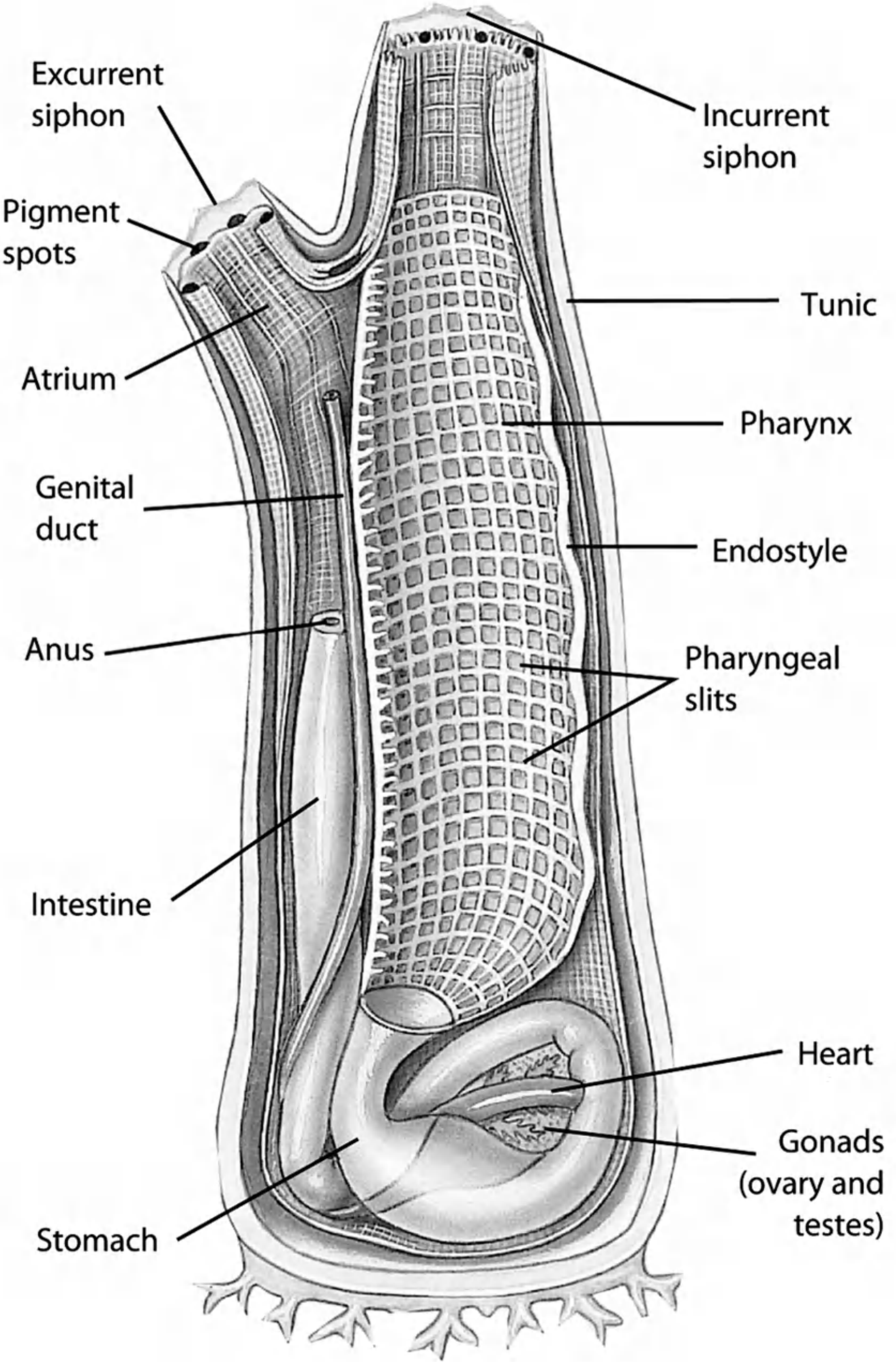
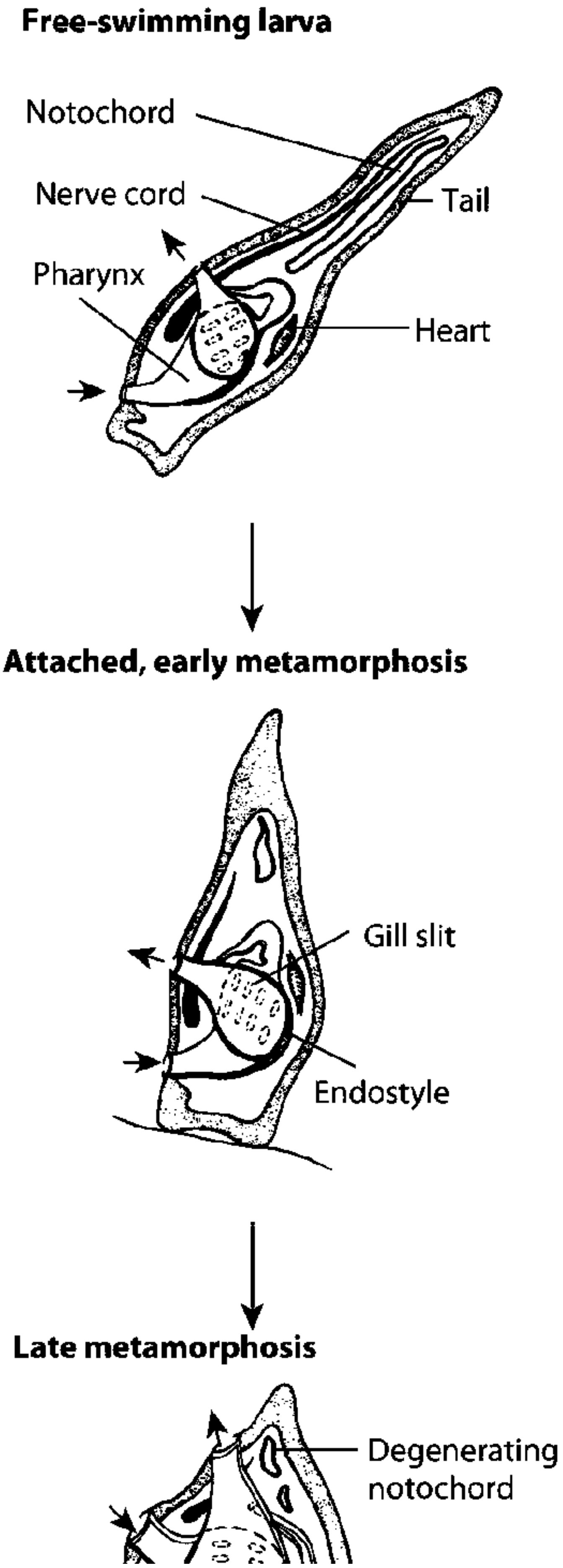


Figure 1.1. Structure of a tunicate, *Ciona* sp.

Subphylum **Urochordata** (tunicates): Adult tunicates, also known as sea squirts, are mostly sessile, filter-feeding marine animals whose gill slits function in both gas exchange and feeding (Fig. 1.1). Approximately 1,600 extant species are known (Nelson, 2016). Water is taken in through an incurrent siphon, goes into a chamber known as the pharynx, and then filters through slits into the surrounding atrium. Larval tunicates, which are free-swimming, possess a muscular larval tail that is used for propulsion. This tail contains a well-developed notochord and a dorsal, hollow nerve cord. The name Urochordate is derived from the Greek *oura*, meaning “tail,” and the Latin *chorda*, meaning “cord”; thus, the “tail-chordates.” When the larva transforms or metamorphoses into an adult, the tail, along with its accompanying notochord and most of the nerve cord, is reabsorbed (Fig. 1.2).

Subphylum **Cephalochordata** (lancelet; amphioxus): Cephalochordates are small—usually less than 5 cm (2 in.) long—fusiform (torpedo-shaped) marine organisms that spend most of their time buried in sand in shallow water. Approximately 30 extant species are known (Nelson, 2016). Their bodies are oriented vertically, with the tail in the sand and the anterior end exposed. A well-developed notochord and long, dorsal, hollow nerve cord extend from the head (*cephalo* means “head”) to the tail and are retained throughout life. The numerous pharyngeal gill slits are used for both respiration and filter-feeding (Fig. 1.3). Cephalochordates have a superficial resemblance to the larvae of lampreys (ammocoete), which are true vertebrates.



Free-swimming larva
Notochord
Nerve cord
Tail
Pharynx
Heart
Attached, early metamorphosis
Gill slit
Endostyle
Late metamorphosis
Degenerating notochord

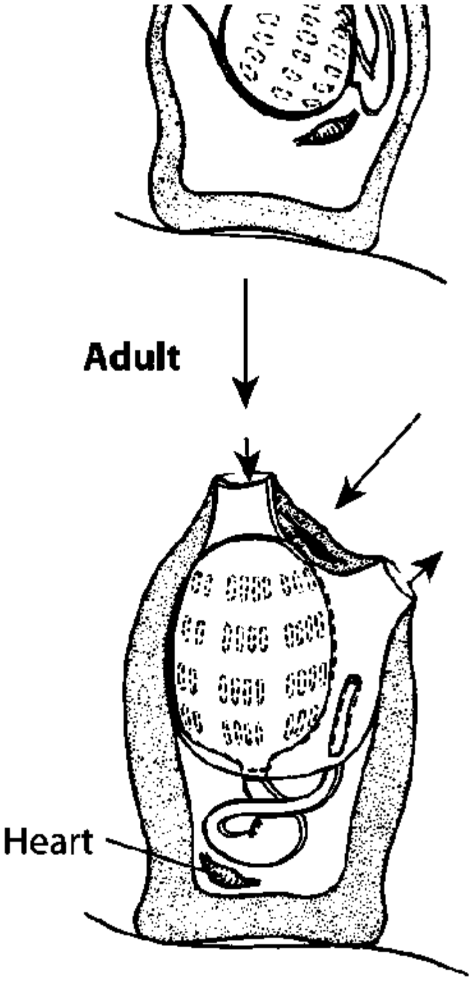
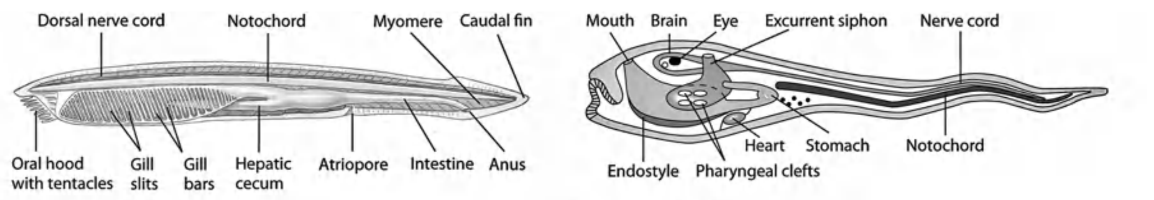
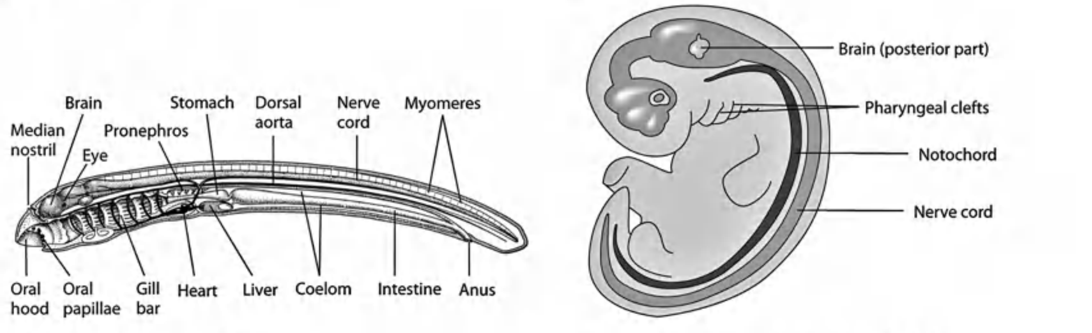


Figure 1.2. Metamorphosis of a free-swimming tunicate (class Ascidiacea) tadpole-like larva into a solitary, sessile adult. Note the dorsal nerve cord, notochord, and pharyngeal gill slits.



(a) Cephalochordate **(b) Larval tunicate**



(c) Larval lamprey (ammocoete) **(d) Tetrapod embryo, early development stage**

Figure 1.3. Three chordate characters (dorsal tubular nerve cord, notochord, and pharyngeal clefts) as seen in (*a*) a cephalochordate (amphioxus), (*b*) a larval tunicate, (*c*) a larval lamprey, and (*d*) a tetrapod embryo.

Serially arranged blocks of muscle known as **myomeres** occur along both sides of the body of the lancelet. Because the notochord is flexible, alternate contraction and relaxation of the myomeres bend the body and propel it. Other similarities to vertebrates include a closed cardiovascular system with a two-chambered heart, similar muscle proteins, and the organization of cranial and spinal nerves. No other group of living animals shows closer structural and developmental affinities with vertebrates, but there are some fundamental differences. For example, the functioning units of the excretory system in cephalochordates are known as protonephridia. They represent a primitive type of kidney design that removes wastes from the coelom. In contrast, the functional units of vertebrate kidneys, which are known as nephrons, are designed to remove wastes by filtering the blood. What long had been thought to be ventral roots of spinal nerves in cephalochordates have now been shown to be muscle fibers (Flood, 1966). Spinal nerves alternate on the two sides of the body in cephalochordates rather than lying in successive pairs as they do in vertebrates (Hildebrand and Goslow, 2001).

Subphylum **Craniata** consists of individuals possessing a cranium, a well-developed brain, 10 to 12 pairs of cranial nerves, and an epidermis composed of several layers of cells. Cartilaginous or bony vertebrae are usually present. (The term **Craniata**, although commonly equated with **Vertebrata**, is preferred by many authorities because it recognizes that some jawless vertebrates have a cranium but no vertebrae.) Nephridia are absent. The subphylum is composed of two infraphyla: **Myxinomorphi** (hagfishes) and **Vertebrata** (vertebrates). Hagfishes are thought to be the sister group of vertebrates and to be the most primitive known craniate taxon. Extant hagfishes are excluded from the Vertebrata by some authorities primarily because they lack arcualia (embryonic or rudimentary vertebral elements) (Nelson, 2016).

Infraphylum **Myxinomorphi** (hagfishes) have an eel-like body, no paired fins, no dorsal fin, and no trace of a lateral-line system in adults. Neuromasts are absent, and the eyes are degenerate. One to sixteen pairs of external gill openings are present. Hagfishes are unique among vertebrates in having only one semicircular canal, which is oriented so that it projects onto all three planes of rotation (J. M. Jorgensen, 1998; McVean, 1998).

Infraphylum **Vertebrata** (vertebrates) are chordates with a “backbone”—either a persistent notochord as in lampreys or a vertebral column of cartilaginous or bony vertebrae that more or less replaces the notochord as the main support of the long axis of the body (Fig. 1.4). All vertebrates possess a cranium, or braincase, of cartilage or bone, or both. The cranium supports and protects the brain and major special sense organs. In addition, all vertebrate embryos pass through a stage when pharyngeal pouches are present (see Fig. 1.3). Most living forms of vertebrates also possess paired appendages and limb girdles.

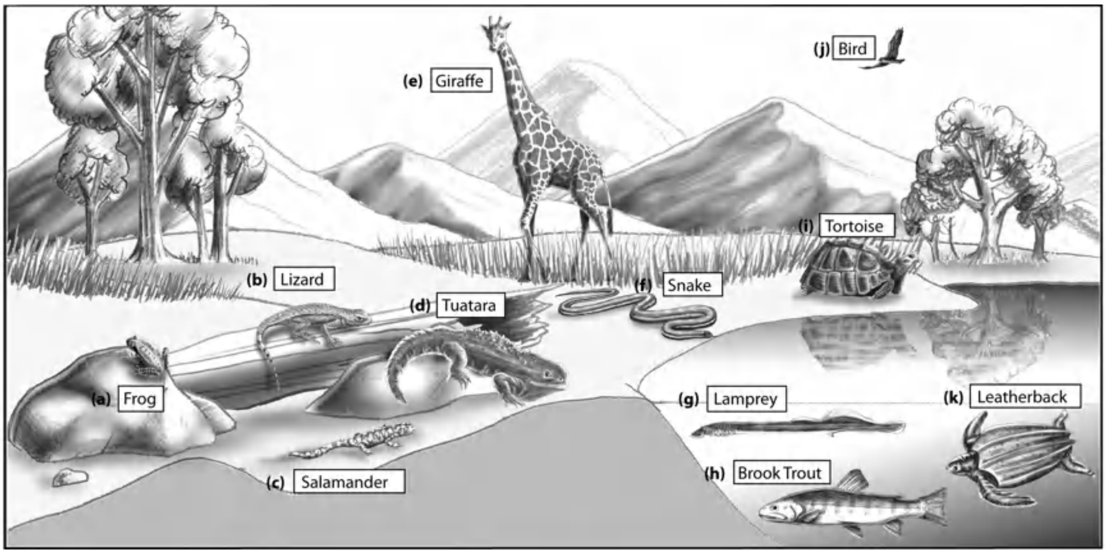


Figure 1.4. Representative vertebrates: (*a*) wood frog, class Amphibia; (*b*) fence lizard, class Reptilia; (*c*) spotted salamander, class Amphibia; (*d*) tuatara, class Reptilia; (*e*) giraffe, class Mammalia; (*f*) garter snake, class Reptilia; (*g*) lamprey, class Cephalaspidomorphi; (*h*) brook trout, class Osteichthyes; (*i*) gopher tortoise, class Reptilia; (*j*) red-tailed hawk, class Reptilia; (*k*) leatherback sea turtle, class Reptilia.

Vertebrate classification is ever-changing as relationships among organisms are continually being clarified. For example, hagfishes and lampreys, which were formerly classified together, each have numerous unique characters that are not present in the other. They have probably been evolving independently for many millions of years. Reptiles are no longer a valid taxonomic category because they have not all arisen from a common ancestor (monophyletic lineage). Recent research, led by the American Museum of Natural History (Barrowclough et al., 2016), suggests that there are about 18,000 bird species in the world—nearly twice as many as previously thought. The work focuses on "hidden" avian diversity—birds that look similar to one another, or were thought to interbreed, but are actually different species. Although differences of opinion exist, most vertebrate biologists now divide the more than 66,000 living vertebrates (craniates)into the major groups depicted in Table 1.1.

Adult vertebrates range in size from the tiniest fishes—*Paedocypris progenetica*, a member of the carp family from Thailand that grows to less than 7.9 mm (0.3 in.) long, and *Photocorynus spiniceps*, with males as small as 6.2 mm (0.25 in.) (Fig. 1.5a, b, c)—to the tiniest amphibians—the New Guinea microhylid, *Paedophryne amauensis* with an average body size of 7.7 mm (0.3 in.), as well as the Brazilian brachycephalid frog, *Psyllophryne didactyla*, and the Cuban leptodactylid frog, *Eleutherodactylus iberia*, with total lengths of only 9.8 mm (0.38 in.)—and the tiniest reptiles—the Jaragua gecko (*Sphaerodactylus ariasae*), found only on Beata Island in the Caribbean, which is just a little more than 14 to 15 mm (0.5 in.) (Fig. 1.6), and the threadsnake (*Leptotyphlops carlae*) from Barbados, which averages only 100 mm (4 in.) in length (Fig. 1.7)—to the largest mammal—the blue whale (*Balaenoptera musculus*), which can attain a length of 30 m (98 ft.) and a mass of 123,000 kg (271,168 lb.) (Estrada and Hedges, 1996; Vergano, 1996; Pietsch, 2005; Kottelat et al., 2006; Hedges, 2008; Rittmeyer et al., 2012).

Wide-ranging and diverse, vertebrates successfully inhabit areas from the Arctic (e.g., polar bears) to the Antarctic (e.g., penguins). During the course of vertebrate evolution, which dates back some 500 million years, species within each vertebrate group have evolved unique anatomical, physiological, and behavioral characteristics that have enabled them to successfully occupy a wide variety of habitats. Many vertebrates are aquatic (living in salt water or fresh water); others are terrestrial (living in forests, grasslands, deserts, or tundra). Some forms, like blind salamanders (*Typhlomolge*, *Typhlotriton*, *Haideotriton*), mole salamanders (*Ambystoma*), caecilians (Gymnophiona), and moles (Talpidae), live beneath the surface of the Earth and spend most or all of their lives in burrows or caves.

Table 1.1. Major Groups of Living Craniates

Group	Number of Species (approx.)
Hagfishes (Myxinoidea)	78
Lampreys (Petromyzontida)	40
Sharks, skates/rays, and ratfish (Chondrichthyes)	1,423
Lobe-finned fishes (Sarcopterygii)	8
Ray-finned fishes (Actinopterygii)	30,500

Group	Number of Species (approx.)
Salamanders, caecilians (Lissamphibia)	931
Frogs (Anura)	6,973
Turtles (Anapsida or Testudines)	340
Diapsids (Diapsida), tuatara, lizards, snakes (Lepidosauria)	9,400
Crocodiles, birds (Archosauromorpha)	10,736
Mammals (Synapsida)	6,399
Total	66,828

(a)

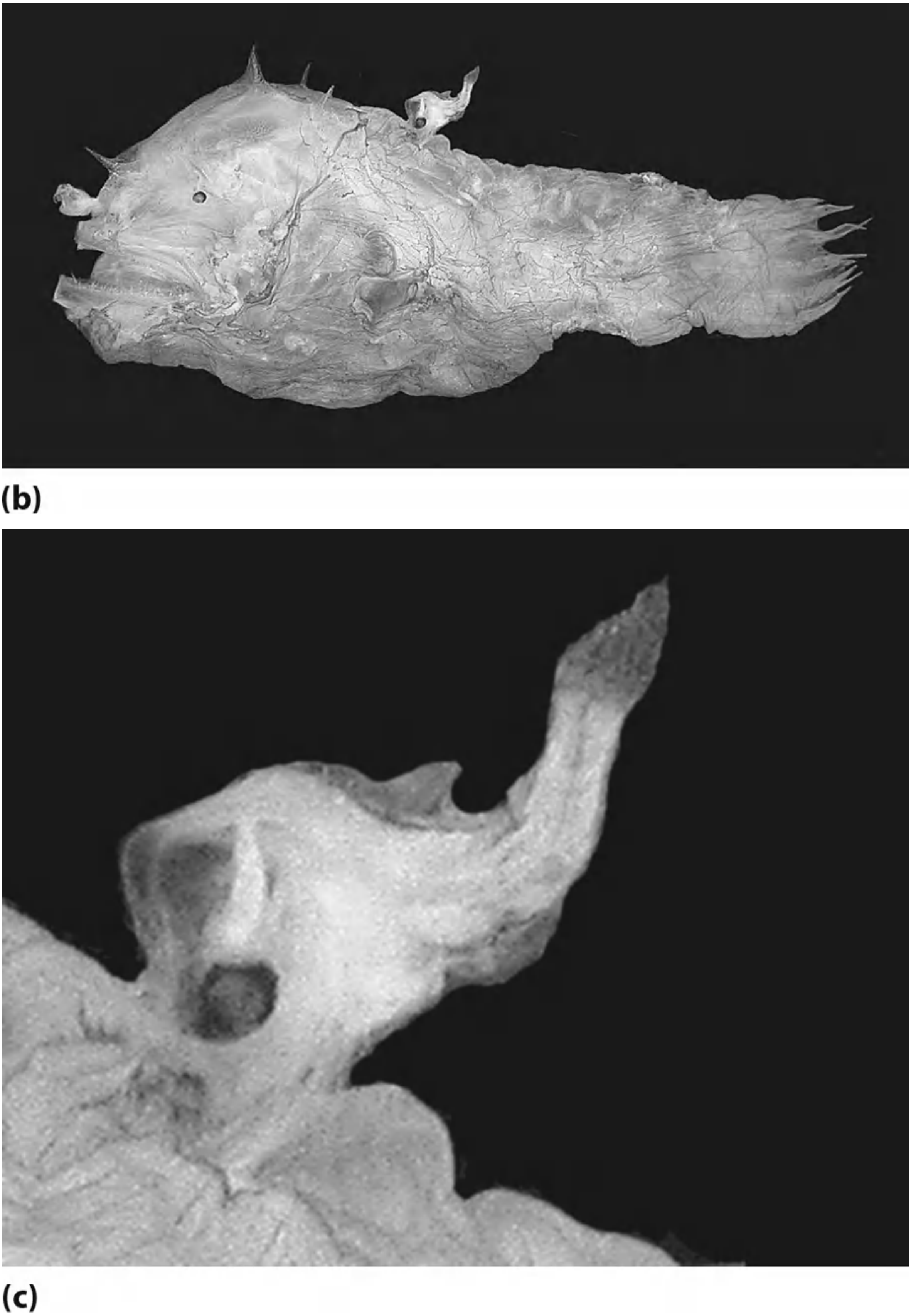


Figure 1.5. (*a*) *Paedocypris progenetica*. (*b*) A male anglerfish (*Photocorynus spiniceps*) fused to the back of a much larger female. Males bite into females and fuse for life. They supply sperm; females supply eggs, food, and locomotion. (*c*) Enlargement of male anglerfish.

(a)

(b)

Figure 1.6. (*a*) *Paedophryne amauensis*, the world's smallest frog and the smallest known animal with a backbone. (*b*) The Jaragua gecko (*Sphaerodactylus ariasae*), the smallest known lizard.

Most fishes, salamanders, caecilians, frogs, turtles, and snakes are unable to maintain a constant body temperature independent of their surrounding environmental temperature. Thus, they have a variable body temperature, a condition known as **poikilothermy**, derived from heat acquired from the environment, a situation called **ectothermy**. Although lizards are poikilothermic, many species are very good thermoregulators. Birds and mammals, on the other hand, are able to maintain relatively high and relatively constant body temperatures, a condition known as **homeothermy**, using heat derived from their own oxidative metabolism, a situation called **endothermy**. During periods of inactivity during the summer (**torpor**) or winter (**hibernation**), some birds and mammals often become poikilothermic. Under certain conditions, some poikilotherms, like pythons (*Python*), are able to increase their body's temperature above that of the environmental temperature when incubating their clutch of eggs (see discussion of parental care in Chapter 7).

Figure 1.7. The threadsnake (*Leptotyphlops carlae*), the world's smallest known snake.

VERTEBRATE FEATURES

Although vertebrates have many characteristics in common, they are very diverse in body form, structure, and the manner in which they survive and reproduce. A brief overview and comparison of these aspects of vertebrate biology at this point, as well as the introduction of terminology that applies to all classes, will provide a firm foundation for more substantive discussions throughout the remainder of the text. Specific adaptations of each class are discussed in Chapters 3–5 and 7–9.

Body Form

Most fishes are fusiform (Fig. 1.8a), which permits the body to pass through the dense medium of water with minimal resistance. The tapered head grades into the trunk with no constriction or neck, and the trunk narrows gradually into the caudal (tail) region. The greatest diameter is near the middle of the body. Various modifications on this plan include the dorsoventrally flattened bodies of skates and rays, the laterally compressed bodies of angelfish, and the greatly elongated (anguilliform) bodies of eels (Fig. 1.8g). Many larval amphibians also possess a fusiform body; however, adult salamanders may be fusiform or anguilliform. Aquatic mammals, like whales, whose ancestral forms reinvaded water, also tend to be fusiform.

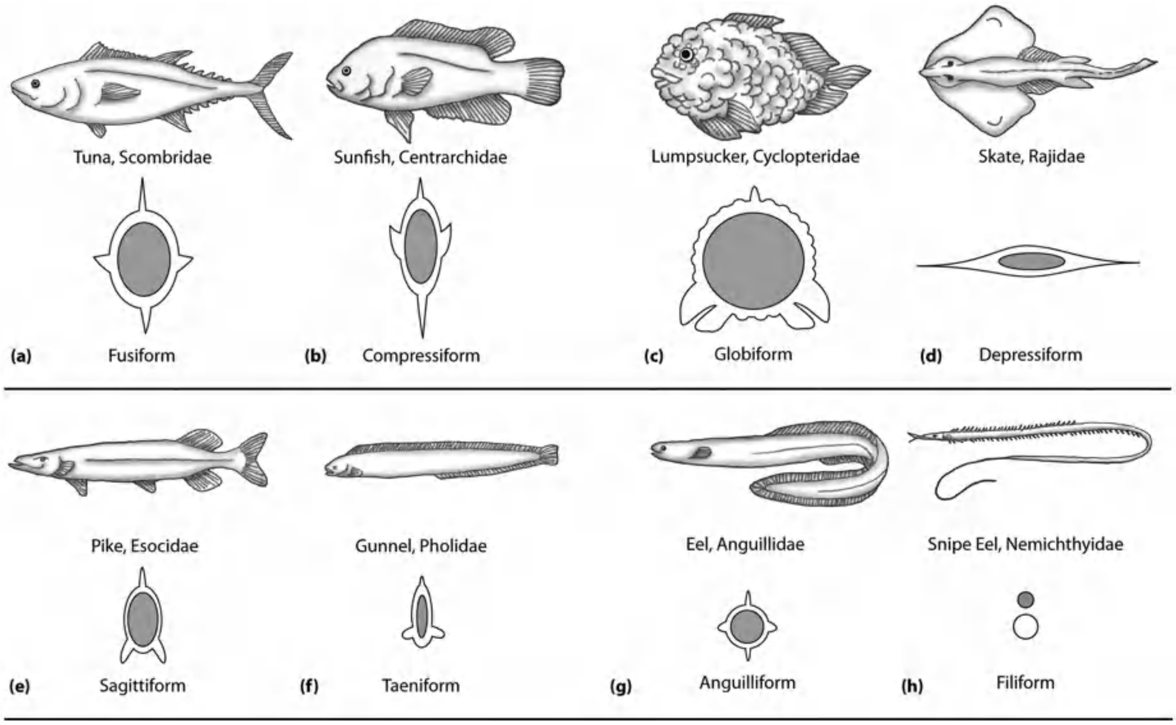


Figure 1.8. Representative body shapes and typical cross sections of fishes: (*a*) fusiform (tuna, Scombridae); (*b*) compressiform (sunfish, Centrarchidae); (*c*) globiform (lumpsucker, Cyclopteridae); (*d*) depressiform (skate, Rajidae), dorsal view; (*e*) sagittiform (pike, Esocidae); (*f*) taeniform (gunnel, Pholidae); (*g*) anguilliform (eel, Anguillidae); (*h*) filiform (snipe eel, Nemichthyidae).

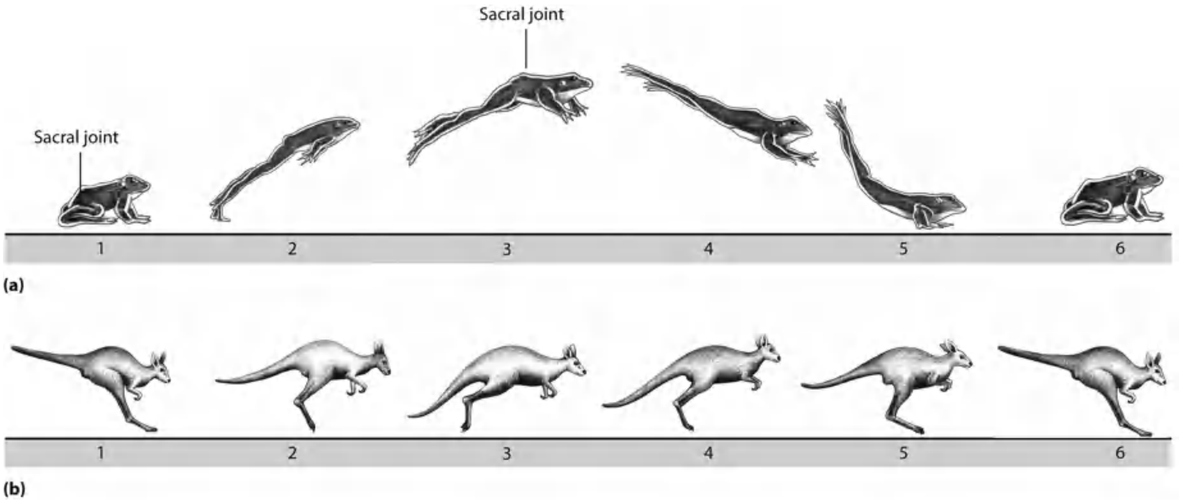


Figure 1.9. Saltatorial locomotion in (*a*) a frog and (*b*) a kangaroo. Saltatorial locomotion provides a rapid means of travel, but requires enormous development of hindlimb muscles. The large, muscular tail of the kangaroo is used for balance.

As vertebrates evolved, changes to terrestrial and aerial locomotion brought major modifications in body form. The head became readily movable on the constricted and more or less elongated neck. The caudal region became progressively constricted in diameter, but usually remained as a balancing organ. The evolution of bipedal locomotion in ancestral reptiles and in some lines of mammals brought additional changes in body form. Saltatorial (jumping) locomotion is well developed in modern anuran amphibians (frogs and toads), and it brought additional shortening of the body, increased development of the posterior appendages, and loss of the tail (Fig. 1.9a). In saltatorial mammals like kangaroos and kangaroo rats, the tail has been retained to provide balance (Fig. 1.9b). Elongation of the body and reduction or loss of limbs occurred in some lineages (caecilians, legless lizards, snakes) as adaptations for burrowing.

Aerial locomotion occurred in flying reptiles (pterosaurs), and it is currently a method of locomotion in birds and some mammals. Although pterosaurs became extinct, flying has become the principal method of locomotion in birds and bats. The bodies of gliding and flying vertebrates tend to be shortened and relatively rigid, although the neck is quite long in many birds (see Fig. 8.9).

Integument

The skin of vertebrates is composed of an outer layer known as **epidermis** and an inner layer known as **dermis** and serves as the boundary between the animal and its environment. Among vertebrates, skin collectively functions in protection, temperature regulation, storage of calcium, synthesis of vitamin D, maintenance of a suitable water and electrolyte balance, excretion, gas exchange, defense against invasion by microorganisms, reception of sensory stimuli, and production of pheromones (chemical substances released by one organism that influence the behavior or physiological processes of another organism). The condition of an animal's skin often reflects its general health and well-being. Significant changes, particularly in the epidermis, occurred as vertebrates adapted to life in water and later to the new life on land.

The entire epidermis of fishes consists of living cells. Numerous epidermal glands secrete a mucous coating that retards the passage of water through the skin, resists the entrance of foreign organisms and compounds, and reduces friction as the fish moves through water. The protective function of the skin is augmented by dermal scales in most fishes.

The move to land brought a subdivision of the epidermis into an inner layer of living cells, called the **stratum germinativum**, and an outer layer of dead cornified cells, called the **stratum corneum**. In some vertebrates, an additional two to three layers may be present between the stratum germinativum and stratum corneum. The stratum corneum is thin in amphibians, but relatively thick in the more terrestrial lizards, snakes, crocodilians, birds, and mammals, where it serves to retard water loss through the skin. Terrestrial vertebrates developed various accessory structures to their integument like scales, feathers, and hair as adaptations to life on land. Many ancient amphibians were well covered with scales, but dermal scales occur in modern amphibians only in the tropical, legless, burrowing caecilians, in which they are rudimentary or degenerate (vestigial) and embedded in the dermis. The epidermal scales of turtles, lizards, snakes, and crocodilians serve in part to reduce water loss through the skin, provide protection from aggressors, and, in some cases (snakes), aid in locomotion. The evolution of endothermy in birds and mammals is associated with epidermal insulation that arose with the development of feathers and hair, respectively. Feathers are modified reptilian scales that provide an insulative and contouring cover for the body; they also form the flight surfaces of the wings and tail. Unlike feathers, mammalian hair is an evolutionarily unique epidermal structure that serves primarily for protection and insulation.

Figure 1.10. The interlocking plates of the nine-banded armadillo (*Dasypus novemcinctus*) provide protection for the back and soft undersides. Armadillos, which can run rapidly and burrow into loose soil with lightning-like speed, are also good swimmers.

Some land vertebrates have epidermal scales underlain by bony plates to form a body armor. For example, turtles have been especially successful with this type of integumental structure. Among mammals, armadillos (*Dasypus*) and pangolins (*Manis*) have similar body armor (Fig. 1.10). Cornified (keratinized) epidermal tissue has been modified into various adaptive structures in terrestrial vertebrates, including scales, feathers, and hair. The tips of the digits are protected by this material in the form of claws, nails, or hooves. The horny beaks of turtles, birds, and various extinct diapsids have the same origin.

Skeleton

The central element of the skeleton is the vertebral column, which is made up of individual vertebrae. There is no typical vertebra; a composite is shown in Fig. 1.11. Each vertebra consists of a main element, the centrum, and various processes. The vertebral column of fishes consists of trunk and caudal vertebrae, whereas in tetrapods (four-legged vertebrates), the vertebral column is differentiated into a neck (cervical) region, trunk region, sacral region, and tail (caudal) region. In some lizards and in birds and mammals, the trunk is divided into a rib-bearing thoracic region and a ribless lumbar region. Two or more sacral vertebrae often are fused in tetrapods for better support of body weight through the attached pelvic girdle; this is carried to an extreme in birds with the fusion of lumbar, sacral, and some caudal vertebrae. Neural arches project dorsally to enclose and protect the nerve cord, and in fishes hemal arches project ventrally to enclose the caudal artery and vein.

The skull supports and protects the brain and the major special sense organs. In hagfishes, lampreys, and cartilaginous fishes, the skull is cartilaginous and is known as the **chondrocranium**, but in other vertebrates, bones of dermal origin invade the chondrocranium and tend to progressively obscure it. It is believed that primitive vertebrates had seven gill arches and that elements of the most anterior gill arch evolved into the vertebrate jaw, which was braced by elements of the second gill arch (see discussion in Chapter 4). As vertebrates continued to evolve, dermal plates enclosed the old cartilaginous jaw and eventually replaced it.

Teeth are associated with the skull, although they are derived embryologically from the integument and, functionally, are a part of the digestive system. The original function of teeth was probably simple grasping and holding of food organisms. These teeth were simple, conical, and usually numerous. All were similar in shape, a condition called **homodont dentition**. In fishes, teeth may be located on various bones of the palate and even on the tongue and in the pharynx, in addition to those along the margin of the jaw. Teeth adapted for different functions, a situation called **heterodont dentition**, have developed in most vertebrate lines from cartilaginous fishes to mammals (Fig. 1.12). The teeth of modern amphibians, lizards, snakes, and crocodilians are of the conical type. The teeth of mammals are restricted to the margins of the jaw and are typically (but not always) differentiated into **incisors** (chisel-shaped for biting), **canines** (conical for tearing flesh), **premolars** (flattened for grinding), and **molars** (flattened for grinding). Many modifications occur, like the tusks of elephants (modified incisors) and the tusks of walruses (modified canines). Teeth have been lost completely by representatives of some vertebrate lines, like turtles and birds, where the teeth have been replaced by a horny beak.

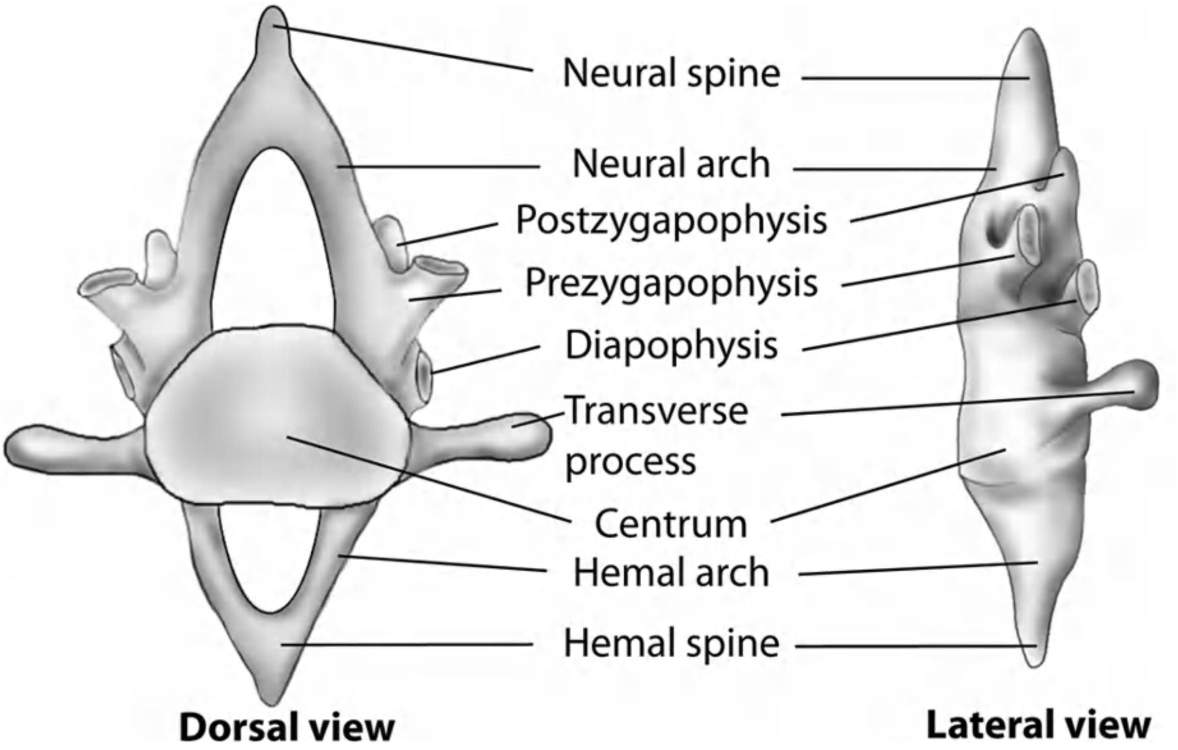


Figure 1.11. A composite vertebra. The neural arch is dorsal to the centrum and encloses the spinal cord. The hemal arch, when present, is ventral to the centrum and encloses blood vessels.

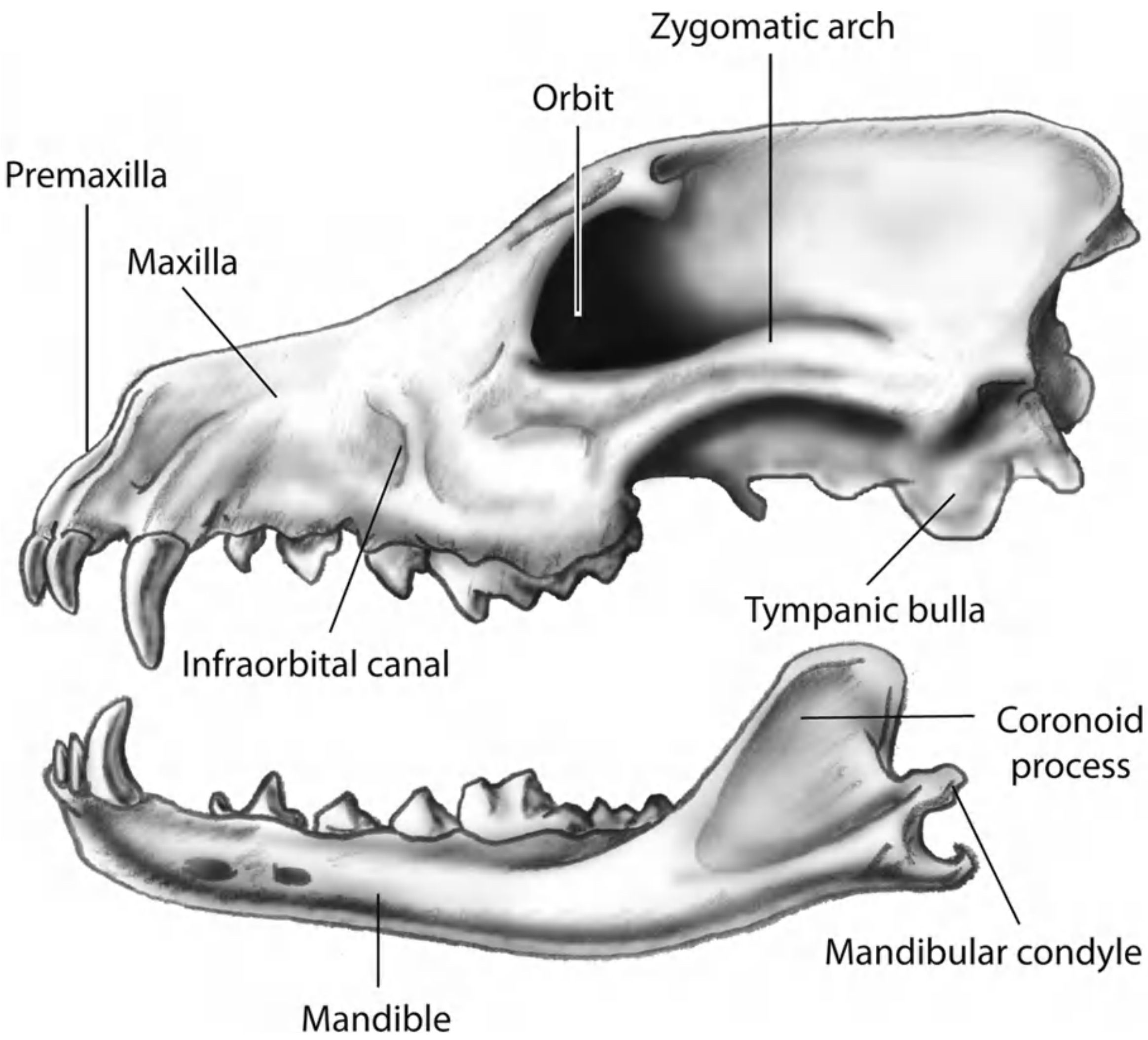


Figure 1.12. Heterodont dentition of a wolf (*Canis lupus*).

Appendages

All available evidence (Rosen et al., 1981; Forey, 1986, 1991; Panchen and Smithson, 1987; Edwards, 1989; Gorr et al., 1991; Meyer and Wilson, 1991; Ahlberg, 1995; Clack, 2006; and many others) suggests that tetrapods evolved from lobe-finned fishes; therefore, tetrapod limbs most likely evolved from the paired lobed fins. Fins of fishes typically are thin webs of membranous tissue, with an inner support of hardened tissue, which propel and stabilize the fish in its aquatic environment. With the move to land, the unpaired fins (dorsal, anal) were lost, and the paired fins became modified into limbs for support and movement. Lobe-finned fishes of today still possess muscular tissue that extends into the base of each fin and a fin skeleton that in ancestral forms could have been modified into that found in the limbs of tetrapods by losing some of its elements (Fig. 1.13). The earliest known amphibians had a limb skeletal structure intermediate between a lobe-finned fish and the limb skeleton of a terrestrial tetrapod.

Terrestrial limbs differ from fish fins in that the former are segmented into proximal, intermediate, and terminal parts, often with highly developed joints between the segments. Limbs of tetrapods generally contain large amounts of muscular tissue because their principal function is to support and move the body. Posterior limbs are usually larger than the anterior pair because they provide for rapid acceleration and often support a greater part of the body weight. Enormous modifications occurred in the types of locomotion used by tetrapods as they exploited the many ecological niches available on land; this is especially evident in mammals (Fig. 1.14). Mammals may be graviportal (adapted for supporting great body weight, e.g., elephants), cursorial (running, e.g., deer), volant (gliding, e.g., flying squirrels), aerial (flying, e.g., bats), saltatorial (jumping, e.g., kangaroos), aquatic (swimming, e.g., whales), fossorial (digging, e.g., moles), scansorial (climbing, e.g., gray squirrels), or arboreal (adapted for life in trees, e.g., monkeys). A drastic reduction in the number of functional digits tends to be associated with the development of running types of locomotion, as in various ancient diapsids, in ostriches among living birds, and in horses, deer, and their relatives among living mammals.

A similar structure found in two or more organisms may have formed either from the same embryonic tissues in each organism or from different embryonic tissues. A structure that arises from the same embryonic tissues in two or more organisms sharing a common ancestor is said to be **homologous**. Even though the limb bones may differ in size, and some may be reduced or fused, these bones of the forelimb and hindlimb of amphibians, diapsids, and mammals are homologous to their counterparts (Fig. 1.15a). The wings of insects and bats, however, are said to be **analogous** to one another (Fig. 1.15b). Although they resemble each other superficially and are used for the same purpose (flying), the flight surfaces and internal anatomy have different embryological origins.

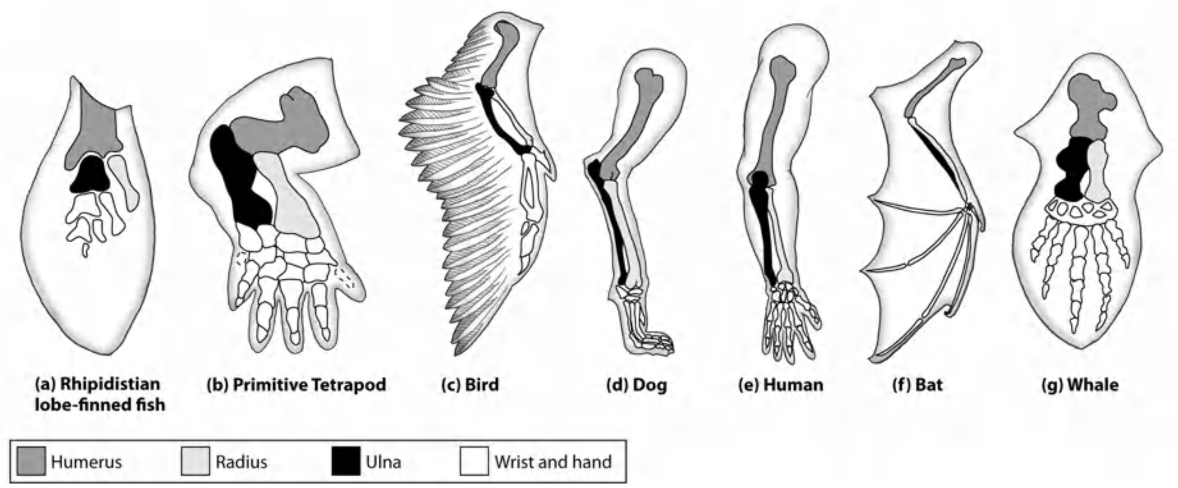


Figure 1.13. Homologous bones in the front limbs of various vertebrates: (*a*) rhipidistian lobe-finned fish (Eusthenopteron); (*b*) primitive tetrapod (Eryops); (*c*) bird; (*d*) dog; (*e*) human; (*f*) bat; (*g*) whale. *Key:* dark shading: humerus; light shading: radius; black: ulna; white: wrist and hand.

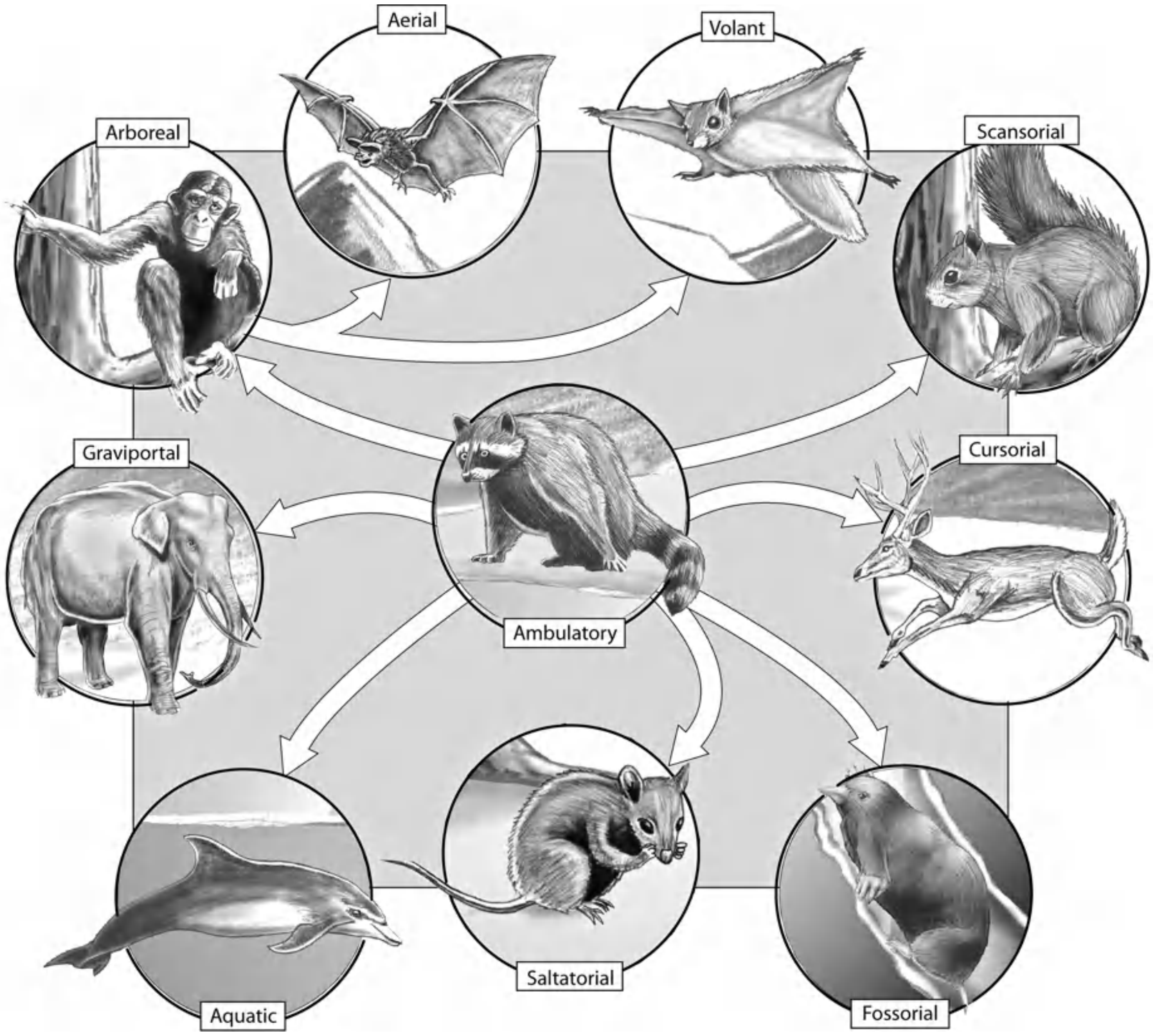
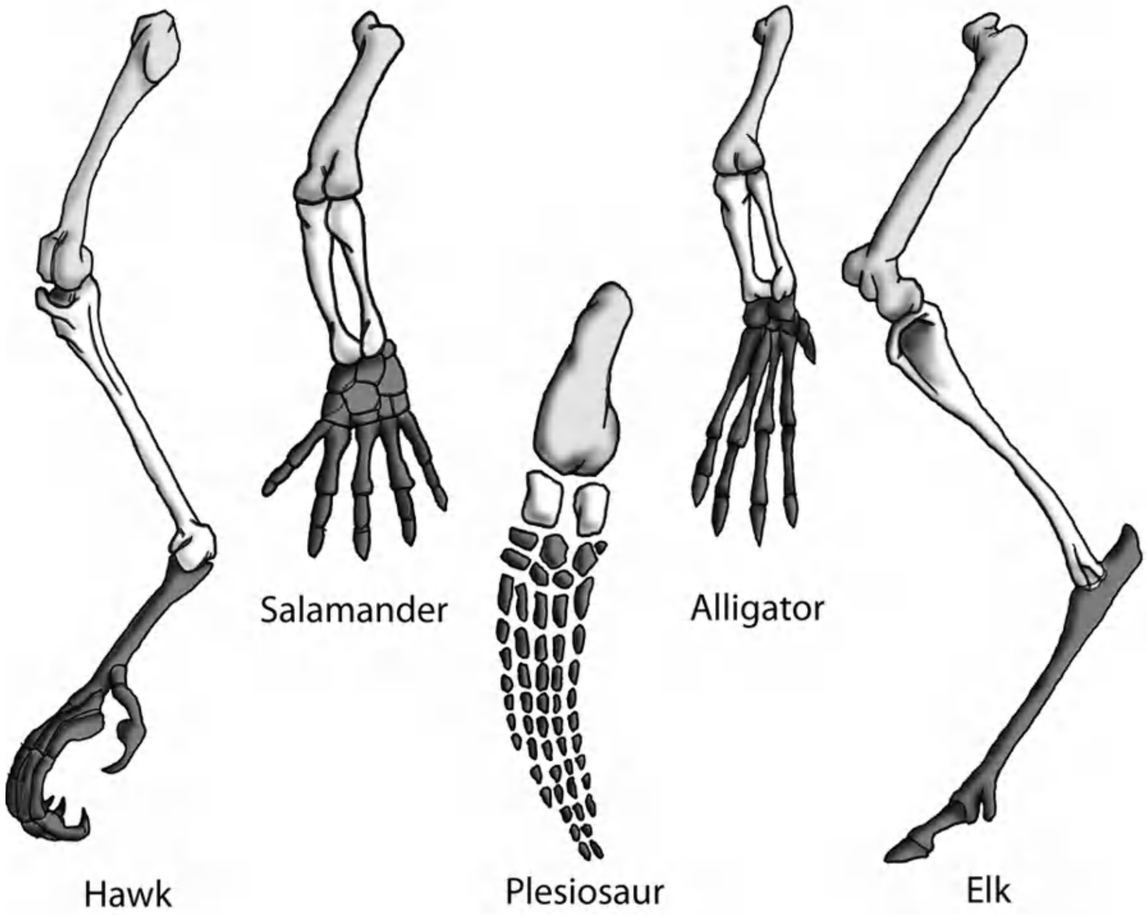


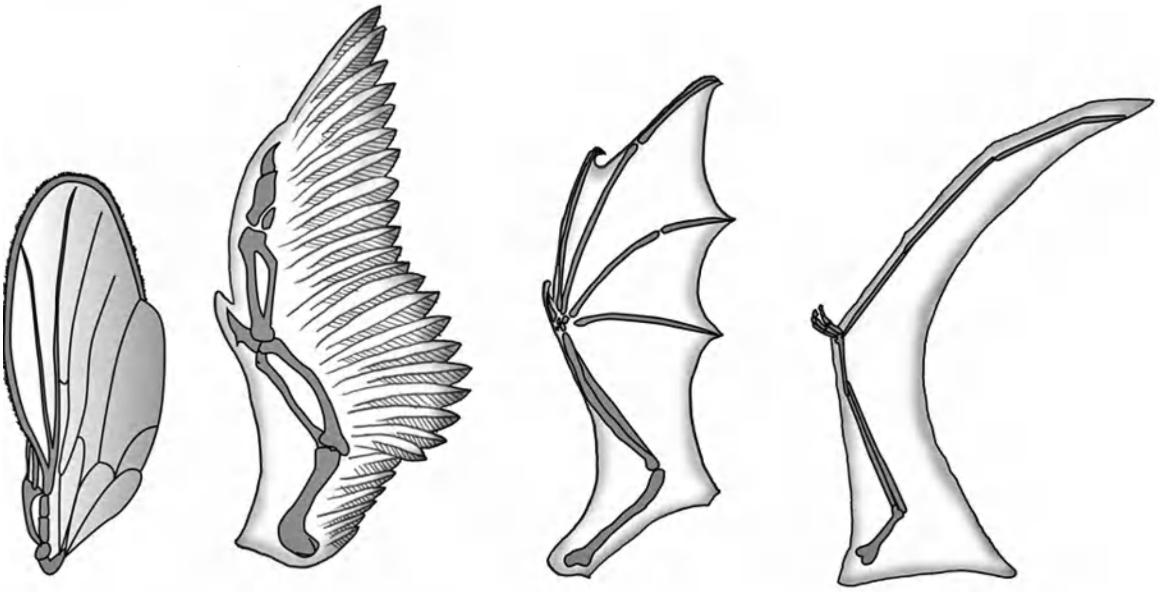
Figure 1.14. Types of locomotion in mammals. The specialized types of locomotion probably resulted from modifications of the primitive ambulatory (walking) method of locomotion.

The return of various lines of tetrapods to an aquatic environment resulted in modification of the tetrapod limbs into finlike structures, but without the loss of the internal tetrapod structure. This is seen in various lines of extinct plesiosaurs, as well as in sea turtles, in birds like penguins, and in mammals like whales, seals, and manatees. All are considered to be homologous structures because they arise from modifications of tetrapod limb-buds during embryogenesis.

The forelimbs of sharks, penguins, and porpoises provide examples of convergent evolution. When organisms that are not closely related become more similar in one or more characters because of independent adaptation to similar environmental situations, they are said to have undergone **convergent** evolution, and the phenomenon is called **convergence**. Sharks use their fins as body stabilizers; penguins use their “wings” as fins; porpoises, which are mammals, use their “front legs” as fins. All three types of fins have become similar in proportion, position, and function. The overall shape of penguins and porpoises also converged toward that of the shark. All three vertebrates have a streamlined shape that reduces drag during rapid swimming.



(a) Homology



(b) Analogy

Figure 1.15. (*a*) Homology: hindlimbs of a hawk, a salamander, a plesiosaur, an alligator, and an elk. Bones with the same intensity of shading are homologous, although they are modified in size and in details of shape by reduction or, even, fusion of bones (as in the elk and the hawk). Identical structures have been modified by natural selection to serve the needs of quite different animals. (*b*) Analogy: wings of an insect, a bird, a bat, and a pterosaur. In each, the flight surfaces and internal anatomy have different embryological origins; thus, the resemblances are only superficial and are not based on common ancestry or embryonic origin.

Musculature

The greatest bulk of the musculature of fishes is made up of chevron-shaped (*V*-shaped) masses of muscles (myomeres) arranged segmentally (metamerically) along the long axis of the body and separated by thin sheets of connective tissue known as **myosepta** (Fig. 1.16). A horizontal septum divides the myomeres into dorsal, or **epaxial**, and ventral, or **hypaxial**, muscles. Coordinated contractions of the body (axial) wall musculature provide the main means of locomotion in fishes. In the change to terrestrial life, the axial musculature decreased in bulk as the locomotory function was taken over by appendages and their musculature. The original segmentation became obscured as the musculature of the limbs and limb girdles (pectoral and pelvic) spread out over the axial muscles. In fishes, the muscles that move the fins are essentially within the body and are, therefore, **extrinsic** (originating outside the part on which it acts) to the appendages. As vertebrates evolved the abilities to walk, hop, or climb, many other muscles developed, some of which are located entirely within the limb itself and are referred to as **intrinsic** muscles. In flying vertebrates like birds and bats, the appendicular musculature reaches enormous development, and the axial musculature is proportionately reduced.

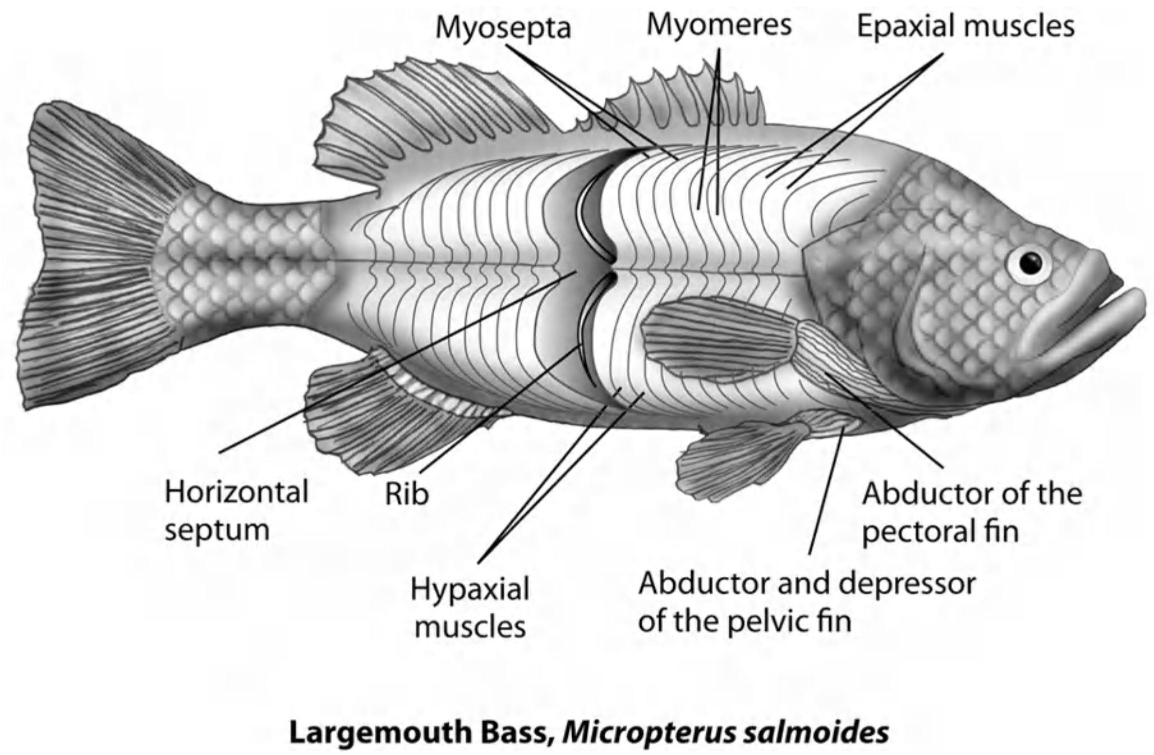
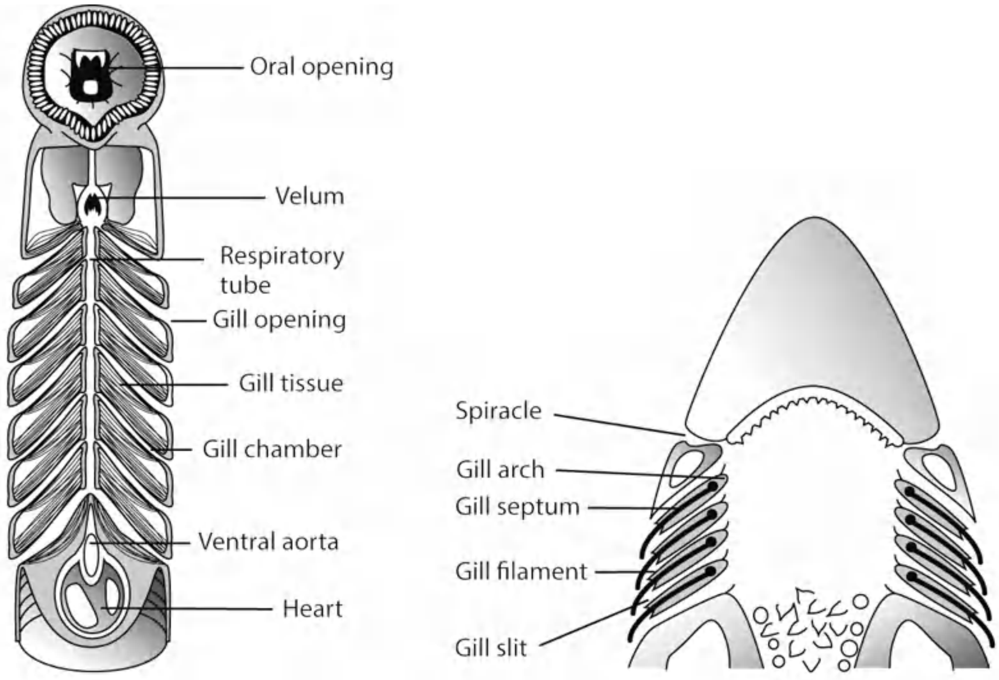


Figure 1.16. Musculature of a teleost with two myomeres removed to show the shape of the myosepta. Abductor muscles move a fin away from the midline of the body; depressors lower the fin. The horizontal septum divides the myomeres into dorsal (epaxial) and ventral (hypaxial) muscles.

Respiration

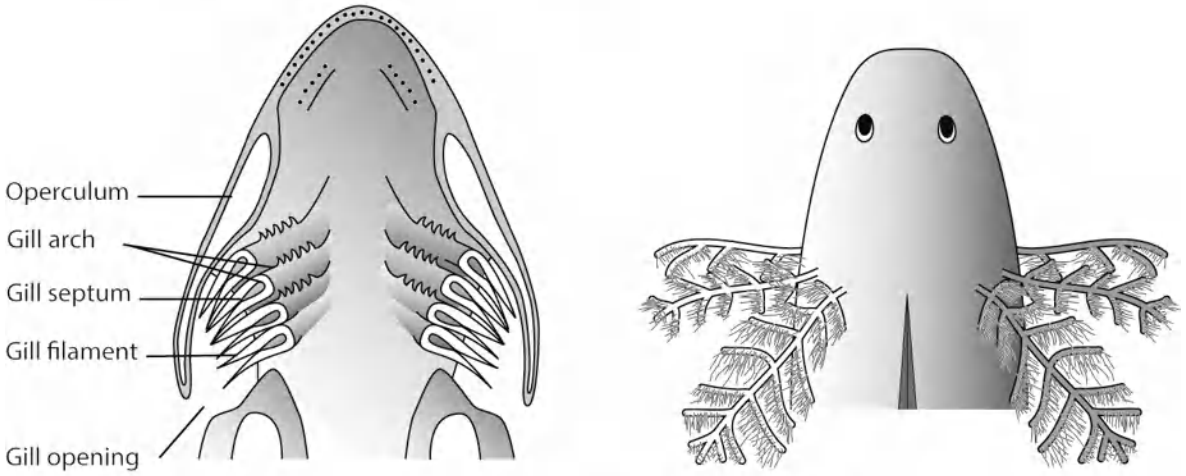
Gas exchange involves the diffusion of oxygen from either water or air into the bloodstream and carbon dioxide from the bloodstream into the external medium. Fishes acquire dissolved oxygen from the water that bathes the **gills** located in the pharyngeal region. Gas exchange is accomplished by diffusion through the highly vascularized gills, which are arranged as lamellar (platelike) structures in the pharynx (Fig. 1.17). An efficient oxygen uptake mechanism is vital because the average dissolved oxygen concentration of water is only 1/30 that of the atmosphere.

In most air-breathing vertebrates, oxygen from a mixture of gases diffuses through moist, respiratory membranes of the **lungs**, which are located deep within the body. Filling of the lungs can take place either by forcing air into the lungs, as in amphibians, or by lowering the pressure in and around the lungs below the atmospheric pressure, thus allowing air to be pulled into the lungs, as is the case with turtles, lizards, snakes, and crocodilians as well as with all birds and mammals. The moist skin of amphibians permits a considerable amount of integumental gas exchange, with land-living members of one large family of lungless salamanders (Plethodontidae) using no other method of respiration as adults. Structures known as **swim bladders** that are homologous to the lungs of land vertebrates first appeared in bony fishes; some living groups of fishes (lungfishes, crossopterygians, garfishes, bowfins) use swim bladders as a supplement to gill-breathing. In most living bony fishes, however, these structures either serve as hydrostatic (gas-regulating) buoyancy organs or they are lost.



(a) Lamprey

(b) Shark



(c) Bony fish

(d) Salamander

Figure 1.17. Vertebrate gills: Internal gills of (*a*) a lamprey, (*b*) a shark, and (*c*) a bony fish. External gills of (*d*) a salamander. Gills allow aquatic vertebrates to acquire oxygen from water by diffusion across the gill lamellae.

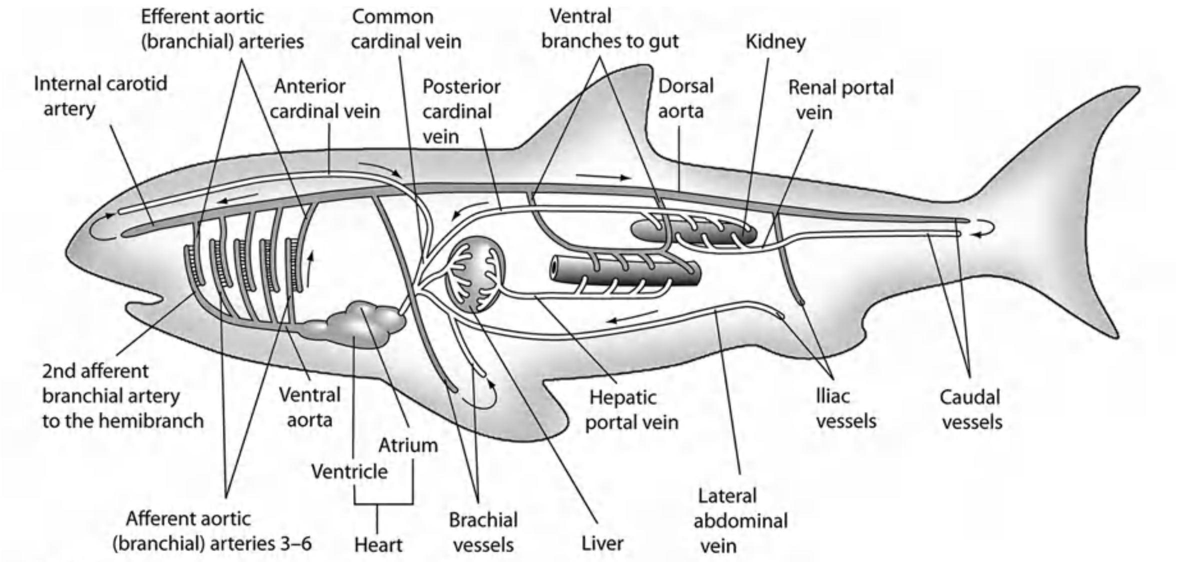
Circulation

Vertebrate cardiovascular systems consist of a **heart**, **arteries**, **veins**, and **blood**. The blood, which consists of cells (**erythrocytes**, or red blood cells; **leukocytes**, or white blood cells; **thrombocytes**, or platelets) and a liquid (**plasma**), is designed to transport substances (e.g., oxygen, waste products of metabolism, nutrients, hormones, and antibodies) rapidly to and from all cells in the body. In homeotherms, cardiovascular systems also regulate and equalize internal temperatures by conducting heat to and from the body surface. In fishes, a two-chambered (**atrium** and **ventricle**) tubular heart pumps blood anteriorly, where it passes through **aortic arches** and capillaries of the gill tissues before being distributed throughout the body (Fig. 1.18a). The blood is oxygenated once before each systemic circuit through the body.

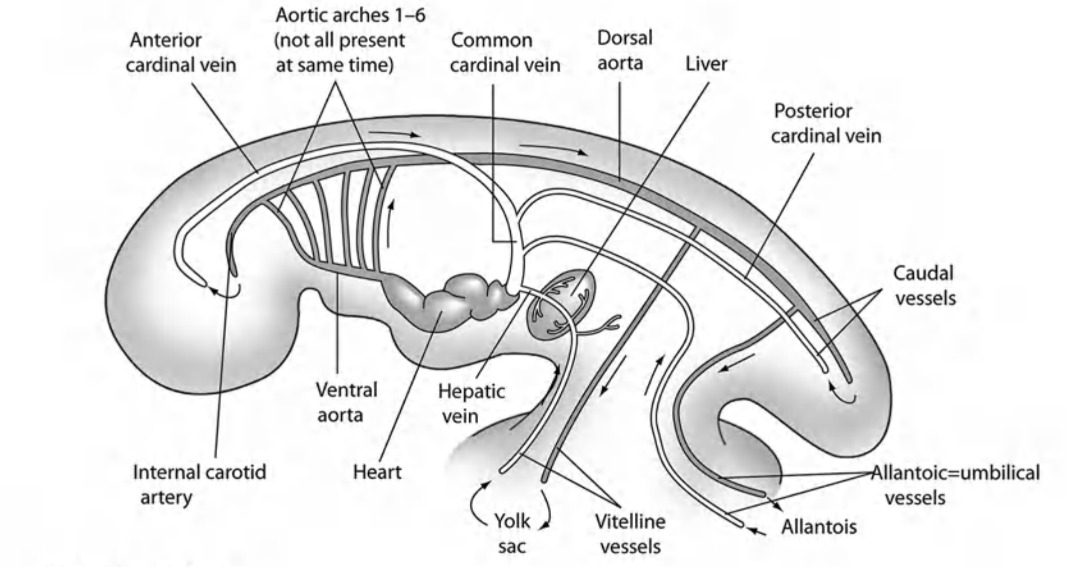
The evolutionary change to lung-breathing involved major changes in circulation, mainly to provide a separate circuit to the lungs (see Fig. 1.18b; 6th aortic arch becomes the pulmonary artery supplying the lungs). The heart became progressively divided into a right side that pumps blood to the lungs after receiving **oxygen-depleted blood** from the general circulation and a left side that pumps **oxygen-rich blood** into the systemic circulation after receiving it from the lungs. This separation of the heart into four chambers (**right** and **left atria**, **right** and **left ventricles**) first arose in some of the bony fishes (lungfishes) and became complete in crocodilians, birds, and mammals.

Digestion

Vertebrates, like other animals, obtain most of their food by eating parts of plants or by eating other animals that previously consumed plants. Fishes may ingest food along with some of the water that they use for respiration. In terrestrial vertebrates, **mucous glands** are either present in the mouth or empty into the mouth to lubricate the recently ingested food.



(a) Shark



(b) Amniote embryo

Figure 1.18. Basic pattern of the vertebrate circulatory system as seen in (*a*) a shark and (*b*) an amniote embryo. All vessels are paired except the dorsal and ventral aortas, the caudal vein, and the vessels of the gut.

The digestive tube is modified variously in vertebrates, mostly in relation to the kinds of foods consumed and to the problems of food absorption. The short **esophagus** of fishes became elongated as terrestrial vertebrates developed a neck and as digestive organs moved posteriorly with the development of lungs. In most vertebrate groups, the **stomach** has been a relatively unspecialized structure; however, it has become highly specialized in many birds, where it serves to both grind and process food, and in ruminant mammals, where a portion of the stomach has been modified into a fermentation chamber. The **intestine**, which generally is longer in herbivorous vertebrates than in carnivorous vertebrates as an adaptation for digesting vegetation, is modified variously internally to slow the passage of food materials and to increase the area available for absorption. A **spiral valve** that also increases the absorptive area of the intestine is present in cartilaginous and some bony fishes and in some lizards. **Pyloric caeca** (blind-ended passages at the junction between the stomach and first part of the intestine) serve the same function in most bony fishes and also may be present in some diapsids and mammals. In teleosts, caeca number from several to nearly 200 and serve as areas for digestion and absorption of food. The mammalian small intestine is lined with tiny, finger-like projections known as **villi** that serve to increase the absorptive surface area.

Nervous System

The nervous and endocrine systems control and coordinate the activities of the vertebrate body. The **brain**, as the most important center of nervous coordination, has undergone great changes in the course of vertebrate evolution. In addition, various sense organs have developed to assist in coordinating the activities of the vertebrate with its external environment.

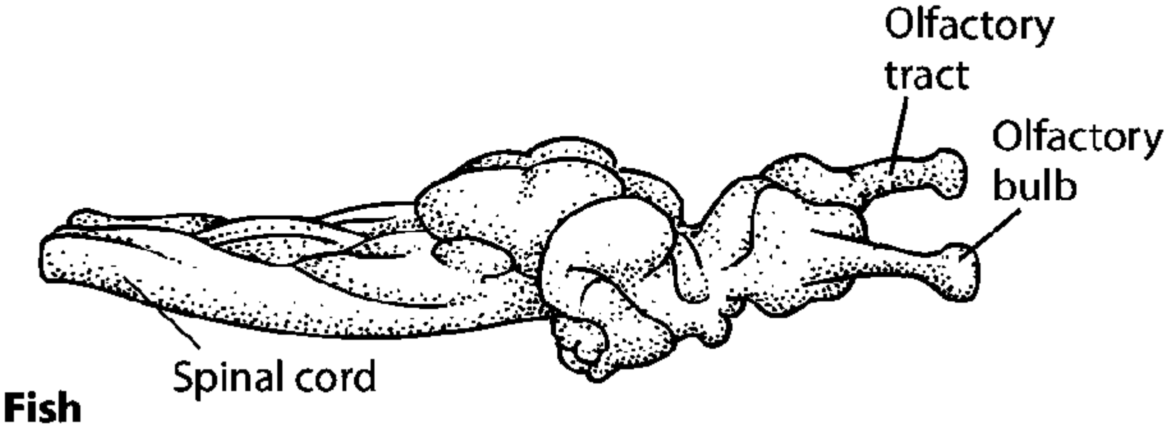
The relative development of the different regions of the brain in vertebrates is related largely to which sense organs are primarily used in obtaining food and mates. The **forebrain** (telencephalon and diencephalon) consists of the **olfactory bulb**, **cerebrum**, **optic lobe**, **parietal eye**, **pineal body**, **thalamus**, **hypothalamus**, and **hypophysis** (**pituitary**). In hagfishes, lampreys, and cartilaginous fishes, the forebrain is highly developed because these vertebrates locate food mainly through olfactory stimuli (Fig. 1.19). The **cerebral hemispheres** of the forebrain (formerly olfactory in function only) become increasingly important association centers of the brain. The **midbrain** (mesencephalon) is most highly developed in many bony fishes and in birds because of the importance of vision in obtaining food and for flight. The **hindbrain** (rhombencephalon) consists of the **cerebellum**, **medulla oblongata**, and **pons**. The cerebellum is responsible for muscular control and coordination; the medulla and pons serve as relay centers and also contain control centers that regulate such functions as respiration and blood pressure. Both the brain and spinal cord are enclosed in protective membranes known as **meninges**.

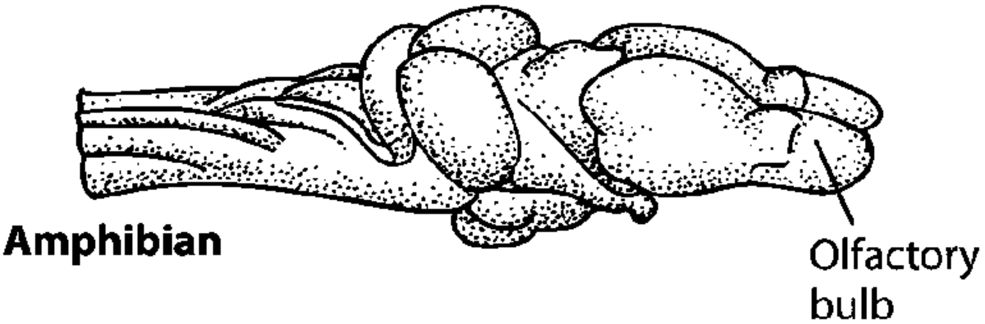
Olfaction

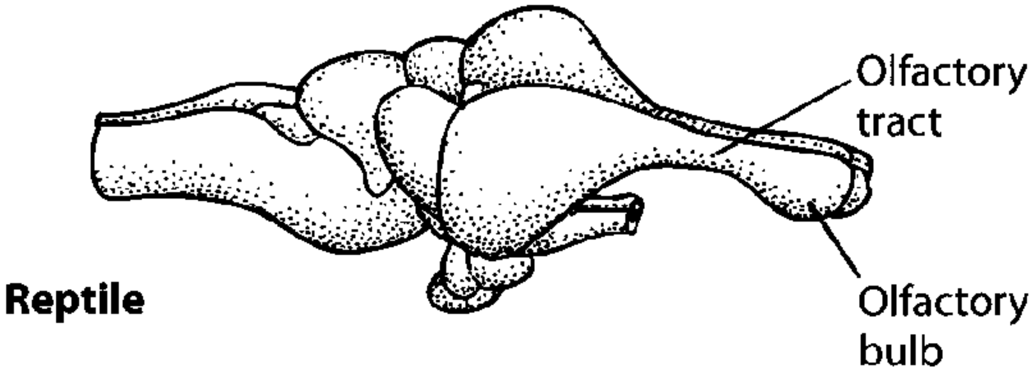
All vertebrates possess a sense of smell (**olfaction**). In hagfishes, lampreys, and all fishes except the sarcopterygians (lobe-finned fish), the olfactory receptors are recessed in paired, blind-ended pits known as **nasal sacs**. In all other vertebrates, the olfactory region is connected to the oral cavity.

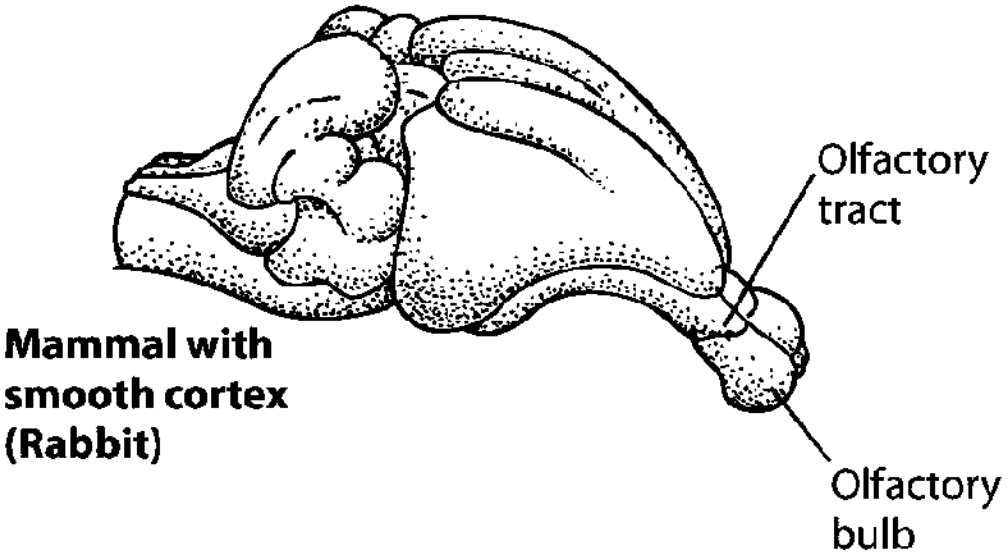
Vision

The paired **eyes** of vertebrates are remarkably constant structures throughout most vertebrates (Fig. 1.20). They tend to be reduced or lost, however, in vertebrates that have adapted to cave or subterranean life where light is dim or absent. An additional medial, unpaired eye is present in hagfishes, lampreys, and some diapsids. Among diapsids, this well-developed parietal eye functions as a light-sensitive organ in the tuatara (*Sphenodon*), and a vestigial parietal eye may be seen as a light-colored spot beneath a medial head scale in many kinds of lizards.


Olfactory tract
Olfactory bulb
Spinal cord
Fish


Amphibian
Olfactory bulb


Olfactory tract
Reptile
Olfactory bulb


Olfactory tract
Mammal with smooth cortex (Rabbit)
Olfactory bulb

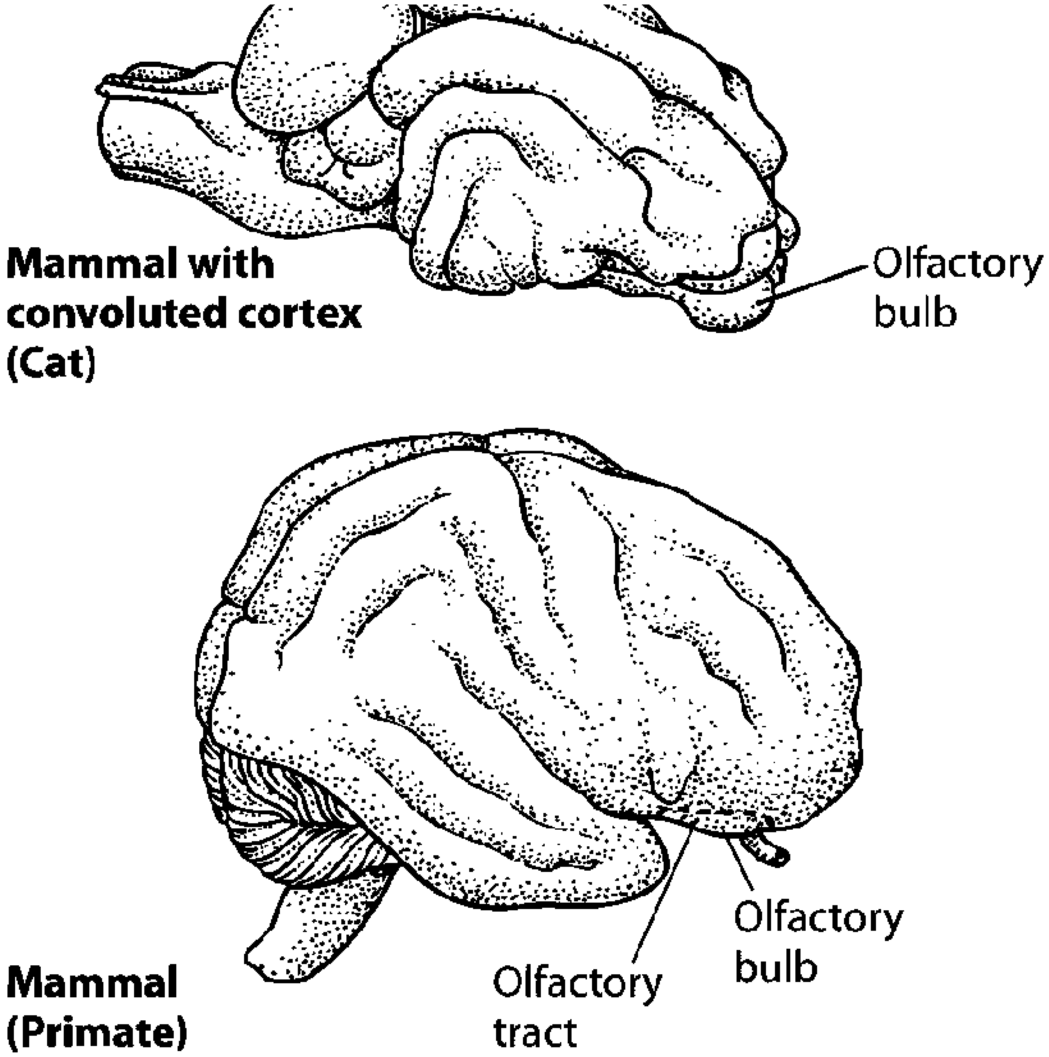


Figure 1.19. Comparison of the olfactory tract portion of the brain in representative vertebrates. The end of the tract is usually expanded into an olfactory bulb, which receives the olfactory nerves leading from the olfactory epithelium in the nasal region.

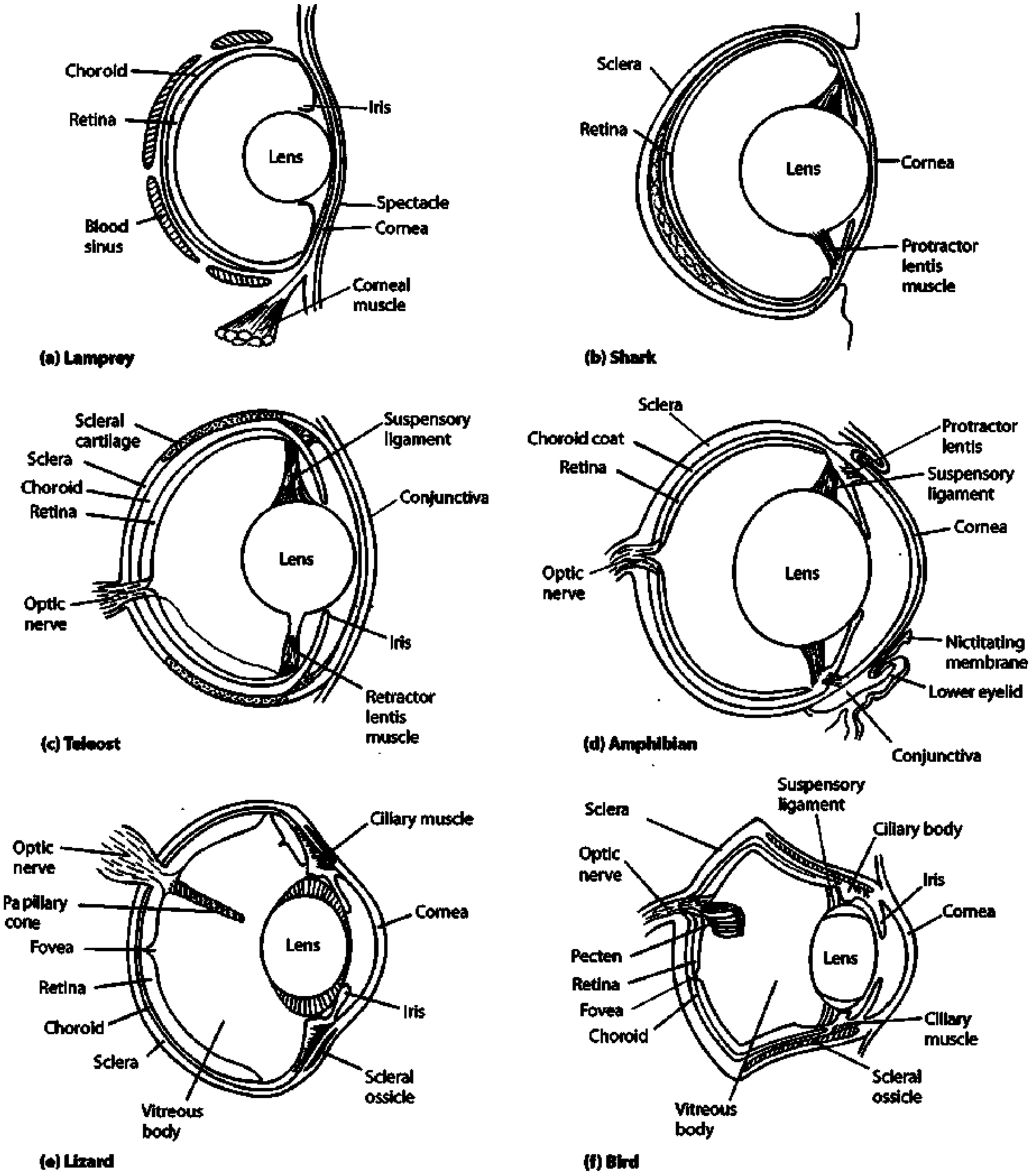
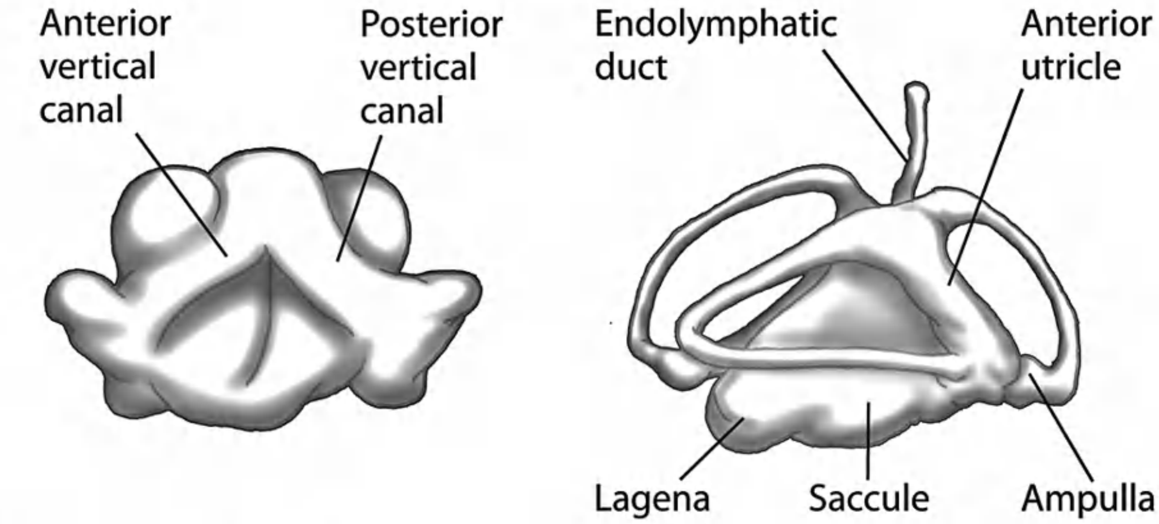


Figure 1.20. Comparison of the eye in representative vertebrates: (*a*) lamprey, (*b*) shark, (*c*) teleost, (*d*) amphibian, (*e*) lizard, (*f*) bird.

Hearing and Vibration Receptors

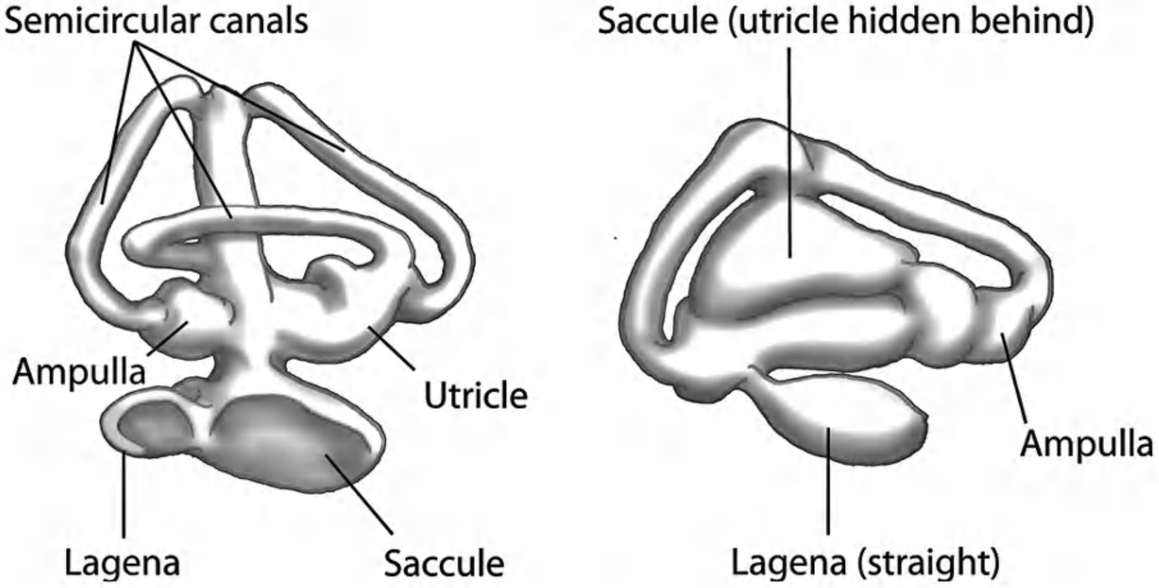
The ability to detect sound is essential to most vertebrates. The receptors for sound waves, as well as the receptors for equilibrium, are located within the **labyrinth** in the inner ear (Fig. 1.21). Sound may be used as a warning, for attracting mates, for aggression, for locating food, or for maintaining contact between members of a group.

Some vertebrates can detect sound below and above the range of human hearing, called **infrasound** and **ultrasound**, respectively. Some aquatic vertebrates have systems of **neuromasts**, hair cells embedded in a gelatinous matrix widely distributed over the body surface. Neuromasts open to the outside and are responsive to vibrations in the water; they have been lost in terrestrial vertebrates.



(a) Lamprey (only 2 semicircular canals)

(b) Elasmobranch



(c) Teleost

(d) Lizard

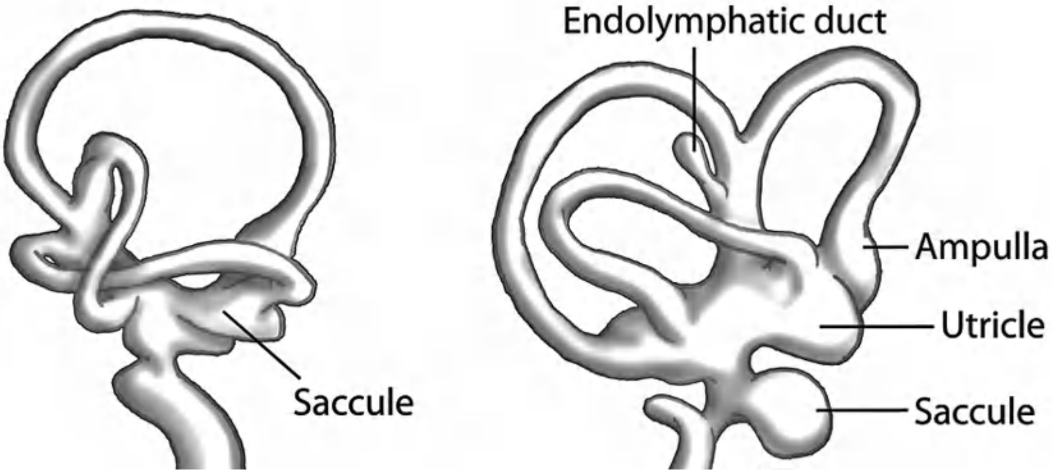


Figure 1.21. Comparison of the structure of the labyrinth of the inner ear in representative vertebrates (lateral view of the right organ): (*a*) lamprey, (*b*) elasmobranch, (*c*) teleost, (*d*) lizard, (*e*) bird, (*f*) mammal.

Endocrine System

Chemical control of coordination is accomplished by means of **hormones** secreted by endocrine glands. In most cases, endocrine organs of different groups of vertebrates are homologous, and similar endocrine controls operate throughout all vertebrates. However, similarities among hormones of different vertebrate groups do not necessarily imply similar function. Prolactin, for example, regulates such activities as nest-building, incubation of eggs, and protection of young in many vertebrates. In female mammals, however, prolactin stimulates milk production by the mammary glands.

Kidney Excretion

The vertebrate kidney has evolved through several stages: **pronephros**, **opisthonephros**, and **metanephros**. The pronephros develops from the anterior portion of tissue (**nephrogenic mesoderm**) that gives rise to the kidney and forms as a developmental stage in all vertebrates. It is functional, however, only in larval fishes and amphibians, and it remains throughout life only in lampreys, hagfishes, and a few teleosts. Even then it functions as an adult kidney only in hagfishes; in all other vertebrates, it ceases to function as a kidney and becomes a mass of lymphoid tissue. An **opisthonephros** serves as the functional kidney of adult lampreys, as well as fishes and amphibians. The kidneys of adult reptiles, birds, and mammals (**metanephros**) develop from the posterior portion of the nephrogenic mesoderm.

Nitrogenous wastes from metabolism and excess salts mostly are removed through the kidney by functional units called **nephrons** (Fig. 1.22). Excretion maintains proper concentrations of salts and other dissolved materials in body fluids. Freshwater fishes live in water that has lower salt concentrations than their own body fluids; they have large nephrons and use water freely to dilute metabolic wastes during excretion. Marine fishes, on the other hand, live in water in which the salt concentrations are higher than in their own body fluids, and as a result, they are in danger of losing water to their environment. Bony marine fishes solve this problem by reducing the size of their nephrons and by excreting salt through their gills. Cartilaginous marine fishes solve the problem by retaining nitrogenous wastes in the body fluids in the form of urea, thereby raising the total osmotic pressure of their internal fluids without increasing the salt concentration.

Terrestrial vertebrates also face the problem of water conservation when excreting metabolic wastes. The filtering portion of the nephron (**renal corpuscle**) is relatively small, and much water is reabsorbed in the tubule portion of the nephron. Many turtles, lizards, snakes, crocodilians, and most birds excrete crystalline **uric acid**; mammals, however, excrete a solution of **urea**, although the solution may be very concentrated in desert inhabitants like kangaroo rats (*Dipodomys*).

Reproduction

Reproductive output among vertebrates is influenced by sexual state, method of fertilization, and environmental factors like temperature, photoperiod, and availability of water. Much of this variation in reproductive output arises because some vertebrates are ectothermic (animals whose body temperature is variable and fluctuates with that of the thermal environment), whereas others are endothermic (animals that use heat derived from their own oxidative metabolism to elevate their internal body temperature independently of the thermal environment). Hormones and environmental factors like temperature, rainfall, and sunlight control the periodicity of breeding and exert a much greater influence on ectothermic species. The age at which an organism reaches sexual maturity and can breed is a major factor in determining growth and size of its population, whereas factors like floods, droughts, extreme temperatures, parasites, predators, and availability of food can significantly affect the number of individuals reaching sexual maturity.

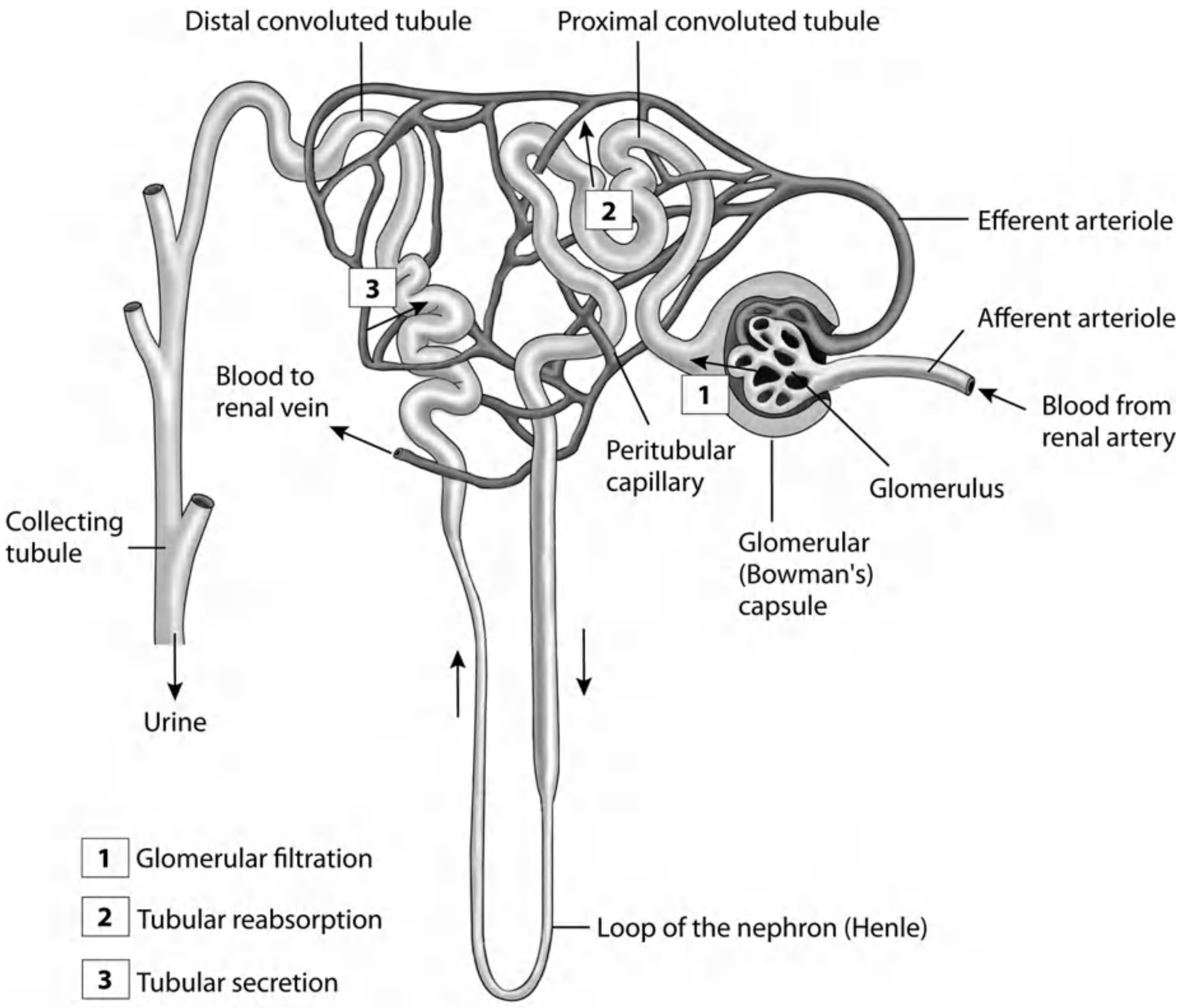


Figure 1.22. A mammalian nephron. Wastes are filtered out of the glomerulus and travel through the nephron to the collecting tubule.

Vertebrate young are typically born or hatched during the period of the year when environmental conditions are most favorable for their survival. In tropical and subtropical areas, many species are able to breed throughout the year, so that distinct periods of breeding (**breeding seasons**) are not as pronounced as they are in areas of greater latitude or altitude. In nonequatorial regions, breeding is controlled by cyclic environmental factors like photoperiod, temperature, and the availability of water. Other factors, like availability of food and the production of hormones, are influenced by these cyclic environmental factors. Thus, breeding in many vertebrates has a periodicity correlated with the environmental conditions in their region of the world.

Some species have high reproductive rates and produce a large number of offspring with rapid developmental rates but low survival. Such species, which are generally small and provide minimal parental care, are known as **r-strategists** (Table 1.2). They are opportunistic and often inhabit unstable or unpredictable environments where mortality is environmentally caused and is relatively independent of population density (Smith, 1996). Species that are r-strategists allocate more energy to reproductive activities and less to growth and maintenance. They are good colonizers and are usually characteristic of early successional stages.

Other species have low reproductive rates and produce relatively few young, which mature slowly but are long-lived. These species, known as **K-strategists**, are relatively large and provide care for their young. They are competitive species whose stable populations are limited by available resources. Mortality is generally caused by density-dependent factors rather than by unpredictable environmental factors. K-strategists allocate more energy to nonreproductive activities, are poor colonizers, and are characteristic of later stages of succession.

The ability of the sexes of a given species to recognize one another is of utmost importance for generating offspring. This is accomplished in a variety of ways that involve one or more of the sense organs of smell, sight, touch, and hearing. Colorful features, pheromones, vocalizations, and courtship behavior may all be employed by one sex in their search for a suitable mate.

The complexity of courtship ranges from being almost nonexistent to very elaborate and extensive, like that found in humans. In each vertebrate group, members of some species come together solely to breed, whereas members of other species mate for life. A great deal of variation between these two extremes also occurs.

Most vertebrates are **dioecious**, meaning that male and female reproductive organs are in separate individuals. A few hagfishes and lampreys, as well as some other fishes, are **hermaphroditic** (both male and female reproductive organs develop in the same individual, but normally do not function simultaneously). A few genera of bony fishes and lizards have **parthenogenetic** species in which females produce young without being fertilized by males.

Table 1.2. Demographic and Life-History Attributes Associated with r- and K-Type Populations of Amphibians and Reptiles

Attributes	r-type	K-type

Attributes	r-type	K-type
Population size (density)	Seasonally variable; highest after breeding season, lowest at beginning of breeding season	High to low, but relatively stable from year to year
Age structure	Seasonally and annually variable; most numerous in younger classes, least in adults	Adult age classes relatively stable; most numerous in adult classes
Sex ratio	Variable, often balanced	Variable, often balanced
Population turnover	Usually annual, rarely beyond 2 years	Variable, often > 1.5 times age of sexual maturity; to decades
Age at sexual maturity	Usually ≤ 2 years	Usually ≥ 4 years
Longevity	Rarely ≥ 4 years	Commonly > 8 years
Body size	Small, relative to taxonomic group	Small to large
Clutch size	Moderate to large	Small to large
Clutch frequency	Usually single breeding season, often multiple times within season	Multiple breeding seasons, usually once each season
Annual reproductive effort	High	Low to moderate

Source: From Zug, 1993. Copyright © Academic Press, New York. Used by permission.

Modes of reproduction vary among vertebrates. They include **oviparous** development (egg-laying) and **viviparous** development (giving birth to nonshelled young). Oviparity is probably the ancestral mode of reproduction, whereas viviparity represents an evolutionary advance because a smaller number of larger offspring, which have a better chance of survival, are produced. According to Blackburn (1992), viviparity originated on at least 132 independent occasions among vertebrates, with 98 of these having occurred in reptiles.

Ova are fertilized in a variety of ways. Fertilization occurs outside the body of the female (**external fertilization**) in some species; in others, it occurs within the female's body (**internal fertilization**). In some species, sperm is stored within the body of the female for extended periods of time. Howarth (1974) reports that the extended storage of sperm and the resultant **delayed fertilization** is represented in every vertebrate class with the exception of jawless fishes (classes Myxini and Petromyzontida). Female diamondback terrapins (*Malaclemys terrapin*), for example, have been reported to lay fertile eggs four years following mating (Hildebrand, 1929). Other examples include most temperate species of bats, which mate in the fall just prior to entering hibernation, with viable sperm remaining in the female's reproductive tract until her emergence from hibernation in the spring.

Most ray-finned fishes and many amphibians reproduce by external fertilization. Eggs are discharged into the water, and sperm are released in the general vicinity of the eggs. Many eggs and sperm must be produced to ensure that enough of the eggs are fertilized; even so, fertilized eggs (zygotes) may be exposed immediately to the uncertainties of independent existence. Internal fertilization, on the other hand, increases the chances of fertilization and consequently reduces the number of eggs and sperm that must be produced. Internal fertilization has appeared in various groups of ray-finned fishes, some amphibians, and universally in cartilaginous fishes, turtles, lizards, snakes, crocodilians, birds, and mammals. Retention of developing zygotes within the reproductive tract of the mother (viviparous development) provides a more stable environment for development and has the advantage of protecting the developing young at a stage when they cannot escape predators or unfavorable environmental conditions.

Most fishes that use internal fertilization are viviparous. Zygotes are retained within the mother's body until they are ready to emerge as free-swimming juveniles. Among terrestrial vertebrates, turtles, lizards, and crocodilians lay eggs (oviparous). Snakes may be oviparous or viviparous. All birds are oviparous. Two groups of mammals—the duck-billed platypus and the echidnas—are oviparous; all other mammals are viviparous. Mammalian zygotes retained by the mother must be attached to the wall of the reproductive tract by a highly efficient connection (**placenta**) so that the zygotes can receive nourishment and oxygen from the mother and have their wastes removed.

Embryos of reptiles, birds, and mammals are enclosed in a protective membrane known as an **amnion**. The amnion, which forms a fluid-filled sac in which the embryo floats during its development, is one of four extraembryonic membranes that are present in these groups of vertebrates. Therefore, reptiles, birds, and mammals are referred to as **amniotes**; fishes and amphibians, which lack an amnion, are known as **anamniotes**.

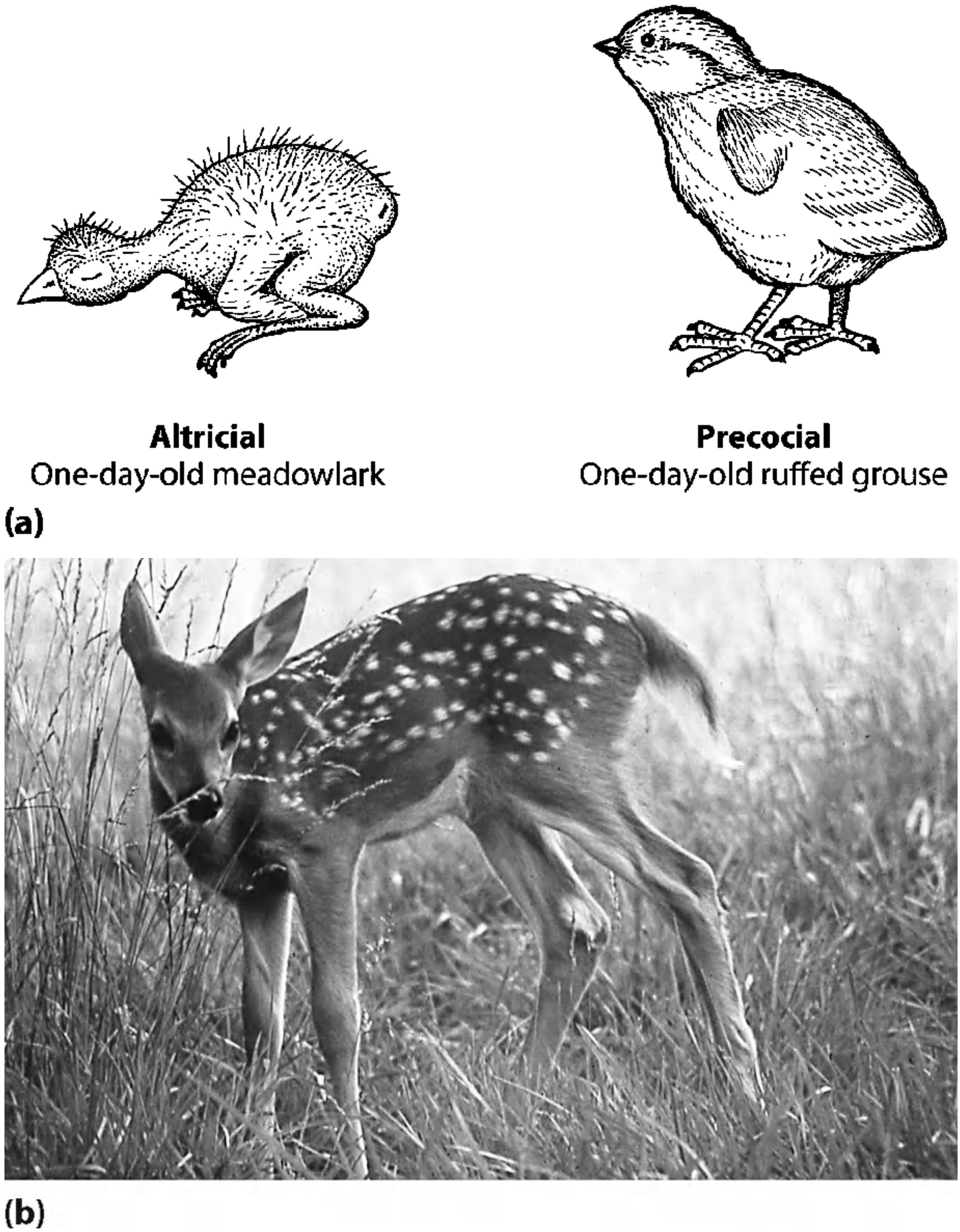
Some kinds of fishes, like bluegills, protect their nest (**redd**) until the young have hatched, and some kinds of fishes even carry the zygotes in their mouth (some catfishes, mouthbreeders in the family Cichlidae) or in a pouch (sea horses) until they hatch (see Fig. 4.36). Many salamanders (Fig. 1.23), some anurans, some lizards, some snakes, all crocodilians, most birds, and all egg-laying mammals guard and protect their eggs during incubation. Some birds and mammals are well developed at birth, have their eyes and ears open, are covered with feathers or hair, and can walk or swim shortly after birth (Figs. 1.24a, b). Ducks, geese, jackrabbits, and deer are examples of such **precocial** young. Other birds and mammals, which are born naked and with their eyes and ears sealed, are referred to as **altricial** young. Parents of altricial young show more highly developed parental care than parents of precocial young, feeding and caring for the young during their early helpless stages of development. In birds, extensive parental care seems related to the fact that young are mostly helpless until they have learned to fly. In mammals, nourishment is provided by the **mammary glands** of the mother.

Figure 1.23. Female dusky salamander (*Desmognathus*) guarding her eggs. Many salamanders and some frogs remain with their eggs to prevent predation by arthropods (like ants, beetles, and millipedes) and by other salamanders and frogs. In some cases, the male parent guards the eggs.

Growth and Development

Prenatal (embryonic) **development** in all vertebrates follows the same basic pattern: general characters develop first, then the more specific characters. For example, the dorsal nerve tube, notochord, and pharynx are among the first structures to develop. These are followed by gill pouches, aortic arches, and pronephric kidneys in all vertebrates. Then, in tetrapods, pentadactyl limbs, mesonephric and metanephric kidneys, and specific amphibian, reptilian, avian, and mammalian characters appear.

Parental care among vertebrates ranges from being nonexistent in many species to lasting many years in some higher primates. The young of many species are born as miniature adults and do not pass through a larval stage of development. Others, like many salamanders and frogs, pass through a larval stage of development before transforming or metamorphosing into the adult form. The time required to reach sexual maturity ranges from several weeks in some fishes to several years in some birds and mammals.


Altricial
One-day-old meadowlark

Precocial
One-day-old ruffed grouse

Figure 1.24. (*a*) Comparison of one-day-old altricial and precocial young. The altricial meadowlark (*left*) is born nearly naked, blind, and helpless. The precocial ruffed grouse (*right*), however, is born covered with down, is alert, and is able to walk and feed itself. (*b*) White-tailed deer fawns are well developed at birth, have their eyes and ears open, and are covered with hair.

The length of time an animal survives depends on its species as well as on factors like food availability, shelter, and competition. Few animals die of old age in the wild. They may be eaten, killed by hunters, succumb to parasites and/or disease, suffer from climatic events like drought or flooding, or die because their habitat has become polluted, reduced, or destroyed.

ROLE OF VERTEBRATES

Vertebrates play major roles in the ecosystems of the Earth. They form an essential link in the ecological processes of life and often have close-knit interactions with plants and invertebrates. For example, hummingbirds and some bats (Fig. 1.25) pollinate plants, whereas other birds and mammals assist in transporting seeds (see Chapters 8 and 9). Seeds may pass through the digestive tract and are often dispersed long distances from their place of origin, or they may be transported by attachment to the fur of mammals. Some species, like gopher tortoises (*Gopherus*) and woodchucks and marmots (*Marmota*), excavate burrows that may be used by a wide array of invertebrates as well as by other vertebrate species (see Chapter 14). Many vertebrates feed on invertebrates, including insects. Conversely, many vertebrates serve as food for other species (see Chapter 14).

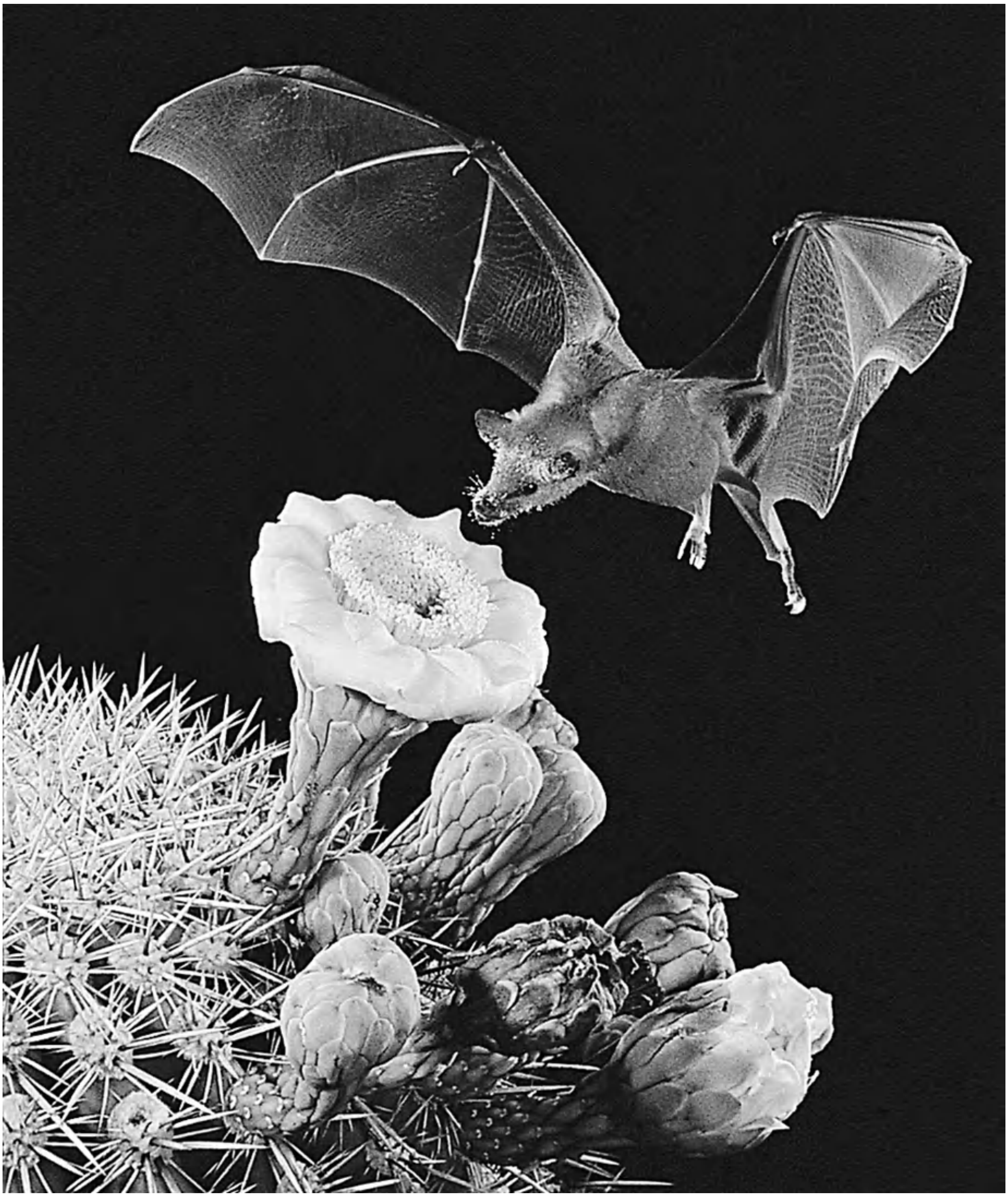


Figure 1.25. Although insects and hummingbirds are widely known as pollinators, some bats, like this lesser long-nosed bat (*Leptonycteris curasoae*), also facilitate the transfer of pollen. Note the saguaro cactus pollen on the bat's face.

Humans are playing an ever-increasing role in the distribution and abundance of vertebrates. The contamination of natural resources (soil, water, air) has a negative impact on most forms of life. The release of human-made chemicals, the destruction of ozone molecules, global warming, and the buildup of estrogen compounds have all had detrimental effects on other species (see Chapters 14, 19, and 20). Thus, a critical role for humanity is to develop a sustainable, nondestructive lifestyle in order to live in harmony with all other vertebrates.

Humans long have hunted other vertebrates for their meat, fur, skin, feathers, ivory, and oil (see Chapters 14 and 16). The commercial fishing industry forms a major component of the economy of many nations, and whaling was formerly a significant activity in many countries. Sport fishing and hunting are of major importance in some regions. In recent years, many countries have commercialized wildlife species in order to attract tourists for tours and photographic safaris, a practice called **ecotourism** (see Chapter 18). Such activities offer an excellent means of using renewable resources in a less destructive way while providing educational and economic opportunities.

The domestication of many species has provided humans with food, clothing, work animals, and companionship. Many new laws and regulations have affected the collection of native vertebrates, as well as the importation of certain foreign species that are considered endangered (see Chapters 14, 16, and 18 and Appendix B). Zoos, theme parks, and aquariums typically feature vertebrate species. In the past, zoos have been composed largely of caged animals whose natural instincts and behavior generally deteriorated the longer they were in captivity. The emphasis now is on providing natural habitats for as many species as possible, supplying educational information about each species, and creating suitable conditions for selected species to breed and produce offspring. Captive breeding programs, which have been established at various zoos around the world, exchange zoo-reared offspring as a means of helping maintain genetic diversity within the species.

FUTURE RESEARCH

The literature on vertebrates is voluminous. For example, in 1991 alone, *Wildlife Review* (formerly an abstracting service of the US Fish and Wildlife Service) listed 13,632 citations just for articles on amphibians, reptiles, birds, and mammals. By 1995, the number of citations had risen to 15,586. Since that time, the number of publications dealing with vertebrates has continued to increase. A great deal of time and effort is required to keep current with research and developments involving even one group of vertebrates. For this reason, most vertebrate biologists concentrate their attention on only one group, on one aspect of vertebrate life (like reproductive physiology), or on a particular aspect of comparison among two or more groups (like their systematic relationships).

Much important and significant information has yet to be discovered concerning the biology, ecology, genetics, evolution, and behavior of vertebrate species. For example, what mechanisms are used for communication? How do many species communicate with one another? Is infrasound important in more than just a few species? Which species possess color vision and/or vision outside of the visible spectrum, and exactly what can they see? Why can some vertebrates regenerate limbs and other portions of their bodies but others cannot? Can domestic animals produce beneficial substances like hemoglobin and hormones in significant quantities for human use? Can squalamine, a water-soluble compound derived primarily from livers of dogfish sharks, cure cancer in humans? Squalamine inhibits the growth of tumor-induced new blood vessels (angiogenesis) in animal systems and also reduces the spread of tumor metastases. It inhibits bacterial activity against both gram-negative and gram-positive bacteria, is fungicidal, and induces osmotic lysis of protozoa. Clinical trials of squalamine are currently underway for several types of cancer as well as for its use in eye drops for the treatment of "wet" age-related macular degeneration (AMD) and its effects in improving visual acuity in persons with AMD. Can the toxic alkaloid components of poison dart frogs be beneficial as drugs for humans (Fig. 1.26)? Scientists know the activity of only about 60 of at least 500 different toxins. One epidermal compound—epibatidine—has been found to be 200 times more potent than morphine at blocking pain (Bradley, 1993). By studying the mode of action of another compound—batrachotoxin—researchers are gaining an understanding of the role electrical impulses play in fundamental processes like human heart function and the sensation of pain. At least one species of Australian frog (*Litoria caerulea*) may have evolved a natural protection against mosquitoes (Williams et al., 2006). Could frog secretions be the next great mosquito repellant?

Figure 1.26. Blue poison dart frogs (*Dendrobates azureus*) produce toxic alkaloids in their skin as a chemical defense against predation.

Efforts to control wild populations of certain abundant mammals, like white-tailed deer (*Odocoileus*), wild horses (*Equus*), raccoons (*Procyon*), skunks (*Mephitis*, *Spilogale*), and woodland voles (*Microtus*), continue. Fertility-inhibiting implants and immunocontraceptive vaccines are the latest techniques being tested for birth control purposes and are discussed in Chapter 11.

The mysteries of migration have yet to be fully understood. How do some young birds, migrating alone for the first time and with no previous knowledge of the terrain, successfully migrate to their overwintering grounds?

New undescribed species continue to be discovered, particularly in tropical areas (Figs. 1.27 and 1.28). Techniques like DNA sequencing and hybridization will continue to provide data concerning the relationships of living populations and also of some forms now extinct. DNA dated at least 47,000 years BP (before the present) has been recovered from Siberian woolly mammoths (*Mammuthus primigenius*) (Hagelberg et al., 1994). Tests on human bones hidden in a Spanish cave for some 400,000 years set a new record for the oldest human DNA sequence ever decoded (Gruber, 2013). Paleontological discoveries will continue to add to our knowledge of vertebrate species that previously inhabited the Earth.

A great deal of future research will be directed toward saving endangered species—both wild populations and those in captive breeding programs (see Chapters 16 and 17). New techniques and procedures will need to be developed to enhance the success of these programs. The reintroductions of species such as the red wolf and timber wolf into suitable areas must be based on sound biological data and not political rhetoric. Public education will be critical to the success of every one of these programs.

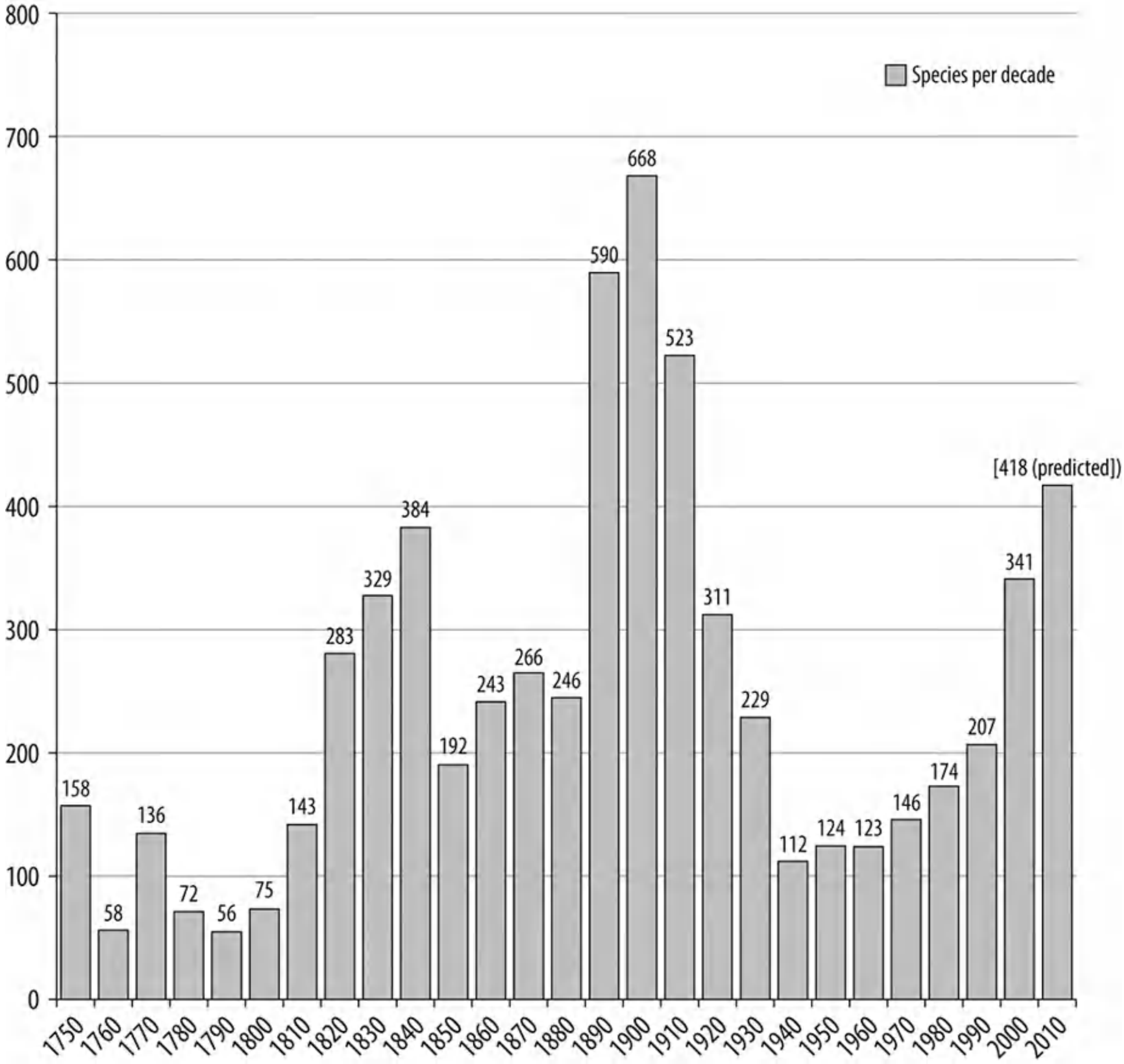


Figure 1.27. The number of new mammal species discovered (some resulting from taxonomic revisions) from 1758 to August 15, 2017. Although the biggest burst of discovery is over, the number of new mammals is rising again, with additions from mice to monkeys.

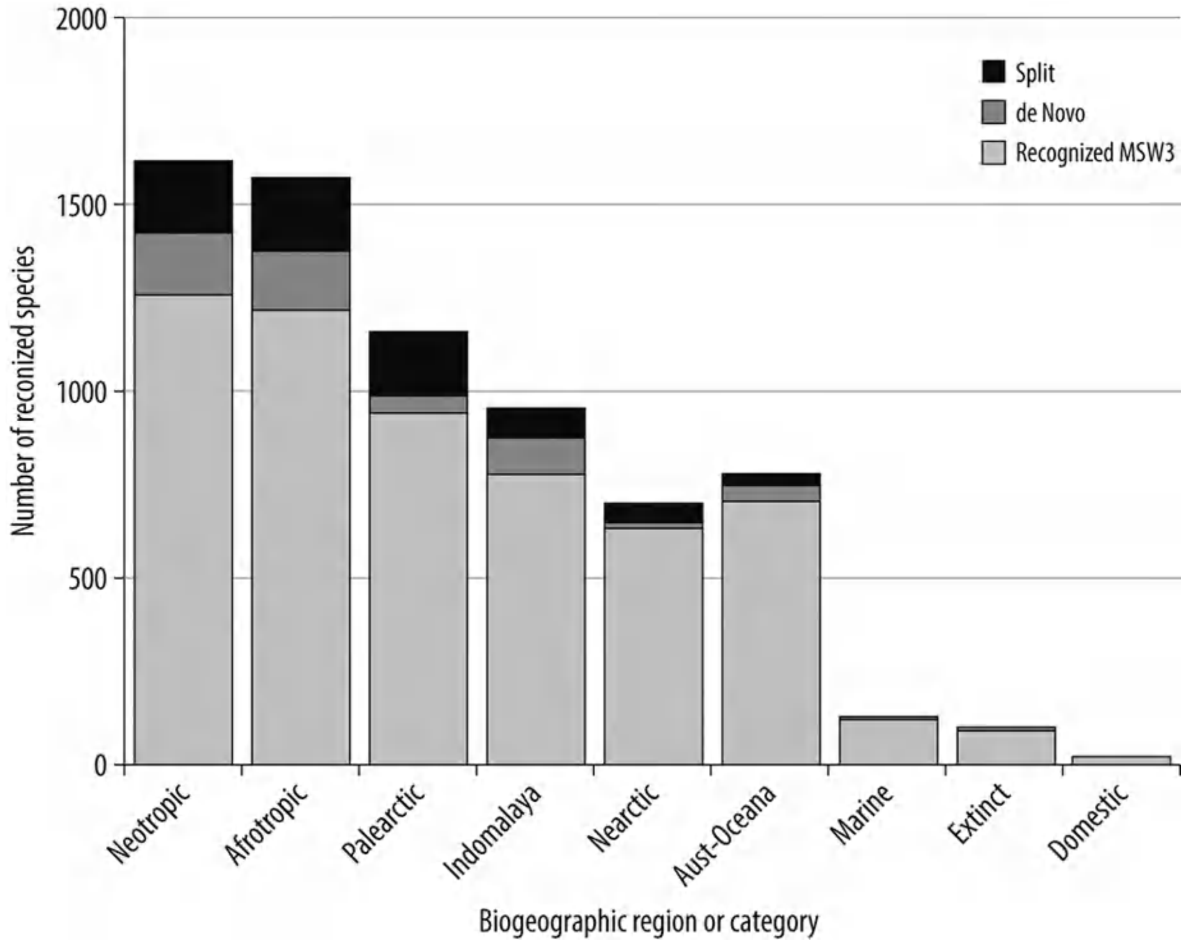


Figure 1.28. The number of mammalian species distributed in each biogeographical region: Palearctic, Afrotropic, Indomalayan, Nearctic, Neotropic, and Australasia-Oceania, with marine, extinct, and domestic species in separate categories.

Many exciting and challenging research activities await interested researchers. You may be one of those researchers who, one day, will add to our knowledge of this large and fascinating group of animals.

DISCOVERING NEW VERTEBRATE SPECIES

The discovery of a new species is an exciting part of scientific research. Although the majority of newly described species are plants and invertebrates, many vertebrates are still "unknown" to science. In some cases, DNA evidence has shown that individuals of a single species are different enough that they should be considered to be two species. Such was the case in 2001, when the genetic dissimilarity between the forest and savanna elephants was found to be as great as that between lions and tigers. Thus, the former “African” elephant was reclassified as two different species: the savanna elephant (*Loxodonta africana*) and the African forest elephant (*Loxodonta cyclotis*). Also in 2001, the orangutans of Sumatra and Borneo were recognized as distinct species, *Pongo abelii* and *Pongo pygmaeus*. An isolated population of orangutans at the southern limit of Sumatran orangutans in the Batang Toru area of South Tapanuli was reported in 1939. The population was rediscovered by an expedition to the area in 1997, but it was not recognized as a distinct species at the time. In 2017, after examining morphometric, behavioral, and genomic evidence, an international team of researchers identified *Pongo tapanuliensis* as a distinct species from both northern Sumatran and Bornean species. This new species became recognized as the most imperiled great ape in the world. In 2013, the olinguito (*Bassaricyon neblina*) was recognized as a new species—the first carnivore species to be discovered in the Americas in 35 years. It had previously been mistaken for its close relative, the olingo.

Although mammals are well studied in comparison to other animal groups, a number of new species and subspecies are still being discovered. From 2005 through 2017, more than 300 new species or subspecies have been discovered, formally named, or reclassified based on DNA analyses. Examples include a new species of monkey (the lesula, *Cercopithecus lomamiensis*), from the Democratic Republic of the Congo, the three-toed pygmy sloth (*Bradypus pygmaeus*) from a small island off the coast of Panama in 2001, a blossom bat from New Guinea in 2010, the saola from Vietnam in 2010, a new species of dolphin from Australia in 2011, and a toothless rat (*Paucidentomys vermidax*) from Sulawesi in 2011.

During the past 20 to 25 years, new species of vertebrates never seen before by scientists are being discovered at a surprisingly rapid rate, especially in those regions of the world that, for one reason or another, have not been accessible to researchers in the past. In 1996, scientists reported discovering the Laotian rock rat (*Laonastes aenigmamus*), a ratlike rodent known locally as khanyou. The mammal, with the face of a rat and the body of a skinny squirrel, belongs to a rodent family that was thought to have died out 11 Mya.

During a two-week period in July 1996, evolutionary biologist James L. Patton discovered four new species of mice, a shrew, and a marsupial in Colombia’s central Andes. In 1991, Patton discovered a new species of spiny mouse (*Scolomys juaraense*) in Brazil whose nearest relatives had been known only from the Andean foothills in Ecuador, 1,500 km (932 mi.) away. Between 1991 and 1996, Philip Hershkovitz of Chicago's Field Museum discovered 2 new genera and 16 new species of field mice in Brazil's Cerrado grasslands. In late 1997, a plump, 23 cm (9 in.) long, almost tailless bird, known as an antpitta, was discovered for the first time in the Ecuadorian Andes. A new species of parrot (*Pionopsitta aurantiocephala*) endemic to Brazil was reported in 2002.

Between 1997 and 2016, the World Wildlife Fund (WWF) reported 2,523 new species of plants, birds, mammals, reptiles, amphibians, and fishes—an average of two a week—from Southeast Asia's region of the Greater Mekong River, which flows 4,500 km (2,796 mi.) through Cambodia, Laos, Vietnam, Thailand, Burma, and South China's Yunnan Province. Among the vertebrate species was the mountain horseshoe bat (*Rhinolophus monticolus*), two moles, a green viper snake that can grow to about 1.3 m (4 ft.) and sense its prey by its thermal energy, the Vietnamese crocodile lizard (*Shinisaurus crocodilurus vietnamensis*), a snail-eating turtle (*Malayemys isan*), a tree frog with green blood and turquoise bones, the Khorat big-mouthed frog (which has fangs and lies in wait along streams for prey), a vibrantly colored frog (*Odorrana mutschmanni*), and a freshwater loach fish. Stuart Chapman, Director of WWF's Greater Mekong Program, stated: "More than two new species a week and 2,500 in the past 20 years speaks to how incredibly important the Greater Mekong is to global diversity. While the threats to the region are many, these discoveries give us hope that species from the tiger to the turtle will survive." Floods often devastate the river's banks during monsoons, and China's damming of the river on its northern stretches is drying the river in the south, killing many species that thrive on the Mekong's banks. Culture is another barrier to protecting rare species, as many restaurants serve them as food.

In 2009, the WWF issued a report entitled "The Eastern Himalayas—Where Worlds Collide" in which it reported 354 new species from the Eastern Himalayas—a biological treasure trove now threatened by climate change. The new species included 244 plants, 14 fishes, 16 amphibians, 16 reptiles, 2 birds, 2 mammals, and at least 60 new invertebrates. The new species included a catfish that has evolved unique adhesive undersides to stick to rocks in fast-moving streams, a "flying frog" that uses its long webbed feet to glide in the air, and the miniature muntjac (also called the “leaf deer”), which is the oldest and second-smallest deer species.

In August 1999, a new species of striped rabbit, named the Annamite rabbit (*Nesolagus timminsi*), was discovered in the remote, forested mountains between Laos and Vietnam (Surridge et al., 1999). The furry, red-bottomed creatures have black and brown stripes across their face and back (Fig. 1.29).

Scientists working in Madagascar announced in 2000 the discovery of three previously unknown species of mouse lemurs, the world’s smallest primate. Madagascar is a large island off Africa’s east coast. It is believed to have split off from the continent about 165 Mya, and many of its plant and animal species are unique to the island. In 1990, Bernhard Meier captured the world’s second-smallest lemur, the hairy-eared dwarf lemur (*Allocebus trichotis*), in Madagascar. This was the first time that scientists had ever seen this animal alive.

Figure 1.29. The striped Annamite rabbit (*Nesolagus timminsi*) is named for the Annamite Mountains that straddle Laos and Vietnam.

In 2009, Conservation International announced the discovery of 10 new amphibians, including a spiky-skinned, orange-legged rain frog, three poison dart frogs, and three glass frogs, so called because their transparent skin can reveal internal organs. These amphibians were discovered in Colombia's mountainous Tacarcuna area of the Darién, near the border with Panama. This area of the Darién is isolated from the Andes mountain range and is recognized as a center of endemism and as valuable for its high biological diversity.

Also in 2009, Conservation International scientists discovered four amphibian species (*Dendrobates* sp., *Pristimantis* sp., *Osteocephalus* sp., and *Bolitoglossa* sp.) and one lizard (*Enyalioides* sp.) potentially new to science in the Tepuyes of the Upper Nangaritza River and Cordillera del Condor region of southwestern Ecuador. They also recorded the glass frog (*Nymphargus chancas*) for the first time in Ecuador. This species was only known from one locality in northeastern Peru.

From 1999 to 2009, the WWF reported 1,200 new species of plants and animals (from bald parrots to translucent frogs)—an average of 111 new species a year, or one new species every three days—in the Amazon region (World Wildlife Fund, 2010). The 2014 WWF report revealed that at least 602 new species were discovered from 2010 to 2013—a rate of one new species every 2.5 days. In 2017, WWF reported that 381 new species were discovered in the Amazon during 2014–2015, including 216 plants, 93 fishes, 32 amphibians, 20 mammals (including a new species of pink river dolphin, *Inia araguaiaensis* (the first discovery in 100 years of a new river dolphin), the fire-tailed titi monkey, and 2 fossil species), 19 reptiles (including a yellow-moustached lizard and a blind snake), and 1 bird (Chico's tyrannulet) (World Wildlife Fund, 2017). This latest survey resulted in the highest rate of discovery yet, with a new species identified every 1.9 days.

In 2002, Marc Van Roosmalen, a Dutch scientist working at Brazil's National Institute for Amazon Research in Manaus, 2,897 km (1,800 mi.) northwest of Rio de Janeiro, described his fourth and fifth new species of monkeys. The two titi monkeys have been identified as *Callicebus bernhardi* and *Callicebus stephennashi*. Van Roosmalen says that he has discovered another 20 unnamed species in the same central Amazon region. These two new monkey species are the 37th and 38th new primate species described since 1990, according to Conservation International's President Russell Mittermeier. Van Roosmalen described the black-headed sagui dwarf marmoset (*Callithrix humilis*) (Fig. 1.30a) from Brazil in 1998. It is the second-smallest monkey species, with an average adult measuring 9 to 10 cm (3.5–4 in.) and weighing between 170 and 190 g (6 and 6.7 oz.). This newly discovered monkey may also have the world's smallest distribution for a primate: it is found only between the Amazon tributaries Rio Madeira and Rio Aripuanã, in an area 250,000 to 300,000 hectares (617,763–714,316 acres) in size—an area smaller than the state of Rhode Island. This is by far the smallest distribution of any primate in the Amazon. Brazil has the largest number of the world's 331 known monkey species—96 endemic species (29 percent).

Scientists working with the Wildlife Conservation Society (WCS) reported eight new frog species in Laos in 2006. One species features a male half the size of the female and another has a row of spines running down its belly.

(a)

(b)

Figure 1.30. (*a*) The black-headed sagui dwarf marmoset (*Callithrix humulis*) is the seventh new monkey discovered in Brazil since 1990. (*b*) The tree kangaroo (*Dendrolagus mbaiso*), another newly discovered mammal, inhabits an area of Indonesia so remote that the kangaroo had never been seen by scientists.

Since 2000, scientists from the Chicago Field Museum have described 8 new species of forest frogs and 16 new mammals in the Philippine Islands. Since 2003, Delhi University herpetologist S. D. Biju and his colleagues have described 25 new species of frogs from the Western Ghats area of India, a region considered as a global biodiversity hotspot for its species richness. An international team of scientists coordinated by Italy's MUSE science museum reported the discovery of 27 new vertebrate species (including 23 amphibians and reptiles) from the Eastern Arc Mountains of Tanzania and Kenya during 2005 to 2009.

An arboreal African monkey, *Rungwecebus* (*Lophocebus*) *kipunji*, was originally thought to be a type of mangabey when discovered by researchers in 2005, but DNA studies concluded that it was more closely related to the baboon and that it should be considered not only a new species but a new genus of primates—the first such primate discovery in Africa in 83 years. A new species of monitor lizard, *Varanus bitatawa*, was reported from the Philippines in April 2010.

In May 2010, Conservation International announced the discovery of a spike-nosed tree frog, a new woolly rat, a new imperial pigeon, a bent-toed gecko with yellow eyes, a new blossom bat, a new tree-mouse, and a tiny forest wallaby that is believed to be the smallest member of the kangaroo family documented in the world. These discoveries were the result of an expedition in late 2008 to the Foja Mountains in the Indonesian province of Papua on the island of New Guinea.

Other recent discoveries have included a new species of tree-dwelling kangaroo (*Dendrolagus mbaiso*) discovered in Indonesia in 1994 (see Fig. 1.30b); a new parrot from Brazil in 2002; a new finch (the Carrizal seedeater, *Amaurospiza carrizalensis*) in eastern Venezuela in 2003; the Yariguies brush-finch from the Andean cloud forest of Colombia in 2004; a wattled smoky honeyeater (bird) in New Guinea in 2005; a catfish with protruding teeth, six species of Siamese fighting fish, and the Kapuas mud snake (which has the ability to change its skin color) on the southeast Asian island of Borneo in 2005 and 2006; a giant elephant-shrew (*Rhynchocyon udzungwensis*) in Tanzania's Udzungwa Mountains in 2008; and Zeigler's crocodile newt (*Tylototriton ziegleri*) from a small habitat of montane forest and wetlands in Vietnam (Nishikawa, Matsui and Nguyen, 2013).

In 2012, a previously unknown Bangladeshi cricket frog (*Zakerana dhaka*) was discovered in the middle of the capital of Bangladesh, one of the world's most densely populated cities. In 2011, a tiny 13 mm (1/2 in.) long, orange-colored poison dart frog with a unique call (*Andinobates geminisae*) was discovered in the district of Donoso, Colón Province, Panama (Batista et al., 2014).

In 2013, a James Cook University–National Geographic expedition to Cape York Peninsula in north-east Australia discovered three vertebrate species new to science and isolated for millions of years: a bizarre-looking Cape Melville leaf-tailed gecko (*Saltuarius eximius*), a golden-colored Cape Melville shade skink (*Saproscincus saltus*), and a blotched boulder-frog (*Cophixalus petrophilus*) (Hoskin, 2013a, b; Hoskin et al., 2013). A new species of flying squirrel (*Biswamoyopterus laoensis*) was described in 2013 from Laos.

In 2015, seven new species of frogs were discovered just in southern Brazil's Atlantic Forest. Also in 2015, Diane's bare-hearted glass frog (*Hyalinobatrachium dianae*) was discovered in Costa Rica.

In 2017, researchers at the California Academy of Sciences added 85 new plant and animal species to Earth's tree of life, including 10 sharks, 22 fishes, a lizard, and an elephant-shrew. In the dark abyss of the Mariana Trench in the western Pacific Ocean lies the deepest spot in the world's oceans and the deepest-dwelling fish ever discovered with verified depth (ScienceDaily, May 23, 2018). Swire's snailfish (*Pseudoliparis swirei*) is a small, tadpole-like fish measuring a little over 112 mm (4 in.) in length and appears to be the top predator in its benthic community.

A third species of orangutan was discovered in a Sumatran forest (Nater et al., 2017). *Pongo tapanuliensis* is the first new great ape to be discovered since the bonobo in 1929. The new species comprises the Batang Toru population, of which fewer than 800 individuals survive, making *P. tapanuliensis* one of the most endangered great apes.

The Census of Marine Life (Ausubel et al., 2010) was an unprecedented decade-long $650-million scientific initiative involving a global network of 2,700 researchers, from more than 80 nations, who logged 540 ocean expeditions. The Census investigated life in the global ocean from microbes to whales, from top to bottom and from pole to pole. It has been described as one of the largest scientific collaborations ever conducted. As of January 2011, 30 million distribution records had been recorded. The main goal of the global marine census was to provide a baseline for future measurements in three areas: diversity, distribution, and abundance. To date, researchers have formally described more than 1,200 new marine species, with another 5,000 or more in the pipeline awaiting formal description. The most common additions were crustaceans, followed by mollusks. Scores of new fish species were discovered. Researchers have confirmed that, excluding microbes, approximately 250,000 valid marine species have been formally described in the scientific literature, with an estimated 750,000 more species remaining to be described.

All discoveries need not be in relatively remote areas. For example, a new species of paedomorphic salamander, the Ouachita streambed salamander (*Eurycea subfluvicola*) was discovered in a mountain creek in Lake Catherine State Park in Arkansas in 2011 (Steffen et al., 2014). A new species of leopard frog (*Rana* (*Lithobates*) *kauffeldi*) was discovered inhabiting the I-95 corridor from Connecticut to North Carolina—one of the most developed, heavily populated areas in the world (Feinberg, 2014). A new species of flying squirrel—Humboldt's flying squirrel (*Glaucomys oregonensis*)—has a geographic range extending along the Pacific Coast from southern British Columbia to southern California (Arbogast et al. 2017). A new legless salamander (*Siren reticulata*) was described from coastal Florida and Alabama by Graham et al. (2018).

When all of the new genera and species are officially named and described, researchers estimate that the number of known mammals alone will jump by at least 15 percent.

Review Questions and Topics

1. Why are tunicates and cephalochordates classified in the phylum Chordata? What do they have in common with vertebrates?
2. Differentiate between poikilothermy and homeothermy. Give several examples of vertebrates exhibiting each type of thermoregulation.
3. Compare the adaptive advantages of hair, feathers, and reptilian scales.
4. List the four types of teeth that may be found in mammals. Give the function of each type.
5. Define the terms *homologous* and *analogous*. Give two examples for each.

6. Distinguish among the following types of locomotion in mammals: cursorial, volant, arboreal, aerial, saltatorial, and fossorial. Give an example for each.
7. What are the two main control systems in the body of a vertebrate?
8. Discuss the adaptations that freshwater bony fishes, marine bony fishes, and cartilaginous fishes have evolved to maintain the proper concentrations of salts and other dissolved materials in their body fluids.
9. Differentiate between viviparous and oviparous. Give examples of each.
10. List several characteristics that distinguish altricial from precocial species. Give several examples.

Supplemental Reading

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Vertebrate Internet Sites

1. Introduction to the Urochordata

   www.ucmp.berkeley.edu/chordata/urochordata.html

   Provides an introduction to the urochordates. Electron microscope images.

2. Introduction to the Cephalochordata

   www.ucmp.berkeley.edu/chordata/cephalo.html

   Provides an introduction to the cephalochordates. Includes a sketch and a photograph.

3. Morphology of the Chordata

   www.ucmp.berkeley.edu/chordata/chordatamm.html

   Discusses morphological characteristics of the chordates and serves as a link to additional information.

4. Introduction to the Vertebrates

   www.ucmp.berkeley.edu/vertebrates/vertintro.html

   Introduction to the vertebrates with links to additional information.

5. Introduction to the Amniota

   www.ucmp.berkeley.edu/vertebrates/tetrapods/amniota.html

Discusses the structure of the amniote egg with links to other sites.

6. Chordata (Phylum)

   http://tolweb.org/Chordata/2499

   Overview, origins, classification, photos, taxonomy, classes, references, and links to additional information.

7. Encyclopedia of Life

   www.eol.org

   Website of the free, multilanguage, web-based guide that was begun in 2007 and covers the known living species, plus new discoveries. As of 2019, EOL has trait data available for over 1,999,000 species and higher taxa. Every living thing has its own page in this grand encyclopedia of life. Viewers may set the level of complexity they will encounter.

8. The Census of Marine Life

   www.ocean.si.edu/census-marine-life

   Discusses projects and findings.

9. The Census of Marine Life

   www.coml.org

   Results from the full Census of Marine Life.

10. Bioscience Careers

    www.aboutbioscience.org/category/careers

    Discusses the major disciplines of bioscience. Learn about job descriptions, salary ranges, educational requirements and places where you can find even more information. Select profiles are accompanied by short videos.

2 | Systematics and Vertebrate Evolution

The evolution of a single species is a process which may take millions of years and which can never be duplicated.

Michael Berger, 1978

INTRODUCTION

Biologists attempt to classify living things according to their evolutionary relationships. Because these relationships can probably never be known exactly, several systematic schools of thought have arisen, each of which has developed its own classification system.

The first step in classification is the grouping together of related forms; the second is the application of names to the groups. Some refer to the first step as systematics and the second as taxonomy; others use the two terms interchangeably to describe the entire process of classification.

Systematics comes from the Latinized Greek word *systema*, which was applied to early systems of classification. It is the development of classification schemes in which related kinds of animals are grouped together and separated from less related kinds. Simpson (1961) defined systematics as “the scientific study of the kinds and diversity of organisms and of any and all relationships among them.” Systematics, which endeavors to order the rich diversity of the animal world and to develop methods and principles to make this task possible, is built on the basic fields of morphology, embryology, physiology, ecology, and genetics.

Taxonomy is derived from two Greek words: *taxis*, meaning "arrangement," and *nomos*, meaning "law." It is the branch of biology concerned with applying names to each of the different kinds of organisms. Taxonomy can be regarded as that part of systematics dealing with the theory and practice of describing diversity and erecting classifications. Thus, systematics is the scientific study of classification, whereas taxonomy is the business and laws of classifying organisms.

Frequently, the two disciplines overlap. Taxonomists may attempt to indicate the relationships of the organism they are describing; systematists often have to name a new form before discussing its relationships with other forms. In both disciplines, distinctions must be made among various levels of differences. Individual differences must be eliminated from consideration, and features characteristic of the populations of different species must be used as the basis for forming groups. A **population** is a group of organisms of the same species sharing a particular space, the size and boundaries of which are highly variable. Similar and related populations are grouped into **species**, and species are then described. Thus, the species, not individuals, are the fundamental units of systematics and are the basis of classification.

If the fossil record were complete and all of the ancestors of living animals were known, it would be straightforward to arrange them according to their actual relationship. Unfortunately, the fossil record is not complete. Many gaps exist. As a result, the classification of organisms is based primarily on the presence of similarities and differences among groups of *living* organisms. These similarities and differences reflect genetic similarities and differences, and in turn, genetic similarities and differences reflect evolutionary origins. Fossilized remains are used whenever possible to extend lineages back into geologic time and to clarify the evolution of groups. For example, paleontological discoveries have clarified our understanding of the development of the tetrapod limb as well as the groups from which birds and mammals arose. Many controversies currently exist due to differences in interpreting the paleontological evidence (Gould, 1989). As techniques improve and more fossils are discovered, the gaps in the fossil record will become fewer, and our understanding of vertebrate evolution and the relationships among the different taxa will increase.

BINOMIAL NOMENCLATURE

The current system of naming organisms is based on a method gradually developed over several centuries. It was not finally formalized, however, until the mid-eighteenth century.

In 1753, the Swedish naturalist Carl von Linne (1707–78), better known as Carolus Linnaeus, published a book, *Species Plantarum*, in which he attempted to list all known kinds of plants. In 1758, he published the 10th edition of a similar book on animals entitled *Systema Naturae*. In that edition, the binomial system of nomenclature (two names) was applied consistently for the first time. The scientific name (binomen) of every species consisted of two Latin or latinized words: the first was the name of the **genus** to which the organism was assigned, and the second was the **trivial** name. In addition, this work was characterized by clear-cut species descriptions and by the adoption of a hierarchy of higher groupings, or taxa, including family, order, and class.

Linnaeus's methods were by no means entirely original. Even before Linnaeus, there was recognition of the categories "genus" and "species," which in part goes back to the nomenclature of primitive peoples (Bartlett, 1940). Plato definitely recognized two categories, the genus and the species, and so did his pupil Aristotle. But Linnaeus's system was quickly adopted by zoologists and expanded because of his personal prestige and influence. Thus, this was the beginning of the binomial system of nomenclature and of the modern method of classifying organisms. Any zoological binomial published in the year 1758 or later can be considered a valid scientific name; those published prior to 1758 are not. For this reason, Linnaeus is often called the father of taxonomy.

In his 10th edition of *Systema Naturae*, Linnaeus listed 4,387 species of animals. This was a substantial increase over the 549 species mentioned in the first edition in 1735. Since these represented a large variety of different forms, shapes, and sizes of organisms, Linnaeus adopted a system of grouping similar genera together as orders and similar orders together as classes. He grouped all the classes of animals together as members of the Animal Kingdom, as distinct from the Plant Kingdom.

The classes established by Linnaeus were as follows:

I. Quadrupeds: Hairy body; four feet; females viviparous, milk-producing

II. Birds: Feathered body; two wings; two feet; bony beak; females oviparous

III. Amphibia: Body naked or scaly; no molar teeth; other teeth always present; no feathers

IV. Fishes: Body footless; possessing real fins; naked or scaly

V. Insects: Body covered with bony shell instead of skin; head equipped with antennae

VI. Worms: Body muscles attached at a single point to a quasi-solid base

Classes I, II, and IV correspond to the traditional evolutionary taxonomic classes (mammals, birds, and fishes) used today. Class III, however, included both amphibians and reptiles.

Common names create difficulties because they often vary with locality, country, or other geographic subdivision. For example, the term *salamander* may mean an aquatic amphibian, or (to many persons in the southeastern United States) it may refer to a mammal, the pocket gopher (*Geomys*). In the latter instance, it is probably a contraction of “sandy-mounder,” which refers to the characteristic mounds constructed by the pocket gopher. The word *lizard* is used by many persons to refer to a salamander. The word *gopher* may be used to refer to a ground squirrel, a pocket gopher, a mole, or, in the southeastern United States, a turtle (the gopher tortoise, *Gopherus polyphemus*).

Scientific names are recognized internationally and allow for more precise and uniform communication. Because Latin is not a language in current use, it does not change and is intelligible to scientific workers of all nationalities. An important asset of the scientific name is its relative stability. Once an animal is named, the name remains, or if it is changed, the change is made according to established zoological rules. The scientific name is the same throughout the world.

The mammal that once had the largest range of any mammal in the Western Hemisphere is known variously as puma, cougar, mountain lion, catamount, deer tiger, Mexican lion, panther, painter, chim blea, leon, or leopardo in various parts of its range in Canada, the United States, and Central and South America (Fig. 2.1). It is known to biologists in all of these countries, however, as *Puma concolor*. Other members of the cat family (Felidae) are placed in different genera like the domestic cat (*Felis*), the ocelot and margay (*Leopardus*), the jaguarundi (*Herpailurus*), the Canada lynx and the bobcat (*Lynx*), and the jaguar (*Panthera*). In its complete, official format, the name of the author who described a species may follow the name of the species. For example, the mink is designated as *Mustela vison* Schreber. If a species was described in a given genus and later transferred to another genus, the name of the author of the original species, if cited, is enclosed in parentheses. *Puma concolor* (Linnaeus) indicates that Linnaeus originally classified and named this species. He classified it in the genus *Felis*, but it was later reclassified in the genus *Puma*.

Figure 2.1. The mountain lion (*Puma concolor*) once had the largest range of any mammal in the Western Hemisphere. Other common names for this species include cougar, puma, panther, painter, catamount, and deer tiger.

CLASSIFICATION

The basic unit of classification, and the most important taxonomic category, is the species. Species are the “types” of organisms. Each type is different from all others, yet the species concept probably has been discussed and debated more than any other concept in biology (Rennie, 1991; Gibbons, 1996a). An understanding of the concept of species is indispensable for taxonomic work.

Through the early part of the twentieth century, a morphological species concept was used. Populations were grouped together as species based on how much alike they looked. In the 1930s and 1940s, a more meaningful biological definition of a species emerged. The **biological species concept** was first enunciated by Mayr (1942) as follows: “Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups.” Later, Mayr (1969) reformulated his definition: “Species are groups of interbreeding natural populations that are reproductively isolated from other such groups.” Thus, a species is a group of organisms that has reached the stage of evolutionary divergence where the members ordinarily do not interbreed with other such groups even when there is opportunity to do so, or if they do, then the resulting progeny are selected against. This biological species concept became the textbook standard.

During the ensuing years, as more and more information became available about natural populations, difficulties were encountered in distinguishing one species from another, and many scientists became dissatisfied with Mayr’s definition of a species. The very concept of species has thus fueled debates for decades. At last count, there were at least 26 published concepts attempting to provide a definition of a species (de Queiroz, 2005, 2007; Zimmer, 2008; Wilkins, 2009). Defining species can have a huge effect on whether an endangered group gets protected and whether a habitat is saved or lost. Some critics feel that there is too much species-splitting going on today. A single mutation might, at least theoretically, be enough to earn a small group of animals a species name. Other researchers, however, think that they should go where the data lead rather than worry about oversplitting.

Hybridization between species has long presented a problem for the identification of biological species boundaries and, more recently, for establishing conservation priorities. Although the strict biological definition of a species states that it is reproductively isolated, many clearly defined species regularly hybridize, to the point that new species may emerge. Despite this, classifying hybrids and identifying their conservation status has been problematic. For example, two species of crocodile (American and Morelet's) have been hybridizing for millions of years (Pacheco-Sierra et al. 2018). Although more "pure" populations of each species exist, there is considerable hybridization throughout their range of overlap. Hence, conservation focus on only the nonhybridized populations would exclude a range of natural, and presumably adaptive, hybrids and millions of years of diversity.

Classification involves the recognition of species and the placing of species in a system of higher categories (taxa) that reflect phylogenetic relationships. Mayr (1969) referred to classification as "a communication system, and the best one is that which combines greatest information content with greatest ease of information retrieval." Related species are grouped together in a genus. A **genus**, therefore, is a group of closely related species or a group of species that have descended from a common ancestral group (or species). Because morphological and physiological features are, in part, the result of gene action, more identical genes should be shared by members of a given genus than by members of different genera. In general, members of the various species of a given genus have more morphological and functional features in common than they have in common with species of a related genus. For example, the domestic dog, wolves, and jackals make up the genus *Canis*. When referring to the dog, the trivial name is added—*Canis familiaris*; the wolf, a close relative, is *Canis lupus*. The name of a species is always a binomen and consists of the genus and the trivial name. This system is not unlike our usage of given names and surnames, except that the order is reversed.

In a similar way, a **family** is a group of related genera, an **order** is a group of related families, a **class** is a group of related orders, and a **phylum** is a group of related classes. Related phyla are grouped as a **kingdom**. These various taxonomic categories traditionally have been arranged in a branching hierarchical order that expresses the various levels of genetic kinship. The sequence from top to bottom indicates decreasing scope or inclusiveness of the various levels. For example:

Kingdom—Animalia

Phylum—Chordata
Class—Mammalia
Order—Carnivora
Family—Felidae
Genus—*Puma*
species—*Puma concolor*

Our present classification scheme has been devised by using the genus and trivial name as a base and then grouping them in a hierarchical system. For example, dogs (*Canis familiaris*) are related in a single genus, members of this genus in turn are related to foxes (*Vulpes*, *Urocyon*), and all of these are united in one family, Canidae. This group is somewhat more distantly related to the cats, bears, and other flesh-eaters, and all these forms are united in an order, the Carnivora. This order shares many features like mammary glands and hair, with forms as diverse as bats and whales, and all are grouped in one class, the Mammalia. In turn, mammals have numerous characteristics like an internal skeleton and a dorsal, hollow nerve cord that are also present in fishes, amphibians, and reptiles; thus, all are grouped in one of the major subdivisions of the Animal Kingdom, the phylum Chordata.

These seven categories are considered essential to defining the relationships of a given organism. Often, however, taxonomists find it necessary, because of great variation and large numbers of species, to recognize intermediate, or extra, levels between these seven categories of the taxonomic hierarchy by adding the prefixes *super-*, *infra-*, and *sub-* to the names of the seven major categories just listed (see classifications in Appendix A).

The delineation of taxa higher than the species level is rather arbitrary: a taxonomist may divide a group of species into two genera if he or she is impressed by differences, or combine them into one genus if the similarities are emphasized. For example, some authorities have included the tiger and other large cats in the genus *Felis* with the small cats, whereas other authorities have segregated them as the separate genus, *Panthera*.

All these examples belie the common idea that animal species cannot hybridize or, if they do, will produce inferior or infertile offspring—think mules. Such reproductive isolation is part of the classic definition of a species. But it is now clear that many animals violate that rule: not only do they mate with related species, but hybrid descendants are fertile enough to contribute DNA back to a parental species—a process called introgression (Pennisi, 2016).

With many different organisms being named by many different taxonomists throughout the world, biologists recognized the need for a set of rules governing scientific nomenclature. In 1895, the Third International Zoological Congress appointed a committee that drew up the Règles Internationales de la Nomenclature Zoologique (International Rules of Zoological Nomenclature) (Mayr et al., 1953). The Rules, which were adopted by the Fifth International Zoological Congress in 1901, became the universal Code of Zoological Nomenclature. The adoption of the Rules (Code) has helped to produce stability in nomenclature, and it has also helped to standardize certain taxonomic procedures. The Code established a permanent International Commission of Zoological Nomenclature that serves in a judiciary capacity to render decisions concerning difficult cases ("special cases" when the rules do not clearly solve a particular situation). It is vested with the power to interpret, amend, or suspend provisions of the Code. Some of the Code's basic rules include the following:

1. The generic or specific name applied to a given taxon is the one first published in a generally acceptable book or periodical and in which the name is associated with a recognizable description of the animal.

2. No two genera of animals can have the same name, and within a genus no two species can have the same name.

3. The species name of an animal consists of the generic name plus the trivial name.

4. Names must be either Latin or latinized and are italicized.

5. The name of a genus must be a single word and must begin with a capital letter, while the specific, or trivial, name must be a single or compound word beginning with a lowercase letter.

6. The name of a higher category (family, order, class, etc.) begins with a capital letter, but is not italicized.

7. No names for animals are recognized that were published prior to 1758, the year of publication of the *Systema Naturae*, 10th

edition.

8. The name of a family is formed by adding *-idae* to the stem of the name of one of the genera in the group. This genus is considered the *type genus* of the family.

A complete revision of the Rules was authorized at the International Zoological Congress held in Paris in 1948. All interpretations of the Rules made since 1901 were incorporated into the Revised Rules. The Code was rewritten in 1958, as the International Code of Zoological Nomenclature. The fourth and latest edition was published in 1999 (Pennisi, 2000a).

METHODS OF CLASSIFICATION

Several methods of grouping organisms together in a hierarchical system of classification have been used during the past 2,300 years. These include Aristotelian essentialism, as well as evolutionary, phenetic, and phylogenetic (cladistic) methods of classification. The latter two methods "can be viewed as late-coming developments that at least partly represent reactions against evolutionary systematics" (Eldredge and Cracraft, 1980).

A **taxon** is a taxonomic group of any rank that is sufficiently distinct to be worthy of being assigned to a definite category. Taxa are often subject to the judgment of the taxonomist. The relationship of taxa may be expressed in one of the following forms: monophyly, paraphyly, or polyphyly. A taxon is **monophyletic** (Fig. 2.2a) if it contains the most recent common ancestor of the group and all of its descendants. It is **paraphyletic** (Fig. 2.2b) if it contains the most recent common ancestor of all members of the group but excludes some descendants of that ancestor. A taxon is **polyphyletic** (Fig. 2.2c) if it does not contain the most recent common ancestor of all members of the group, implying that it has multiple evolutionary origins. Both evolutionary and cladistic taxonomy accept monophyletic groups and reject polyphyletic groups in their classifications. They differ on the acceptance of paraphyletic groups, a difference that has important evolutionary implications.

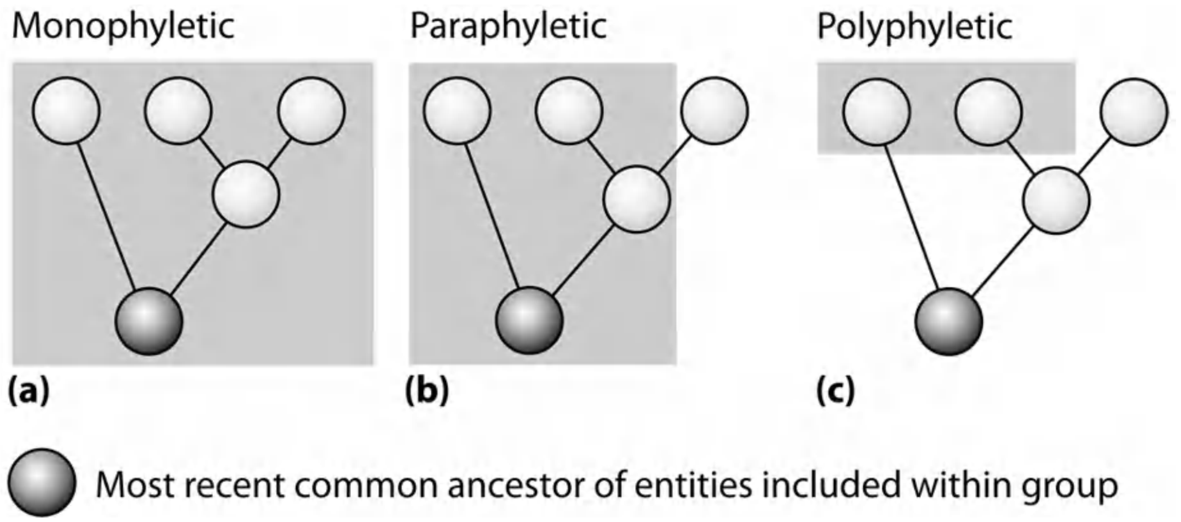


Figure 2.2. Biological taxonomists currently distinguish among three classes of taxa: monophyletic, paraphyletic, and polyphyletic. (*a*) A monophyletic group includes a common ancestor and all of its descendants. (*b*) A paraphyletic group includes a common ancestor and some but not all of its descendants. (*c*) A polyphyletic group is a group in which the most recent common ancestor of the entities included within the group is not itself included within the group.

Aristotelian Essentialism

Pre-Darwinian systems of classification were arbitrarily based on only one or a few convenient (i.e., essential) morphological characters. Aristotle (384–322 BC) did not propose a formal classification of animals, but he provided the basis for such a classification by stating that "animals may be characterized according to their way of living, their actions, their habits, and their bodily parts." In other words, animals could be characterized based on the degree of similarity of shared "essential" traits (e.g., birds have feathers, mammals have hair) of those animals. "According to Aristotle, all nature can be subdivided into natural kinds that are, with appropriate provisions, eternal, immutable, and discrete. For example, living organisms are of two sorts—plants and animals… . He subdivided animals into those that have red blood and give birth to their young alive and those that do not. He further subdivided each of these groups until finally he reached the lowest level of the hierarchy—the species" (Hull, 1988).

Aristotle's "classification" is known as the "A and not-A" system of classification:

Animals with blood (the "A" group)

Viviparous quadrupeds

    Oviparous quadrupeds
    Fishes
    Birds
  Animals without blood (the “not-A” group)
    Mollusks
    Crustaceans
    Testaceans
    Insects

Since Aristotle, philosophers have divided organisms into animals (sensible, motile) and plants (insensible, nonmotile)—a perfect example of “A” and “not-A” groups. Pliny (AD 23–79) divided animals into Aquatilia, Terrestria, and Volatilia based on their habitat. The classification of Linnaeus was similar. The class Worms (Vermes) of Linnaeus was reserved for those animals lacking both skeletons and articulated legs.

Evolutionary (Classical or Traditional) Classification

In the years following Darwin’s *On the Origin of Species* (1859), the theory of evolution replaced the concept of special creation in the scientific community. It was found that living species are not fixed and unchanging, but had evolved from preexisting species during geological time. In other words, organisms in a “natural” systematic category shared characteristics because they were descendants of a common ancestor. The more recent the divergence from a common ancestor, the more characteristics two groups would normally share. It is now considered that, in general, similarities in structure are evidence of evolutionary relationships. This is because similarities in structure are caused by similar genetic material. Organisms that share the greatest number of similar characteristics are assumed to be most closely related to one another and are grouped together. A certain degree of subjectivity is present in this system; therefore, experience and judgment on the part of the taxonomist is important.

Cladistic (Phylogenetic) Classification

In 1950, the German entomologist Willi Hennig proposed a systematic approach emphasizing common descent based on the cladogram of the group being classified. This approach, **cladistic analysis**, is a systematic method that focuses on shared, derived characters. **Derived traits** are new characteristics that appear as a new species arises from its ancestor, and hence they represent recent rather than ancient adaptations. Cladistics holds that a classification should express the branching (cladistic) relationships among species, regardless of their degree of morphological similarity or difference.

Cladistics aims specifically to create taxonomic groupings that more accurately reflect organisms' evolutionary histories (de Queiroz, 1988; de Queiroz and Gauthier, 1992). It recognizes only monophyletic taxa (all taxa evolved from a single parent stock) that include all the descendants from a single ancestral group. Cladists feel that their methods allow for better analyses and testing than those of earlier systematists. Shared characters are separated into three clearly defined groups: those shared by living organisms because they have evolved from recent common ancestors, called shared derived characters or **synapomorphies** (Gr. *synapsis*, joining together, + *apo*, away, + *morphe*, form); primitive traits inherited from an ancestor, called **plesiomorphies** (Gr. *plesi*, near); and primitive traits shared by larger groups of organisms because they have been inherited from an ancient common ancestor that had them, which are known as **symplesiomorphies** (Gr. *synapsis*, joining together, + *plesio*, near, + *morphe*, form).

A character state present in all members of a group is **ancestral** for the group as a whole. **Derived characters** are those characters that have newly evolved from the ancestral state, are shared by a more limited set of taxa, and that therefore define related subsets of the total set. The organisms or species that share derived character states, called **clades** (Gr. *klados*, branch), form subsets within the overall group. Relationships among species are portrayed in a **cladogram** (Figs. 2.3 and 2.4). A cladogram is an evolutionary diagram that depicts a sequence in the origin of uniquely derived characters: traits that are found in *all* of the members of the clade and *not* in any others. It therefore represents the sequence of origin of new groups of organisms. Although its branching pattern is somewhat similar to that of a phylogenetic tree, a cladogram is different because it does not incorporate information on the time of origin of new groups nor on how different closely related groups are. A cladogram is not based on overall similarity of species, and so it may differ substantially from a phenogram.

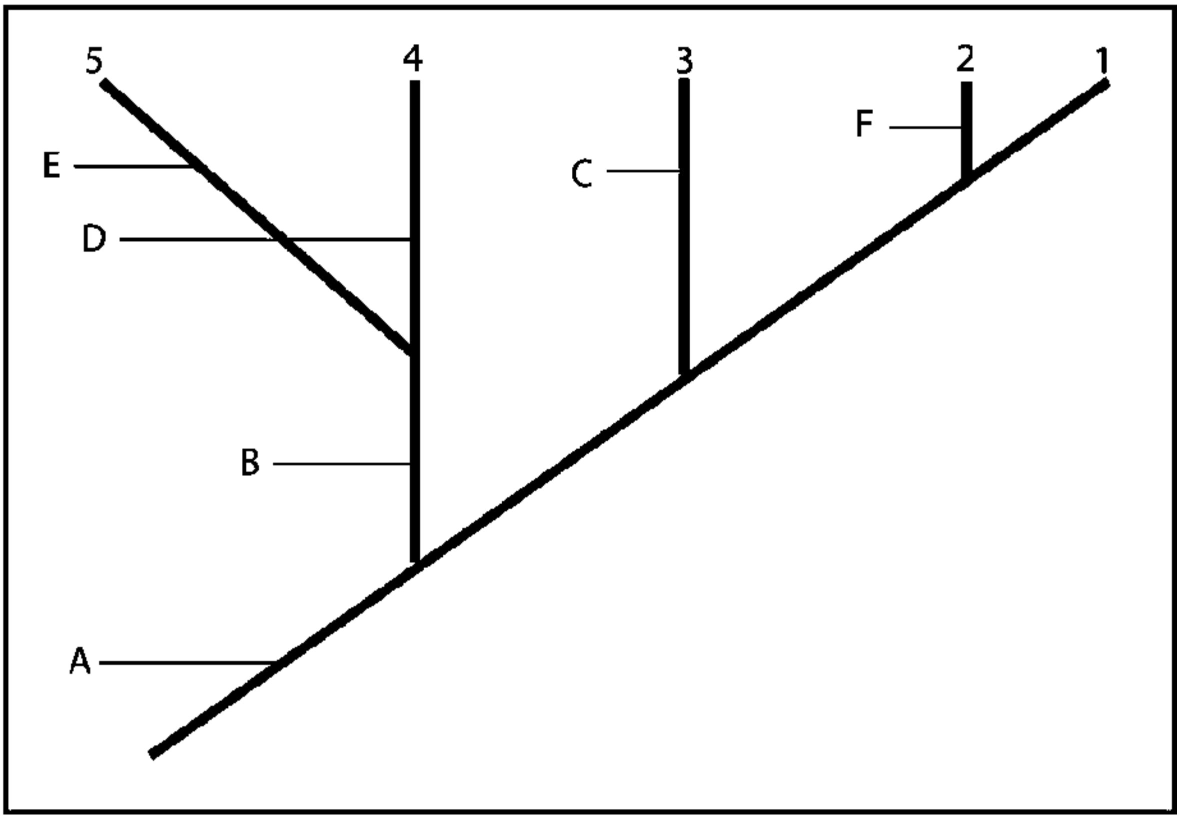


Figure 2.3. This hypothetical cladogram shows five taxa (1–5) and the characters (A–F) used in deriving the taxonomic relationships. Character A is a symplesiomorphy (shared, ancestral characteristic) because it is shared by members of all five taxa. Because it is present in all taxa, character A cannot be used to distinguish members of this monophyletic lineage from each other. Character B is a synapomorphy (derived, ancestral character) because it is present in taxa 4 and 5 and can be used to distinguish these taxa from 1–3. Character B, however, is on the common branch giving rise to taxa 4 and 5. Character B is, therefore, symplesiomorphic for those two taxa. Characters D and E are derived traits and can be used to distinguish members of taxa 4 and 5.

A cladogram uses a method known as outgroup comparison to examine a variable character. A group of organisms that is phylogenetically close but not within the group being studied is included in the cladogram and is known as the **outgroup**. Any character state found both within the outgroup and in the group being studied is considered to be ancestral for the study group. For example, if the study group consisted of four vertebrates (frog, snake, fox, and antelope), *Amphioxus* could serve as the outgroup. In this example, characters like vertebrae and jaws are common only to the study group and are not found in the outgroup.

Species within a single genus resemble each other because they share a recent common ancestor. Similarly, members of a family represent a larger evolutionary lineage descended from common stock in the more remote past. Because cladistic classifications are based on shared derived character states, they may radically regroup some well-recognized taxa. Furthermore, because a cladogram is based on monophyletic taxa, each group that arises from a particular branch point along a cladogram is related through the characters that define that branch point. A group of organisms most closely related to the study taxon is known as a **sister group**. Traditional evolutionary taxonomy using such characters as scales, feathers, and hair is compared with a cladistic classification linking the same organisms through shared characteristics in Fig. 2.4.

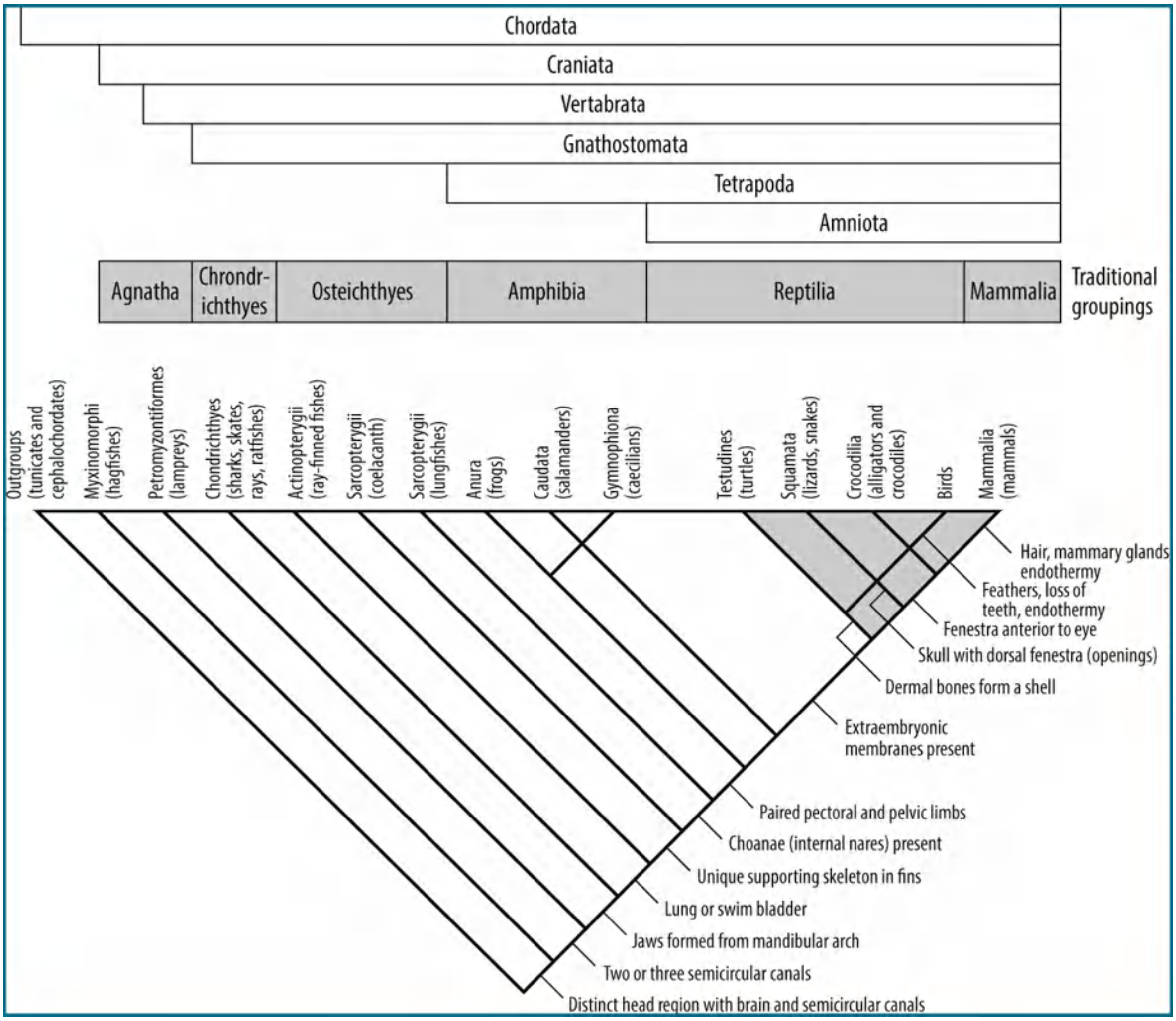


Figure 2.4. A cladogram is constructed by identifying the point or node at which two groups diverged. Animals that share a branching point are included in the same taxon. Time scales are not given or implied, and the relative abundances of taxa are not shown. This diagram of extant (living) vertebrates shows birds and crocodilians sharing a common branch, indicating that these two groups share many common characters and are more closely related to each other than either is to any other group of extant animals.

Constructing a Cladogram

The first step in constructing a cladogram is to summarize the characters of the taxa being compared. Knowledge of the organisms is essential for choosing the characters for analysis, since a cladogram is constructed on the basis of unique derived characters. In the example presented in Figure 2.8, the study group consists of four vertebrates: brook trout, tiger salamander, giraffe, and gray squirrel. The lancelet is included as the **outgroup**, a taxon outside of the study group but consisting of one or more of the study group’s closest and more primitive relatives. Any character found in both the outgroup and the study group is considered to be primitive, or **plesiomorphic** (ancestral), for the study group. Traits that are common to some, but not all, of the species in the study group are used to construct the simplest and most direct (parsimonious) branching diagram.

This cladogram is made up of three clades, with each clade consisting of all the species descended from a common ancestor. Clades differ in size because the first clade (vertebrae and jaws) includes the other two, and the second clade (four legs, lungs) includes the third clade, which contains the giraffe and squirrel.

All of the study groups belong to the first clade because they all possess vertebrae and jaws. The tiger salamander, giraffe, and gray squirrel are in the clade that has lungs and four legs. Only the giraffe and gray squirrel (of the animals considered here) have a four-chambered heart, are endothermic, and have an embryo surrounded by an amnion.

Phenetic approaches focus on degrees of difference, whereas cladists concentrate on specific differences or character states (derived traits). Each synapomorphic trait is given equal weight, with the number of trait differences between each pair of organisms being used to create the simplest branching diagram.

To represent the phylogeny of vertebrates in a cladistic classification, animals are arranged on the basis of their historical divergences from a common ancestral species. Animals with similar derived characters are considered more closely related than animals that do not share the characters. The results of such an analysis should produce a cladogram that approximates the phylogeny of the animals considered. Unfortunately, problems arise in actual practice. Evolution may not always occur by what appears to be the simplest route. As in all forms of systematics, similarities and differences like convergent evolution (the evolution of similar adaptations in unrelated organisms to similar environmental challenges), loss or reversal of characters, and parallelism (evolution of similar structures in related [derived] organisms) can be misinterpreted easily. The greatest problem in creating groupings is the difficulty of determining which character states are primitive and which are derived.

A major difference between evolutionary and phylogenetic systematics is seen, for example, in the classification of reptiles and birds (Fig. 2.5). The tuatara, lizards, snakes, crocodilians, and birds all possess a skull with two pairs of depressions in the temporal region (diapsid condition). Phylogenetic systematists (cladists) place all of these forms in one monophyletic group (Diapsida). When this group is subdivided, the birds and crocodilians (Archosauromorpha) and the tuatara, snakes, and lizards (Lepidosauromorpha) are placed in a separate taxonomic rank. Evolutionary systematists, on the other hand, place crocodilians, tuataras, lizards, snakes, and turtles (which are anapsids) in the class Reptilia and birds in a separate class (Aves). Evolutionary systematists attribute great significance to such "key characteristics" in birds as the presence of feathers and endothermy, and they group the diapsid crocodilians and squamates with the turtles, which are morphologically distinct, because they share many primitive characters. Cladists, however, make the point that the use of “key characteristics” involves value judgments by systematists that cannot be tested scientifically.

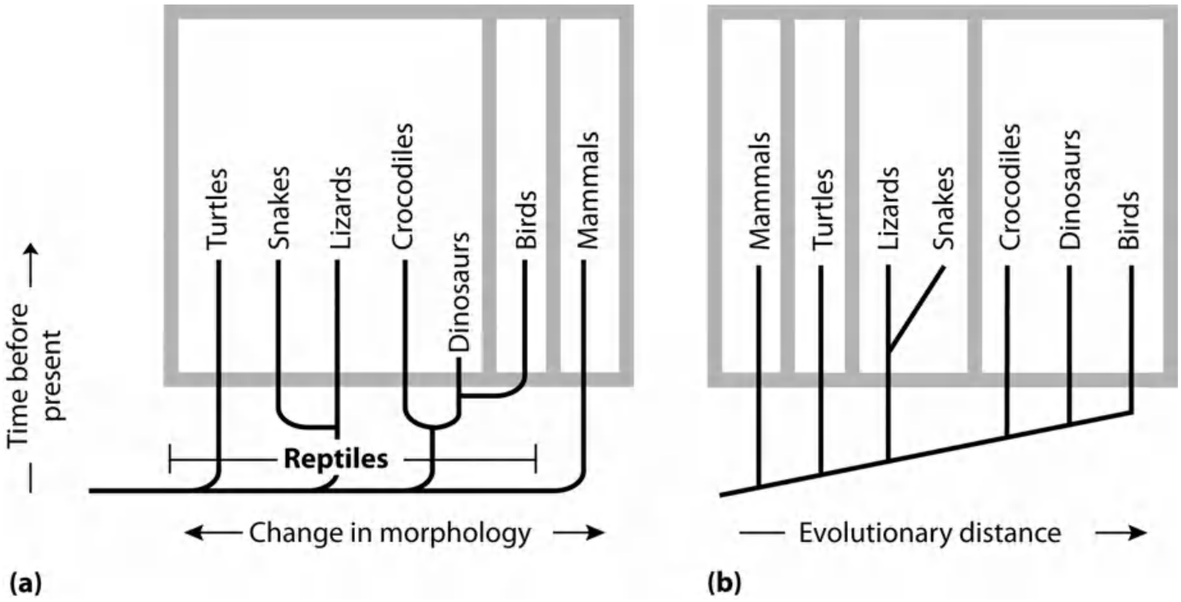


Figure 2.5. Comparison of evolutionary and cladistic systematics among the amniotes. (*a*) In evolutionary taxonomy, traditional key characteristics like scales for reptiles, feathers for birds, or fur for mammals are used to differentiate the groups. (*b*) A cladistic classification links organisms with uniquely derived characters and shared ancestries.

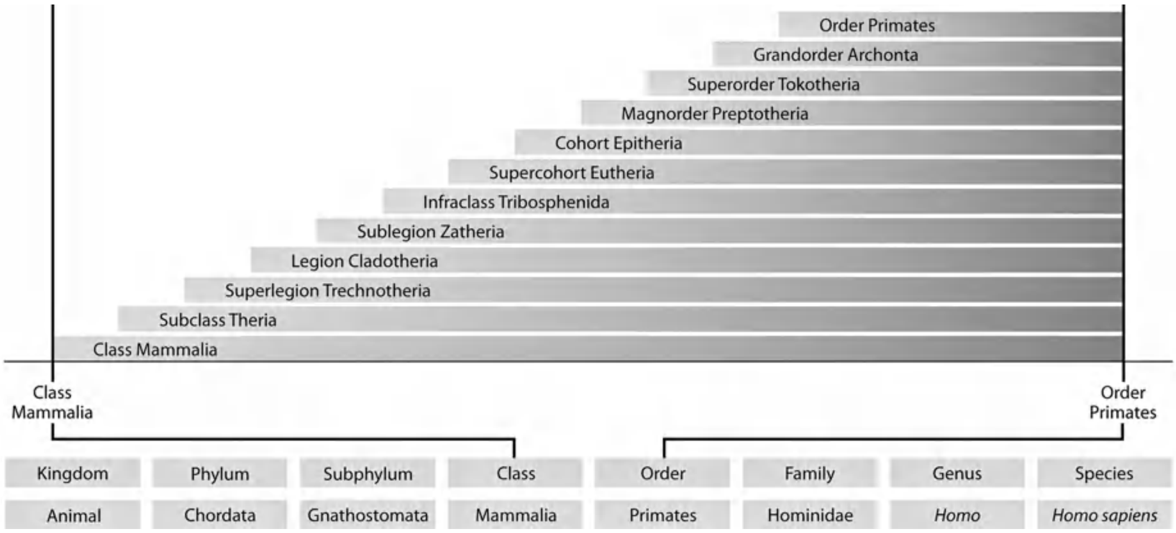


Figure 2.6. A classification of the primates based on cladistics. *Bottom:* The major taxonomic categories as they are used in the classification of humans without regard to cladistics.

"Traditional evolutionary" systematists are attempting to achieve the same goal as "phylogenetic" systematists: the accurate interpretation of the pattern of evolutionary descent of specific groups of organisms, like vertebrates. Thus, both current approaches are phylogenetic and evolutionary. While the goal is the same, the methods differ. Each method has its proponents and its critics. Some have even attempted to combine the best features of both evolutionary and cladistic methods. Wiley (1981) summarized the principles of cladistics, and Cracraft (1983) described the use of cladistic classifications in studying evolution. Additional information concerning phylogenetic systematics can be found in Eldredge and Cracraft (1980), Nelson and Platnick (1981), Halstead (1982), Ghiselin (1985), Abbott et al. (1985), Hull (1988), Nelson (2006), and Hamilton (2014).

To the extent possible, classifications in this text will use monophyletic taxa that are consistent with the criteria of both evolutionary and cladistic taxonomy. Complete revision of vertebrate taxonomy utilizing cladistic criteria would result in vast changes, including the probable abandonment of Linnaean ranks. In many cases, classifications based strictly on cladistics would require numerous taxonomic levels and be too complex for convenience (Fig. 2.6). A separate category must be created for every branch derived from every node in the tree. Not only must many new taxonomic categories be employed, but older ones must be used in unfamiliar ways. For example, in cladistic usage, the category of "reptiles" includes birds with traditional reptiles (turtles, lizards, snakes, crocodilians) but exclude some fossil forms, like the mammal-like reptiles, that have traditionally been classified in the Reptilia.

Some cladistic classifications require compromises. For example, a cladogram showing the evolutionary history of the tuna, lungfish, and pig requires that the lungfish and pig be placed in a group separate from the tuna (Fig. 2.7). The lungfish is obviously a fish, but the pig and all mammals (including humans) have shared a common ancestor with it more recently than its common ancestor with the tuna.

Cladograms for each class of vertebrates are given in Chapters 3, 5, 6, and 9.

EVOLUTION

Evolution is the underlying principle of biology. The modern theory of evolution includes two basic concepts: first, the characteristics of living things change with time; second, the change is directed by natural selection. **Natural selection** is the nonrandom reproduction of organisms in a population that results in the survival of those best adapted to their environment and the elimination of those less well adapted. If the variation is heritable, natural selection leads to evolutionary change. The change referred to here is not change in an individual during its lifetime, but change in the characteristics of populations over the course of many generations. An individual cannot evolve, but a population can. The genetic makeup of an individual is set from the moment of conception; in populations, though, both the genetic makeup and the expression of the developmental potential can change. Natural selection is thoroughly opportunistic. A population responds to a new environmental challenge by appropriate adaptations or becomes extinct. The fossil record bears witness to the fact that a majority of the species living in the past eventually became extinct. The organisms likely to leave more descendants are those whose variations are most advantageous as adaptations to the environment. Natural selection occurs in reference to the environment where the population presently lives; evolutionary adaptations are not anticipatory of the future. The change in the genetic makeup of a population over successive generations is **evolution**.

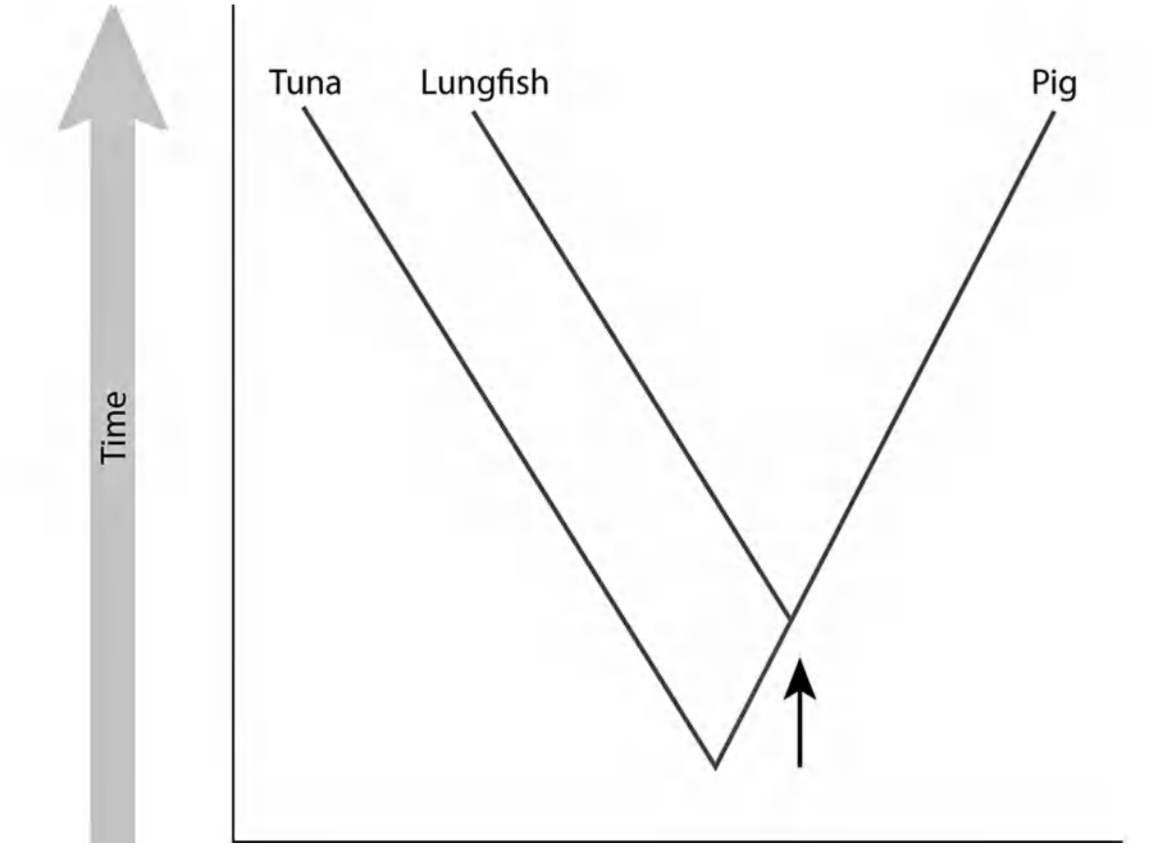


Figure 2.7. Cladogram showing the evolutionary relationship between the tuna, lungfish, and pig. It is traditional to classify the tuna and lungfish together in the class Osteichthyes (bony fishes) and to classify the pig in the class Mammalia (mammals). However, this violates the basic rule of cladistics: all members of a taxonomic group must have shared a common ancestor with each other more recently than they have with members of any other group. The lungfish, which possesses internal nostrils and an epiglottis, is descended from an ancestor (*arrow*) that is also the ancestor of all land-living vertebrates (including humans).

A population is made up of a large number of individuals that share some important features but differ from one another in numerous ways, some rather obvious, some very subtle. In human beings, for example, we are well aware of the uniqueness of the individual, for we are accustomed to recognizing different individuals on sight, and we know from experience that each person has distinctive anatomical and physiological characteristics as well as distinctive abilities and behavioral traits. It follows that if there is selection against certain variants within a population and selection for other variants within it, the overall makeup of that population may change with time since its characteristics at any given time are determined by the individuals within it.

Darwin recognized that in nature the majority of the offspring of any species die before they reproduce. If survival of the young organisms were totally random and if every individual in a large population had exactly the same chance of surviving and reproducing as every other individual, then there would probably be no significant evolutionary change in the population. But survival and reproduction are never totally random. Some individuals are born with such gross defects that they stand almost no chance of surviving to reproduce. In addition, differences in the ability to escape predators, to obtain nutrients, to withstand the rigors of the climate, to find a mate, and so forth, ensure that survival will not be totally random. The individuals with characteristics that weaken their capacity to escape predators, to obtain nutrients, to withstand the rigors of the climate, and the like will have a poorer chance of surviving and reproducing than individuals with characteristics enhancing these capabilities. In each generation, therefore, a slightly higher percentage of the well-adapted individuals will leave progeny. If the characteristics are inherited, those favorable to survival will slowly become more common as the generations pass, and those unfavorable to survival will become less common. Given enough time, these slow shifts can produce major evolutionary changes.

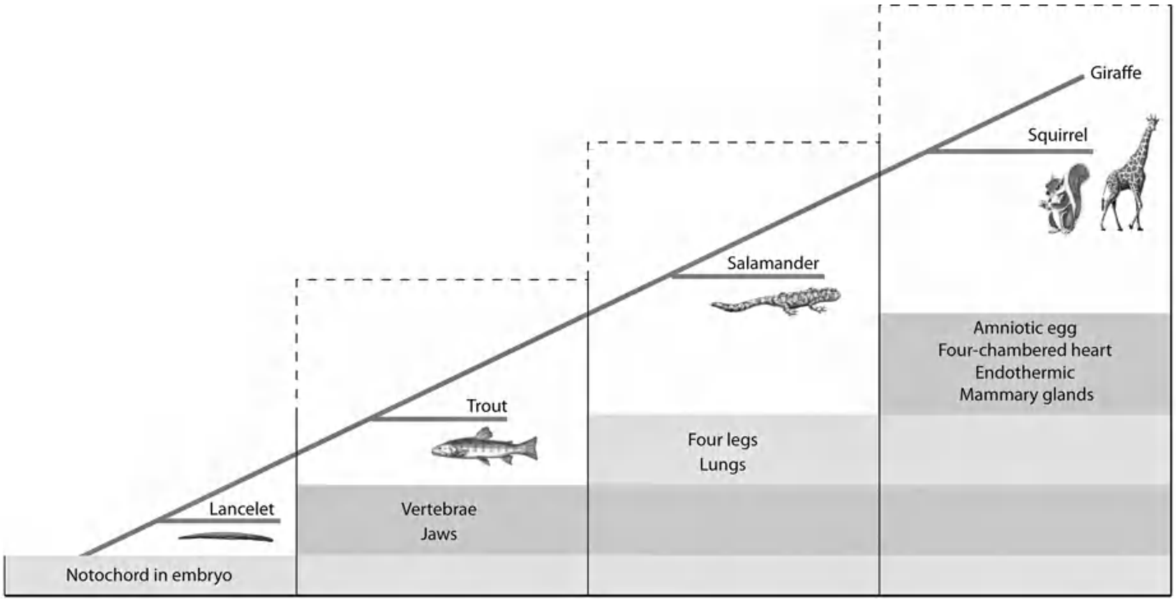


Figure 2.8. Construction of a cladogram involving four vertebrates: a fish, an amphibian, and two mammals. The lancelet serves as the outgroup.

High-Speed Evolution

In certain situations, evolution may proceed at a rapid rate. For example, in Trinidad's Aripo River, a species of cichlid fish feeds primarily on relatively large, sexually mature guppies (*Poecilia reticulata*); in nearby tributaries, killifish prefer tender young fish. In response to these different pressures, the guppies have evolved two different life-history strategies. Those in the Aripo River reach sexual maturity at an early age and bear as many young as possible before succumbing to a predator. The guppies in the tributaries bear fewer young and have delayed sexual maturity because their focus is surviving into adulthood. By transplanting guppies from the Aripo River to a tributary that happened to be empty of guppies and where killifish were the only predators, researchers were able to prove that predation caused this pattern. Within four years, transplanted male guppies were already detectably larger and older at maturity when compared with the control population; they had switched strategies, delaying their sexual maturity and living longer. Seven years later, females were also noticeably larger and older. Some of these adaptations occurred in just four years—a rate of evolutionary change some 10,000 to 10 million times faster than the average rates determined from the fossil record.

In another study, small populations of the brown anole (*Anolis sagrei*) were transplanted from Staniel Cay in the Bahamas to several nearby islands in 1977. Staniel Cay has scrubby to moderately tall forests, whereas the experimental islands have few trees and are mostly covered by vegetation with narrow stems. Within a 10- to 14-year period, the displaced lizards were found to have shorter rear legs than their ancestors, an apparent adaptation to the bushy vegetation that dominated their new island. Whereas species living on tree trunks have longer legs for increased speed, shorter legs provide increased agility for species living on bushy vegetation. The more different the recipient island's vegetation from that of Staniel Cay, the greater the magnitude of adaptation. Such changes could in time turn each island's population into a separate species.

The house sparrow (*Passer domesticus*) was introduced into North America from western Europe during the period 1852–60. Studies of color and of 16 skeletal characters from 1,752 specimens from 33 localities taken between 1962 and 1967 throughout North America revealed color and size differentiation in all 16 characters. This adaptive radiation occurred in just 50 to 115 generations.

Geographic variation in the house sparrows was most pronounced in color. In many cases, the color differences were both marked and consistent, permitting specimens from several localities to be consistently identified solely on the basis of color. One measurable component, gross size, showed strong inverse relationships with measures of winter temperature. This adaptation (larger body size in colder regions) is consistent with the ecogeographic rule of Bergmann. The adaptive variation found in limb size (shorter limb size in colder regions) was consistent with Allen's Rule. These latter adaptations are designed to conserve heat in colder climates and radiate heat in warmer regions. Since sparrows did not reach Mexico City until 1933, Death Valley before 1914, or Vancouver before 1900, the data suggest that racial differentiation in house sparrow populations may require no more than 50 years.

Johnston and Selander, 1964, 1971; Case, 1997; Losos et al., 1997; Morell, 1997b; Reznick et al., 1997

Thus, Darwin's explanation of evolutionary change in terms of natural selection depends on five basic assumptions:

1. Many more individuals are born in each generation than will survive and reproduce.
2. There is variation among individuals; they are not identical in all their characteristics.
3. Individuals with certain characteristics have a better chance of surviving and reproducing than individuals with other characteristics.
4. At least some of the characteristics resulting in differential reproduction are heritable.
5. Enormous spans of time are available for slow, gradual change.

Natural selection is a creative process that generates novel features from the small individual variations that occur among organisms within a population. It is the process whereby organisms adapt to the demands of their environment. Over many generations, favorable new traits will spread through the population. Accumulation of such changes leads, over long periods of time, to the production of new organismal features and new species.

Species and Speciation

Speciation, the process by which new species of organisms evolve in nature from an ancestral species, is generally considered to be a population phenomenon. A small local population, like all the perch in a given pond or all the deer mice in a certain woodlot, is known as a **deme**. Although no two individuals in a deme are exactly alike, the members of a deme do usually resemble one another more closely than they resemble the members of other demes for two reasons: (1) they are more closely related genetically because pairings occur more frequently between members of the same deme than between members of different demes; and (2) they are exposed to more similar environmental influences and hence to more nearly the same selection pressures.

It must be emphasized that demes are not clear-cut units of population. Although the deer mice in one woodlot are more likely to mate among themselves than with deer mice in the next woodlot down the road, there will almost certainly be occasional matings between mice from different woodlots. The woodlots themselves are not permanent ecological features. They have only a transient existence as separate and distinct ecological units: neighboring woodlots may fuse after a few years, or a single large woodlot may become divided into two or more separate smaller ones. Such changes in ecological features will produce corresponding changes in the demes of deer mice. Demes, then, are usually temporary units of population that intergrade with other similar units. The deme is the ultimate systematic unit of species in nature. In some cases, a deme may correspond to a subspecies, but it is almost always a decidedly smaller group. Demes do not enter into classification because they do not have long-continuing evolutionary roles and because adjacent demes often have no observable differentiation.

Demes often differ from one another in a geographic series of gradual changes. A gradual geographic shift in any one genetically controlled trait is known as a character **cline** (Fig. 2.9). A series of samples from along a cline reveals a gradual shift in a particular character, like body size, tail length, number of scales, or even intensity of coloration. Because such situations add to the difficulty of deciding the true phylogenetic relationships of populations, the experience and judgment of the systematist play an important role.

Intergradation occurs between “similar” demes. Some interbreeding can be expected between deer mice from adjacent demes, but we do not expect interbreeding between deer mice and house mice or between deer mice and gray squirrels. We recognize the existence of units of population larger than demes that are more distinct from each other and longer lasting than demes. One such unit of population is that containing all the demes of deer mice. We call these larger units species. A species is a genetically distinctive group of natural populations (demes) that share a common gene pool and that are reproductively isolated from other such groups. In other words, a species is the largest unit of population within which effective **gene flow** (exchange of genetic material) occurs or can occur.

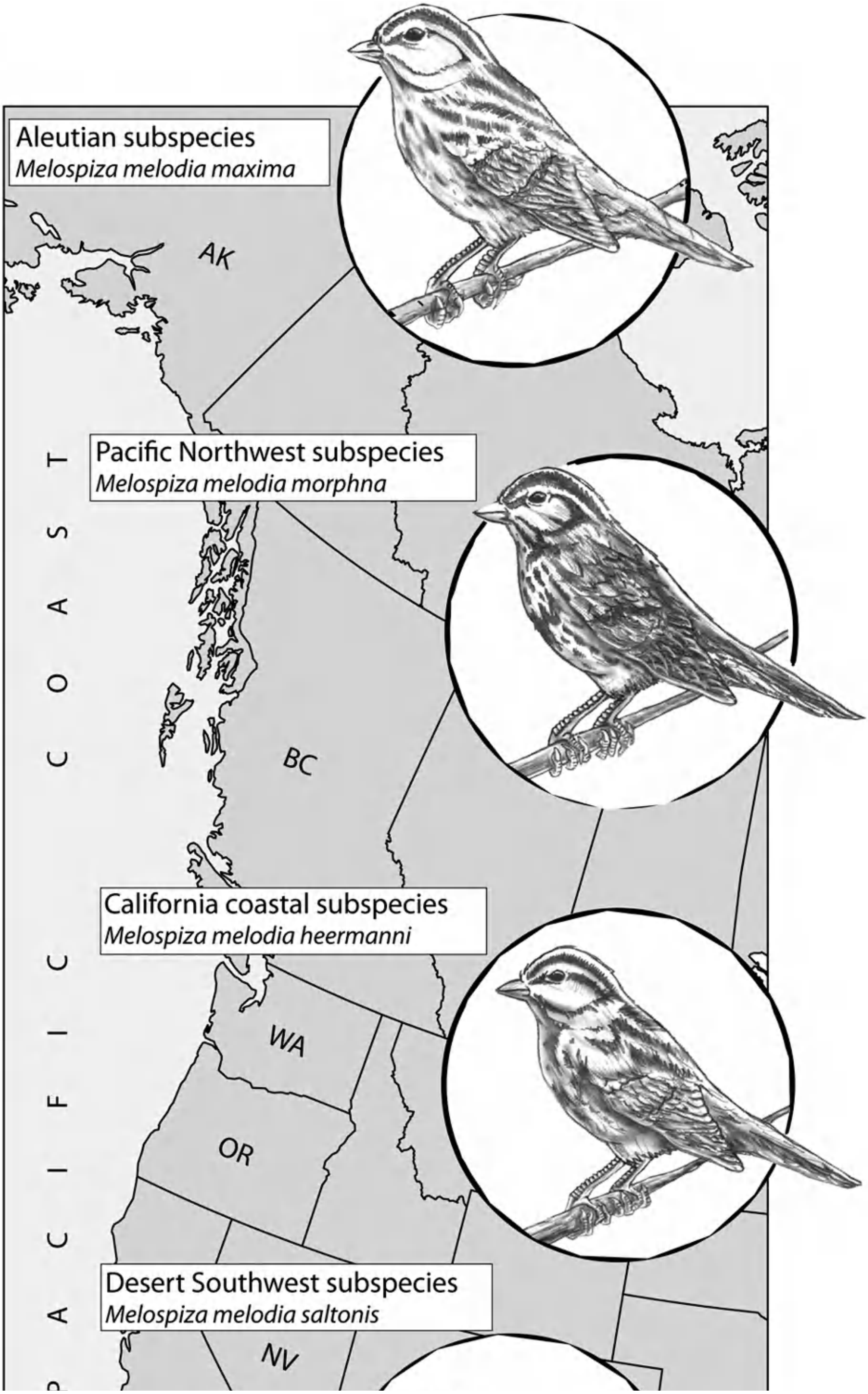

Aleutian subspecies
Melospiza melodia maxima
Pacific Northwest subspecies
Melospiza melodia morphna
California coastal subspecies
Melospiza melodia heermanni
Desert Southwest subspecies
Melospiza melodia saltonis
AK
BC
WA
OR
NV
PACIFIC COAST

Figure 2.9. On the west coast of North America, subspecies of the song sparrow form a cline in body size, plumage coloration, and song characteristics. There is a dramatic difference in appearance between the small, pale *Melospiza melodia saltonis* subspecies of the southwestern desert region and the large, dark Aleutian subspecies, *M. m. maxima*. It seems unlikely that the desert-dwelling subspecies *saltonis* would easily breed with the large Alaskan subspecies *maxima*, even if the ranges of the two subspecies were to overlap in the future. If some catastrophe completely eliminated the central west coast populations of the song sparrow, the northern and southern ends of the cline would likely become two distinct species of sparrow.

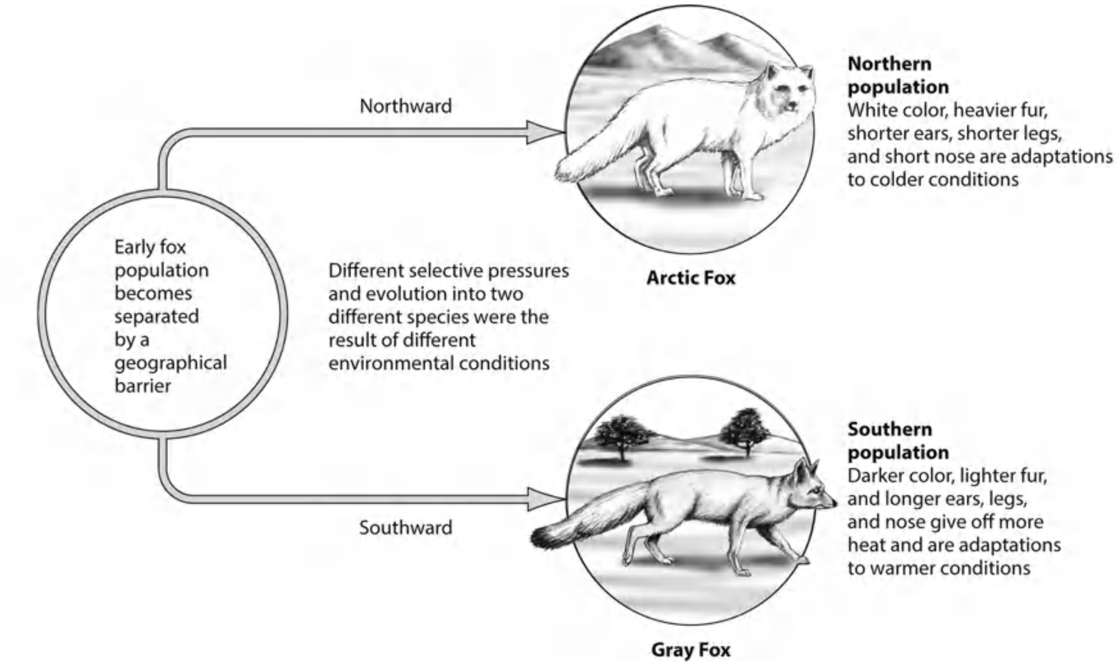


Figure 2.10. Speciation of an ancestral species of fox into two different species, resulting from migration of portions of the original fox population into geographically isolated areas with different climates.

According to Mayr's biological species concept, a species consists of a collection of interbreeding individuals. The biological species concept is based on reproductive isolation—related species may occasionally hybridize but cannot and do not reproduce regularly.

Sometimes, there may be a rather abrupt shift in some character in a particular part of the range of the species. When such an abrupt shift in a genetically determined character occurs in a geographically variable species, some biologists designate the populations on the two sides of the step as **subspecies** or **races**.

Subspecies (and species) were formerly described solely on the basis of their morphological characteristics—primarily differences in external and skeletal form and appearance. Whitaker (1970) proposed a biological subspecies concept to replace the morphological subspecies concept. Whitaker proposed that subspecies should be restricted to situations wherein populations or groups of populations appear to be on their way toward becoming new species.

The initial step in speciation is the introduction of a **primary isolating barrier** that tends to prevent or reduce the opportunity for interbreeding between closely related species. Physical barriers like mountain ranges, deserts, bodies of water, canyons, and differences in physical size would be examples of primary isolating barriers.

Allopatric populations, those that live in different regions, may have no common borders between their distributional areas; such isolated populations have no natural means of gene exchange. This **geographic isolation** serves as a primary isolating barrier. Elevation often serves as a geographic barrier, particularly in the tropics. Many of the isolated mountains in the southwestern United States exist as cool, moist forests in a sea of hot, dry desert. The small mammals, reptiles, and amphibians currently inhabiting these forests traveled there when the mountains were connected by corridors of suitable forested habitat during the Pleistocene. Today, these animals exist as isolated populations.

Islands also provide geographic isolation for many species. The California Channel Island fox (*Urocyon littoralis*) is a dwarf island species found only on six of the Channel Islands off the coast of California (Gilbert et al., 1990). It is thought that the foxes probably dispersed to the northern islands by floating on debris from the mainland during a storm, earthquake, or other natural event more than 18,000 years ago, when the distance would have been approximately 6.5 km. Populations were probably transported to the two southern islands by Native Americans between 2,200 and 3,800 years ago. These are now genetically isolated populations that are evolving independently.

When a primary isolating barrier is in place, the development of **secondary isolating barriers** can occur. These are mechanisms that, over time, prohibit interbreeding even if the primary isolating barrier is removed (Fig. 2.10). The advertisement calls of most male anurans are excellent examples of secondary reproductive isolating barriers—no two male frogs have identical calls. If the secondary isolating barriers have developed to the point that the two populations would be unable to breed even if the primary isolating barrier were removed and they were in contact with one another, then speciation has occurred.

Premating, or **prezygotic**, barriers prevent successful fertilization. They may be **ecological** (differences in minor habitat requirements), **ethological** (differences in mating behavior), **morphological** (differences in structure that prevent mating), or **physiological** (different mating seasons, gamete incompatibility). **Postmating**, or **postzygotic**, barriers operate after fertilization. They may be **physiological** (hybrid inviability, hybrid sterility, etc.) or **cytological** (differences in chromosome structure may prevent development of the fertilized egg). Even if successful mating occurs, offspring may be weak or abnormally developed, they may fail to reach sexual maturity, or they may be sterile. Any of these conditions would disrupt the continuity of genetic exchange between populations.

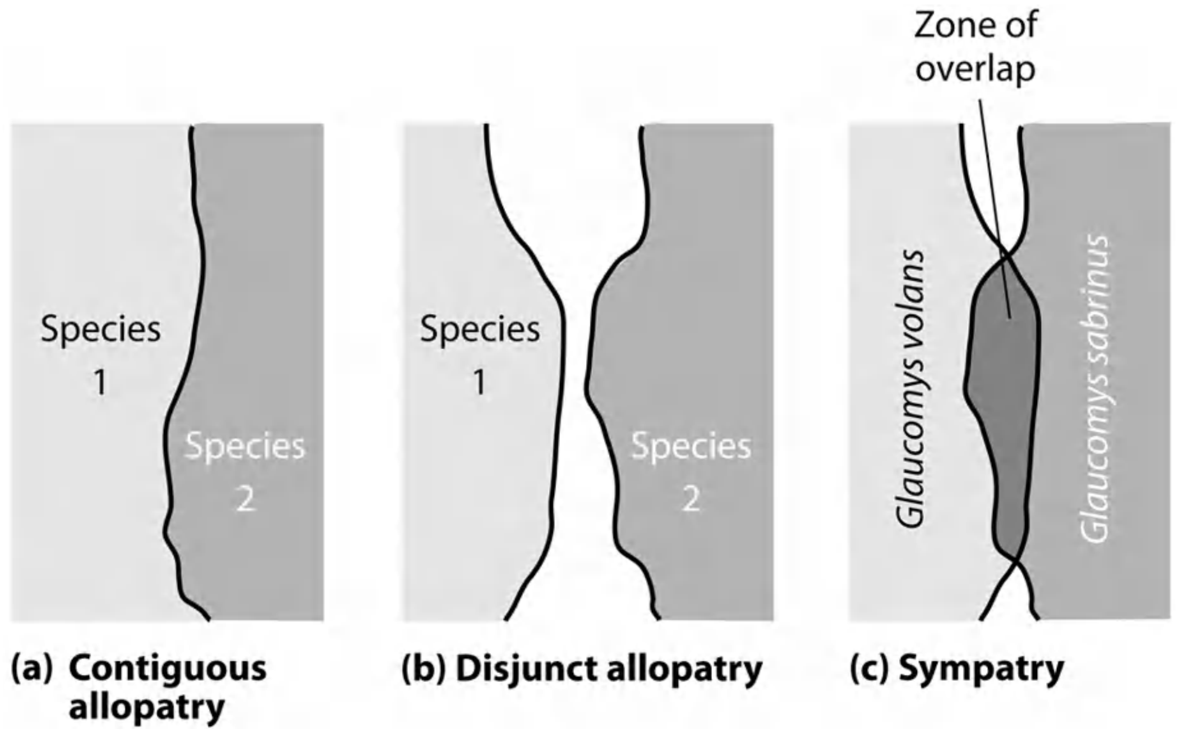
Thus, Whitaker's (1970) criteria for the recognition of subspecies are: (1) a primary isolating barrier is in place but secondary isolating barriers are not; and (2) the results of evolution can be observed as morphological (or other) variations between the mutually isolated populations.

When segments of a population become isolated geographically, the two isolated segments of the population might well accumulate enough genetic differences (secondary isolating barrier) to prevent interbreeding and the exchange of genetic information even if the original barrier were removed. This is known as **allopatric speciation** and is the most common type of speciation among animals (Fig. 2.11). Allopatric speciation may occur when climatic or geological changes produce impenetrable barriers that separate a species into different populations. It also may occur when a small number of individuals either disperse or are transported to a new and distant environment. Known as the **founder effect**, speciation can proceed rapidly since only a portion of the original gene pool is normally present in the small, newly relocated population, and natural selection can work more quickly on smaller gene pools. The founder effect may allow the new population to establish itself in a much shorter period of time than might be expected; however, if the gene pool is so limited that the individuals cannot adapt to the new environment, the entire population may be lost through the process of natural selection.

Songbird Divergence

Songbird species that have distinct eastern and western North American populations have long been thought to have diverged during the Late Pleistocene glaciations, approximately 100,000 years ago. However, analyses of mitochondrial DNA (mtDNA) of 35 pairs of songbirds indicate that while some diverged relatively recently (e.g., the timberline and Brewer's sparrows about 35,000 years ago), many diverged much earlier (Steller's jay and blue jay as long as 5 Mya). The average mtDNA difference was 5.1 percent for all pairs of eastern and western songbirds, suggesting that they have been evolving separately for 2.5 million years.

Klicka and Zink, 1997



(a) Contiguous allopatry **(b) Disjunct allopatry** **(c) Sympatry**

Figure 2.11. (*a*) Contiguous allopatry occurs when the ranges of two populations meet, but without interbreeding. (*b*) Disjunct allopatry occurs when two populations are separated spatially or temporally. (*c*) Sympatry occurs when the ranges of two populations overlap but no interbreeding occurs, as with the southern flying squirrel (*Glaucomys volans*) and the northern flying squirrel (*Glaucomys sabrinus*).

Two major types of allopatry are recognized. **Contiguous allopatry** (see Fig. 2.11a) occurs when the ranges of two populations meet and interdigitate (but do not overlap) without interbreeding between the two groups. The usual evidence of contiguous allopatry is the absence of morphologically distinct intermediate forms. Different ecological requirements for sandy and clay soils, for example, may account for interdigitation of the two populations/species where the respective environments meet. As long as interbreeding does not occur, each population is defined as a separate species.

Disjunct allopatry (see Fig. 2.11b) occurs when two more or less morphologically differentiated populations are separated by a wide geographic gap where neither population occurs. Such instances are numerous because geographic separation of populations is one important method by which speciation is initiated. Although such populations are prevented from interbreeding by one or more geographic barriers, the natural situation gives no clue as to whether they have developed reproductive isolating mechanisms. A fairly reliable decision could be reached if individuals of both populations are brought together under controlled conditions and given the opportunity to breed. For example, orangutans (*Pongo pygmaeus*) from the island of Sumatra and the mainland appear to be distinct species, yet in captivity they interbreed and have healthy hybrid offspring. Zoos are now keeping the two groups separate and destroying any hybrids. Some species, however, refuse to mate in captivity. If successful mating results in inviable offspring because of genetic, ethological, physiological, or other differences, it demonstrates that the parents belong to different species. Little information of this sort is available for disjunct allopatric populations of vertebrates.

Once isolation occurs, each population (initially a subspecies) follows its own evolutionary course. If two populations are **sympatric**—that is, they exist in the same region, with either a broad or narrow zone of overlap—and do not interbreed, this demonstrates that they have evolved into two distinct species (see Fig. 2.11c). By their coexistence, such populations show that they have developed effective secondary isolating barriers.

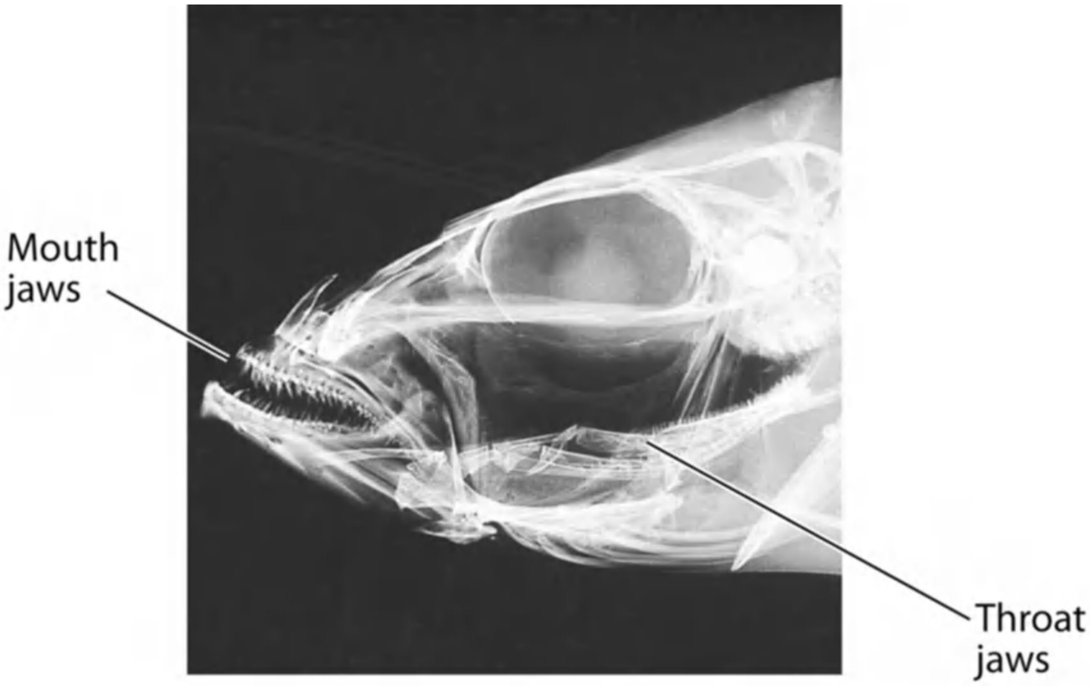
In some cases, speciation can proceed at rapid rates. Members of the freshwater family Cichlidae exhibit exceptional diversity wherever they occur in Africa, Madagascar, southern India, Sri Lanka, South and Central America, and the southwestern United States. By far, however, the most abundant diversity occurs in the East African lakes of Victoria, Malawi, and Tanganyika (Stiassny and Meyer, 1999; Pennisi, 2018a). Lake Victoria formed between 250,000 and 750,000 years ago; it contains approximately 400 species of cichlids. Lake Malawi is about 4 million years old and contains 300 to 500 cichlid species. Lake Tanganyika is 9 to 12 million years old and has approximately 200 species.

Several factors have allowed cichlids to diversify and exploit a variety of habitats. Cichlids are the only freshwater fishes to possess a modified second set of jaws (remodeled gill arches) (Fig. 2.12a). The jaws in the mouth are used to suck, scrape, or bite off bits of food; the jaws in the throat are used to crush and macerate food. Both the jaws and the teeth—sharp, pointed piercers (Fig. 2.12b) and flat, molar-like crushers (Fig. 2.12c)—can change shape within the lifetime of a single animal. The unique jaws and teeth allow each species to specialize and occupy its own specific ecological niche (see discussion of scale-eating cichlids in Chapter 4). All cichlids care for their broods long after hatching; many are mouthbrooders and hold fertilized eggs or young in their mouths.

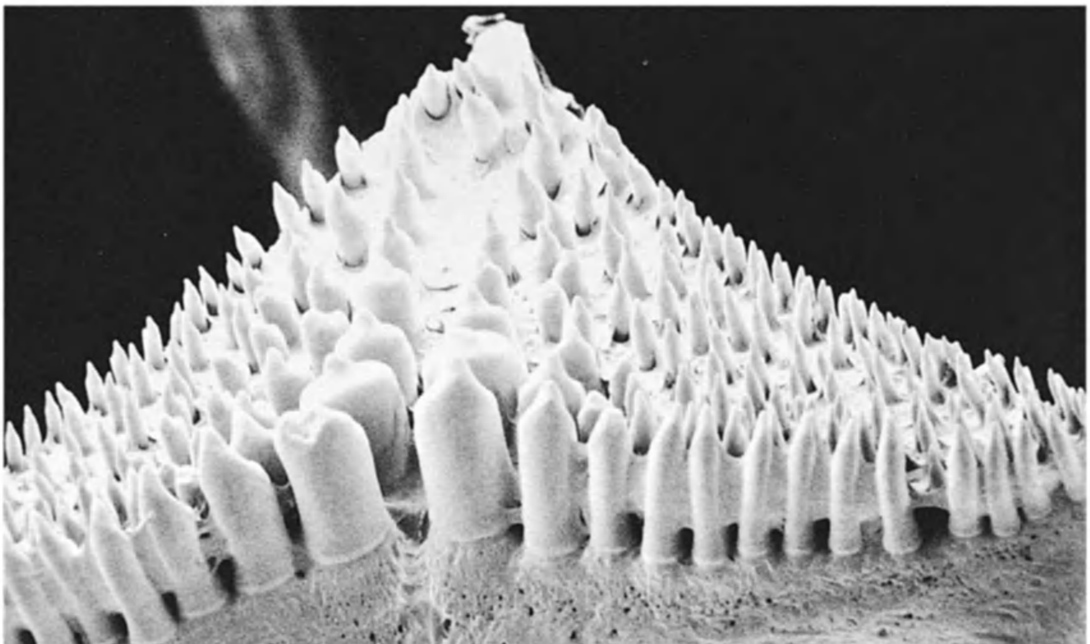
Studies of mitochondrial DNA (mtDNA) show that the cichlids in Lake Victoria are genetically very close to one another—far closer than to morphologically similar cichlids in the other two lakes (Fig. 2.13). Thus, almost identical evolutionary adaptations can and did evolve many times independent of one another (Stiassny and Meyer, 1999). Molecular clocks that are roughly calibrated on the rate of mutations in mtDNA suggest that the 400 species in Lake Victoria arose within the past 200,000 years—an amazingly short period of time.

Geographic Variation

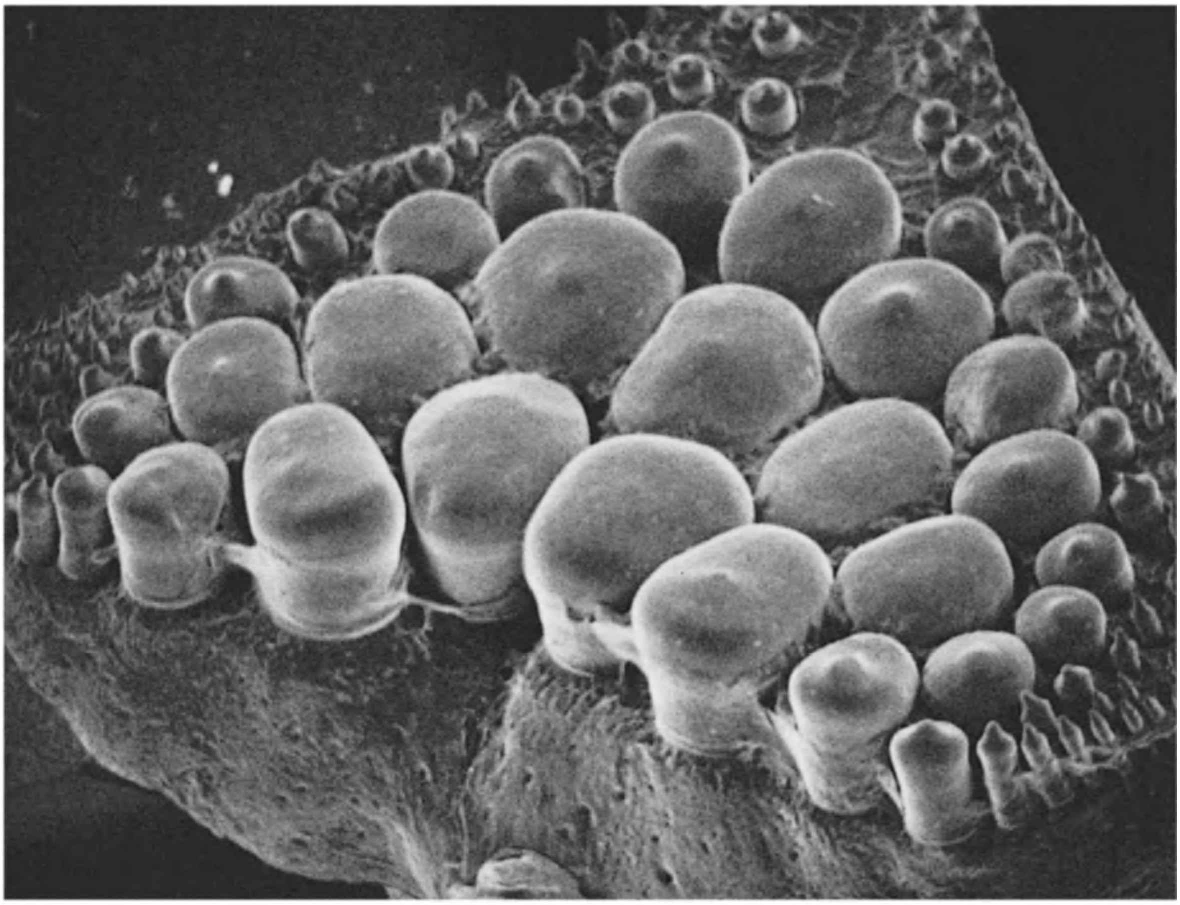
Many species of birds and mammals vary in a somewhat similar manner under similar environmental conditions. These differences have resulted in several "rules" of variation.



(a)



(b)



(c)

Figure 2.12. (*a*) Radiograph of the cichlid (*Cichlasoma citrinellum*) showing the two sets of jaws: one in the mouth and the other in the throat. The teeth of *Cichlasoma* may be in the form of sharp, pointed piercers (*b*) or flat, molar-like crushers (*c*). The teeth can change shape within the lifetime of a single animal.

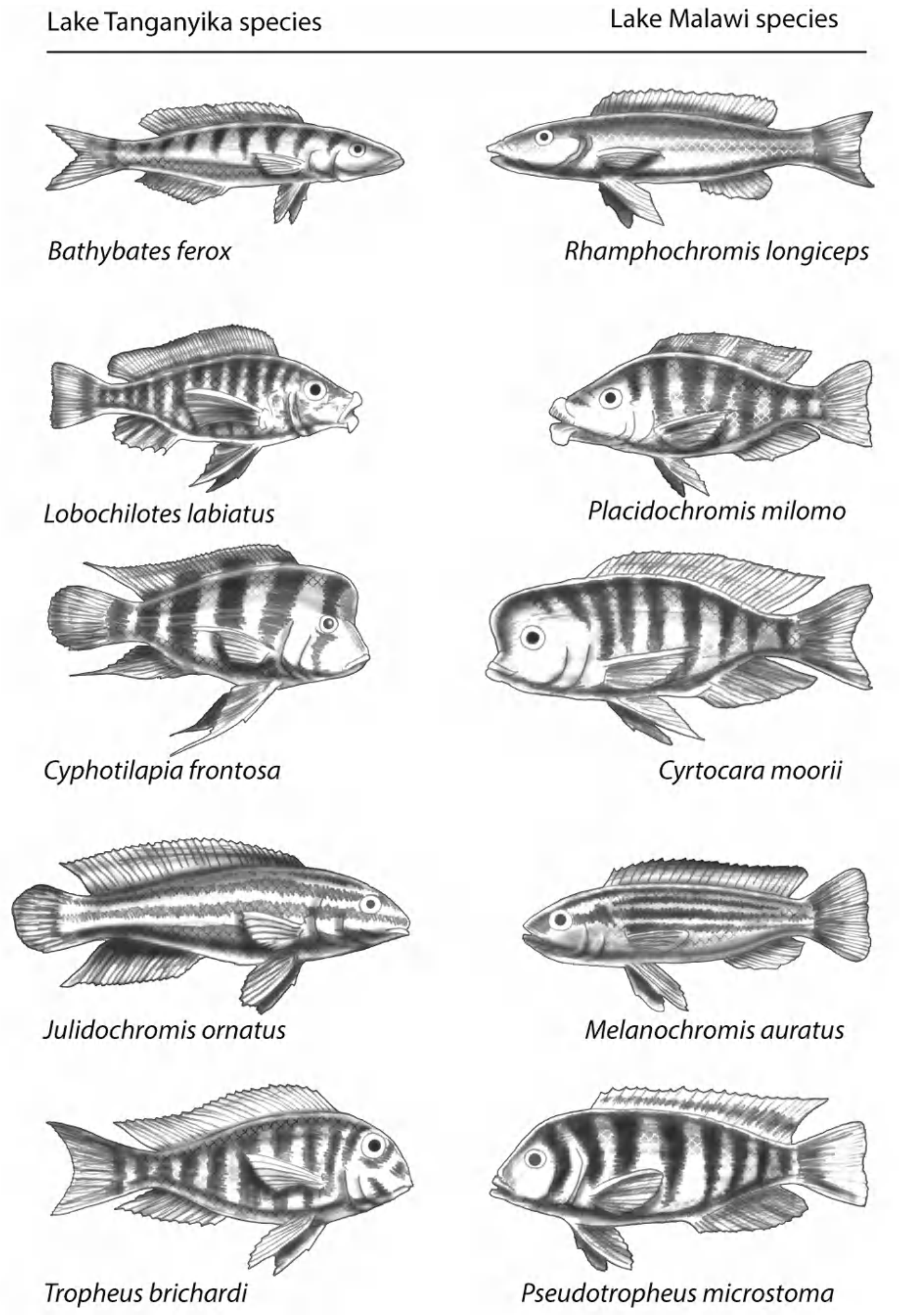


Figure 2.13. Distantly related cichlids from Lakes Tanganyika and Malawi have evolved to become morphologically similar by occupying similar ecological niches. They demonstrate that there may be little correlation between morphological resemblance and genetic closeness or

evolutionary lineage. All of the cichlids of Lake Malawi are more closely related to one another than to any cichlids in Lake Tanganyika.

1. **Bergmann's Rule.** Many endotherms tend to be larger in colder climates than their relatives in warmer regions. This tendency toward less body surface area in proportion to volume in northern areas is thought to be a means of conserving body heat. One of the best examples of Bergmann's Rule is the song sparrow (*Melospiza melodia*) (see Fig. 2.9). Specimens from the northern part of their range in North America are much larger than their paler relatives from the southwestern United States.

2. **Allen's Rule.** The extremities of many endotherms show a tendency to vary inversely with body size (Fig. 2.14). The ears, feet, and tail of many northern species are proportionately smaller in order to conserve body heat, whereas these parts of the body are larger in members of the same species living in warmer environments in order to lose additional heat by convection and radiation.

3. **Gloger's Rule.** Some endotherms living in arid regions tend to be lighter in color than their relatives living in more humid regions (see Fig. 2.14). Fox sparrows (*Passerella iliaca*) illustrate this principle, with eastern forms being reddish and their western relatives that breed on arid mountains being pale grayish. The black-tailed jackrabbit (*Lepus californicus*), which ranges from the humid Pacific coast to the arid southwestern deserts, is another species in which the individuals exhibit marked contrast in coloration. Lower humidity does not always result in paler coloration. Benson (1933) noted that in certain desert areas where extensive black lava beds exist, some species of small mammals tend to be very dark, perhaps to blend in with the color of the habitat and to enhance the absorption of radiant energy for thermoregulation.

Red crossbills (*Loxia curvirostra*) and lodgepole pine in the South Hills of Idaho illustrate the process of coevolution leading to divergence and speciation (Benkman and Parchman, 2009). Although still considered to be a single species, red crossbills have evolved unique bill sizes, bill shapes, and body sizes depending on the kind of conifer seeds they eat. There is a crossbill that specializes on ponderosa pine seeds, one that is equipped to eat lodgepole pine seeds, and another that feeds on western hemlock. Each type of crossbill has a different call and refrains from breeding with other types. Throughout most of the red crossbill's Rocky Mountain range, red squirrels have the upper hand in seed retrieval because they harvest and cache whole cones in early fall while crossbills must mine seeds from the cones that remain on trees. The squirrel’s taste for lodgepole seeds has encouraged the trees to evolve short, wide cones—more difficult for the rodents to bite off—with thick scales at the base. In Idaho’s South Hills, however, there are no squirrels. Lodgepole pines there have longer, thinner cones whose scales are thicker at the tips where seeds are housed. To pry open these cones, South Hills crossbills have developed bigger bills than other crossbills. Crossbills that fly into the South Hills from other areas rarely stay long enough to breed with the locals because they cannot extract seeds from the tougher cones.

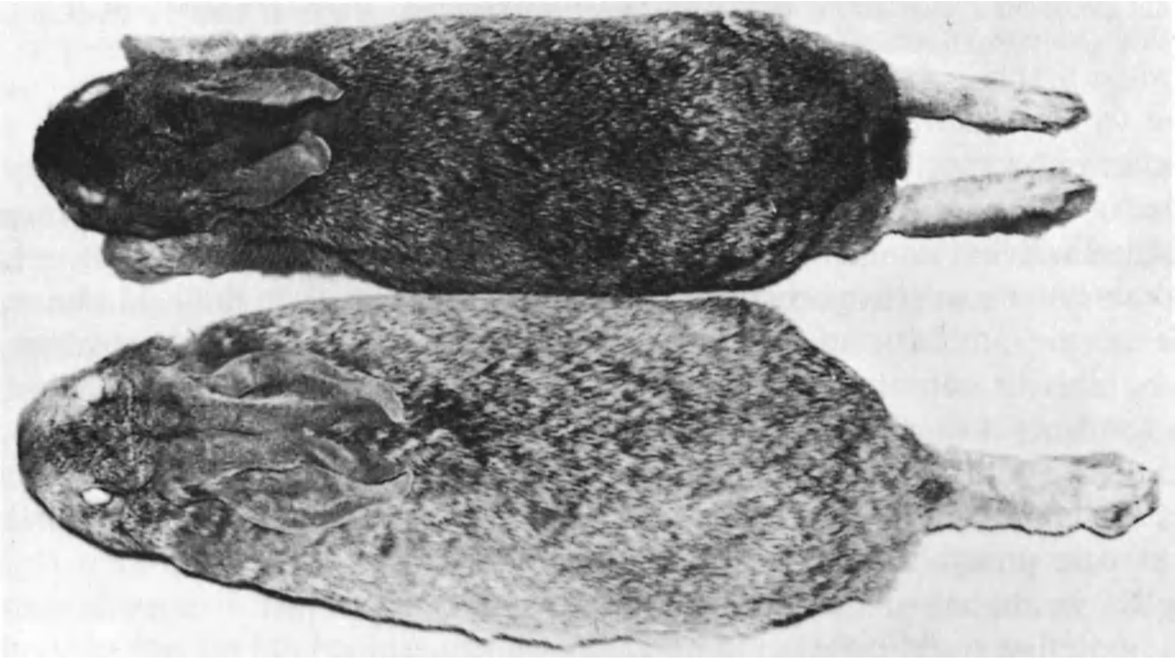


Figure 2.14. The brush rabbit (*Sylvilagus bachmani*) illustrates both Allen's Rule and Gloger's Rule. The dark, small-eared specimen on top is from the cool, humid coast of northern California; the pale, large-eared specimen is from the hot, arid interior of Baja California.

Molecular Evolution and Techniques

In many cases, the degree of variation in morphological characters (e.g., scale counts, skull measurements) has been the most frequently used taxonomic character because this type of variation is most easily seen, measured, and compared in preserved material. However, all evolutionary change results from alterations in the sequence of bases of the DNA in the nucleus of reproductive cells and, therefore, the subsequent sequence of amino acids in the proteins of offspring. Molecular evolution is the process of evolution at the scale of DNA, RNA, and proteins. Molecular evolution emerged as a scientific field in the 1960s as researchers from molecular biology, evolutionary biology, and population genetics sought to understand recent discoveries on the structure and function of nucleic acids and proteins. As a result, more sophisticated laboratory methods were developed to assay variation in chromosomes, proteins, and nucleic acids. Some of the key topics that spurred development of the field have been the evolution of enzyme function, the use of nucleic acid divergence as a "molecular clock" to study species divergence, and the origin of nonfunctional, or junk, DNA.

Studies of molecular evolution compare gene and protein sequences in different species, subspecies, or populations and are providing systematists with much new evolutionary information. Macromolecules —mtDNA, RNA, enzymes (isozymes), and the amino acid sequences of proteins like hemoglobin and cytochrome c—are being analyzed in order to determine how distantly or closely related the organisms in the study groups are to one another (Highton and Webster, 1976; Highton and Larson, 1979; Larson et al., 1981; Sibley and Ahlquist, 1984; Maxson and Heyer, 1988; Meyer et al., 1990; Bowen et al., 1991; Highton, 1991; Larson, 1991; McKnight et al., 1991; Shaffer et al., 1991; Peterson, 1992; Kumar and Hedges, 1998; Graur and Li, 2000; Li, 2006; Nachman, 2006; Hay et al., 2008; and many others).

DNA sequencing (genome sequencing) is the process of determining the precise order of nucleotides within a DNA molecule along chromosomes and genomes. It includes any method or technology that is used to determine the order of the four bases—adenine (A), guanine (G), cytosine (C), and thymine (T)—in a strand of DNA. It requires breaking the DNA of the genome into many smaller pieces, sequencing the pieces, and assembling the sequences into a single long “consensus.” The human genome, for example, is made up of over 3 billion of these bases.

Two indirect measures of DNA sequence variation led to major advances in systematics and population biology during the 1980s and 1990s but have given way to direct amplification and sequencing methods. Whole-genome DNA hybridization was used primarily for phylogeny reconstruction in marsupials, rodents, bats, and primates. Restriction-site analysis led to the development of DNA fingerprinting and intraspecific phylogeography, and it has been applied widely in studies of parentage, kinship, speciation, hybridization, conservation genetics, and phylogeny (Feldhamer et al. 2015).

Today, DNA sequencing on a large scale—the scale necessary for ambitious projects such as sequencing an entire genome—is mostly done by high-tech machines. Much as your eye scans a sequence of letters to read a sentence, these machines “read” a sequence of DNA bases.

Because DNA and proteins are composed of many bits of information (nucleotides and amino acids, respectively), molecular similarities between two or more species likely reflect a shared common ancestor in the same way that morphological or other similarities do. Thus, the greater the molecular similarities between two species, the closer their likely evolutionary ancestry. Because differences in nucleotide sequences arise through mutations, and mutations accumulate with time, if two organisms once shared a common ancestor, the time that has passed since they diverged into two distinct species can be estimated by analyzing the mutations that have accumulated in their genes (Fig. 2.15). Evolutionary trees based on biochemical data are, in most cases, quite similar in appearance to those based solely on anatomical data.

Chimpanzees are more closely related to humans than to any other primate. While monkeys, humans, and chimpanzees are thought to have shared a common ancestor about 13 Mya, humans and chimpanzees are thought to have shared a common ancestor as recently as 5 to 7 Mya, although just what that ancient primate looked like is unknown. Since then, chimpanzees and humans have evolved separately, with humans developing a brain about twice the size of a chimp's brain. Thus, some researchers feel that chimpanzees should be included in the human branch of the family tree (Elango et al., 2006, 2009). Currently, humans are alone in the species group *Homo*. The authors argue that humans appear "as only slightly remodeled chimpanzee-like apes," with humans and chimps sharing 98.8 percent of their DNA. The reports propose establishing three species under *Homo*: humans, common chimpanzees, and pygmy chimpanzees.

Scientists long thought that the forest elephant of Africa was a separate subspecies from the more familiar savanna elephant. New analyses of mtDNA now show that the two are entirely different species (Tangley, 1997). The forest elephant has rounder ears and thinner, straighter tusks than its larger relative. Unlike savanna elephants, which feed on grass, forest elephants feed on the leaves, twigs, bark, and fruit of rain forest trees.

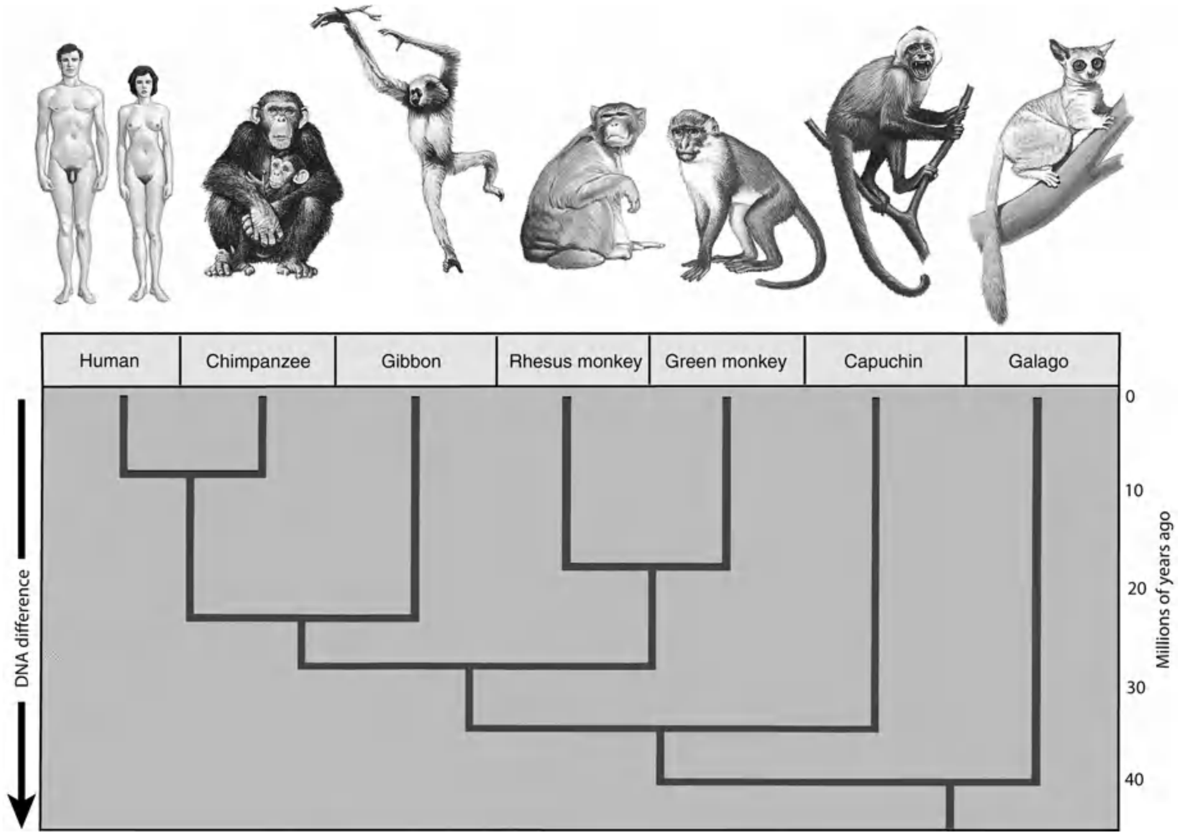


Figure 2.15. The relationship of certain primate species, based on a molecular comparison of their genomes. The lengths of the branches indicate the relative number of nucleotide pair differences that were found among groups. By using the fossil record as a comparative tool, it is possible to approximate the date at which each group diverged from the other.

DNA analysis confirmed that while olinguitos and olingos both belong to the raccoon family, they are "sister groups" in the same way that humans are closely related to chimpanzees (Helgen et al., 2013). Genetic analysis was employed in confirming a new leopard frog species (*Rana kauffeldi*) from New York City and surrounding Atlantic Coast regions (Feinberg et al., 2014).

There has always been much debate about whether the woolly mammoth (*Mammuthus primigenius*) was more closely related to the African (*Loxodonta africanus*) or Asian (*Elephas maximus*) elephant. Analysis of the complete mitochondrial genome of a mammoth reveals that mammoths are more closely related to Asian elephants, but not by much. The lineages leading to mammoths and the three living elephant species diverged about 6 Mya in Africa. The new data suggest that the African lineage split first, followed around 440,000 years later by the separation between Asian elephants and mammoths (Krause et al., 2006).

On the other hand, extensive genetic analysis has revealed just 6, rather than 32, subspecies of puma (*Puma concolor*) in the Western Hemisphere (Culver et al., 2000). Blood and tissue samples were secured from 209 pumas in zoos, museums, and the wild across North and Central America, and from 106 of the animals in South America. The researchers found no differences in the mtDNA from North American pumas, suggesting that only one kind of puma inhabits North America, rather than the 15 subspecies previously identified on the basis of where they live and differences in appearance. The DNA analyses also showed that only one subspecies lives in Central America and that just four others roam South America. The team found the most genetically diverse pumas in Paraguay and Brazil south of the Amazon River. This indicates that these populations are the oldest, dating back some 250,000 years, and that northward migrations gave rise to the others over time.

Present-day domestic goats harbor more genetic diversity than any other livestock species. In fact, analyses of goats' mtDNA have shown that these animals evolved through five distinct maternal lines that spread from the Near East and Central Asia across Europe. Molecular evidence from both modern and ancient wild horses is providing clues to the origins of domestic horses. DNA analysis has shown that California beaked whales are a separate species from their southern Pacific cousins (Dalebout et al., 2002).

Classifying the Quagga

The quagga (*Equus quagga*) (see Fig. 2.16) is an extinct southern African mammal that resembled a zebra. The last known individuals died in captivity in 1875 (in Berlin) and 1883 (in Amsterdam). Some observers considered it to be most closely related to the horse based on analyses of mainly cranial characters. Others thought it was a distinct species of zebra related to the three living species. Still others felt it was merely the southern end of a cline and a subspecies of the plains zebra. Both DNA and protein analyses of samples from quagga skin confirmed that it was, indeed, related to the plains zebra (*E. burchelli*). A breeding program, started in 1987, is underway in an attempt to "re-create" the quagga by repeated inbreeding of the most quagga-like plains zebras—those with a brownish basic color and/or reduced striping. As of 2018, project animals were on four large properties in the Western Cape of South Africa. Six other properties had private breeding herds. Molecular studies may thus prove responsible, if only indirectly, for the return of one extinct subspecies to its native habitat (at least one that superficially resembles the quagga, since we can never be sure of the evolutionary pathways that created it).

Lowenstein, 1991; Burroughs, 1999; Murphy, 2000; www.quaggaproject.org/latest-news.

Biochemists are now able to extract proteins and DNA from some extinct organisms, like mammoths (*Mammuthus*) and mastodons (*Mammut*), from the dung of a 20,000-year-old extinct ground sloth, and even from fossils in order to establish their relationship to living organisms. A team from the American Museum of Natural History analyzed nuclear DNA from a 27,000-year-old fossilized female mammoth jawbone recovered in Siberia. The scientists found that the specimen DNA nearly perfectly matched the known genetic code of today's African elephants (*Loxodonta africana*), one of mammoth's closest living relatives. These studies are possible because all organisms, living or extinct, share some of the same types of molecules. Comparative biochemistry, immunology, protein-sequencing, and DNA studies have corroborated, for the most part, earlier evolutionary findings and, at the same time, have provided new understanding of molecular processes in evolution.

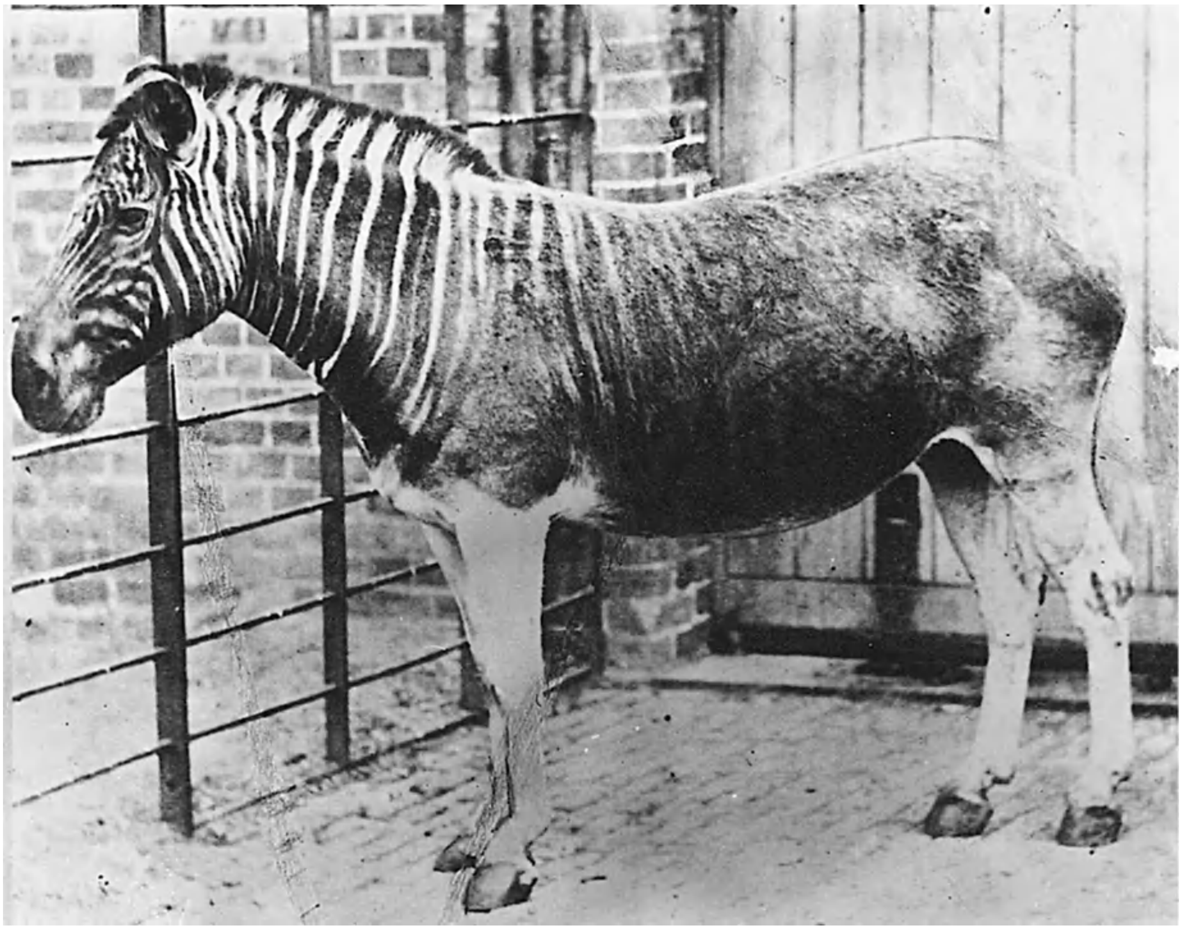


Figure 2.16. The quagga (*Equus quagga quagga*), an extinct southern African mammal resembling a zebra. The last known individual died in 1883.

In 2014, China's Beijing Genomics Institute (BGI), the world's largest genomics center, reported 45 new, fully sequenced bird genomes. They were the result of a four-year megasequencing project, led by BGI, involving hundreds of researchers from more than 80 institutions across 20 countries. BGI has also led the sequencing of the giant panda and 38 different types of pigeon. BGI is a leader in de novo whole genome sequencing—sequencing a novel genome where there is no reference sequence available for alignment.

The Genome 10K Project (https://genome10k.soe.ucsc.edu/; https://www.rockefeller.edu/research/vertebrate-genomes-project), begun in 2009, has a goal of sequencing the genomes of at least one individual from each vertebrate genus—approximately 10,000 genomes. It served as part of the motivation for the Vertebrate Genomes Project (VGP), organized in March 2017, whose mission is "to provide high quality genome assemblies of all vertebrate species to address fundamental questions in biology and disease" (Wellcome Sanger Institute, n.d.). The

VGP is headquartered at the Sanger Institute on the Wellcome Genome Campus in the village of Hinxton, Cambridge, United Kingdom, but collaborates with research laboratories throughout the world (https://www.sanger.ac.uk/news/view/genetic-code-66000-uk-species-be-sequenced). The deciphering of genomes is used to study the phylogeographic genomic diversity of closely related species such as elephants and, in the case of elephants, helps in conservation efforts including legal investigations of the ivory trade.

Museum specimens provide a wealth of information to biologists, but obtaining genetic material from formalin-fixed and fluid-preserved specimens has always been a challenge. While DNA sequences have been recovered from such specimens, most approaches are time-consuming and produce low quality data. Ruane and Austin (2017), however, used a modified DNA extraction protocol combined with high-throughput sequencing to recover DNA from formalin-fixed and fluid-preserved snakes that were collected over a century ago and for which little or no modern genetic materials exist in public collections.

DNA fingerprinting (profiling) has proved valuable in studying paternity and genetic variability in whooping cranes. This information helps prevent inbreeding in captive breeding programs (Longmire et al., 1992). DNA analysis of the 52 remaining California condors in 1992 (50 in captivity, 2 released in January 1992) revealed that they were divided into three distinct ancestral groups (Hedrick, 1992). DNA probes have revealed population differentiation in California Channel Island foxes (*Urocyon littoralis*) inhabiting six of the Channel Islands off the coast of Southern California. Morphologic and genetic distinctions support the classification of six separate subspecies, one on each island (Gilbert et al., 1990; Parker, 2002). DNA analysis has also revealed the general rule for kinship in lion (*Panthera leo*) prides: female companions are always closely related, male companions are either closely related or unrelated, and mating partners are usually unrelated (Packer et al., 1991). By applying a genetic probe that selectively binds to gender-specific DNA fragments, Demas et al. (1990) could distinguish sexes in the hatchlings of endangered sea turtles. A review of DNA fingerprinting methods in zoology, including discussions of minisatellite and microsatellite DNA genotyping methods, has been presented by Chambers et al. (2014).

Species relatedness can also be estimated by comparing the number of chromosomes, chromosome band patterns, and the order of genes on stained chromosomes. **Karyotypes**, or chromosome pictures, are used to depict gross relationships between species. When chromosome banding patterns between humans and six other species of mammals are compared, regions of apparently conserved chromosomal banding are revealed (Sawyer, 1991). Among primates, the banding pattern of humans most closely matches those of chimpanzees, then gorillas, then orangutans.

Comparison of amino acid sequences in different species often supports fossil or anatomical evidence, but it also may provide evidence refuting long-held traditional schemes of classification. For example, the nucleotide and amino acid sequences of six different genes show that the elephant shrew, the elephant, the aardvark, and the hyrax are all closely related (Balter, 1997). Researchers used genes and proteins with widely different structures and functions to construct their proposed phylogenies. These included a protein that aids water transport across cell membranes, a component of the lens of the eye, and a blood-clotting protein. Rabbits and rodents also appear to be close cousins. Many proteins in humans and chimpanzees are 99 percent similar in their amino acid sequencing, and several sequences are identical. Cytochrome c, an ancient and well-studied protein, is identical in humans and chimpanzees, as are the alpha and beta chains of hemoglobin from both species. Human and chimpanzee cytochrome c differs from horse cytochrome c by 12 amino acids and from kangaroo cytochrome c by only 8 amino acids (Fig. 2.17). The amino acid sequence between humans and rhesus monkeys varies by only one amino acid.

For centuries, the guinea pig (*Cavia*) had been classified in the suborder Hystricomorpha in the monophyletic order Rodentia. In 1990, 15 proteins, including insulin, were analyzed from a variety of mammals (Graur et al., 1991). Of the 51 amino acids that make up insulin, humans and mice had all but four in precisely the same sequence. Guinea pigs, however, had insulin that differed from mice and humans by 18 amino acids. In addition, guinea pigs differed from cows by 19 amino acids and from the opossum—a marsupial—by 20 amino acids. This pattern was repeated in a number of other proteins as well. The protein analysis revealed that the distance between the two “rodents”—guinea pigs and mice—was significantly longer than the distance between other animals that are not even in the same order. Thus, Graur et al. (1991) proposed that the guinea pig be placed in its own order (Caviomorpha). This suggestion, which is still highly controversial, radically contradicts the traditional view of rodent monophyly, which until recently has been based primarily on comparative morphology.

Vertebrates for which complete genome sequences have been assembled, annotated, and published as of September 2018 include: Chondrichthyes, 2; Osteichthyes, 19 (including *Latimeria chalumnae*, West Indian coelacanth and oldest known living lineage of Sarcopterygii); Amphibia, 5; Reptilia, 14; Aves, 61; and Mammalia, 50.

Among the mammals whose DNA has been decoded are the dog, domestic cat, horse, house mouse, duck-billed platypus, gray short-tailed opossum, giant panda, chimpanzee, rhesus macaque, gibbon, orangutan, gorilla, marmoset, and humans. Evidence from comparative DNA sequencing of the duck-billed platypus, a monotreme, shows that the DNA crosses different classifications of animals. It has reptilian, avian, and mammalian genome features in one organism. Although long thought to represent one of the earliest mammalian lineages, genetic evidence now shows conclusively that it should be placed with the other mammals, specifically on the lineage leading to marsupials (Janke et al., 1996) (see Chapter 9). A related study (Warren et al., 2008) found that the platypus shares 82 percent of its approximately 18,500 genes with the human, mouse, dog, opossum, and chicken. The analysis identified families of genes that link the platypus to reptiles (like those for egg-laying, vision, and venom production) as well as to mammals (antibacterial proteins and lactation) (Fig. 2.18). The link with marsupials is strongly questioned by most nonmolecular mammalogists.

A small kangaroo known as a tammar wallaby has had its DNA decoded (Gelineau, 2008). Although the kangaroo last shared a common ancestor with humans approximately 150 Mya, the genomes are surprisingly similar. In addition, researchers discovered 14 previously unknown genes in the kangaroo and suspect the same ones are also in humans. Eighty-two percent of the gray short-tailed opossum's genes have clear human counterparts, and many of the rest have near-matches (Mikkelsen et al., 2007). Only 8 opossum genes (of about 19,500) have no known relatives in humans. In their study of the dog genome, researchers determined 77 percent of the genome and found canine DNA fragments corresponding to 18,473 of the 24,567 previously documented human genes (Kirkness et al., 2003).

	10	20	30	40	50	
Human	--------GD	VEKGKKIFIM	KCSQCHTVEK	GGKHKTGPNL	HGLFGRKTGQ	APGYS
Rhesus monkey	--------GD	VEKGKKIFIM	KCSQCHTVEK	GGKHKTGPNL	HGLFGRKTGQ	APGYS
Horse	--------GD	VEKGKKIFVQ	KCAQCHTVEK	GGKHKTGPNL	HGLFGRKTGQ	APGFT
Dog	--------GD	VEKGKKIFVQ	KCAQCHTVEK	GGKHKTGPNL	HGLFGRKTGQ	APGFS
Gray whale	--------GD	VEKGKKIFVQ	KCAQCHTVEK	GGKHKTGPNL	HGLFGRKTGQ	AVGFS
Rabbit	--------GD	VEKGKKIFVQ	KCAQCHTVEK	GGKHKTGPNL	HGLFGRKTGQ	AVGFS
Kangaroo	--------GD	VEKGKKIFVQ	KCAQCHTVEK	GGKHKTGPNL	NGIFGRKTGQ	APGFT
Penguin	--------GD	IEKGKKIFVQ	KCSQCHTVEK	GGKHKTGPNL	HGIFGRKTGQ	AEGFS
Snapping turtle	--------GD	VEKGKKIFVQ	KCAQCHTVEK	GGKHKTGPNL	NGLIGRKTGQ	AEGFS
Bullfrog	--------GD	VEKGKKIFVQ	KCAQCHTCEK	GGKHKVGPNL	YGLIGRKTGQ	AAGFS
Tuna	--------GD	VAKGKKTFVQ	KCAQCHTVEN	GGKHKVGPNL	WGLFGRKTGQ	AEGYS
Silkworm moth	----GVPAGN	AENGKKIFVQ	RCAQCHTVEA	GGKHKVGPNL	HGFYGRKTGQ	APGFS
Wheat	ASFSEAPPGN	PDAGAKIFKT	KCAQCHTVDA	GAGHKQGPNL	HGLFGRQSGT	TAGYS
Fungus (*Neurospora*)	----GFSAGD	SKKGANLFKT	RCAECHGEGG	NLTQKIGPAL	HGLFGRKTGS	VDGYA

	60	70	80	90	100	110
Human	YTAANKNKGI	IWGEDTLMEY	LENPKKYIPG	TKMIFVGIKK	KEERADLIAY	LKKATNE
Rhesus monkey	YTAANKNKGI	TWGEDTLMEY	LENPKKYIPG	TKMIFVGIKK	KEERADLIAY	LKKATNE
Horse	YTDANKNKGI	TWKEETLMEY	LENPKKYIPG	TKMIFAGIKK	KTEREDLIAY	LKKATNE
Dog	YTDANKNKGI	TWGEETLMEY	LENPKKYIPG	TKMIFAGIKK	TGERADLIAY	LKKATNE
Gray whale	YTDANKNKGI	TWGEETLMEY	LENPKKYIPG	TKMIFAGIKK	KGERADLIAY	LKKATNE
Rabbit	YTDANKNKGI	TWGEDTLMEY	LENPKKYIPG	TKMIFAGIKK	KDERADLIAY	LKKATNE
Kangaroo	YTDANKNKGI	IWGEDTLMEY	LENPKKYIPG	TKMIFAGIKK	KGERADLIAY	LKKATNE
Penguin	YTDANKNKGI	TWGEDTLMEY	LENPKKYIPG	TKMIFAGIKK	KSERADLIAY	LKDATSK
Snapping turtle	YTEANKNKGI	TWGEETLMEY	LENPKKYIPG	TKMIFAGIKK	KAERADLIAY	LKDATSK
Bullfrog	YTDANKNKGI	TWGEDTLMEY	LENPKKYIPG	TKMIFAGIKK	KGERQDLIAY	LKSACSK
Tuna	YTDANKSKGI	VWNNDTLMEY	LENPKKYIPG	TKMIFAGIKK	KGERQDLVAY	LKSATS-
Silkworm moth	YSNANKAKGI	TWGDDTLFEY	LENPKKYIPG	TKMVFAGLKK	ANERADLIAY	LKESTK-
Wheat	YSAANKNKAV	EWEENTLYDY	LLNPKKYIPG	TKMVFPGLKK	PQDRADLIAY	LKKATSS
Fungus (*Neurospora*)	YTDANKQKGI	TWDENTLFEY	LENPKKYIPG	TKMAFGGLKK	DKDRNDIITF	MKEATA-

A	Alanine	F	Phenylalanine	K	Lysine	P	Proline	T	Threonine
C	Cysteine	G	Glycine	L	Leucine	Q	Glutamine	V	Valine
D	Aspartic acid	H	Histidine	M	Methionine	R	Arginine	W	Tryptophan
E	Glutamic acid	I	Isoleucine	N	Asparagine	S	Serine	Y	Tyrosine

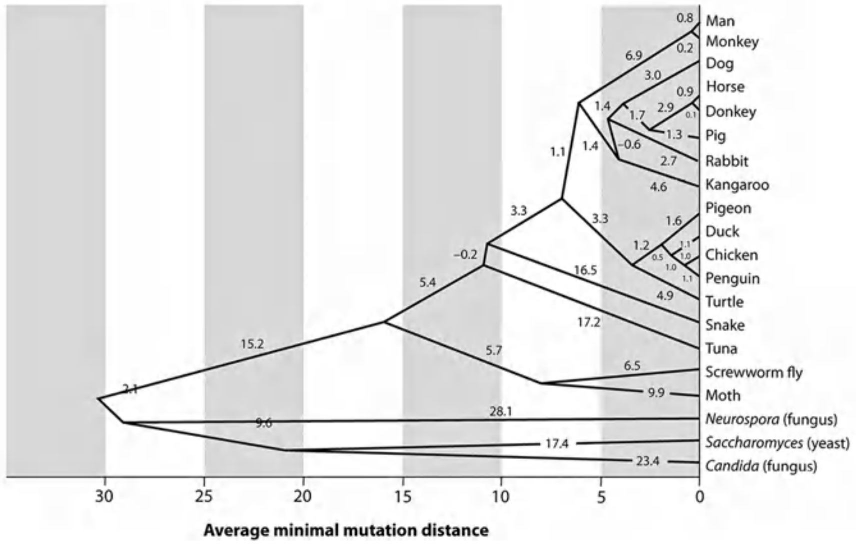


Figure 2.17. (*Facing page*) The amino acid sequences of cytochrome c (*top*) show a striking similarity among living organisms. Each amino acid is represented by a single letter. (*Bottom*) A phylogenetic table depicting evolutionary relationships derived by comparing the differences among amino acid sequences of cytochrome c in different species. The numbers on the lines show the number of nucleotide substitutions that have taken place.

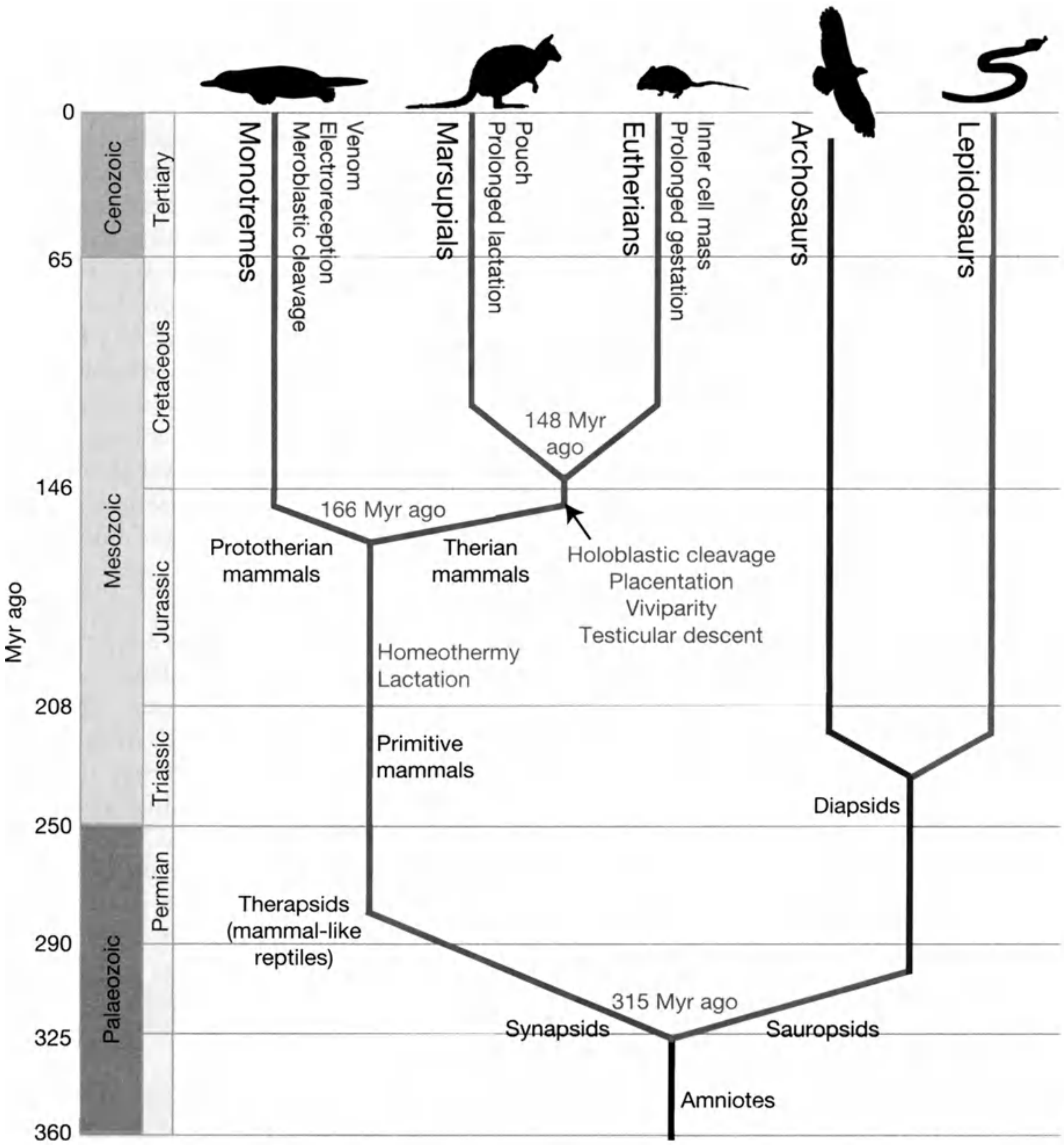


Figure 2.18. Amniotes split into the sauropsids (leading to birds and reptiles) and the synapsids (leading to mammal-like reptiles). These small early mammals developed hair, homeothermy, and lactation. Monotremes diverged from the therian mammal lineage about 166 Mya and developed a unique suite of characters. Therian mammals with common characters split into marsupials and eutherians around 148 Mya.

DNA analyses produced data showing that skunks should be removed from the family Mustelidae and placed in their own family, Mephitidae (Dragoo and Honeycutt, 1997). Researchers at the US National Cancer Institute in Frederick, Maryland, studied the DNA from 979 domestic cats and wild cats from across Europe and Asia. The DNA from the wild cats broke down into five different groups of the wild cat *Felis silvestris*: the European wildcat, the southern African wild cat, the central Asian wild cat, the Chinese desert cat, and the Near Eastern wildcat. All domestic cats belong to the Near Eastern wildcat group.

Developing methods of preserving the DNA of endangered and threatened species has been a topic of discussion among scientists for many years (Ryder et al., 2000). There needs to be a coordinated worldwide effort to store samples of DNA, DNA libraries, or frozen cells or tissues that could readily yield DNA for every endangered animal species. Conservation management and policy could benefit from the laboratory research of such a coordinated and cooperative effort. A portion of the collected DNA, tissues, and cell lines, equivalent to the human genome diversity cell line collection, plus an archive of tissues for physiological and DNA expression studies, needs to be maintained and made available to researchers. Conservation biologists, managers, and policymakers need access to technology and expertise in genetics research. The major problem lies in the long-term preservation of the DNA. Procedures need to be developed to ensure that damage during storage is minimal and (preferably) repairable, for a bank with poorly preserved DNA will be of little use 100 years from now. In 2000, the Zoological Society of San Diego Zoo and Amersham Pharmacia Biotech announced that they were launching the first systematic effort to decode the DNA of endangered species. Using DNA samples from the Zoological Society's "Frozen Zoo," the biotech firm works with researchers from the society's Center for Reproduction of Endangered Species (CRES) to sequence the mtDNA of endangered species. The project is collecting and sequencing complete mtDNA from one member of each of the 146 mammalian families. Begun in 1976, the Frozen Zoo of stockpiled DNA from more than 3,200 individual mammals represents 355 species and subspecies from rare Przewalski's horses to western lowland gorillas. Additional samples come from other zoological organizations and field researchers.

The Frozen Ark Project, with headquarters at the University of Nottingham in the United Kingdom and collaborating with a number of zoos and aquaria, strives to collect, preserve, and conserve tissue, gametes, viable cells, and DNA of animal species facing extinction by providing infrastructure, expertise, partnership, and coordination for endangered animal biobanking.

More recently, it has turned out that differences in appearance are deceiving: very different animals have very similar sets of genes. Devices are now being found within DNA—genetic "switches"—that do not encode any proteins but that regulate *when* and *where* genes are used. Changes in these switches are crucial to the evolution of anatomy and provide new insights into how the seemingly endless forms of the Animal Kingdom have evolved (Carroll et al., 2008). The study of the pivotal role played in evolution by genes and processes associated with the development of anatomy has earned the nickname "evo-devo."

Traditional methods for classifying animals and plants demand great skill and time in looking at color, shape, and even behavior. Some researchers have proposed a faster and easier method that involves examining a small portion of the DNA. The idea of establishing an identification system for all plant and animal life using genetic sequences from a uniform locus was first proposed in 2003. The new method is called **barcoding**, because it was inspired by the barcode on products (Stoeckle and Hebert, 2008). It is proposed that a segment of mtDNA can distinguish animal species. **Mitochondria** are the energy-producing subunits of cells that are inherited from the mother. In the future, it may be possible to use a handheld scanner, similar to a GPS (global positioning system) device, to link to a database of the barcodes of all species. Then, by inserting a snippet of tissue into the scanner, anyone can get an instant identification of an animal or a plant. For animal species, researchers are using a gene that gives rise to an enzyme called cytochrome c oxidase subunit 1, or CO1 for short. The CO1 barcode region is small enough that the sequence of its nucleic acid base pairs (the "rungs" of the famous double helix) can be deciphered in one read with current technology. And, although it is a tiny fraction of the DNA inside each cell, it captures enough variation to tell most species apart.

To help coordinate the enormous effort involved in the assembly of such a comprehensive library, the Consortium for the Barcode of Life (CBOL) was established in 2005. It currently includes 427 sequencing laboratories worldwide that support the development of DNA barcoding as a global standard for the identification of species. The actual assembly of records is driven by the International Barcode of Life Project. Such a system allows biologists to quickly identify organisms in the field to assess biodiversity, allows taxonomists to spot genetically distinct specimens and speed up cataloging of new species before they become extinct, and allows museums to analyze backlogs of collected specimens to find undescribed species.

A public database called the Barcode of Life Data System, or BOLD (online at www.barcodinglife.org), has been established. BOLD is an informatics workbench aiding the acquisition, storage, analysis, and publication of DNA barcode records. By assembling molecular, morphological, and distributional data, it bridges a traditional bioinformatics chasm. BOLD is freely available to any researcher with interests in DNA barcoding. It aids the assembly of records that meet the standards needed to gain barcode designation in the global sequence databases. As of September 2018, BOLD had 8,782,278 specimen records, including plants, fungi, protists, invertebrates, and vertebrates. Of these, 613,068 are Chordate records. There are 34,815 chordate species with barcodes and 476,333 chordate specimens with barcodes. Each record contains the species name, barcode sequence, collection location, links to the voucher specimen, photographs, and other biological data.

Barcoding has already been successfully used in a number of instances to identify new species. For example, researchers examined the DNA of 643 North American species of birds and discovered 15 that are genetically distinct from currently accepted species. In Guyana, they analyzed 87 kinds of bats and identified 6 new species.

Decisions made by systematists are not final. When new data show that forms originally described as separate species are really geographic races of the same species or that a subspecies should be elevated to the rank of a full species, appropriate changes are made in the nomenclature. Similarly, reclassification is also often necessary at higher taxonomic levels. Vertebrate classification is in a dynamic state and all groups are subject to change. Because particular classifications eventually become obsolete, they should be regarded as frameworks that will provide a basis for building as advances are made.

The classification of vertebrates is an extraordinarily difficult undertaking because of the diversity of vertebrates (66,139 living species and perhaps many times that number of species now extinct) and also because of convergent evolution. Species are not static and immutable; thus, simply classifying species is no longer an adequate means of comprehending vertebrate diversity. It is now necessary to include genealogical information in the system of classification in order to express the evolutionary relationships among species.

Review Questions and Topics

1. What is meant by the binomial system of nomenclature?
2. Why do biologists use scientific names for species?
3. Describe the hierarchical system used to classify organisms. List in order, from most inclusive to least inclusive, the principal taxa.
4. How does a phylogenetic tree differ from a cladogram?
5. Define the term *species*, using the various schools of systematic thought.
6. In your opinion, should birds be classified in a separate class (Aves), or should they be classified with the reptiles in one monophyletic group (Diapsida)? Why?
7. How do new species evolve? List several types of isolating barriers.
8. Give two examples of reproductive isolating barriers and discuss what they accomplish.
9. Distinguish between allopatry and sympatry.
10. Differentiate among a deme, a cline, and a species.
11. List several molecular techniques that are providing systematists with new evolutionary information.

Supplemental Reading

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Vertebrate Internet Sites

1. Animal Diversity Web: Kingdom Animalia

   http://animaldiversity.ummz.umich.edu/site/index.html

   Vast collection of links to vertebrate sites.

2. Journey into Phylogenetic Systematics

   www.ucmp.berkeley.edu/clad/clad4.html

   This site discusses the introduction, methodology, implications, and the need for cladistics.

3 | Early Chordates and Jawless Fishes

We need to appreciate that a species, of whatever form, is a unique manifestation of life, the final product of some evolutionary development.

Irston R. Barnes, 1968

INTRODUCTION

There are many hypotheses concerning the evolution of vertebrates. These hypotheses are continually being changed and refined as new studies uncover additional evidence of evolutionary relationships and force reassessments of some earlier ideas about vertebrate evolution (Fig. 3.1). New fossil evidence, morphological studies, and comparative studies of DNA and RNA are gradually filling gaps in our knowledge and providing a more complete understanding of the relationships among vertebrates.

Evolution takes place on many scales of time. Gingerich (1993) noted that field and laboratory experiments usually are designed to study morphological and ecological changes on short time scales; in contrast, fossils provide the most direct and best information about evolution on long time scales. The principal problem with the fossil record is that the time scales involved, typically millions of years, are so long that they are difficult to relate to the time scales of our lifetimes and those of other organisms. Many biologists have difficulty understanding evolution on a geological scale of time, and many paleontologists have difficulty understanding evolution on a biological scale of time. One reason for this is that we have almost no record of changes on intermediate scales of time—scales of hundreds or thousands of years—which would permit evolution on a laboratory scale of time to be related to evolution on a geological scale.

Paleontologists have long suspected that vertebrates diverged from a lancelet-like relative sometime in the Cambrian period, which began 545 Mya. Meanwhile, molecular studies of gene similarities between lancelets and today's vertebrates suggest that the vertebrate lineage goes all the way back to 750 Mya. But the fossil record provides few clues to help resolve this contradiction because there are no animal fossils that old and no examples of an intermediate species.

Studies of living vertebrates reveal that as an embryo forms, a sheet of cells on its surface curls up into a tube that sinks into its body. This structure, called the neural tube, eventually becomes the central nervous system, including the brain and spinal cord. Along the edges of the sheet, a special collection of cells called neural crest cells breaks away and wanders around the embryo, helping to shape many structures like eyes, nose, nerves, head muscles, and skull bones. The lancelet does not have a true neural crest, but it does have cells in the same position as neural crest cells, and they express some of the same genes that neural crest cells express before they begin to migrate (Holland and Holland, 1999). These cells also migrate, but only as a sheet moving on the surface of an embryo, not as small clusters traveling inside it. The development of a wandering neural crest was a major innovation of vertebrates.

No living protochordate (tunicate and lancelet) is regarded as being ancestral to the vertebrates, but their common ancestry is evident. In 1928, Garstang proposed a hypothesis by which larval tunicates could have given rise to cephalochordates and vertebrates (Fig. 3.2). Garstang suggested that the sessile adult tunicate was the ancestral stock and that the tadpole-like larvae evolved as an adaptation for spreading to new habitats. Furthermore, Garstang suggested that larval tunicates failed to metamorphose into adults but developed functional gonads and reproduced while still in the larval stage. As larval evolution continued, the sessile adult stage was lost, and a new group of free-swimming animals appeared. This hypothesis, known as **paedomorphosis** (the presence of evolutionary juvenile or larval traits in the adult body), allowed traits of larval tunicates to be passed on to succeeding generations of adult animals. Delsuc et al. (2006) present a phylogenetic data set from genome-sequencing that provides evidence that tunicates, not cephalochordates, represent the closest living relatives of vertebrates (Fig. 3.3).

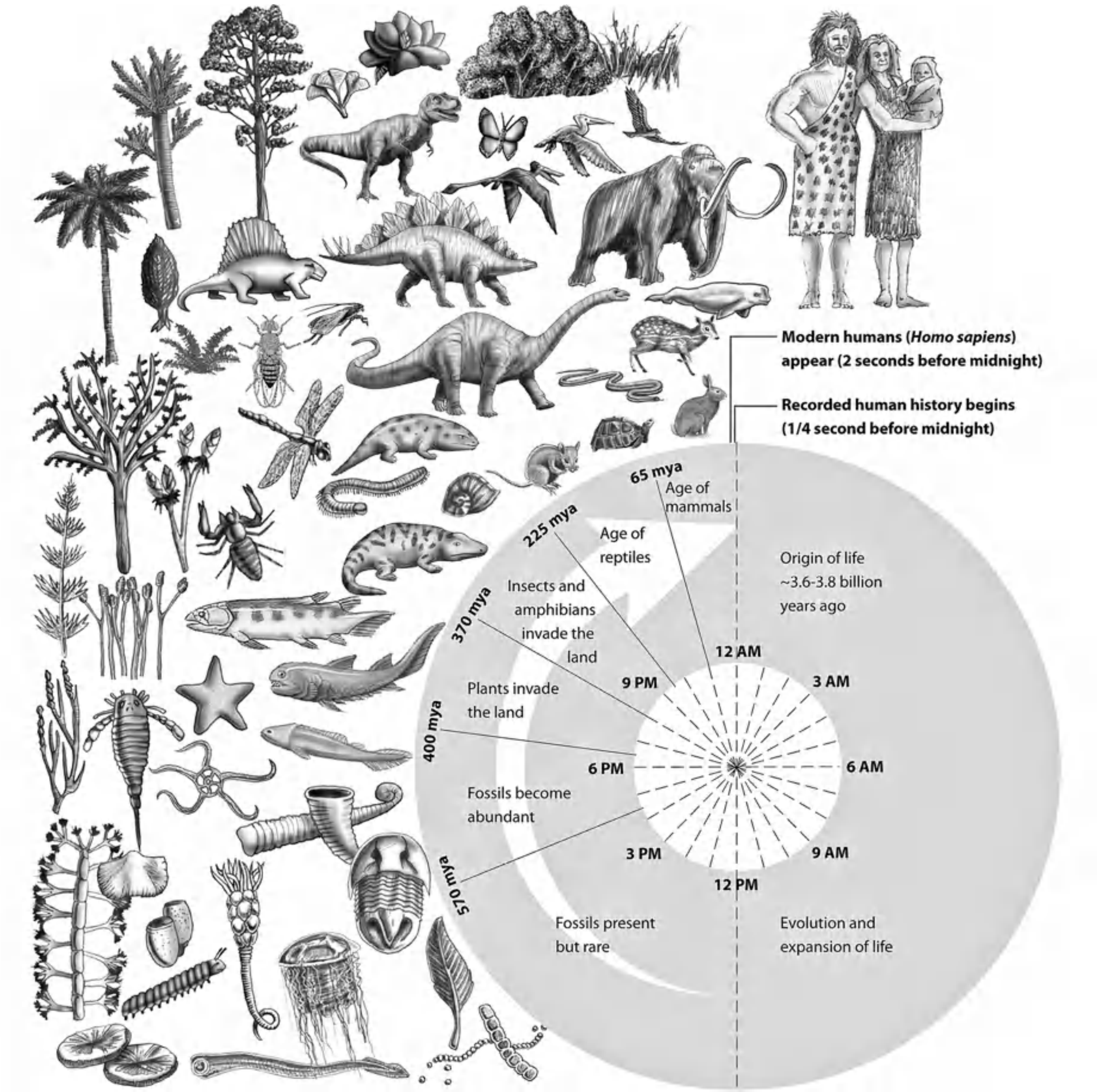


Figure 3.1. Greatly simplified timeline showing the history of the evolution of different forms of life on Earth compared to a 24-hour time scale. The human species evolved only about 2 seconds before the end of this 24-hour period.

The first vertebrate is thought to have used internal gills for respiration and feeding while swimming through shallow water. It was probably similar in appearance and mode of living to the lancelet or amphioxus, *Branchiostoma*, which currently lives in shallow coastal waters. Cephalochordates possess symplesiomorphic features (see Chapter 2, page **31**) that ancestral vertebrates are presumed to have inherited, like a notochord, a dorsal, hollow nerve cord, and pharyngeal gill slits, and they occurred earlier in geological time than the first known fossil vertebrates.

Studies have revealed that the lancelet nerve cord is divided like a vertebrate brain (Holland and Holland, 1999; Lacalli and Kelly, 2000). In the regions of the lancelet nerve cord where the Hollands found forebrain and midbrain genes at work, the neuronal structure matches that of the vertebrate forebrain and midbrain. Lacalli and Kelly (2000) claim that clusters of neurons in the lancelet brain seem to perform the same functions as their vertebrate counterparts—even though in the lancelet brain these clusters may be made up of only a handful of neurons. Lacalli and Kelly also claim that lancelets have a rudimentary limbic system. They have found lancelet neurons whose structure and organization resemble those of vertebrate limbic neurons and that are located in the corresponding parts of the midbrain and forebrain.

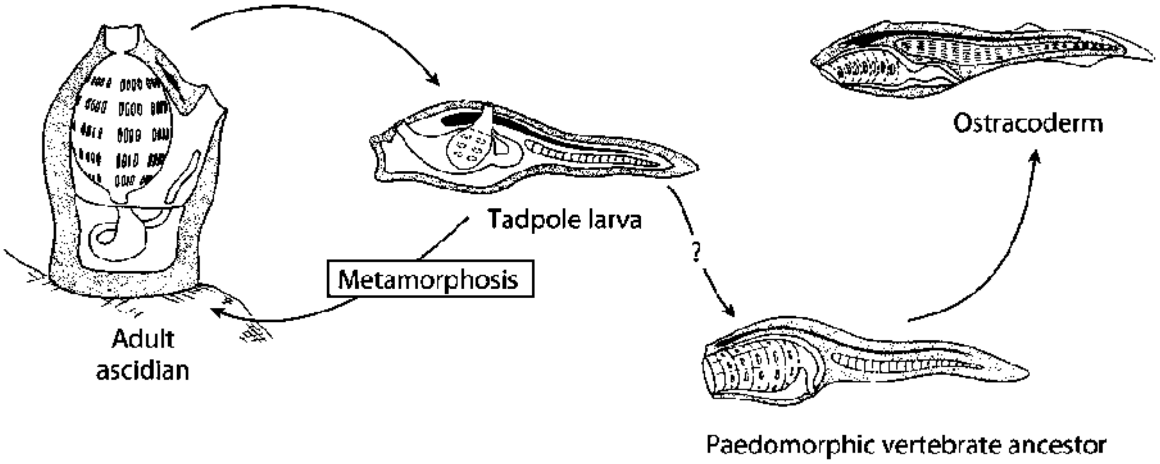


Figure 3.2. Garstang's hypothesis of larval evolution from paedomorphic urochordate larvae. Adult tunicates live on the seafloor but reproduce through a free-swimming "tadpole" stage. More than 500 Mya, some larvae began to reproduce in the swimming stage. These are believed to have evolved into the ostracoderms, the first known vertebrates.

Even though the lancelet is primitive, its asymmetry and unusual pattern of nerves appear to make it too specialized to be considered a truly ancestral type.

Feduccia and McCrady (1991) believed that cephalochordates were the probable vertebrate ancestors. As evidence, they cited the discovery of the mid-Cambrian 520-million-year-old *Pikaia gracilens*, a cephalochordate fossil found in the Burgess Shale formation in British Columbia, Canada. *Pikaia* possessed a notochord and segmented muscles, and, in 1991, it was the earliest known chordate (Fig. 3.4). Since that time, an even earlier possible chordate, *Yunnanozoon lividum*, from the Early Cambrian (525 Mya), has been reported from the Chengjiang fauna in China (Chen et al., 1995). It possessed a spinelike rod believed to be a notochord, metameric (segmental) branchial arches that possibly supported gills, segmented musculature, and a row of gonads on each side of the body. Not everyone is convinced that *Yunnanozoon* is a chordate. In fact, another Chinese researcher and his colleagues (Shu et al., 1996a) have classified it in another closely related phylum—the phylum Hemichordata (acorn worms).

In 1996, researchers discovered a 530-million-year-old fossil from the same Chengjiang fossil site and proclaimed it to be the oldest chordate fossil (Monastersky, 1996c; Shu et al., 1996b). *Cathaymyrus diadexus* (Fig. 3.5a) is 2.2 cm (0.86 in.) long, has *V*-shaped segments that closely resemble the stacked muscle blocks in primitive living chordates like amphioxus, and a creaselike impression running partway down the back of the body that scientists interpret as the imprint left by the animal's notochord.

More than 300 fossil specimens of another craniate-like chordate, *Haikouella lanceolata*, were recovered from Lower Cambrian (530-million-year-old) shale in central Yunnan in southern China (Chen et al., 1999). The 3 cm (1.2 in.) *Haikouella* fossils are similar to *Yunnanozoon* but they have several additional features: a heart, ventral and dorsal aortae, gill filaments, a caudal projection, a neural cord with a relatively large brain, a head with possible lateral eyes, and a ventrally situated buccal cavity with short tentacles.

Researchers continue to search for the earliest vertebrate (Janvier, 1999). Several groups of organisms—calcichordates and conodonts—have been proposed as "possible" chordates and vertebrates. Their inclusion in the vertebrate group is still uncertain, and their significance to the vertebrate story remains unclear. In addition, in 2003, Australian scientists claimed that a 560-million-year-old, 6.5 cm (2.56 in.) fishlike fossil discovered in the Flinders Ranges of South Australia was the earliest known vertebrate (Salleh, 2003; Anonymous, 2003). They claimed that it had bilateral symmetry, a distinct head, a dorsal fin, and segmentation that looked like bundles typical of a chordate. Other paleontologists contested that it was really a nonvertebrate fossil of the Ediacaran period known as *Charnia* or *Kimberella*.

CALCICHORDATES

One of these groups, the **calcichordates**, comprise marine organisms, usually classified as echinoderms, known only from fossils dated from 600 to 400 Mya (Jefferies, 1986) (see Fig. 3.5b). Calcichordates were covered by small plates of calcium carbonate, possibly representing incipient bone. Although they possessed indentations on their sides and an expanded anterior chamber, there is no evidence that these structures formed a pharyngeal gill apparatus. Other vertebrate-like characteristics pointed out by proponents include an expanded anterior nervous system (brain?) and a whiplike stalk (postanal tail?). However, there is no evidence of a notochord, nerve cord, or segmented musculature.

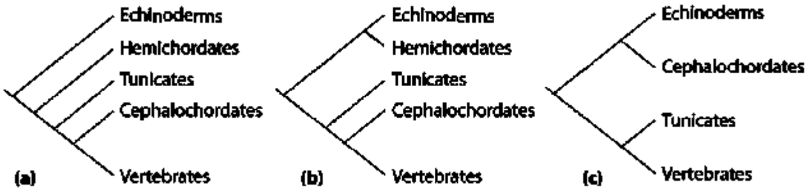


Figure 3.3. Deuterostome relationships. (*a*) The classic, textbook view, implying a smooth increase in complexity from a relatively simple and sedentary deuterostome ancestor to motile vertebrates. (*b*) A more recent view, informed by molecular evidence, in which hemichordates are allied with echinoderms, implying a more complex echinoderm history. (*c*) The topology suggested by the results of Delsuc et al. (2006). This implies that the deuterostome ancestor would have been motile and relatively complex, and that the sessile habits of most echinoderms and tunicates evolved later. Hemichordates are notably absent.

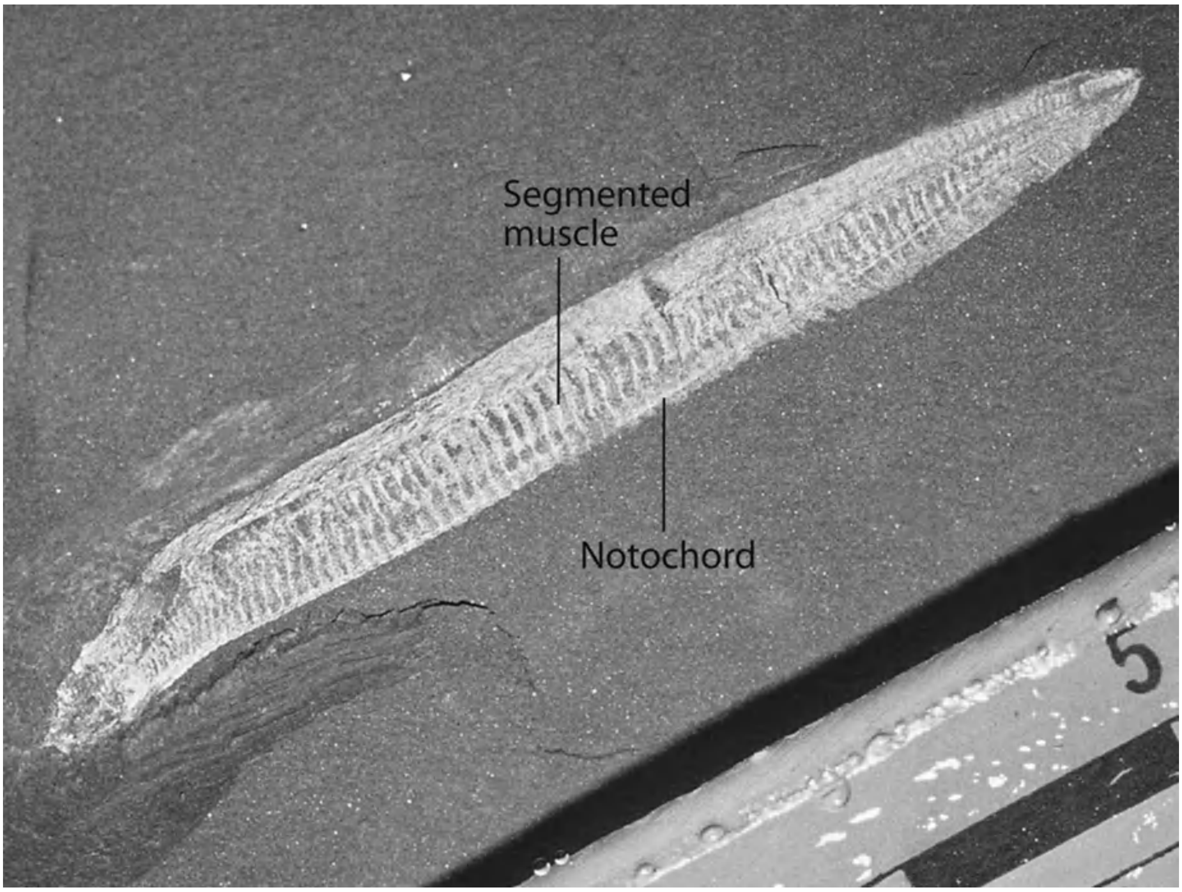


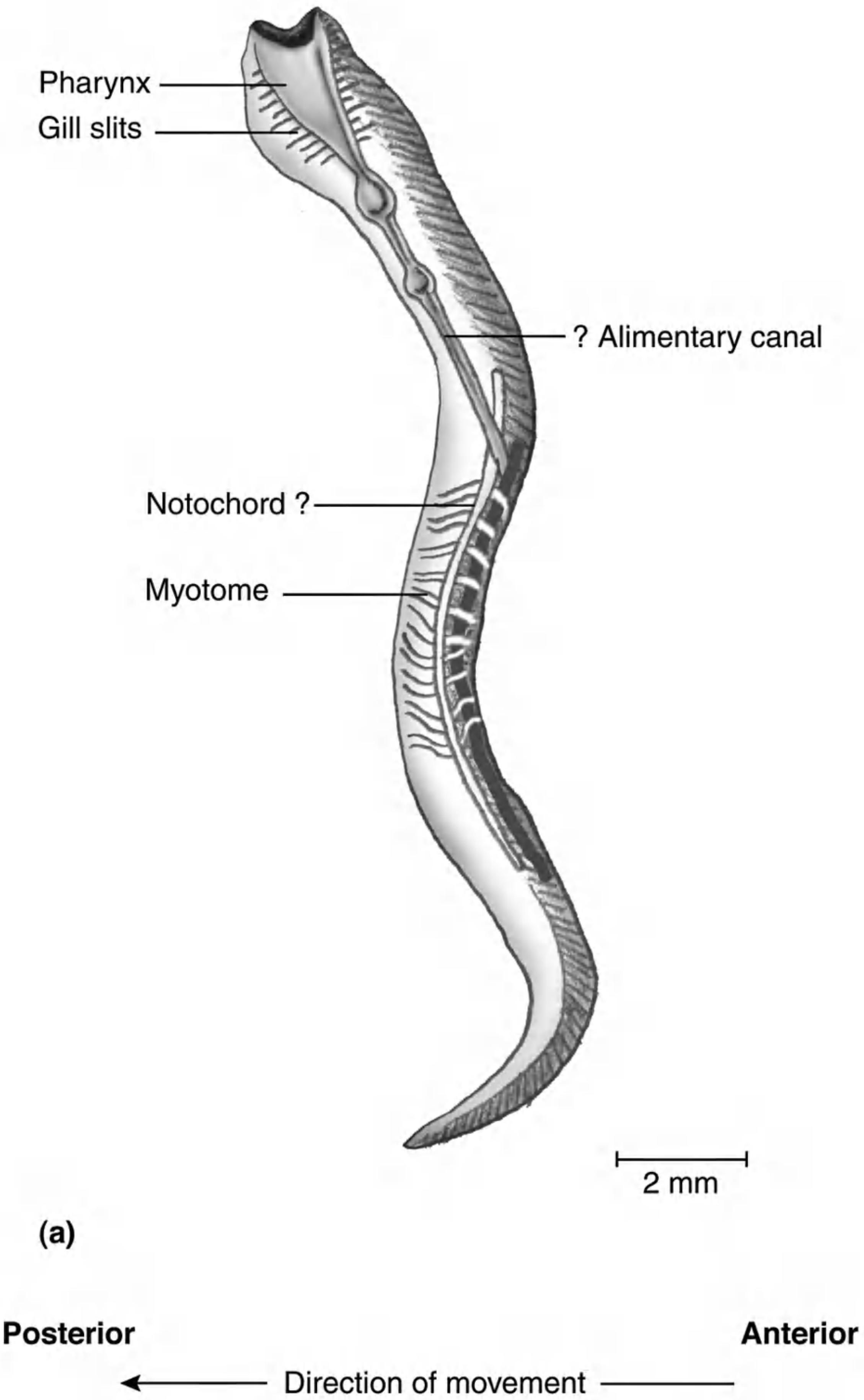
Figure 3.4. *Pikaia gracilens*, an early chordate, from the Burgess Shale of British Columbia, Canada.

CONODONTS

The second group recently proposed as possible vertebrates are the conodonts (Fig. 3.6a, b). These were small, 4 cm (1.6 in), wormlike marine organisms known only from some fossils with small teeth containing calcium phosphate. Some segmented muscle was present in a bilaterally symmetrical body. They appeared in the Cambrian (510 Mya), approximately 40 million years before the earliest vertebrate fossils, and lasted until the Triassic (200 Mya). Evidence of large eyes with their associated muscles, fossilized muscle fibers strikingly similar to fibers in fossil fishes; a mineralized exoskeleton, the presence of dentine, and the presence of bone cells make it a likely candidate as a near-gnathostome (jawed) vertebrate. The absence of a gill apparatus, however, is still puzzling (Sansom et al., 1994; Gabbotts et al., 1995; Janvier, 1995). The discovery of microscopic wear patterns on the teeth, perhaps produced as food was sheared and crushed, supports the hypothesis that these early forms were predators (Purnell, 1995) (Fig. 3.6b).

EARLY CAMBRIAN FISHLIKE FOSSILS

Shu et al. (1999, 2003) described two distinct types of agnathan from the mid-Lower Cambrian (530 Mya) Chengjiang fossil site. One form, *Haikouichthys ercaicunensis*, has structures resembling a branchial basket and a dorsal fin with prominent fin-radials and is lamprey-like. The second fossil, *Myllokunmingia fengjiaoa*, has well-developed gill pouches with probable hemibranchs and is closer to hagfishes. Shared features include complex myomeres and a notochord as well as probable paired ventral finfolds. The zigzag arrangement of segmented muscles is the same type of pattern seen in fishes today. The arrangement of the gills is more complex than the simple slits used by amphioxus. These agnathan vertebrates predate previous records by at least 20 million years and possibly as many as 50 million years (Shu et al., 1999).


Pharynx
Gill slits
? Alimentary canal
Notochord ?
Myotome
2 mm
(a)
Posterior
Anterior
Direction of movement

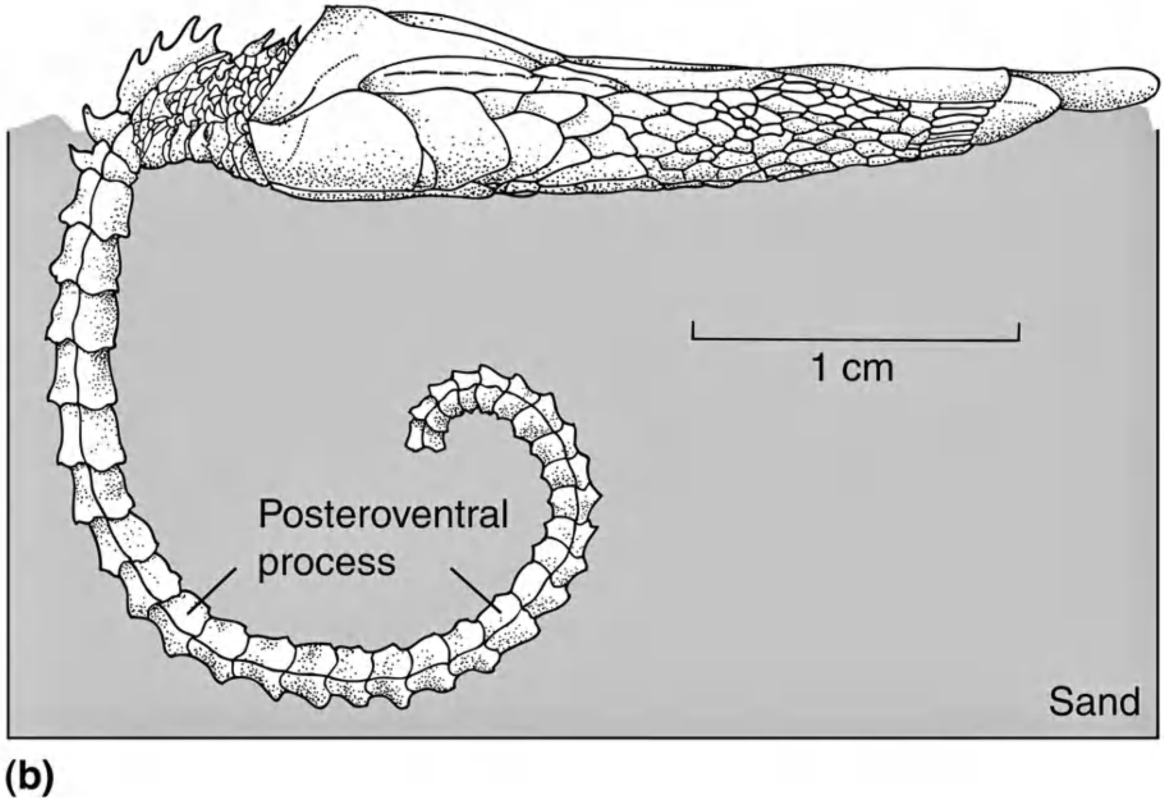


Figure 3.5. (*a*) Camera lucida drawing of *Cathaymyrus diadexus*, a new species. (*b*) Lateral view of a calcichordate, showing small, overlapping plates of calcium carbonate covering the surface of the animal's body.

Although both *Haikouichthys* and *Myllokunmingia* lack the bony skeleton and teeth seen in most, but not all, members of the infraphylum Vertebrata, they appeared to have had skulls and other skeletal structures made of cartilage. They are regarded as the earliest vertebrate fossils. Shu et al. (1999) proposed that vertebrates evolved during the explosive period of animal evolution at the start of the Cambrian and only some 30 million years later developed the ability to accumulate minerals in their bodies to form bones, teeth, and scales.

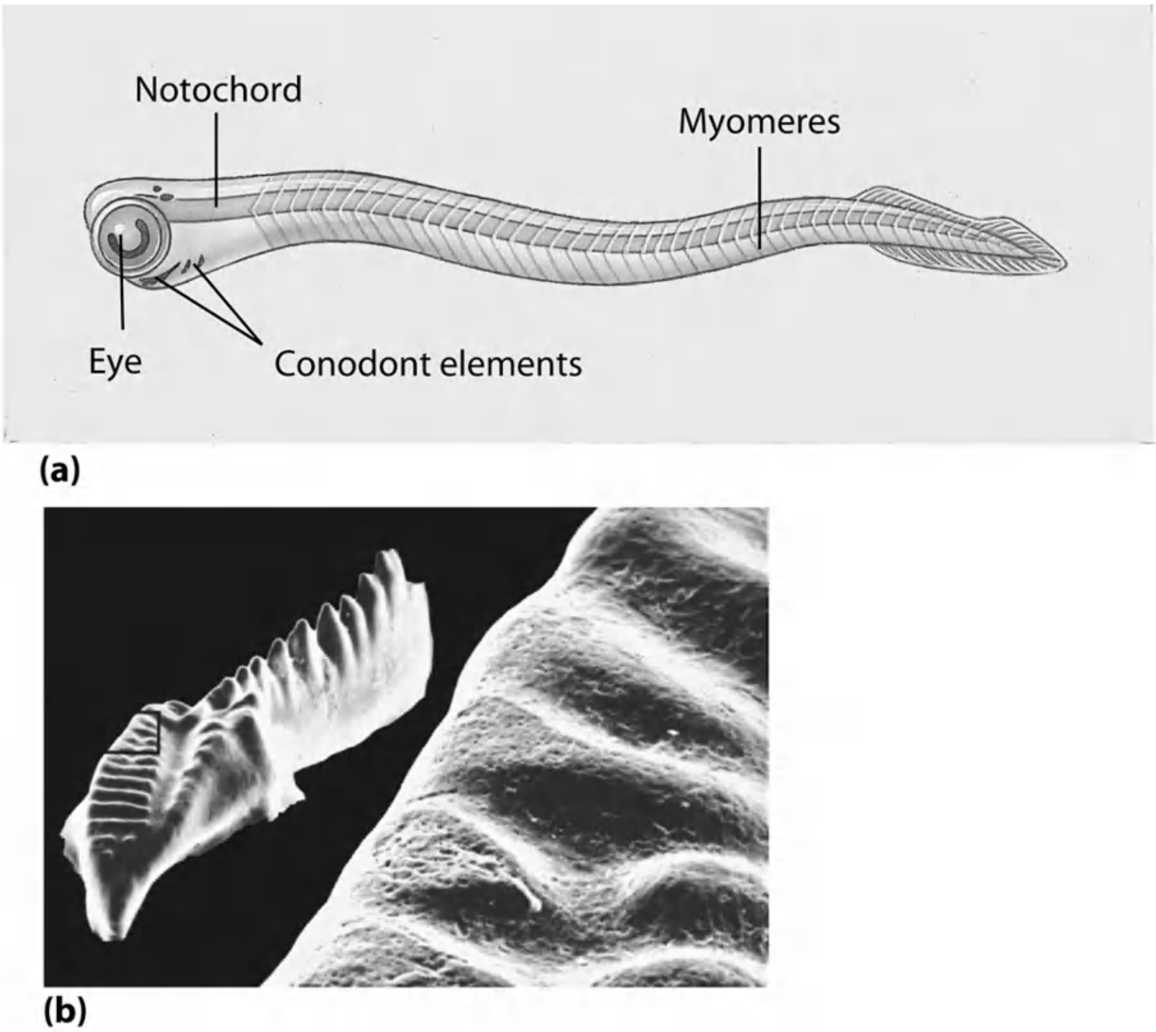


Figure 3.6. (*a*) Restoration of a living conodont. Although superficially resembling an amphioxus, the conodont possessed a much greater degree of encephalization (large, paired eyes; possible auditory capsules) and bonelike mineralized elements—all indicating that the conodont was a vertebrate. The conodont elements are believed to be gill-supporting structures or part of a suspension-feeding apparatus. (*b*) Micrograph shows single conodont tooth with closeup of ridges worn down by crushing food.

Metaspriggina, a 5 cm (2 in.), 505-million-year-old creature, is considered to represent a primitive chordate, possibly transitional between cephalochordates and the earliest vertebrates (Morris and Caron, 2014; Long, 2014). It had most of the characteristics attributed to vertebrates: a notochord, a pair of prominent camera-type eyes, paired nasal sacs, *W*-shaped myomeres, and a postanal tail. It had a weakly developed cranium along with seven pairs of well-developed cartilaginous gill arches that were external as in jawed fishes. The anterior-most pair of arches was slightly thicker than the remainder and is thought to have eventually led to the evolution of jaws in vertebrates, the first time this feature has been seen so early in the fossil record. It is thought to have lived as a filter-feeder swimming above the seafloor. Phylogenetic analysis places *Metaspriggina* as a basal vertebrate, apparently close to *Haikouichthys* and *Myllokunmingia* (Morris and Caron, 2014).

EVOLUTION

The evolution of the major groups of hagfishes, lampreys, and fishes and their relationships to each other, to amphibians, and to amniotes are shown in Fig. 3.7. A cladogram showing probable relationships among the major groups of fishes is depicted in Fig. 3.8. Because taxonomy is constantly undergoing refinement and change, the relationships depicted in this cladogram, along with others used in this text, are subject to considerable controversy and differences of opinion among researchers (see Supplemental Reading at the end of this chapter).

Homeobox Genes

Some researchers believe that *all* animals are descended from a common ancestor and share a special family of genes (the homeobox, or *Hox*, genes) that are important for determining overall body pattern. The protein product of *Hox* genes controls the activation of other genes, ensuring that various body parts develop in the appropriate places. *Hox* genes are "organizer" genes; they switch other genes "on" and "off." Garcia-Fernandez and Holland (1994) have described a single cluster of *Hox* genes from an amphioxus, *Branchiostoma floridae*, that matches the 38 *Hox* genes in four clusters on different chromosomes known from mammals. Each amphioxus *Hox* gene can be assigned to one of the four clusters, and they are even arranged in the same order along the main axis of each chromosome. These genes are involved in embryonic patterning and development and serve as blueprint genes. Patterns of *Hox* gene expression are established that give cells a positional address, and then the interpretation of this positional information leads to the appropriate development of particular bones, appendages, and other structures. Most vertebrates, including mammals, have four *Hox* clusters, suggesting that two genome duplications occurred since these lineages split from the invertebrates, which typically have only one *Hox* cluster.

A change in *Hox* gene number has been hypothesized as a significant factor in the evolution of vertebrate structures. For example, at the 1998 meeting of the Canadian Institute for Advanced Research Programs in Evolutionary Biology, John Postlethwait and his colleagues at the University of Oregon announced that they had found that zebra fish have seven *Hox* clusters on seven different chromosomes. They hypothesize that the doubling might have occurred very early in the ray-finned fish (Actinopterygii) lineage and might explain how the 25,000 species came to evolve such diverse forms. Although their respective evolutionary histories are unique, vertebrate, insect, and other animal appendages are organized via a similar genetic regulatory system that may have been established in a common ancestor.

Garcia-Fernandez and Holland, 1994; Gee, 1994; Shubin et al., 1997; Vogel, 1998; Smith et al., 2018.

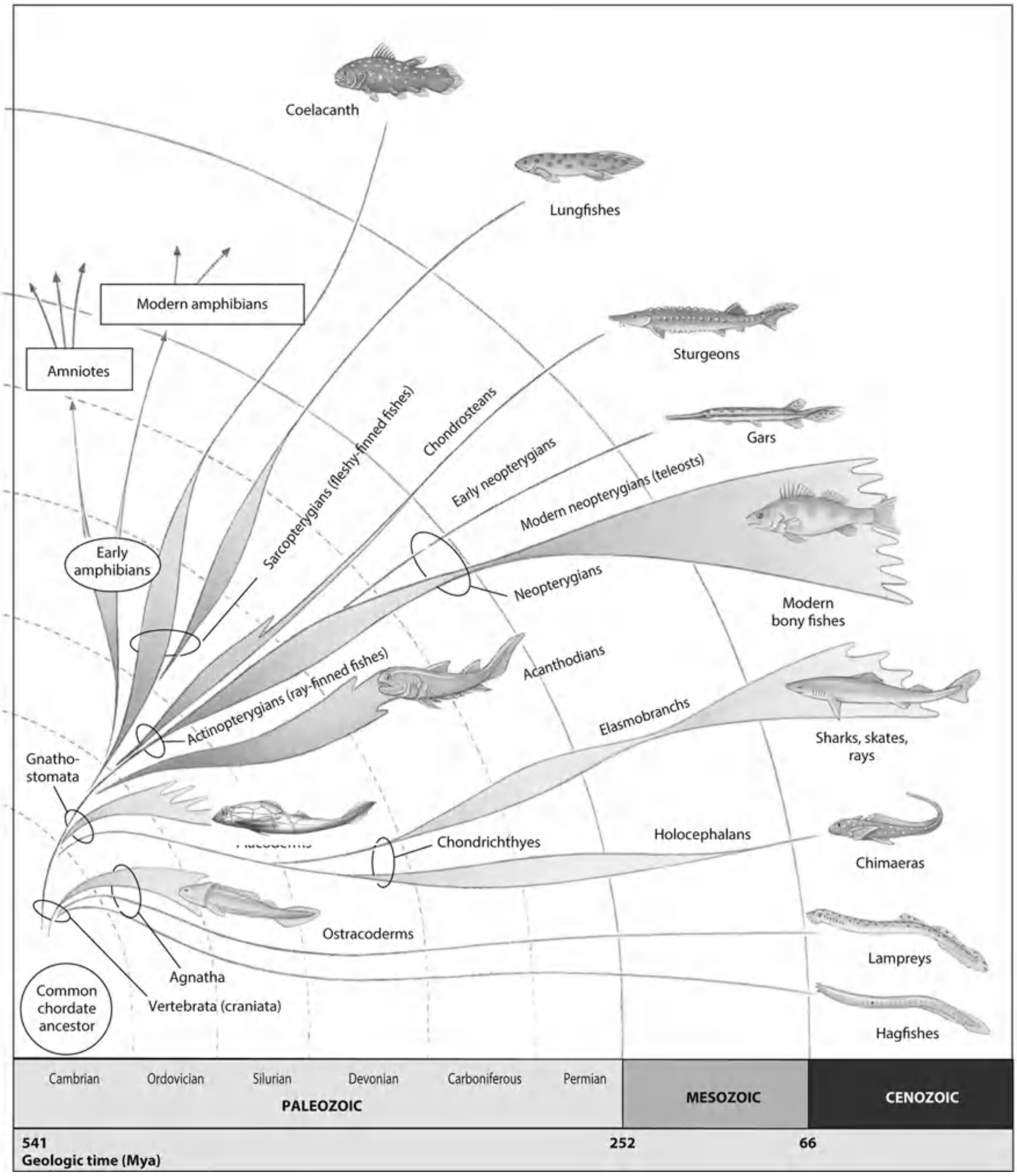


Figure 3.7. Graphic representation of the family tree of fishes, showing the evolution of major groups through geological time. Many lineages of extinct fishes are not shown. Widths of lines of descent indicate relative numbers of species. Widened regions of the lines indicate periods of adaptive radiation. The fleshy-finned fishes (sarcopterygians), for example, flourished in the Devonian period but declined and are today represented by only four surviving genera (lungfishes and the coelacanth). Homologies shared by the sarcopterygians and tetrapods suggest that they are sister groups. The sharks and rays, which radiated during the Carboniferous period, apparently came close to extinction during the Permian period but recovered in the Mesozoic era. Modern bony fishes, or teleosts, currently make up most of the living fishes.

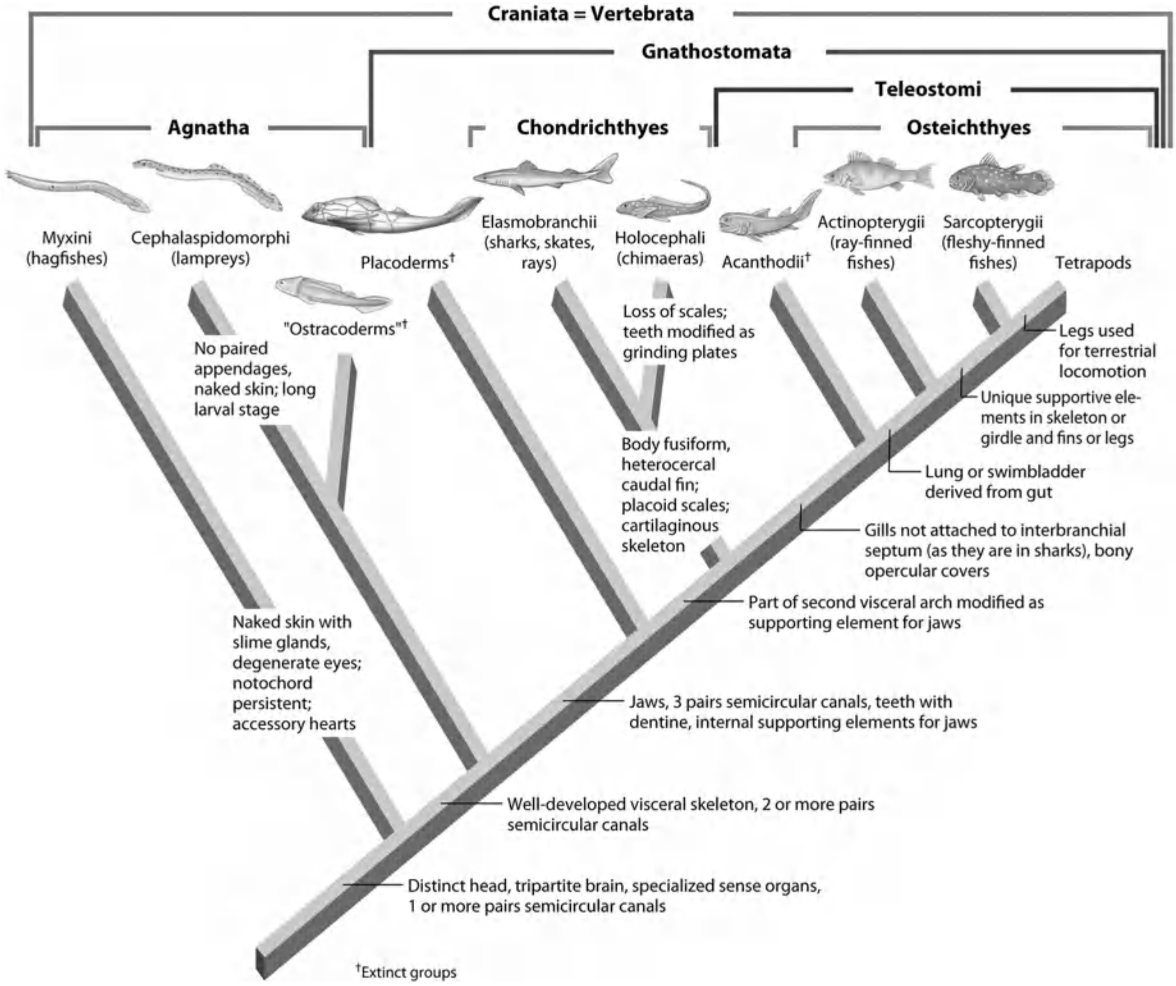


Figure 3.8. Cladogram of the fishes, showing the probable relationships of major monophyletic fish taxa. Several alternative relationships have been proposed. Some of the shared derived characters that mark the branchings are shown to the right of the branch points.

The earliest vertebrate remains were thought to consist of fossil remnants of bony armor of an ostracoderm (*Anatolepis*) recovered from marine deposits in Upper Cambrian rocks dating from approximately 510 Mya (Repetski, 1978). More recent studies, however, have identified these remains of "bone" as the hardened external cuticles of early fossil arthropods (Long, 1995). Since bone is found only in vertebrates, the presence of bone in a fossil is highly significant. Young et al. (1996) and Janvier (1996) reported fragments of bony armor from a possible Late Cambrian (510 Mya) early armored fish from Australia. The fragments have rounded projections, or tubercles, that bear a striking resemblance to those of arandaspids, a group of jawless vertebrates from the Ordovician period. The Australian fragments, unlike arandaspid armor (which is composed of bone), are made up of enamel-like material. Both arandaspids and the Australian fragments also lack dentin (a substance softer than enamel but harder than bone). Dentin is deposited by specialized cells derived from ectomesoderm, thus providing indirect evidence of the presence of a neural crest, a unique vertebrate tissue found nowhere else in the Animal Kingdom (Kardong, 2012).

The cradle of vertebrate evolution was limited to a zone of shallow coastal waters, no more than 60 meters deep (Sallen et al. 2018). In those waters, fish appeared about 480 Mya. For nearly 100 million years, those fish rarely strayed from that habitat, where they diversified into an array of new forms and acquired adaptations before eventually moving into new areas. Some fish gained streamlined, graceful bodies good for fast swimming in deeper waters. Others had stronger, armored bodies and stayed close to shore or moved into rivers or lakes.

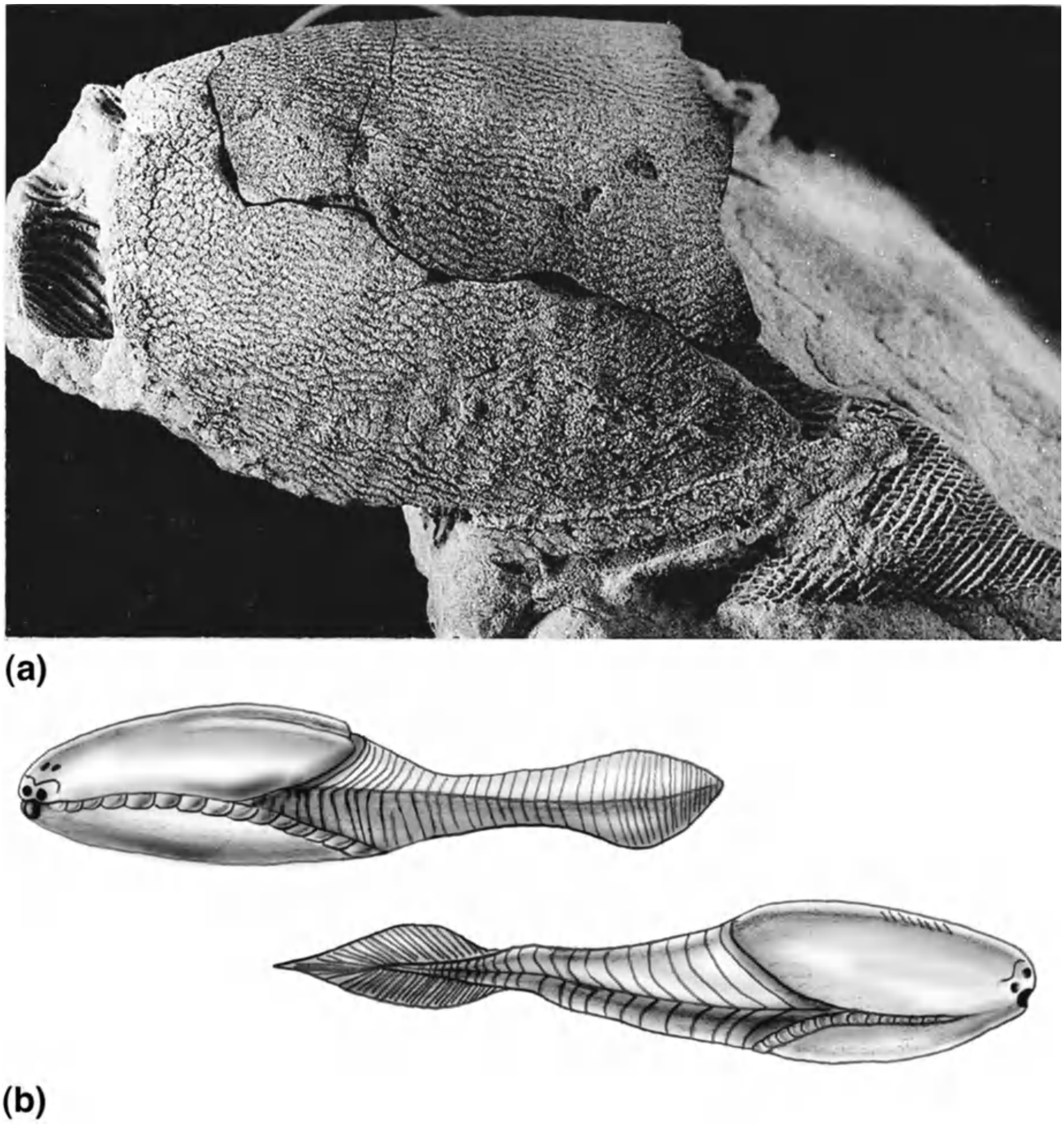
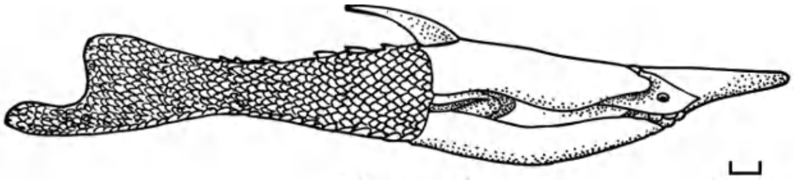


Figure 3.9. (*a*) *Arandaspis*, a 470-million-year-old jawless fish found near Alice Springs in central Australia. The fossilized impression of the bony plates was preserved in sandstone. The impression of the ribbed clam shell is approximately where the mouth of the fish would have been. The length of this specimen is approximately 20 cm (8 in.). (*b*) Reconstructions of the primitive Ordovician fishes *Arandaspis* (*above*) and *Sacabambaspis* (*below*).

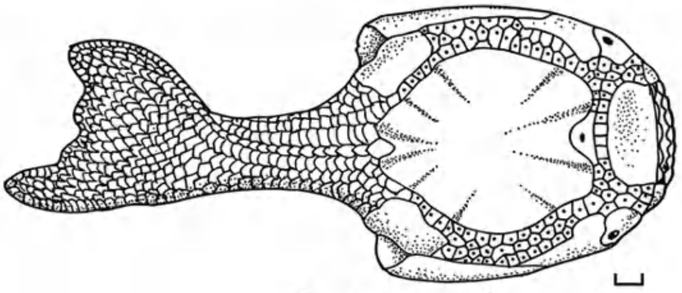
At present, the oldest identifiable vertebrate fossils with real bone are fragmentary ostracoderm fossils (*Arandaspis*) that have been found in sedimentary rocks formed in fresh water near Alice Springs in central Australia during the Ordovician period, approximately 470 Mya (Long, 1995) (Fig. 3.9a). The bony shields were not preserved as bone but as impressions in the ancient sandstones. The first complete Ordovician ostracoderm fossils (*Sacabambaspis*) were discovered in central Bolivia in the mid-1980s by Pierre Yves-Gagnier (Long, 1995) (Fig. 3.9b). They have been dated at about 450 Mya and, thus, are slightly younger than the Australian fossils, but they are much more completely preserved.

Although ostracoderms presumably possessed a cartilaginous endoskeleton, the head and front part of the body of many forms were encased in a shieldlike, bony, external cover (Fig. 3.10). Bony armor, together with a lack of jaws and paired fins, characterized these early vertebrates (heterostracans), which presumably moved along the bottom sucking up organic material containing food.

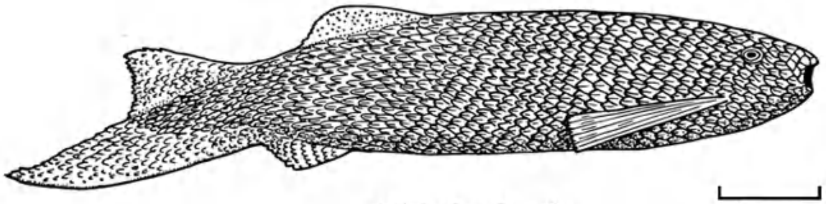
Heterostracan skeletons are made of a really strange tissue called aspidin. For years, scientists have wondered if aspidin was a transitional stage in the evolution of mineralized tissues. Scientists at the universities of Manchester and Bristol used a special type of CT scanning technology (synchrotron tomography), using very high energy X-rays produced by a particle accelerator, to image the internal structure of heterostracan skeletons (Keating et al., 2018). The images suggest the aspidin skeleton’s tiny tubes were once filled with bundles of collagen fibers. Thus, aspidin, once thought to be the precursor of vertebrate mineralized tissues, has been shown to be, in fact, a type of bone.



Pteraspis

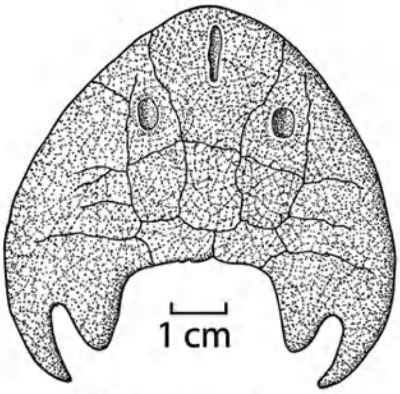


Drepanaspis

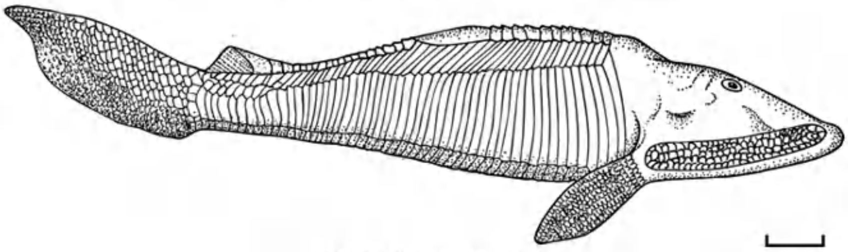


Phlebolepis

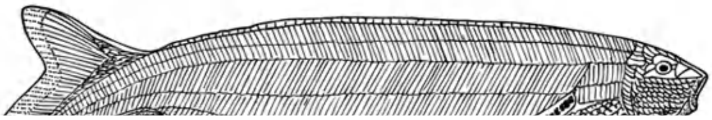
(a)



Yunnanogaleaspis



Hemicyclaspis



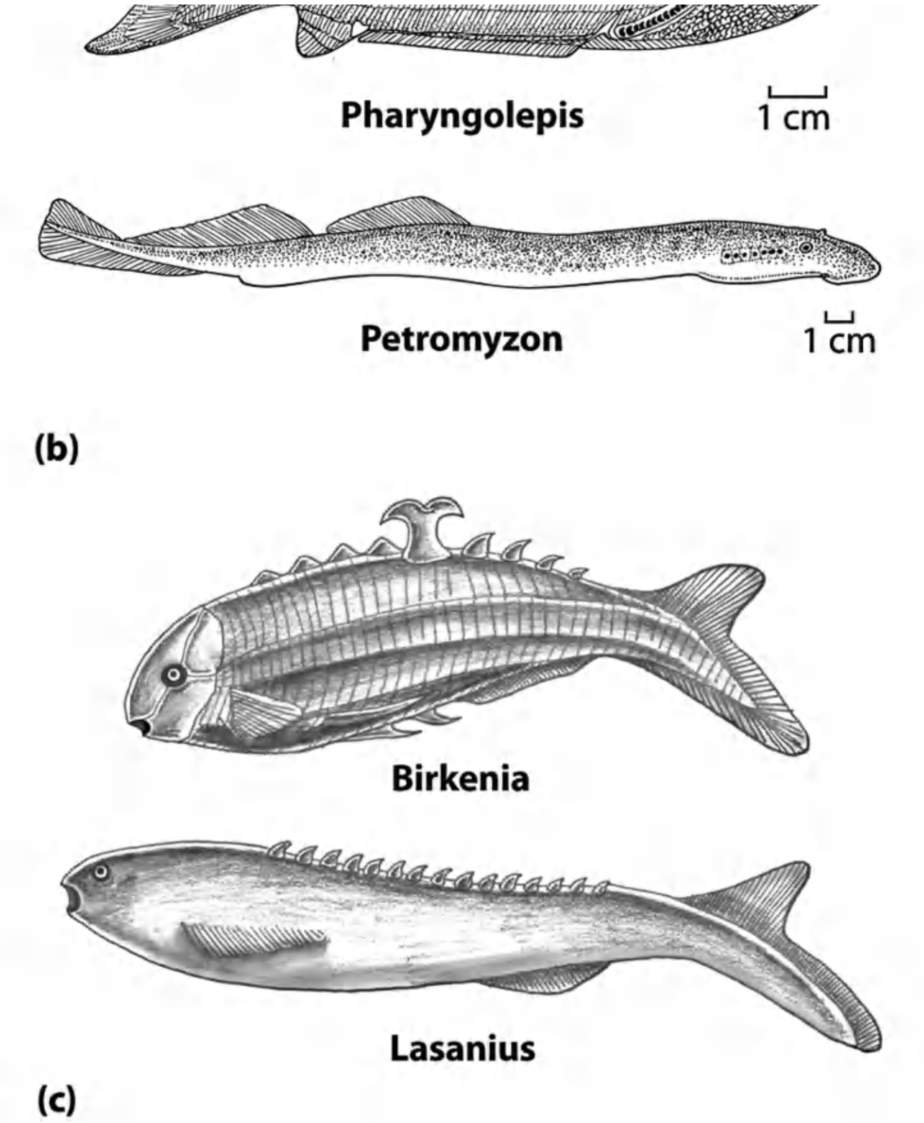


Figure 3.10. Representative ostracoderms. (*a*) Pteraspidomorphs, from the Early Paleozoic, with plates of bony armor that developed in the head. All are extinct. (*b*) Representative cephalaspidomorphs. All are extinct except the lamprey. (*c*) Representative anaspidomorphs. All are extinct.

Heterostracan tails consisted of two lobes, with the distal end of the notochord extending into the larger lobe. If the larger lobe was dorsal, the tail was known as an epicercal tail; if ventral, it was known as a hypocercal tail. Later ostracoderms (cephalaspidiforms) developed paired “stabilizers” behind their gill openings that probably improved maneuverability. Most of these stabilizers were extensions of the head shield rather than true fins, although some contained muscle and a shoulder joint homologous with that of gnathostomes.

Ostracoderms, which are considered to be a sister group to the lampreys (Cephalaspidomorphi), survived some 100 million years before becoming extinct at the end of the Devonian period. Two relatives of this group—hagfishes and lampreys—exist today.

The earliest hagfish (class Myxini) fossil comes from the Pennsylvanian epoch, approximately 330 Mya (Bardack, 1991). Whereas lampreys occur in both freshwater and marine habitats, hagfishes are strictly marine animals and live in burrows on the ocean bottom in waters cooler than 22°C (72°) (Martini, 1998). They occur worldwide, except in the Arctic and Antarctic oceans, and serve as prey for many marine animals, including codfish, dogfish sharks, octopuses, cormorants, harbor porpoises, harbor seals, elephant seals, and some species of dolphins (Martini, 1998).

Hagfishes have been evolving independently for such an extremely long time—probably more than 530 million years, according to Martini (1998)—and are so different from other vertebrates that many researchers question their relationship to vertebrates. They appear to have changed little over the past 530 million years. Some researchers, like Janvier (1981), do not classify hagfishes as vertebrates because there is no evidence of vertebrae either during their embryonic development or as adults. However, because they have a cranium, they are included in the Craniata by phylogenetic systematists; they are considered the most primitive living craniates. The Craniata includes all members of the subphylum Vertebrata in the traditional method of classification.

The earliest fossil lamprey (class Cephalaspidomorphi) dates from the Late Devonian period, some 360 Mya (Gess et al., 2006). *Priscomyzon riniensis* shows characteristic lamprey features, like a grotesquely large sucker armed with horny teeth that surrounds the mouth and a basket-like gill skeleton. This shows that lamprey morphology has been astonishingly stable for 360 million years and proves that lampreys and hagfishes had already diverged by Late Devonian times, earlier than previously thought. All cephalaspids possess a distinctive dorsally placed nasohypophyseal opening. The single nasal opening merges with a single opening of the hypophysis to form a common keyhole-shaped opening. This is a synapomorphy of the group. In addition, the brain and cranial nerves are strikingly similar. Fossils differ little from modern forms and share characteristics, and presumably ancestry, with two groups of ostracoderms (anaspids and cephalaspids).

As is the case with many issues discussed in this text, there is considerable controversy concerning the evolutionary history of these groups. Both lampreys and hagfishes possess many primitive features. Besides the absence of jaws and paired fins, both groups lack ribs, vertebrae, a thymus, lymphatic vessels, and genital ducts. Both possess cartilaginous skeletons. Based on these shared primitive characteristics, many researchers and taxonomists feel that lampreys and hagfishes form a monophyletic group—the agnathans. Phylogenetic comparisons of ribosomal RNA sequences from hagfishes, lampreys, a tunicate, a lancelet, and several gnathostomes provide additional evidence to support the proposed monophyly of the agnathans (Stock and Whitt, 1992).

Hagfishes, however, lack some structures found in lampreys, like well-developed eyes, extrinsic eyeball muscles, and the radial muscles associated with the median fins (Stock and Whitt, 1992). They possess only a rudimentary braincase, or cranium. Also, the primary structure of insulin, a hormone secreted by the pancreas, has been found to differ in the two groups, leading researchers to note that the most likely conclusion would be that lampreys and hagfishes descended from different ancestors (Mommsen and Plisetskaya, 1991). Differences between adult lampreys and hagfishes are presented in Table 3.1. Based on such morphological analyses, other researchers believe that agnathans are paraphyletic, with lampreys being more closely related to gnathostomes than either group is to hagfishes (Janvier, 1981; Hardisty, 1982; Forey, 1984; Maisey, 1986). Additional studies, including analyses of sequences from other genes, are needed to clarify the phylogenetic relationships of the agnathans.

MORPHOLOGY

Integumentary System

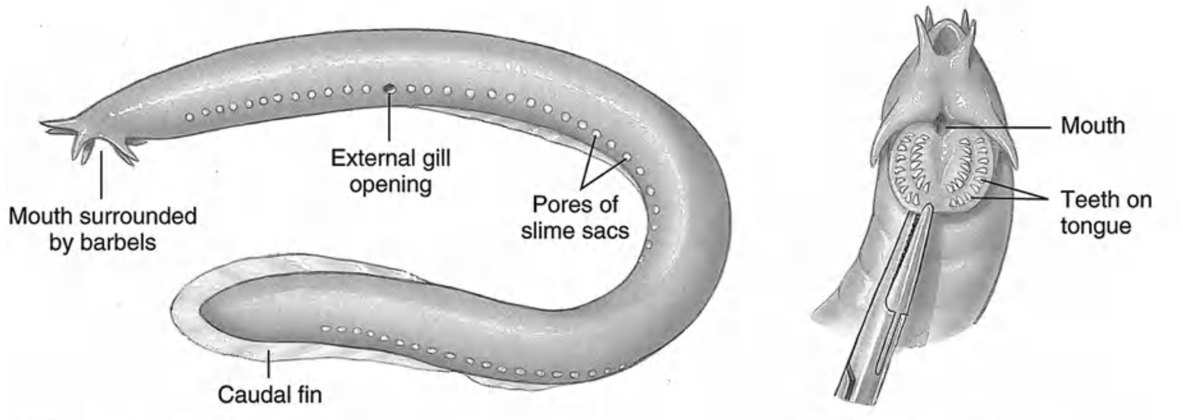
The outer surface of the body of extant jawless fishes is smooth and scaleless (Figs. 3.11 and 3.12). The skin consists of a thin **epidermis** composed of living cells and a thicker, more complex **dermis** consisting of multiple dense layers of collagen fibers. The skin of hagfishes is attached to underlying muscles only along the dorsal midline and along the ventral surface at the level of the slime glands (Martini, 1998). Tanned hagfish skin is sold as “eel-skin” and is used to produce designer handbags, shoes, wallets, purses, and briefcases (Martini, 1998). A nonliving secretion of the epidermis, called **cuticle**, covers the epidermis in lampreys. Within the dermis of jawless fishes are sensory receptors, blood vessels, and chromatophores. Several types of unicellular glands are normally found in the epidermis; they contribute to a coating of mucus that covers the outside of the body. A series of pores along the sides of the body of a hagfish connect to approximately 200 slime glands that produce the defensive slime (mucus) that can coat the gills of predatory fish and either suffocate them or cause them to leave the hagfish alone (Fig. 3.11a). To clean the mucus off their own bodies, hagfishes have developed the remarkable ability to tie themselves in a knot, which passes down the body, pushing the mucus away (Fig. 3.11d). The knotting behavior is also useful in giving hagfishes extra leverage when feeding on large fish (Barton, 2007).

Table 3.1. Comparison of Anatomical and Physiological Characteristics between Adult Lampreys and Hagfishes

Characteristics	Lampreys	Hagfishes
Dorsal fin	1 or 2	None
Pre-anal fin	Absent	Present
Eyes	Well developed	Rudimentary
Extrinsic eye muscles	Present	Absent
Oral disc	Present	Absent
Lateral-line system	Well developed	Absent
Semicircular canals	2 on each side of head	1 on each side of head
Barbels	Absent	3 pairs
Intestine	Ciliated	Unciliated
Spiral valve intestine	Present	Absent

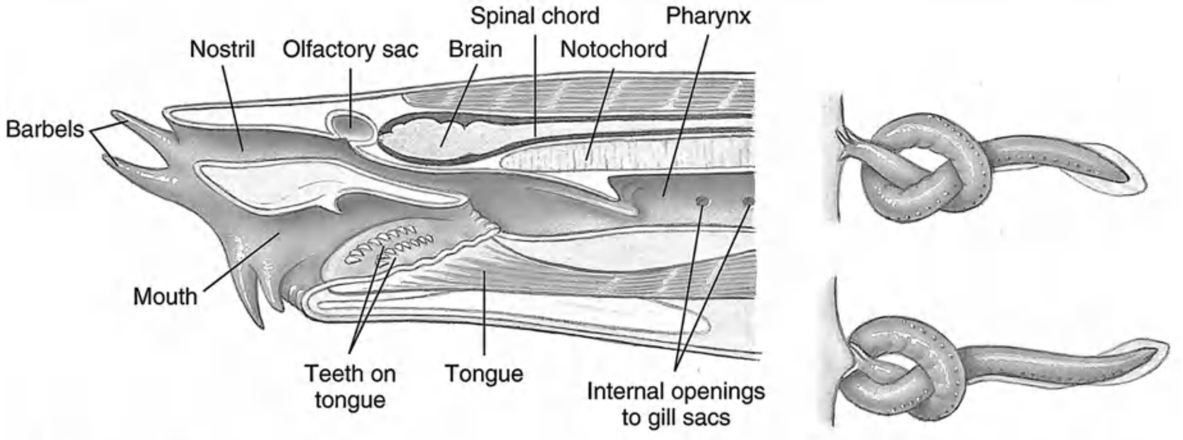
Characteristics	Lampreys	Hagfishes
Buccal glands	Present	Absent
Nostril location	Top of head	Front of head
Nasohypophyseal sac	Does not open into pharynx	Opens into pharynx
External gill openings	7	1 to 14
Internal gill openings	United into single tube connecting to oral cavity	Each enters directly into pharynx
Cranium	Cartilaginous	Poorly developed
Branchial skeleton	Well developed	Rudimentary
Vertebrae (cartilaginous)	Present	Absent
Spinal nerve pairs per body segment	2	1
Ducts of Cuvier to heart	Right only	Left
Pronephric kidney	Absent	Present
Osmoregulation	Hyper- or hypoosmotic	Isosmotic
Eggs	Small, without hooks	Very large, with hooks
Cleavage of embryos	Holoblastic	Meroblastic

Source: From Moyle and Cech, Jr., 2004. Copyright © 2004 Pearson Benjamin Cummings, San Francisco. Adapted by permission.



(a) External anatomy

(b) Ventral view of head



(c) Sagittal section of head region

(d) Knotting action used to tear flesh from prey

Figure 3.11. The Atlantic hagfish, *Myxine glutinosa*: (*a*) external anatomy; (*b*) ventral view of head with mouth held open, showing horny plates used to grasp food during feeding; (*c*) sagittal section of head region; (*d*) knotting action, illustrating how the hagfish obtains leverage to tear flesh from its prey.

Skeletal System

Cartilages supporting the mouthparts and the gills are suspended from the skull, which is little more than a troughlike plate of cartilage on which the brain rests. The rest of the branchial (gill) skeleton consists of a fenestrated, basket-like framework under the skin surrounding the gill slits (see Fig. 3.12). This branchial basket supports the gill region. Although a true vertebral column is lacking in jawless fishes, paired lateral neural cartilages are located on top of the notochord lateral to the spinal cord in lampreys. These cartilaginous segments are the first evolutionary rudiments of a backbone, or vertebral column. In hagfishes, however, lateral neural cartilages are found only in the tail. While these segments are reminiscent of neural arches, it is unclear whether they represent primitive vertebrae, vestigial vertebrae, or entirely different structures. Anteriorly, only an incomplete cartilaginous sheath covers the notochord in hagfishes.

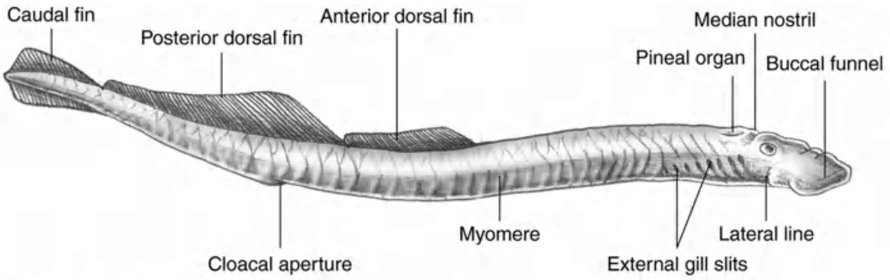
All jawless fishes lack paired appendages, although all possess a caudal fin. In addition, one or two dorsal fins are present in lampreys. Hagfishes lack dorsal fins but have a pre-anal fin.

Muscular System

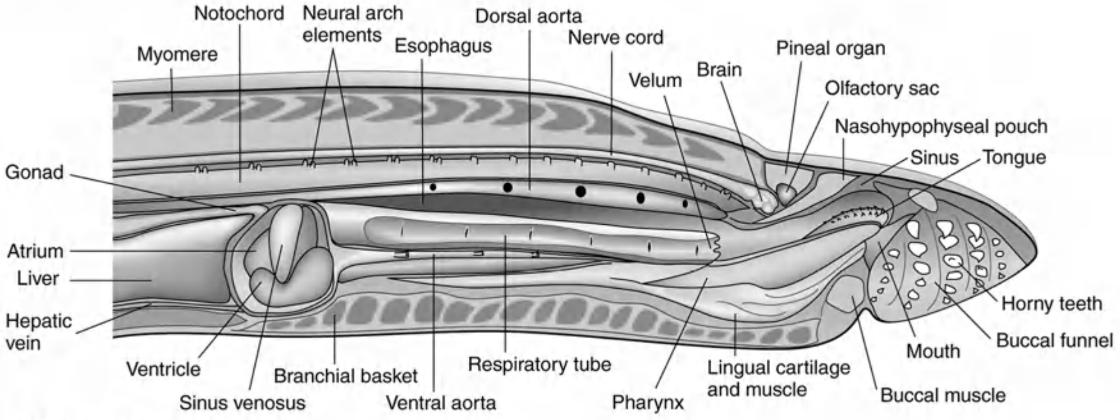
Body muscles are segmentally arranged in a series of **myomeres**, each of which consists of bundles of longitudinal muscle fibers that attach to thin sheets of connective tissue, called **myosepta**, between the myomeres (see Fig. 3.12). There is no further division of body wall musculature in these primitive vertebrates. Waves of contraction passing alternately down the two sides of the body cause the lateral undulation of the trunk and tail. Jets of water expelled from the gill slits may also aid in locomotion. Buccal and lingual muscles are situated in the buccal funnel and pharyngeal regions (see Fig. 3.12).

Cardiovascular System

The heart in hagfishes and lampreys is located in the **pericardial cavity** ventral to the pharynx (see Fig. 3.12). It consists of four parts: from posterior to anterior, these are the **sinus venosus**, **atrium**, **ventricle**, and **conus arteriosus** (blood flows through the heart in that sequence). Hagfishes have three additional sets of accessory hearts along their venous system: the **portal heart**, which receives venous blood from the cardinal vein and from the intestine and pumps this blood to the liver; **cardinal hearts**, which are located in the cardinal veins and help to propel the blood; and **caudal hearts**, which are paired expansions of the caudal veins (Johansen, 1960). These accessory hearts have their own intrinsic pumping rhythm and are not coordinated by the central nervous system. Despite the presence of these accessory hearts, blood pressure in hagfishes is very low (Randall, 1970a). The pooling of blood in large blood sinuses also contributes to the low blood pressure in hagfishes.



(a) Sea lamprey, external anatomy



(b) Sea lamprey, sagittal section

Figure 3.12. (*a*) Lateral view of the sea lamprey, *Petromyzon marinus*. The dorsal fins, eyes, and lateral-line system are well developed. These structures are either absent or rudimentary in hagfishes. (*b*) Sagittal section through the anterior portion of a lamprey. Note the prominent buccal funnel.

Respiratory System

Living jawless fishes have between 5 and 15 pairs of external gill openings (see Figs. 3.11 and 3.12). In hagfishes, water enters the nostril and passes through the nasopharyngeal duct to the pharynx. Afferent branchial ducts lead from the pharynx to the gill pouches, while water is carried from the pouches to the outside through efferent branchial ducts. In parasitic lampreys, however, the direction of water flow has been modified. Water enters the external gill slits and is ejected by the same route. This modification is essential so that the lamprey can carry on respiration when it is attached by its buccal funnel to a host fish. The nasal duct ends in a **nasohypophyseal sac** and does not lead to the pharynx. At metamorphosis in the lamprey, the pharynx differentiates into an esophagus dorsally and pharynx ventrally, so that, in adults, the pharynx terminates blindly.

Digestive System

Lampreys have a round, suctorial mouth (oral disk) located inside a **buccal funnel** (see Fig. 3.12b). Within the buccal funnel is a thick, fleshy, rasping “tongue” armed with horny epidermal “teeth” for scraping flesh. Many lampreys are parasitic, attaching to a host with their oral disks and using their rasping teeth to bore into the host’s body wall (Fig. 3.13). Blood and other body fluids are sucked from the host while the lamprey secretes an anticoagulant. Parasitic lampreys generally do not kill their hosts, but detach, leaving a weakened animal with an open wound. For this reason, some biologists prefer to regard parasitic lampreys as predators, rather than parasites. During its lifetime, each sea lamprey can kill 40 or more pounds of fish.

Food passes through the pharyngeal region and into the esophagus (see Fig. 3.12b). Because lampreys have no true stomach, the esophagus leads directly into a straight intestine that contains a region of longitudinal folds, known as a typhlosole, whose function is to increase the absorptive area. The intestine opens into the cloaca. Swim bladders, which are derivatives of the digestive tract in many fishes, are not present in agnathans.

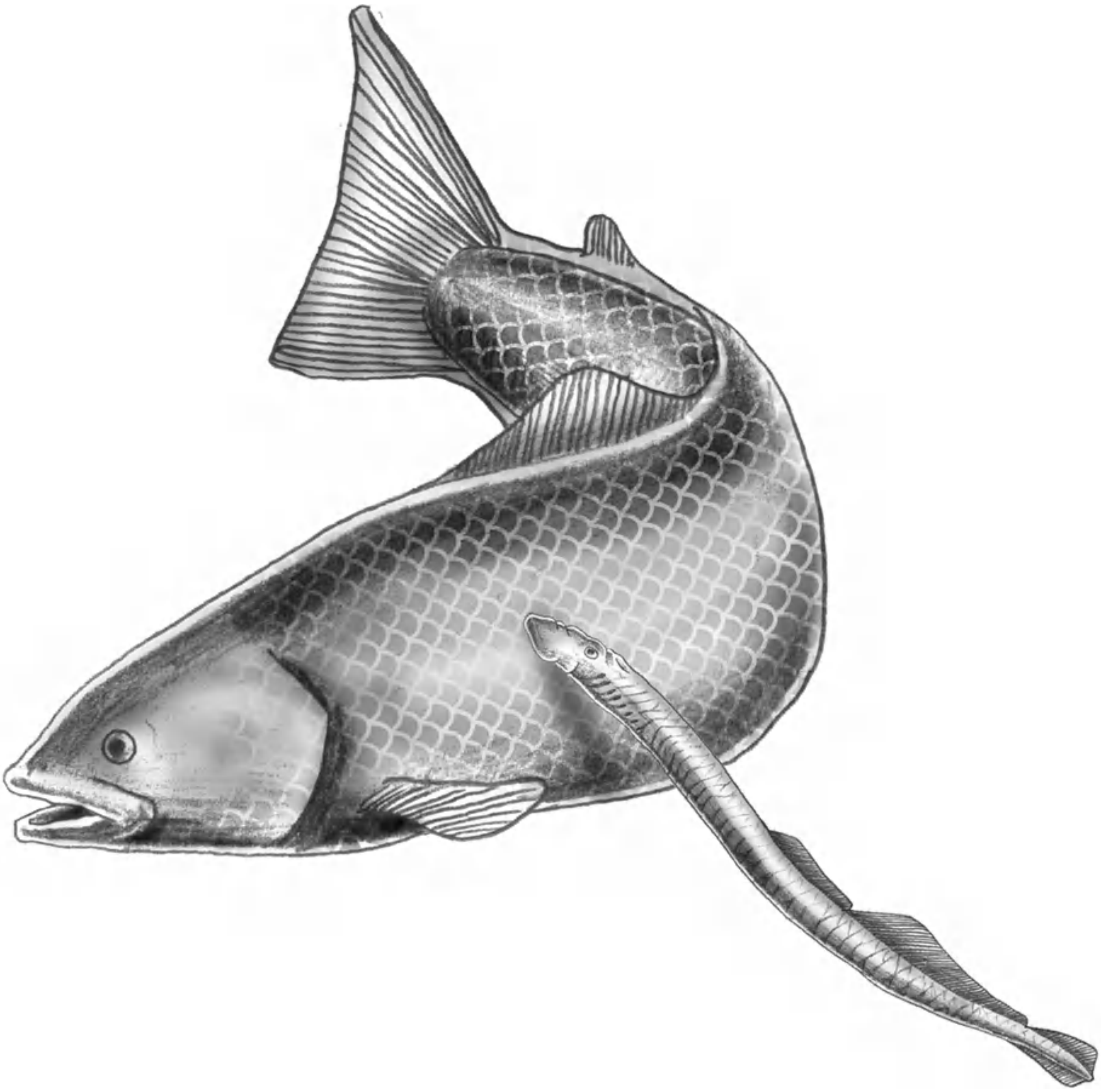


Figure 3.13. Sea lampreys are parasites that attach themselves to the body of fish like lake trout and salmon. Using their horny teeth, sea lampreys scrape a hole in the skin of their host and suck out its blood and other body fluids. An adult sea lamprey can kill approximately 18 kg (40 lb.) of fish annually.

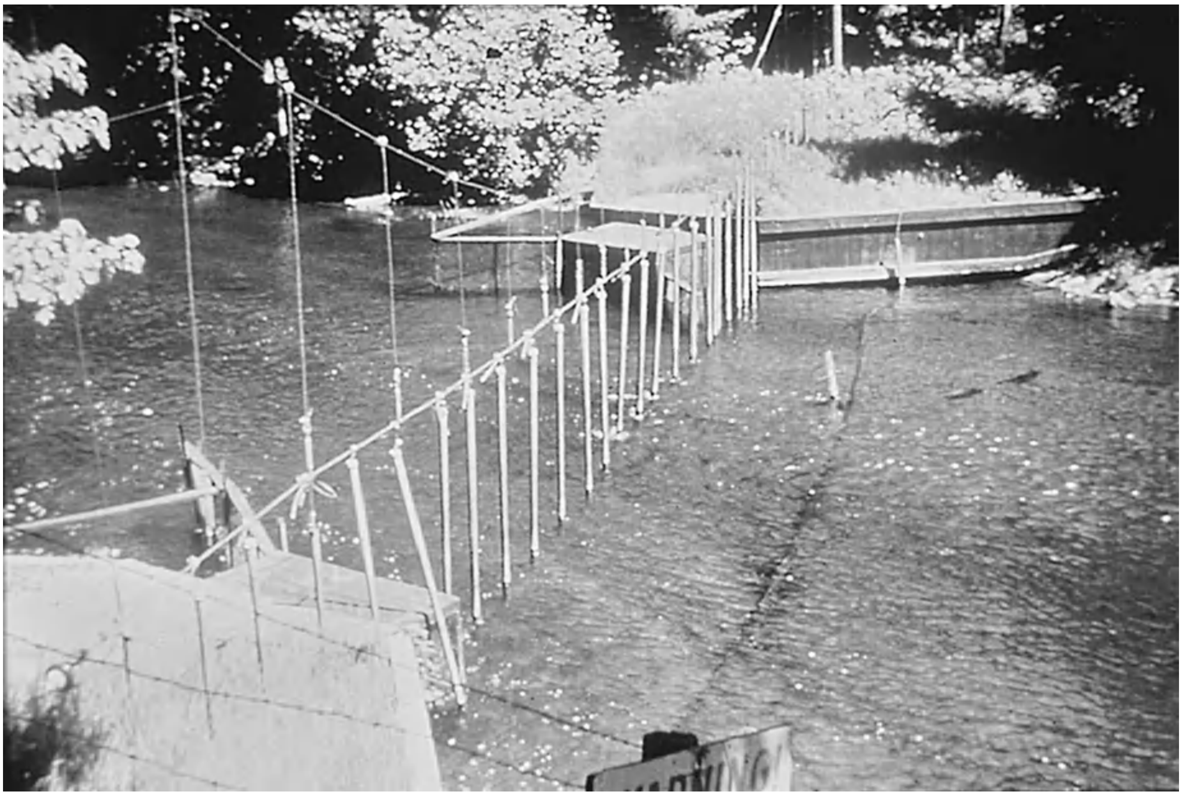
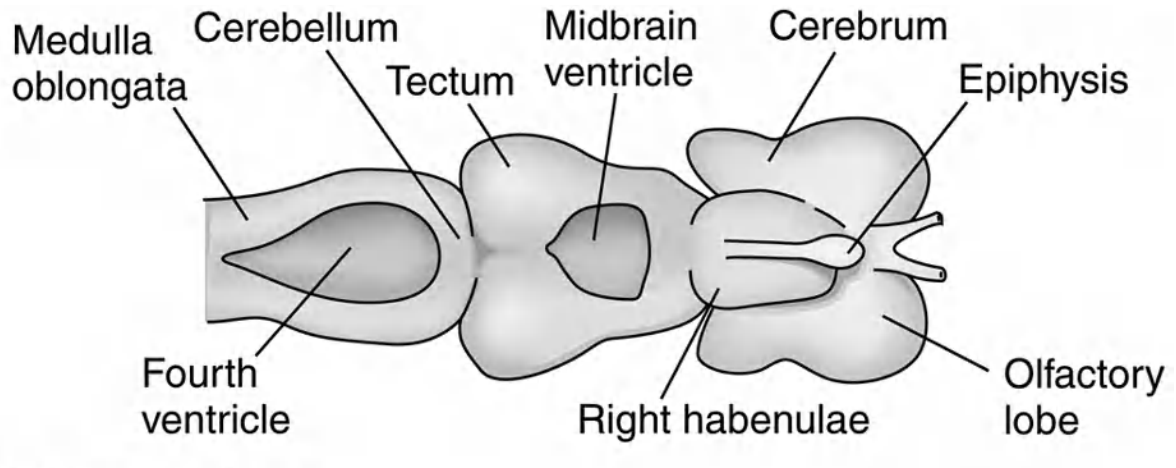
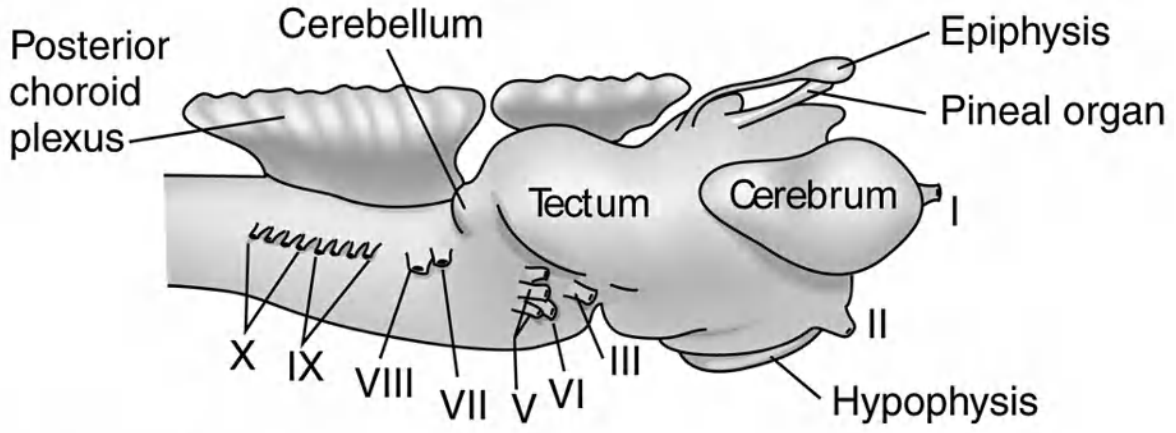


Figure 3.14. Electrical barriers spanning tributary streams of the Great Lakes have proven effective in preventing adult lampreys from entering the streams to spawn.

Hagfishes are usually scavengers and lack oral disks (see Fig. 3.11c). Their feeding apparatus consists of two dental plates, hinged along the midline, each with two curved rows of sharp, horny cusps (see Fig. 3.11b). They feed primarily on small, soft-bodied living invertebrates and also on dead and dying fish, making them important scavengers on the ocean floor. In the Gulf of Maine, Martini (1998) recorded an average of 59,700 *Myxine glutinosa* per square kilometer of seafloor. Although individual hagfishes have extremely low metabolic rates, Martini (1998) calculated that 59,700 animals needed to consume the caloric equivalent of 18.25 metric tons (20 US tons) of shrimp, 11.7 metric tons (12.9 US tons) of sea worms, or 9.9 metric tons (10.9 US tons) of fish every year to maintain themselves at rest. When actively swimming or burrowing, their energy demands increase four-to fivefold. Like lampreys, hagfishes also lack a stomach. Food passes through the pharynx and esophagus into a straight intestine, which opens into the cloaca.



(a) Dorsal view



(b) Lateral view

Figure 3.15. (*a*) Dorsal and (*b*) lateral views of the brain of a lamprey.

Nervous System

Even though the brains of vertebrates have undergone great changes in the course of vertebrate evolution, they are all similar in basic design. The anterior portion of the lamprey brain consists of inconspicuous cerebral hemispheres and rather prominent olfactory bulbs (Fig. 3.15). The pineal organ (epiphysis), a photoreceptor, is absent in hagfishes but is present in lampreys (Wurtman et al., 1968), where it lies just beneath the connective tissue covering most of the brain; it is usually connected to the posterior roof of the brain's diencephalon by a stalk.

A prominent parietal (parapineal) organ is found only in lampreys, where it serves as a photoreceptor. Even though the pineal and parapineal organs are light-sensitive, they do not form images like the lateral eyes. Rather, they monitor the intensity and duration of light. Feduccia and McCrady (1991) suggested that the single median "eye" present in many vertebrates is not homologous because in some the eye corresponds to the parietal body and in others to the pineal body. The cerebellum, which aids in maintaining balance and posture, is not well developed in lampreys and hagfishes. A discussion of the cranial nerves is included in Chapter 4.

The dorsoventrally flattened spinal cord lies dorsal to the notochord and is surrounded by a fibrous neural sheath. Paired spinal nerves arise from the spinal cord. In lampreys, spinal nerves are completely separated into dorsal and ventral portions, a characteristic not found in any other living vertebrate. Grillner (1996) found that the neural controls for the lateral undulatory mode of locomotion utilized by the lamprey were distributed throughout the spinal cord. Axons extend from cells in the brain stem and lead to the specialized motor neurons involved in locomotion. In response to signals from the brain, local networks of cells generate bursts of neural activity. These networks act as specialized circuits, stimulating the neurons on one side of a segment of the lamprey's body while suppressing the neurons on the opposite side. The resultant bursts of muscle activity occur in smooth waves that alternately bend segments of the body from one side to the other.

Sense Organs

The lamprey is the only living jawless fish that has an evident **lateral-line system** (see Fig. 3.12). This system consists of superficial sensory organs, called **neuromasts**, arranged in several noncontinuous lines on the head and around the branchial chambers. Indistinct dorsal, lateral, and ventral portions of the lateral-line system are present on the body behind and above the branchial openings. Hagfish apparently lack a lateral-line system, although canals (without neuromasts) are present in some species.

Lampreys, like most vertebrates, possess two lateral eyes that serve as their primary receptors of light. In hagfishes, however, the rudimentary eyes are light-sensitive. Small light-colored areas often mark the site for the eyes, although no eyeball ever forms.

Olfactory organs are well developed in lampreys and hagfishes. The single, median, dorsal nostril leads into a short nasal tube that ends in a nasohypophyseal sac at the level of the second internal gill slit. In lampreys, the pouch ends blindly, but in hagfishes the pouch connects with the gut. Three pairs of sensory barbels are located around the mouth and nostril of hagfishes.

In most vertebrates, three semicircular canals located in the inner ear provide the organism with its sense of dynamic equilibrium. One end of each canal is enlarged into a swelling, called an **ampulla**, which contains a patch of sensory cells known as **cristae**. Lampreys, however, have only the anterior and posterior semicircular canals, whereas in hagfishes the two semicircular canals are connected in such a manner that they appear as one (Berg, 1940).

Endocrine System

Endocrine organs and their functions in jawless fishes and gnathostomes are discussed in Chapter 4.

Urogenital System

With the exception of hagfishes, whose body fluids have salt concentrations similar to that in seawater (isotonic), all other marine vertebrates maintain salt concentrations in their body fluids at a fraction of the level in the water (hypotonic) (Schmidt-Nielsen, 1997).

Lampreys can live in both seawater and fresh water. In the ocean, they prevent osmotic water loss by having a tough skin, by using salt-excreting cells in their gills to rid themselves of salt absorbed in their gut, and by reabsorbing water in their kidneys. In fresh water, the kidneys excrete large amounts of excess water while retaining essential proteins and salts.

Hagfish embryos possess a primitive kidney known as an archinephros (Fig. 3.16a). It is replaced by a pronephric kidney (Fig. 3.16b), which forms from the anterior portion of the nephrogenic mesoderm and functions as the adult kidney in hagfishes. In lampreys, the anterior portion of the nephrogenic mesoderm forms a pronephric kidney and the posterior portion forms an opisthonephric kidney (Fig. 3.16c). The pronephric kidney consists of segmentally arranged pronephric tubules with ciliated funnels that extend into the peritoneal (or body) cavity and receive materials directly from this cavity. The opisthonephric kidney consists of longer tubules (nephrons) that usually lack peritoneal funnels. Each tubule partially encloses a specialized cluster of capillaries, known as a glomerulus, thereby increasing the efficiency of the filtering process. A pronephros forms as a developmental stage in all vertebrates. It is functional, however, only in larval fishes and amphibians and remains throughout life only in lampreys, hagfishes, and a few teleosts. Even then, it functions as an adult kidney only in hagfishes; in all other vertebrates, it ceases to function as a kidney and becomes a mass of lymphoid tissue. An opisthonephros serves as the functional kidney of adult lampreys, as well as fishes and amphibians.

Hagfishes and lampreys possess only a single gonad (ovary or testis). Occasionally, individuals with both an ovary and a testis are found, but only one gonad is functional. There are no oviducts or sperm ducts; thus, eggs and sperm are released directly into the abdominal cavity and pass into the cloaca through an abdominal pore.

Lampreys in the Great Lakes

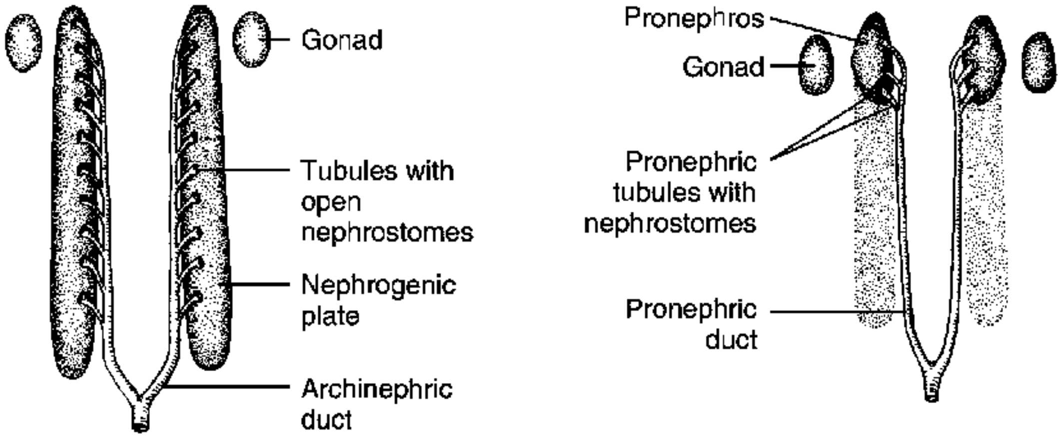
The only natural connection between Lake Ontario and Lake Erie is the Niagara River. Falls and rapids, including Niagara Falls, made the river useless as a commercial waterway and had always served as a barrier to the upstream movement of aquatic organisms. The completion of the Welland Canal by Canada in 1829, however, created a navigable waterway 43 km (26 mi.) long between the two lakes. The canal also provided a means by which the sea lamprey (*Petromyzon marinus*) was able to invade the remaining four Great Lakes. The lamprey was first recorded in Lake Erie about 1921, in Lake Michigan in 1936, in Lake Huron in 1937, and in Lake Superior in 1938. As the sea lamprey invaded each lake, populations of larger fish species like lake whitefish, lake trout, and burbot collapsed, as did the commercial fisheries that depended on them.

Prior to the invasion, about 9 million kg (20 million lb.) of fish were harvested commercially each year in the upper Great Lakes (Superior, Huron, and Michigan). By the 1960s, that amount was reduced to about 136,077 kg (300,000 lb.) per year—about 2 percent of the previous average, while sea lamprey were killing close to 45.4 million kg (100 million lb.) of fish each year, and 85 percent of the remaining fish were scarred with lamprey attack wounds.

Each year, the Great Lakes Fishery Commission traps 50,000 to 100,000 lampreys—sterilizing and releasing the males and killing the females. Intensive research has resulted in the development of a lampricide (poison) that is known as TFM (3-trifluoromethyl-4-nitrophenol) and is specific for the ammocoete larvae in their nursery tributaries. TFM kills larvae before they develop lethal mouths and migrate to the lakes to feed on fish, while most other organisms are unaffected. A second lampricide, Bayluscide, is sometimes combined with TFM to reduce the amount of TFM needed during treatments. Additionally, a granular form of Bayluscide, consisting of Bayluscide-coated grains of sand covered with a time-release coating, is applied to slow-moving or stationary waters where it sinks to the bottom before releasing its payload. This enables control of larvae in areas where TFM cannot be used. As a result of these and other control measures, sea lamprey populations have been reduced and most fish populations are recovering. Since the introduction of TFM as a management tool in 1958, the sea lamprey population in the Great Lakes has been reduced by about 90–95 percent from their peak in the late 1950s and dropped the amount of fish killed by the lamprey to about 4.5 million kg (10 million lb.) a year. Eventually, the species may coadapt to one another and reach an equilibrium so that they can coexist without the need for any control programs.

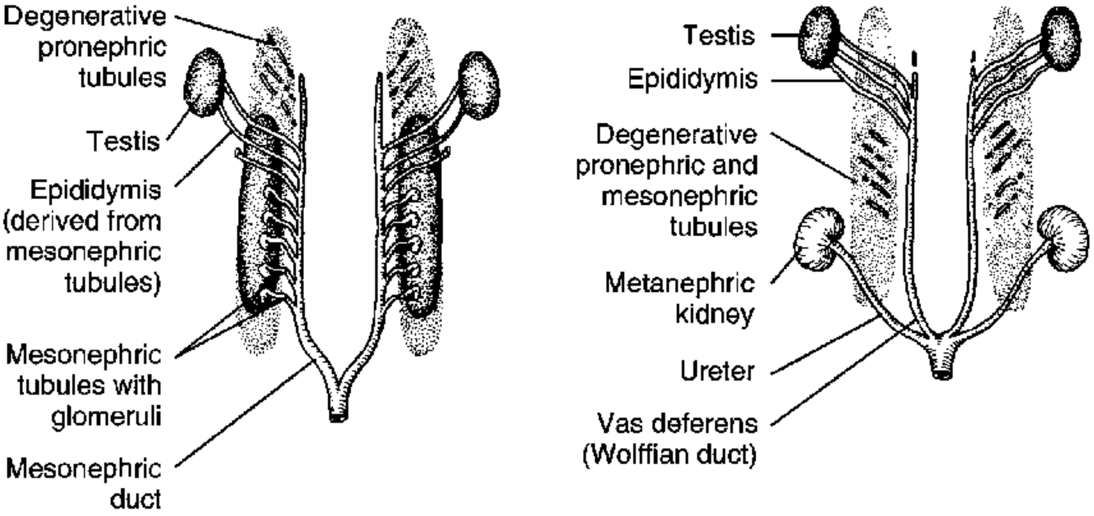
Lampreys spawn in streams draining into the Great Lakes. Electrical barriers are effective in preventing adult lampreys from entering tributary streams to spawn (see Fig. 3.14). Researchers have found that migrating adult lampreys are attracted to particular spawning streams by the smell of two bile acids secreted by larval lampreys in those streams. By using this knowledge, researchers can alter lamprey migration patterns, and lampreys can be more efficiently lured into traps.

Nicholson, 1996; Bunch, 2017; Great Lakes Fishery Commission, 2018, www.glfc.org/control.php



(a) Archinephros: Kidney found in embryo of hagfish; this is the inferred ancestral condition of the vertebrate kidney.

(b) Pronephros: Functional kidney in adult hagfish and embryonic fishes and amphibians; fleeting existence in embryonic reptiles, birds, and mammals



(c) Mesonephros (Opisthonephros): Functional kidney of adult lampreys, fishes, and amphibians; transient function in embryonic reptiles, birds, and mammals

(d) Metanephros: Functional kidney of adult reptiles, birds, and mammals

Figure 3.16. (*a*) Archinephric kidney found in hagfish embryos. (*b*) The pronephros is the functional kidney found in adult hagfishes and embryonic fishes and amphibians. It is present only for a short time in embryonic reptiles, birds, and mammals. (*c*) The functional kidney of adult lampreys, fishes, and amphibians is the mesonephros (opisthonephros). It functions for only a short time in embryonic reptiles, birds, and mammals. (*d*) Metanephric kidney of adult reptiles, birds, and mammals.

REPRODUCTION

Little is known about hagfish reproduction. There is no information about when breeding occurs or how the eggs are fertilized. Few fertilized eggs have ever been found (Martini, 1998). It is known that female hagfishes produce between 20 and 30 large, yolky eggs, which possess hooked filaments by which they can be attached to the sea bottom and to each other (Fig. 3.17).

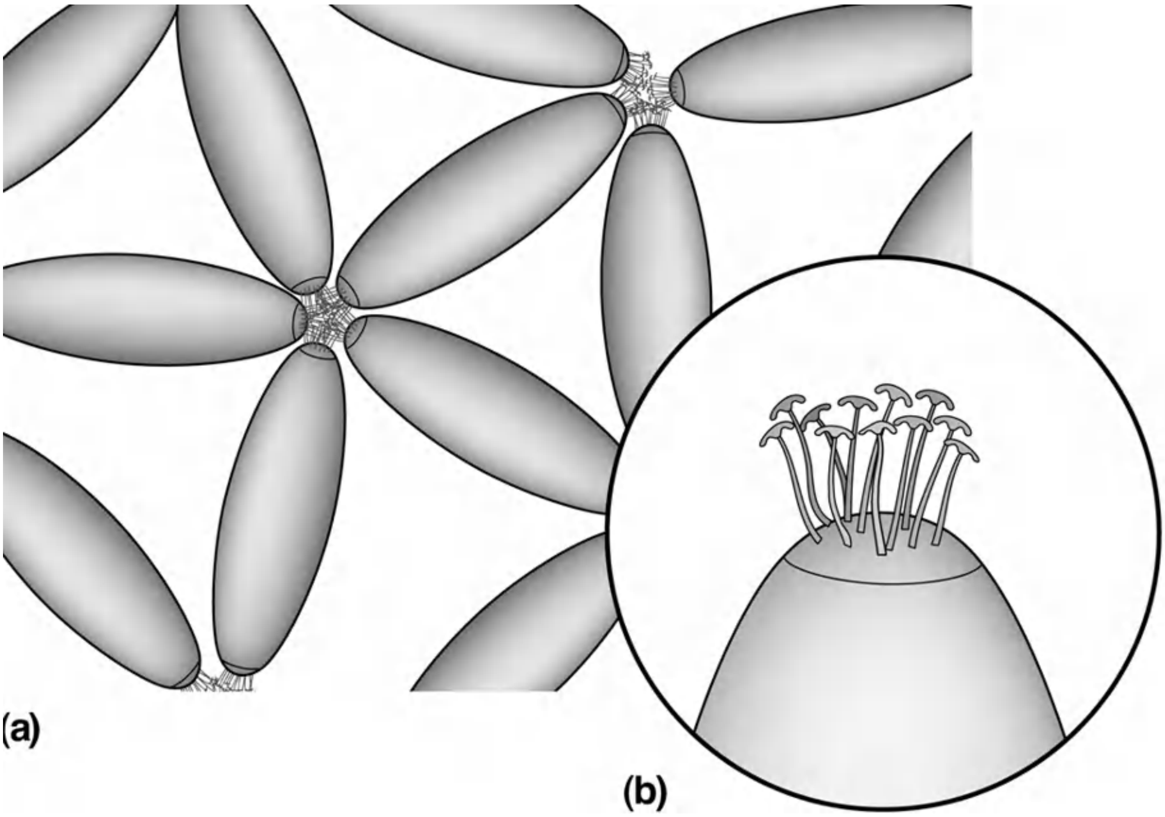


Figure 3.17. (*a*) Cluster of eggs of the hagfish (Myxinidae) connected by the interlocking of their anchor-shaped filaments (*b*).

Adult lampreys may live in either salt water or fresh water, but all species spawn only in fresh water, indicating that this group evolved in fresh water and secondarily invaded marine environments. Both eggs and sperm are shed directly into the body cavity and exit through one or more abdominal pores. Female parasitic sea lampreys (*Petromyzon marinus*) may deposit as many as 260,000 eggs, whereas most nonpredatory female lampreys produce only 1,000 to 2,000 eggs (Barton, 2007). Most lampreys spawn in shallow, gravel-bottomed streams in late winter or early spring. Following their release from the female, eggs require approximately two weeks to hatch.

Cleavage in the large, yolky egg of hagfishes is termed **meroblastic** because only a portion of the cytoplasm is cleaved (divided). Cleavage is **holoblastic** in the sparsely yolked egg of lampreys, in which the mitotic cleavage furrows pass through the entire egg.

GROWTH AND DEVELOPMENT

Young hagfishes hatch as small, fully formed hagfishes. Since no larval hagfishes have ever been found, it is presumed that development is direct and without metamorphosis. Details of their life history (e.g., life span, age at reproduction, breeding sites, juvenile habitat) are unknown.

After hatching, lampreys undergo an extended larval period, during which they are known as **ammocoetes**. The blind, toothless ammocoete larvae (see Fig. 1.3c) drift with the current until they come to an area of quiet water with a muddy bottom. They burrow into the mud until only the oral hood is left exposed and feed by straining microorganisms and organic detritus from the water. Larval development may last from three to seven years, depending on the species (Hardisty and Potter, 1971). Those species that are parasitic generally have a shorter larval life and longer adult life than nonparasitic species. Following metamorphosis, some will migrate to the ocean, and others will migrate to large bodies of fresh water. The adult stage generally lasts from five to six months in nonparasitic species and up to two years in parasitic species. Lampreys die after breeding once. Some nonparasitic lampreys live as larvae for seven years and then metamorphose into nonfeeding adults. The adults live for a few weeks, reproduce, and die.

Adult hagfishes are generally less than 1 m (3 ft.) in total length. Parasitic marine lampreys attain a larger adult size, 30 to 80 cm (12–31 in.), than parasitic species living in fresh water, which are usually less than 30 cm (12 in.). Adults of both freshwater and marine parasitic forms are larger than adults of nonparasitic forms, usually less than 20 cm (8 in.).

Review Questions and Topics

1. Do you feel that calcichordates and conodonts should be classified as vertebrates? Explain.
2. What characteristics do lampreys and hagfishes have in common?
3. Compare and contrast the digestive systems of hagfishes and lampreys.
4. Explain (or attempt to explain) why lampreys spawn in freshwater environments but may live their adult lives in marine environments.

Supplemental Reading

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Garcia-Fernàndez, J., and E. B. Gutiérrez. 2009. It's a long way from amphioxus: Descendants of the earliest chordate. *BioEssays* 31(6):665–675.

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Gee, H. 2018. *Across the Bridge: Understanding the Origin of the Vertebrates*. Chicago: University of Chicago Press.

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Martini, F. H. 1998. Secrets of the slime hag. *Scientific American* 279(4):70–75.

Northcutt, R. G. 1996. The agnathan ark: The origin of craniate brains. *Brain, Behavior, and Evolution* 48:237.

Svingen, T., and P. Koopman. 2007. Involvement of homeobox genes in mammalian sexual development. *Sexual Development* 1:12–23.

Zeller, R., and J. Deschamps. 2002. Developmental biology: First come, first served. *Nature* 420:138–139.

Zimmer, C. 2000. In search of vertebrate origins: Beyond brain and bone. *Science* 287:1576–1579.

Vertebrate Internet Sites

1. Introduction to the Cephalochordata

   www.ucmp.berkeley.edu/chordata/cephalo.html

   Introduction, description, phylum characteristics, paleontology, drawing, and photograph.

2. Amphioxus

   www.britannica.com/animal/amphioxus

   Classification, natural history, and anatomy.

3. Conodonts

   www.ucl.ac.uk/GeolSci/micropal/conodont.html

Introduction, history of study, range, classification, lifecycle, observation techniques, and images.

4. Hyperotreti (Hagfishes)

   www.tolweb.org/Hyperotreti

   Arizona's Tree of Life Web Project. An introduction, pictures, characteristics, discussion of the skull, phylogenetic relationships, and references on hagfishes.

5. Hyperoartia (Lampreys)

   www.tolweb.org/Hyperoartia

   Arizona's Tree of Life Web Project. An introduction, pictures, characteristics, discussion of the skull, phylogenetic relationships, and references on lampreys.

6. Introduction to the Myxini

   www.ucmp.berkeley.edu/vertebrates/basalfish/myxini.html

   University of California at Berkeley, Museum of Paleontology. Images, photos, systematics, life history, and links.

7. Hagfish

   www.aquaticcommunity.com/mix/hagfish.php

   Taxonomy, geographical distribution, habitat, description and characteristics, sliming and knotting, ecology, predators, evolutionary history, importance in research, reproduction, commercial importance and conservational concerns, and web links.

4 | Gnathostome Fishes

> It is a curious situation that the sea, from which life first arose, should now be threatened by the activities of one form of that life.
>
> Rachel Carson, 1951

INTRODUCTION

The two groups of living gnathostome (jawed) fishes are the Chondrichthyes, or cartilaginous fishes (sharks, skates, rays, and ratfishes), and the Osteichthyes, or bony fishes (Fig. 4.1). Both groups may have evolved in separate but parallel fashion from placoderm ancestors and are the survivors of hundreds of millions of years of evolution from more ancient forms. Fishes are the most diverse group of vertebrates with approximately 31,931 species of bony and cartilaginous fishes extant in the world today (Nelson, 2016).

EVOLUTION

The evolution of the major groups of hagfishes, lampreys, and gnathostome fishes, and their relationships to each other, to the amphibians, and to amniotes, are shown in Fig. 3.7. In Fig. 3.8 is presented a cladogram showing probable relationships among the major groups of fishes. Because taxonomy is constantly undergoing refinement and change, the relationships depicted in this cladogram, along with others used in this text, are subject to considerable controversy and differences of opinion among researchers (see Supplemental Reading at the end of this chapter).

Evolution of Jaws

The development of hinged jaws from the most anterior pair of primitive pharyngeal arches was one of the most important events in vertebrate evolution. Jaws permitted the capture and ingestion of a much wider array of food than was available to the jawless ostracoderms, and jaws also permitted the development of predatory lifestyles. Fish with jaws could selectively capture more food and occupy more niches than ostracoderms and, thus, were more likely to survive and leave offspring. They could venture into new habitats in search of food, breeding sites, and retreats. Jaws, which also could be used for defensive purposes, could have aided these primitive fish in both intraspecific and interspecific combat. Thus, hinged jaws made possible a revolution in the method of feeding and hence in the entire mode of life of early fishes. The term **gnathostome** includes all of the jawed fishes and the tetrapods.

The discoveries of *Entelognathus primordialis*, a three-dimensionally preserved 419-million-year-old placoderm fish (Zhu et al., 2013), and *Qilinyu rostrata*, a 423-million-year-old placoderm (Zhu et al., 2016), both found at the Xiaoxiang fossil site in Yunnan, China, are helping rewrite the story of vertebrate evolution. The jaws of all bony vertebrates contain three bones: the maxilla and premaxilla of the upper jaw and the dentary of the lower jaw. Prior to these discoveries, scientists knew that placoderms were early jawed animals, but their jaws consisted of unusual bladelike structures that were thought to be only very distantly related to the three-part jaw found in modern bony fishes and land vertebrates, including humans. The bones in placoderm jaws generally sit farther inside the animal’s mouths than do human jawbones, and they do not contribute to the outer structure of the face. The blades, called gnathal plates, looked so peculiar that most scientists thought that the three-part jaw originated in an early bony fish and that placoderms were just a side branch in the vertebrate family tree. However, the jaws of *Entelognathus* and *Qilinyu* both had the three-part jaw of a bony fish. The two fossils form almost perfect intermediates between placoderms and bony fishes. The authors propose that the maxilla, premaxilla, and dentary are homologous to the gnathal plates of placoderms and that all belong to the same dental arcade and that the key jaw elements of bony fishes (and all land vertebrates) evolved from those bony blades of placoderms.

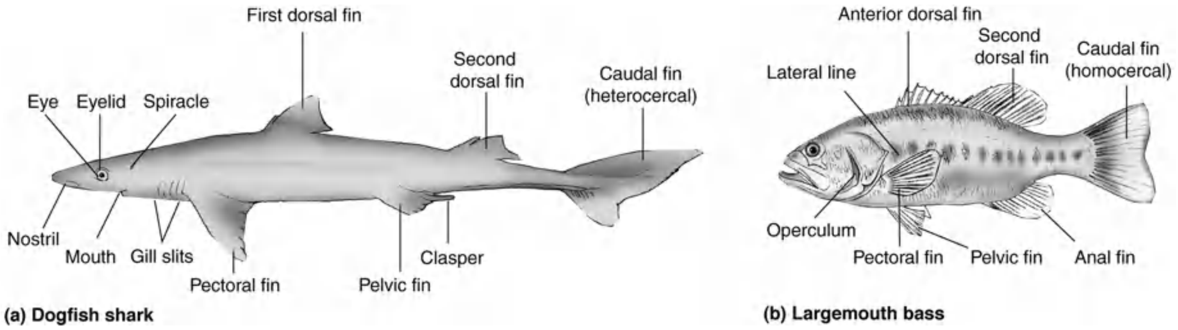


Figure 4.1. External anatomy of (*a*) the dogfish shark (Chondrichthyes) and (*b*) the largemouth bass (Osteichthyes).

Mallatt (1996) reassessed homologies between the oropharyngeal regions of jawless fishes and Chondrichthyes and proposed that jaws originally evolved and enlarged for a ventilatory function—namely, closing the jaws prevented reflux of water through the mouth during forceful expiration. As the jaws enlarged further to participate in feeding, they nearly obliterated the ancestral mouth in front of them, leading to the formation of a new pharyngeal mouth behind the jaws. The secondary function of jaws was to grasp prey in feeding. Thus, Mallatt (1996) proposed the following stages in the evolution of gnathostomes: (1) ancestral vertebrate (with unjointed branchial arches); (2) early pregnathostome (jointed internal arches and stronger ventilation); (3) late pregnathostome (with mouth-closing, ventilatory “jaws”); and (4) early gnathostome (feeding jaws).

Evolution of Paired Fins

A second major development in the evolution of vertebrates was the evolution of paired appendages. As early fishes became more active, they would have experienced instability while in motion. Presumably, just such conditions favored any body projection that resisted roll (rotation around the body axis), pitch (tilting up or down), or yaw (swinging from side to side), and it led to the evolution of the first paired fins (pectoral and pelvic). Force applied by a fin in one direction against the water is opposed by an equal force in the opposite direction. Thus, fins can resist roll if pressed on the water in the direction of the roll; fins projecting horizontally near the anterior end of the body similarly counteract pitch. (Yaw is controlled by vertical fins along the mid-dorsal and mid-ventral lines.) Thus, fins bring stability to a streamlined body. Pectoral fins, which project laterally from the sides of the body, are used for balancing and turning, whereas pelvic fins serve as stabilizers. The associated girdles stabilized the fins, served as sites for muscle attachment, and transmitted propulsive forces to the body.

The origin of paired fins has long been debated and even today remains unresolved. The **Gill Arch Theory** of Gegenbaur (1872, 1876) proposed that posterior gill arches became modified to form pectoral and pelvic girdles and that modified gill rays formed the skeletons of the fins. Pectoral girdles superficially resemble gill arches and are located behind the last gill in some fish, which provided early support for this theory. However, a rearward migration of branchial parts would have been necessary to form the pelvic girdle. There is no embryological or morphological evidence to support this theory.

A second theory, the **Fin Fold Theory**, was originally proposed independently in 1876 by J. K. Thacher and F. M. Balfour. It has been further developed and modified by later investigators, including Goodrich (1930) and Ekman (1941), who provided evidence that the paired fins of sharks develop from a continuous thickening of the ectoderm. This theory suggests that paired fins arose within a paired but continuous set of ventrolateral folds in the body wall. This continuous fold became interrupted at intervals, forming a series of paired appendages. Intermediate fins were lost, and the remaining portions supposedly evolved into pectoral and pelvic fins. Some primitive ostracoderms had such folds, although they were higher on the sides of the body. The primitive shark *Cladoselache* (class Chondrichthyes), whose paired fins are hardly more than lateral folds of the body wall, is cited often as possible evidence of this theory. However, there is no supporting fossil evidence.

The most recent hypothesis is the **Fin Spine Theory**. Spiny sharks (acanthodians) possessed as many as seven pairs of spiny appendages along their trunks (Fig. 4.2). These appendages are thought to have served as stabilizers. In some forms, a fleshy, weblike membrane was attached to each spine (Romer, 1966). All of the spines may have been lost except for two pairs—an anterior pair that would develop into pectoral fins and a posterior pair that would become pelvic fins.

Although paired fins are the phylogenetic source of tetrapod limbs, a definitive explanation for their origin is lacking, and the fossil record provides no clear answer. The possibility exists that paired fins may have originated independently more than once (convergent evolution); if so, more than one of these theories could be accurate.

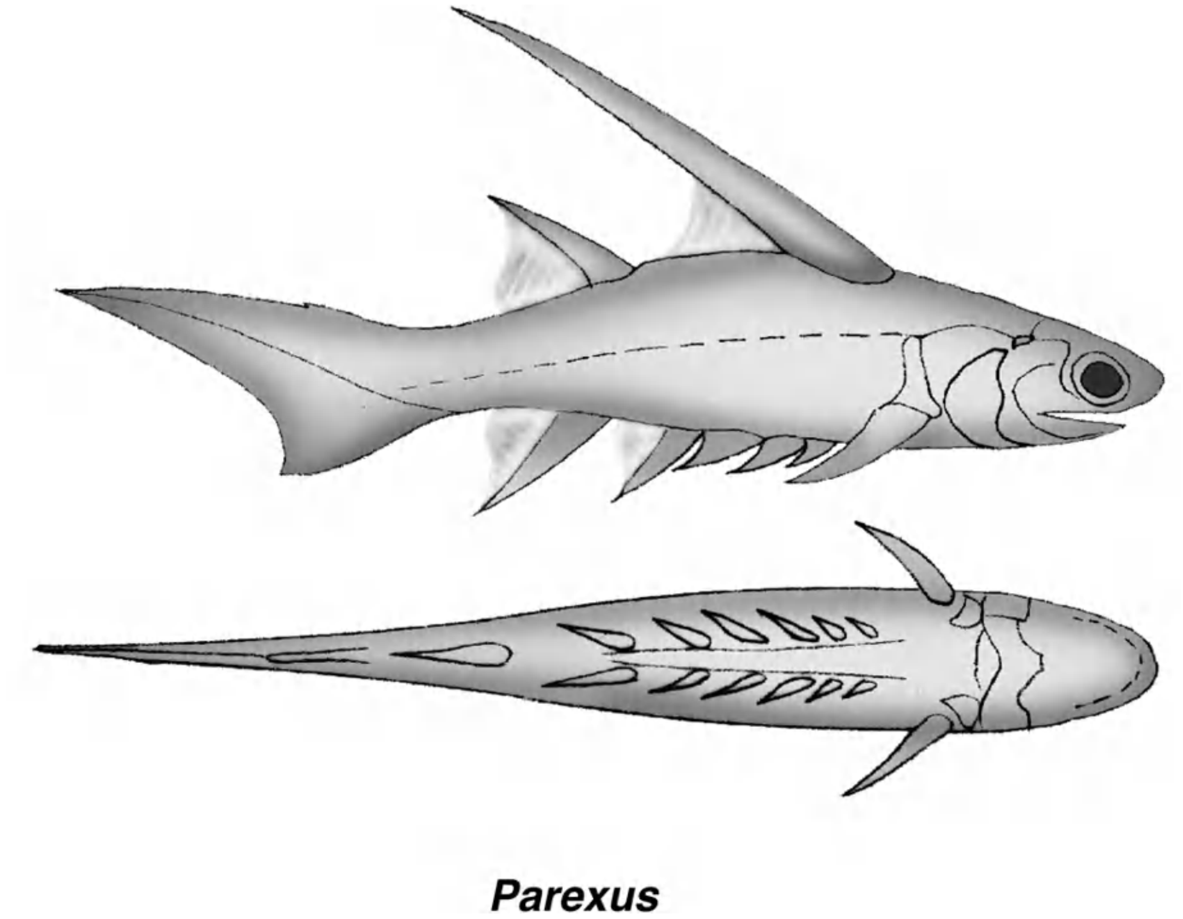
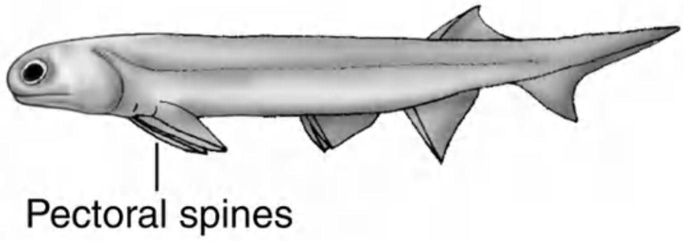
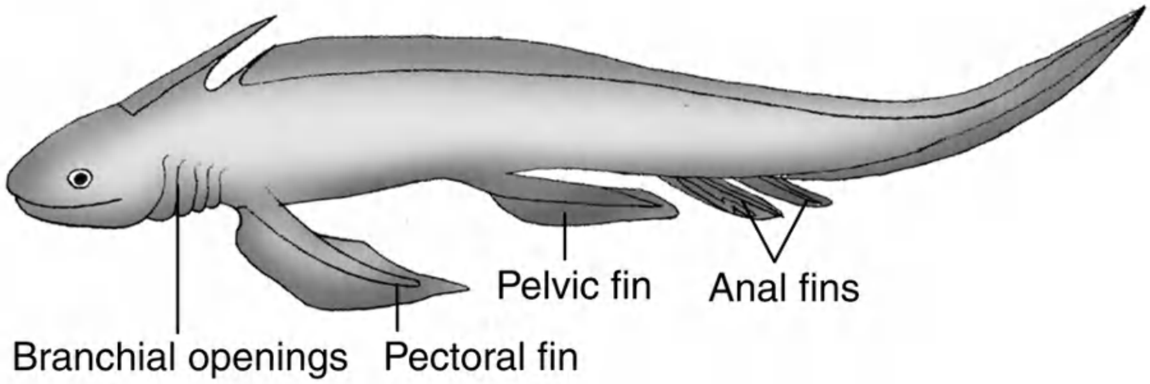


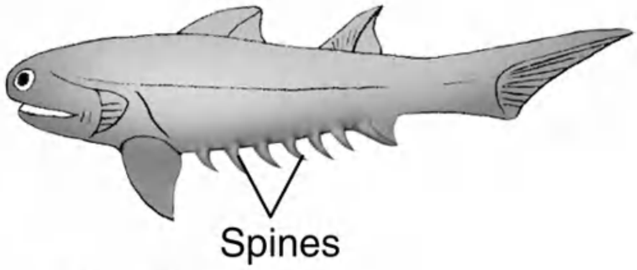
Figure 4.2. *Parexus*, a typical acanthodian genus whose members often had a series of spiny appendages along the trunk. A fleshy, weblike membrane was attached to some of the spines.



(a) ***Acanthodes***



(b) ***Pleuracanthus***



(c) ***Climatius***

Figure 4.3. Representative acanthodians, or spiny sharks, the earliest known jawed vertebrates.

Acanthodians and Placoderms

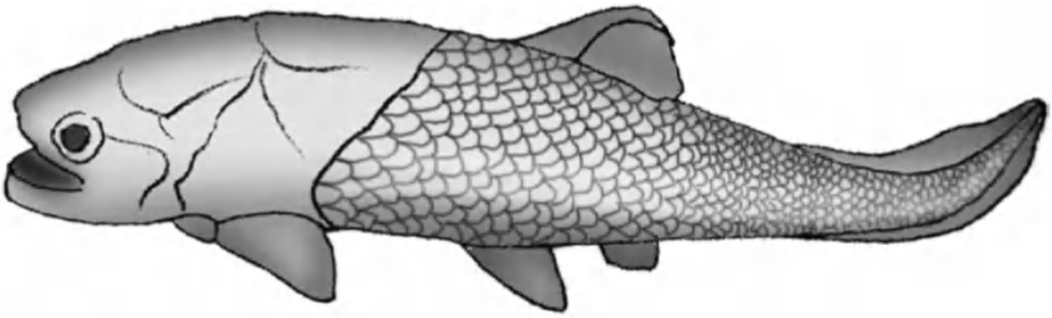
Long before ostracoderms became extinct, the jawed vertebrates (gnathostomes) appeared. The earliest known jawed vertebrates were the spiny sharks, or acanthodians (class Acanthodii), which appeared approximately 440 Mya in the Silurian period (Fig. 4.3). These were mostly small fishes, with the majority of individuals less than 20 cm in length. They had large eyes, small nostrils, an internal skeleton composed partly of bone, and a well-developed lateral-line system. Their bodies were covered with a series of small, flat, bony, diamond-shaped ganoid scales, so called because overlying the basal plate of each scale were layers of a shiny, enamel-like substance known as ganoin. The gill region typically was covered by a flap (operculum), presumably composed of folds of skin reinforced by small dermal scales. A row of ventral paired fins was present along each side of the body of some individuals. All fins, both paired and unpaired (except the caudal fin), had strong and apparently immovable dermal spines at their front edges that are believed to have been highly developed scales. These active, swimming fishes, which were adapted to open water, have sometimes been included with the placoderms in the class Placodermi. Romer (1966) considered acanthodians as an early branch from the unknown ancestral stock from which the Osteichthyes (bony fishes) arose. Moyle and Cech (2004) noted that acanthodians may represent an independent evolutionary line intermediate between Osteichthyes and Chondrichthyes (cartilaginous fishes). Most researchers now regard them either as a separate class of early vertebrates or as a subclass of the class Osteichthyes (Feduccia and McCrady, 1991). Although acanthodians survived into the Lower Permian period, they were never a dominant group and were overshadowed by the placoderms.

Counting Genes in Vertebrates and Invertebrates

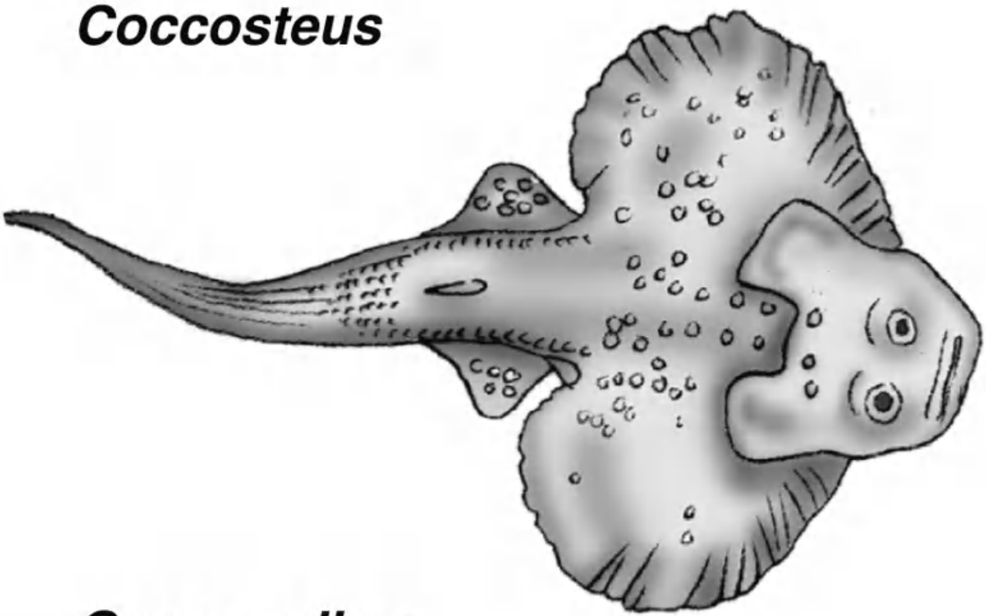
Molecular zoologists have found that all vertebrates have roughly the same number of genes and that all invertebrates have roughly the same number of genes. However, there was a distinct jump in the *total number* of genes from invertebrates to vertebrates. Peter Holland has suggested that a mutation in an animal similar to a lancelet resulted in a doubling of chromosomes and a second copy of all genes. This initial gene doubling occurred more than 500 Mya, just before vertebrates originated. It is hypothesized that the additional genes enabled the hypothetical vertebrate ancestor to evolve entirely new body structures—in particular, a more complex head and brain. There is some evidence that a second genome duplication occurred later and resulted in the appearance of jaws.

Holland, 1992

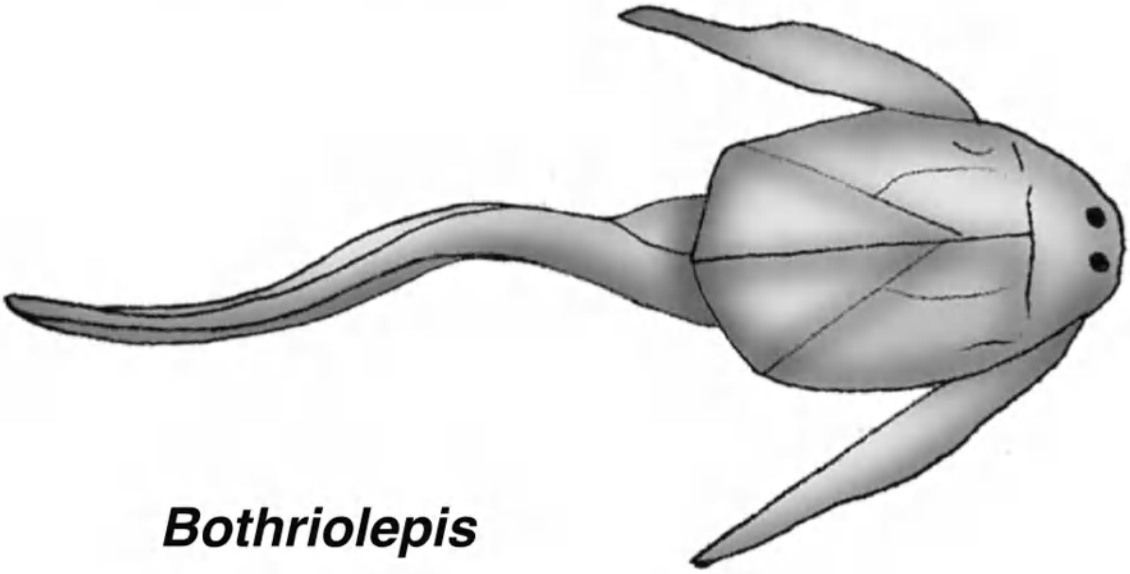
Placoderms (Fig. 4.4), which also possessed jaws and whose bodies were covered with dermal bony plates, became the dominant fishes during most of the Devonian period. In addition, they possessed an internal skeleton of bone and cartilage and sharp dermal armor on the margins of their jaws, which functioned like teeth for seizing, tearing, and crushing a wide variety of food. Fundamental differences in jaw structure and musculature, together with the absence of true teeth, are often thought to indicate that placoderms are the most primitive of the gnathostomes. The dorsoventrally flattened body in many forms suggests they were primarily bottom-dwellers.



Coccosteus



Gemuendina



Bothriolepis

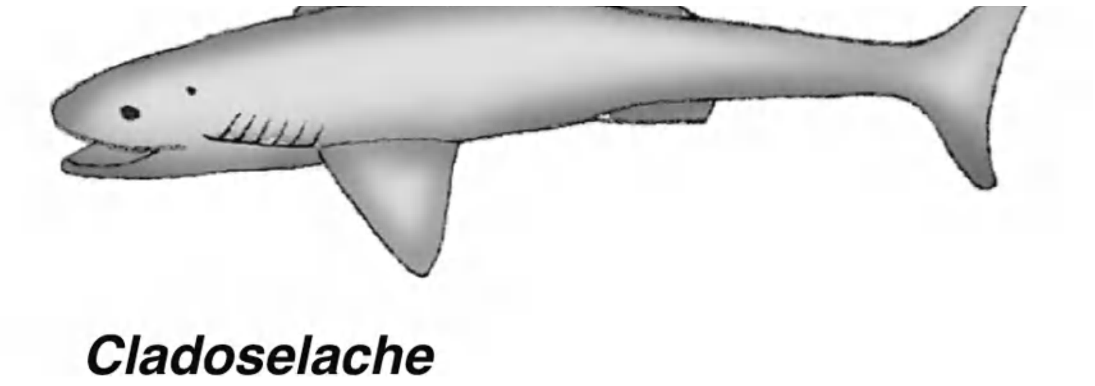


Figure 4.4. Representative placoderms with jaws and paired appendages. Most possessed a dermal armor composed of bony plates that were broken up into small scales on the midbody and tail. Most placoderms were active predators.

The largest group of placoderms, and the most common Devonian vertebrates, were the jointed-necked, armored fishes (arthrodires), which ranged in length from 0.3 to 9.0 m. Their bony armor was arranged in two rigid parts: one covering the head and gill region, and the second enclosing much of the trunk. The latter segment articulated with the anterior shield by ball-and-socket joints. Thus, the head was for the first time freely movable up and down on the trunk, allowing for a wider field of vision, a wider gape, and increased efficiency in securing food.

The oldest record of a live-bearing vertebrate has been documented in a ptyctodontid placoderm, *Materpiscis attenboroughi*, from the Late Devonian Gogo Formation of Australia (approximately 380 Mya) (Long et al., 2008). The fossil contains a single, intrauterine embryo connected by an umbilical cord. Another ptyctodont from the same formation, *Austroptyctodus gardineri*, also shows three small embryos inside it in the same position. These discoveries point to internal fertilization and viviparity in vertebrates as originating earliest within placoderms.

Placoderms were too specialized to be directly intermediate between ostracoderms and modern groups of fishes. Although they dominated the Devonian seas, they were rather abruptly replaced in the Early Carboniferous by the cartilaginous fishes (Chondrichthyes) and the bony fishes (Osteichthyes). Placoderms became extinct in the Mississippian period (approximately 345 Mya) and left no modern living descendants.

Chondrichthyes

The class Chondrichthyes consists of sharks, skates, rays, and chimaeras (Fig. 4.5). These fishes are distinguished by their predominantly cartilaginous skeletons and placoid scales with a posteriorly projecting spine of dentin (see Fig. 4.8). The near absence of bone in the skeleton, except for traces of bone in the placoid scales and teeth, apparently represents a secondary loss, because bone was more extensive in the ostracoderms (largely in the dermis).

Cartilaginous fishes are thought to have arisen from placoderm ancestors. Fossil finds from China indicate the existence of several different jawed fishes in the Silurian, which began approximately 438 Mya (Monastersky, 1996a). These discoveries imply that the first jaws appeared well before that time. The presence of sharks, possible acanthodians, conodonts, and heterostracan-like fish presumably indicates that the major period of diversification within these vertebrates was well under way during the Ordovician period.

Color in Ancient Fishes

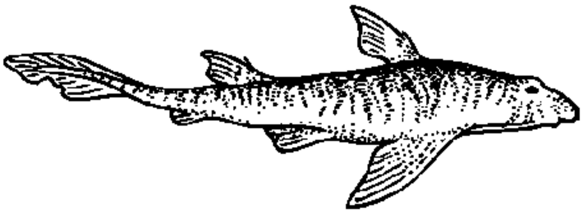
Red and silver pigment cells have been found in a 370-million-year-old placoderm found in the Antarctic. Previously, the oldest known animal pigment cells were from a 50-million-year-old frog found in Messel, Germany. When transparently thin sections of fragments of the fish were prepared, silver iridescence-producing cells were found on the fish's belly and red pigment cells were found on its back. By mapping the cells' distribution, a partial color model of the ancient fish was prepared. The finding of color cells on the fossil fish provides evidence that Devonian animals or their predators may have had color vision.

Parker, 1997

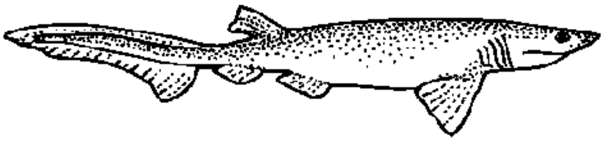
Sharks

Mustelus, Smooth dogfish shark

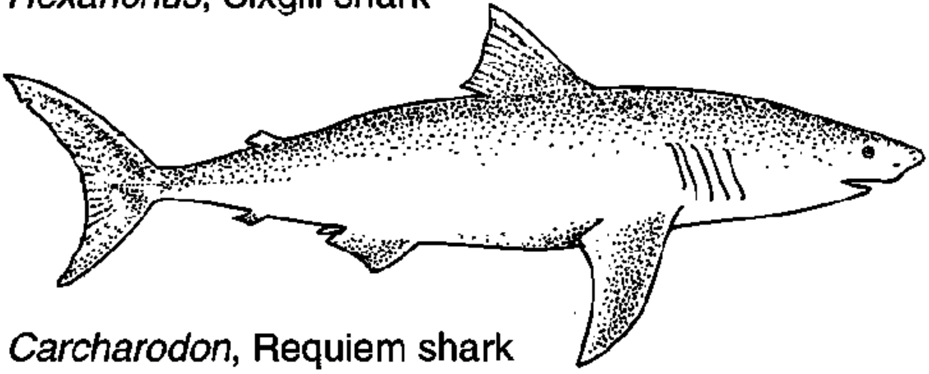
Squalus, Spiny dogfish shark



Heterodontus, Horn shark

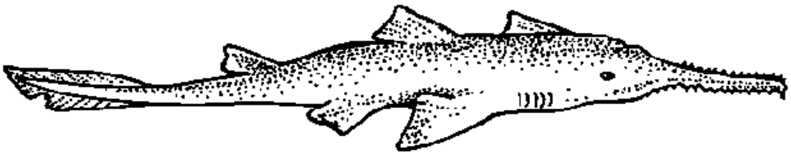


Hexanchus, Sixgill shark

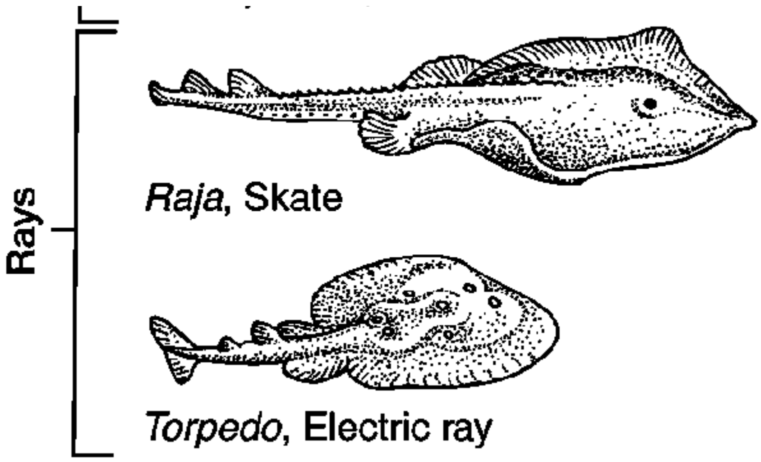


Carcharodon, Requiem shark

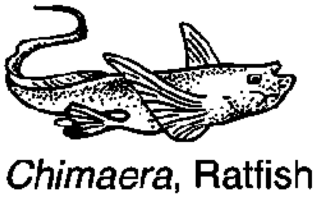
Pristis, Sawfish



Pristiophorus, Saw shark



(a) Elasmobranchs



(b) Holocephalans

Figure 4.5. Representative chondrichthyans: (*a*) elasmobranchs, including sharks, skates, and rays; (*b*) holocephalans.

In spite of a rather good fossil record, the taxonomic relationships of cartilaginous fishes remain unclear. By the Cenozoic era, however, they were present in large numbers and had diversified greatly (see Fig. 4.5). Approximately 970 species, mostly marine, are living today. They comprise two subclasses: Elasmobranchii (sharks, skates, rays) and Holocephali (chimaeras or ratfishes). Male chondrichthyans possess claspers on their pelvic fins, which are specializations associated with the practice of internal fertilization.

Skates and rays (superorder Batoidea) are primarily adapted for bottom-living. Rays make up more than half of all elasmobranchs and include electric rays, sawfishes, stingrays, manta rays, and eagle rays. Skates differ from rays in that skates have a more muscular tail, usually have two dorsal fins and sometimes a caudal fin, and lay eggs rather than giving birth to living young. Skates and rays differ from sharks in having enlarged pectoral fins that attach to the side of the head, no anal fin, horizontal gill openings, and eyes and spiracles located on the top of the head; in sharks, the eyes and spiracles are situated laterally. With the exception of whales, sharks include the largest living marine vertebrates. The whale shark (*Rhincodon typus*), which may attain a length of up to 15 m, is the world's largest fish. Manta rays (*Manta* sp.) and devil rays (*Mobula* sp.) may measure up to 7 m in width from fin tip to fin tip.

The Holocephali contains the chimaeras (ratfishes), which have a long evolutionary history independent of that of the elasmobranchs. They have large heads, long, slender tails, and a gill flap over the gill slits similar to the operculum in bony fishes. In addition to pelvic claspers, males possess a single clasper on their head, which is thought to clench the female during mating.

Osteichthyes

Bony fishes, the largest group of living fishes, have been the dominant form of aquatic vertebrate life for the last 180 million years. Comprising approximately 97 percent of all known species of fishes, they first appear in the fossil record in the Late Silurian period, and they are very closely related to acanthodians. Because most early fossils are from freshwater deposits, it is thought that bony fishes, which possess well-ossified internal skeletons, probably evolved in fresh water.

It is unclear how the common osteichthyan ancestor of actinopterygians and sarcopterygians arose from non-osteichthyan gnathostome ancestors. Zhu et al. (1999) reported a 400-million-year-old sarcopterygian-like fish (*Psarolepis*) from China with an unusual combination of osteichthyan and non-osteichthyan features. Zhu and colleagues feel that this early bony fish provides a morphological link between osteichthyans and non-osteichthyan groups. Whether *Psarolepis* turns out to be a stem-group osteichthyan or a stem-group sarcopterygian, its combination of unique characters will probably have a marked impact on studies of osteichthyan evolution.

Two major groups currently are recognized: lobe-finned fishes (subclass Sarcopterygii) and ray-finned fishes (subclass Actinopterygii) (see Figs. 3.7, 3.8, and 4.6). The subclass Sarcopterygii contains the coelacanths (Fig. 4.6a) and the lungfishes (Fig. 4.6b). These fishes possess muscular, lobed, paired fins supported by internal skeletal elements. Each group is treated separately because recent studies indicate that each is derived from a long independent evolutionary line. The evolutionary histories of lungfishes and coelacanths are of great interest because one or the other is considered by different investigators to be a sister group of all land vertebrates (tetrapods). In addition, the only living coelacanth, *Latimeria*, is the only living animal with a functional intracranial joint (a complete division running through the braincase and separating the nasal organs and eye from the ear and brain) and paired fins that are coordinated, not like most fishes, but in a fashion identical to human limbs.

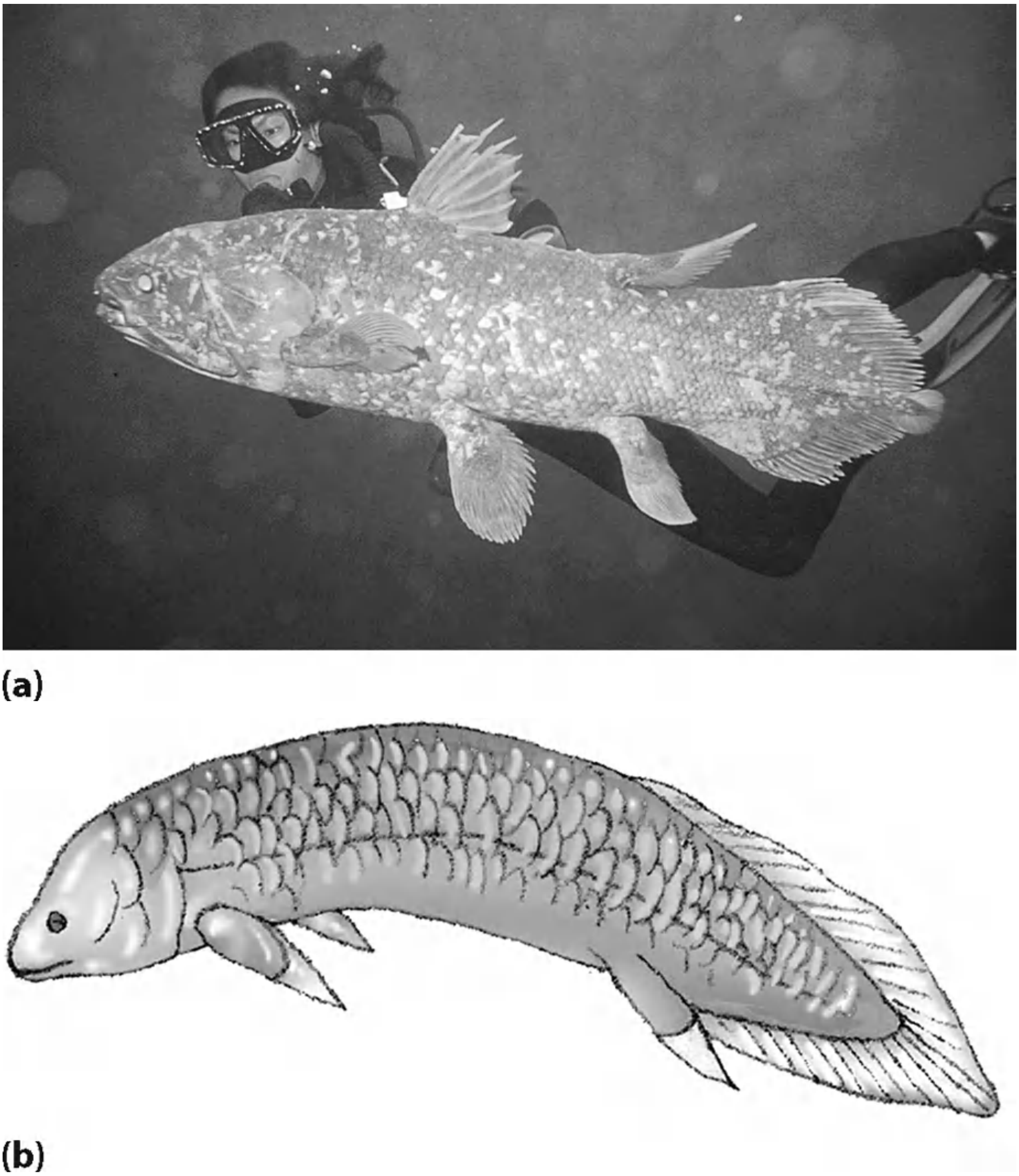


Figure 4.6. Representative sarcopterygians: (*a*) coelacanth; (*b*) lungfish.

The Actinopterygii formerly were classified into three groups: Chondrostei (primitive ray-finned fishes), Holostei (intermediate ray-finned fishes), and Teleostei (advanced ray-finned fishes). Currently, two major divisions of Actinopterygii are recognized: Chondrostei (primitive ray-finned fishes) and Neopterygii (advanced ray-finned fishes).

MORPHOLOGY

Integumentary System

Unlike most other vertebrates, most fishes have an epidermis that consists entirely of living cells. Multicellular glands that produce mucus, various toxic secretions, and other substances are present in most species and are particularly abundant in those fishes that lack scales.

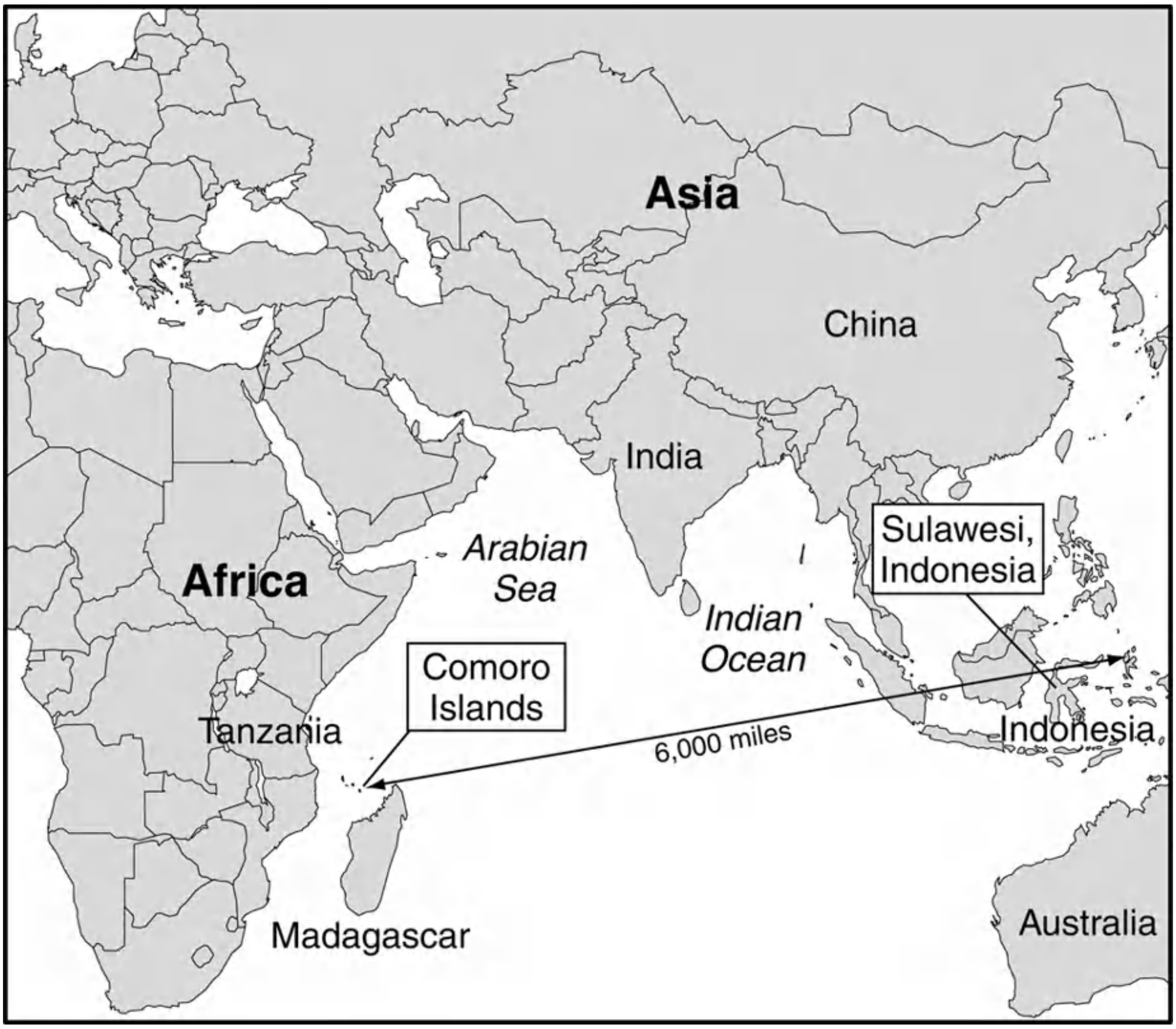


Figure 4.7. The first living coelacanth was taken near the mouth of the Chalumna River, southeast of East London in South Africa's Cape Province. A second population was discovered in Indonesia, 10,000 km (6,000 mi.) east of the Comoro Islands, by Mark Erdmann in 1997.

These glands may be confined to the epidermis, or they may grow into the dermis.

The dermis in most fishes is characterized by the presence of scales composed of bony and fibrous material (Fig. 4.8). Broad plates of dermal bone were present in the earliest known vertebrates, the ostracoderms, or armored fishes, and they were well developed in the extinct placoderms. These large, bony plates have gradually been reduced to smaller bony plates or scales in modern fishes. Five types of scales—cosmoid, placoid, ganoid, cycloid, and ctenoid—occur.

Cosmoid scales are small, thick scales consisting of a dentine-like material, known as cosmine, overlaid by a thin layer of enamel. Although many extinct lobe-finned fishes possessed cosmoid scales, the only living fish having this type of scale is the lobe-finned coelacanth (*Latimeria*).

Placoid scales (see Fig. 4.8a) are characteristic of elasmobranchs and consist of a basal plate embedded in the dermis with a caudally directed spine projecting through the epidermis. Both the plate and spine are composed of dentine, a hard, bonelike substance. Each spine is covered by enamel and contains a central pulp cavity of blood vessels, nerve endings, and lymph channels from the dermis. Modified placoid scales form a variety of structures, including shark teeth, dorsal fin spines, barbs, sawteeth, and some gill rakers.

Ganoid scales (see Fig. 4.8b) are rhomboidal in shape and composed of bone. On the surface of the bone is a hard, shiny, inorganic substance known as ganoin. Today, these scales are found only on bichirs and reedfish (*Polypterus* and *Erpetoichthys*), sturgeons (*Acipenser*), paddlefishes (*Polyodon* and *Psephurus*), and gars (*Lepisosteus*). In gars, these scales fit against each other like bricks on a wall, whereas in sturgeons five rows of scales form ridges of armor along portions of their sides and back.

Cycloid and **ctenoid scales** (see Fig. 4.8c, d) closely resemble one another, and both may occur on the same fish. They consist of an outer layer of bone and a thin inner layer of connective tissue. The bony layer is usually characterized by concentric ridges that represent growth increments during the life of the fish. Ctenoid scales possess comblike or serrated edges along their rear margins, whereas cycloid scales have smooth rear margins. They both are thin and flexible, have their anterior portions embedded in the dermis, and overlap each other like shingles on a roof. Cycloid and ctenoid scales are characteristic of teleost fishes. Together with reduction in heaviness and complexity, these scales allow increased flexibility of the body.

Considerable variation exists in both the abundance and size of fish scales. Most species of North American catfishes (Ictaluridae) are “naked,” or smooth-skinned, whereas the scales of eels are widely separated and buried deep in the skin. Paddlefishes and sculpins have only a few scales. The scales of trout are tiny (more than 110 in the lateral line), and those of mackerels are even smaller.

Coelacanths

Coelacanths constitute a rare order of fish that includes two living species: the West Indian Ocean coelacanth (*Latimeria chalumnae*), primarily found near the Comoro Islands off the east coast of Africa, and the Indonesian coelacanth (*Latimeria menadoensis*) from Indonesia.

Amemiya et al. (2013) sequenced and assembled the first genome sequence of *Latimeria chalumnae*. It was discovered that the coelacanth is more closely related to lungfishes, reptiles, and mammals than to ray-finned fishes. Genome sequencing also revealed that coelacanths are still evolving today at a relatively slow rate, presumably due to the lack of evolutionary pressure. They have few predators and live deep in the ocean where conditions are very stable.

The first living coelacanth (see Fig. 4.6a) was discovered on December 23, 1938, when natives caught one while fishing in deep water off the coast of South Africa in the Indian Ocean. Prior to this time, coelacanths were known only from Mesozoic fossils and were thought to have become extinct some 75 Mya.

The 1938 specimen was taken in a trawling net in water approximately 73 m (239 ft.) deep near the mouth of the Chalumna River. It initially was examined by Marjorie Courtenay-Latimer, the curator of the museum in nearby East London, South Africa. Although she could not make a positive identification, she notified J. L. B. Smith, an ichthyologist, who identified the fish as a coelacanth and named it in honor of the curator and the river.

Since 1938, about 200 coelacanths have been taken in deep waters, 73 to 146 m (239–479 ft.), around the Comoro Islands off the coast of Madagascar, as well as in the waters of Kenya, Tanzania, Mozambique, and in iSimangaliso Wetland Park, KwaZulu-Natal, South Africa. Known coelacanth populations have been monitored for a number of years and show an alarming decline in numbers. A study of underwater caves along 8 km (5 mi.) of coastline off Grande Comore revealed a decline from an average of 20.5 individuals in all underwater caves in 1991 to an average of 6.5 in 1994. A total of 59 coelacanths were counted in 1991, but only 40 in 1994. The total estimated population around the Comoro Islands in 2008 was probably less than 400 individuals. The decline is thought to be due to overfishing by native Comorans, who often get paid by scientists eager to obtain a specimen.

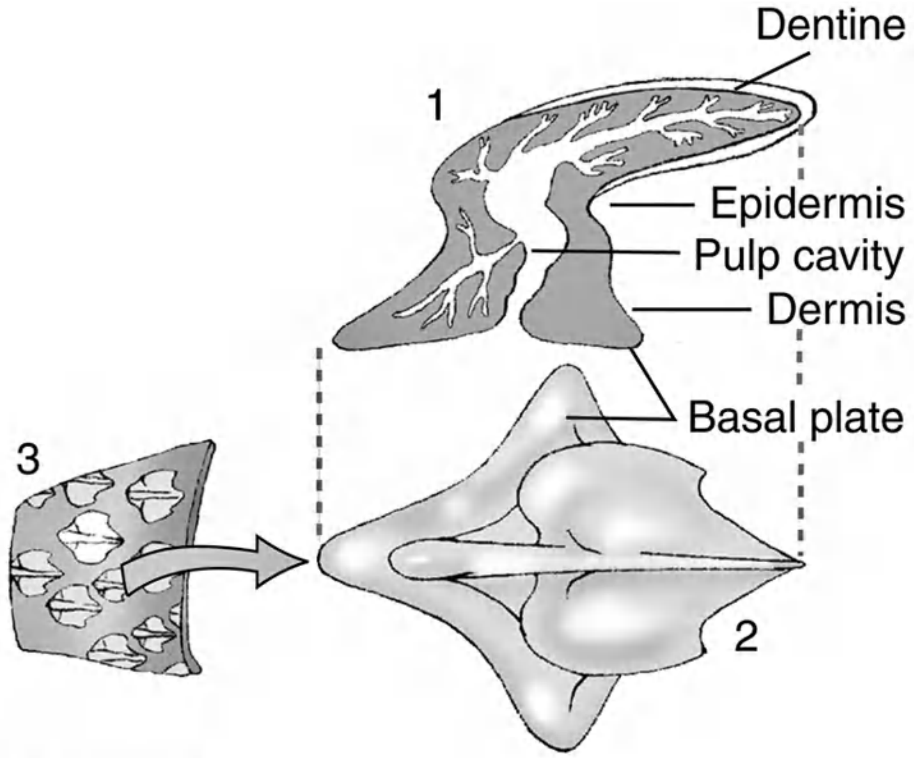
A previously unrecorded population of coelacanths was discovered off the Indonesian island of Manado Tua in North Sulawesi in the Celebes Sea, some 10,000 km (6,200 mi.) east of Africa's Comoran Archipelago, by Mark Erdmann in 1997 (see Fig. 4.7). The Indonesian coelacanth was described as a new species, *Latimeria menadoensis*, by Pouyaud et al. (1999). Molecular analyses concluded that the Comoran and Sulawesi populations diverged 5.5 Mya, and perhaps as long as 16 Mya, but morphological analyses remain inconclusive until additional specimens are examined. Researchers have recorded live sightings in the Sulawesi Sea as well as in the waters of Biak in Papua.

Latimeria chalumnae is listed as critically endangered by the International Union for the Conservation of Nature, while *Latimeria menadoensis* is listed as vulnerable. Trade is banned for *Latimeria chalumnae* under the Convention on International Trade in Endangered Species, and the US National Marine Fisheries Service has recently listed coelacanths as threatened under the Endangered Species Act.

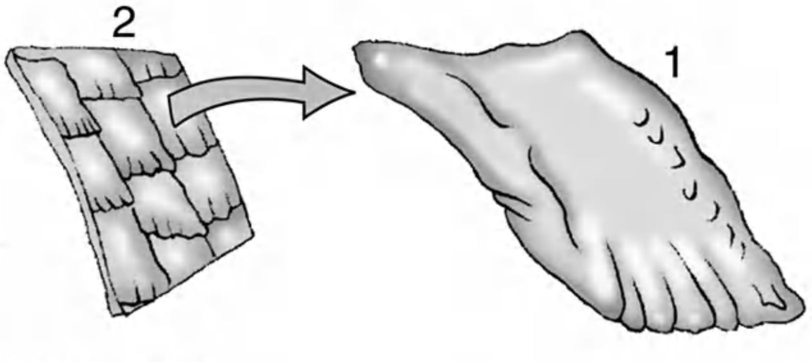
To coordinate and promote conservation efforts, a Coelacanth Conservation Council was formed with branches in Comoros, South Africa, Canada, the United Kingdom, the United States, Japan, and Germany. The Council prints periodic newsletters. In 2002, the African Coelacanth Ecosystem Programme was launched to help further the studies and conservation of the coelacanth. In 2011, a plan for a Tanga Coelacanth Marine Park was designed to conserve marine diversity for marine animals including the coelacanth. The fourth 5-year phase began in 2018.

A website on coelacanths entitled “The Fish Out of Time” can be accessed at www.dinofish.com. Sections include recent history, news, biology and behavior, online videos, and more.

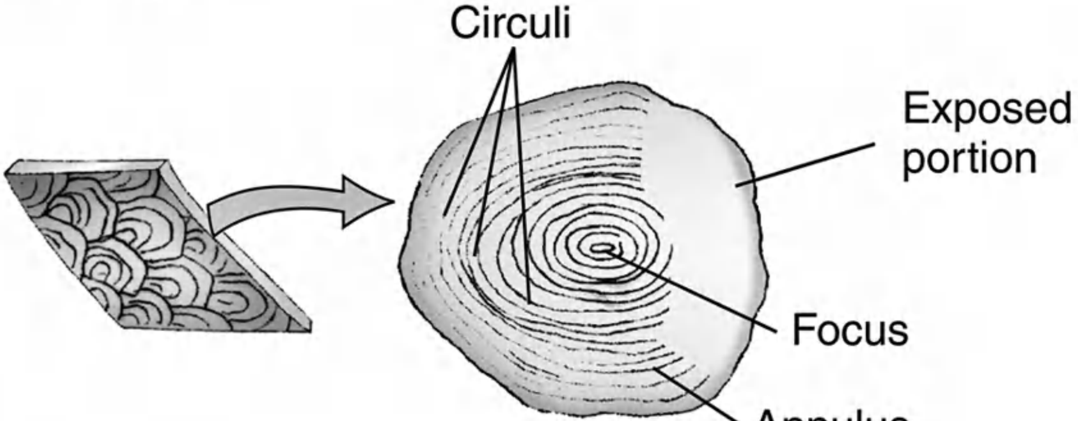
Fricke et al., 1995; Forey, 1998; Erdmann, 1999, 2008; Erdmann et al., 1999; Holder et al., 1999; Pouyard et al., 1999; Fricke, 2001; Anonymous, 2002b; Nulens et al., 2011; Amemiya et al., 2013; Platt, 2015; Syaihailatua, 2015; Insacco et al., 2016



(a) Placoid



(b) Ganoid



(c) Cycloid

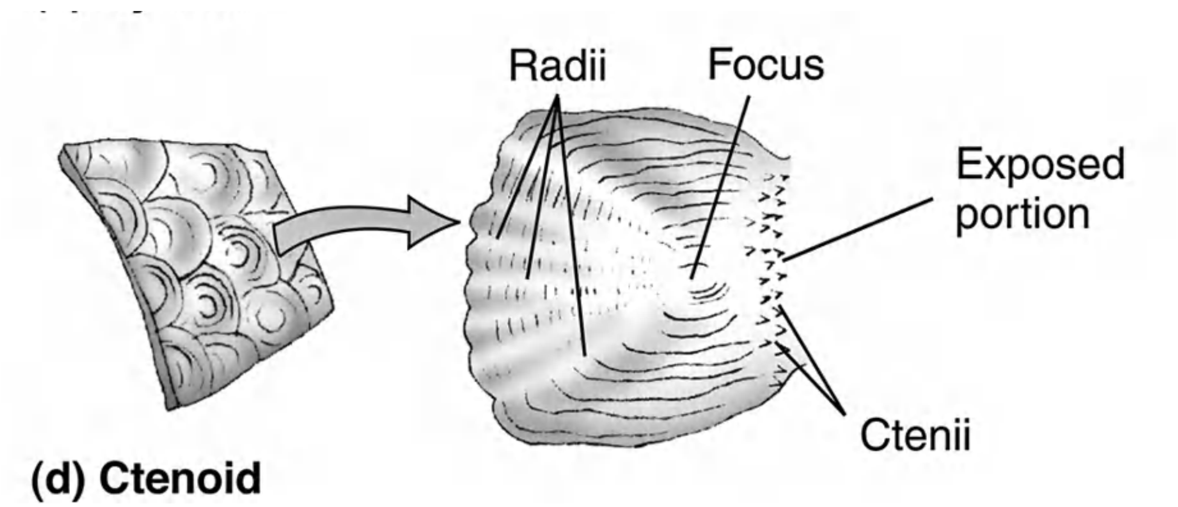


Figure 4.8. Scale types. (*a*) Placoid: 1, sagittal section; 2, dorsal view; 3, normal arrangement on skin, that is, not overlapping. (*b*) Ganoid: 1, single scale; 2, normal arrangement on skin, that is, slightly overlapping. (*c*) Cycloid. (*d*) Ctenoid. Cycloid and ctenoid scales overlap extensively.

Fishes that either lack scales entirely or have a reduced number of scales are typically bottom-dwellers in moving water (like sculpin); fishes that frequently hide in caves, crevices, and other tight places (like many catfishes and eels); or fast-swimming pelagic fishes (like swordfish and some mackerels). The loss of scales increases flexibility and decreases friction. Many ecologically similar fishes that appear to be scaleless, like most tunas and anguillid eels, in fact have a complete covering of deeply embedded scales.

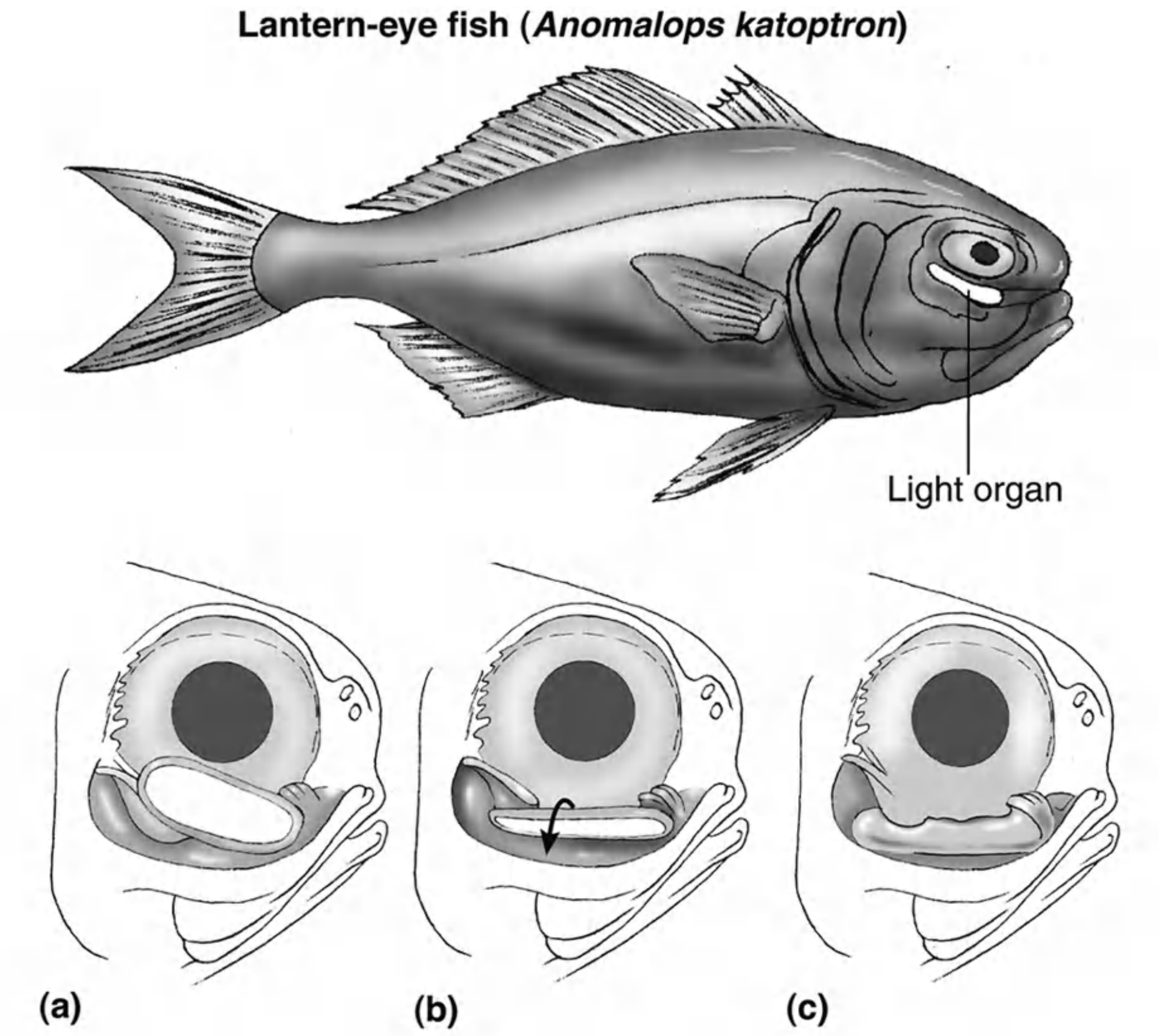


Figure 4.9. The bioluminescent light organ of the lantern-eye fish (*Anomalops katoptron*) is hinged at the front by a muscle (*a*). This muscle is used by the fish to rotate the organ downward into a pouch (*b* and *c*). These fish blink several times per minute.

Coloration is produced by pigment-bearing cells known as **chromatophores**. Many kinds of pigments are found in fishes, but the most common are melanins, carotenoids, and purines. Those chromatophores containing the pigment melanin are known as **melanophores** and produce brown, gray, or black colors. **Lipophores** are the pigment-bearing cells that contain the carotenoids, which are responsible for yellow, orange, and red colors. **Purines** are crystalline substances that reflect light. The most common purine in fishes is guanine, which is contained in special chromatophores known as **iridophores** or guanophores. Iridophores reflect and disperse light and are responsible for iridescence.

Color change is controlled by the nervous and endocrine systems. It involves reflex activities brought about by visual stimulation of the eyes, and/or the pineal body, through hormones like adrenaline and acetylcholine and through the stimulus of light on the skin and/or chromatophores. Color change may be brought about either by a change in the shape of the chromatophores or by a redistribution of the pigment within the chromatophores.

Multicellular epidermal glands of at least 42 families of fishes are modified to function as light-emitting organs known as **photophores** (Fig. 4.9). Most of these families are teleosts (bony fishes); only two families of elasmobranchs (sharks, skates, and rays) are known to be luminous. Most live at depths of 300 to 1,000 m, although many move vertically into surface waters on nightly feeding migrations.

Color Change in Flounders

Flounders (order Pleuronectiformes) are famous for their ability to match their background either to avoid predators or to enhance their ability to capture prey. The initiation of a color change usually comes from visual cues. A flounder with its head on one background and its body on another will have a body color matching that of the background around its head.

In the laboratory, tropical flounders (*Bothus ocellatus*) can transform their markings in less than eight seconds to match even unusual patterns put on the floor of their laboratory tanks. They changed their markings even faster—in as little as two seconds—when exposed to the same pattern for the second or third time. When swimming over sand, flounders look like sand. Above a pattern of polka dots, they develop a pattern of dots. They can even match a checkerboard fairly well when placed on one in the laboratory.

Bothus ocellatus possesses at least six types of skin markings, including *H*-shaped blotches, small dark rings, and small spots. The darkness of these figures is adjusted to blend into the different backgrounds. The neural mechanisms that enable a flounder to alter its spots are still not known, but it is thought that cells in its visual system may respond specifically to shapes in its environment.

Ramachandran et al., 1996

Light in some luminous fishes is produced chemically by the interaction of an enzyme (luciferase) with a phenol (luciferin) (Barton, 2007). In others, including many marine species that live in deeper waters (orders Stomiiformes, Myctophiformes, Batrachoidiformes, Lophiiformes, and others), bioluminescent bacteria reside in specialized glandlike organs (Foran, 1991). Because these bacteria glow continuously, fishes have evolved methods of covering and uncovering the pouches to produce light signals for intraspecific communication, camouflage, and attracting food. Some have evolved a pigmented iris-like shutter to conceal the light; others rotate the light organ into a black-pigmented pocket (see Fig. 4.9).

Lanternfishes (Myctophidae) are small, blunt-headed fishes with large eyes and rows of photophores on the body and head. Photophore patterns are different for each species and also different for the sexes of each species. This sexual dimorphism led some early investigators to describe males and females of the same species as separate species.

Skeletal System

A fish's skeleton is composed of cartilage and/or bone. It provides a foundation for the body and fins, encases and protects the brain and spinal cord, and serves as an attachment site for muscles. The **axial skeleton** of a fish consists of the skull and vertebral column; the **appendicular skeleton** consists of the fin skeleton.

Skull

The skull consists of the chondrocranium, splanchnocranium, and dermatocranium. The **chondrocranium** (neurocranium) surrounds the brain and the special sense organs. It develops from paired cartilages, most of which eventually fuse with one another. The **splanchnocranium** arises from arches of cartilage that develop in association with the pharynx. It develops into the branchial (visceral, pharyngeal) arches that support the gills and make up the skeleton of the jaws and gills in fishes and amphibians that breathe by means of gills. The splanchnocranium may remain cartilaginous or become ensheathed by dermal bones. The **dermatocranium** (Fig. 4.10), which develops in the dermis, is formed of dermal bones that overlie the chondrocranium and splanchnocranium and completes the protective cover of the brain and jaws.

In the Chondrichthyes, the skull consists of a cartilaginous chondrocranium and splanchnocranium. The splanchnocranium in Chondrichthyes includes seven pairs of branchial cartilages and a series of median cartilages in the pharyngeal floor. The first pair of branchial cartilages, called the **mandibular arch**, consists of a dorsal **palatoquadrate (pterygoquadrate) cartilage** and a ventral **Meckel's cartilage** on each side (Fig. 4.11). The upper jaw is formed by the palatoquadrates, and the lower jaw is formed on each side by Meckel's cartilages. The second pair of visceral cartilages, called the **hyoid arch**, consists of several elements, with the most dorsal being known as **hyomandibular** cartilages. Ligaments hold the jaws together and bind them to the hyomandibular cartilages, which suspend the entire splanchnocranium from the skull. The last five pairs of visceral cartilages consist of four segments each (pharyngobranchial, epibranchial, ceratobranchial, and basibranchial) and are similar to one another. Embryological evidence and comparative anatomy studies indicate that jaws evolved from the first gill arch (Feduccia and McCrady, 1991).

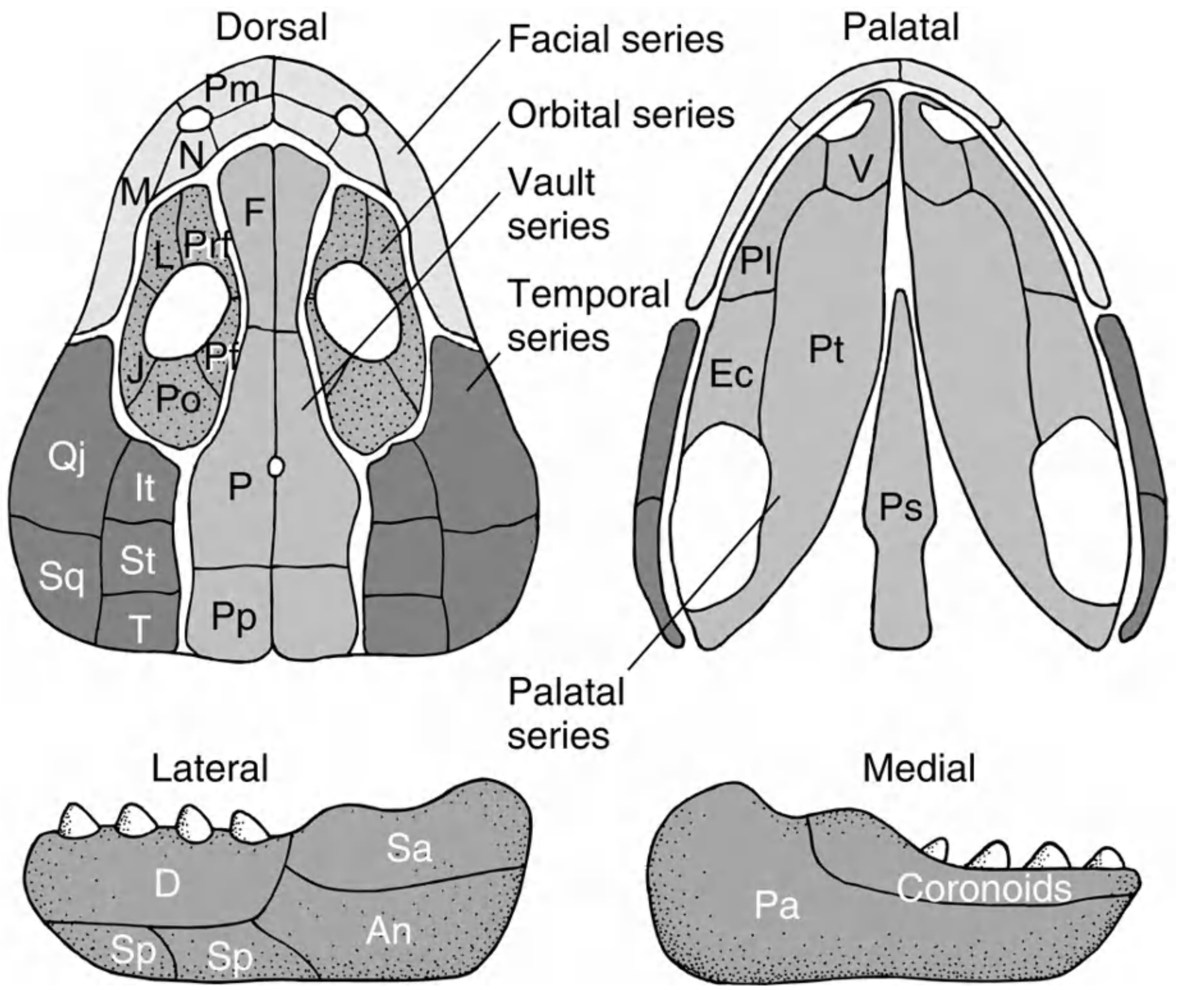


Figure 4.10. Major bones of the dermatocranium. Meckel's cartilage (not shown) is encased by the bones forming the mandible. *Key:* An, angular; D, dentary; Ec, ectopterygoid; F, frontal; It, intertemporal; J, jugal; L, lacrimal; M, maxilla; N, nasal; P, parietal; Pa, prearticular; Pf, postfrontal; Pl, palatine; Pm, premaxilla; Po, postorbital; Pp, postparietal; Prf, prefrontal; Ps, parasphenoid; Pt, pterygoid; Qj, quadratojugal; Sa, surangular; Sp, splenial; Sq, squamosal; St, supratemporal; T, tabular; and V, vomer.

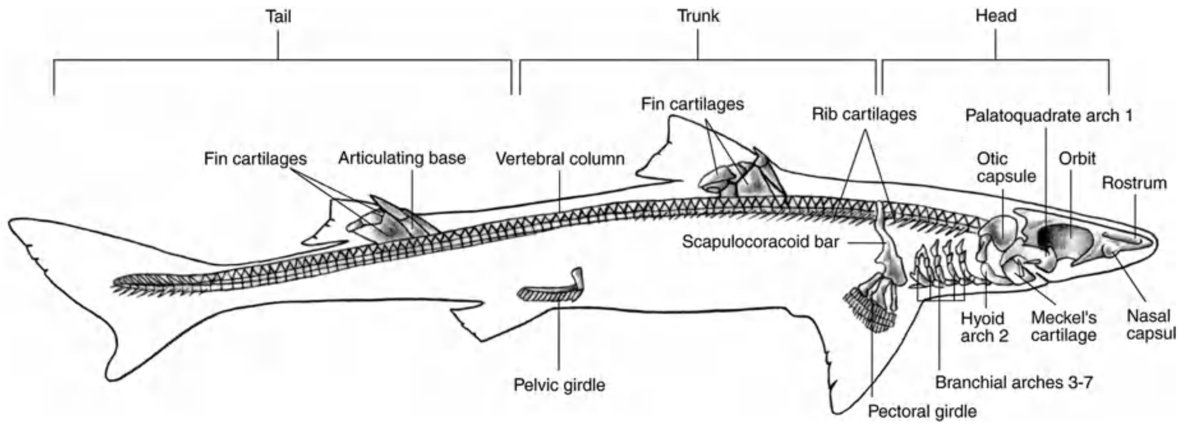


Figure 4.11. Lateral view of the skeleton of a dogfish shark (*Squalus*) with detail of the head and visceral arches.

The skulls of bony fish are compressed laterally. They are cartilaginous initially, but are partly or wholly replaced by bone as development progresses. The only portions of the embryonic palatoquadrate cartilages that contribute to the upper jaws in bony fish are the caudal ends, which become **quadrate bones** (Fig. 4.12); the remainder of the palatoquadrate cartilages are replaced by several bones, including the **premaxillae** and **maxillae**. Teeth are usually present on the premaxillae and maxillae (as well as on many bones forming the palate), but in teleosts, maxillae may be toothless, reduced, or even lost from the upper jaw margin. The posterior tip of Meckel's cartilage ossifies and becomes the **articular bone**; the remainder of Meckel's cartilage becomes ensheathed by dermal bones like the **dentary** and **angular** bones.

Light Organs in Predatory Fishes

Anglerfish have a long "fishing rod" attached to the skull, with a luminous bulbous light lure at the tip that can be wiggled about. Viperfish, on the other hand, have light organs directly inside their mouths to lure prey into a waiting stomach. The most specialized light source, however, may belong to a small predatory fish in the genus *Pachystomias*, which emits a red beam from an organ directly under its eye. Because most fishes cannot see red, this fish can use its beam like a sniperscope, sighting and then moving in on its target without detection.

The hyoid skeleton of bony fishes undergoes extensive ossification and performs key roles in the specialized movements of ingestion and respiration. The **operculum**, which is of dermal origin, extends backward over the gill slits and regulates the flow of water across the gills. Movements of the operculum and hyoid, therefore, must be well coordinated. An operculum is absent in most cartilaginous fishes.

Jaw suspension in fishes is accomplished in three ways (Fig. 4.13). In some sharks, the jaws and hyoid arch are braced directly against the braincase, an arrangement called **amphistylic** suspension. In lungfishes and chimaeras, the hyomandibular cartilage is not involved in bracing the jaws. This “self-bracing” condition, known as **autostylic** suspension, is also utilized by all of the tetrapods. In most of the Chondrichthyes and in some of the bony fishes, the hyomandibular cartilage is braced against the chondrocranium, and the jaws are braced against the hyomandibular cartilage, a condition known as **hyostylic** jaw suspension.

Vertebral Column

The vertebral column in fishes ranges from a column having cartilaginous vertebrae with centra in elasmobranchs (see Fig. 4.11) to one having vertebrae of solid bone in teleosts (see Fig. 4.12). Extending from the skull to the tip of the tail, fish vertebrae are differentiated into **trunk vertebrae** and **caudal** (tail) **vertebrae**. Both ends of the **centra** (body) of a vertebra in most fishes are concave, a condition known as **amphicoelous** (Fig. 4.14). A greatly constricted notochord runs through the center of each centrum and also fills the spaces between adjacent vertebrae.

Fin Skeleton

The pectoral and pelvic girdles together with the skeleton of the paired fins make up the appendicular skeleton of fishes (see Figs. 4.11 and 4.12). Most gnathostome fishes have both pectoral and pelvic fins, although pelvic fins are lost in elongate fishes, like eels, which wriggle along the bottom.

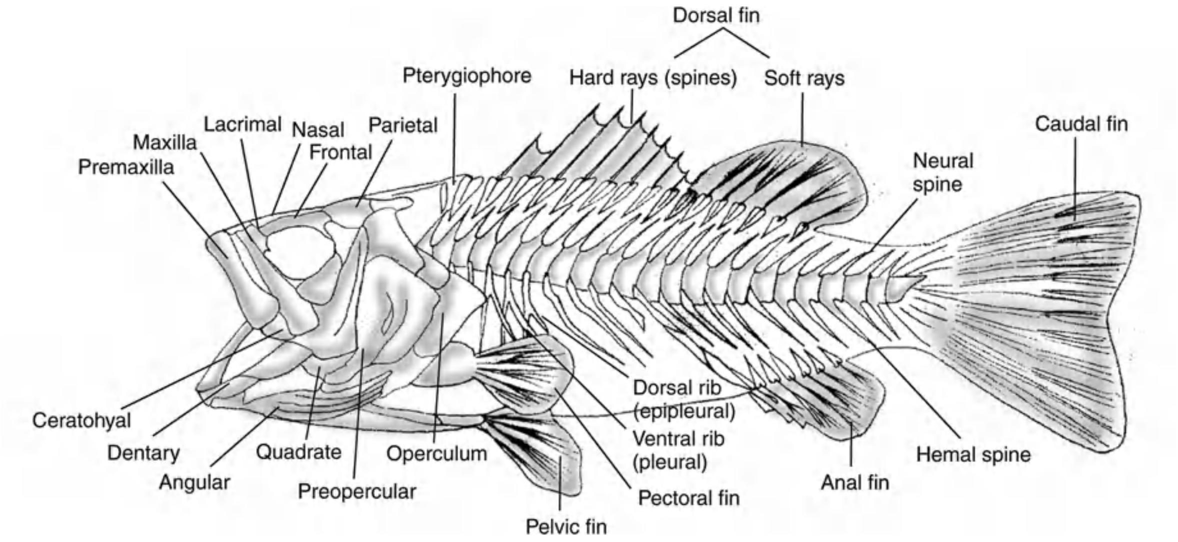


Figure 4.12. Lateral view of the skeleton of a bony fish (Teleostei). Note the position of the paired and unpaired fins and the hyostylic method of jaw suspension.

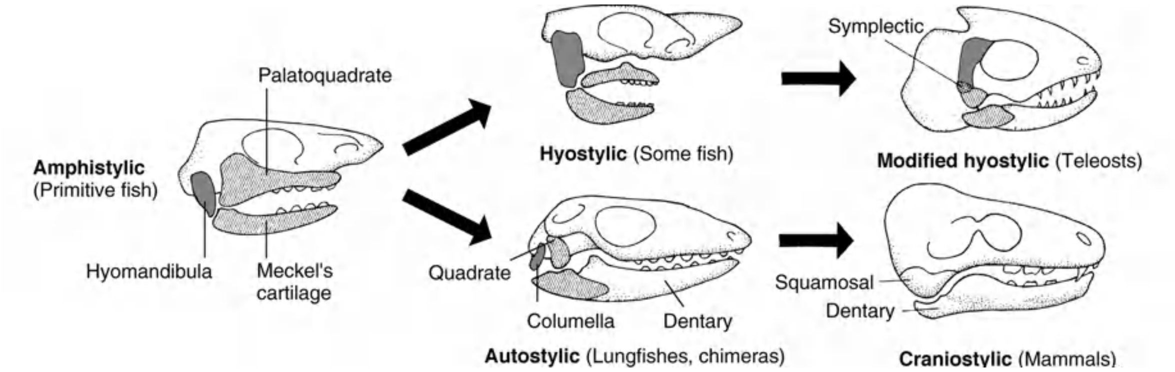
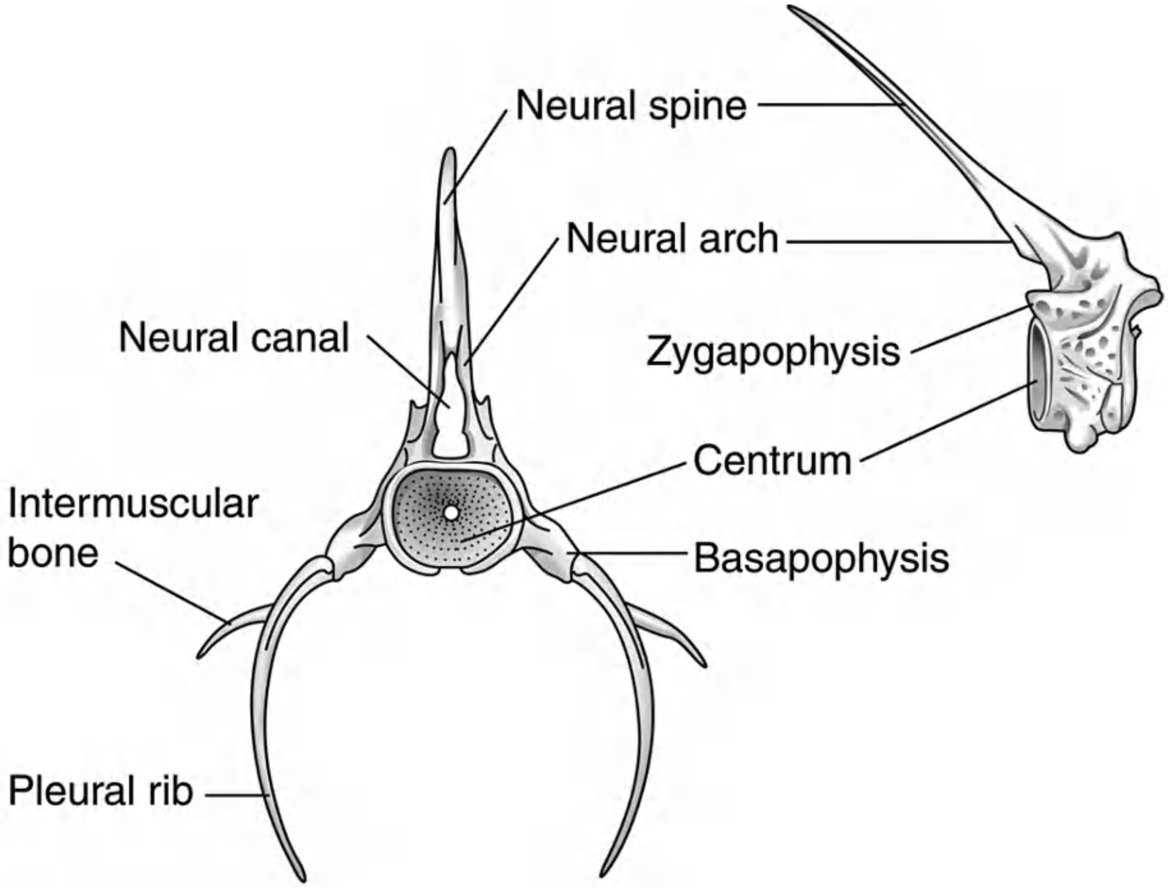


Figure 4.13. Evolution of jaws and jaw suspension. The types of jaw suspension are defined by the points at which the jaws attach to the rest of the skull. Note the mandibular arches (crosshatched areas) and hyoid arches (shaded areas). The dermal bone (white areas) of the lower jaw is the dentary.

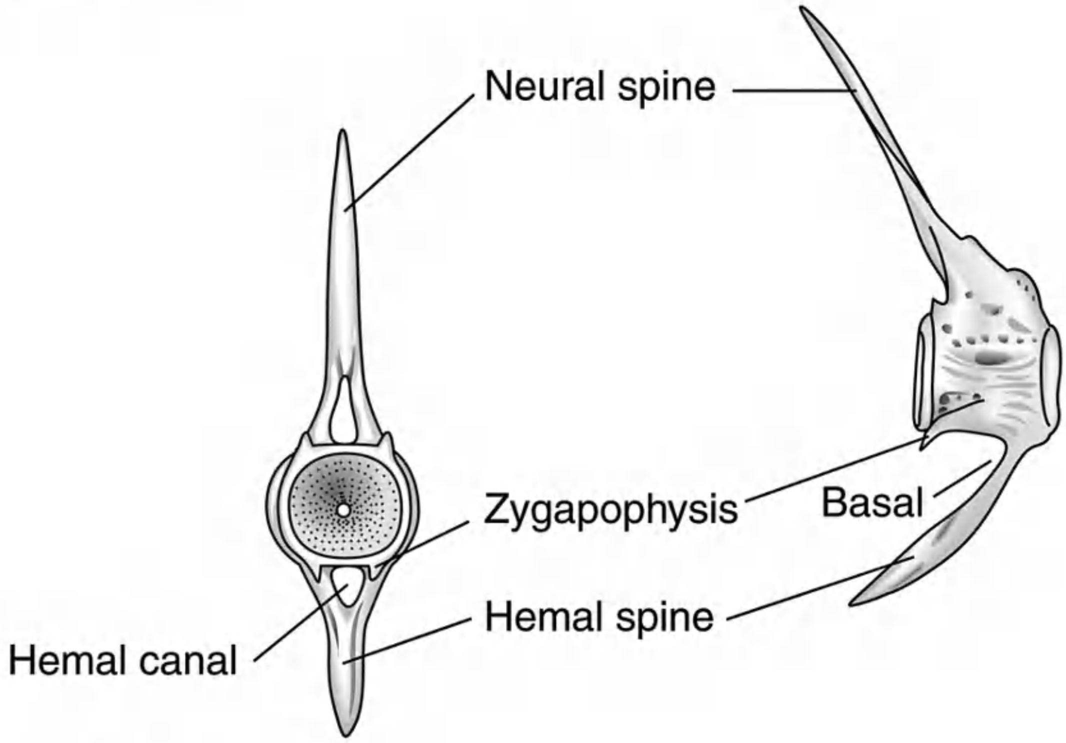
The **pectoral girdle** braces the anterior pair of appendages (pectoral fins) of fishes. Pectoral fins may be located high on the sides of the body, more toward the midline, or below the midline (Fig. 4.15). They may be long and pointed or broader and more rounded. In most fishes, these fins operate not only as stabilizers, but also as "diving planes." They are set at an angle to generate lift for the anterior part of the body and, in some species, are important in thrust generation. In threadfins (Polynemidae) (Fig. 4.15d), the pectoral fins are divided into two parts, with the lower portion consisting of several long filaments that are thought to function as tactile organs. The pectoral fins of batfishes (Ogcocephalidae) (Fig. 4.15f) are located posterior to the pelvic fins. They are used for "walking" over the bottom.

The pelvic girdle braces the posterior pair of appendages (pelvic fins). In sharks and in the more ancestral bony fishes, like salmon, shad, and carp, pelvic fins are located ventrally, toward the rear of the fish; this is called the **abdominal position** (Fig. 4.16a). In more recently evolved teleosts, many of which are deep-bodied, the pelvic fins are more anterior and are located either slightly behind the pectoral fins, in the **subabdominal position** (Fig. 4.16b); below the pectoral fins, in the **thoracic position** (Fig. 4.16c); or even in front of the pectoral fins, in the **jugular position** (Fig. 4.16d). In some teleosts, like eels and eel-like fishes, the pectoral and pelvic fins are frequently absent or greatly reduced in size, whereas in bottom-dwelling fishes, pelvic fins are frequently modified into organs for holding on to the substrate (Figs. 4.16e–g).

Most fishes also have unpaired **median fins** that assist in stabilizing their bodies during swimming (see Figs. 4.11 and 4.12). These include one or two **dorsal fins**, a ventral **anal fin** behind the anus or vent, and a **caudal fin**. Some primitive bony fishes, including salmon, trout, and smelts (Salmoniformes), as well as catfishes (Siluriformes) and characins (Characiformes), possess an **adipose fin**, a median, fleshy dorsal fin that lies near the caudal fin and has no internal stiffening rays or bony elements. It probably plays a minor role in propulsion. Eel-like fishes have long dorsal and anal fins that frequently run most of the length of the body.



(a) Trunk



(b) Caudal

Figure 4.14. Structure of the two kinds of vertebrae found in teleosts: (*a*) trunk; (*b*) caudal.

Caudal fins are modified in three major ways. They are unlobed, or **diphycercal**, in lungfishes and bichirs (Fig. 4.17a). Sharks, in contrast, possess **heterocercal** fins (Fig. 4.17b), in which one lobe is larger than the other. If the vertebral column extends into the dorsal lobe, the caudal fin is **epicercal**; if the vertebral column extends into the ventral lobe, it is **hypocercal**. Such fins, which provide lift for the posterior part of the body, counter the shark's tendency to sink and also assist in lifting the body off the substrate following periods of rest. In most bony fishes, the upper and lower lobes of the caudal fin are about the same size, or **homocercal** (Fig. 4.17c). The vertebral column does not extend into either lobe.

Pelvic fins in male chimaeras, skates, and oviparous sharks, all of which utilize internal fertilization, have been modified by the addition of skeletal elements to form intromittent organs known as **claspers** (see Fig. 4.35). The anal fin is modified into an intromittent organ known as a **gonopodium** in some male teleosts, like guppies and mollies (*Poecilia*), swordtails (*Xiphophorus*), and mosquitofish (*Gambusia*). These organs, which have evolved to improve fertilization of the eggs, are inserted into the genital openings of females and guide sperm into the female reproductive tract.

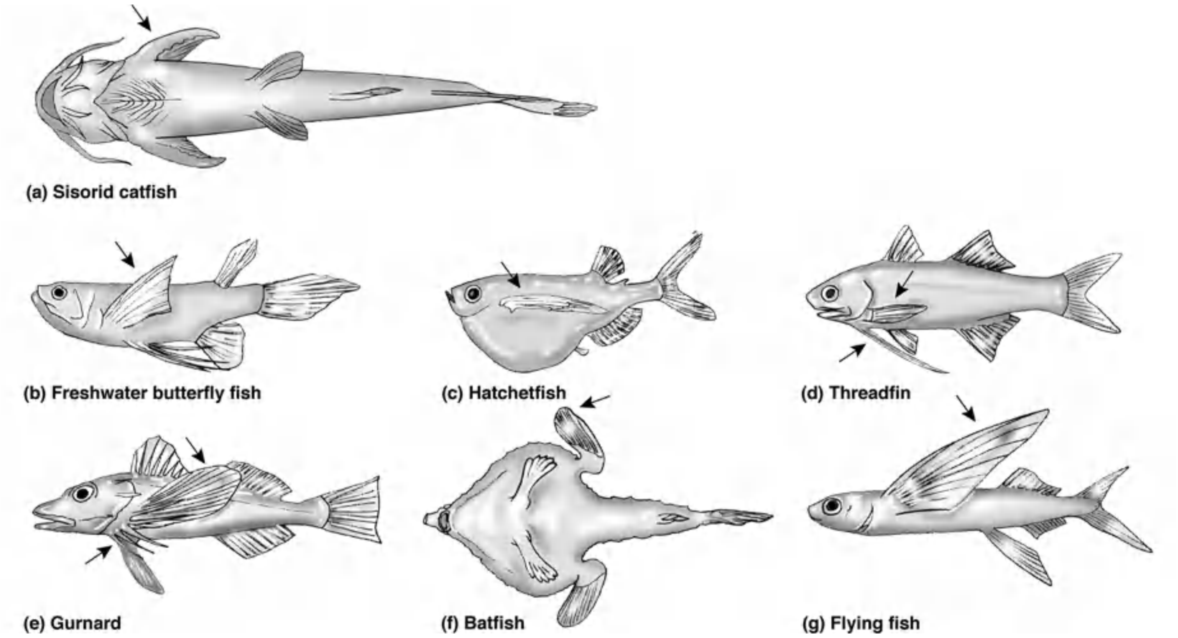
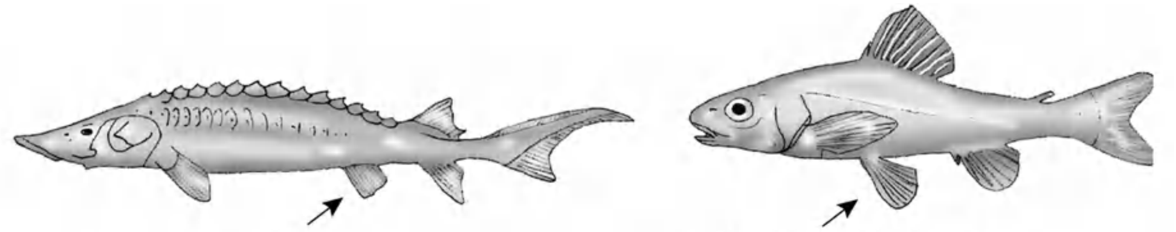


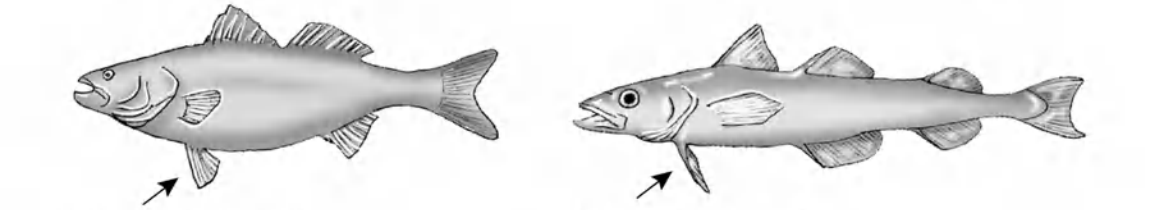
Figure 4.15. Modifications of pectoral fins (*indicated by arrows*) in several fish genera: (*a*) ventral view of sisorid catfish (*Glyptothorax*); (*b*) freshwater butterfly fish (*Pantodon*); (*c*) hatchetfish (*Gasteropelecus*); (*d*) threadfin (Polynemidae); (*e*) gurnard (Triglidae); (*f*) ventral view of batfish (Ogcocephalidae) with armlike pectoral fins well behind pelvic fins; (*g*) flying fish (Exocoetidae).

Fishes are propelled through the water by fins, body movement, or both. In most fishes, both paired and unpaired fins serve primarily for steering and stabilizing rather than for propulsion. In general, the main moving force is created by the caudal fin and the area immediately adjacent to it, known as the **caudal peduncle**. It long had been hypothesized that the anterior musculature generated most of the power and that the posterior musculature transmitted the force to the tail. By analogy, the anterior muscle was thought to act as the "motor," the tail as the "propeller," and the posterior muscle as the "drive shaft." However, through a combination of filming, electrical impulse recordings, and mathematical modeling of red muscle bundles in the scup (*Stenotomus chrysops*), Rome et al. (1993) showed that most of the power for normal swimming came from muscle in the posterior region of this fish, and relatively little came from the anterior musculature. Eels rely on extreme, serpent-like body undulations to swim, with fin movement assisting to a minor extent. Fishes with a fairly rigid body like the filefish, trunkfish, triggerfish, manta, and skate, however, depend mostly on fin action for propulsion.



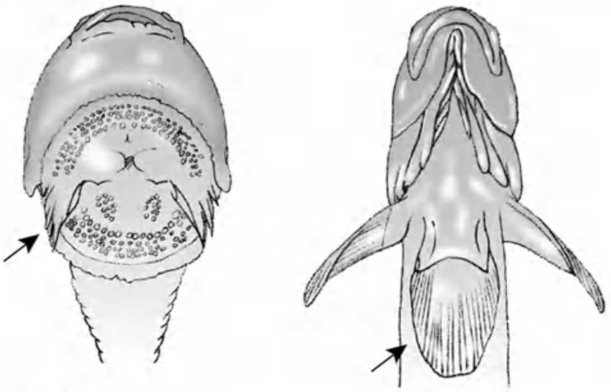
(a) Abdominal pelvic fins

(b) Subabdominal pelvic fins



(c) Thoracic pelvic fins

(d) Jugular pelvic fins



(e) Clingfish

(f) Goby

(g) Snailfish

Figure 4.16. Modifications of pelvic fins and their positions (*pelvic fins indicated by arrows*): (*a*) abdominal (sturgeon, Acipenseridae); (*b*) subabdominal (sand roller, Percopsidae); (*c*) thoracic (bass, Moronidae); (*d*) jugular (pollock, Gadidae). Some pelvic fins have been modified for holding on to the substrate: (*e*) clingfish (Gobiesocidae); (*f*) goby (Gobiidae); (*g*) snailfish (Liparidae).

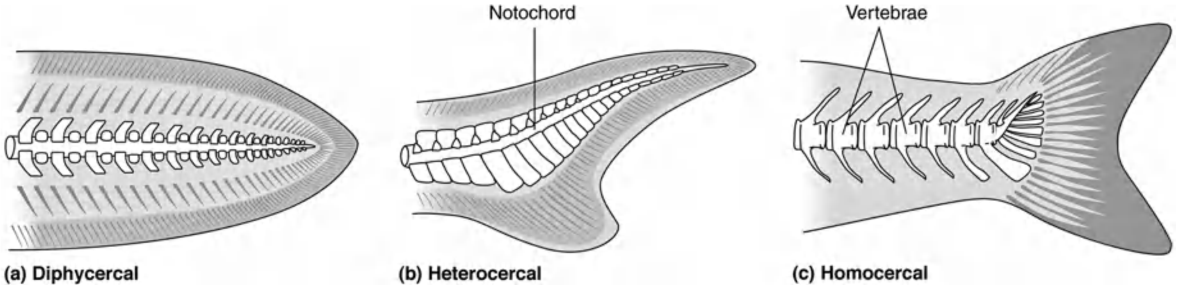
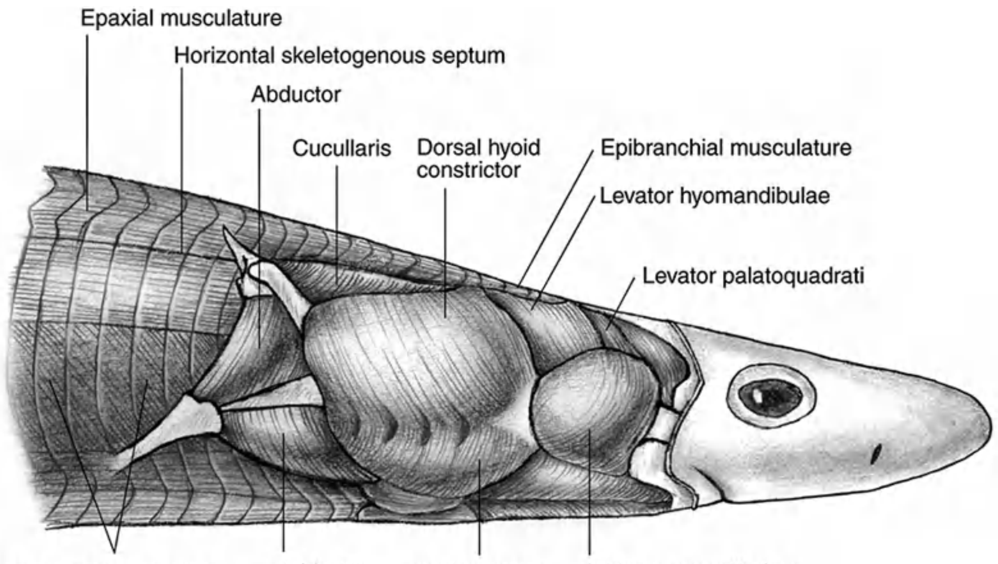


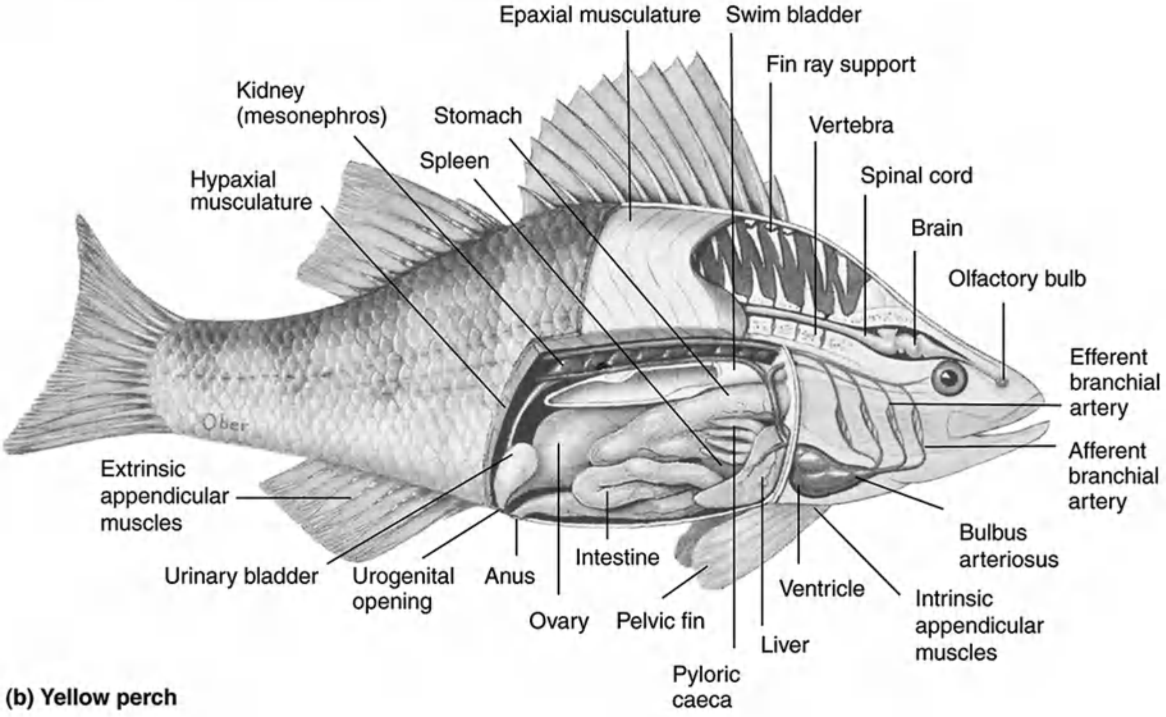
Figure 4.17. Major caudal fin (tail) modifications in fishes: (*a*) diphycercal (lungfishes and bichirs); (*b*) heterocercal (sharks); (*c*) homocercal (most bony fishes). Heterocercal tails may be further subdivided: if the dorsal lobe is larger than the ventral lobe, it is designated as an epicercal tail; if the ventral lobe is larger, it is known as a hypocercal tail.

Muscular System

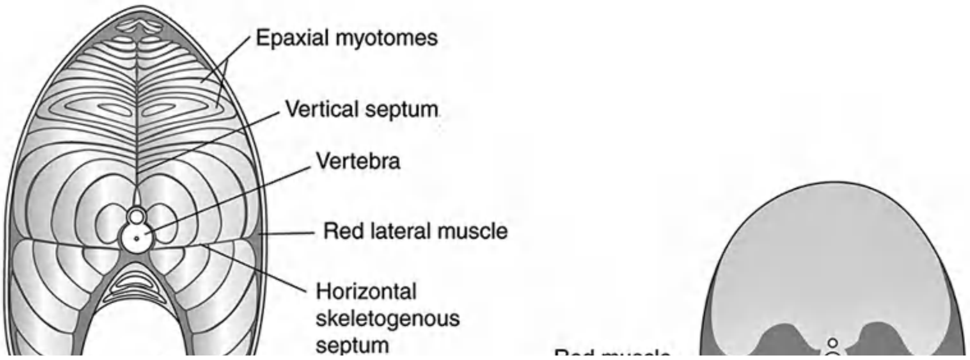
The metamerically arranged body wall muscles are composed of a series of zigzag-shaped **myomeres** (Fig. 4.18a, b), with each myomere constituting one muscle segment. Coordinated contractions (contraction on one side accompanied by relaxation on the opposite side) of posterior myomeres produce waves of contraction that provide the main locomotor mechanism of most fishes. As this propulsive wave moves posteriorly, the water adjacent to the fish is accelerated backward until it passes over the posterior margin of the caudal fin, producing thrust (Lighthill, 1969).



(a) Dogfish shark



(b) Yellow perch



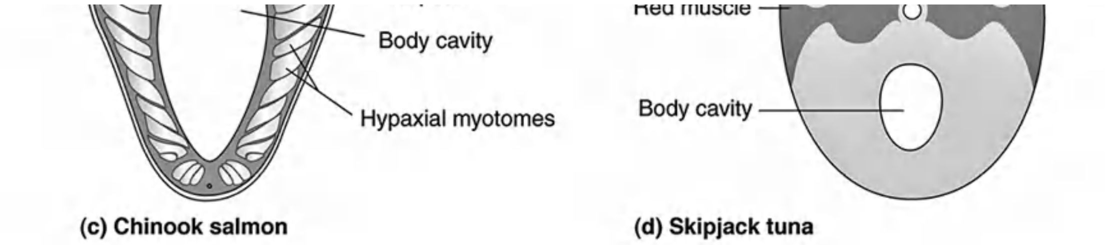


Figure 4.18. (*a*) Lateroventral view of the head of a dogfish shark (*Squalus*) showing epibranchial (above the gills), hypobranchial (below the gills), and branchiomeric musculature. (*b*) Muscles and internal anatomy of the yellow perch (*Perca flavescens*), a freshwater teleost fish. (*c*) Cross section of body musculature in a chinook salmon (*Oncorhynchus tshawytscha*). (*d*) Diagram showing approximate extent of red muscle (*darker shading*) in skipjack tuna (*Katsuwonus pelamis*).

In most fishes, white muscles predominate and may comprise up to 90 percent or more of the entire body weight. White muscle has relatively thick fibers, contains no fat or myoglobin (a protein that bonds with oxygen), and primarily utilizes anaerobic metabolism. However, in those fishes that swim most of the time and have an adequate oxygen supply, like tuna, bonito, and marlin, red muscles make up a greater portion of the body muscle mass (Cailliet et al., 1986; Barton, 2007) (see Fig. 4.18d). Red muscle consists of thin-diameter fibers, contains fat and myoglobin, and utilizes aerobic respiration.

Six groups of fishes (Rajidae, Torpedinidae, Mormyriformes, Gymnotiformes, Malapteruridae, and Uranoscopidae) are known to possess electric organs derived from muscle fibers. Certain muscle masses in these fishes are highly modified to produce, store, and discharge electricity. Specialized cells known as electrocytes are stimulated by signals from spinal nerves to generate small voltage gradients. Because electrocytes are arranged in columns surrounded by insulating tissues, voltages are linearly increased, similar to a series of small batteries (Heiligenberg, 1977). Because these groups of fishes are only remotely related, electric organs appear to have evolved several times independently in Africa and South America after the two continents separated. Although this capability evolved in early vertebrates, only some of the primitive fishes living today have retained this ability.

Some marine and freshwater fishes can produce charges up to approximately 500 volts, although most species are limited to weak electric discharges in the range of millivolts to volts. Most are nocturnal, have poorly developed eyes, and live in dark, murky water where visibility is poor.

The electric ray (*Torpedo*) has two dorsal electric organs in the pectoral fins, which are apparently used to immobilize prey. In another ray (*Raja*) and the electric eel (*Electrophorus*), electric organs lie in the tail and are modifications of the hypaxial musculature. Electric organs can be used for defense or to stun prey, to scan the environment and locate enemies or prey, and for social communication. (See the section on Sense Organs, pages **117–118**, for additional information on electroreceptors.)

Cardiovascular System

In fishes, the **sinus venosus** is a thin-walled sac that serves chiefly as a collecting chamber for venous blood it receives from all parts of the body (Fig. 4.19a, b). Blood flows from the sinus venosus into a large, thin-walled muscular sac—the atrium (auricle). From the atrium, blood enters the **ventricle** through an atrioventricular aperture guarded by valves. The ventricle, a relatively large chamber with heavy walls of cardiac muscle, functions as the primary pump distributing blood anteriorly. The anterior end of the ventricle becomes a muscular tube, the **conus arteriosus**, which connects with the **ventral aorta** and serves to moderate blood pressure. In teleosts, the conus is short, and its function is assumed by the **bulbus arteriosus**, an expansion of the ventral aorta. A series of semilunar valves in the conus arteriosus prevents the backflow of blood. Cameron (1975) found that the teleost heart in three species of freshwater fishes requires up to 4.4 percent of the total energy of the fish.

The ventral aorta carries blood forward beneath the pharynx, where six pairs of **aortic arches** connect the ventral aorta with the **dorsal aorta**. The dorsal aorta carries blood above the digestive tract toward the tail. It continues into the tail as the **caudal artery**.

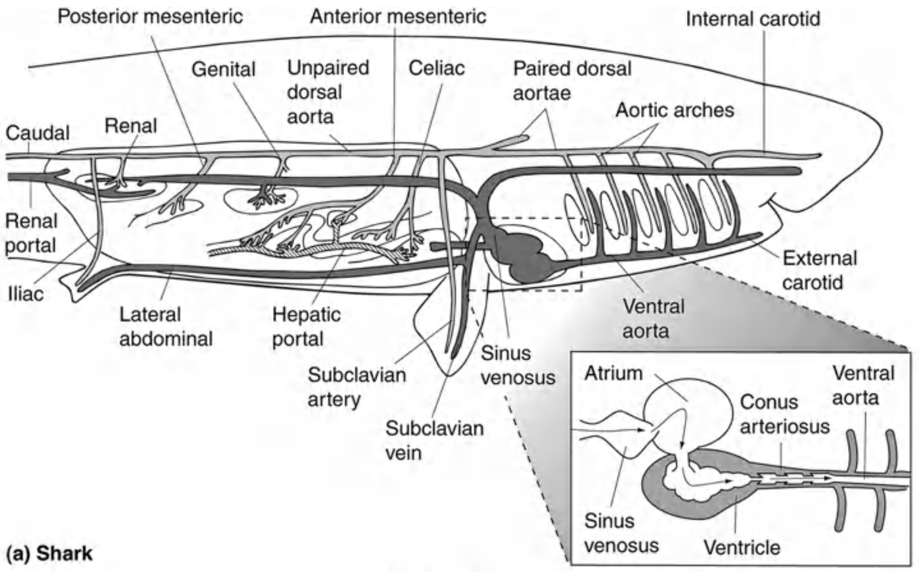
In most Chondrichthyes, branchial arteries form in the aortic arches. Blood entering an aortic arch from the ventral aorta must pass through gill capillaries before continuing to the dorsal aorta. This arrangement allows aortic arches to serve a gas exchange (respiratory) function. In most teleosts, the first and second aortic arches disappear during development. The remaining pairs are converted to branchial arteries.

In fishes, all blood must traverse through at least two capillary systems (gills and tissue) before returning to the heart (Fig. 4.20a). A drop of blood passes through the heart of a fish only one time during each circuit of the body. After passing through the heart, the blood is carried to the gills for aeration and then is distributed to all parts of the body. In most fishes, all of the blood flowing through the heart is venous blood. In contrast, a drop of blood in amphibians, reptiles, birds, and mammals must pass through the heart twice during any single circuit of the body (Fig. 4.20b). As a result of this difference in circulation pattern, the pressure of blood supplying the tissues is lower in fishes than in reptiles, birds, and mammals.

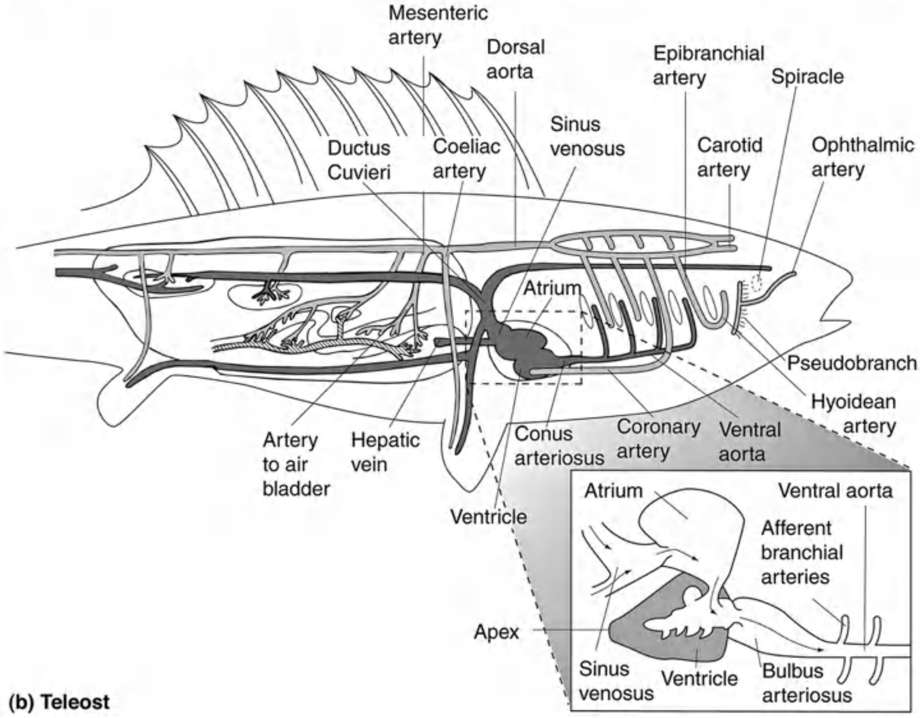
Endothermy

Some degree of endothermy is present in sharks of the family Lamnidae and Alopiidae and in certain oceanic teleost fishes like mackerels, tunas, and billfishes. The development of endothermy requires the elevation of aerobic capacity and the reduction of heat loss. Tunas have exceptionally high metabolic rates and are able to reduce their overall heat loss. They retain metabolic heat by way of vascular countercurrent heat exchangers located in the brain, muscle, and viscera. Red aerobic muscle contributes the majority of metabolically derived heat and is centrally located near the vertebral column rather than laterally as in most teleosts. Thus, these fishes warm their brain, muscle, and viscera. Billfishes, however, use cranial endothermy and warm only the brain and eyes by passing blood through the superior rectus eyeball muscle. A countercurrent heat exchanger retains the heat beneath the brain, and a distinct arterial supply directs warm blood to the retina. The butterfly mackerel also uses cranial endothermy, but the thermogenic tissue is derived from the lateral rectus eyeball muscle. The development of endothermy may have permitted range expansion into cooler waters.

Block et al., 1993



(a) Shark



(b) Teleost

Figure 4.19. (*a*) Basic vertebrate circulatory pattern in a shark. Blood is pumped by the heart to the ventral aorta. It flows through the gill region via the branchial arteries and the paired aortic arches, which lead to the dorsal aortae. The dorsal aortae carry blood anteriorly to the head and posteriorly to the remainder of the body. The aortae give off major branches to the viscera and somatic tissues. (*b*) Diagram of the branchial circulation of a teleost fish. Blood is pumped anteriorly by the heart into the ventral aorta. After being aerated by passing through the gills, the blood flows into the dorsal aorta.

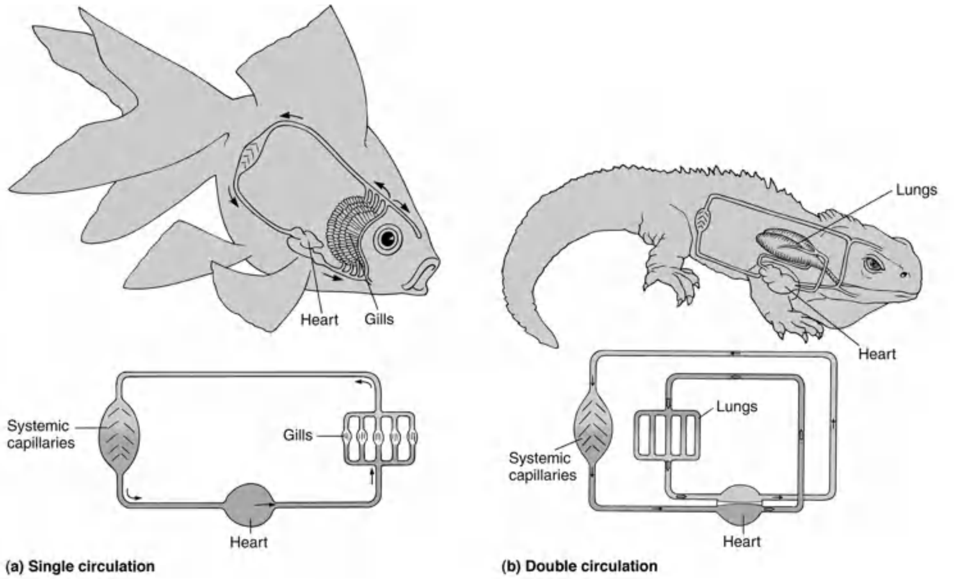


Figure 4.20. Single and double circulation. (*a*) The single circulation of fishes includes the heart, gills, and systemic capillaries in series with one another (*arrows indicate the path of the blood flow*). A drop of blood passes through the heart only once during each circuit of the body. (*b*) The double circulation of most amniotes includes the heart, lungs, and systemic capillaries. A drop of blood passes through the heart twice during each circuit of the body.

The blood of fishes contains nucleated erythrocytes, leukocytes, and thrombocytes. Seasonal changes in red blood cell production have been reported in some fishes (Hevesy et al., 1964). For example, when oxygen demands of tissues are relatively low, as when water temperatures are low and the fish is not very active, large numbers of erythrocytes are not required and the number tends to drop.

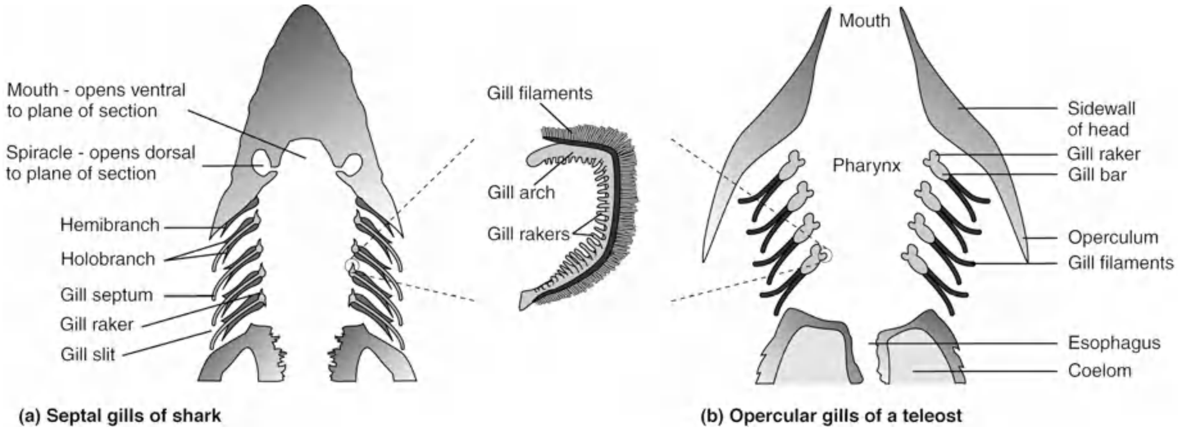
Respiratory System

In most fishes, **external nares** lead to blind olfactory sacs that contain the olfactory epithelium. Water usually enters the external nares through an incurrent aperture, flows over the olfactory epithelium, and exits through an excurrent aperture. In many lobe-finned fishes, nasal canals lead from the olfactory sacs and open into the oral cavity via **internal nares (choanae)**. However, these are not used in aquatic respiration.

Internal nares are thought to have first served to increase the effectiveness of olfaction by making possible more efficient sampling of the environment. Their first respiratory function was probably to help prevent desiccation of the gills and lungs by serving as devices for aerial respiration. Thus, internal nares in crossopterygians may have been preadapted for use in aerial respiration.

In fishes, gills function primarily for respiration. They are ventilated by a unidirectional flow of water, created either actively by branchial pumping or passively by simply opening the mouth and operculum while swimming forward. The gill system consists of several major gill arches on each side of the head (Fig. 4.21) with two rows of gill filaments extending from each gill arch. Each filament consists of rows of densely packed flat **lamellae** (primary and secondary). **Gill rakers**, which project from gill arch cartilages into the pharynx, serve to protect the gills and to direct food in the water toward the esophagus. Tips of filaments from adjoining arches meet, forcing water to flow between the filaments.

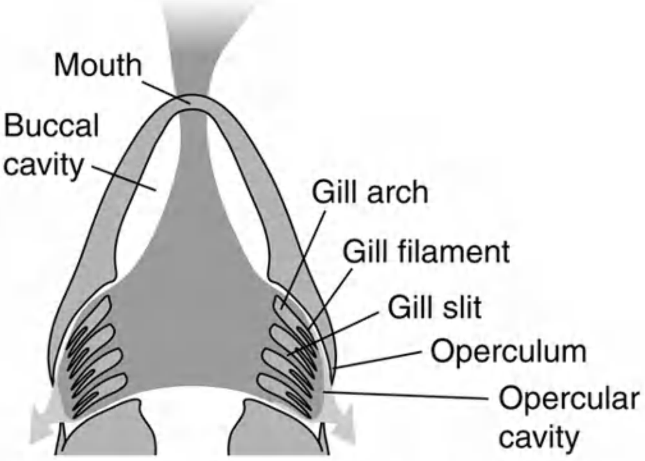
Most elasmobranchs possess five exposed (naked) gill slits that are visible on the surface of the pharyngeal region (see Fig. 4.21a). They are exposed because no operculum is present. Each gill slit opens into a gill chamber whose anterior and posterior walls possess gills that are supported by gill arches. These are the sites of gas exchange. Water enters the pharynx through the mouth or spiracle and passes into the gill chambers, where it bathes the gill surfaces (Fig. 4.22). As water flows from front to rear through the slits between the lamellae, gas exchange takes place in the lamellae. At the same time, blood flows through capillaries in the opposite direction (rear to front). This **countercurrent flow** greatly increases the efficiency of gills as gas exchangers by allowing better exploitation of the low oxygen content of the water. Water is forced from the gill chambers by contraction of branchiomeric muscles. Water may leave the gills of bony fishes with a loss of as much as 80 or 90 percent of its initial oxygen content (Hazelhoff and Evenhuis, 1952). In contrast, mammalian lungs remove only about 25 percent of the oxygen present in inhaled air. (While gill respiration is more efficient than mammalian respiration in terms of percent saturation, it must be remembered that the amount of oxygen available in air is approximately 20 times that in an equal volume of water.)



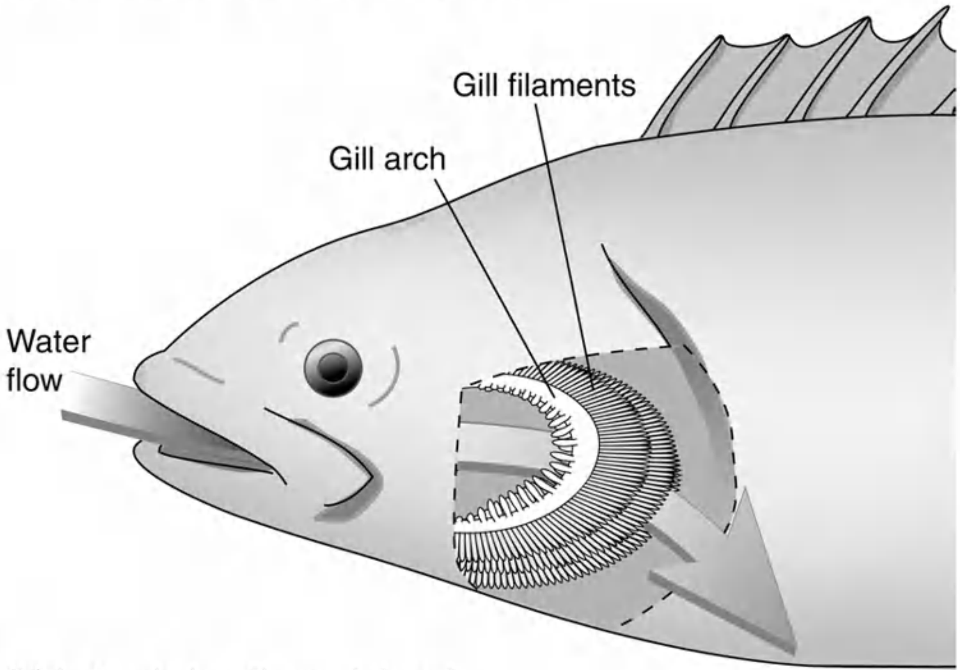
(a) Septal gills of shark

(b) Opercular gills of a teleost

Figure 4.21. Gill coverings: (*a*) In sharks, valves formed from the individual gill septa guard each gill chamber. (*b*) In most teleosts and some other species, a common operculum covers the gills. *Inset*: A single gill arch. The gill filaments play a role in gas exchange, whereas the gill rakers strain water entering the gill chamber from the pharynx.



(a) Horizontal section through head



(b) Lateral view through head

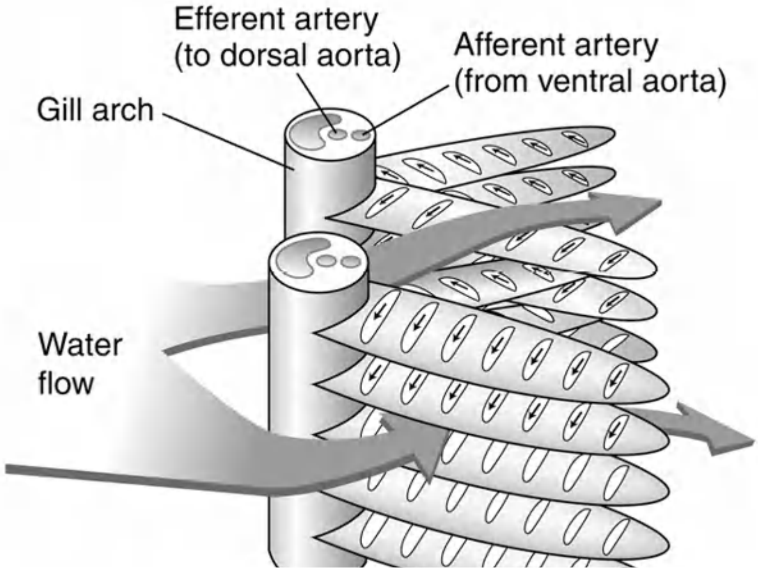


Figure 4.22. Morphology of teleost gills: (*a*) position of the gills in the head and the general flow of water; (*b, c*) water flow (*shaded arrow*) and blood flow (*solid arrows*) patterns through the gills.

Gills have become modified in some species like the “walking catfish” (*Clarias batrachus*) of southeastern Asia and now introduced to southern Florida. In these species, the second and fourth gill arches possess modified gill filaments that do not collapse when exposed to the air. Ordinarily, gills tend to adhere to one another and lose much of their effective surface area when removed from water. Walking catfish usually leave the water during periods of rain so that the gills can be kept moist while moving about on land (Jordan, 1976).

Digestive System

Fishes may consume a variety of foods: filter-feeders feed on plankton, herbivores feed on plant material, detritivores consume partly decomposed organic matter, carnivores feed on animal material, and omnivores consume a variety of plant and animal material.

In most fishes, the mouth is terminal in position (see Figs. 4.1b and 4.12a), although in some, especially sharks and rays, it is located ventrally and often well back from the tip of the head (subterminal) (see Figs. 4.1a and 4.11). Still others, like barracudas, have projecting lower jaws, and some, like the swordfish, have elongated upper jaws.

Most fishes possess a flat, rigid, cartilaginous tongue that arises from the floor of the oral cavity. It is not always sharply demarcated and is not freely movable.

The roof of the oral cavity is formed by the primary palate. If internal nares are present, they open into the anterior portion of the oral cavity. Oral glands are sparse and consist primarily of mucus-secreting cells.

Teeth are numerous and may occur on the jaws, palate, and pharyngeal bones. Teeth composed of epidermal cells are present in lampreys, hagfishes, and adult sturgeons. Teeth may be attached to the outer surface, or summit, of the jawbone, a situation called **acrodont dentition**, or rooted in individual bony sockets, a situation called **thecodont dentition**. Most fishes have **polyphyodont dentition**—that is, they can replace damaged or injured teeth.

Food and water, which are taken into the oral cavity together, are separated in the pharynx, with gill rakers preventing the food from passing out through the gill slits. The pharyngeal region is thus a vital portion of both the digestive and respiratory systems.

The stomach, a muscular organ at the end of the esophagus, secretes digestive enzymes and serves as a temporary storage site (see Fig. 4.18b). The distinction between the esophagus and stomach is poorly delineated in fishes. Blind pouches known as **pyloric caeca** are found near the junction of the stomach and intestine in ray-finned fishes, especially teleosts (see Fig. 4.18b). Their primary function appears to involve fat absorption, although they secrete a variety of digestive enzymes. No other vertebrate group possesses pyloric caeca.

The digestive tract of most fishes is a relatively straight tube terminating at the cloaca or anus (Fig. 4.23). Predators have relatively shorter intestines than herbivorous species because meaty foods are more easily digested than plant foods. Sharks, chimaeras, lungfishes, and some primitive teleosts have intestines that incorporate a **spiral valve** that aids in digestion by increasing the absorptive area (Fig. 4.23b–d).

In most fishes, the colon (large intestine) leads to the rectum, which then opens into the cloaca. The cloaca is the common chamber at the end of the digestive tract in elasmobranchs and lungfishes. It receives the colon, the urinary tract, and the genital tract and opens to the exterior via the vent. In most of the remaining fishes, the digestive, genital, and urinary systems tend to open separately to the exterior; in some teleosts, the urinary and reproductive systems may unite and empty into a common sinus before leaving the body. The alimentary canal and digestion in teleosts are discussed in detail by Kapoor et al. (1975).

Air (gas) bladders, or **swim bladders**, probably originated as modified, paired pharyngeal pouches that were ventral in position (Feduccia and McCrady, 1991). They originally evolved as organs of respiration and, in some species, eventually evolved into true lungs. In many ray-finned fishes (Actinopterygii), they developed into paired swim bladders and then into a single organ on the dorsal side of the gut (Fig. 4.24). The climbing perch (*Erythrinus*) has a lateral attachment of its swim bladder to the gut (Fig. 4.24c) and often is cited as an intermediate stage in the migration of the swim bladder to a dorsal position (Feduccia and McCrady, 1991).

Icefishes

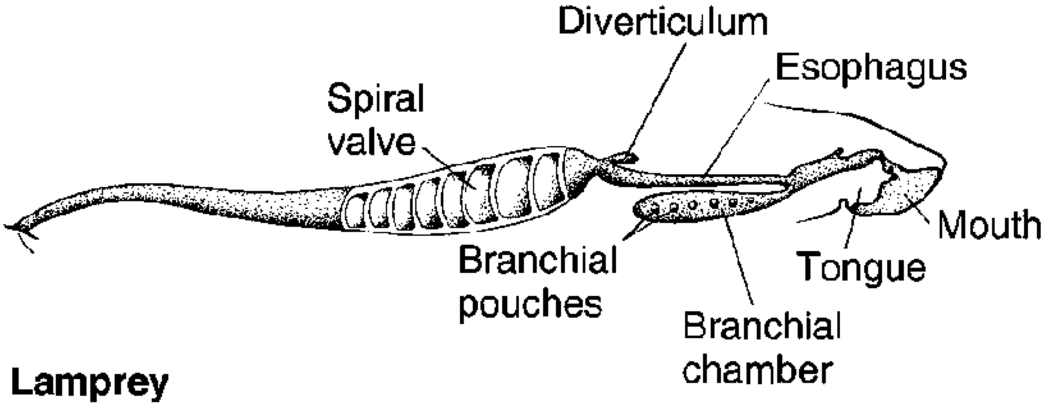
Antarctica's marine fish fauna (there are no freshwater species because there is no permanent liquid water on the continent) comprises approximately 275 species, 95 of which belong to the perciform suborder Notothenioidei. This group contains many species with unusual adaptations. Members of one family—Channichthyidae—are known as icefishes and are unique among vertebrates in that they totally lack the respiratory pigment hemoglobin (although some nonpigmented erythrocytes are present), and their muscles contain only minute traces of myoglobin. These fishes, also commonly known as "white-blooded fish," lack scales, lack a swim bladder, possess creamy-white gills, yellowish-tinted blood, and yellow muscles. The first icefish was discovered in 1927 by zoologist Ditlef Rustad, who pulled up a strange pale fish with large eyes, a long, toothed snout, soft white gills, and fins stretched across fans of slender quills during an expedition to Antarctic waters. He named it the "white crocodile fish."

Oxygen is carried throughout the body in simple dissolved solution, a process that reduces the oxygen-carrying capacity of the blood to only about 10 percent of that of red-blooded fishes. Although dissolved oxygen is high in the consistently cold Antarctic waters, these sluggish fishes have low metabolic oxygen requirements. Physiological compensation is achieved through adaptations like large ventricles, low arterial pressure, large diameter vessels, and low erythrocyte densities that serve to increase blood volume and flow rate. Although icefishes pump unusually thin blood through their bodies, their circulatory systems handle huge volumes. Whereas fishes in temperate zones devote no more than 5 percent of their resting metabolic rate to their hearts, icefishes invest a whopping 22 percent of their body's available energy to their large hearts.

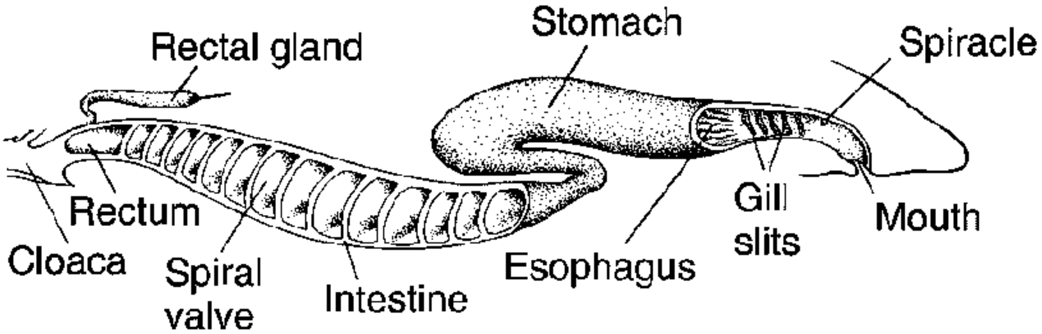
Researchers are studying the low-density bones of icefish in the hope of learning more about the human disorders known as osteopenia and osteoporosis. Icefish blood provides insights into other conditions, such as anemia and how bones develop. The ability of icefish to live in freezing water without freezing can also help scientists learn about the formation of ice crystals and storage of frozen foods, and even organs used for transplant.

Today, the biggest threat to icefish is human-caused climate change. The Southern Ocean is getting warmer and possibly more acidic and less nutritious. Adult icefishes are more sensitive to changes in temperature than red-blooded fish—they cannot stand the heat. They will either need to adapt or they will perish.

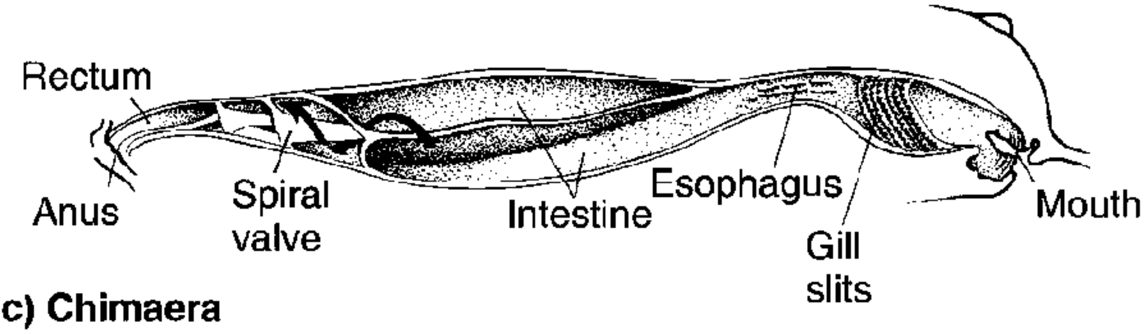
Hemmingsen and Douglas, 1977; Douglas et al., 1985; Harrison et al., 1991; Eastman, 1993; Sidell and O'Brien, 2006; Jabr, 2012



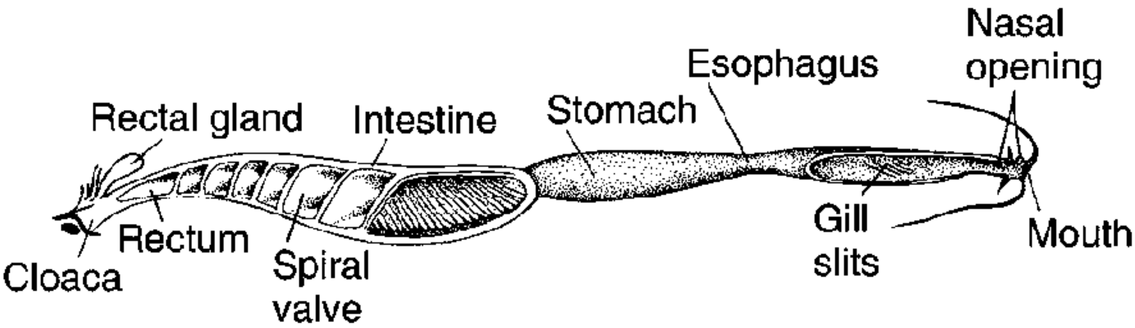
(a) Lamprey



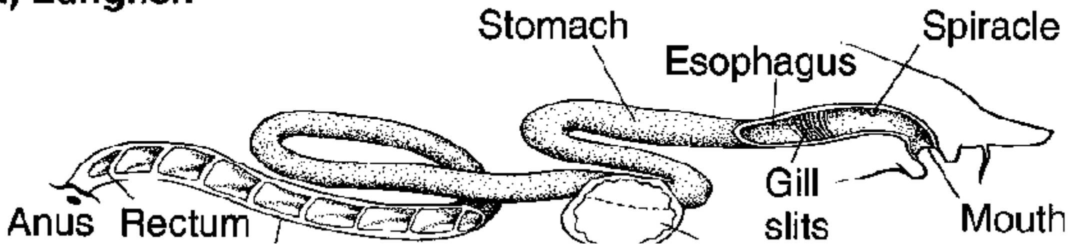
(b) Shark



(c) Chimaera



(d) Lungfish



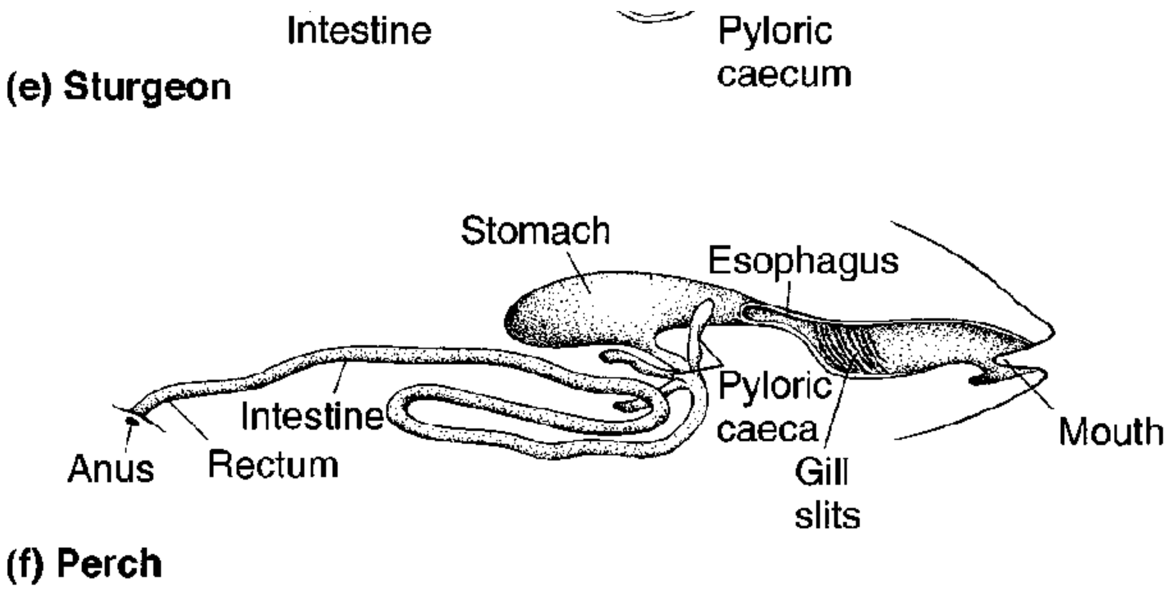


Figure 4.23. Digestive tracts of selected fishes: (*a*) lamprey; (*b*) shark; (*c*) chimaera; (*d*) lungfish; (*e*) sturgeon; (*f*) perch. When a spiral valve is absent, the intestine is often lengthened, as in the perch. A stomach is absent in lampreys and chimaeras.

Because the density of most animal tissues is greater than that of water, water-dwelling species tend to sink. This can be prevented either actively by swimming movements or passively by the development of a gas-filled swim bladder. The primary function of the swim bladder, therefore, is to serve as a hydrostatic organ in which buoyancy can be regulated with water depth. Swim bladders allow a relatively precise control of buoyancy because the volume and pressure of gas they contain can be regulated with comparative ease, thereby altering the specific gravity of the fish and increasing or decreasing its buoyancy. By the processes of diffusion and/or active transport, gas enters the swim bladder. The gases used differ among fishes. Oxygen, carbon dioxide, and nitrogen are found in swim bladders in higher concentrations than would be expected on the basis of their partial pressure in water.

Left- and Right-Mouthed Scale-Eaters

Seven of the thousands of species of cichlid fishes in the lakes of Africa's Rift Valley are scale-eaters—species that exhibit a peculiar feeding habit involving eating the scales from other fish. The prey's behavior (see below) serves to maintain a nearly perfect 1:1 ratio between two genetically determined forms of predatory cichlids. These forms are distinguished by mouths that twist either to the left or to the right. Predators often have been shown to exert such frequency-dependent selection on their prey populations, but this is the first indirect evidence of frequency-dependent selection by prey on predators.

The mouth of a scale-eating cichlid opens either rightward or leftward as a result of an asymmetrical joint of the jaw to the suspensory apparatus. As a result of this lateral asymmetry, the mouth is "frozen open" on one side, which makes the cichlid's attacks more efficient. However, this specialization, which is considered an adaptation for efficiently tearing off a prey’s scales, restricts each fish to attacking from just one side. Left-mouthed scale-eaters only attack the right side of their prey, and vice versa. Stomach analyses from left-mouthed fish were found to contain mostly scales from their prey’s right sides.

This restriction may explain why left-mouthed and right-mouthed populations stay in balance. If, for example, right-mouthed fish became more common, their prey would change their behavior, becoming more alert to activity on their left sides and thus fending off more attacks by right-mouthed fishes. Meanwhile, left-mouthed fish would gain the advantage, and the balance would be restored.

Hori, 1993; Stewart and Albertson, 2010; Lee et al., 2012

Swim bladders are not found in lampreys, hagfishes, and cartilaginous fishes, but they are present in about half of the teleost fishes. Many bottom-dwelling species have lost them as an adaptation to this lifestyle. Some teleosts that lack these organs as adults have them during embryonic development. To retain buoyancy, cartilaginous fishes like sharks never stop swimming. They use their pectoral fins as hydrofoils and their asymmetrically shaped tails to generate lift. To increase their buoyancy, they also accumulate low-density oils and the hydrocarbon squalene in their tissues, particularly the liver.

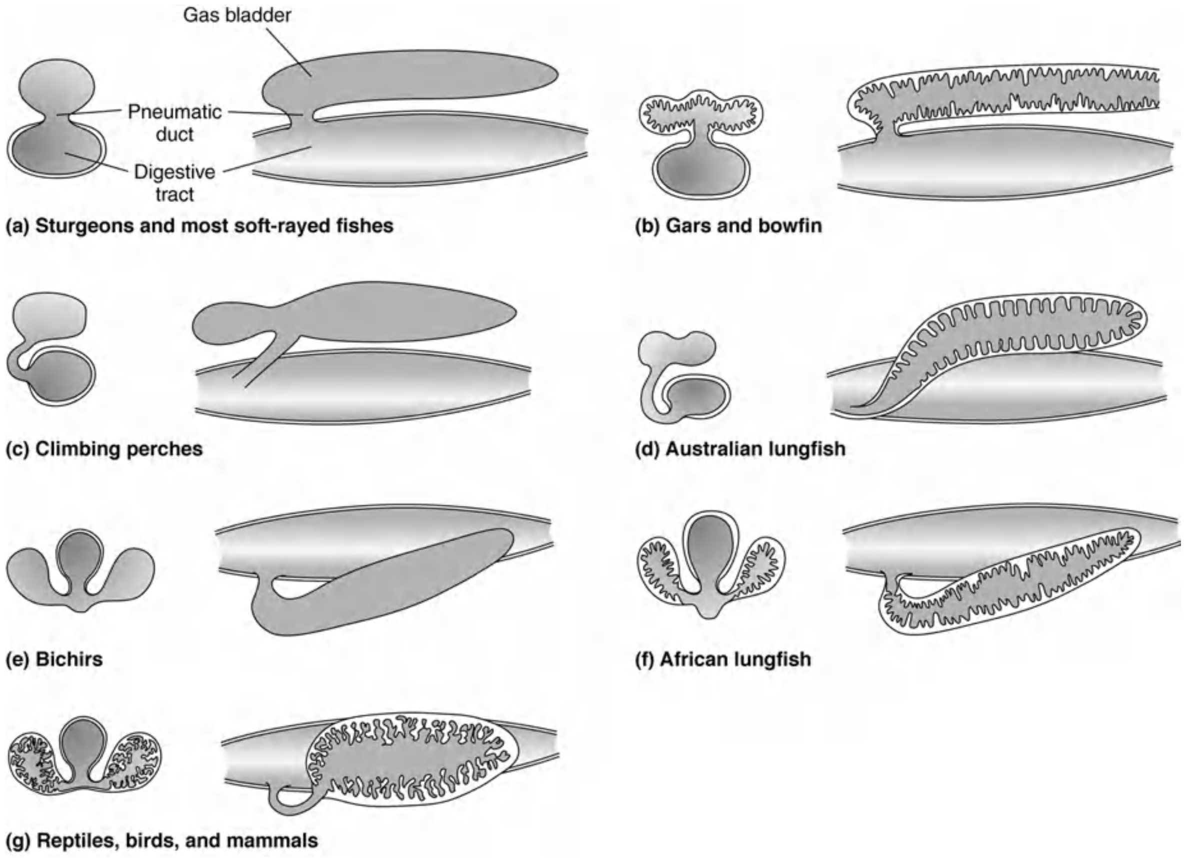


Figure 4.24. Variations of swim bladder relationships to the gut in those fishes whose swim bladder connects to the digestive tract via a pneumatic duct (physostomes) and in reptiles, birds, and mammals: (*a*) sturgeons (*Acipenser*) and most soft-rayed fishes; (*b*) gars (*Lepisosteus*) and bowfin (*Amia*) with roughened lining; (*c*) climbing perches (*Erythrinus*); (*d*) Australian lungfish (*Neoceratodus*) with sacculated lining; (*e*) bichirs (*Polypterus* and *Calamoichthyes*); (*f*) African lungfish (*Protopterus*); and (*g*) reptiles, birds, and mammals.

Swim bladders are more or less oval, soft-walled sacs in the abdominal cavity just below the spinal column (Fig. 4.25). They may be paired or unpaired and may be partitioned into chambers. They lie retroperitoneally (behind the peritoneum) near the kidneys and bulge into the coelomic cavity. A pneumatic duct, when present in adults, usually connects the swim bladder to the esophagus; it may, however, connect the swim bladder to the pharynx or even to the stomach. Fishes in which the swim bladder connects to the digestive tract via a pneumatic duct are termed **physostomes** and include many of the more ancestral soft-rayed teleosts like herrings, salmon, catfishes, eels, pike, and cyprinids. Physostomous species gulp air at the water’s surface and push it through the pneumatic duct into the swim bladder using a force supplied by the buccal cavity (Fänge, 1976). Gas is removed from the swim bladder by bubbling it through the pneumatic duct and mouth.

Bony fishes possessing a closed swim bladder that lacks a pneumatic duct are known as **physoclists**. These fishes have special structures associated with the circulatory system for inflating or deflating the swim bladder. The source of gas is normally from the blood contained in a network of capillaries (*rete mirabile*, or red gland) found in the lining of the swim bladder (see Fig. 4.25). Gas from the blood is moved into the gas gland by the *rete mirabile*. The capillaries of the red gland are usually supplied with arterial blood through branches of the celiac artery and are drained by veins that empty into the hepatic portal vein. More than two-thirds of all teleosts with swim bladders are physoclists.

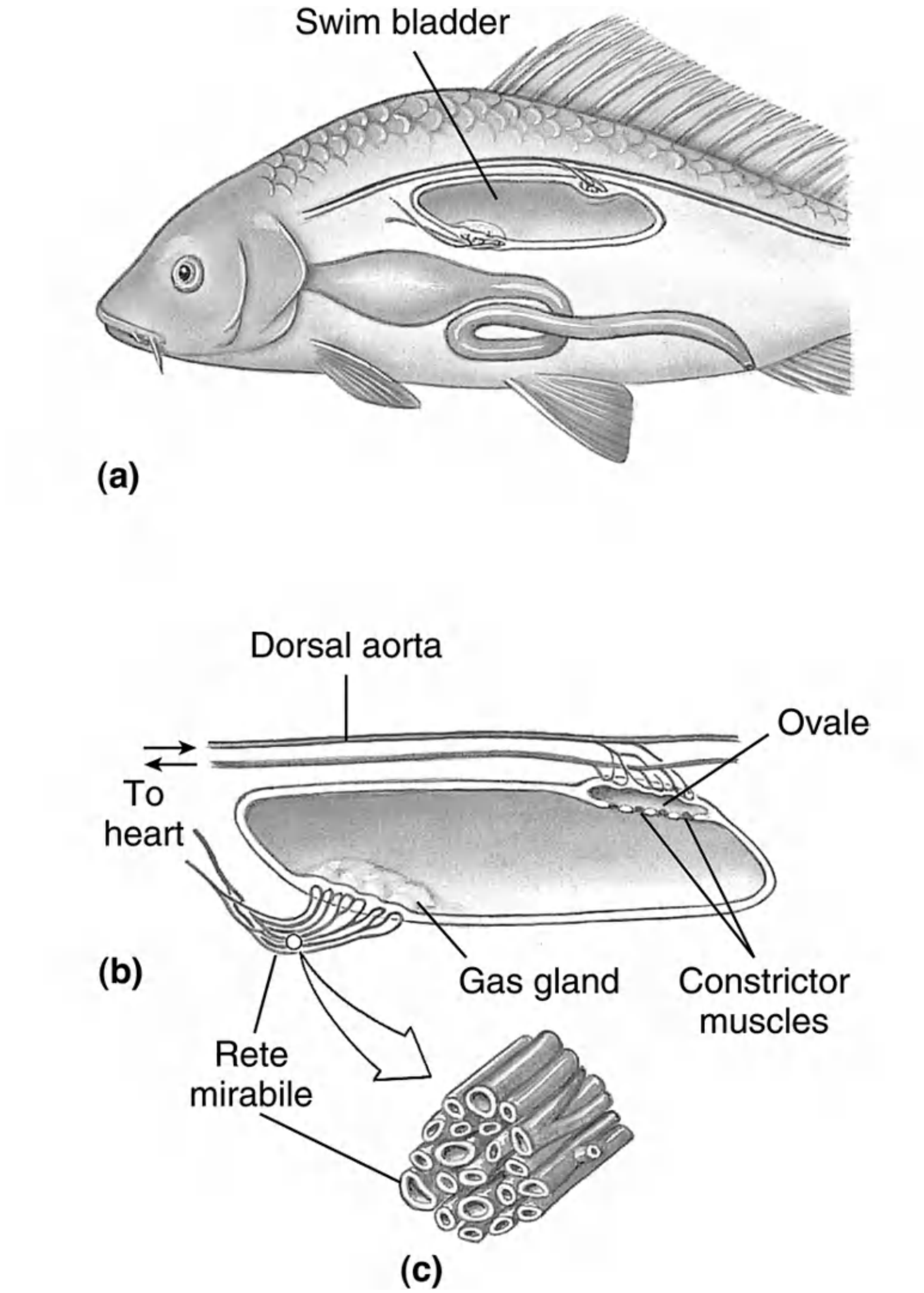


Figure 4.25. (*a*) The swim bladder in a teleost fish lies just beneath the vertebral column. (*b*) Gas is secreted into the swim bladder by the gas gland. Gas from the blood is moved into the gas gland by the *rete mirabile*, an array of tightly packed capillaries that acts as a countercurrent multiplier to build up the gas concentration in the blood vessels. The arrangement of venous and arterial capillaries in the *rete mirabile* is shown in (*c*). Gas is released during ascent by opening a muscular valve; this allows the gas to enter an absorptive area (ovale), from which the gas is removed by blood circulation.

The Root Effect

The hemoglobin of certain fishes have structural characteristics that make them efficient oxygen pumps, able to drive gases into the swim bladder. A network of capillaries (*rete* *mirabile*) secretes lactic acid, which forces nitrogen out of solution and also causes a marked reduction in the oxygen affinity of blood hemoglobin—a phenomenon known as the Root effect. It is this pH-dependent release of oxygen from Root-effect hemoglobin that largely accounts for the ability of fishes to "compress" oxygen and force it into the swim bladder when extra buoyancy is needed.

Mylvaganam et al., 1996; Berenbrink et al., 2005; Verde et al., 2007; Rummer et al., 2013

Because the density of the gases is much less than that of the body tissues, slight changes in pressure will have a pronounced effect on a fish's buoyancy. Pressure on the body of a fish increases significantly after a descent of only a fraction of a meter. The pressure compresses the swim bladder, making the fish denser and less buoyant, thereby increasing the rate of its descent. To counteract this descent, the fish must expend energy either by secreting more gas into its swim bladder or by actively swimming. Thus, gas must be secreted into the swim bladder against a pressure gradient; the deeper the fish swims, the greater the gradient.

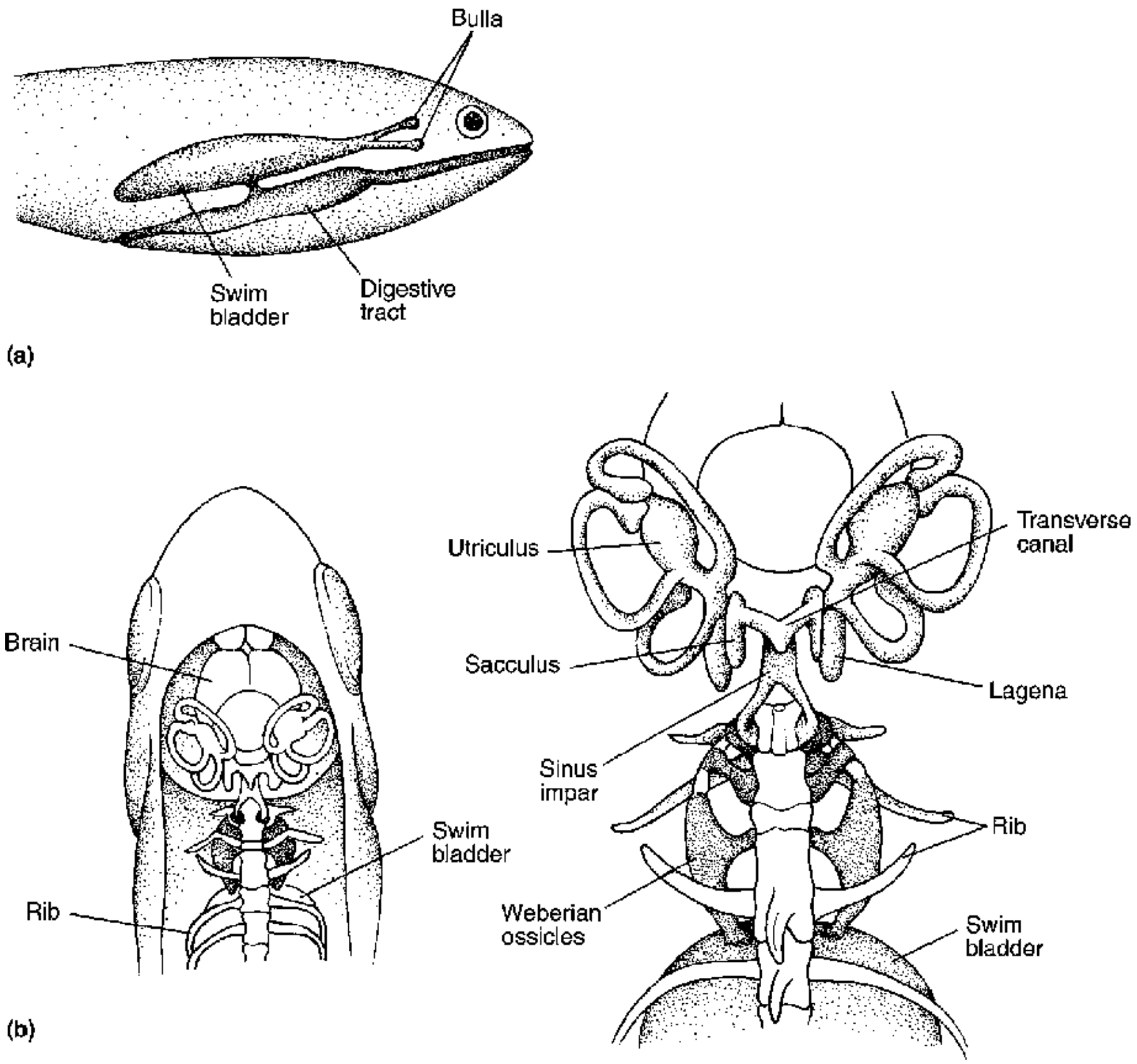


Figure 4.26. Route of sound transfer in fishes. (*a*) In some fishes, the swim bladder includes anterior extensions that contact the inner ear. (*b*) In other fishes, the Weberian ossicles, a tiny series of bones, connect the swim bladder to the inner ear.

Besides their role in regulating buoyancy, swim bladders are modified to perform other functions in some fishes. In minnows, carp, catfishes, and other members of the order Cypriniformes, the swim bladder is involved in the sense of hearing (Fig. 4.26b). A chain of small bones known as Weberian ossicles joins together the anterior end of the swim bladder and a *Y*-shaped lymph sinus known as the sinus impar (Fig. 4.26b). The connecting bones are modified portions of the first four vertebrae. The sinus impar lies adjacent to a lymph-filled canal that joins the sacculi of the right and left ears. Movements in the water cause vibrations of the gas within the swim bladder. These vibrations are transmitted by the Weberian ossicles to the inner ear. Some squirrelfishes (Holocentridae), the tarpon (Elopidae), featherbacks (Notopteridae), deepsea cods (Moridae), and sea breams (Sparidae) have forked, forward extensions of the swim bladder that end near the ear and serve to amplify sound waves (Moyle and Cech, 2004) (Fig. 4.26a). Herrings (Clupeidae) and elephantfishes (Mormyridae) have similar extensions that enter the auditory capsule and are in contact with the inner ear. Their function also is to amplify sound.

Many fishes make rasping, squeaking, grunting, or squealing noises. In some, like croakers and grunts, the noises are the result of muscles attached to the swim bladder. These contractions may cause the swim bladder to emit thumping sounds, or they may cause air to be forced back and forth between the chambers within the swim bladder.

Courtship and the Swim Bladder

The "fastest" muscle among vertebrates is used neither for fleeing predators nor for capturing food, but for sex—the courtship part. The swim bladder muscle of the toadfish (*Opsanus tau*) contracts and relaxes 200 times per second (i.e., at 200 Hz) as it makes its boat-whistle-like mating call—compared with 0.5 to 5.0 Hz for the fish's locomotory muscles. Calcium, which triggers muscle contraction, cycles through the swim bladder muscle 50 times as fast as in locomotory muscle. The muscle also may have an unusually fast version of a protein—troponin—which binds and releases calcium, and the rate at which myosin crossbridges detach from actin filaments in the muscle is 100 times as fast as in muscles used for locomotion.

Rome et al., 1996

Nervous System

Brain

In fishes, the anterior portion of the brain (telencephalon) (Fig. 4.27) consists of rather prominent olfactory bulbs and inconspicuous cerebral hemispheres. A pineal organ (epiphysis), which serves as a photoreceptor, is present in most fishes. Remnants of the parapineal organ (parietal eye) are found in some bony fishes. The cerebellum is particularly large and assists in the maintenance of posture and balance. In some species of fishes, it overlies the medulla and the midbrain.

Cranial Nerves

The conventional view that vertebrates possess 12 cranial nerves is based on mammalian anatomy, and its application to the vertebrates as a group is inaccurate. In fishes and amphibians (anamniotes), the 11th nerve is an integral part of the 10th and whether or not a 12th nerve should be recognized is controversial. Furthermore, following establishment of the nomenclature for the basic 12, a 13th anteriormost nerve was identified, and to avoid disrupting the time-honored numbering system, it was given the number 0. So anamniotes actually possess 11 cranial nerves, and amniotes have 13.

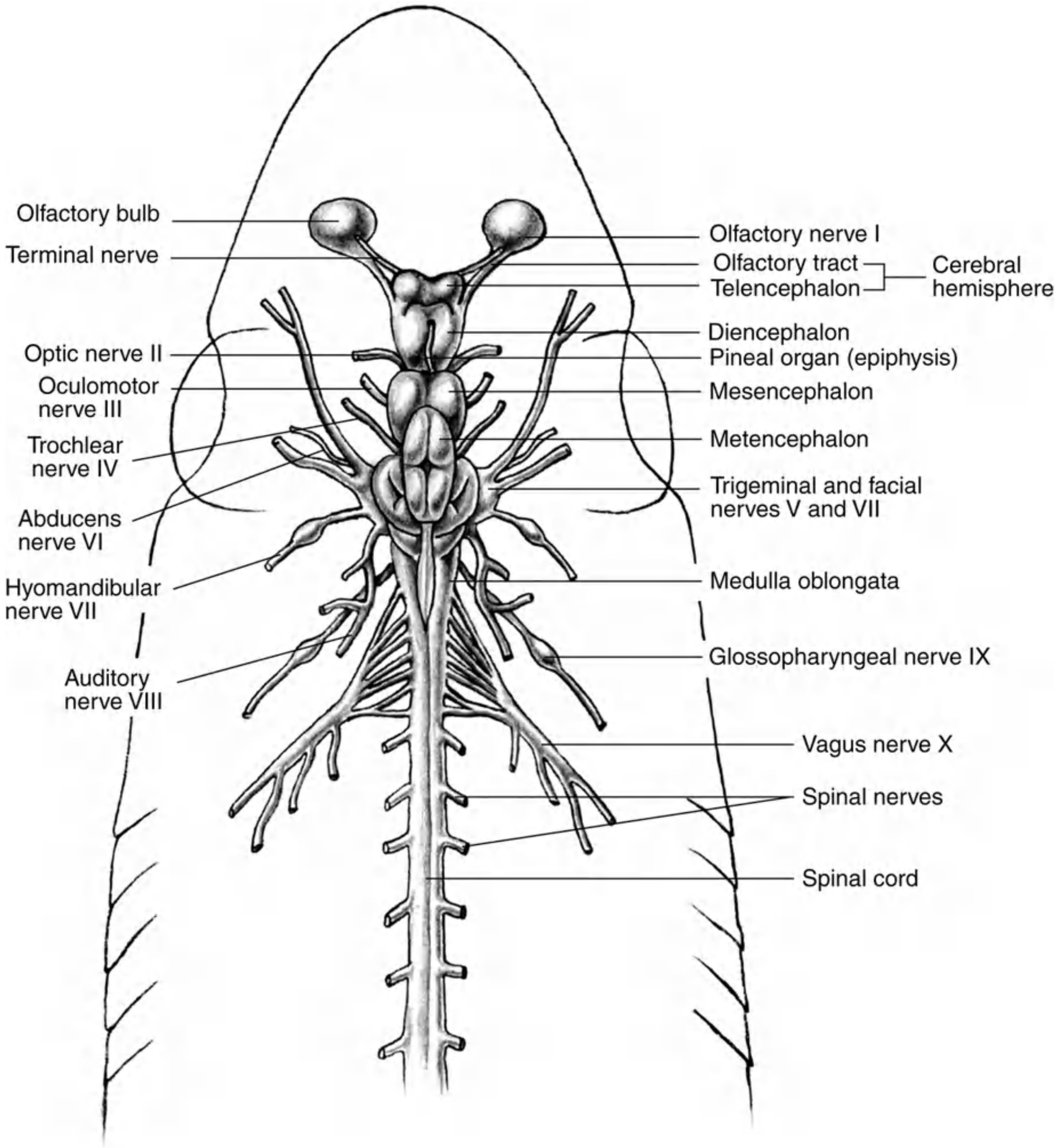


Figure 4.27. Brain, cranial nerves, and anterior portion of the spinal cord of a shark.

The first 10 (or 11) cranial nerves of all vertebrates (see Fig. 4.27) may be grouped into three categories: predominately sensory nerves (0: terminal; I: olfactory; II: optic; and VIII: vestibulocochlear), mixed nerves containing both sensory and motor fibers and serving the eyeball muscles (III: oculomotor; IV: trochlear; and VI: abducens), and mixed branchiomeric nerves (V: trigeminal; VII: facial; IX: glossopharyngeal; and X: vagus) supplying the head, neck, stomach, heart, and lungs.

The spinal cord, a portion of the central nervous system, technically begins at the **foramen magnum**, where it merges imperceptibly with the brain. It is protected by the centra and neural arches of the vertebrae as well as by fat and one or more connective tissue membranes (meninges). Paired spinal nerves emerge at regular intervals along the length of the spinal cord and innervate each body segment. In all vertebrates except lampreys, each nerve arises by a dorsal and ventral root, which then join to form the spinal nerve. In lampreys, dorsal and ventral roots alternate.

In most vertebrates, the spinal cord occupies the bony vertebral canal and extends for most of the length of the vertebral column. In fishes, however, the length of the spinal cord varies considerably. In fishes with abundant tail musculature, the cord tapers gradually and extends to the end of the tail. In some teleosts, however, the spinal cord is shortened and terminates at various distances from the end of the vertebral column. In a few species, the spinal cord is actually shorter than the length of the brain. For example, the marine sunfish *Orthagoriscus* spp. may reach a length of 2.5 m and weigh 900 kg or more. Its spinal cord, however, is less than 2 cm in length (Weichert, 1965).

Sense Organs

Sensory receptors monitor the external and internal environments. Some receptors are widely distributed over the body; others are localized. Most receptors transmit nerve impulses to the brain, where they are interpreted as sensations; some impulses are transmitted to the spinal cord and result in reflex actions.

NEUROMAST SYSTEM

Fish possess a **neuromast system** consisting of fluid-filled **pits**, **ampullae**, and **canals**. Some neuromasts open onto the surface of the skin via pores, whereas others consist of sunken canals beneath the skin. Examples of neuromast organs include lateral-line canals, cephalic canals, ampullae of Lorenzini, and pit organs. The neuromast system, which responds primarily to mechanical stimulation like water movement and sound waves, enables fish to avoid potential enemies, to orient themselves, to locate food, and to participate in schooling.

Portions of the neuromast system in some fishes, like the ampullae of Lorenzini in elasmobranchs, are sensitive to minute electrical currents in the water and are known to be **electroreceptors**. Electric currents are generated by such processes as the exchange of ions across the gills and by the contraction of respiratory muscles (see discussion on page **107**).

Whenever an electric pulse is emitted, the fish is surrounded by an electric field. When the pulse stops, the field disappears. Any object near the fish will distort the electric field and change the way the current flows over the fish's body (Cooper, 1996). This creates an electric "shadow" on the fish's body surface, which is covered with electroreceptors. From this information, the fish will sense an image and discern its size, shape, movement, and electrical properties. The weakly electric fish *Gnathonemus petersii* can measure the distance of stationary objects, independent of the objects' size, shape, or constituent material, by instantaneously analyzing the electric image of objects with a single array of electroreceptors embedded in its skin in the tail region (von der Emde et al., 1998). Because most electric fishes are nocturnal, the evolution of an electric sense was a valuable adaptation. The ability to perceive such electric fields helps these fishes orient themselves, communicate with one another, and locate prey, and it assists males in locating females during the mating season (Anonymous, 1992).

Variations in temperature as small as 1°C (1.8°F) in the gel of glycoproteins filling the ampullae in black-tip reef and white sharks has been found to produce a voltage as large as 300 microvolts (Brown, 2003). Brown concluded that a temperature change in seawater of less than a thousandth of a degree Celsius would induce a voltage in the gel filling the ampullae large enough for the shark to detect. Scientists have known for years that sharks can home in on prey that congregate at thermal boundaries, where the ocean's temperature varies by several degrees over a kilometer or so. It is thought that sharks may use their supersensitive gel to detect these subtle boundaries and assist them in finding their food.

Imprinting

Imprinting is a process of rapid, irreversible learning of a particular visual, auditory, or olfactory stimulus that occurs in the cerebrum at a critical or sensitive period during development and that influences the future behavior of the animal. Imprinting is known to occur in fishes. Juvenile salmon, for example, imprint on the distinctive odor of their natal stream before migrating to sea. The timing at which imprinting occurs has been studied extensively, and there is strong evidence that salmon imprint on their natal water during the Parr-Smolt transformation as well as during their alevin and smolt stages. Several years later, as adults, salmon use built-in geomagnetic orientation to find and return to the river's plume and mouth, and then mostly follow olfactory cues to their spawning grounds.

Hasler and Wisby, 1951; Hasler et al., 1978; Lohmann et al., 2008; Noakes, 2016; Nolan et al., 2016; Havey et al., 2017

In a school of fish, movements of individuals are extremely well coordinated and almost perfectly synchronized. Fish in a school often swim at a constant pace and maintain characteristic individual distances. They are able to monitor the swimming speed and direction of travel of neighboring fish. Thus, the school as a whole can execute complicated maneuvers that require individuals to respond quickly to changes in the velocity and direction of their neighbors.

EARS

All fishes have a series of closed tubes and sacs that compose the membranous labyrinths (inner ears) embedded in the auditory region of the skull (see Fig. 1.21). The fluid within the labyrinth is known as **endolymph**. Each labyrinth consists of three semicircular canals and two sacs (utriculus and sacculus), with each of the sacs containing particles of calcium carbonate known as **otoliths**. The utriculus and sacculus are involved primarily in maintaining **static equilibrium**, or posture: the position of the body (mainly the head) relative to the Earth's surface (i.e., with respect to gravity). The semicircular canals are involved primarily with **dynamic equilibrium**: the maintenance of the body's position in response to sudden movements like rotation, acceleration, and deceleration.

Although the membranous labyrinth serves primarily as an organ of equilibrium in fishes, in a few species it has developed the accessory function of sound transmission. A series of modified transverse processes of the first four trunk vertebrae in some fishes serve as auditory structures (see Fig. 4.26). Portions of the first four vertebrae are actually separated from the vertebrae themselves and form a chain of tiny bones that connect the swim bladder to the inner ear. This arrangement provides acute hearing. The tiny bones are known as Weberian ossicles; their action, in conjunction with the swim bladder, was discussed on page **87**.

Sound consists of regular compression waves that can be transmitted through air, water, or solids; thus, "hearing" cannot be restricted to the perception of compression in air only. Because of its greater density, water is a much more effective conductor of sound than air. Underwater, sounds will carry much farther and travel on average 4.8 times faster than in air (Moyle and Cech, 2004).

It has long been thought that most teleost fishes cannot detect sounds higher than 2 or 3 kHz (Fay, 1988). However, Mann et al. (1997) report that the American shad (*Alosa sapidissima*) can detect ultrasounds up to 180 kHz. These researchers speculate that the American shad, as well as other clupeid fishes, may be able to detect the ultrasonic clicks of one of their major predators, echolocating cetaceans (whales).

EYES

The structure of the vertebrate eye has remained remarkably constant throughout vertebrate evolution. Most fishes have two lateral eyes that serve as primary receptor sites of light (see Fig. 4.18a, b). Fishes that live in caves have vestigial eyes, are frequently blind, and, in many cases, have eyelids that do not open.

In fishes, adjustments in focus for near and far vision (called optical accommodation) are accomplished by movement of the spherical lens closer to or farther away from the cornea by muscles within the eye. This is achieved without changing the shape of the eye. The **retina**, located at the rear of the vitreous chamber, contains light-sensitive cells known as **rods** and **cones**. Colorless oil droplets are found in the cone photoreceptors of some fishes, an indication that they lack color vision (Bowmaker, 1986). Robinson (1994), however, reported colored oil droplets, and possibly tetrachromatic (color) vision in the Australian lungfish (*Neoceratodus forsteri*).

Morphological adaptations to amphibious vision are found in several groups of teleost fishes. *Anableps*, the "four-eyed fish," uses an aspherical lens and two pupils for amphibious vision (Fig. 4.28). The division of the eye into two functionally separated areas allows the fish to have optical accommodation both in water and in air. Other fishes, like the amphibious clinids *Dialommus* and *Mnierpes* and the blenniid *Coryphoblennius*, have flattened corneas that reduce refraction in air. The Atlantic flying fish *Cypselurus* uses a prism-like cornea (Jermann and Senn, 1992).

The only fishes in which adults are not bilaterally symmetrical are the soles and flounders (Pleuronectiformes). Larval flatfish are bilaterally symmetrical and possess one eye on each side of their head. As they mature and adapt to a bottom-dwelling existence, however, they become asymmetrical: one eye moves to the opposite side of the body. This movement causes modifications of muscles, skull bones, blood vessels, and nerves. Those species of flatfishes that lie on the right side of their body have both eyes on their left side; those that lie on their left side have both eyes on their right side. Although the movement of the eye is generally species-specific, there are some species that have both left- and right-eyed forms.

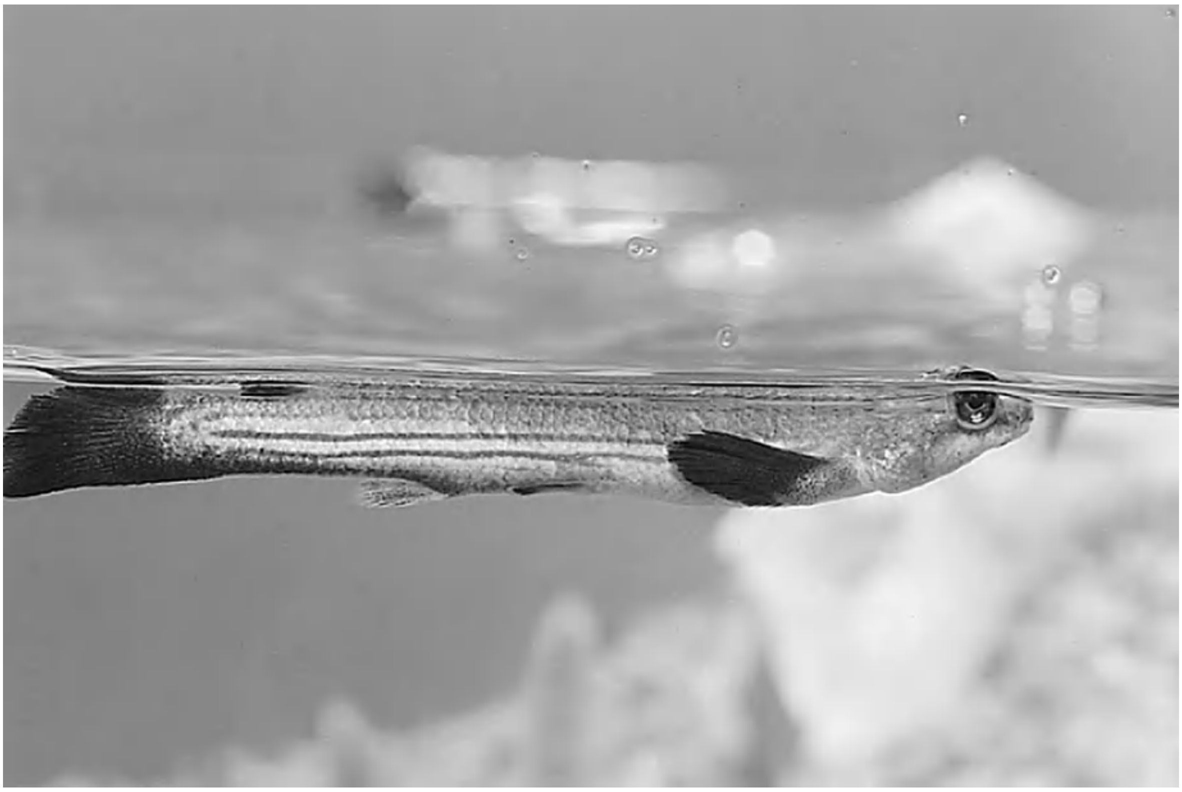


Figure 4.28. The "four-eyed" fish has the upper half of its eye adapted for vision in air above the water line while the lower half is adjusted to seeing in the water. A dumbbell-shaped pupil makes it possible to use both parts of the eye simultaneously. Most of the time, this fish is found at or close to the surface.

PINEAL AND PARAPINEAL ORGANS

Light-sensitive organs develop as a pair of sacs in the roof of the diencephalon of most fishes (see Fig. 4.27). The larger and more dorsal sac develops on the right side and is known as the **pineal organ (epiphysis)**. A **parapineal organ** develops on the left side. In lampreys and some larval fishes, the pineal and parapineal organs are both light-sensitive, but unlike lateral eyes, they do not form images. Instead, they monitor the duration of the photoperiod and intensity of solar radiation. Pineal organs are also sensitive to light in most adult fishes and appear to have importance in the control of daily and seasonal circadian rhythms (Kavaliers, 1980). These organs appear to be ultrasensitive light sensors closely connected to the brain. Gruber et al. (1975) showed that the chondrocrania of three species of sharks were modified for light transmission, and that seven times more light reached the pineal receptors than surrounding areas of the brain.

OLFACTION (SMELL)

Olfactory organs are well developed in fishes, and chemoreception in general plays an important and indispensable role in their behavior. Chemoreception is involved in the procurement of food, the recognition of sex, the discrimination between individuals of the same or different species, defense against predators, parental behavior, and migration and orientation, as well as many other activities.

The olfactory region is a blind sac in all fishes except lobe-finned fishes; in all other vertebrates, the olfactory region is connected to the oral, or pharyngeal, cavity. In fishes, each naris is divided into incurrent and excurrent apertures, so that the forward motion of the fish propels a stream of water into one aperture and out the other. Water is induced to flow through the olfactory sacs by the action of cilia within the sac, by the muscular movement of the branchial pump, by swimming, or by a combination of these actions. Olfactory cells in the olfactory epithelium monitoring the water stream can detect extremely small concentrations of certain chemicals dissolved in water. Olfactory cues have been shown to be extremely important to salmon in locating their natal stream once they have reached the vicinity of the river mouth (Hasler and Wisby, 1951; Hasler and Scholz, 1983; Brannon and Quinn, 1990; Barinaga, 1999). Researchers have found that the telencephalon and olfactory bulbs are larger in the brains of wild trout than in hatchery-reared trout (Holden, 2000b). The difference is thought to be due to environmental factors. Wild trout must contend with everything from predators to unpredictable edibles, whereas domestic fish are raised in austere environments. Sharks also possess an extremely acute sense of smell.

Magnetoreceptor cells have been located in the nose of the rainbow trout (*Oncorhynchus mykiss*) (Walker et al., 1997). Behavioral and electrophysiological responses to magnetic fields have been recorded.

TASTE

Gustatory cells (**taste buds**) are located in the roof, side walls, and floor of the oral cavity and pharynx, where they monitor incoming water, as well as on the fins and body of some species of fishes. The number of taste buds may vary greatly from one region of the body to another, but the greatest number are found in regions most closely associated with food contact. Bottom-feeders or scavengers like catfishes, carp, and suckers have sensitive chemoreceptors distributed over the entire surface of the body. Gustatory cells are also abundant on the barbels surrounding the mouth of a catfish. As taste is primarily a close-range sense, it is used in food item discrimination after other senses like smell, sight, or hearing have recognized the presence of food. Besides its function in identifying nutrients and verifying their palatability, taste receptors also permit fishes to avoid noxious substances. The gustatory system in fishes has been reviewed by Kapoor et al. (1975).

Endocrine System

Since many of the endocrine glands and hormones are similar in the different groups of vertebrates, they will be discussed here. In the other vertebrate groups, discussion will focus only on instances where a hormone has a different function from that discussed here.

The anterior lobe (adenohypophysis) of the **pituitary gland** secretes a number of hormones, some of which control the activities of other endocrine glands. **Growth hormone (GH)** stimulates body cells to grow and to maintain their size once growth is attained. **Adrenocorticotropic hormone (ACTH)** stimulates the adrenal cortex to secrete its hormones. **Thyroid-stimulating hormone (TSH)** stimulates the thyroid gland to synthesize and release thyroid hormones. Two **gonadotropic hormones** are released cyclically in response to exterior stimuli. **Follicle-stimulating hormone (FSH)** stimulates the development of ovarian follicles in the female and the development of spermatozoa in the seminiferous tubules in the male. In the female, **luteinizing hormone (LH)** induces development of a new endocrine gland, the corpus luteum, following ovulation. In males, LH is better known as **interstitial cell-stimulating hormone (ICSH)** and induces interstitial cells of the testes to produce testosterone. **Melanocyte-stimulating hormone (MSH)** controls skin pigmentation by regulating production of the pigment melanin. **Prolactin (PRL)** regulates a wide range of processes in the different groups of vertebrates. Certain parental behavior patterns are brought about by the effects of prolactin. These include activities like nest-building, the incubation of eggs, and the protection of young.

The **posterior lobe** (neurohypophysis) of the pituitary serves solely for the storage and release of neurosecretions synthesized in the hypothalamus. These include **arginine vasotocin** (oxytocin), which is a smooth muscle contractor, and **vasopressin** (antidiuretic hormone [**ADH**]), which regulates water loss.

The **thyroid gland** may be paired or unpaired. It secretes **thyroxin** and **triiodothyronine**, which control the processes of metabolism, metamorphosis, and maturation. Production of thyroxin is regulated by TSH secreted by the anterior lobe of the pituitary gland. An increase in TSH causes an increase in thyroid output, which in turn depresses the secretion of TSH. A sufficient quantity of iodine is also necessary for thyroid hormones to be produced. A third hormone, **calcitonin**, permits calcium in the circulating blood to be used for metabolic functions like bone formation, muscle contraction, and nerve transmission. Calcitonin reduces calcium levels in the blood and prevents bone resorption. Fishes lack parathyroid glands.

Adrenal glands are located on or near the kidneys. The inner portion (adrenal medulla), or its equivalent, produces **epinephrine** (**adrenaline**) and **norepinephrine** (**noradrenaline**) in all vertebrates. Both epinephrine and norepinephrine are vasoconstrictors of the circulatory system. They increase the amount of blood sugar in times of sudden metabolic need and stimulate increased production of adrenocortical hormones in times of prolonged stress. These hormones cause acceleration of the heartbeat and increased blood pressure, with increased blood flow to the heart muscle, skeletal muscle, and lungs, and decreased blood flow to smooth muscle of the digestive tract and skin. They are the primary hormones involved in the “fight-or-flight” response to fear, pain, and aggression. They help mobilize the physical resources of the body in response to emergency situations.

The outer portion of the adrenal gland (**adrenal cortex**) is essential to life. It produces **corticoids** like **aldosterone**, which regulates sodium levels by acting on the gills and/or kidneys. Secretion of aldosterone promotes the retention of sodium and the excretion of potassium by the kidney. Other corticoids secreted include the glucocorticoids **cortisone**, **cortisol**, and **corticosterone**. Together with aldosterone, glucocorticoids regulate the metabolism of carbohydrates, proteins, and fats, as well as the use of electrolytes and water.

The pancreas is a unique organ in that some cells, the **acinar** cells, function as an **exocrine gland** to aid in digestion, while other cells are part of the endocrine system and secrete hormones. Hormone-secreting cells are known as **pancreatic islets** (islets of Langerhans), and in fishes, like most vertebrates, the islets are dispersed throughout the secretory tissue of the pancreas. Islet cells in fishes may also be found in scattered locations around the gallbladder and between the pyloric caeca. Although the location of islet cells may vary somewhat in different vertebrates, the function of the pancreas is similar in all groups.

The two major pancreatic hormones are **insulin** and **glucagon**, which function antagonistically to regulate blood glucose levels. Insulin, secreted by beta cells of the islets, facilitates the assimilation of sugar by tissues and stimulates the formation of glycogen in muscle tissue and in the liver from blood glucose. Glucagon, a product of alpha cells, has the opposite action and increases blood glucose concentration.

Gonads act as endocrine organs. The ovaries and testes of most vertebrates produce three types of steroid hormones: estrogens, androgens, and progesterone. Secretion of these hormones is controlled by pituitary gonadotropins. **Estrogen** is produced by ovarian follicles. It causes formation of primary follicles and also the development of the accessory sex organs, including the reproductive tract. Maturation of follicles depends on FSHs from the pituitary gland. Secretion of estrogen is partly responsible for differentiation of the Müllerian ducts into uteri and oviducts in female embryos. Estrogen also regulates reproductive behaviors. In males, LH, also known as ICSH, from the anterior pituitary gland causes the interstitial cells of the testes to produce the male androgen, **testosterone**. Increased levels of testosterone cause the development of secondary sex characteristics and initiate the process of spermatogenesis. The failure of Müllerian ducts to develop in males is caused by increased levels of androgens. Larger muscles and bones in males are also a result of androgens. In addition, androgens regulate reproductive behavior.

Ultimobranchial bodies develop from the last pair of pharyngeal (branchial) pouches in all vertebrates. They may be known as postbranchial bodies or, in bony fishes, as suprapericardial bodies. In some fishes, amphibians, reptiles, and birds, they produce calcitonin, which removes calcium and phosphates from the circulating blood so these ions can be utilized for essential functions like bone formation, muscle contraction, and nerve transmission.

A **thymus gland** is found in all vertebrates except lampreys and hagfishes. The thymus secretes the hormone **thymosin**, which stimulates lymph glands to produce lymphocytes. It is also involved in producing antibodies and in the maturation of **T lymphocytes**, or T cells, which can distinguish foreign cells and/or substances in the body (e.g., viruses, bacteria) and destroy them; thus, the thymus provides a major defense mechanism to keep bodies free of foreign substances. It increases in size until the animal reaches sexual maturity, and then it steadily shrinks.

The pineal region in some lower vertebrates, like lampreys, contains highly specialized cells that function as photoreceptors. They function in a manner similar to that of the mammalian retina and generate impulses that are carried to the brain. As vertebrates evolved and the cerebrum grew back over the dorsal portion of the brain, the pineal organ lost much of its photoreceptivity and became primarily an endocrine organ.

The pineal gland secretes the hormone **melatonin**, which causes melanophores to aggregate in lower vertebrates. The pineal is negatively light-sensitive and secretes melatonin during darkness. Thus, pineal and blood melatonin levels exhibit daily (diurnal) rhythms. The weight of the pineal gland varies within a 24-hour cycle: its weight is lowest at the end of the daily light period (Wurtman et al., 1968; Falcon et al., 1987; Kezuka et al., 1988), and continuous light reduces the weight of the pineal gland. Considering its 24-hour cycle, the pineal may play a role in the synchronization of other 24-hour **circadian cycles** like sleeping, eating, and adrenocortical function. Although diurnal rhythms of the melatonin level in the retina have been reported in amphibians, birds, and mammals, the lateral eyes of trout apparently have no significant endocrine function as far as regulating melatonin levels in the blood (Zachmann et al., 1992).

Urogenital System

Freshwater fishes live in water that has a lower salt concentration (hypotonic) than that of their own body fluids (Fig. 4.29). They have large renal corpuscles and use water freely in excreting nitrogenous wastes. Marine fishes, on the other hand, live in water in which the salt concentration is normally higher (hypertonic) than in their own body fluids. They are in danger of losing water to their environment.

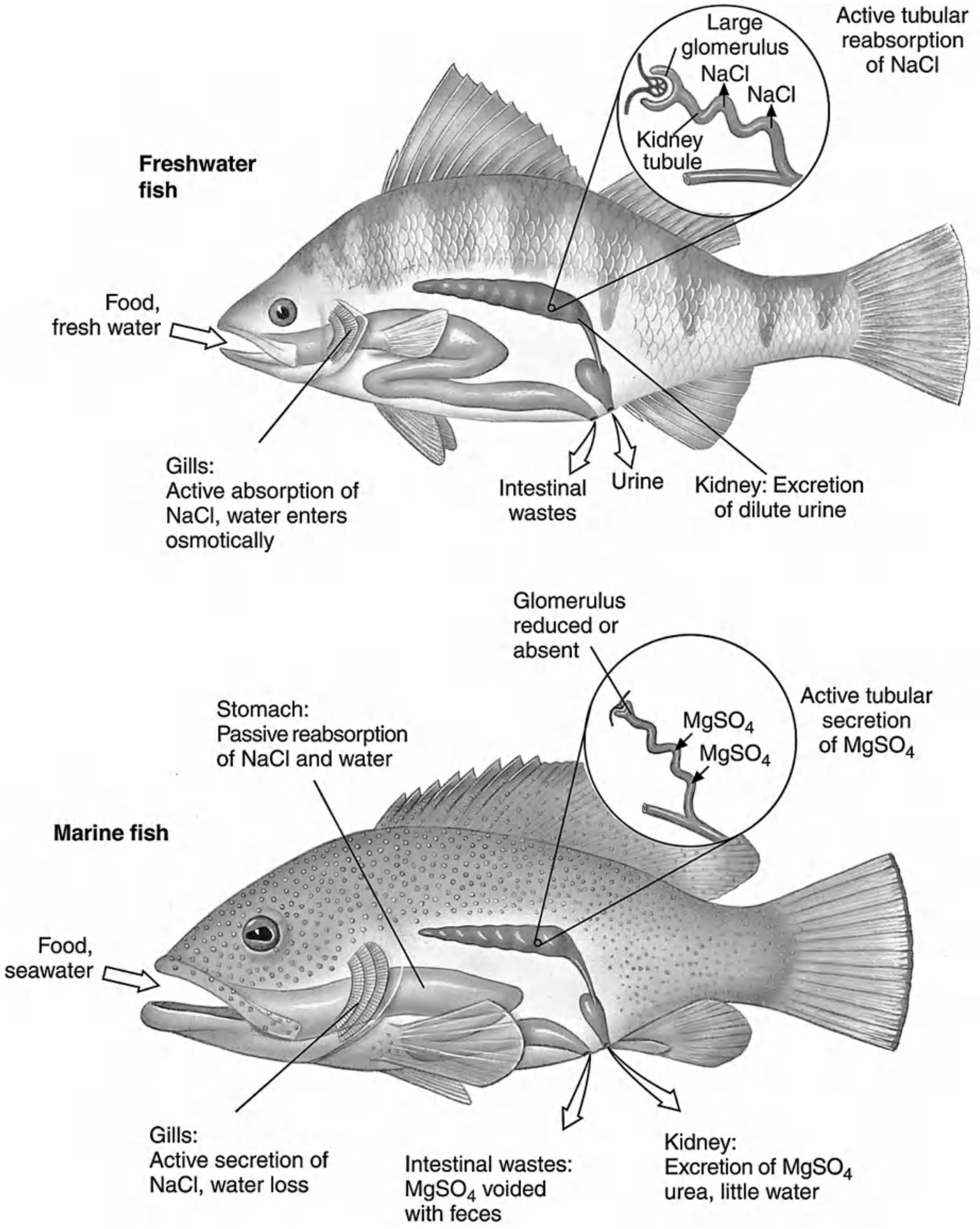


Figure 4.29. Osmotic regulation in freshwater and marine bony fishes. Freshwater fishes maintain osmotic and ionic balance in their dilute environment by actively absorbing sodium chloride across their gills (some salt is also gained with food). To flush out excess water that constantly enters the body, a glomerular kidney produces a dilute urine by reabsorbing sodium chloride. Marine fishes drink seawater to replace water lost osmotically to their salty environment. Sodium chloride and water are absorbed from the stomach. Excess sodium chloride is actively transported outward by the gills. Other sea salts, mostly magnesium sulfate, are eliminated with the feces and secreted by the tubular kidney.

With the exception of hagfishes, whose body fluids have salt concentrations similar to that of seawater, all other marine vertebrates maintain salt concentrations in their body fluids at a fraction of the level in the water (Schmidt-Nielsen, 1997). Bony marine fishes maintain osmotic concentrations of about one-fourth to one-third the level in seawater. They have reduced the size of their renal corpuscles, and they excrete excess salt through the gills. Cartilaginous fishes maintain salt concentrations in their body fluids at roughly one-third the level in seawater. They maintain osmotic equilibrium by retaining large amounts of organic compounds, primarily urea, in their body fluids. This allows these fishes to raise the total osmotic concentration of their blood so that it is equal to, or slightly exceeds, that of seawater without increasing the overall salt concentration of their body (Schmidt-Nielsen, 1997).

Many modern fishes (e.g., salmon, eels, shad, smelt) migrate during their lives between oceanic and fresh waters. Animals that do this require adaptations to control the osmotic pressure of their internal fluids. Osmoregulation is thought to be controlled by hormones: thyroxin from the thyroid gland and corticosteroids from the adrenal glands. Fishes that are **anadromous**—that is, spend most of their life in the sea and migrate to fresh water to breed, like Chinook salmon (*Oncorhynchus tshawytscha*)—must be able to prevent dilution of their fluids by the inward diffusion of water from the less concentrated external medium. In contrast, freshwater fishes passing into the sea to spawn—called **catadromous**—must prevent concentration of their fluids by loss of water to the more concentrated external medium. The most common catadromous fish in North America is the American eel (*Anguilla rostrata*). Fishes whose migration from fresh water to the sea, or vice versa, is not for the purpose of breeding but occurs regularly at some other stage of the lifecycle are referred to as **diadromous**. For example, bull sharks (*Carcharhinus*) and sawfishes (*Pristis*) move in and out of Lake Nicaragua in Central America.

Natural "Antifreeze" in Antarctic Fishes

Antarctic icefishes inhabit seawater with temperatures generally between –2°C and 4°C (28°F and 39°F). Seawater temperatures below the freezing point of fresh water (0°C or 32°F) are possible due to the dissolved salts.

Dr. Arthur DeVries discovered antifreeze proteins in Antarctic notothenioid fish in the late 1960s and was the first to describe how the proteins bind to ice crystals in the blood to prevent the fish from freezing.

Small ice crystals, inadvertently swallowed when drinking seawater, presumably exist in the bodies of notothenioid Antarctic fishes (suborder Notothenioidei). A major physiological-biochemical adaptation of these fishes is the presence of macromolecular "antifreeze" substances (sugars and amino acids) in their body fluids. Glycopeptides (glycoproteins) inhibit ice growth through a process known as adsorption-inhibition. By adsorption onto existing ice crystals, the glycopeptides produce a barrier between the ice surface and water molecules, thereby preventing further growth of the ice crystals, which could cause tissue damage. Antifreeze glycopeptides are synthesized in the liver and are found in most of the body fluids. Peak effectiveness is reached when antifreeze levels reach about 4 percent by mass.

The same molecules that keep fish from freezing in frigid polar waters may one day enable blood banks to refrigerate platelets for weeks at a time. Human platelets are disk-shaped cell fragments that help clot blood after injury. They are often given to surgery patients to limit bleeding. But unlike red blood cells, they cannot be frozen and must be used within five days. Even so, recent studies have shown that platelet mitochondrial respiratory function and activation response decrease significantly in platelets stored for three or more days. However, platelets kept in a solution containing glycoproteins derived from the blood of Antarctic or Arctic fishes last up to 21 days at 5°C (41°F). This is a completely new and innovative approach to the long-term storage problem of blood products and warrants further analysis.

Eastman, 1993; Tablin et al., 1996; Villarroel et al., 2013.

A pronephric kidney forms as a developmental stage in all vertebrates but is functional only in larval fish and amphibians. It remains throughout life only in lampreys, hagfishes, and a few teleosts as a mass of lymphoid tissue.

As differentiation of the embryo proceeds, more and more tubules form behind the pronephric tubules (see Fig. 3.16). The anteriormost tubules usually are little different from the pronephric tubules (segmentally arranged with nephrostomes), but soon the segmented arrangement (metamerism) is lost and internal glomeruli and tubules develop that lack nephrostomes. With the disappearance of pronephric tubules, the pronephric duct becomes the **opisthonephric** (mesonephric) **duct** and the newer kidney is known as the **opisthonephros** (mesonephros). The latter is the functional kidney of adult fishes and amphibians (opisthonephros) and functions as an embryonic kidney in reptiles, birds, and mammals (mesonephros). The term *mesonephros* is used in reference to the kidney that serves as an intermediate stage in the development of a vertebrate, whereas the term *opisthonephros* is used in reference to the adult kidney. They both develop from the same portion of the nephrogenic mesoderm.

The opisthonephros may extend for most of the length of the coelom as in sharks, or it may be confined to more caudal regions. In males, the anteriormost tubules of the opisthonephros have no association with glomeruli and are used solely to conduct sperm to the opisthonephric duct. This part of the kidney becomes known as the epididymal kidney, and the highly coiled part of the opisthonephric duct that drains it is the **epididymis**. The corresponding part of the opisthonephros in females may or may not degenerate.

Although most teleosts excrete ammonia, African lungfishes (*Protopterus*) are capable of excreting either ammonia, while living in an aquatic environment, or urea, while in **estivation** (i.e., in a dormant condition during droughts). Elasmobranchs, as well as the coelacanth (*Latimeria*), filter urea from the blood plasma at the glomerulus and excrete it as the primary nitrogenous end product. However, much of the urea is reabsorbed from the filtrate by the kidney tubules, thus preventing major losses of urea in the urine (Schmidt-Nielsen, 1997). The urea is retained and gives their body fluids a nearly isosmotic relationship with their environment.

Most fishes, with the exception of lampreys, hagfishes, and elasmobranchs, have a **urinary bladder**. Bladders of most fishes are terminal enlargements or evaginations of the mesonephric ducts known as **tubal bladders**.

The caudal ends of the opisthonephric ducts may enlarge to form urinary bladders or seminal vesicles for the temporary storage of sperm. In some fishes, like the lamprey and dogfish shark, the two opisthonephric ducts empty caudally into a urinary, or urogenital, papilla. When accessory urinary ducts are numerous in males, the opisthonephric ducts may be used chiefly, or entirely, for sperm transport.

Both testes and ovaries are usually paired and are suspended by mesenteries from the wall of the body cavity near the kidneys. During the spawning season, the testes are smooth, white structures that rarely account for more than 12 percent of the weight of the fish, whereas the ovaries are large, yellowish structures, granular in appearance, that may make up 30 to 70 percent of a fish’s weight (Moyle and Cech, 2004). The ovaries of most teleosts are hollow and saccular, whereas the ovaries of most other fishes are solid. A few hermaphroditic species have ovotestes, which are part ovary and part testis, and these species are capable of self-fertilization. Synchronous (or simultaneous) hermaphrodites have ripe ovaries and testes at the same time but usually spawn with one or more other individuals, alternately taking the role of male or female. Some, like the belted sandfish (*Serranus subligarius*), a small bass found only along the Florida coast, have fertilized their own eggs in captivity, but in the wild, self-fertilization is unlikely to happen because other spawning individuals are usually in close proximity. The neotropical cyprinodont *Rivulus marmoratus* can fertilize its eggs internally prior to oviposition (Harrington, 1961). Synchronous hermaphrodites are known from the following families: Chlorophthalmidae, Bathypteroidae, Alepisauridae, Paralepididae, Ipnopidae, Evermannellidae, Cyprinodontidae, Serranidae, Maenidae, and Labridae.

Female elasmobranchs have a pair of ovaries, but the left one may be greatly reduced in size in some genera (*Scyliorhinus*, *Pristiophorus*, *Carcharhinus*, *Galeus*, *Mustelus*, and *Sphyrna*). In rays, the left ovary is functional in *Urolophus*; the right ovary is completely absent in *Dasyatis* (Kardong, 2009).

A pair of oviducts and a pair of uteri arise from the Müllerian ducts (originally called pronephric ducts) in female elasmobranchs (Fig. 4.30). Oviducts possess **oviducal** (nidamental or shell) **glands** that secrete albumen (protein) and shells around the eggs. The paired ostia (anterior openings of the oviducts) unite to form a single ostium in the falciform ligament.

Most female teleosts have paired ovaries. Fusion of the ovaries occurs in some genera, like the perches (*Perca*), so that there is only one functional ovary. In the Japanese ricefish (*Oryzias latipes*) and the guppy (*Poecilia reticulata*), only one gonad develops.

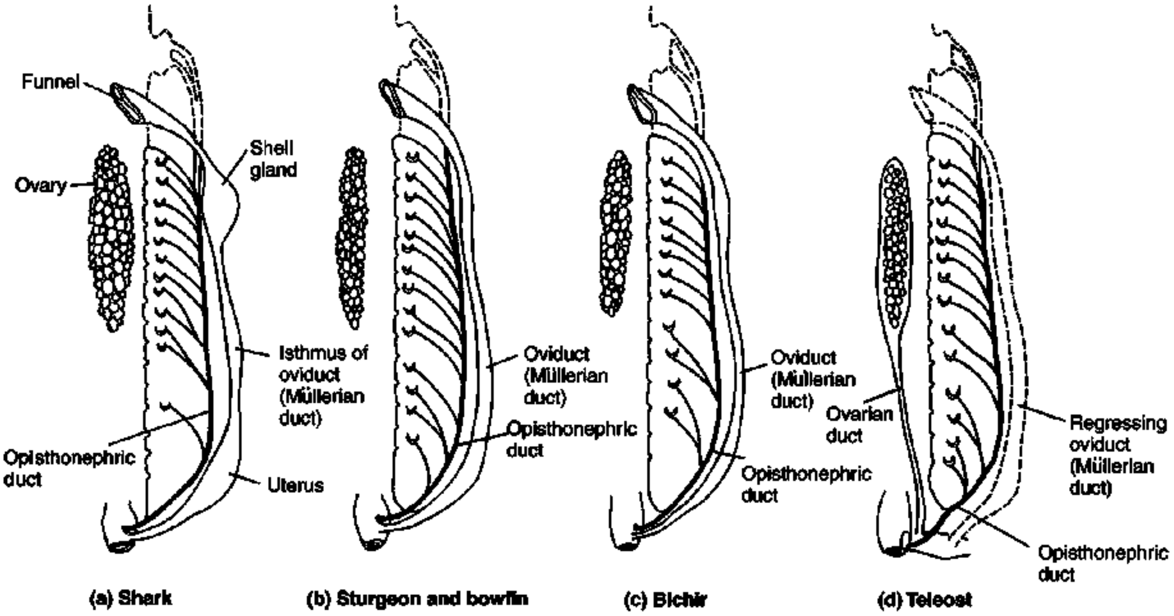


Figure 4.30. Oviducts of female fishes: (*a*) shark; (*b*) sturgeon (*Acipenser*) and bowfin (*Amia*); (*c*) bichir (*Polypterus*); (*d*) teleost. The oviduct (Müllerian duct) arises adjacent to and parallel with the opisthonephric duct in most fishes. In teleosts, the oviduct is usually replaced by an ovarian duct that is derived separately.

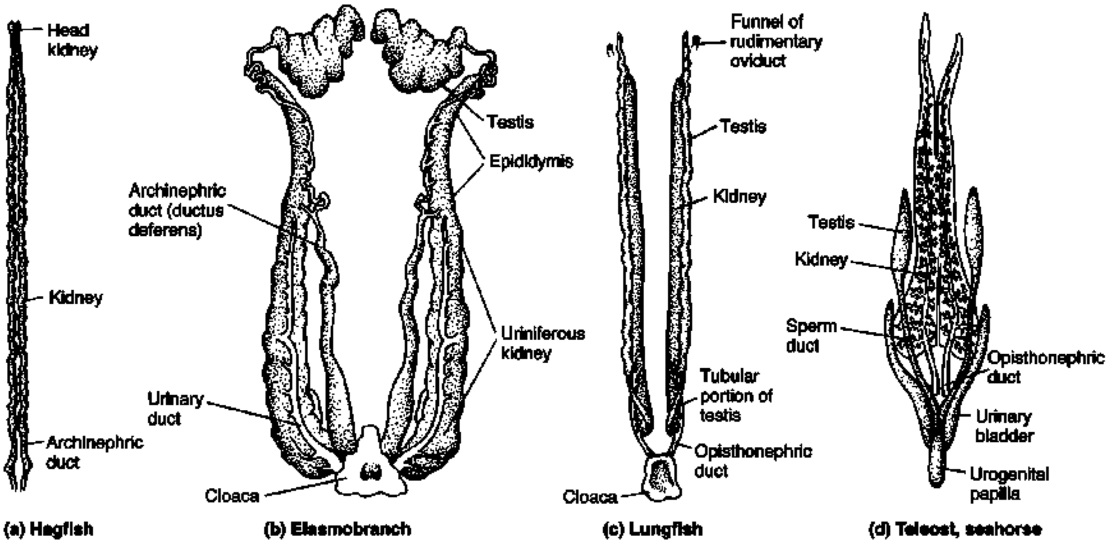


Figure 4.31. Urogenital systems of male fishes: (*a*) hagfish (*Bdellostoma*)—the single testis of the hagfish hangs in the dorsal body wall between the kidneys; (*b*) elasmobranch (*Torpedo*); (*c*) lungfish (*Protopterus*); (*d*) teleost, seahorse (*Hippocampus*).

In contrast with most vertebrates, most teleosts have oviducts that are continuous with the covering of the ovaries, so that the ova are not shed into the body cavity. Ovaries in this saccular ovary-oviduct system are known as **cystovarian ovaries** (Hoar, 1969). Most non-teleosts and a few teleosts have **gymnovarian ovaries**, in which the ovaries open into the body cavity and the ova are conveyed through an open funnel to the oviduct. These include the loach (*Misgurnus*), as well as members of the Anguillidae, Salmonidae, and Galaxiidae (Barton, 2007).

In some male fishes, like the bowfin (*Amia*), sturgeon (*Acipenser*), and gar (*Lepisosteus*), the opisthonephric duct conducts sperm as well as urine (Fig. 4.31). Connections between the opisthonephros and testes are established early in embryonic life when some of the anterior mesonephric tubules connect with a network of channels within the testes. These modified mesonephric tubules become structures known as **vasa efferentia** and carry sperm from the testes to the opisthonephric duct.

In the Salmonidae, sperm are shed directly into the body cavity and exit through an abdominal pore or pores. In Chondrichthyes, sperm pass through a duct shared with the kidney (opisthonephric duct) and may be stored in a seminal vesicle for a short time before being expelled. It is the same situation in most non-teleost bony fishes, except that a seminal vesicle is lacking. Most teleosts possess separate sperm ducts (Moyle and Cech, 2004).

Some male fishes, including sharks, skates, rays, sawfish, and guitarfish, possess intromittent organs. Elasmobranchs possess claspers—grooved digitiform appendages of the pelvic fins (see Fig. 4.35). Associated with each clasper is a muscular saclike siphon that lies just beneath the skin and fills with water just prior to mating. During copulation, the male inserts one of his claspers into the female's reproductive tract. Sperm are washed along the groove in the clasper and into the female by seawater discharged from one of the siphon sacs. The siphon sac also contributes large quantities of an energy-rich mucopolysaccharide to the seminal fluid. In many teleosts, the anal fin is modified for sperm transport and is known as a gonopodium.

REPRODUCTION

Reproductive cycles of temperate fishes are closely tied to seasonal changes in temperature, day length, and, in some cases, acidity of the water (Lam, 1983; Weiner et al., 1986). Under the influence of increasing light and temperature, the hypothalamus and pituitary glands are stimulated to produce hormones that control the development of the gonads and initiate reproductive behavioral activities and the development of secondary sexual characteristics. Temperatures above a certain level will inhibit spawning (Moyle and Cech, 2004), whereas low pH caused by acid rain has been shown to delay maturation of gonads in rainbow trout (*Salmo gairdneri*) (Weiner et al., 1986). Some fishes spawn only once as adults and then die (e.g., Chinook salmon, *Oncorhynchus tshawytscha*); others reproduce for several years (e.g., bass, *Micropterus*). In other species, sperm can be stored in females and remain viable for many months and possibly for several years.

The onset of reproductive activity (generation time) in fishes varies with sex. In many species, especially those with sexual differences in size (e.g., striped bass, *Morone saxatilis*, and sturgeon, *Acipenser*) and live-bearers (e.g., guppies, *Poecilia*, and many species of sharks), males mature at a smaller size and younger age than do females. Reproductive activity also varies with the nature of the population because a larger size may be attained at a younger age in expanding populations inhabiting favorable environments. Where the environment is favorable for growth and favors high adult survival, fishes tend to delay maturation, whereas if conditions are unfavorable, so that growth and adult survival are low, reproduction tends to take place at a younger age. Females that belong to an expanding population tend to reproduce at an earlier age than those in more stable populations (Moyle and Cech, 2004).

Various means of sexual recognition have evolved among fishes. Some, like female stingrays (*Dasyatis*), passively emit electric fields that attract males (Anonymous, 1992). A difference in form or color between the sexes of a given species is known as **sexual dimorphism** (Fig. 4.32). In many fishes, adult females are larger than adult males. This sexual dimorphism is particularly evident in those fishes that bear live young, like members of the family Poeciliidae (guppies, mollies, swordtails, and mosquitofish). In others, especially species in which males compete for females, the males are the larger sex (e.g., many coral-reef fishes).

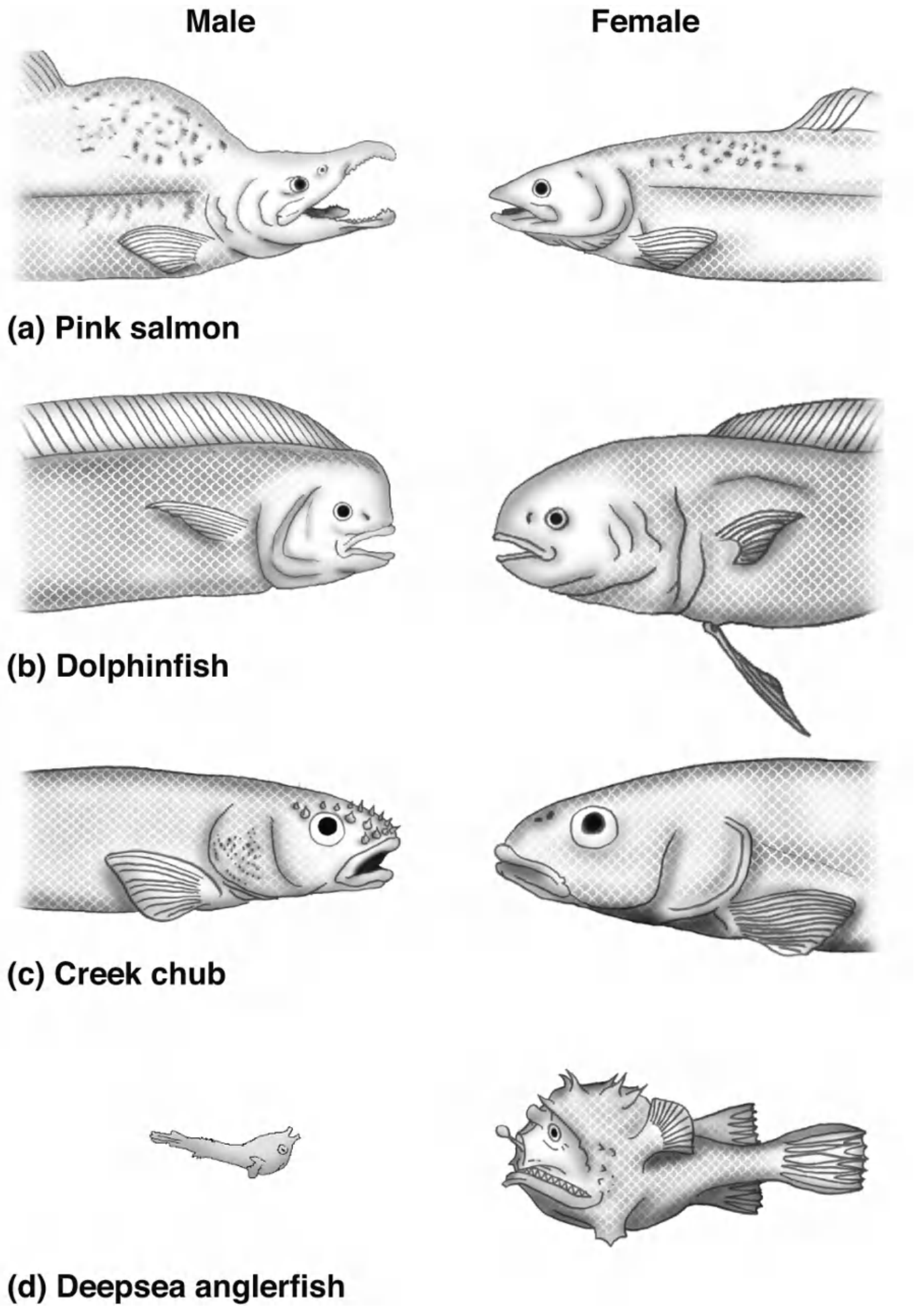


Figure 4.32. Sexual dimorphism in fishes: (*a*) humped back and hooked jaws of the male pink salmon (*Oncorhynchus gorbuscha*); (*b*) domed forehead and anterior position of the dorsal fin in a dolphinfish, or mahi-mahi (*Coryphaena hippurus*); (*c*) nuptial tubercles on the snout and forehead of a male creek chub (*Semotilus atromaculatus*); (*d*) parasitic male of the deepsea anglerfish (*Photocorynus spiniceps*).

Sexual dimorphism also may involve the development of tubercles on the heads and/or scales of males during the breeding season (see Fig. 4.32c). These structures often develop on body parts that come into contact with females and may stimulate the females to lay eggs and assist males in maintaining contact during spawning (Moyle and Cech, 2004). Males of some species, like three-spined sticklebacks (*Gasterosteus aculeatus*) and guppies (*Poecilia reticulata*), become brightly colored during the breeding season. Male sticklebacks develop a red belly or throat and a whitish back. Female sticklebacks exhibit a significant preference for males having the most intense coloration (Milinski and Bakker, 1990). Parasitization of male sticklebacks by the ciliate that causes "white spot" significantly decreases the intensity of the male's coloration and reduces the male's acceptance by females. Because tropical fishes breed all year, males typically retain their bright colors throughout the year.

Some fishes engage in elaborate courtship behavior (Fig. 4.33). The male three-spine stickleback, for example, constructs a tubelike nest and then, using a complex courtship ritual, entices the female to enter the nest. Her occupation of the nest, in turn, stimulates the male to thrust his snout against her rump in a series of quick, rhythmic, trembling movements. This induces the female to spawn. Without the stimulus of the male's tremble-thrusts, the female is incapable of spawning. Male gouramis (Helostomatidae) and Siamese fighting fish (Belontiidae) build bubble nests as part of their courtship behavior (Fig. 4.34b). As a female expels eggs from her body, the male blows them upward and into the floating nest, which he then maintains until the eggs hatch.

Most fishes do not establish long-lasting pair bonds. Males and females come together to breed and then go their separate ways. Some female mosquitofish (*Gambusia*) will mate with dozens of males during one breeding cycle. Offspring of these multiple unions are genetically more diverse than offspring of females who mate with just one male (Evans and Magurran, 2000). In addition, larger females breed many times and produce larger broods, both of which have definite survival value. Female Mediterranean blenniid fish (*Aidablennius sphynx*) may use "test" eggs to assess paternal quality (Kraak and Van Den Berghe, 1992). Females initially lay a small quantity of eggs at a male-guarded site. If the male guards the eggs successfully, she will continue laying at his site.

Most female bony fishes release eggs into the water, where sperm are deposited by males (see Fig. 4.34a). Although all sperm consist of a head containing the nucleus, a midpiece containing mitochondria that serve as an energy source, and a tail (flagellum) for locomotion, they exhibit much variation in shape. These species of fishes usually spawn in groups and do not have elaborate courtship displays or specialized reproductive structures. They depend on water currents for egg dispersal. Other fishes hide their eggs among gravel or rocks, or build nests in which eggs are buried (see Fig. 4.34b). Female salmon and trout (Salmonidae), for example, excavate redds (nests) in gravel substrates by digging with their tails. Redds are defended by both sexes. Some fishes protect the eggs while spawning and also guard the embryos until they hatch, for example, many North American minnows (Cyprinidae); in some cases, guarding extends through larval development, for example, sunfish and bass (Centrarchidae) (see Fig. 4.34b). In addition to providing extensive protection for their young, these fishes usually exhibit elaborate courtship behavior.

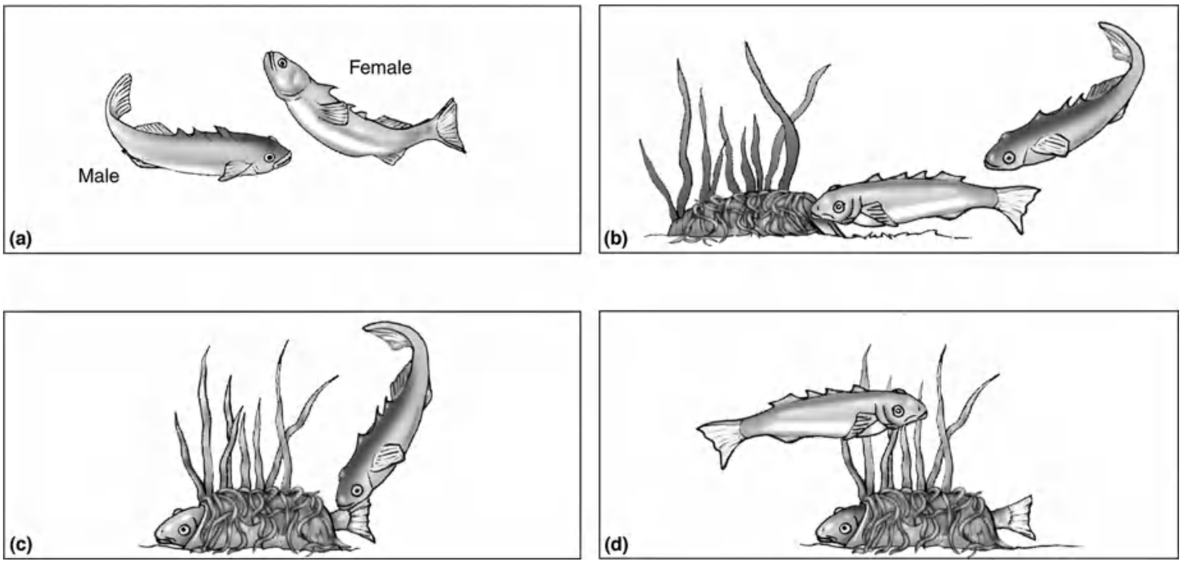


Figure 4.33. Mating behavior in the three-spined stickleback (*Gasterosteus aculeatus*). The movements that make up the courtship behavior of this species can be traced down to the activity of single muscles or groups of muscles like those that move a single fin. It has repeatedly been shown that in this species one particular movement in the behavior train acts as a stimulus for the next. The instinctive movements imply a course of patterned rather than haphazard activity. In early spring in shallow ponds and lakes, the male builds a nest of vegetation that is held together with a sticky secretion from his kidneys. After excavating a hole through the mass of vegetation, the male changes color, with his chin becoming red and his back a bluish white. (*a*) Upon finding a female, the male swims to his nest, thrusts his red snout into it, and then turns on his side and presents the fins across his back to the female. (*b*) The female then swims into the burrow in the nest. (*c*) The male follows and touches the base of her tail, an action that stimulates the female to deposit 50 to 100 eggs. (*d*) The male then enters the nest, fertilizes the eggs, and, by using his fins and tail, moves water over them to bring in additional oxygen. With fertilization accomplished, the male leaves the nest.

Fertilization in fishes is usually external. As females release eggs, sperm are released by one or more males in the same general area. In some teleosts, like *Fundulus*, the male and female interlock their anal and pelvic fins and then execute external fertilization.

Internal fertilization occurs in most cartilaginous fishes and in some teleost fishes. Males of some teleost species possess an intromittent organ known as a gonopodium that may be formed from a thickened anal spine (e.g., Embiotocidae) or a modified anal ray (e.g., Poeciliidae). Gonopodia have grooved passageways that guide sperm into the female during copulation. The shape and structure of the gonopodium in poeciliids is a key feature in the classification of this family. Sharks and rays have modified pelvic fins known as claspers (Fig. 4.35). A clasper is inserted into the female, and sperm are transported along a groove into her cloaca. Many fishes with internal fertilization, like guppies (*Poecilia* *reticulata*), dogfish sharks (*Squalus*), and coelacanths (*Latimeria*), carry the embryos until the time of birth.

Some fishes protect their eggs and/or offspring by carrying them in their mouths or in special pouches (see Fig. 4.34c). Maternal mouthbrooding is found in sea catfishes (Ariidae), cichlids (Cichlidae), cardinal fishes (Apogonidae), and bonytongues (Osteoglossidae). Females take eggs into their mouths during spawning and inhale sperm to ensure fertilization in the mouth. The brood is carried in the mouth until the young are able to swim and feed. Male sea horses (Syngnathidae), as well as some pipefishes (Syngnathidae), have a brood pouch (marsupium) on the belly into which females deposit eggs (see Figs. 4.34c and 4.36). Following incubation, the young are carried in the pouch until they can swim actively on their own.

Some fishes are **hermaphroditic**, a condition in which one individual is both male and female. Some hermaphrodites possess both male and female sex organs at the same time and are called **synchronous hermaphrodites**; others change sex as they grow and are called **sequential hermaphrodites**. Sea basses (Serranidae), for example, are synchronous hermaphrodites. Fertilization is external, and each member of the pair assumes a specific sex role associated with the release of eggs or sperm. Individuals release only one type of gamete during a spawning episode. Individuals of other species, like black hamlets (*Hypoplectrus nigricans*), take turns releasing eggs for their partners to fertilize, a mating system referred to as “serial monogamy.” Serial monogamy is common among parrotfishes (Scaridae), wrasses (Labridae), and groupers (Serranidae). The most common form of sequential hermaphroditism, called **protogyny**, occurs when females turn into males. A less common form is **protandry**, a change from male to female. Protandrous species are found among the moray eels (Muraenidae), damselfishes (Pomacentridae), and anemonefishes and porgies (Sparidae). These processes allow eggs and/or sperm to be produced when the numbers of one sex in the population are low.

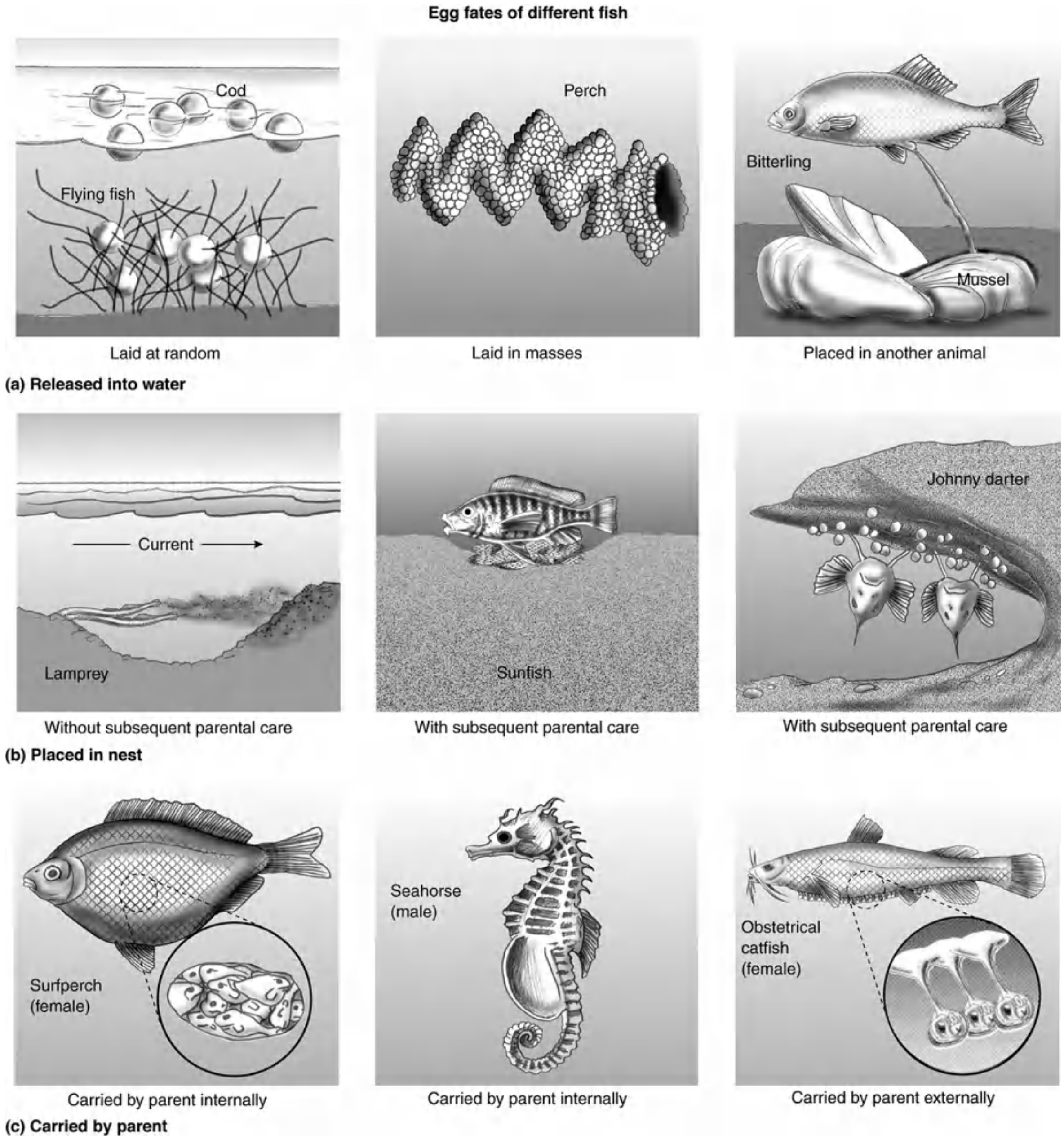


Figure 4.34. Methods of egg deposition in fishes are diverse. They range from (*a*) simply releasing the eggs into the water to (*b*) depositing the eggs in a carefully constructed nest. (*c*) In some species, the eggs are carried on or within the body of one of the parents.

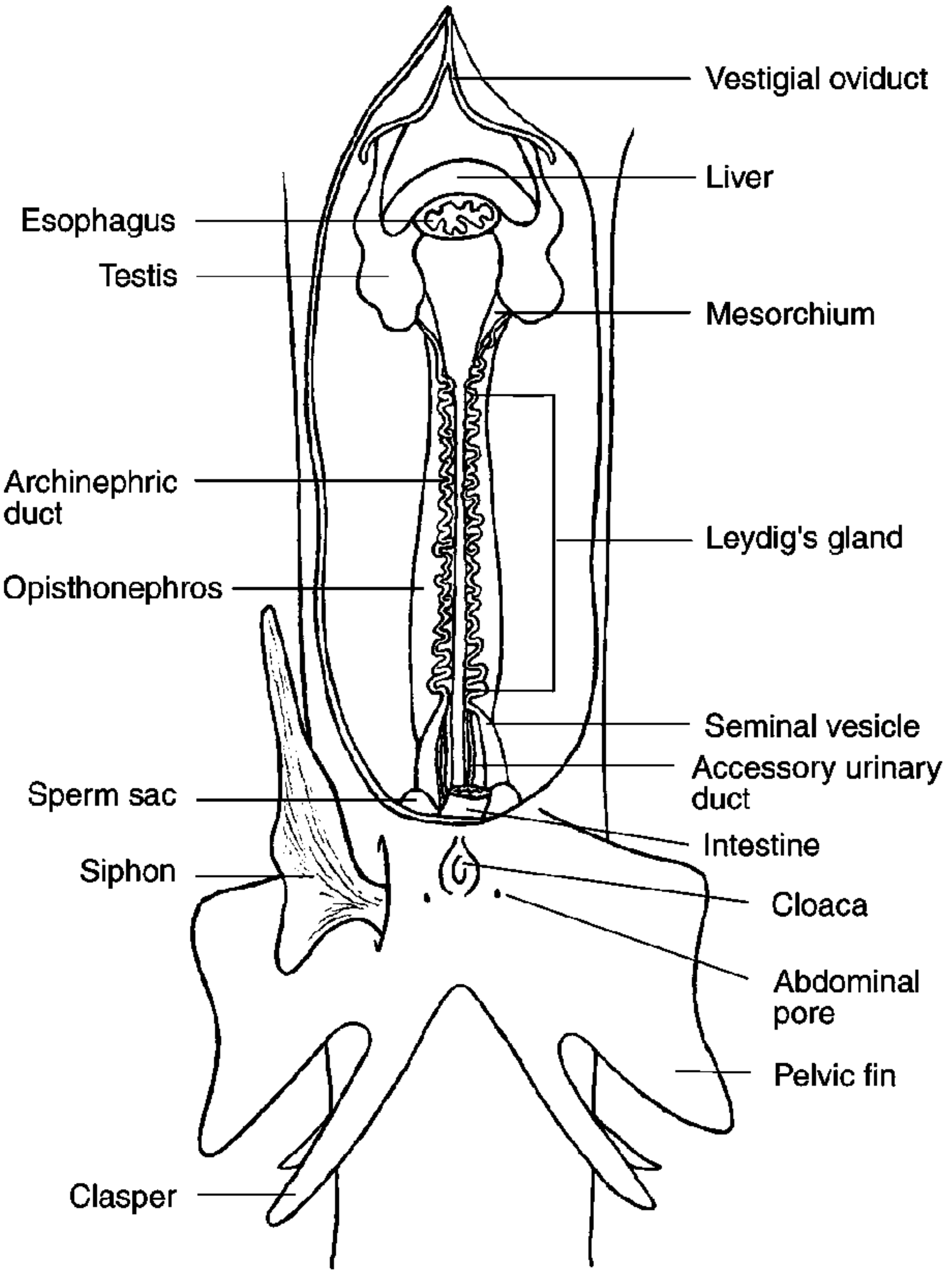


Figure 4.35. Male intromittent organs of the horn shark (*Heterodontus francisci*). Each pelvic fin is modified into a clasper (myxopterygium).

Most marine teleosts release large numbers of small, buoyant eggs that contain relatively small amounts of yolk. Some sturgeons (*Acipenser*, *Huso*), for example, may deposit as many as 5 million eggs

(Herald, 1967) and the king mackerel (*Scomberomorus cavalla*) lays more than 6 million eggs (Elgar, 1990) during each annual breeding cycle. The eggs are fertilized externally and develop and hatch while drifting in the water. This method of reproduction, which provides for wide dispersal of the young, may have evolved as a means of decreasing predation and the possibly adverse effects of local environmental changes (Moyle and Cech, 2004). Marine larvae, which usually are very different in appearance from their parents, are specialized to feed and grow for weeks or months while adrift at sea.

Freshwater fishes, on the other hand, deposit fewer eggs than marine species; these eggs are significantly larger than those of marine species because of a greater amount of yolk. Eggs hatch into juveniles with adult-like body forms. In addition, nest-building and parental care are more common in freshwater species than in marine species. Clutch size in both freshwater and marine fishes is correlated positively with fish length (Elgar, 1990): larger fishes tend to lay a greater number of relatively small eggs.

GROWTH AND DEVELOPMENT

Prenatal Development

Oviparous Species

All skates, some sharks, and many bony fishes are oviparous. Some female sharks that can store sperm release fertilized eggs over an extended period of time. These shark eggs are large and covered with tough, leathery cases, many of which have tendrils at the corners, apparently to attach the egg cases to seaweeds. Other species of oviparous fishes tend simultaneously to release vast quantities of eggs and sperm into the water. Fertilized eggs may drift with the current, or they may be deposited within a nest constructed by one or both parents. The developing embryo is nourished by yolk contained within the egg.

Viviparous Species

Viviparity is defined as the retention of fertilized eggs within the female reproductive tract. Embryos may be enclosed in a thin membrane or envelope along with a yolk supply, or they may be nourished by direct transfer of nutrients from the mother. Young are born alive. Most sharks, all rays, sawfish, guitarfish, and some bony fishes, including the coelacanth (*Latimeria chalumnae*), are viviparous. The eggs of the coelacanth are reported to be as “big as a grapefruit, the largest in any animal,” by David Noakes of the University of Guelph in Ontario (Milius, 1998c). The 12 m (39 ft.) long whale shark (*Rhincodon typus*), the largest fish in the oceans, is viviparous.

In some sharks, like the hammerhead sharks (*Sphyrna* spp.) and requiem sharks (*Carcharhinus* spp.), embryos are initially nourished by yolk, but the yolk supply is used up early in development. Remnants of the yolk sac form a placenta-like connection to the wall of the uterus, which supplies the developing young with nourishment during the remainder of the 9- to 12-month gestation period.

In the lamnoid shark (order Lamniformes), which includes the makos (*Isurus* spp.), threshers (*Alopias* spp.), crocodile sharks (*Pseudocarcharias* spp.), great white (*Carcharodon carcharias*), and sand tiger (*Carcharias taurus*), the embryos use up their yolk supply and “hatch” in the uterus after the first several months of their 10- to 12-month gestation period. The female continues to ovulate throughout the gestation period, and when the yolk supply runs out, the young ingest the nutritious eggs (Luer and Gilbert, 1991). In some species of rays that use up their supply of yolk before development is complete, young are nourished by a fluid known as uterine milk secreted by stringlike “trophonemata” that line the inner wall of the uterus (Luer and Gilbert, 1991).

Multiple matings in female guppies provide several advantages for females, including shorter pregnancies, greater numbers of offspring, and progeny that are better at evading predators (Evans and Magurran, 2000). Multiple mated females gave birth to an average of nine per brood versus only five per brood for singly mated fish. The number of days from insemination to birth was reduced by an average of eight days.

Several methods of nutrient exchange exist in viviparous bony fishes. In some, placenta-like growths form in the posterior portion of the maternal reproductive tract. Surfperches (Embiotocidae) are a small group of fishes found only along the northern Pacific coasts of North America and Asia. Females carry young in uterus-like sacs in the ovary. Body fluids of the mother that contain nutrients diffuse through greatly enlarged and highly vascularized dorsal, pelvic, and anal fins of the embryos, which are in close contact with the mother’s tissues (Moyle and Cech, 2004)

Duration of Embryonic Development

Live-bearing sharks and rays have gestation periods of 6 to 22 months (Moyle and Cech, 2004). Hatching in oviparous fishes, however, may be as short as 1 to 2 days in gouramis and coral fishes or as long as 16 months in some sharks and rays (Moyle and Cech, 2004). The rate of development generally is temperature-dependent. For example, at 10°C (50°F), trout and salmon eggs hatch in about 50 days, but at 2°C (36°F), incubation requires about 6 months. Incubation temperature also influences the development of certain segmental features of the body, like vertebrae, scale rows, and fin rays. Typically, individuals from a selected batch of eggs incubated at low temperatures will have more vertebrae, scale rows, and fin rays than their siblings incubated at higher temperatures. The opposite is true in a few species. In some species, the temperature experienced by embryos during development influences sex determination (Barton, 2007).

Hatching and Birth

Most fish embryos produce hatching enzymes that assist in digesting the membrane enclosing them at the time of hatching. In many bony fishes, secretions come from special glands on the head or inside the mouth (Barton, 2007).

Turquoise killifish (*Nothobranchius furzeri*) that hatch after unpredictable rains in Mozambique can mature from hatchling to ready-to-breed adult in 14 days (Vrtilek et al., 2018). A rapidly vanishing puddle dictates the need for speed. This is the record for the fastest known sexual maturity among vertebrates. When puddles dry, fertilized eggs can stay viable without hatching for months until it rains again.

The sex of some fishes, like the Atlantic silverside (*Menidia menidia*), is determined in part by the temperature of the water when the young are born (Conover and Kynard, 1981). Low temperatures early in the season produce females; higher temperatures later in the year yield males.

Parental Care

Parental care is lacking in oviparous elasmobranchs and in most other fishes. However, some species spend a great deal of time preparing a nest, oxygenating the eggs, and guarding the eggs and young. All three genera of lungfishes lay large, yolky eggs in nests formed by scooping out depressions in the pond bottom where the water is shallow. In the African lungfish, *Protopterus*, males guard their nests and may beat the water with their tails to scare away predators and, perhaps, to aerate the nest (Thomson, 1991).

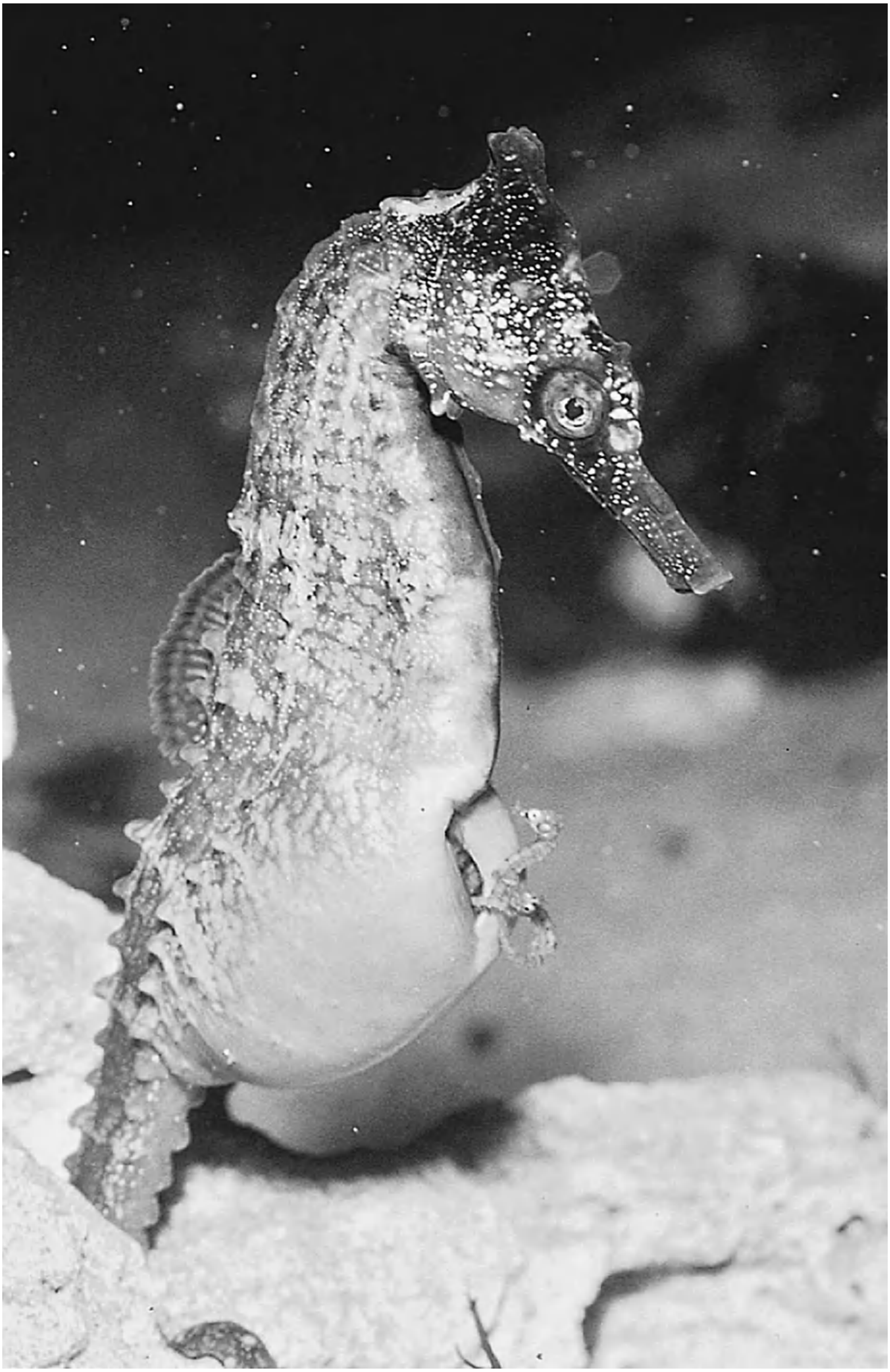


Figure 4.36. Female sea horses deposit their eggs in a brood pouch on the abdomen of the male. The eggs are incubated and hatched inside the sealed brood pouch. The young are expelled once they are capable of swimming on their own.

Salmon and trout excavate a nest (redd) and bury the eggs for protection. Several species, like gouramis, build bubble nests for their floating eggs. Eggs of some species adhere to the bodies of adult fish and are transported with them. Some fishes carry eggs and/or young with them in brood pouches (sea horses, pipefishes, some catfishes) (Fig. 4.36). Mouth-brooders, like sea catfishes (Aridae), cichlids (Cichlidae), cardinal fishes (Apogonidae), and bonytongues (Osteoglossidae), carry the eggs, embryos, and sometimes even larval fishes in their mouth cavities.

Growth and Metamorphosis

The life of an oviparous fish is divided into four stages: embryo, larva, juvenile, and adult. Most of the embryonic stage is passed within the egg, although it may continue for a short time after hatching while the embryo’s nutrition is still derived from yolk (Fig. 4.37). The **larval** period begins when the fish is able to catch food organisms. During this time, the skeleton and other organ systems become fully formed, and the fins develop. In most species, there is no dramatic development that signals the end of the larval stage and the beginning of the juvenile stage; it is a gradual, progressive transition. In the **juvenile** stage, the fish and its organ systems grow considerably in size; thus, this is usually a period of rapid growth. During this stage, which lasts until the gonads mature, the fishes may be distinctively colored. When gonads mature, the fish is able to spawn and is considered to be an **adult**.

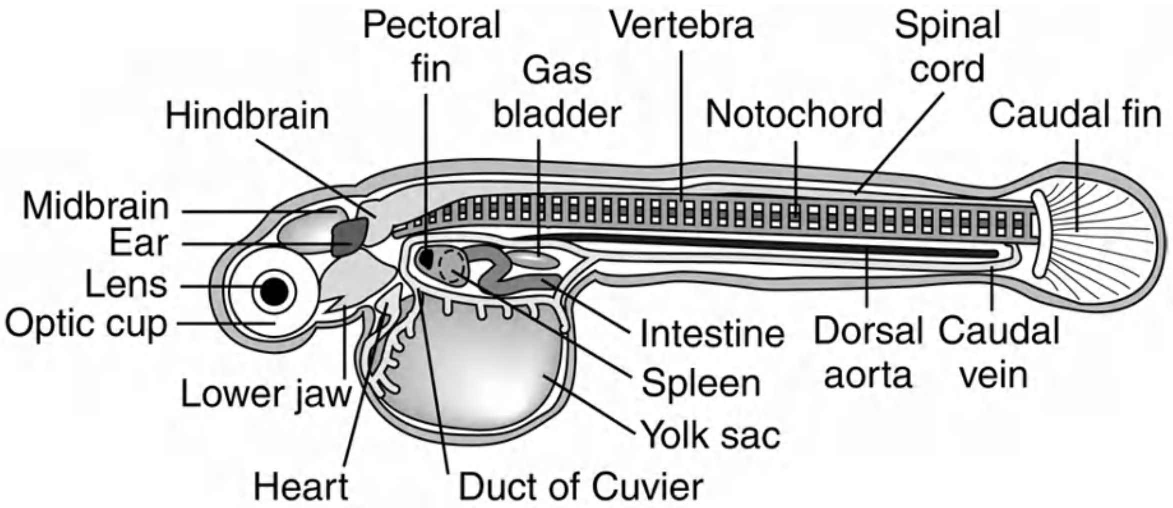


Figure 4.37. Embryo of the mummichog (*Fundulus heteroclitus*) at hatching. The embryo is nourished by the yolk contained within the egg. At hatching, a small amount of yolk remains within the yolk sac.

Those species of fishes that have undergone their development within the female's reproductive tract are well developed at birth and are born as miniature adults. Thus, there is no larval life stage.

Adult fishes range in size from about 6 to 8 mm (1/4 to 1/3 in.) to the giant whale shark, which is 12 m (39 ft.) long. The largest freshwater fish ever captured is believed to be a 294 kg (646 lb.), 2.7 m (9 ft.) long Mekong giant catfish that was caught in May 2005.

Attainment of Sexual Maturity

The time required to reach sexual maturity in most fishes ranges from several weeks to several years. Some, like members of the viviparous perch family (Embiotocidae), become sexually mature a few weeks after birth (Moyle and Cech, 2004). Other species, like salmon (*Oncorhynchus*), usually spawn when 4 or 5 years of age.

Longevity

Nelson (2016) noted that maximum longevity in fishes was probably about 120 years, with some sharks along with such species as sturgeons and paddlefishes probably being among the longest-lived. Researchers can learn about the age of marine creatures by finding traces of atomic radiation in their tissues, resulting from atmospheric tests of thermonuclear weapons since the mid-1950s. Dating based on forms of carbon found in sharks' eye lenses suggests that a large female

Greenland shark (*Somniosus microcephalus*) was about 392 years old (give or take 120 years) when she died (Nielsen et al., 2016). Even with the uncertainty, the shark outdoes the previous marine record holder: a bowhead whale estimated to have lived 211 years. The Greenland shark is one of the largest carnivores in the world. Unlike bony fishes, such as salmon and cod, sharks do not have ear bones that build up calcified rings that reveal age. Some sharks, such as great whites, have some calcified vertebrae, but the Greenland shark is a "soft shark."

Review Questions and Topics

1. What advantages are conferred on an organism by having vertebrae that are differentiated into various types?
2. Distinguish between ostracoderms and placoderms. What important evolutionary advances did each contribute to vertebrate evolution?
3. Discuss the theories concerning the origin of paired fins.
4. Why was the discovery of the first living coelacanth (Latimeria) in 1938 of such great importance to scientists?
5. Compare the functions of paired fins and unpaired median fins like the dorsal and caudal fins.
6. What is the function of the bulbous arteriosus in fish? Why is it not present in birds and mammals?
7. Why is an operculum important to bony fishes and not to most cartilaginous fishes? What functions does it perform?
8. Explain the mechanism by which bony fishes control their buoyancy.
9. Trace the pathway that food would follow from the time it enters the mouth of a largemouth bass until it is absorbed into the bloodstream.
10. How are spiral valves and villi similar?
11. Why wouldn't you expect birds to have taste buds distributed over their entire body surface, as a catfish does? What adaptive advantage does this arrangement afford the catfish?
12. When (or under what conditions) are freshwater fishes in danger of excessive water intake ("drowning") and marine fishes in danger of dehydration? What mechanisms has each group evolved to counteract these problems?

13. Which hormones influence male reproductive function?
14. Differentiate between oviparous and viviparous. Give an example for each.
15. Compare and contrast the advantages and disadvantages to the female of external versus internal fertilization.

Supplemental Reading

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Vertebrate Internet Sites

1. Introduction to the Chondrichthyes

   www.ucmp.berkeley.edu/vertebrates/basalfish/chondrintro.html

   University of California at Berkeley, Museum of Paleontology. Images, photos, and systematics.

2. Sharks and Their Relatives

   www.seaworld.org/animals/all-about/sharks-and-rays

   Classification, habitat and distribution, physical characteristics, senses, behavior, diet, reproduction, anatomy and physiology, longevity, photographs, and bibliography.

3. Neopterygii

www.ucmp.berkeley.edu/vertebrates/actinopterygii/neopterygii.html

Characteristics, range, photos, and links.

4. Teleostei

   www.ucmp.berkeley.edu/vertebrates/actinopterygii/teleostei.html

   Images, photos, systematics, and links.

5. Actinopterygii

   www.tolweb.org/Actinopterygii

   Photos, classification, and links.

6. Teleostei

   www.tolweb.org/Teleostei

   A cladogram, phylogenetic relationships, characteristics, and references on teleost fishes.

7. Introduction to the Actinopterygii

   www.ucmp.berkeley.edu/vertebrates/actinopterygii/actinintro.html

   Images, photos, systematics, and links.

5 | Amphibians

Many of the medicines we use today, to fight everything from AIDS to cancer, originate as a toxin in an amphibian skin. When we lose these animals, we lose resources. We lose keystone species in the environments where they live.

Jeff Corwin, 2009

INTRODUCTION

Amphibians are the first quadrupedal vertebrates evolutionarily that can support themselves and move about on land. They have a strong, mostly bony, skeleton and usually four limbs (tetrapod), although some are legless. Webbed feet are often present, and no claws or true nails are present. The glandular skin is smooth and moist. Scales are absent, except in some caecilians that possess concealed dermal scales. Gas exchange is accomplished either through lungs (absent in some salamanders), through gills, or directly through the skin. Amphibians have a double circulation consisting of separate pulmonary and systemic circuits, with blood being pumped through the body by a three-chambered heart (two atria, one ventricle). They are able to pick up airborne sounds because of their tympanum and columella and to detect odors because of their well-developed olfactory epithelium.

The emergence of a vertebrate form onto land was a dramatic development in the evolution of vertebrates. Some ancestral vertebrate evolved a radically different type of limb skeleton with a strong central axis perpendicular to the body and numerous lateral branches radiating from this common focus. This transition had its beginnings during the Early to Middle Devonian period and took place over many millions of years (Fig. 5.1). It involved significant morphological, physiological, and behavioral modifications. A cladogram showing presumed relationships of early amphibians with their aquatic ancestors, as well as with those amphibians that arose later, is shown in Fig. 5.2. Phylogenetic relationships depicted in such diagrams are controversial and subject to a wide range of interpretations.

EVOLUTION

Controversy surrounds the ancestor of the amphibians. Was it a lungfish, a lobe-finned rhipidistian, or a lobe-finned coelacanth? Rhipidistians, which are now extinct, were dominant freshwater predators among bony fishes. Did amphibians arise from more than one ancestor and have a polyphyletic origin, or did they all arise from a common ancestor, illustrating a monophyletic origin? Are salamanders and caecilians more closely related to each other than either group is to the anurans?

Great gaps in the fossil record make it difficult to connect major extinct groups and to link extinct groups to modern amphibians. These so-called missing links are a natural result of the conditions under which divergence takes place. Evolution at that point is likely to have been rapid. Any significant step in evolution probably would take place in a relatively small population isolated from the rest of the species. Under such conditions, new species can evolve without being swamped by interbreeding with the ancestral species, and the new species and new habits of life have more chance of survival. The chances of finding fossils from such populations, however, are minute. In addition, as amphibians became smaller, their skeletons became less robust and more delicate due to an evolutionary trend toward reduced ossification. These factors increased the likelihood of the skeletons being crushed before they could fossilize intact.

The extinct lobe-finned rhipidistian fishes, which were abundant and widely distributed in the Devonian period some 400 Mya, have been regarded by some investigators as the closest relatives of the tetrapods (Panchen and Smithson, 1987). One group of rhipidistians, the osteolepiforms (named in reference to the earliest described genus *Osteolepis*, from the Devonian rocks of Scotland), had several unique anatomical characters. One of the best-known osteolepiforms was *Eusthenopteron foordi* (see Fig. 5.3). These fishes possessed a combination of unique characteristics in common with the earliest amphibians (labyrinthodonts) (Figs. 5.4 and 5.5). Along with most of the bony fishes (Osteichthyes), rhipidistians had both gills and air passageways leading from their external nares to their lungs, so that they presumably (there is no concrete evidence, because no fossils of lungs exist) could breathe atmospheric air. If the oxygen content of the stagnant water decreased, respiration could be supplemented by using the lungs to breathe air. The skeletons of rhipidistians were well ossified, and their muscular, lobed fins contained a skeletal structure amazingly comparable to the bones of the tetrapod limb. Such fins may have given these fishes an adaptive advantage by facilitating mobility on the bottoms of warm, shallow ponds or swamps with abundant vegetation (Edwards, 1989), to move short distances over land to new bodies of water, and/or to escape aquatic predators (Fig. 5.6). Palatal and jaw structures, as well as the structure of the vertebrae, were identical to those of early amphibians. The teeth have the complex foldings of the enamel—visible as grooves on the outside of each tooth—that are also found in the earliest labyrinthodont ("labyrinth tooth") amphibians.

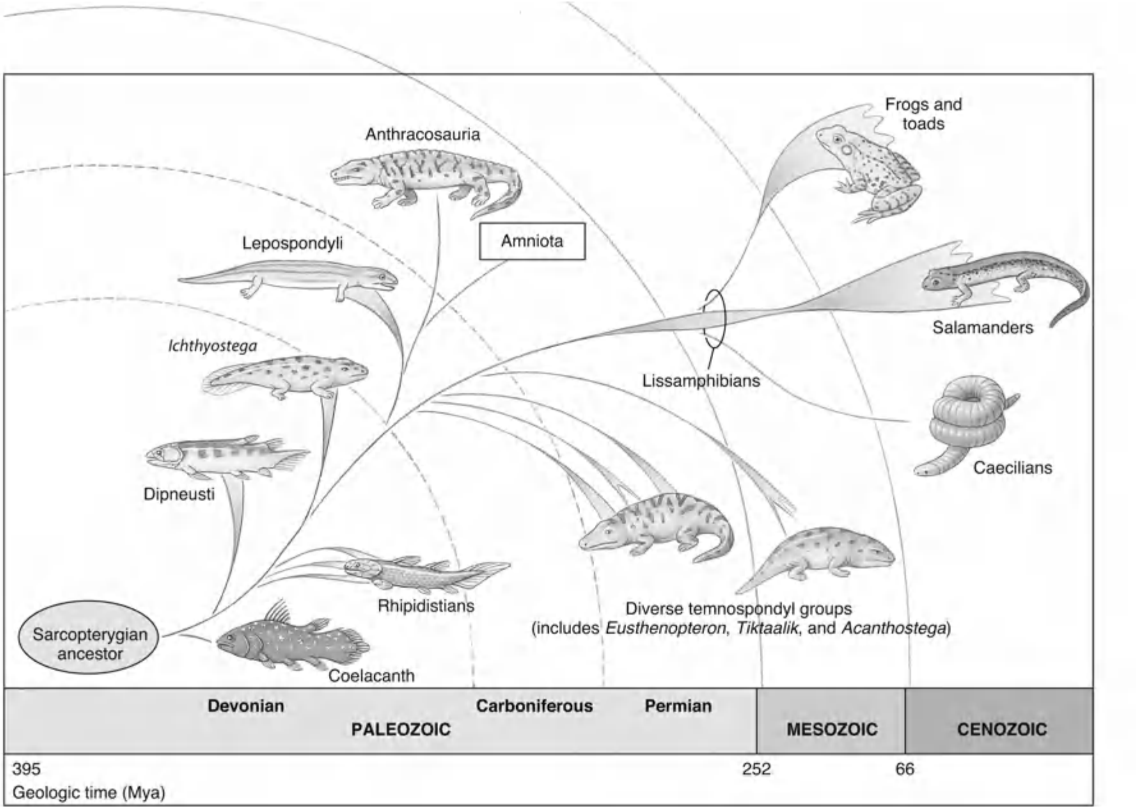


Figure 5.1. Early tetrapod evolution and the rise of amphibians. The tetrapods share their most recent common ancestry with the rhipidistians of the Devonian. Amphibians share their most recent common ancestry with the temnospondyls of the Carboniferous and Permian periods of the Paleozoic and the Triassic period of the Mesozoic.

The skull and jaw bones of *Elginerpeton pancheni* from the Upper Devonian (approximately 368 Mya) in Scotland exhibit a mosaic of fish and amphibian features (Ahlberg, 1995). Appendicular bones (amphibian-like tibia, robust ilium, incomplete pectoral girdles) exhibit some tetrapod features, but whether this genus had feet like later amphibians or fishlike fins has not been established. The genera *Elginerpeton* and *Obruchevichthys* from Latvia and Russia possess several unique derived cranial characters, and so they cannot be closely related to any of the Upper Devonian or Carboniferous amphibians. Instead, they form a clade that is the sister group of all other Tetrapoda.

Specimens of 382-million-year-old fossils from Canada's Ellesmere Island, above the Arctic Circle, are remarkably complete and currently represent the oldest known stem tetrapod (Daeschler et al., 2006). The find included three nearly complete skeletons of *Tiktaalik roseae*, a creature with the fins, scales, and gills of a fish ranging in size from 1 to 2.7 m (3–9 ft.) long. The front fins had bones analogous to a shoulder, upper arm, elbow, forearm, and a primitive version of a wrist (Shubin et al., 2006). From the shoulder to the wrist area, the fin basically looked like a scale-covered arm. In addition, *Tiktaalik* had nostrils, a neck, and tetrapod-like ribs that could help support its body on land (Clack, 2006). *Tiktaalik* probably spent most of its time in shallow water, but it could also come out onto land in search of prey. It probably relied on both gills and lungs to obtain oxygen.

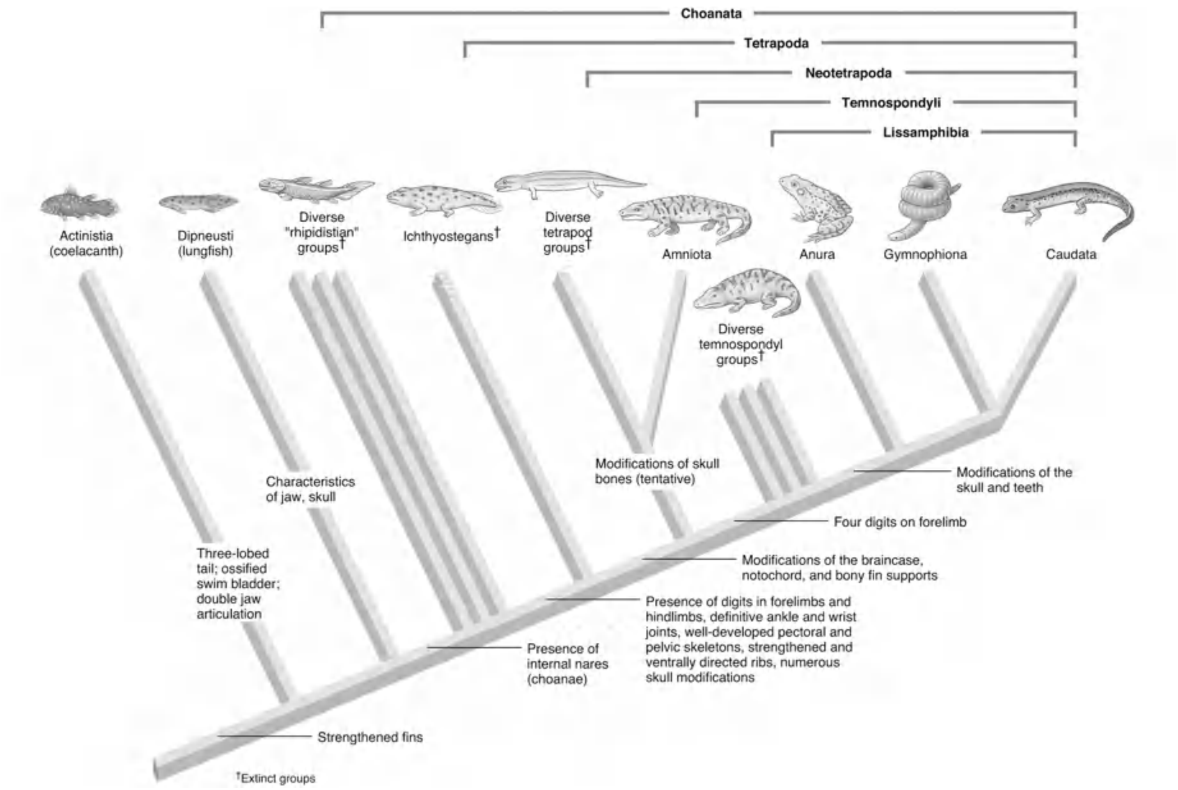


Figure 5.2. Tentative cladogram of the Tetrapoda, with emphasis on the rise of the amphibians. Some of the shared derived characters are shown to the right of the branch points. All aspects of this cladogram are controversial, including the monophyletic representation of the Lissamphibia. The relationships shown for the three groups of Lissamphibia are based on recent molecular evidence.

Prior to the discovery of *Tiktaalik*, the closest known relative to early tetrapods was a 376-million-year-old fish known as *Panderichthys*. Its proto-limbs were fleshy and ended in fins.

The 365-million-year-old fossil skull, shoulders, and part of the pelvis of a primitive four-legged creature, *Ventastega curonica*, was reported from Latvia in 2008 (Ahlberg et al., 2008). While *Elginerpeton* was slightly older, it was more fish than tetrapod. *Ventastega* is more tetrapod than fish. *Ventastega* was 1 to 1.2 m (3–4 ft.) long and probably swam through shallow brackish waters and ate other fish.

Pederpes finneyae, a 350-million-year-old fossil from Dumbarton, Scotland (Clack, 2002), is advanced over its Devonian predecessors in having only five toes on the foot, yet it has a relic of a tiny finger on the forelimb reminiscent of the supernumerary digits of the best-known amphibians—*Ichthyostega* and *Acanthostega*—from the Upper Devonian. The toes are pointed forward like those of modern tetrapods rather than sideways like those of its aquatic ancestors. Although the foot structure indicates that the animal could walk on land, its ear structure and other features of its skull, like grooves for lateral-line canals—a characteristic of fish—suggest that *Pederpes* spent much of its time immersed in the brackish waters of coastal wetlands. It was a short-limbed, large-skulled predator, resembling an especially ungainly crocodile. Although the full length of the tail is not known, the animal was probably nearly a meter in length. It almost certainly reproduced in the water.

Claims of tetrapod trackways predating *Panderichthys* and *Tiktaalik* have remained controversial with regard to both age and the identity of the track makers. However, Niedźwiedzki et al. (2010) present well-preserved and securely dated tetrapod tracks from Polish marine tidal flat sediments of early Middle Devonian age that are approximately 18 million years older than the earliest known tetrapod body fossils and from 10 million years before *Tiktaalik*.

Some researchers feel that the sole surviving crossopterygian, the coelacanth (see Fig. 4.6a), is the closest extant relative of tetrapods. Evidence supporting this hypothesis has been presented by Gorr et al. (1991), who analyzed the sequence of amino acids in hemoglobin, the protein that carries oxygen through the bloodstream. This study concluded that coelacanth hemoglobin matched larval amphibian hemoglobin more closely than it matched the hemoglobin of any other vertebrate tested (several cartilaginous and bony fishes, larval and adult amphibians). As might be expected, considerable controversy has been generated by these findings since extinct forms like rhipidistians could not be analyzed for comparison.

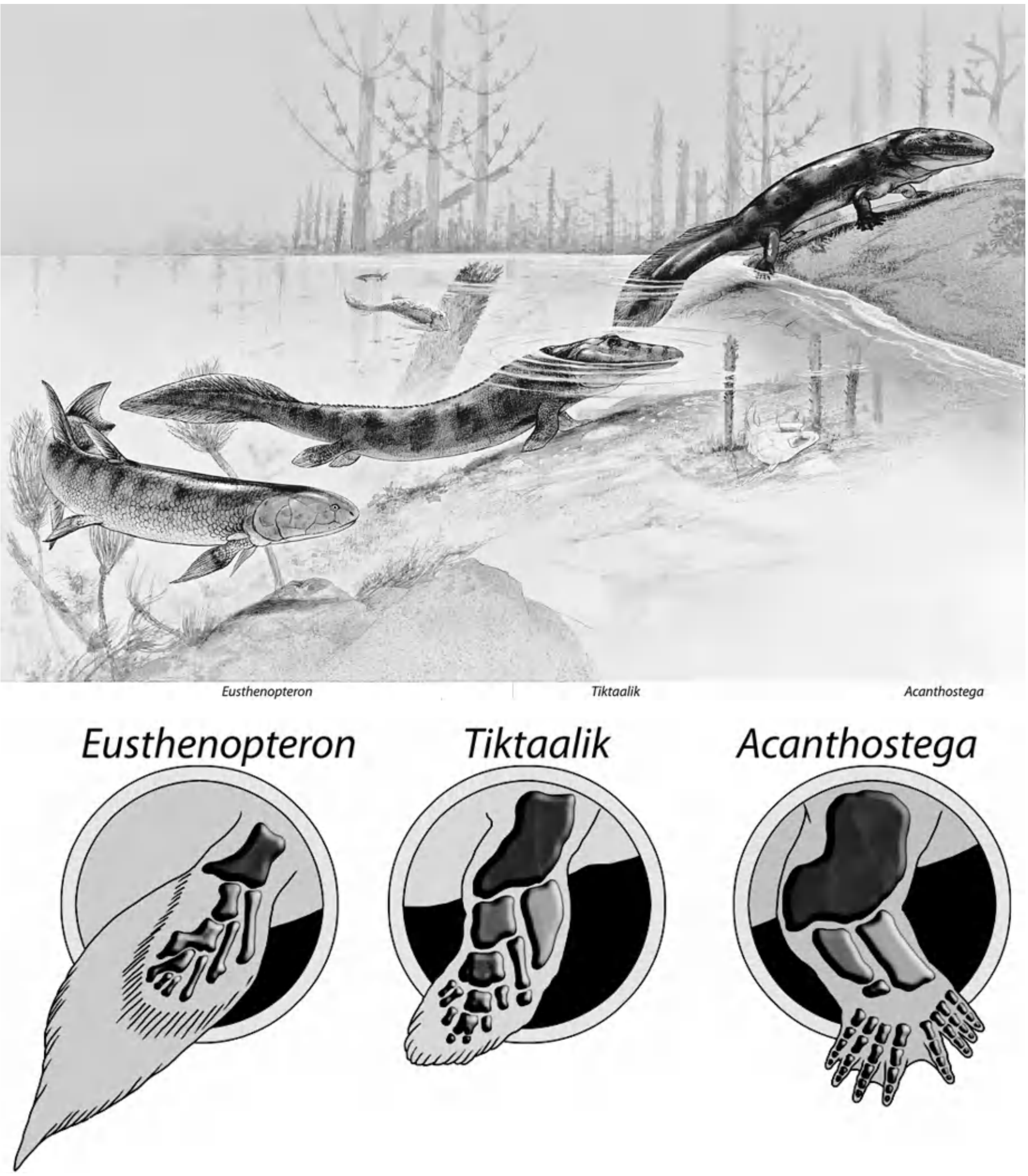


Figure 5.3. From fish to amphibian. An artist's rendering of the functional evolution of tetrapod limbs from a lobe-finned fish (*left*) through an intermediate transition stage represented by *Tiktaalik* (*center*) to a labyrinthodont amphibian (*right*).

Based on the most extensive character set ever used to analyze osteolepiform relationships, Ahlberg and Johanson (1998) presented evidence showing that osteolepiforms were paraphyletic, not monophyletic, to tetrapods. Their analyses revealed that tetrapod-like character complexes (reduced median fins, elaborate anterior dentition, morphology of a large predator) evolved three times in parallel within closely related groups of fishes (rhizodonts, tristichopterids, and elpistostegids). Thus, Ahlberg and Johanson concluded that tetrapods are believed to have arisen from one of several similar evolutionary "experiments" with a large aquatic predator.

Still other researchers (Rosen et al., 1981; Forey, 1986, 1991; Meyer and Wilson, 1991) have presented convincing anatomical and molecular evidence favoring lungfishes as the ancestor. Forey (1986) concluded that "among recent taxa, lungfishes and tetrapods are sister-groups, with coelacanths as the plesiomorphic sister-group to that combined group." Meyer and Wilson (1991) found lungfish mitochondrial DNA (mtDNA) was more closely related to that of the frog than the mtDNA of the coelacanth. Zardoya and Meyer (1997a) reported that a statistical comparison using the complete coelacanth mtDNA sequence did not point unambiguously to either lungfishes or coelacanths as the tetrapods' closest sister group. However, when Zardoya and Meyer (1997b) reanalyzed their data, they concluded that they could "clearly reject" the possibility that coelacanths are the closest sister group to tetrapods. (The possibility that coelacanths and lungfishes are equally close relations of tetrapods, although unlikely, could not be formally ruled out.) At present, most paleontologists and ichthyologists reject the lungfish hypothesis.

Some researchers consider tetrapods to have arisen from two ancestral groups. Holmgren (1933, 1939, 1949, 1952) considered tetrapods to be diphyletic, with the majority being derived from one group of fossil fish, the Rhipidistia, and the rest (the salamanders) being derived from lungfishes (Dipneusti). As recently as 1986, Jarvik (1980, 1986) continued to argue that tetrapods were diphyletic, with salamanders being separately derived from a different group of rhipidistians (the Porolepiformes) than were other tetrapods, whose ancestry is traced to the rhipidistian Osteolepiformes. Benton (1990) considered the class Amphibia to be "clearly a paraphyletic group if it is assumed to include the ancestor of the reptiles, birds, and mammals (the Amniota)."

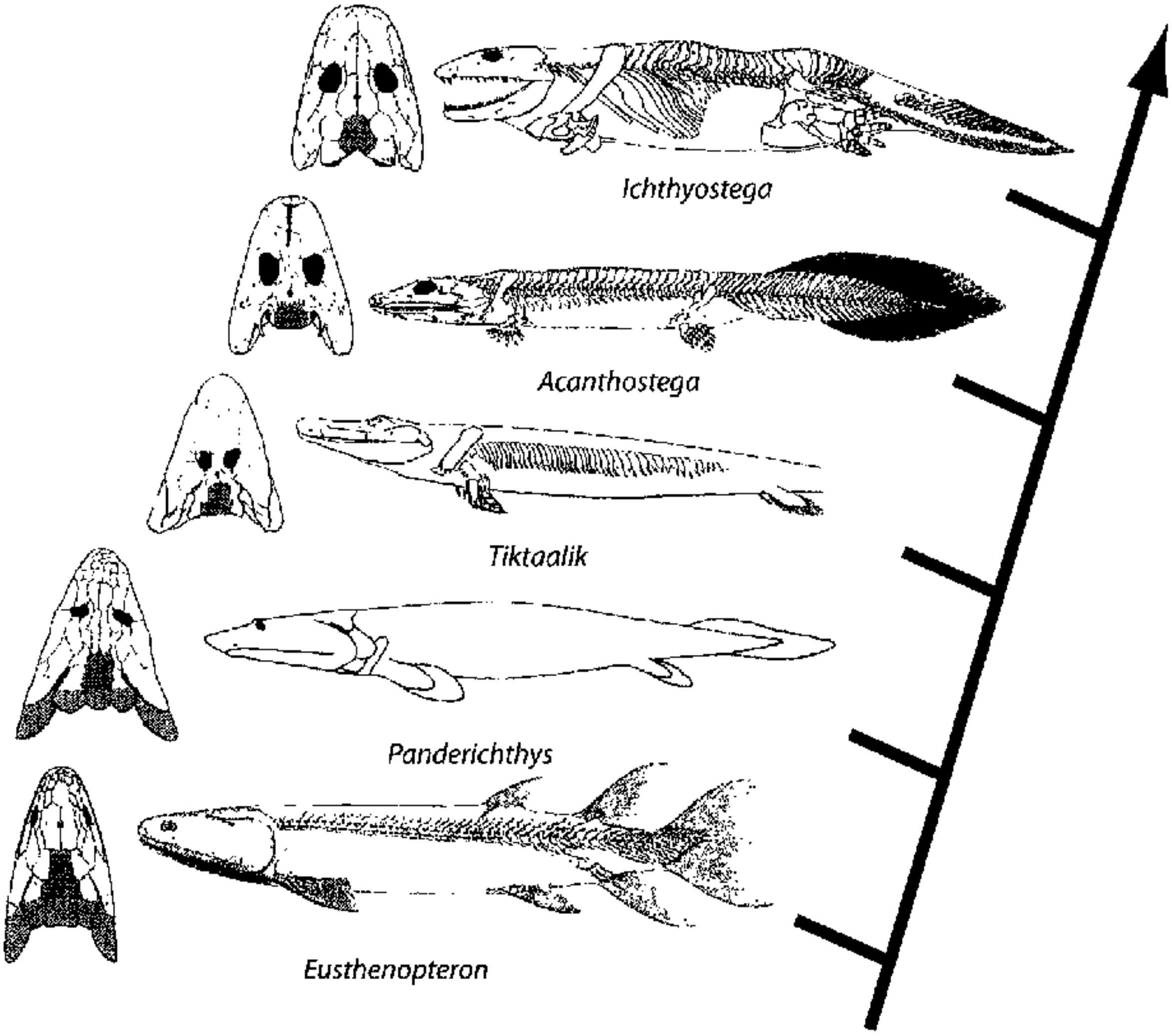


Figure 5.4. *Tiktaalik* in context. The lineage leading to modern tetrapods includes several fossil animals that form a morphological bridge between fishes and tetrapods. Five of the most completely known are the osteolepiform *Eusthenopteron*, the transitional forms *Panderichthys* and *Tiktaalik*, and the primitive tetrapods *Acanthostega* and *Ichthyostega*. The vertebral column of *Panderichthys* is poorly known and not shown. The skull roofs show the loss of the gill cover, reduction in size of the postparietal bones, and gradual reshaping of the skull.

The Devonian period saw great climatic fluctuations, with wet periods followed by severe droughts. As bodies of water became smaller, they probably became stagnant and more eutrophic as dissolved oxygen dropped dramatically. They also probably became overcrowded with competing fishes. With their lobed fins and their ability to breathe air, ancestors to the tetrapods could have moved themselves about in the shallow waters and onto the muddy shores (see Fig. 5.3). Lobed fins with their bony skeletal elements, along with lateral undulations of the fish's body wall musculature, could have allowed these fishes to move across land in search of other bodies of water. This movement would be similar to the movements of the walking catfish (*Clarias*) of today, which uses its pectoral spines along with lateral undulations to “walk” on land, or mudskippers (*Periophthalmus*), which climb out of the water and “walk” on mudflats and along mangrove roots on their pectoral fins. Thus, lobed fins and the ability to breathe air may have allowed increased survival as an aquatic animal, and then later allowed movement overland. These ancestral semiamphibious groups may have been moving temporarily onto land to avoid predators or to seek arthropod prey. Early Devonian arthropod faunas are known from North America, Germany, and the United Kingdom and may well have been an abundant food source (Kenrick and Crane, 1997). These arthropods included centipedes, millipedes, spiders, pseudoscorpions, mites, primitive wingless insects, and collembolans. Little by little, modifications occurred that allowed increased exploitation of arthropod prey, and time spent on land increased.

The class Amphibia is divided into three subclasses: Labyrinthodontia, Lepospondyli, and the subclass containing all living amphibians, Lissamphibia.

Labyrinthodontia

The earliest known amphibians are the labyrinthodonts (order Ichthyostegalia) (see Fig. 5.6), and the earliest known labyrinthodont fossils are from Upper Devonian freshwater deposits in Greenland. Labyrinthodonts appear to have been the most abundant and diverse amphibians of the Carboniferous, Permian, and Triassic periods. At the present time, two families and three genera are recognized, with the best-known genera being *Ichthyostega* and *Acanthostega*. The name *Ichthyostega* means “fish with a roof,” referring to its primitive fishlike structure and the thick roof of its skull. The first *Ichthyostega* fossils were discovered in 1932. Both *Ichthyostega* and *Acanthostega* lived about 365 Mya in what is now Greenland.

Ichthyostega was a fairly large animal (approximately 65–70 cm) that exhibited characters intermediate between crossopterygians and later tetrapods (see Figs. 5.1 and 5.2). It had short, stocky limbs instead of fins. Jarvik (1996) provided evidence of pentadactyl hind feet (five digits) and refuted the statements of Coates and Clack (1990) that each hind foot contained seven digits. The pentadactyl limb is an ancestral vertebrate characteristic. The skull was broad, heavily roofed, and flattened, and it possessed only a single occipital condyle (rounded process on the base of the skull that articulates with the first vertebra). Ichthyostegids possessed rhachitomous “arch vertebrae” similar to those of some crossopterygians. The snout was short and rounded, and an opercular fold was present on each side of the head. The tail was fishlike and had a small dorsomedial tail fin partially supported by dermal rays. *Ichthyostega* probably was primarily aquatic, as evidenced by the presence of lateral-line canals, but it likely could move about on land using its short, but effective, limbs (Clack, 2006).

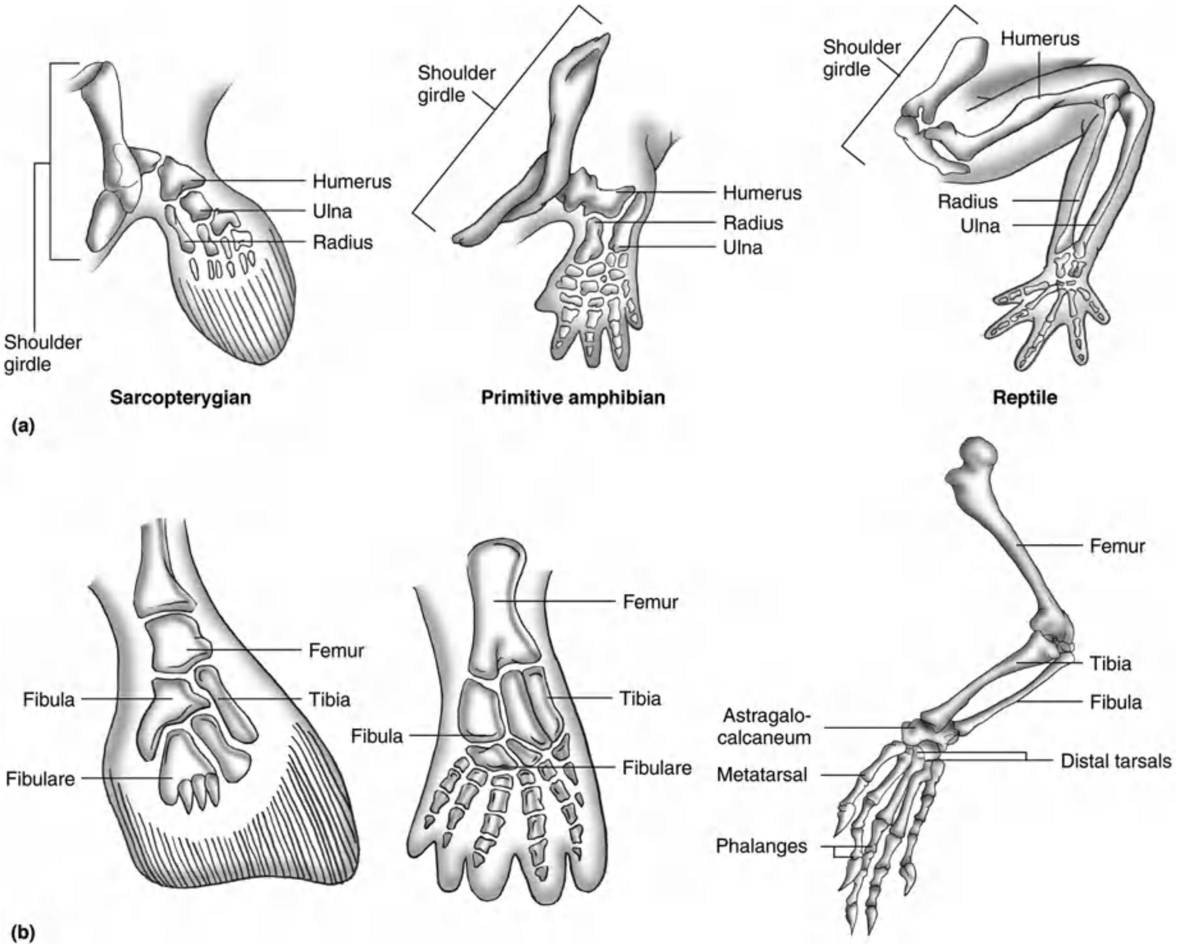


Figure 5.5. Forelimbs (*a*) and hindlimbs (*b*) of a sarcopterygian, a primitive amphibian, and a reptile.

The branchial (gill) skeleton of *Acanthostega gunnari* from the Upper Devonian (about 363 Mya) has revealed structural details similar to those of modern fishes (Coates and Clack, 1991; Coates, 1996). These features indicate that *Acanthostega* "retained fish-like internal gills and an open opercular chamber for use in aquatic respiration, implying that the earliest tetrapods were not fully terrestrial" (Coates and Clack, 1991). Fishes differ from tetrapods in that their pectoral girdles are firmly attached to the back of the skull by a series of dermal bones; these bones are reduced or lost in tetrapods. *Acanthostega* retains a fishlike shoulder girdle, similar to that in lungfishes, *Neoceratodus*. Both forelimbs and hindlimbs are thought to have been flipper-like, and the forelimb contained eight fingers (Coates and Clack, 1990, 1991). Limbs with digits probably evolved initially in aquatic ancestors rather than in terrestrial ones. They could have provided increased maneuverability among aquatic plants and fallen debris in shallow waters near the edges of ponds and streams.

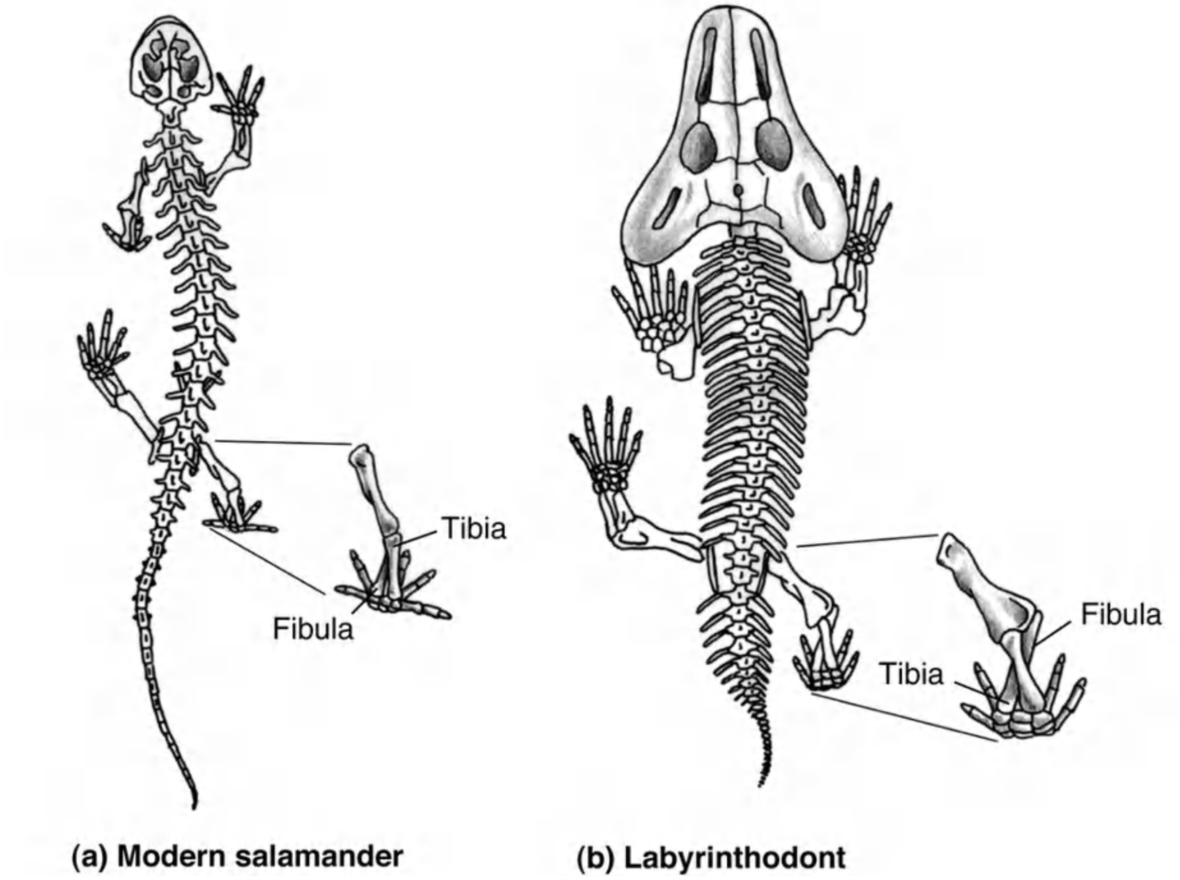


Figure 5.6. Modern salamander (*a*) and ancient labyrinthodont (*b*). Lateral undulations of the body are used to extend the stride of the limbs. The forward planting of the feet requires the crossing of the tibia by the fibula and thus places twisting stress on the tarsus.

In a comparative study of the forelimb bones from several individuals of both *Ichthyostega* and *Acanthostega*, Callier et al. (2009) concluded that the pattern of muscle attachment processes on small humeri in *Ichthyostega* resembled that in "fish" members of the tetrapod stem group, like *Tiktaalik*, whereas large humeri approached the tetrapod crown-group condition; in *Acanthostega*, both small and large humeri exhibited the crown-group pattern. They concluded that *Ichthyostega* underwent greater locomotory terrestrialization (more time spent on land by older individuals than by younger ones) during ontogeny, and that the newly recognized characteristics suggest that *Ichthyostega* could be phylogenetically more basal than *Acanthostega*. The authors concluded that they had captured the oldest fossil evidence for a developmental transition between aquatic and terrestrial environments.

The discovery in Upper Devonian deposits in Scotland of the tibia of *Elginerpeton* bearing articular facets for ankle bones (and thus feet) is strongly suggestive of tetrapod affinity and represents the earliest known tetrapod-type limb (Ahlberg, 1991). This find pushed back the origin of tetrapods by about 10 million years. Previously, the closest known relative to early tetrapods was a 376-million-year-old fish known as *Panderichthys*, whose proto-limbs were fleshy and ended in fins. Because tetrapod or near-tetrapod fossils have been described from the Upper Devonian (about 370 Mya) of Pennsylvania in the United States, Greenland, Scotland, Latvia, Russia, and Australia (Ahlberg, 1991; Daeschler et al., 1994), a virtually global equatorial distribution of these early forms was established by the end of the Devonian.

Two other groups of labyrinthodonts evolved: the temnospondyls and the anthracosaurs. Members of the order Temnospondyli had two occipital condyles and a tendency toward a flattened skull. They were more successful as amphibians than the order Anthracosauria, which was a short-lived group (but which were ancestral to the turtles and diapsids). The ancestor of turtles and diapsids is thought to have diverged from the main anthracosaur line during the Late Mississippian period (approximately 360 Mya). The temnospondyls, which may have given rise to the living amphibians, died out by the end of the Triassic (245 Mya). Three full-body imprints of foot-long temnospondyls were discovered in sandstone rocks from eastern Pennsylvania in 2007 (Lucas, 2007). The imprints show the shape of the body and the texture of the skin, features that are not discernible in bones.

Numerous problems had to be overcome in order to survive on land. Some have been solved by the amphibians; others were not overcome until reptiles evolved. One major problem was locomotion. The weight of the body in a terrestrial vertebrate is passed to the legs through the pectoral and pelvic girdles. The general consensus is that the primitive bony elements of the ancestral fish fin gradually differentiated into the bones of the tetrapod forelimb (humerus, radius, ulna, carpals, metacarpals, and phalanges) and hindlimb (femur, tibia, fibula, tarsals, metatarsals, and phalanges). The girdles and their musculature were modified and strengthened. Even today, however, most salamanders cannot fully support the weight of their bodies with their limbs. They still primarily use a lateral undulatory method of locomotion, with their ventral surfaces dragging on the ground. Salamander appendages project nearly at right angles to the body, thus making the limbs inefficient structures for support or rapid locomotion. Not until reptiles evolved did the limbs rotate to a position more beneath the body.

Although the earliest amphibians probably were covered by scales, the evolution of the integument and the subsequent loss of scales in most forms made desiccation a significant threat to survival. The problem of desiccation was solved partly by the development of a **stratum corneum** (outermost layer of the epidermis) and by the presence of mucous glands in the epidermis. The entire epidermis of fishes consists of living cells, whereas the stratum corneum in amphibians is a single layer of dead keratinized cells. The keratinized layer is thin and does not prevent the skin from being permeable. These developments were especially vital in preventing desiccation in derived groups that used cutaneous gas exchange to supplement oxygen obtained through their lungs. In forms that lost their lungs completely and now rely solely on cutaneous gas exchange (family Plethodontidae), these changes became absolutely critical.

Most fishes deposit eggs and sperm in water, and fertilization is external. One problem that most amphibians did not solve was the ability to reproduce away from water. Desiccation risk to eggs greatly limits the distribution of amphibians and the habitats that can be exploited. Fertilization of eggs is external in some salamanders and most anurans. In most salamanders, however, fertilization occurs internally but without copulation. In these forms, males deposit spermatophores (see Fig. 5.33) whose caps are full of sperm. The caps are removed by the female's cloaca (the posterior chamber of the digestive tract, which receives feces and urogenital products), and sperm are stored in a chamber of the cloaca known as the spermatheca. As eggs pass through the cloaca, they are fertilized and must be deposited in a moist site. Many amphibians undergo larval development within the egg, called **direct development**, and hatch as immature versions of the adult form. Others hatch into aquatic larvae and undergo metamorphosis into terrestrial adults. Some, however, remain completely aquatic as adults. A few species are viviparous, a method of reproduction in which fertilized eggs develop within the mother's body and hatch within the parent or immediately after laying.

Lepospondyli

Lepospondyls were small, salamander-like amphibians that appear in the fossil record during the Carboniferous and Permian periods. They are distinguished from the labyrinthodonts primarily on the basis of their vertebral construction. The vertebral centra were formed by the direct deposition of bone around the notochord; their formation was not preceded by cartilaginous elements as in the temnospondyls and anthracosaurs. Little is known regarding their relationships to each other or to other groups of amphibians.

Lissamphibia

Lissamphibia include the salamanders, frogs, toads, and caecilians. Fossil salamanders are represented reasonably well in the fossil record beginning in the Upper Jurassic of North America and Eurasia (approximately 145 Mya) (Estes, 1981). Blair (1976) noted that all fossil salamanders were from land masses of the Northern Hemisphere. Currently, the oldest known fossils of the most successful family in North America, the Plethodontidae, date back only to the Lower Miocene of North America (Duellman and Trueb, 1994).

Salamander-like fossil amphibians, the albanerpetontids, are known from the mid-Jurassic to mid-Tertiary (Miocene epoch) across North America, Europe, and Central Asia (McGowan and Evans, 1995). Some investigators place this group within the salamanders, whereas others consider them to be a separate amphibian group. Although they resemble salamanders by having an unspecialized tailed body form, cladistic analysis using a data matrix of 30 skeletal characters suggests that they represent a distinct lissamphibian lineage (McGowan and Evans, 1995).

Caecilians were unknown as fossils until Estes and Wake (1972) described a single vertebra from Brazil. It was recovered from Paleocene deposits approximately 55 million years old. Since then, additional fossils have been recovered from Jurassic deposits, pushing the age of caecilians back to approximately 195 Mya (Benton, 1990; Monastersky, 1990c). Jurassic specimens apparently had well-developed eyes, sensory tentacles, and small, functional limbs, and were about 4 cm long. Because of the diminished role of the limbs for terrestrial locomotion, most researchers presume that these ancient caecilians also burrowed underground.

The nature and origin of caecilians continues to be open to debate. We still do not know whether caecilians evolved from a group of early lepospondyl amphibians known as microsaurs and developed separately from salamanders and anurans, or whether the three groups of amphibians are more closely related (Feduccia and McCrady, 1991; Zardoya and Meyer, 2000).

The oldest known froglike vertebrate was taken from a Triassic deposit (200 Mya) in Madagascar (Estes and Reig, 1973). Its relationship to modern frogs is still unclear; therefore, it is placed in a separate order, the Proanura. The 190-million-year-old *Prosalirus bitis*, the oldest true frog yet discovered, comes from the Jurassic period in Arizona (Shubin and Jenkins, 1995). The fossil includes hind legs, which were long enough to give it a powerful forward spring, and a well-preserved pelvis. The fossilized skeleton of a 41 cm (16 in.) long, 4.5 kg (10 lb.) frog was recently discovered in Madagascar (Evans et al., 2008). Its closest relatives live in South America.

Four frogs preserved in amber from a tropical rain forest in Myanmar date back 99 million years (Xing et al., 2018). The best-preserved frog is a newly discovered (but extinct) species the researchers named *Electrorana limnoae*. Previous frogs preserved in amber date back 40 million years in the Caribbean and 25 million years in Mexico.

In the end, the primitive paired fins of an ancestral fish, used originally for steering and maneuverability, evolved into appendages able to support the weight of an animal and provide locomotion on land. Additional limb modifications have evolved in the turtles, diapsids, and mammals.

MORPHOLOGY

Integumentary System

An amphibian’s skin is permeable to water and gases and also provides protection against injury and abrasion. Many species of salamanders and anurans absorb moisture from the soil or other substrates via their skins (Packer, 1963; Dole, 1967; Ruibal et al., 1969; Spotila, 1972; Marshall and Hughes, 1980; Shoemaker et al., 1992). Water uptake in anurans occurs primarily through the pelvic region of the ventral skin, a region that is heavily vascularized and typically thinner than the dorsal skin. Called the “seat patch” or “pelvic patch,” it accounts for only 10 percent of the surface area but 70 percent of the water uptake in dehydrated red-spotted toads (*Anaxyrus* [*Bufo*] *punctatus*) (McClanahan and Baldwin, 1969). In dehydrated giant toads (*Rhinella marinus*), the hydraulic conductance of pelvic skin is six times that of pectoral skin (Parsons and

Mobin, 1989). In addition, some minerals, like sodium, are absorbed from the aqueous environment through the skin. Rates of absorption depend on soil moisture and the animal's internal osmotic concentration. Thus, in addition to protection, amphibian skin is important in respiration, osmoregulation, and, to some extent, thermoregulation.

The skin consists of an outer thin epidermis and an inner thicker dermis (Fig. 5.7a). The epidermis is composed of an outermost single layer of keratinized cells that form a distinct stratum corneum, a middle transitional layer (stratum spinosum and stratum granulosum), and an innermost germinative layer (stratum germinativum or stratum basale), which is the region that gives rise to all epidermal cells. Mucous and granular (poison) glands may also be present. Aquatic amphibians have many mucus-secreting glands and usually few keratinized cells in their epidermis. Terrestrial forms, however, have fewer mucus-secreting glands and a single layer of keratinized cells. The keratinized layer is thin and does not prevent the skin from being permeable. As in fishes, the epidermis of most amphibians lacks blood vessels and nerves.

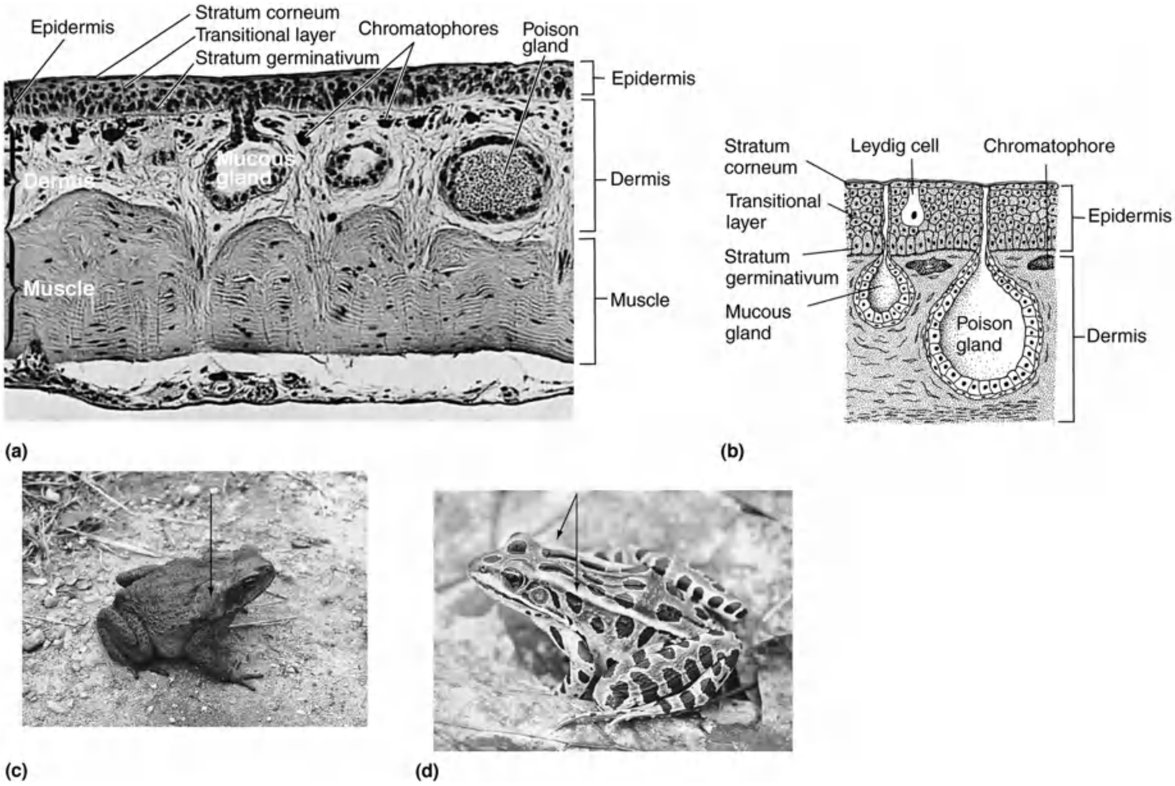


Figure 5.7. Amphibian skin. (*a*) Section through the skin of an adult frog. The epidermis consists of a basal stratum germinativum (stratum basale), a transitional layer consisting of a stratum spinosum and a stratum granulosum, and a thin, superficial stratum corneum. (*b*) Diagrammatic view of amphibian skin showing the mucous and poison glands that empty their secretions through short ducts onto the surface of the epidermis. (*c*) Warts and parotoid glands (*arrow*) of the giant toad (*Bufo marinus*). (*d*) Dorsolateral ridges (*arrows*) of the leopard frog (*Lithobates [Rana] pipiens*).

Molting or shedding of outer keratinized epidermal tissue occurs in both aquatic and terrestrial salamanders and anurans. It involves the separation of the upper keratinized layer (stratum corneum) from the underlying transitional layer. Prior to shedding, mucus is secreted beneath the layer of stratum corneum about to be shed in order to serve as a lubricant. The separated stratum corneum is shed either in bits and pieces or in its entirety, and it is consumed by most species immediately after sloughing. The period between molts is known as the **intermolt**, and its duration is species-specific. Both the shedding of the stratum corneum and the intermolt frequency are under endocrine control, with molting being less frequent in adult amphibians than in juveniles (Jorgensen and Larsen, 1961). In the laboratory, molt frequency has been shown to increase with temperature (Stefano and Donoso, 1964). Photoperiod is less important (Taylor and Ewer, 1956), whereas the relationship of food intake to molting is variable and unclear.

Multicellular mucous and granular glands are numerous and well developed (see Fig. 5.7b). These glands originate in the epidermis and are embedded in the dermis. Mucous glands, which continuously secrete mucopolysaccharides to keep the skin moist in air and allow it to continue serving as a respiratory surface, are especially advantageous to aquatic species that spend some time out of water. Excessive secretion of mucus when an animal is captured can serve as a protective mechanism by making the animal slimy, slippery, and difficult to restrain.

Granular glands produce noxious or even toxic secretions. Such secretions benefit their possessors by making them unpalatable to some predators. These glands often occur in masses and give a roughened texture to the skin. The warts and parotoid glands of toads (see Fig. 5.7c) and the dorsolateral ridges of ranid frogs (see Fig. 5.7d) are examples. Secretions of these integumentary glands consist of amines like histamine and norepinephrine, peptides, and steroidal alkaloids. In some groups of frogs, like the poison dart frogs of Central and South America, phylogenetic relationships have been based on the biochemical differences of integumentary gland secretions.

Two Brazilian hylid frogs, *Corythomantis greeningi* and *Aparasphenodon brunoi*, have bony spines on the skull that pierce the skin in areas with concentrations of granular skin glands and act as a delivery system for the frog venoms (Jared et al. 2015). The venoms, produced by the skin glands, are more lethal than those of deadly venomous Brazilian pit vipers (*Bothrops*). Skin secretions show proteolytic and fibrinolytic activity and have hyaluronidase, which is nontoxic and nonproteolytic but promotes diffusion of toxins. When restrained by hand, these frogs release a sticky secretion and flex the head, jabbing and rubbing the spines into the hand. Many of the spines pierce the skin and are coated with the skin secretion. These frogs have an unusual ability to flex the head laterally and ventrally, as compared to most other frogs, thereby facilitating contact between the spines in the rostral and posterior margin of the head and the hand grasping the frog. This action should be most effective on the mouth lining of an attacking predator.

Toxin-secreting granular glands are most abundant in anurans, but also occur in some caecilians and salamanders. Members of the family Salamandridae and the genera *Pseudotriton* and *Bolitoglossa* (Plethodontidae) are known to secrete toxins (Brodie et al., 1974; Brandon and Huheey, 1981). Toxins, which can be vasoconstrictors, hemolytic agents, hallucinogens, or neurotoxins, may cause muscle convulsions, hypothermia, or just local irritation in a potential predator. For example, *Salamandra* secretes a toxin that causes muscle convulsions, whereas the newts *Notophthalmus* and *Taricha* possess a neurotoxic tetrodotoxin. Sufficient toxin is present in one adult *Taricha granulosa* to kill approximately 25,000 white mice (Brodie et al., 1974). Tetrodotoxin (TTX) is an extremely poisonous substance that binds to sodium channels. It blocks the channels, preventing ions from flowing through them. The result is paralysis of any tissue that contains sodium channels—the nervous system, muscles, heart, and lungs—and ultimately death. Skin secretions of *Bolitoglossa* cause snakes of the genus *Thamnophis* to pause during ingestion, paralyzes their mouth, and may render them incapable of moving or responding to external stimuli. Snakes often die after attempting to eat *Bolitoglossa rostrata* (Brodie et al., 1991).

Bacteria-killing antibiotic peptides—small strings of amino acids, which are the building blocks of all proteins—were originally discovered in the skin of African clawed frogs (*Xenopus laevis*) (Glausiusz, 1998). The peptide was named *magainin* by its discoverer, Michael Zasloff. Magainin filters urea from the blood plasma at the glomerulus; it is discharged onto the frog's skin in response to adrenaline, which is released when pain receptors in the skin send the brain a message that an injury has occurred. Magainins have now been found in many species, ranging from plants and insects to fishes, birds, and humans. These peptides are being turned into antibiotic drugs in hopes of providing an alternative to currently available antibiotics. They can kill a wide range of microorganisms, including gram-positive and gram-negative bacteria, fungi, parasites, and enveloped viruses, without harming mammalian cells. In addition, some can selectively destroy tumor cells. Their mechanism of action is completely different from that of most conventional antibiotics. Instead of disabling a vital bacterial enzyme, as penicillin does, antimicrobial peptides appear to selectively disrupt bacterial membranes by punching holes in them, making them porous and leaky. Efforts are currently underway to chemically synthesize the peptides and make them available for clinical trials.

Although a wide variety of toxic secretions have been identified in many species of anurans, several genera of tropical frogs—*Dendrobates*, *Phyllobates*, and *Epipedibates*—possess extremely toxic steroidal alkaloids (batrachotoxins) in their skin, apparently as a chemical defense against predation (Daly et al., 1978; Myers and Daly, 1983). By studying the mode of action of batrachotoxins, researchers are gaining an understanding of the role electrical impulses play in fundamental processes like human heart function and the sensation of pain. Over 800 alkaloid compounds affecting the nervous and muscular systems have been identified. The alkaloids, which render neurons incapable of transmitting nerve impulses and induce muscle cells to remain in a contracted state, may cause cardiac failure and death. Other alkaloids block acetylcholine receptors in muscles, block potassium channels in cell membranes, or affect calcium transport in the body. Although these frogs rarely exceed 5 cm in length, the combination of toxic alkaloids in the body of a single frog is sufficient to kill several humans (Kluger, 1991). Members of the same species, however, are immune to each other's toxins.

Frogs of the genus *Phyllobates* are the most poisonous. Extrapolating from the lethal dosage (LD) in rats, approximately 136 µg (micrograms) of this alkaloid is the LD for a 150-pound (68 kg) person. This minute amount is roughly equivalent to the weight of 2 or 3 grains of ordinary table salt.

At least three species of the genus *Dendrobates* take up a toxin from their prey and modify the alkaloid to make it about five times as poisonous (Daly, 1999; Daly et al., 2002). The enhanced poison, one of a class called pumiliotoxins, is not as deadly as the batrachotoxins produced by *Phyllobates* and ends up as a protective agent in the frogs' skin. Ants and other arthropods in the frogs' habitat carry most of the poisons that show up in frogs' skin. Poison arrow (poison dart) frog is the common name of frogs in the family Dendrobatidae, which are native to tropical Central and South America. In preparation for hunting, natives rub the tips of their blow darts on the skin of these tiny frogs. They do this to coat their blow dart tips with a toxin that, even in small amounts, can paralyze or kill animals. A diverse array of biologically active, lipid-soluble alkaloids have been discovered in amphibian skin. Almost all of the more than 800 amphibian skin alkaloids appear to be derived from dietary sources (Daly et al., 2005).

Medicinal Compounds from Toads and Frogs

With human diseases becoming alarmingly antibiotic resistant, potential medical compounds in toad secretions and alkaloid substances from tropical frogs may be new sources of drugs for humans.

Fifteen of 47 frog and toad species used in traditional folk medicine belong to the family Bufonidae. For millennia, secretions from their skin and glands, as well as from their bones and muscle tissues, have been used as remedies for infections, bites, cancer, heart disorders, hemorrhages, allergies, inflammation, pain, and even AIDS. New mass spectrometry and nuclear magnetic resonance spectroscopy techniques are now being employed to elucidate chemical structures of the alkaloids, steroids, peptides, and proteins produced by these and other amphibians. It is thought that most of the chemicals produced in frog and toad skin serve to protect them against predators.

In 1992, J. W. Daly and the US National Institutes of Health patented an opioid compound from a poison dart frog (*Epipedibates tricolor*) from Ecuador. The compound, epibatidine, acts as a painkiller that is 200 times more powerful than morphine. Its toxicity stems from its ability to interact with nicotinic acetylcholine receptors, which are involved in the transmission of pain sensations. Epibatidine causes numbness and eventually paralysis. Doses are lethal when the paralysis causes respiratory arrest. Development of epibatidine as an analgesic agent has been precluded because its use is accompanied by adverse effects like hypertension, neuromuscular paralysis, and seizures. However, by using nuclear magnetic resonance spectroscopy to determine epibatidine's structure, and with a little rearranging on the atomic level, researchers at Abbott Laboratories were able to produce a potent synthetic nicotinic (nonopioid) analgesic drug as a less toxic analogue. It apparently acts not through opioid receptors but through non-nicotinic receptors for the neurotransmitter acetylcholine, blocking both acute and chronic pain in rats. Known as Tebanicline (Ebanicline, ABT-594), it got as far as Phase II trials in humans, but was dropped from further development due to unacceptable incidence of gastrointestinal side effects. As of August 2018, further research in this area was ongoing.

Batrachotoxins are extremely potent cardiotoxic and neurotoxic steroidal alkaloids found in certain species of poison dart frogs of the genus *Phyllobates*. Contact with these toxins also causes numbness in human tissue. Upon entering the body, these toxins cause muscle and nerve depolarization, fibrillation, arrhythmias, and heart failure. These deadly effects are caused by the toxins interfering with the body's ability to transmit electrical signals by means of action potentials. Frogs that contain batrachotoxins are unaffected by the deadly compound because they have a form of sodium channel to which the toxins cannot bind.

Research in natural products chemistry involving dendrobatid frogs has become more difficult because these frogs have become rare and have been accorded protection as threatened species under the Convention on International Trade in Endangered Species of Flora and Fauna. Thus, husbandry research and essential nutritional research to allow successful captive breeding and development are essential.

Bradley, 1993; Myers and Daly, 1993; Bannon et al., 1998; Strauss, 1998; Lasley, 1999; Daly et al., 2000, 2005; Dumbacher et al., 2004; Xu and Lai, 2015; Rodriguez et al., 2017; Smithsonian Tropical Research Institute, 2017.

In the wild, about half of the 135 species in the family Dendrobatidae produce poisons. These alkaloids persist for years in frogs kept in captivity but are not present in captive-raised frogs. The alkaloids vanish in the first generation raised outside their natural habitat. Studies at the National Institutes of Health, the National Aquarium, and elsewhere attempted to find the cause of this intriguing situation. At least in some species, the wild diet includes some "cofactor," an organism like an ant or another substance that is not an alkaloid itself but is needed to produce the frogs' alkaloids (Daly et al., 1992, 1994a, b; Dumbacher et al., 2004). For example, offspring of wild-caught parents of *Dendrobates auratus* from Hawaii, Panama, or Costa Rica raised in indoor terrariums on a diet of crickets and fruit flies do not contain detectable amounts of skin alkaloids. Offspring raised in large outside terrariums and fed mainly wild-caught termites and fruit flies do contain the same alkaloids as their wild-caught parents, but at reduced levels. Another hypothesis suggests the frogs need some kind of unknown environmental factor to trigger the production of the toxins, like a combination of sunlight and variable temperatures or the stress of hunting for food.

Most species that possess noxious or toxic secretions are predominantly or uniformly red, orange, or yellow. Such bright **aposematic** (warning) **coloration** is thought to provide visual warning to a predator. Supposedly, predators learn to associate the foul taste with the warning color and thereafter avoid the distasteful species. In some species, these colors are present along with a contrasting background color like black.

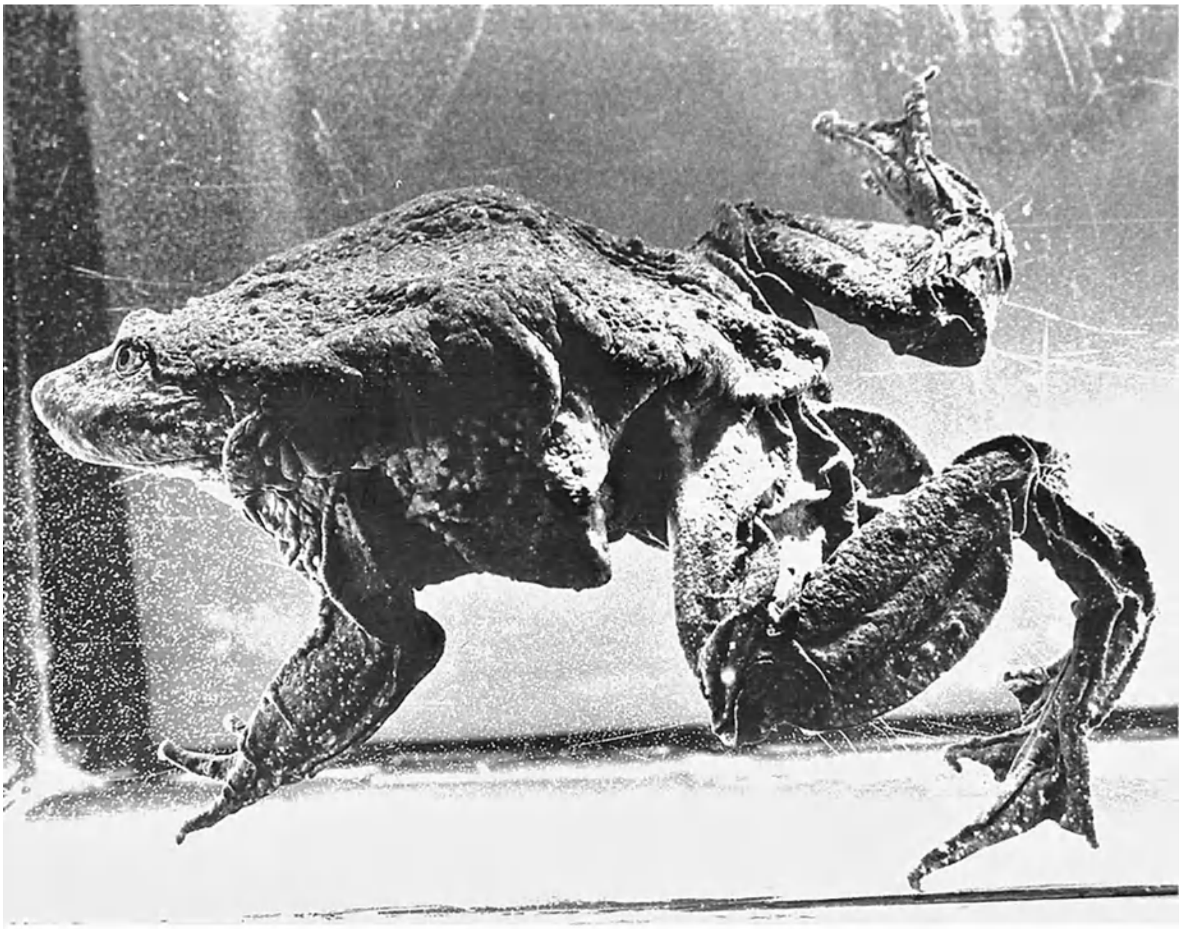
Because their skin has little resistance to evaporation, amphibians experience high rates of water loss when exposed to desiccating conditions. Heat is lost as water evaporates, resulting in decreased skin temperatures (Wygoda and Williams, 1991). Most amphibians are unable to control the physiological processes that result in heat gain and/or loss; thus, thermoregulation is accomplished through changes in their position or location. Some arboreal anurans, like the green tree frog (*Hyla cinerea*), have been shown to have reduced rates of evaporative water loss through the skin, and their body temperatures may be as much as 9°C (16°F) higher than typical terrestrial species (Wygoda and Williams, 1991). The adaptive significance of lower rates of evaporative water loss may be to allow these frogs to remain away from water for longer periods, thus making them less susceptible to predators.

The skin of many amphibians is modified and serves a variety of functions. These modifications include the highly vascularized skin folds of some aquatic amphibians (Fig. 5.8a, b), the annuli or dermal folds of caecilians, and the costal grooves in many salamanders, all of which serve to increase the surface area available for gas exchange. The male hairy frog (*Astylosternus robustus*) of Africa possesses glandular filaments resembling hairs on its sides and hind legs (Fig. 5.8c). These cutaneous vascular papillae develop only during the breeding season and are thought to be accessory respiratory structures that are used when increased activity triggers an increased demand for oxygen. Other integumentary structures, like superciliary processes, cranial crests, and flaps on the heels of some frogs (calcars), are thought to aid in concealment. Metatarsal tubercles that occur on some fossorial forms aid in digging, and toe pads assist in locomotion. Brood pouches occur in South American hylid "marsupial" frogs (*Gastrotheca*) and in the Australian myobatrachium (*Assa*).

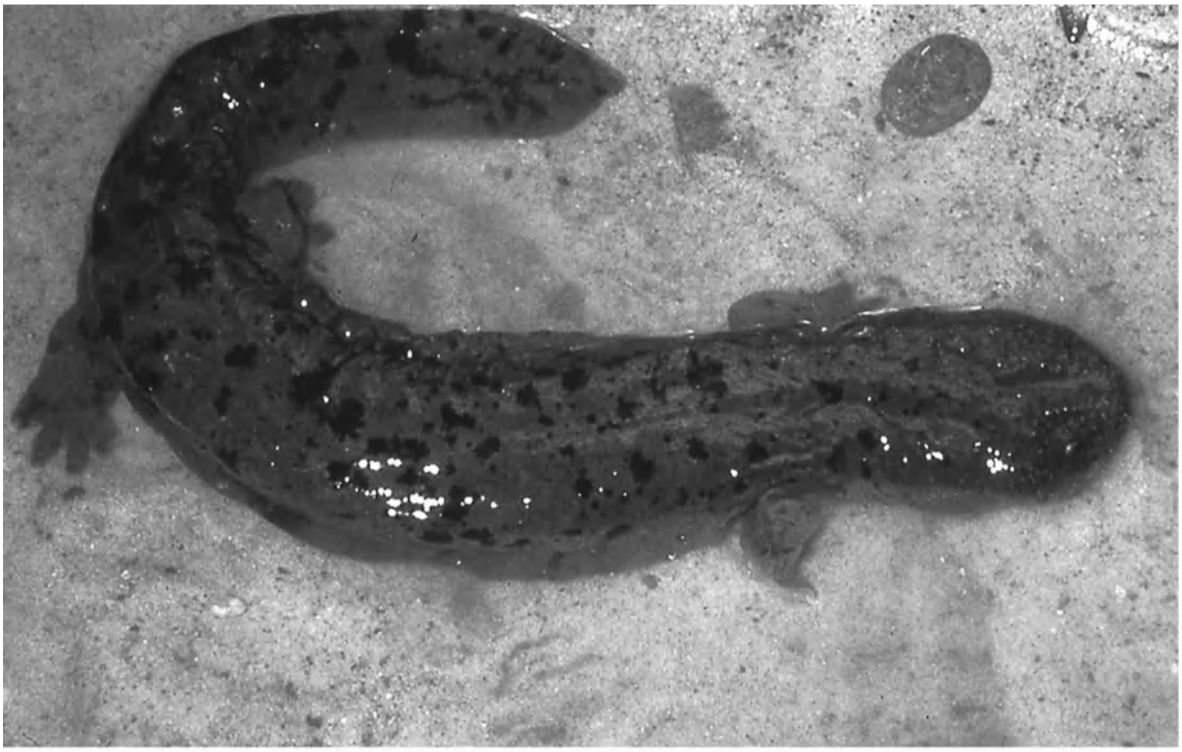
During the breeding season, some male salamanders (ambystomatids, plethodontids, and some salamandrids) develop glands on various parts of their bodies. Such glands may be on the head, neck, chin (mental), or tail. During courtship, these glands come in contact with the female's body. Their secretions, known as pheromones, presumably aid in stimulating the female. The biochemical identification of one such pheromone from the mental gland of a salamander (*Plethodon jordani*) was reported by Rollmann et al. (1999). Similar glands are present on various parts of the bodies of male anurans. In addition, the thumb pads of many breeding male anurans consist of clusters of keratinized mucous glands that help them clasp females.

Webbing between the fingers and toes of anurans is part of the integument. It is most extensively developed on the rear feet of the more aquatic species and provides a broader surface to the foot when swimming. In some species, like the Malaysian flying frog (*Rhacophorus reinwardtii*), both hands and feet are fully webbed and are used in a parachute fashion for controlled jumping from a higher perch to a lower one. The tips of the digits of some salamanders and anurans are modified with thickened, keratinized epidermis.

Many tree frogs possess expanded adhesive **toe pads** with glandular disks at the tips of their toes, which aid in grasping and climbing (Fig. 5.9). Toe pads consist of columnar epithelium whose cells feature stout, hexagonal, flat-topped apices that are separated from each other by deep mucus-filled channels (Fig. 5.10) (Ernst, 1973; Green, 1979). Studies by Emerson and Diehl (1980), Green (1981), and Green and Carson (1988) show that surface tension created by mucous secretions is the primary factor in allowing anurans with toe pads to cling to smooth surfaces. The strength of the adhesive bond, produced by the surface tension of the fluid that lies between the toe pad and the substrate, is a function of the area of contact with the substrate. However, wet adhesion has been found to be only part of the answer. Microscopic bumps on the toe pad jut through the film and make direct, dry contact with a surface (Federle et al., 2006). This arrangement enables the tree frog to toggle between wet adhesion, which is useful on rough surfaces, and dry friction, which gives the frog a grip on smooth terrain. The mucous channels not only produce a mucous film, but on wet surfaces, they funnel away excess fluid. On dry or uneven surfaces, or when a frog hangs upside down, the mucus creates surface tension and viscosity—in other words, extra clinginess. The channels also allow the hexagonal cells to conform to contoured surfaces, like that of a leaf. An **intercalary bone** allows the adhesive toe disk to be offset from the end of the digit so that the entire surface of the toe pad can be in contact with the substrate (Fig. 5.11b). Arboreal salamanders lack toe pads, but may have recurved, spatulate terminal phalanges to assist in grasping (Fig. 5.11c).



(a)



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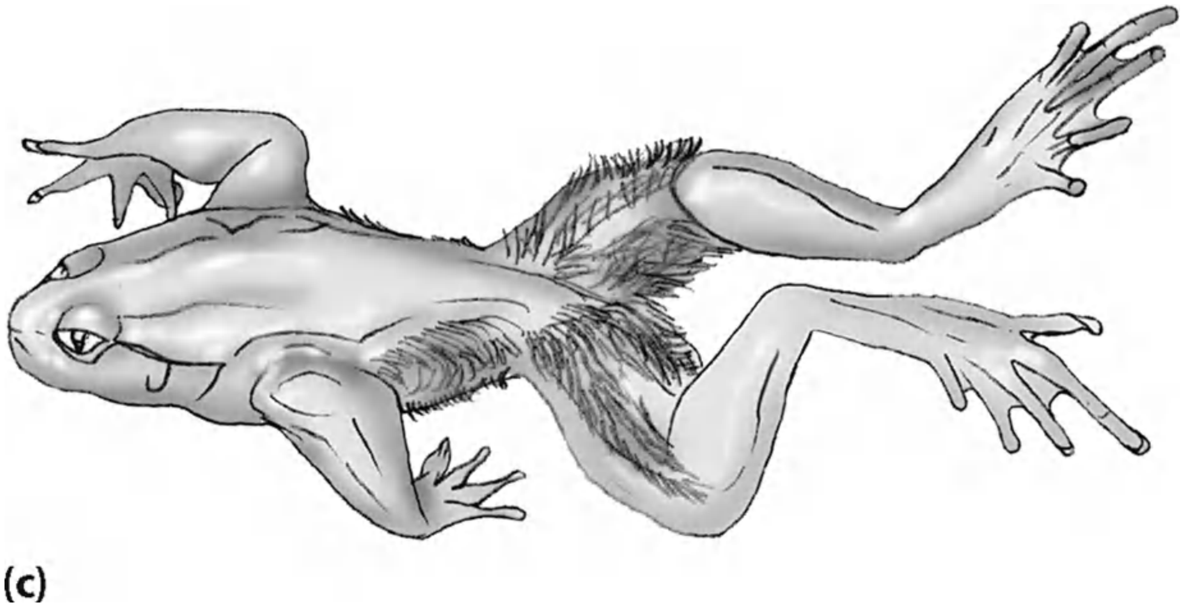


Figure 5.8. (*a*) The Titicaca frog (*Telmatobius culeus*) and (*b*) a hellbender (*Cryptobranchus alleganiensis*), an aquatic salamander—both with highly vascularized skin folds with capillaries penetrating to the epidermis. When submerged in water with a low oxygen pressure, they periodically sway from side to side so as to break up the boundary layer between the water and skin, thereby ventilating the cutaneous surfaces. Oxygen can be obtained entirely by diffusion through the skin surface. (*c*) The "hairy frog" (*Astylosternus robustus*) receives its name from the thick growth of vascular filaments resembling hair that develops in the male during the breeding season. These are respiratory organs that compensate for the reduced lungs of this species at the time of the year when the metabolism increases.

Figure 5.9. Glass frog (*Centrolenella*) with the heart visible through the skin. Adhesive toe pads aid in climbing.

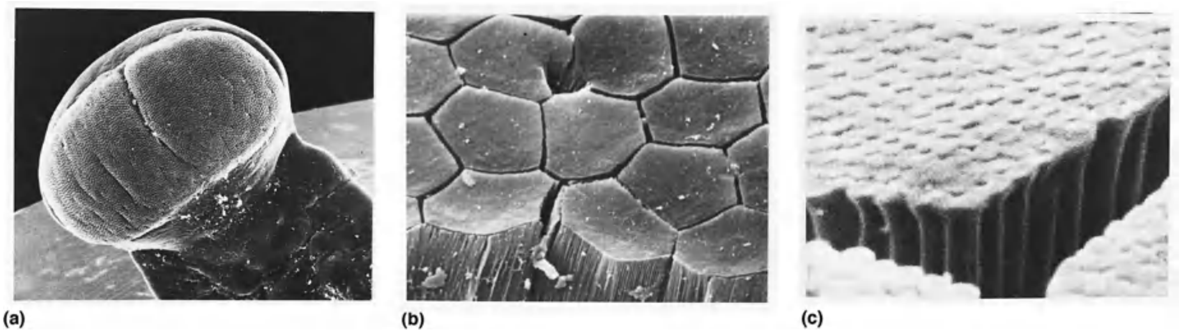


Figure 5.10. Scanning electron micrographs of the toe pad of a frog: (*a*) ventral view of the entire toe pad of *Litoria rubella*; (*b*) the opening of a mucous gland on the epidermal surface of the toe pad in *Eleutherodactylus coqui*; (*c*) fibrous epithelium of individual toe pad cells in *Hyla picta*.

The dermis of amphibians contains a rich network of capillaries that supply nutrients to the epidermis. Dermal scales, or ossicles, are present in several kinds of anurans (*Brachycephalus*, *Ceratophrys*, *Gastrotheca*, *Phyllomedusa*, and others) and in caecilians. The ability to change skin color is advantageous to amphibians, both in providing protective coloration and in regulating temperature. Three types of chromatophores —melanophores, iridophores, and xanthophores (erythrophores)—are present in the epidermis and/or in the dermis. Color change may be effected by the amoeboid movement of the chromatophores or by a shifting of pigment granules within the cell. Color change in adult amphibians appears to be controlled primarily by melanocyte-stimulating hormone (MSH) secreted by the anterior lobe (adenohypophysis) of the pituitary gland (Duellman and Trueb, 1994). Coloration may be the result of the dispersion or concentration of pigments, or a combination of pigments and dermal structures. For example, lightening of the integument is due to secretion of melatonin, a hormone found in the pineal gland, brain, and retina that aggregates melanin granules in dermal melanophores, thus causing the skin to appear lighter in color (Baker et al., 1965; Pang et al., 1985). Melatonin also appears to be responsible for color change in amphibian larvae (Bagnara, 1960).

Skeletal System

Compared with that of fishes, the amphibian skeleton exhibits increased ossification, loss and fusion of elements, and extensive modification of the appendicular skeleton for terrestrial locomotion (Fig. 5.12).

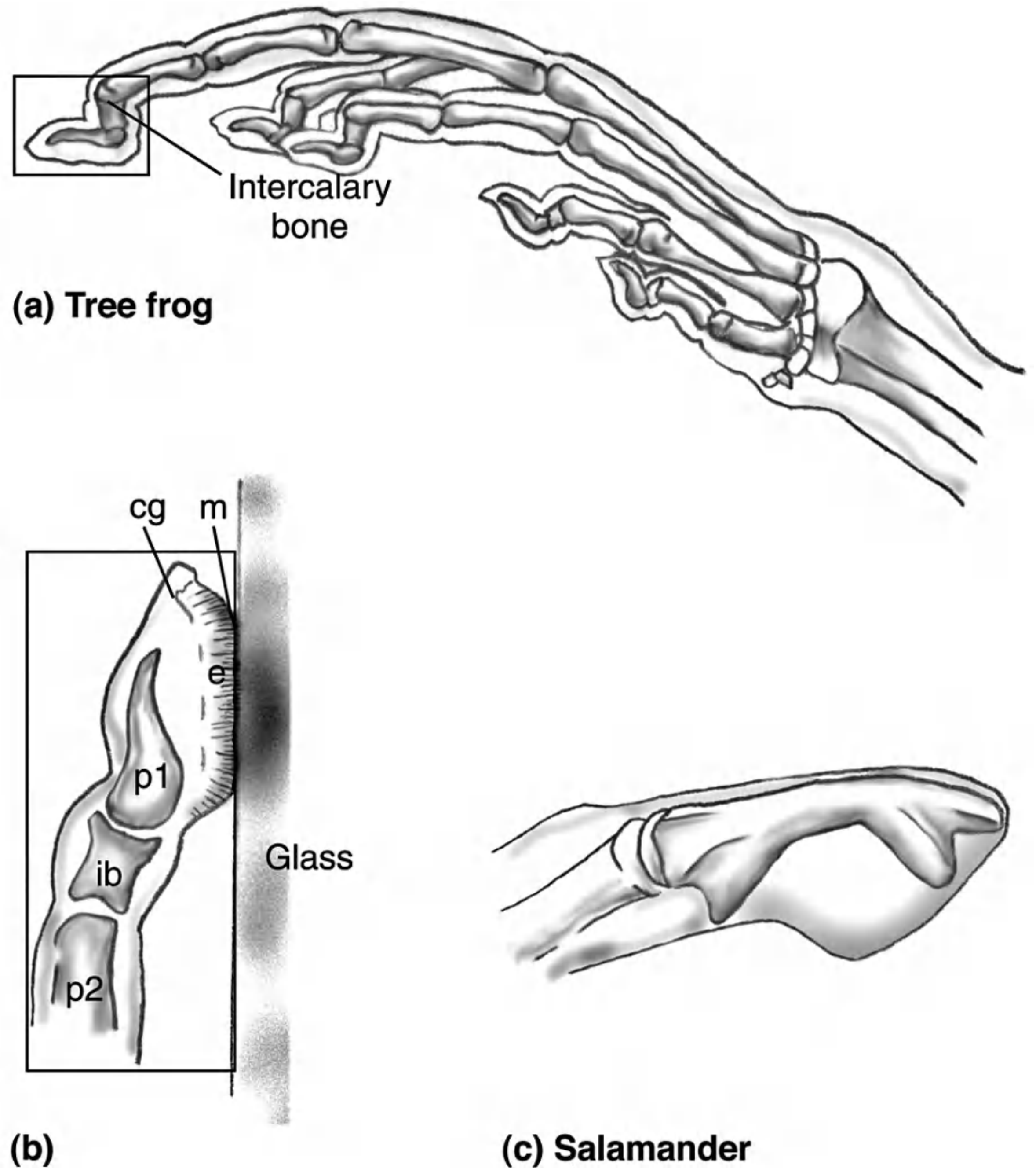


Figure 5.11. Arboreal adaptations in the phalanges of tree frogs and some salamanders. (*a*) Tree frogs have terminal phalanges that rotate on the intercalary bones. (*b*) A diagrammatic cross section of a tree frog's toe pad in contact with a smooth glass surface, illustrating the mechanism of adhesion by surface tension. *Key*: e, adhesive epidermis; cg, circumferal groove of the toe pad; m, meniscus; p1, first phalange; ib, intercalary bone or cartilage; p2, second phalange. (*c*) Arboreal salamanders like *Aneides lugubris* may have recurved, spatulated terminal phalanges.

Terrestrial salamanders have a somewhat arched and narrow skull, whereas in aquatic forms the skull is flatter. Salamander skulls, which may be partly or wholly ossified, contain fewer bones than skulls of teleost fishes. Through loss and fusion, skulls of caecilians and anurans contain even fewer bones than those of salamanders (Fig. 5.13a, b). The broad, flat head of anurans is almost as wide as the body.

The upper jaw of anurans is composed of a pair of premaxillae and a pair of maxillae. Meckel's cartilage in the lower jaw is ensheathed primarily by the dentary and angular bones, with the latter articulating with the quadrate of the skull.

The posterior ends of the embryonic palatoquadrate cartilages serve as the posterior tips of the upper jaws. They may remain as quadrate cartilages, or they may ossify to become quadrate bones. The more anterior part of the palatoquadrate cartilages become ensheathed by dermal bones like the premaxilla and maxilla. The upper jaw is connected directly to the skull in amphibians, a method of jaw suspension known as **autostylic**. The dentary forms the major portion of the mandible (lower jaw).

The hyomandibular cartilage, which in sharks is located between the quadrate region of the upper jaw and the otic capsule, ossifies in tetrapods and becomes the **columella** of the middle ear (see Fig. 5.23). It transmits sound waves from the quadrate bone to the inner ear. The columella serves as an evolutionary stage in conducting airborne sounds in terrestrial vertebrates, a process culminating in the presence of three ear ossicles in mammals.

Larval gill-bearing amphibians have visceral arches that support gills. During metamorphosis, changes occur that result in a pharyngeal skeleton (that initially was adapted for branchial respiration) being converted in the span of a few days to one characteristic of animals that live on land and breathe air. Those amphibians (salamanders) that remain aquatic as adults retain an essentially fishlike branchial skeleton throughout life, except that the number of gill-bearing arches is fewer than in fishes.

As vertebrates became increasingly specialized for life on land, the ancestral branchial skeleton underwent substantial adaptive modifications. Some previously functional parts were deleted, and those that persisted perform new and sometimes surprising functions. For example, the hyobranchial apparatus supports gills in larval salamanders and the complex, projectile tongue in metamorphosed adults. In anurans, however, vocalization is possible because of modifications of the hyobranchial apparatus to form laryngeal cartilages.

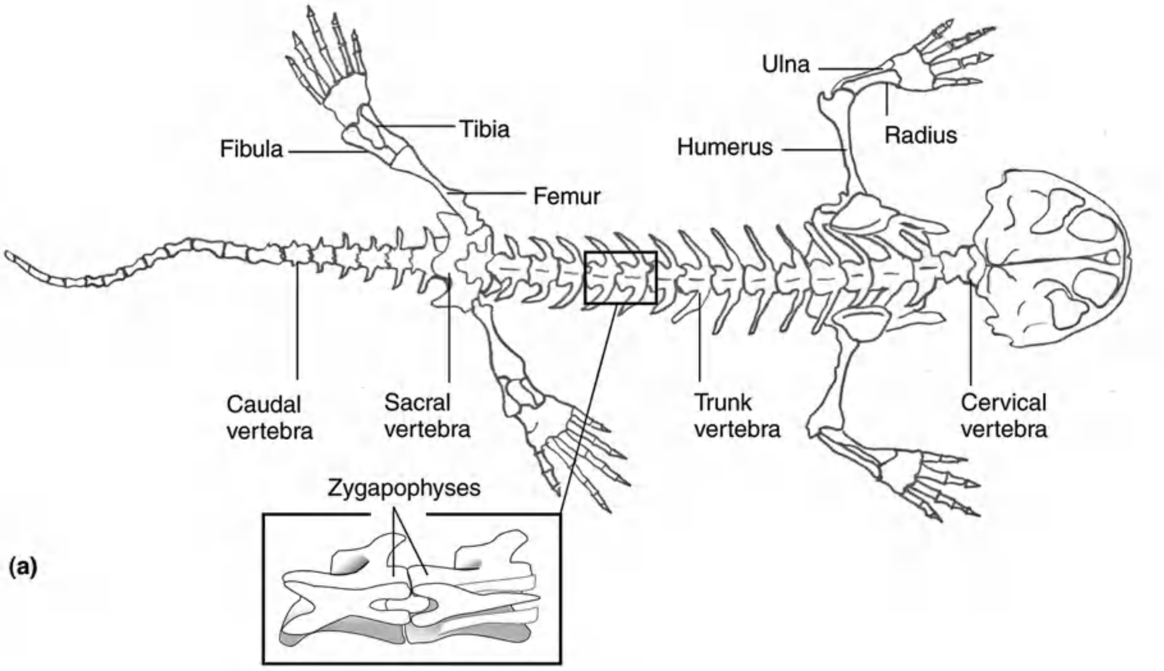
The vertebral column in amphibians varies considerably in length. Some salamanders have as many as 100 vertebrae, and caecilians may have up to 285 (Wake, 1980a). Anurans usually have 8 (excluding the urostyle), though the number may range from 6 to 10.

With the evolution of tetrapods and life on land, the vertebral column has become more specialized. It serves to support the head and viscera and acts as a brace for the suspension of the appendicular skeleton. Four (sometimes five) types of vertebrae are present in most salamanders (see Fig. 5.12a), whereas the anuran vertebral column normally is divided into four regions (see Fig. 5.12c). In salamanders, the first **trunk** vertebra became a **cervical** vertebra, which now provides for an increasingly flexible neck. This single cervical vertebra, the **atlas**, has two concave facets for articulation with the two occipital condyles of the skull. Trunk vertebrae vary in number from approximately 10 to 60, depending on the species.

Why Frogs Are Green

Why do many frogs appear green? Because the epithelium is transparent, a portion of skin appears green from the outside when light of long wavelength passes through the iridophores and is then absorbed by melanophores, whereas light of short wavelength is diffracted and refracted back by the iridophores. Only the green component of this refracted light escapes absorption in the yellow color screen of the lipophores. Other colors like blue, yellow, and black are seen either where the pigment layers are not continuous, or where they are irregularly arranged.

Lindemann and Voute, 1976



(b) Lateral view

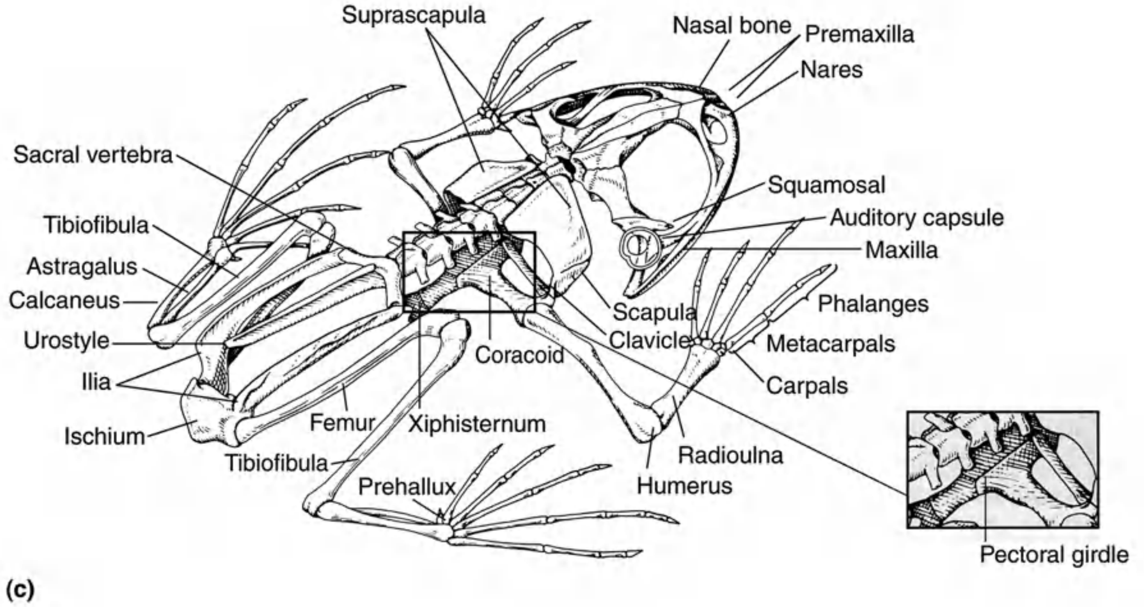


Figure 5.12. (*a*) Dorsal view of a salamander skeleton. (*b*) Lateral view of salamander trunk vertebrae. (*c*) Skeleton of a bullfrog (*Rana catesbeiana*).

Because of the force generated against the vertebral column by the tetrapod hindlimbs and pelvic girdle, the terminal trunk vertebra has become enlarged and modified as a **sacral** vertebra. Salamanders have a sacrum consisting of one sacral vertebra, which serves to brace the pelvic girdle and hindlimbs against the vertebral column. This arrangement does not provide very strong support for the hindlimbs; therefore, most salamanders have difficulty completely raising their bodies off the ground when walking. Their sprawl-legged stance and sinusoidal method of locomotion also contribute to their inability to keep their bellies off the substrate. Most salamanders "wriggle." A **caudal-sacral** region consisting of two to four vertebrae immediately posterior to the sacrum is recognized by some authors. The **caudal**, or tail, vertebrae may range up to 20 or more in salamanders. Some salamanders have weak articulations between their caudal vertebrae that allow them to shed their tails (**caudal autotomy**) when attacked by predators (Wake and Dresner, 1967).

Caecilians have one cervical vertebra (atlas) and a variable number of trunk vertebrae. They lack a sacrum, and most species lack a tail. With the exception of the atlas, all vertebrae of caecilians are nearly identical in shape.

The anuran vertebral column consists of cervical, trunk, sacral, and postsacral regions (see Fig. 5.12c). The presacral region consists of five to eight vertebrae, with the first being modified as a cervical vertebra, the atlas. A single vertebra, the sacrum, is modified for articulation with the pelvic girdle. Postsacral vertebrae are fused into a **urostyle**, an unsegmented part of the vertebral column that is homologous to the separate postsacral vertebrae of early amphibians.

Amphicoelous vertebrae in which both anterior and posterior faces of the centra are concave are found in caecilians, a few primitive anurans, and some salamanders. Most salamanders and a few anurans possess **opisthocoelous** vertebrae, in which the centrum is concave on its posterior face and convex on its anterior face. Most anurans possess **procoelous** vertebrae, in which the concave surface faces anteriorly and the posterior face is convex. Intervertebral joints of amphibians are reinforced by two pairs of processes (**zygapophyses**) arising from the neural arch (see Fig. 5.12b).

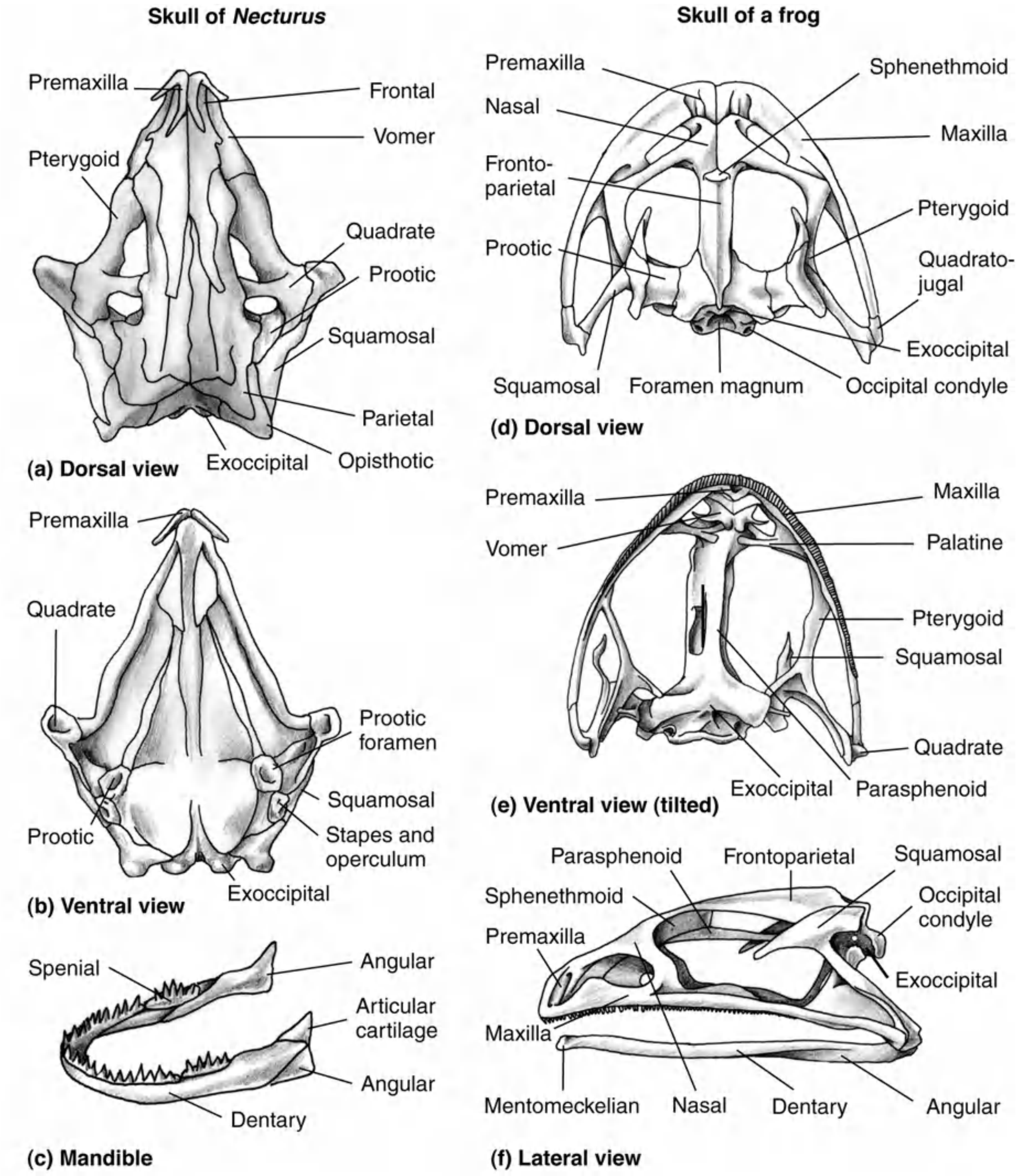


Figure 5.13. (*Left*) Skull of *Necturus*: (*a*) dorsal view; (*b*) ventral view; (*c*) mandible. (*Right*) Skull of a frog: (*d*) dorsal view; (*e*) ventral view, tilted laterally to the left side; (*f*) lateral view.

The earliest amphibians had well-developed ribs on both trunk and tail vertebrae (see Fig. 5.4). In modern amphibians, however, ribs are always absent on the atlas and are either reduced or absent on the other vertebrae. When present, they are usually shortened structures that are fused with transverse processes. They are longest in caecilians, shorter in salamanders, and vestigial or absent in most anurans.

A true **sternum**, characteristic of higher tetrapods, appears for the first time evolutionarily in amphibians. It is absent in caecilians and in some salamanders. In other salamanders, it is poorly developed and exists as a simple, medial triangular plate that articulates with the pectoral girdle. It is poorly developed in primitive frogs, but in more advanced frogs, it may exist as a rod-shaped structure consisting of four elements or as an ossified plate. Although ribs do not attach to it, the amphibian sternum functions as a site for muscle attachment.

The evolutionary origin of the sternum is unclear. One hypothesis is that it resulted from the fusion of the ventral ends of the thoracic ribs. A second hypothesis proposes that the sternum developed independently of the ribs, a view that is supported by the embryonic origin of the sternum in reptiles and mammals. Feduccia and McCrady (1991) noted that it "may even be possible that amphibian and amniote sterna have evolved independently and are not homologous structures."

Early amphibians, which were not truly terrestrial and spent much of their time in water, possessed two pairs of limbs. The pectoral girdle of early tetrapods closely resembled the basic pattern of their crossopterygian ancestors; it did not articulate with the vertebral column, and the coracoid braced the girdle against the newly acquired sternum (see Fig. 5.4).

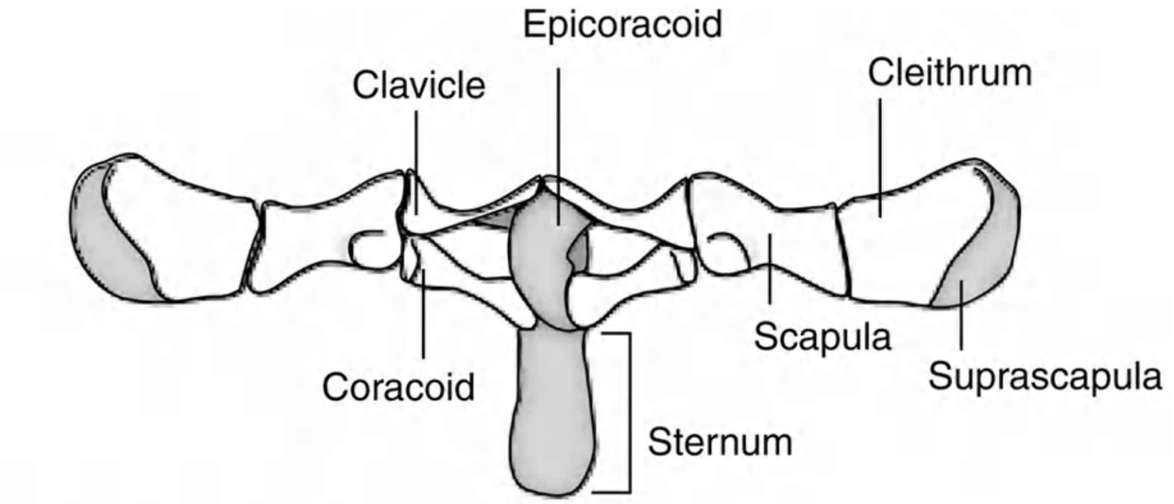
In modern salamanders, the pectoral girdle is mostly cartilaginous, with one-half of the girdle overlapping the other and moving independently. A small ventral, cartilaginous sternum lies posterior to the pectoral girdle in some salamanders.

In most anurans, the scapula and other elements may be ossified or cartilaginous; the girdle is suspended from both the skull and the vertebral column and is designed to absorb the shock of landing on the forelimbs.

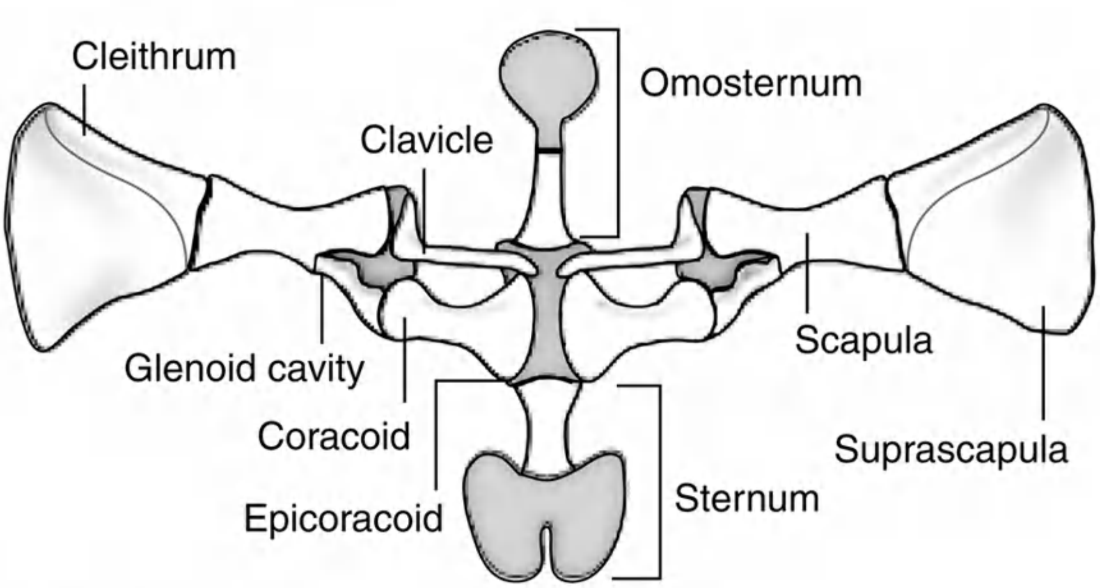
The structure of the pectoral girdle of anurans has been used as an important taxonomic tool. Those families in which the two halves of the pectoral girdle overlap and that possess posteriorly directed epicoracoid horns (Bufonidae, Discoglossidae, Hylidae, Pelobatidae, Pipidae, and Leptodactylidae) have an **arciferous**-type pectoral girdle (Fig. 5.14a). Here, the epicoracoids articulate with the sternum by means of grooves, pouches, or fossae in the dorsal surface of the sternum. Those families in which the sternum is fused to the pectoral arch and the epicoracoid cartilages of each half of the pectoral girdle are fused to one another

(Ranidae, Rhacophoridae, and Microhylidae) have a **firmisternal** type of girdle (Fig. 5.14b).

Considerable diversity in limbs exists among modern amphibians as a result of their locomotion (like hopping or walking) and their various adaptations to aquatic, burrowing, and arboreal habits. Limbs of modern salamanders are short, stout, and directed outward at right angles to the body. Anterior limbs consist of a single upper bone, the **humerus**, two lower forearm bones, the **radius** and **ulna**, as well as **carpals**, **metacarpals**, and **phalanges** (see Fig. 5.12a). The primary function of the forelimbs in salamanders is to raise the body and assist the hindlimbs in moving the body forward. In anurans, the forelimb is considerably shorter than the hindlimb (see Fig. 5.12c). Instead of having two foreleg bones (radius and ulna), the ossification of the ligament between the radius and ulna creates a single bone: the **radio-ulna**. Carpals, metacarpals, and phalanges complete the skeleton of the forelimb.



(a) Arciferous girdle



(b) Firmisternal girdle

Figure 5.14. Anuran pectoral girdles in ventral view. Shaded areas are cartilaginous. (*a*) Arciferal girdle with overlapping halves (*Bufo coccifer*). (*b*) Firmisternal girdle with two halves of girdle fusing in midline (*Rana esculenta*).

Modifications to the front limb in amphibians involve a reduction of bones by loss or fusion. Most modern amphibians have reduced or lost at least one digit and one metacarpal, so that four functional digits are present on each front foot. Others, like members of the genus *Amphiuma*, have girdles, but both forelimbs and hindlimbs are vestigial. Both girdles and limbs are absent in caecilians.

The pelvic girdle of salamanders may be partially ossified and consists of a ventral **puboischiac plate** and a dorsal pair of **ilia** on each side. A median *Y*-shaped **ypsiloid** (**prepubic**) **cartilage** develops just anterior to the pubic area in most salamanders. The ypsiloid cartilage is associated with the hydrostatic function of the lungs. By elevating the cartilage, the salamander is thought to be able to compress the posterior end of its body cavity and force air in its lungs forward, thereby causing its head to rise in the water. When the ypsiloid cartilage is depressed, air is thought to move posteriorly in the lungs, thereby reducing the buoyancy of the head so that it tends to sink in the water (Duellman and Trueb, 1994).

In anurans, each half of the pelvic girdle consists of an ilium, ischium, and pubis (see Fig. 5.12c). Ilia are greatly elongated and articulate with the sacrum. They extend to the end of the urostyle, where they meet the ischia and pubis. Ilia are thus adapted to absorb the shock of impact when frogs land after a jump.

Hindlimbs in salamanders consist of a single upper bone, the **femur**, two lower leg bones, the **tibia** and **fibula**, as well as **tarsals**, **metatarsals**, and **phalanges** (see Fig. 5.12a). Sirens (family Sirenidae) have a pectoral girdle and small forelimbs but lack pelvic girdles and hindlimbs.

The well-developed hindlimbs of anurans are specialized for jumping and swimming (see Fig. 5.12c). The head of the upper leg bone (femur) articulates with the acetabulum (socket) of the pelvic girdle. Distally, the femur articulates with the **tibiofibula**, representing the fusion of the separate tibia and fibula and forming a stronger and more efficient structure for leaping. As in salamanders, the knee joint is directed anteriorly to provide better support and power for forward propulsion. A series of tarsal bones constitutes the ankle. Four or five metatarsals form the foot, and phalanges form the toes. A small additional bone, the **prehallux**, frequently occurs on the inner side of the foot. It commonly supports a sharp-edged tubercle used for digging by burrowing species like spadefoot toads (*Scaphiopus*). Most amphibians have five digits on each of the rear feet. The primary function of the hindlimbs is to provide the power for locomotion.

All anurans, whether primarily walkers, hoppers, or swimmers, use some form of jumping or leaping (saltatorial) locomotion. For this, forelimbs must be positioned differently than those of salamanders and fulfill a different role in locomotion. Duellman and Trueb (1994) describe the mechanism of a frog's leap in the following manner:

> At rest, the shoulder joint tends to be extended with the upper arm lying against the flank rather than held out at a right angle to the body as in salamanders. The elbow joint is flexed and the forearm directed in an anteromedial direction rather than directly forward. Thus, the entire lower arm and hand are rotated inward toward the center of the body. As the animal thrusts itself forward in a leap, it probably rolls off the palmar surface of the hand while straightening the elbow and wrist joints. Thus, the forelimb lies parallel to the body for maximum streamlining. After full thrust has been developed from the hindlimbs, the forelimb is flexed at the elbow, and the upper arm is pulled as far forward as possible. Subsequent flexion of the wrist allows the animal to land on its hands, the force of landing presumably being absorbed by the pectoral girdle.

Muscular System

The body musculature of amphibians varies widely; that of aquatic salamanders is similar to the pattern in fishes, whereas the body musculature of terrestrial species, especially anurans, is markedly different. Metamerism is clearly evident in salamanders, caecilians, and larval anurans. Epaxial myomeres have begun to form elongated bundles of muscle that extend through many body segments. These muscles, which are partially buried under the expanding appendicular muscles, extend along the vertebral column from the base of the skull to the tip of the tail. In salamanders, these muscles are known as the **dorsalis trunci** and allow for side-to-side movement of the vertebral column, the same locomotor pattern as in fishes.

Those amphibians that utilize lateral undulations of their hypaxial muscles for swimming, like most larval forms and adult aquatic salamanders, retain a more fishlike, segmented hypaxial musculature. Even terrestrial salamanders utilize lateral undulations to a great extent. In other amphibians, hypaxial muscle masses begin to lose their segmental pattern and form sheets of muscle (external oblique, internal oblique, transversus), especially in the abdominal region.

As vertebrates evolved into more efficient land-dwelling forms, the axial musculature decreased in bulk as the locomotor function was taken over by the appendages and their musculature. The original segmentation becomes obscured as the musculature of the limbs and limb girdles spreads out over the axial muscles.

The appendicular muscles of most amphibians are far more complicated than those of fishes due to the greater leverage required on land. In amphibians, the limbs (for the first time in the evolution of the vertebrates) must support the entire weight of the body. Due to the difference in locomotion between salamanders and anurans, considerable variation exists in the musculature of the girdles and limbs between these two groups. Even so, many salamanders still drag their bellies over the substrate when they walk. Lateral undulatory movements of the body wall assist the appendicular muscles in this movement.

Forward Motion in Caecilians

Caecilians are legless, wormlike, burrowing tropical amphibians. Unlike other vertebrates, caecilians have muscles that ring the body wall, running from the belly to the back (the muscles in most vertebrates tend to run lengthwise, from head to tail). By contracting these muscles, caecilians pressurize the fluid in their body cavity, creating a hydrostatic force that goes in the direction of the head, driving the animal forward and causing it to become longer and thinner. This remarkably efficient technique permits the caecilian to generate about twice the force of a similar-size burrowing snake, which uses the muscles that run along the vertebral column to twist and arch itself through the soil. By using its entire body as a single-chambered hydrostatic organ, a caecilian applies nearly 100 percent of its muscular energy toward forward motion.

O’Reilly et al., 1997

Hindlimb muscles of frogs that jump must generate maximum mechanical power during jumping. Maximum power is generated by the rapid release of calcium from sarcoplasmic reticula in muscle fibers, which initiates cross-bridge formation between actin and myosin filaments in the sarcomeres, and by having the maximum number of muscle fibers contracting (Lutz and Rome, 1994).

In amphibians, muscles of the first visceral arch continue to operate the jaws. Some of the muscles of the second arch retain their association with the lower jaw, whereas muscles of the third and successive arches operate gill cartilages in those amphibians with gills. In amphibians without gills, these muscles are reduced. They assume new functions like assisting in swallowing and opening and closing of the pharynx and larynx.

Cardiovascular System

The evolution of lungs was a significant development in the evolution of vertebrates. Those mechanisms must have evolved to enable the best use of the oxygenated blood returning from the lungs via pulmonary veins. Development of an interatrial septum in the heart of most amphibians was essential in helping keep oxygenated blood separated from deoxygenated blood.

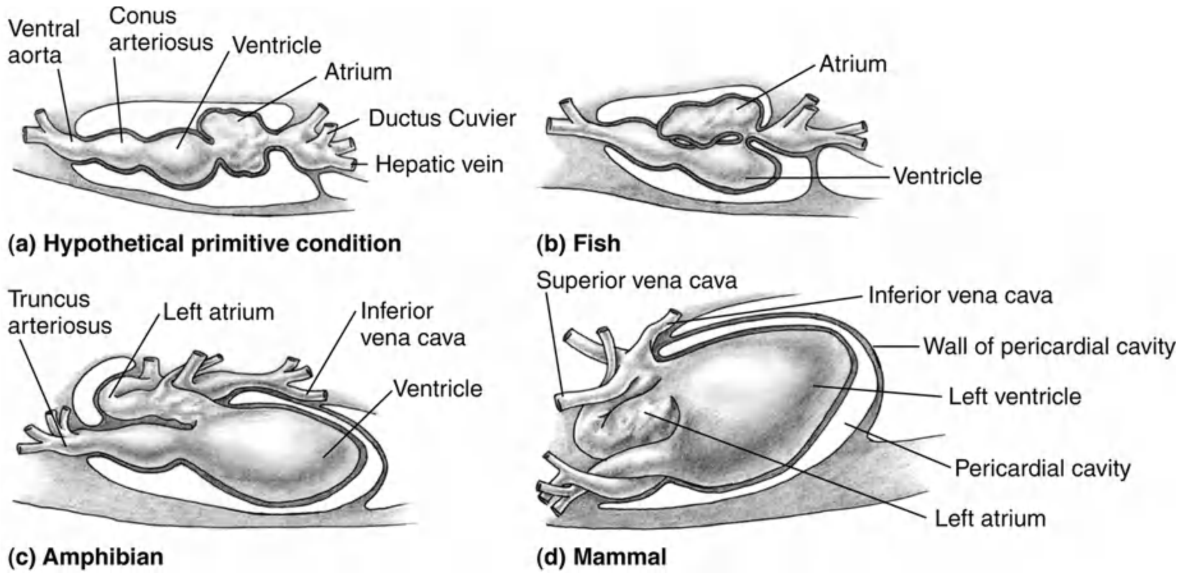


Figure 5.15. Stages in the evolution of the vertebrate heart: (*a*) hypothetical primitive condition; (*b*) fish; (*c*) amphibian; (*d*) mammal. The atrium, which was posterior to the ventricle, moves anteriorly. The original atrium and ventricle become partitioned into right and left chambers.

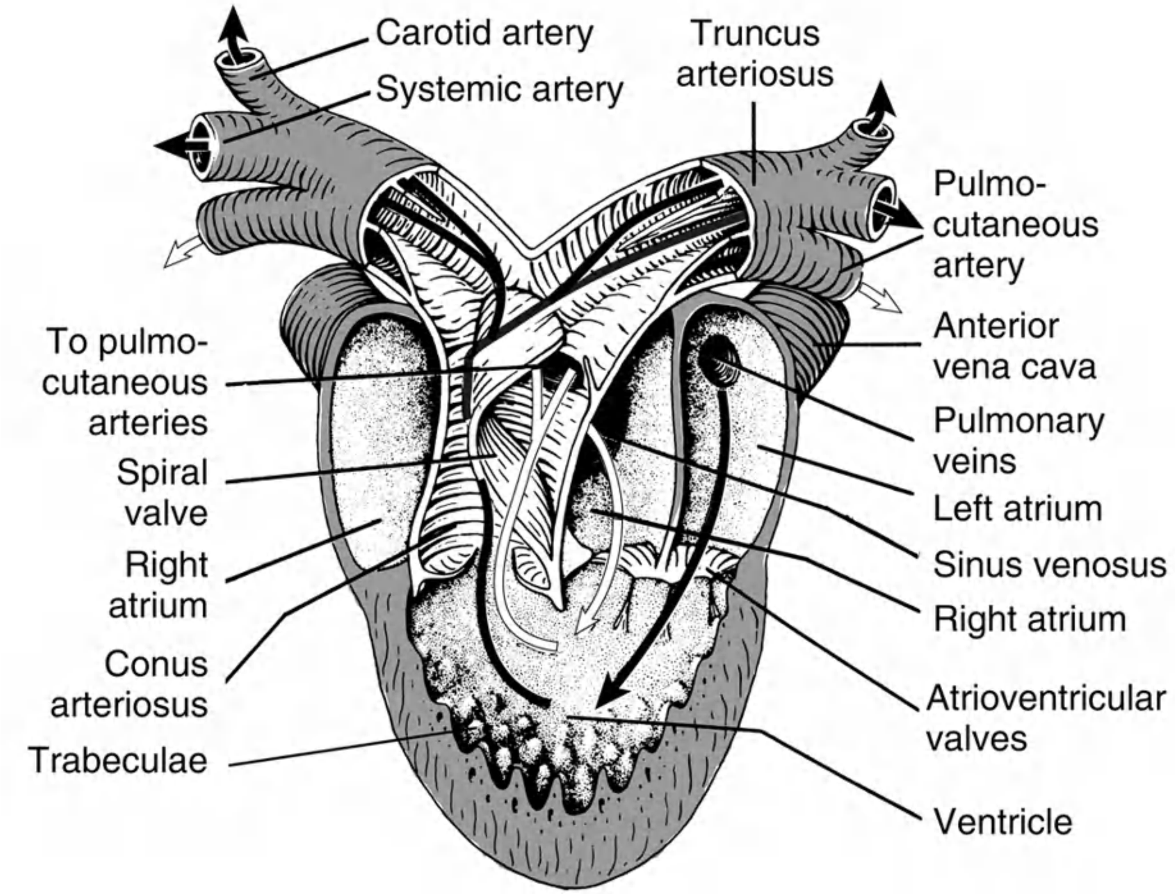


Figure 5.16. Structure of the frog heart. Oxygenated blood is indicated by dark arrows, deoxygenated blood by white arrows.

Instead of the simple two-chambered heart (atrium, ventricle) characteristic of most fishes, many amphibians have a heart with two atria and a single ventricle (Fig. 5.15). Although the interatrial septum is incomplete (fenestrated) in most salamanders and caecilians and is lacking completely in lungless salamanders, it is complete in anurans (Fig. 5.16). The right atrium receives deoxygenated blood from the sinus venosus; the left atrium receives the pulmonary veins (absent in lungless forms) and oxygenated blood. Some blood travels from the heart via pulmonary arteries to cutaneous arteries in the skin in order for cutaneous respiration to occur. Once aerated, the blood returns to the heart via cutaneous and pulmonary veins. **Ventricular trabeculae** (ridges in the ventricular wall) are common in many amphibians and help to keep oxygenated and deoxygenated blood separated in the ventricle. A few salamanders have partial interventricular septa, but no living amphibian is known to have a complete interventricular septum.

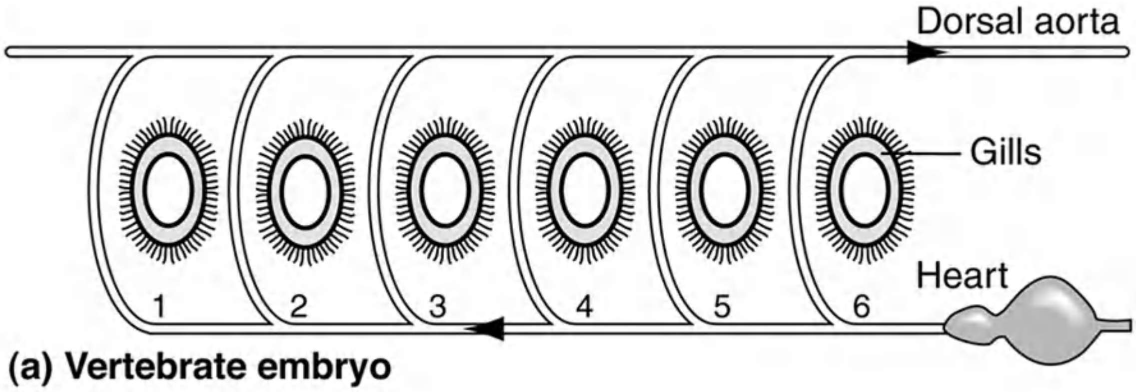
In most fishes, six aortic arches appear between the developing gill slits in embryos (Fig. 5.17). The most anterior aortic arch disappears during embryonic development, so that adult elasmobranchs are left with five arches. Adult teleosts have four aortic arches, the second usually disappearing as well during development. Lungfishes have the same four arches, and the lungs are supplied from the most posterior of these. This is equivalent to the sixth of the original embryonic series. The lungs of all land vertebrates are supplied with blood from this source, indicating common ancestry and homology.

During development, most larval salamanders and all tadpoles pass through a stage in which the arches form gill capillaries and also may supply the external gills. Later, the gill circulations are lost and the adult pattern develops. Aortic arches 3 (carotid), 4 (systemic), and 6 (pulmonary) always are retained, and arch 5 (systemic) is present in some salamanders. All anurans and some salamanders have a spiral valve in the conus arteriosus that shunts oxygenated blood to arches 3 and 4 (to the head and dorsal aorta) and deoxygenated blood to arch 6.

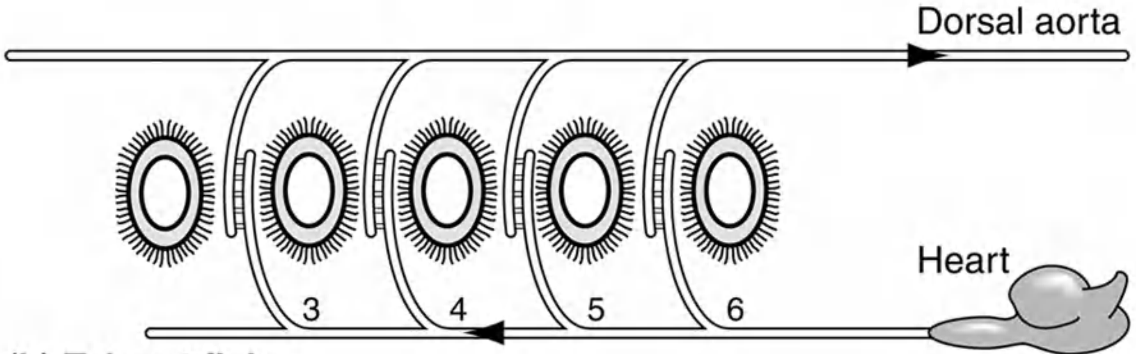
All amphibians utilize cutaneous gas exchange to some degree. The moist skin may play only a minor role in oxygen uptake in some species, whereas in others, like plethodontid (lungless) salamanders, it plays a major role. Branches of the pulmonary artery transport blood to the skin, so that many amphibians lose most of their carbon dioxide through their skin. Blood returning from the skin through the cutaneous vein into the right atrium is oxygenated just as that returning from the lungs into the left atrium is oxygenated. Depending on the extent to which cutaneous respiration is being utilized, keeping the two bloodstreams separate may or may not be an advantage.

The blood of many amphibians consists of plasma, erythrocytes, leukocytes, and thrombocytes. Frogs, however, lack thrombocytes. Normal erythrocytes are elliptical, nucleated disks varying in size from less than 10 mm in diameter in some species to more than 70 mm (in *Amphiuma*), the largest known erythrocyte of any vertebrate.

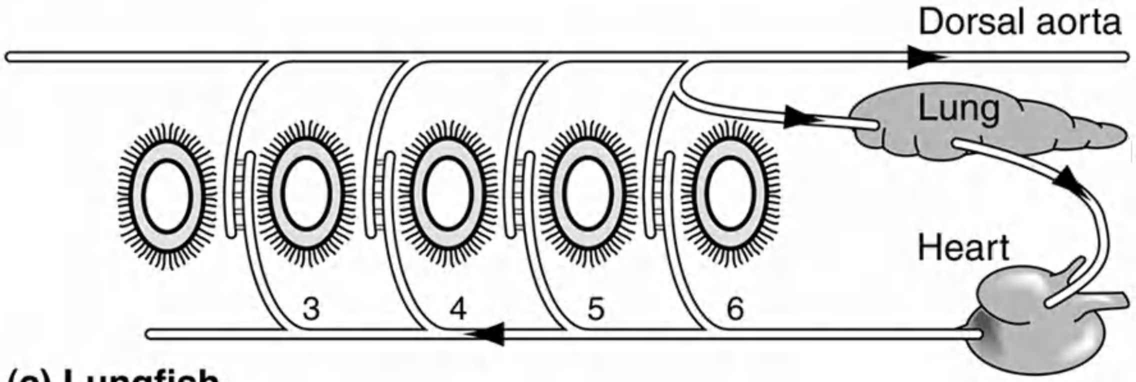
Hematopoiesis (production of all formed elements in the blood—i.e., all red and white blood cells) in salamanders takes place primarily in the spleen, whereas in anurans it occurs in the spleen and in the marrow of the long bones at metamorphosis and upon emerging from hibernation (Duellman and Trueb, 1994). Leukocytes may be formed in the liver, in the submucosa of the intestines, and in the bone marrow.



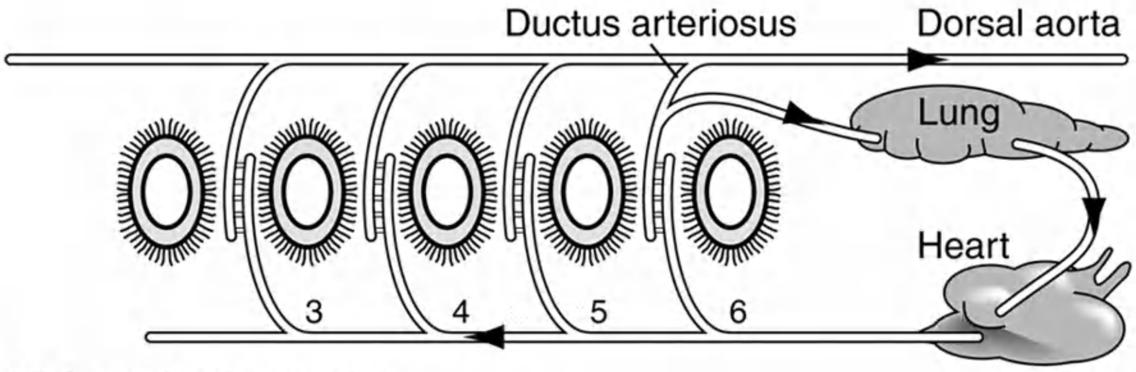
(a) Vertebrate embryo



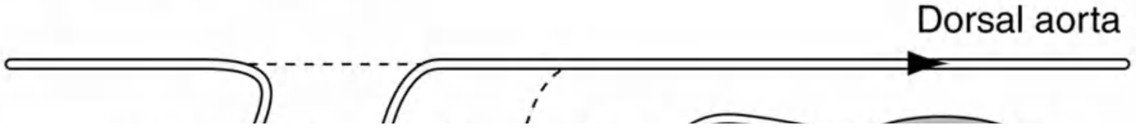
(b) Teleost fish



(c) Lungfish



(d) Larval salamander



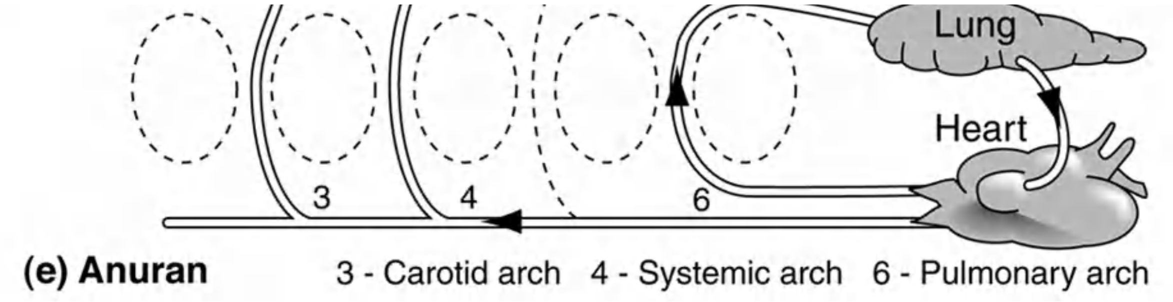


Figure 5.17. Arrangement of the aortic arches in (*a*) vertebrate embryo; (*b*) teleost fish; (*c*) lungfish; (*d*) larval salamander; and (*e*) anuran.

Respiratory System

Body size and temperature influence gas exchange in amphibians. In general, as mass increases, oxygen consumption and carbon dioxide production increase, although the consumption rate declines with increasing mass. Thus, respiratory surfaces may be unable to meet the metabolic needs without modification. Modifications include increasing the surface by additional folds of skin or partitioning of the lungs; increasing vascularization of the skin and/or having blood vessels closer to the surface; increasing the gas transport capacity of the blood and increasing flow rate; and/or similar respiration-enhancing devices.

External nares (nostrils) lead via nasal passages to internal nares (choanae) (Fig.5.18a). Because amphibians lack a secondary palate, the internal nares usually open far forward in the roof of the mouth just inside the upper jaw. From the pharynx, air passes through the **glottis** into a short **trachea**.

Amphibians are the most primitive vertebrates to have the anterior end of the trachea modified to form a voice box, or **larynx**. Voice is well developed in most male frogs and toads, which have two muscular bands stretching across the laryngeal chamber; these form vocal cords that vibrate when air passes over them. Tightening or relaxing these vocal cords causes variations in pitch. Many male anurans have paired or median **vocal sacs**, or resonating chambers (see Fig. 5.18b, c, d). The size, shape, and position of vocal sacs is species-specific. There is increasing evidence that at least some terrestrial anuran species integrate acoustic, visual, and chemical cues in species recognition and mate choice (Starnberger et al., 2014).

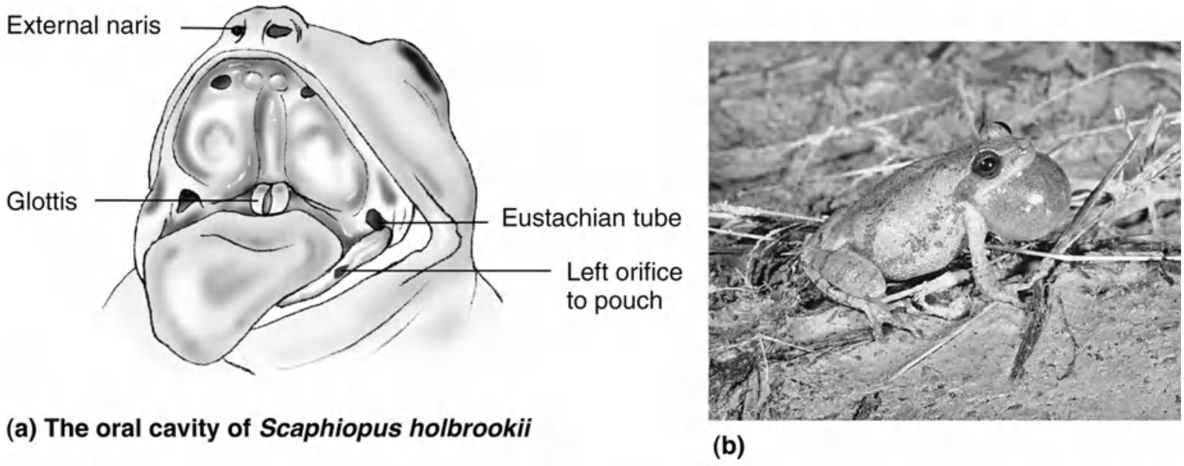
Calls have long been thought to radiate from the vocal sac. However, Alejandro Purgue of the University of California at Los Angeles discovered that the ears account for up to 90 percent of the sound output in the American bullfrog (*Lithobates* [*Rana*] *catesbeiana*) (Purgue, 1997; Pennisi, 1997a). The ears act as loudspeakers, amplifying the sound of the frog's vocal cords. The vocal sac serves primarily to store the air used by the vocal cords. Six additional, closely related frog species have loudspeaker ears, whereas western chorus frogs and California tree frogs use other body parts as resonators.

Female vocalization is rare and has been observed in only a handful of species, including the concave-eared torrent frog (*Odorrana tormota*). Female *O. tormota* have been reported to emit moderate-level calls to attract mates (Zhang et al., 2017).

Although a larynx is present in the mudpuppy (*Necturus*) and a few other salamanders, most lack vocal cords and are voiceless. Sounds reported from salamanders are probably produced by the inspiration and expiration of air. A few, like the Pacific giant salamander (*Dicamptodon ensatus*), have a large larynx and bands, known as **plicae vocales**, which resemble anuran vocal cords. Air from the lungs passes over the plicae, causing them to vibrate. Lungless salamanders (plethodontids) lack both a trachea and a larynx.

A force-pump mechanism (Fig. 5.19) is used by amphibians to get air into their lungs. Air enters the oral cavity through the internal nares. When the nostrils close and the floor of the oral cavity is raised, air is forced through the glottis into the lungs and is retained by closure of the glottis sphincter. While air is in the lungs and the glottis is closed, "throat flutters" can provide additional aeration of oral surfaces (Fig. 5.19c). By taking repeated volumes of air into its lungs several times in succession without letting air out, a frog or toad can blow itself up to a considerable size as a defensive maneuver when confronted by a potential predator.

Amphibians utilize several different methods of gas exchange: cutaneous, buccopharyngeal, branchial, and pulmonary. Some salamanders and two caecilians (*Atretochoana* and *Caecilita iwokramae*) (Anonymous, 1996a, 2010) are the only tetrapods in which the evolutionary loss of lungs has occurred. Land-living members of one large family of salamanders (Plethodontidae), which constitute about 70 percent of existing salamander species, depend *entirely* on gas exchange through the moist, well-vascularized skin (cutaneous gas exchange) and through the lining of the mouth and pharynx (buccopharyngeal gas exchange). Lunglessness, which reduces buoyancy, has been proposed to be adaptive, particularly for larval survival, in flowing, well-oxygenated streams (Wilder and Dunn, 1920; Beachy and Bruce, 1992). Ruben and Boucot (1989), however, suggested terrestrial or semiterrestrial ancestors for plethodontids, which would mean that lungs were lost for reasons other than ballast.



(a) The oral cavity of *Scaphiopus holbrookii*

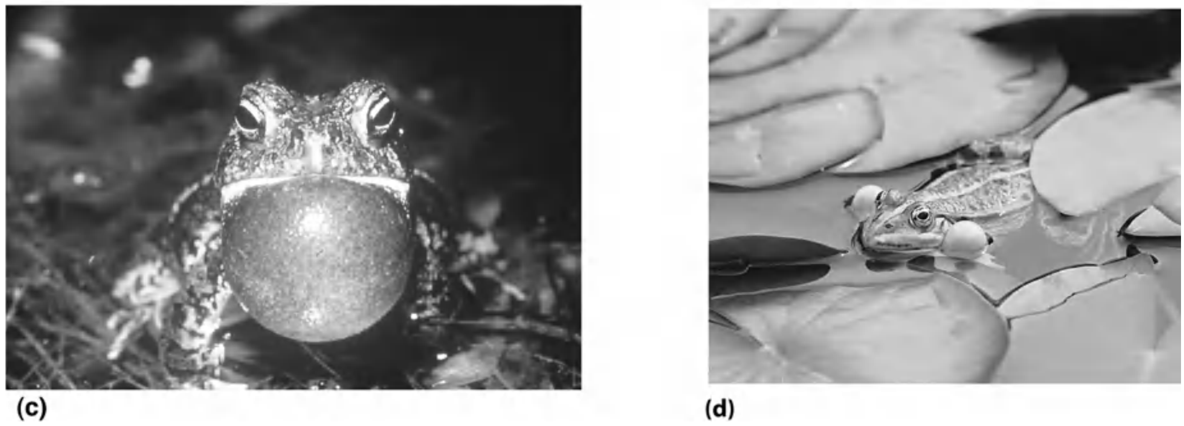


Figure 5.18. (*a*) Oral cavity of toad (*Scaphiopus holbrookii*) showing location of certain respiratory structures. Distended median vocal sacs of (*b*) the spring peeper (*Pseudacris crucifer*) and (*c*) Fowler's toad (*Bufo fowleri*). (*d*) Distended paired vocal sacs of the edible frog (*Rana esculenta*).

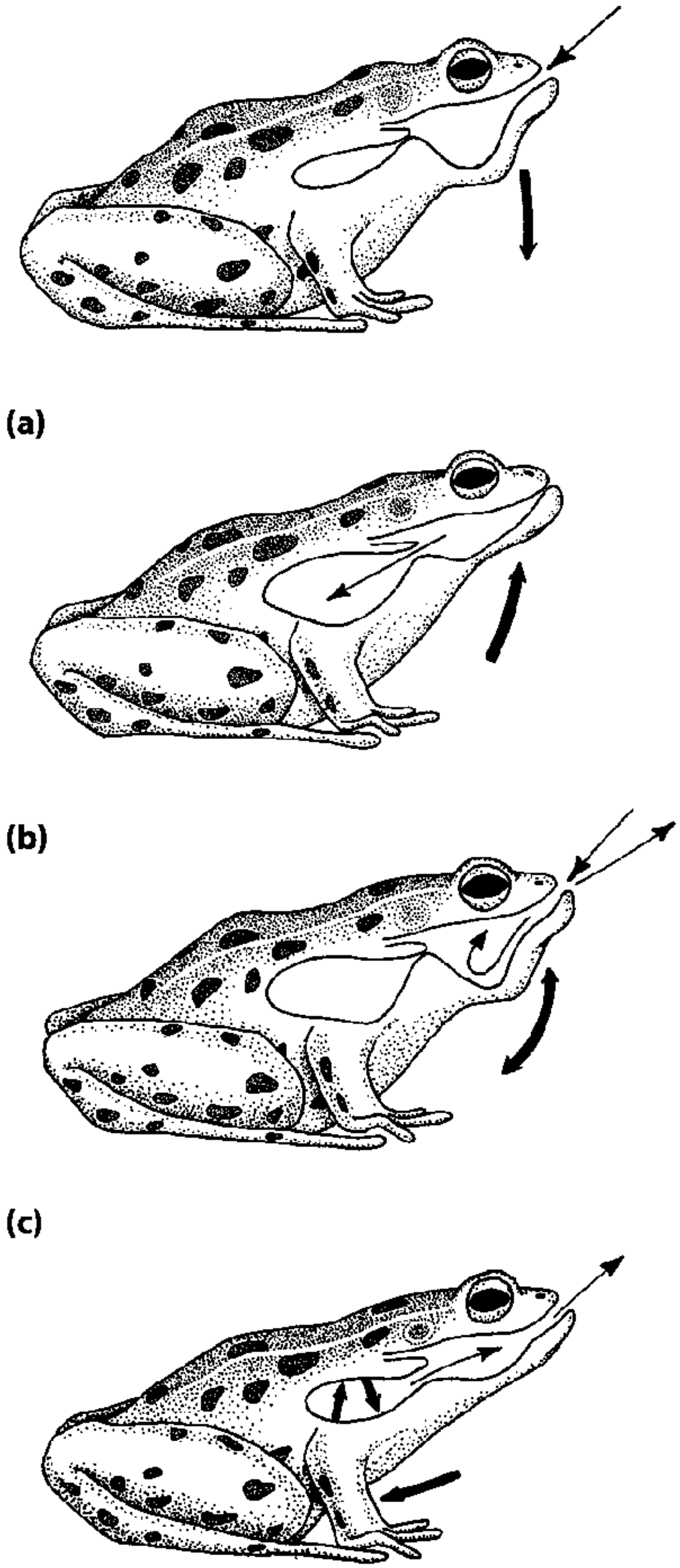
Sounds without Vocal Cords

The totally aquatic pipid anuran *Xenopus borealis* lacks vocal cords yet produces long series of clicklike sounds underwater at night. Although it retains an essentially terrestrial respiratory tract, the larynx is highly modified. Unlike in all other anurans, sound production does not involve a moving air column. Rather, calcified rods with disklike enlargements in the larynx are held tightly together. When muscle tension is developed and exceeds the adhesive force, the disks rapidly separate, leaving a vacuum. A click is produced by air rushing at high speed into the space between the disks.

Yager, 1992a, b

Larval amphibians breathe by means of external gills (branchial gas exchange). In anuran tadpoles, gills are enclosed in an atrial chamber, which may be either ventral or lateral and which opens via a **spiracle**. The position of the spiracle is a generic characteristic. In tadpoles, water enters the atrial chamber via the mouth, flows over the gills, and passes to the outside through the spiracle. Gills of tadpoles are usually smaller and simpler than those of salamander larvae. During metamorphosis, gills of anurans are resorbed, the gill slits close, and gas exchange using lungs takes over.

In larval salamanders and caecilians, gills are exposed on each side behind the head. No atrial chamber develops. As they mature, aquatic amphiumas (*Amphiuma* spp.) and hellbenders (*Cryptobranchus alleganiensis*) develop lungs and lose their gills, but they retain the openings of one pair of gill slits. Some species, however, retain gills throughout their lives (perennibranchiates). The retention of larval or embryonic characters is known as **neoteny**. Adult *Necturus*, for example, possess both gills and lungs, and two gill slits remain open. Adult sirens (Sirenidae) also have lungs, gills, and gill slits. *Necturus* and *Cryptobranchus* are water-breathing aquatic salamanders that utilize aerial gas exchange primarily under stress conditions, like environmental hypoxia, and possibly during recovery from strenuous activity. Sirens and amphiumas, both of which have highly vascularized lungs, are aquatic salamanders that are primarily air-breathers and are known to enter drought-induced estivation, during which time they breathe atmospheric air exclusively. Their aquatic gas exchange mechanism is primarily limited to the integument.

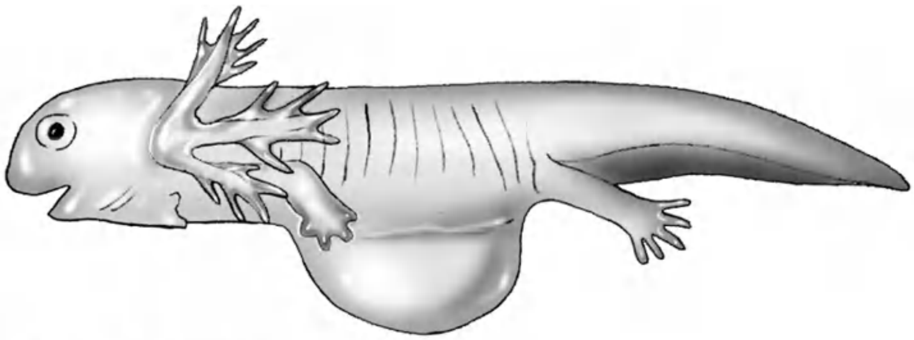

(a)
(b)
(c)

(d)

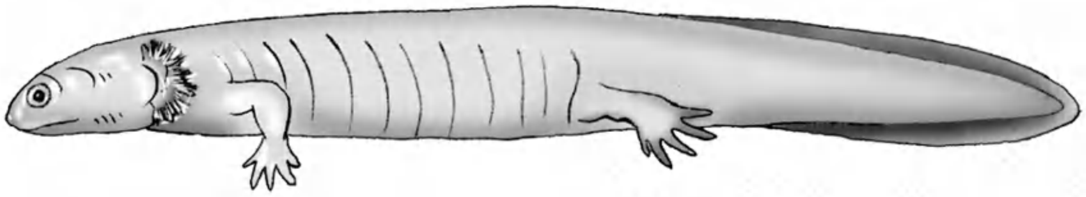
Figure 5.19. Breathing in the frog. Frogs use positive pressure to force air into their lungs. In the sequence shown, air is drawn in through the nostrils by lowering the floor of the mouth (*a*). By closing the nostrils, opening the glottis, and elevating the floor of the mouth, the frog forces the air into its lungs (*b*). The mouth cavity is ventilated rhythmically for a period (*c*), after which the air is forced out of the lungs by contraction of the body wall musculature and by the elastic recoil of the lungs (*d*).

Larval gills in salamanders vary as a result of adaptation to the larval habitat (Fig. 5.20). Terrestrial forms within the family Plethodontidae lay their eggs on land, and the young undergo larval development in the egg. They have staghorn-shaped gills. Stream salamanders have reduced gills with short, broad gill filaments. Pond salamanders have larger, feather-like gills for life in quiet water with reduced oxygen.

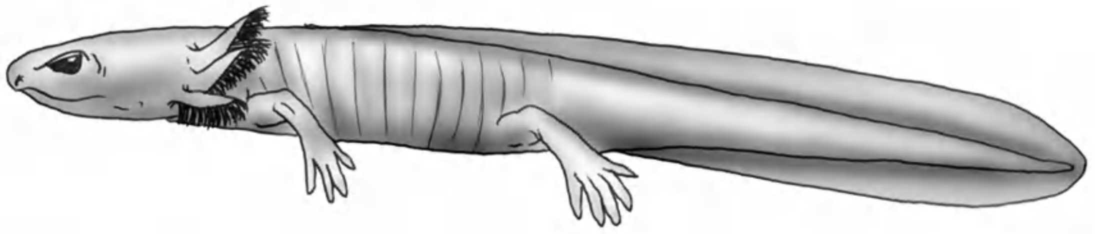
With the development of lungs, oxygen from a mixture of gases (air) passes through moist, gas exchange membranes deep within the body (pulmonary gas exchange), and gas exchange takes place with minimal loss of water through evaporation. Internal lungs must be ventilated by a tidal movement of air to replenish the oxygen supply at the gas exchange surfaces.



(a) Terrestrial type



(b) Mountain stream type



(c) Pond type

Figure 5.20. Gills in larval salamanders: (*a*) terrestrial type (*Plethodon vandykei*); (*b*) mountain stream type (*Dicamptodon ensatus*); (*c*) pond type (*Ambystoma gracile*).

The paired lungs of amphibians develop within the pleuroperitoneal (coelomic) cavity before metamorphosis. Although some salamanders (plethodontids) lack lungs and the lungs of some mountain stream salamanders are extremely small, lungs are present in all other adult amphibians. In caecilians, the right lung is functional and the left lung is rudimentary—presumably an adaptation associated with the elongate body form of caecilians. This adaptation is similar to that found in snakes (see Chapter 7).

The internal lining of amphibian lungs may be smooth, or it may be pocketed to increase the surface area available for gas exchange. Lung linings are more complex in anurans, where the lungs may be made up of many folds lined with **alveoli** (respiratory pockets) that are supplied by dense capillary networks. Pulmonary oxygen uptake (lung and buccopharyngeal surfaces) accounts for only 26 to 50 percent of the total gas exchange in mole salamanders (Ambystomatidae) (Whitford and Hutchison, 1966); however, approximately 80 percent of the carbon dioxide release is through the skin.

Some neotenic salamanders, some adult newts, and pipid frogs apparently utilize the lungs more as hydrostatic organs than as organs for gas exchange. In *Necturus*, for example, only about 2 percent of the oxygen is obtained via lungs when water is well oxygenated. Some of these forms take air in through their mouth, which, along with the pharynx, is lined with highly vascularized epithelium called the **buccopharyngeal mucosa**. In winter, when the oxygen uptake is quite low, the skin takes up more oxygen than the lungs. In summer, when oxygen consumption is high, uptake through the lungs increases several-fold and far exceeds cutaneous uptake (Schmidt-Nielsen, 1997). Oxygen uptake through the skin remains nearly constant throughout the year (Dolk and Postma, 1927).

A Projectile Tongue

Salamanders of the genus *Bolitoglossa*, *Hydromantes*, and *Eurycea* possess tongues that can project distances ranging from 31 to 80 percent of snout-vent length (SVL) (16–60 mm, or 0.6–2.4 in.). The greatest tongue reach occurs in *Hydromantes supramontis*, which has been recorded as having a tongue reach of 60 mm (2.4 in.), or 80 percent of its body length. The tongue is fired from the mouth by a ballistic mechanism and is retracted by muscles that originate at the pelvis. Maximum speeds range from 9.7 to 25.3 km (6–15.7 mi.) per hour and reach accelerations up to 450 *g* (force of acceleration). When the tongue is extended, the entire tongue skeleton leaves the mouth completely. These are the only vertebrates known to shoot part of their visceral skeleton completely out of their body as a projectile. Researchers believe that the speed of this action cannot be accomplished by the direct application of muscle power alone. Rather, the tongue mechanism is thought to be analogous to the components of a crossbow: a muscle to produce energy over time, a spring to store the energy, and a latch to release the spring in an instant.

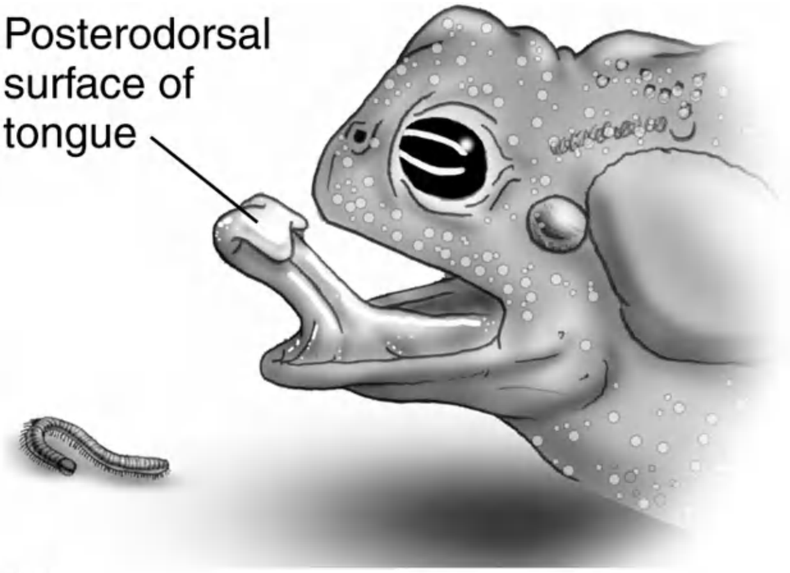
Deban et al., 1997; Deban et al., 2007

Rates of oxygen consumption by larval and adult amphibians at rest and during locomotion have been presented by Gatten et al. (1992). Absolute levels of oxygen uptake during rest and exercise, and the difference between these two measures, were found to be consistently lower in salamanders than in anurans.

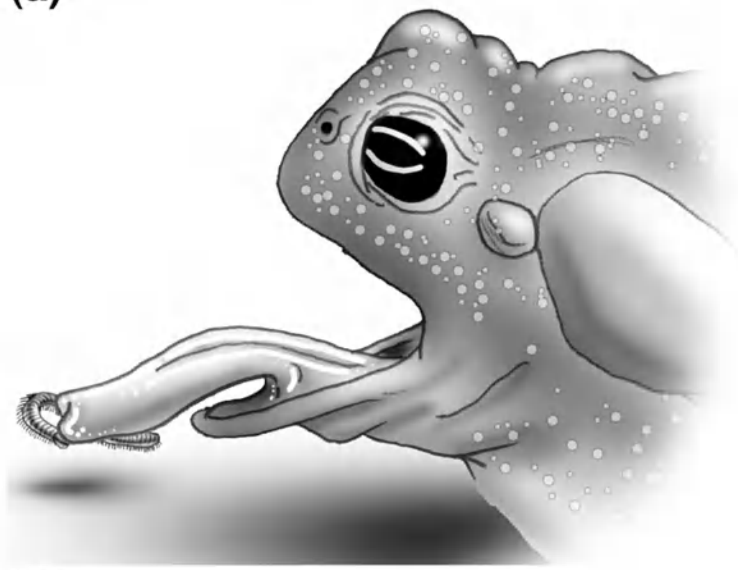
Digestive System

Most species of amphibians possess a tongue in their oral cavity. It may be attached by its anterior end or its posterior end, or it may be mushroom-shaped (boletoid) and consist of a pedestal with a free upper edge. These variations permit the tongue to be used in taxonomic classifications. The tongue is poorly developed in aquatic forms and is absent in pipid frogs (Pipidae).

In those salamanders with protrusible tongues, the tongue is mounted on the hyoid, and hyoid movement serves to evert the tongue beyond the mouth. Tongues of some plethodontid salamanders can be extended several times the length of the head. Anurans lack such an intrinsic lingual skeleton.



(a)



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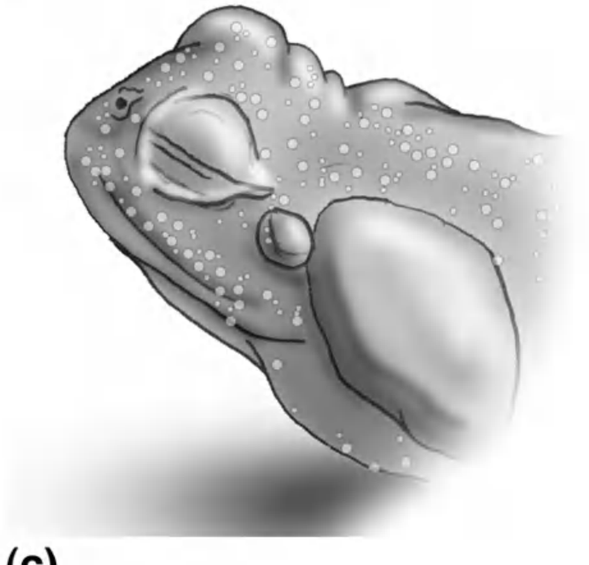


(c)

Figure 5.21. Lingual flipping feeding mechanism in the toad *Bufo marinus*. Note the depressed anterior part of the jaw.

The anuran tongue is a well-developed, sticky prehensile organ that is important in gathering food, particularly insects. Numerous glands and secretory cells maintain a layer of sticky mucus that coats the tongue and assists in capturing prey. Tongues of most anurans are attached anteriorly, are highly flexible, and are used for securing food. Because considerable diversity exists in tongue structure, the mechanism of protraction varies (Gans and Gorniak, 1982; Nishikawa and Cannatella, 1991; Nishikawa and Roth, 1991; Deban and Nishikawa, 1992) (Fig. 5.21). Protrusion involves muscular action with the tongues of some, like *Rana* and *Anaxyrus* (*Bufo*), being highly protrusible, whereas those of *Ascaphus*, *Discoglossus*, and most hylids are weakly protrusible (Deban and Nishikawa, 1992). Food capture involves a lingual flip in which the posterodorsal surface of the retracted tongue becomes the anteroventral surface of the fully extended tongue. The tongue of caecilians is rudimentary, cannot be protruded from the oral cavity, and is capable of only limited movement.

Most amphibians have small teeth (see Fig. 5.13) that are shaped alike (**homodont dentition**) and are found on the palate as well as on the jaws. Teeth are attached to the inner side of the jawbone (**pleurodont dentition**) and are replaced an indefinite number of times if lost or injured (**polyphyodont dentition**). Because amphibians do not chew their food, the function of teeth is to grasp and hold food until it is swallowed. Most frogs lack teeth in the lower jaw.

The boundary between the esophagus and stomach is indistinct. The stomach is generally unspecialized and retains food items for 8 to 24 hours, during which time the food mixes with gastric secretions and digestion begins (Larsen, 1992).

Feeding habits and digestive systems change drastically with metamorphosis. Larval forms with herbivorous diets have longer intestines than those with carnivorous diets in order to more efficiently break down the cellulose cell walls of plant cells.

Anuran larvae have much longer mid- and hindguts than do larval salamanders. Anuran digestive tracts are coiled within the abdominal cavity, and their total length is several times greater than the length of the animal. The maximum length of the gut is reached when the hind legs are well developed. Reduction in length of larval intestines comes from contraction of the circular and longitudinal muscles at both ends. Shortening and reorganization of the gut in *Anaxyrus* (*Bufo*) requires 24 hours and occurs within 10 days after the front legs break through (Bowers, 1909). Larval salamanders tend to be carnivorous and feed on larger prey than anuran tadpoles do.

All amphibians have a cloaca that receives the contents of the digestive, urinary, and reproductive systems. A urinary bladder is connected to the ventral side of the cloaca. The comparative anatomy and phylogeny of the cloacae of salamanders has been discussed by Sever (1991a, b, 1992). Kikuyama et al. (1995) isolated sodefrin from the abdominal gland of the cloaca of the male red-bellied newt (*Cynops pyrrhogaster*). Sodefrin is a species-specific, female-attracting pheromone (a secretion that elicits a behavioral response in another member of the same species), the first ever identified in an amphibian. It is also the first peptide pheromone identified in a vertebrate.

Nervous System

The anterior portion of the brain consists of a pair of olfactory lobes and a pair of cerebral hemispheres (Fig. 5.22). A pineal organ is present and may serve as a photoreceptor, but only remnants of the parapineal organ are found in amphibians. Optic lobes are present; however, the cerebellum is relatively inconspicuous—a condition presumably correlated with the comparatively simple locomotor activities of many amphibians. Impulses from the lateral-line system are directed to the cerebellum, which coordinates and controls voluntary muscular activity. The cerebellum is very poorly developed in those amphibians with a reduced lateral-line system.

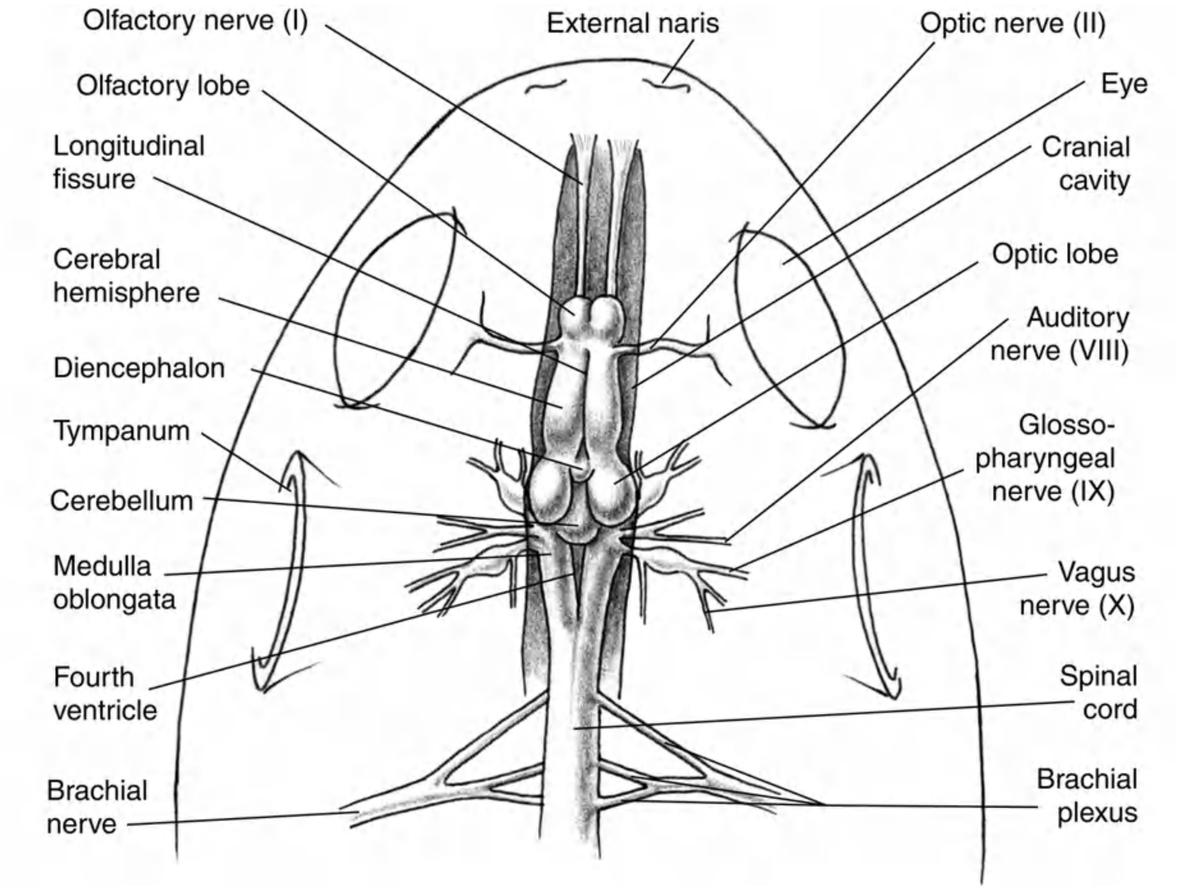


Figure 5.22. Dorsal view of the frog brain within the cranial cavity.

Cranial nerves in anamniotes were discussed in Chapter 4. Amphibians have the same 10 basic cranial nerves as fishes and the same terminalis nerve. However, some authorities recognize two additional nerves: the **accessory nerve** (XI), which supplies the cucullaris muscle in amphibians, and the **hypoglossal nerve** (XII), which innervates muscles of the tongue and supplies hypobranchial muscles in the neck. Primitive fossil amphibians apparently had 12 cranial nerves emerging from their skull. Due to a shortening of the cranium, the 12th, or cranial nerve XII, is now associated with the first two spinal nerves (Duellman and Trueb, 1994).

Right Forelimb Dominance in Toads

Behavioral asymmetry in forelimb usage has been demonstrated in European toads (*Bufo bufo*), which showed a bias for right forepaw use. Toads (and frogs) that ingest undesirable objects like ants and wasps (whose bodies may contain toxins) empty their stomachs by regurgitating (everting) their entire stomach. The stomach hangs out of the side of their mouth, and they use their hand to wipe away remaining vomitus from the surface of the prolapsed stomach before reswallowing it. The right hand is always used for this “gastric” grooming. Why? Because the anuran stomach, like ours, lies somewhat left of center and is held in place by membranes. Because the membrane attached to the right side of the stomach is shorter, it pulls the stomach to the right as it is everted. Toads and frogs cannot reach over to the right corner of their mouth with their left hand because their arms are too short, and so they use their right hand.

Bisazza et al., 1996; Naitoh and Wassersug, 1996

Two **meninges**—an outer **dura mater** and an inner **vascular pia-arachnoid membrane**—surround the spinal cord. In tailed amphibians, the spinal cord extends to the caudal end of the vertebral column, whereas in most frogs it consists of just 11 segments and ends anterior to the urostyle. Cervical and lumbar enlargements occur for the first time evolutionarily because these are the first forms to have appendages modified into true limbs. Eleven pairs of spinal nerves emerge from the spinal cord of anurans by means of ventral and dorsal roots. An autonomic nervous system, which controls activities of smooth muscles, glands, and viscera, is well developed.

Sense Organs

NEUROMAST ORGANS

Larval and adult aquatic amphibians possess **neuromast organs** in the form of lateral-line canals and cephalic canals. Receptors are distributed either singly or in small groups over the dorsal and lateral surfaces of the body and head. Receptors are especially abundant on the head, where they form distinct patterns.

Each neuromast consists of a pear- or onion-shaped group of hair cells embedded in the epidermis. They perceive low-frequency vibrations of the water and water currents and may also be sensitive to pressure (Russell, 1976). Collectively, they enable the animal to maintain equilibrium and posture. In some salamanders, like the axolotl (neotenic *Ambystoma* spp.), the lateral-line system also provides electroreception. In these salamanders, two types of sensory units are present: electrosensitive and mechanosensitive. Electrosensitive units react to minute voltage gradients, whereas mechanosensitive units are extremely sensitive to movements in the water (Münz et al., 1984).

The lateral-line organs of some salamanders regress and regenerate in an annual cycle. Regeneration is associated with the return of the amphibians to an aquatic existence during the breeding season. It is the only special sensory system in vertebrates that alternately regresses and regenerates during the life of the animal (Russell, 1976).

EARS

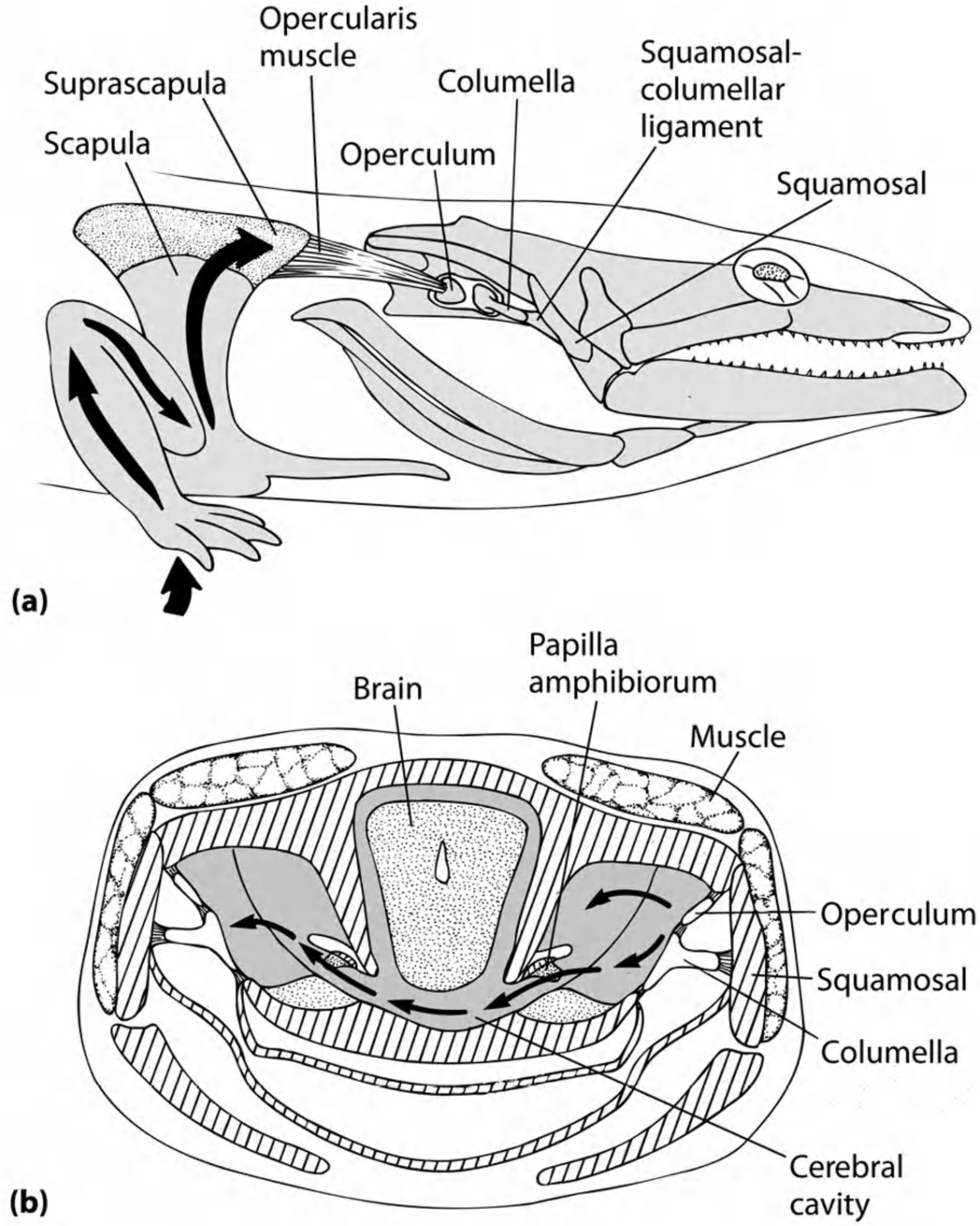
The amphibian ear shows several advances over the ear of fishes. Amphibians possess an auditory system with three main divisions: an outer ear, a middle ear, and an inner ear (Fig. 5.23). The system is sensitive to both ground vibrations and airborne sound waves, with the ears of most anurans being more highly developed than those of salamanders and caecilians.

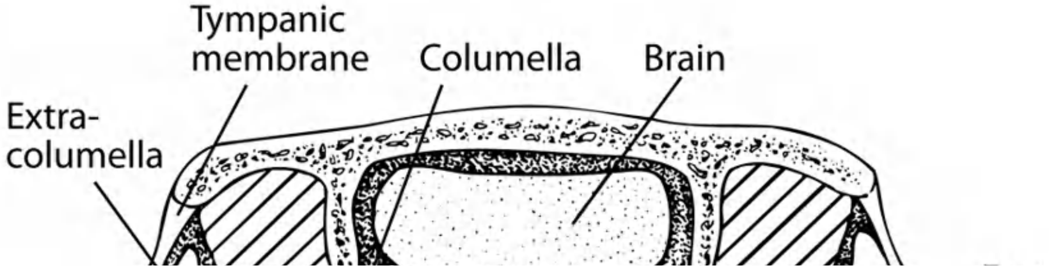
The outer ear of most anurans consists of a **tympanic membrane**, or **tympanum**, which initially receives airborne vibrations; it is absent in larval and adult salamanders and caecilians (Jaslow et al., 1988). In some species, like *Lithobates* [*Rana*], this membrane may be much larger in males than in females, even though the two sexes may be of approximately equal body size (Fig. 5.24). Although Capranica (1976) noted that the functional significance of the size of the eardrum was not clear, new studies (e.g., Purgue, 1997) suggest that its larger size in some male anurans is due to males using their tympanum as an amplification device, as discussed on page **136** in this chapter.

In anuran tadpoles, the developing lungs serve as eardrums. A columella connects the round window membrane of the inner ear with the bronchus and lung sac on the same side of the body. Changes in lung volume result in displacement of the bronchial membranes (Capranica, 1976).

Amphibians are the first group of vertebrates in which the first pair of pharyngeal pouches becomes involved in forming the middle ear. The distal end of each pouch expands to form the tympanic cavity in anurans, while the Eustachian (auditory) tubes form a passageway from the middle ear to the pharynx (Feduccia and McCrady, 1991).

The middle ear, or **tympanic cavity**, is an air-filled chamber that contains the small, rod-shaped **columella** (see Fig. 5.23) and another small, movable bone, the **operculum**. A small opercularis muscle joins the operculum to the pectoral girdle. The primary function of the columella, which is homologous to the dorsal segment of the hyoid arch (hyomandibula) in fishes and transmits vibrations from the tympanum to the oval window, is to convey sound from the external environment to the fluid-filled inner ear. In anurans lacking a tympanum, the columella may be reduced or absent. All salamanders lack tympanic cavities (see Fig. 5.23). The columella, often degenerate, is joined to the squamosal bone by a short squamosal-columellar ligament (see Fig. 5.23) so that sounds can reach the inner ear via a squamosal-columella route.


Opercularis muscle
Suprascapula
Scapula
Operculum
Columella
Squamosal-columellar ligament
Squamosal
(a)
Brain
Papilla amphibiorum
Muscle
Operculum
Squamosal
Columella
Cerebral cavity
(b)


Tympanic membrane
Columella
Brain
Extra-columella

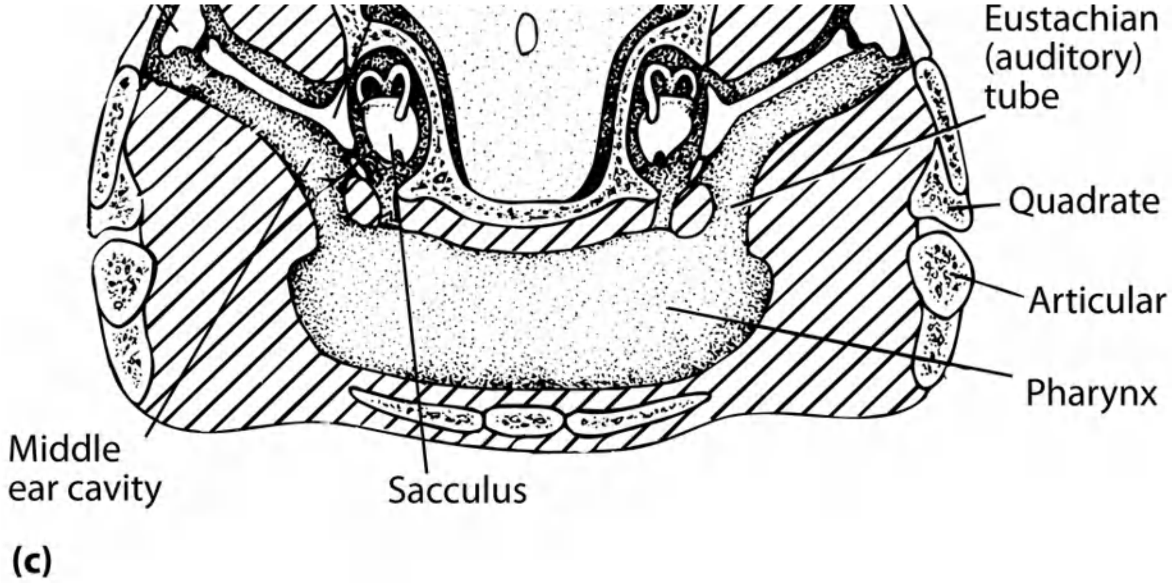


Figure 5.23. (*a*) The inner ear of many salamanders receives sounds via a squamosal-columella route and/or via the opercularis muscle from the scapula. (*b*) As in frogs, the two inner ears on the opposite sides of the salamander's head are connected by means of a fluid-filled channel that passes through the cerebral cavity. This arrangement may allow sound vibrations to spread from one ear to the other (*black arrows*). (*c*) In a frog, both ears are connected via the Eustachian tubes and pharynx; thus, any sound that sets one tympanum in motion also affects the ear on the opposite side. This unique structure is thought to allow frogs to localize the source of sounds.

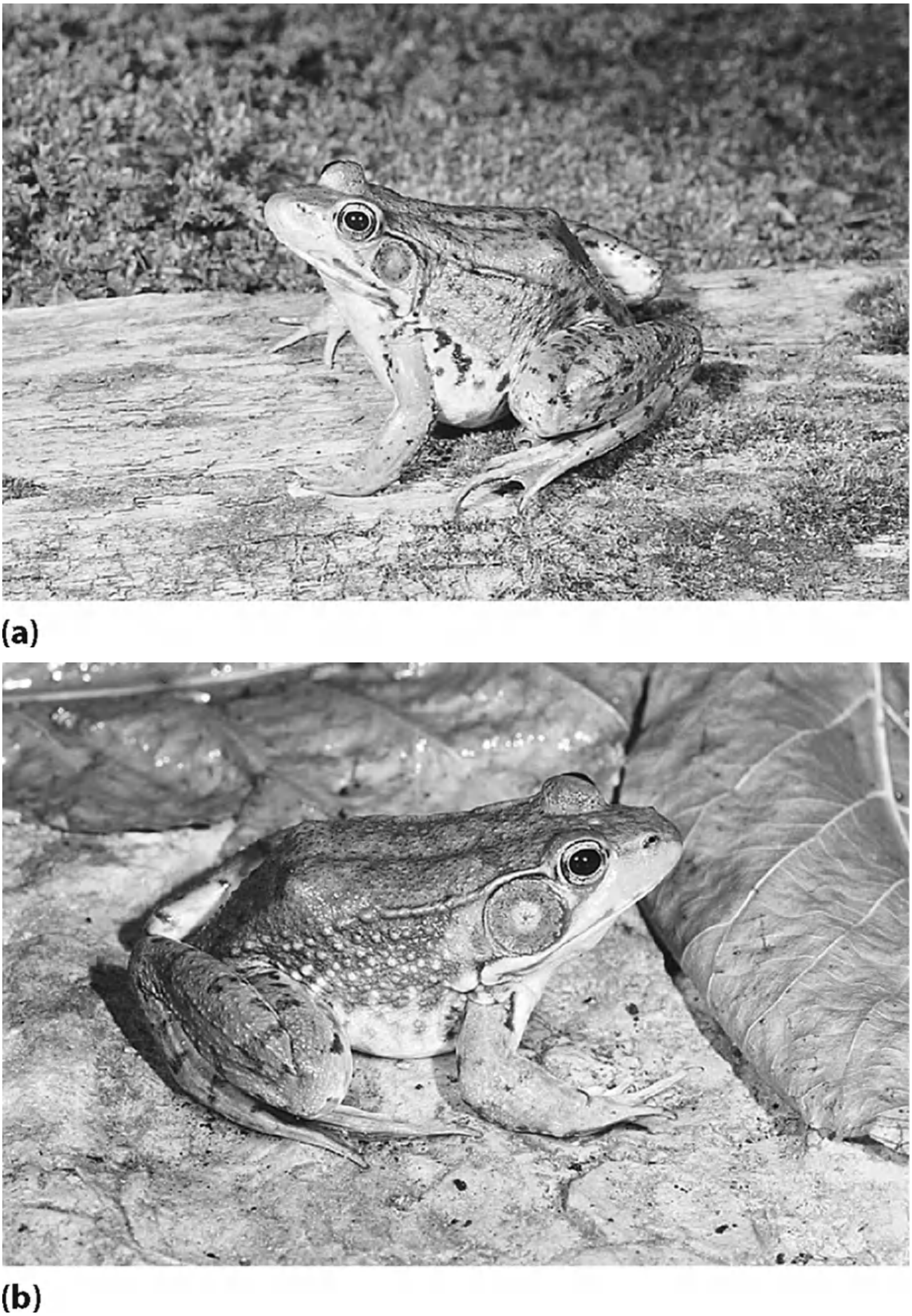


Figure 5.24. Sexual dimorphism. The tympanum is markedly smaller in female green frogs (*Lithobates clamitans*) (*a*) than in male green frogs (*b*).

In addition, sound waves may travel from the ground to the inner ear via the scapula-opercularis muscle-operculum route. In anurans, a **Eustachian (auditory) tube** leads from the middle ear to the pharynx and serves to equalize pressure on both sides of the tympanum. Because salamanders and caecilians lack a middle ear, they also lack a Eustachian tube.

The inner ear consists of a **utriculus**, a **sacculus**, a **lagena** (slight bulge in the ventral wall of the saccule), and three **semicircular canals**, each lying in a different plane. Two fluids—**endolymph** and **perilymph**—are present in the inner ear and function in both hearing and the maintenance of equilibrium. Endolymph is enclosed within the inner ear membranes, whereas perilymph is external to the membranes. Movement of the endolymph stimulates sensory hair receptors and allows vibrations to be transmitted to the brain. The receptor cells, located in ampullae at the base of each canal (at the point where each canal enters the utriculus), are known as **cristae.** By having each canal oriented in a different plane, the endolymph in one or more of the canals will shift with even the slightest movement. Patches of sensory epithelia known as **maculae** are present within the utriculus and sacculus.

EYES

Eyes of terrestrial amphibians are large and well developed, and they show a number of advances over those of fishes (see Fig. 1.20d). Salamanders have good color vision; anurans probably have some color vision (Porter, 1972). Colorless oil droplets are found between the inner and outer segments of cone photoreceptor cells of some species (Bowmaker, 1986). They probably filter out damaging ultraviolet radiation, but they do not appear to contribute to acuity of vision (Hailman, 1976). Their function may be chiefly chemical storage, perhaps in relation to the visual pigment cycle, or they may make wavelength perception more “even” by spreading out the photons.

At times, the eyes may be partially retracted into the orbit, which facilitates the swallowing of large objects. Because the eyeballs protrude into the oral cavity, they assist in forcing food into the esophagus.

Movable eyelids and **orbital glands** (Harderian and lacrimal) are present to afford protection for the eyes in most terrestrial forms. The eyelids and glands develop at metamorphosis in most salamanders and anurans. The lower eyelid has a much greater range of motion than the upper and is better developed in anurans than in salamanders. Eyelids are absent in purely aquatic salamanders and in all amphibian larvae. Harderian glands, which secrete an oily substance, and lacrimal glands, which secrete a watery fluid (tears), are present evolutionarily for the first time in the vertebrates. They serve to lubricate and cleanse the outer surfaces of the eyes.

In many frogs, the lower eyelid has become modified into a translucent or transparent fold of skin called the **nictitating membrane** (Fig. 5.25). This membrane can be drawn up over the retracted eye by tendons encircling most of the eyeball and gives the frog a certain amount of vision even when it appears to be sleeping with partly closed eyes. This membrane is often marbled with a pattern of colored lines or spots in designs characteristic of the species. In water, the nictitating membrane is drawn over the eye to protect it while allowing the frog some degree of vision.

Figure 5.25. Bullfrog (*Rana catesbeiana*) showing the eye partly covered by the nictitating membrane.

The amphibian lens, hard and almost spherical, cannot change shape. Accommodation for near vision is accomplished by contraction of the protractor lentis muscle, which moves the lens closer to the cornea. Relaxation of the protractor muscle allows the eye to focus on distant objects. Further discussion of the amphibian visual system can be found in Fite (1976).

Some cave-dwelling and subterranean salamanders and caecilians may be blind, or the eyes may be vestigial or poorly developed (Fig. 5.26). Cave-dwelling genera include *Typhlomolge*, *Typhlotriton*, and *Haideotriton*—all members of the family Plethodontidae.

PINEAL ORGAN

A pineal organ is present in all amphibians; the parietal organ, however, is present only in anurans. Both organs function as photoreceptors and are located in the top of the head between the eyes. They both appear to be important in the establishment of endogenous rhythms, in thermoregulation, in gonadal development, and in compass orientation (Adler, 1970). The parietal organ is known to be sensitive both to light intensity and to different wavelengths of light (Dodt and Heerd, 1962; Dodt and Jacobson, 1963).

NOSE

Amphibians have a double olfactory system. Air enters the nasal chamber via external nares and exits via internal nares into the oral cavity. Air entering the external nares must flow past the olfactory epithelium on its way to the lungs, thus allowing the olfactory epithelium to sample chemicals in the airflow. The olfactory epithelium, therefore, monitors an airstream instead of a water stream. In addition, rudimentary **vomeronasal**, or **Jacobson's**, **organs** (first described in 1811, by L. Jacobson, a Danish physician), are present for the first time (Fig. 5.27). Each vomeronasal organ consists of a ventral segment of olfactory epithelium that has become isolated from the nasal passageway and usually is located dorsal to the vomer bone in the oral cavity. The organs, consisting of a pair of deep grooves in salamanders and a pair of sacs in anurans, are innervated by a branch of the olfactory nerve. They probably play a role in the recognition of food and are used to test substances held in the mouth. The presence of a vomeronasal system is often an indication of the use of olfactory signals, or **pheromones**, for intraspecific communication. Indeed, chemical signals associated with courtship or territoriality have been demonstrated repeatedly in adult salamanders (Dawley, 1984; Horne and Jaeger, 1988), but not in adult caecilians. An aquatic, female-attracting pheromone named *splendipherin* is the first pheromone to be identified from an adult anuran (Wabnitz et al., 1999). It is secreted from the parotoid and rostral glands of the male magnificent tree frog (*Litoria splendida*).

Figure 5.26. The Texas blind salamander (*Typhlomolge rathbuni*), a plethodontid. Note the poorly developed eyes, external gills, and lack of pigment in the skin.

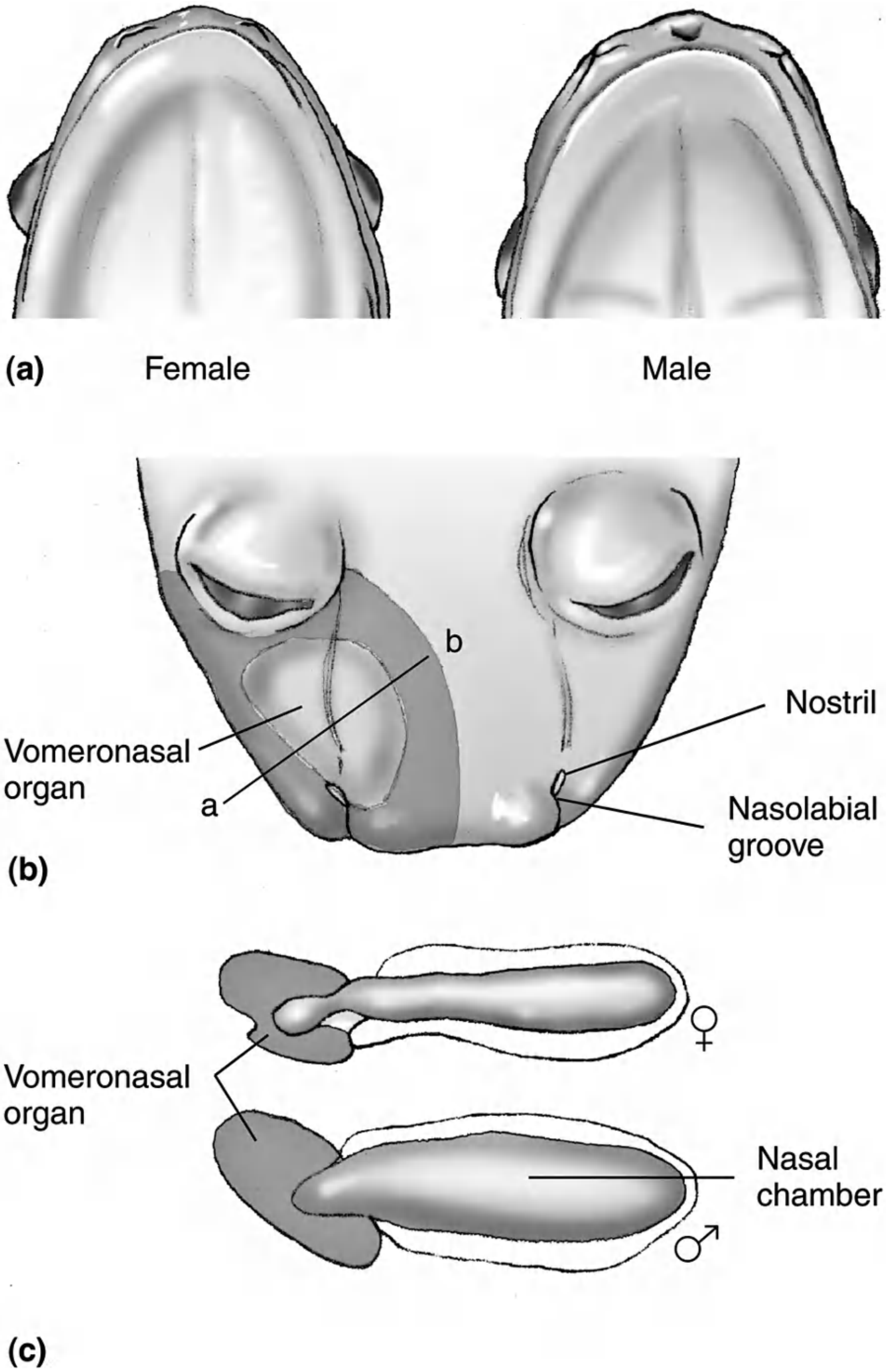

(a)
Female
Male
b
Nostril
Vomeronasal organ
a
Nasolabial groove
(b)
♀
Vomeronasal organ
Nasal chamber
♂
(c)

Figure 5.27. Sexual dimorphism in the nasolabial grooves and vomeronasal organs of plethodontid salamanders. (*a*) Note the difference in forking of the grooves at the edge of the upper lip in ensatina (*Ensatina eschscholtzii*): (*left*) female; (*right*) male. (*b*) Nasal passage of the red-backed salamander (*Plethodon cinereus*) exposed to show the position of the vomeronasal organ. (*c*) Cross section through female (*top*) and male (*bottom*) nasal passages at line a–b in (*b*), showing differences in the size of the vomeronasal organ.

The sense of smell has been shown to be particularly well developed among plethodontid salamanders (see Jaeger and Gergits, 1979, for review; Dawley, 2017). The presence of **nasolabial grooves** in these salamanders is thought to aid in their olfactory reception and is unique among terrestrial vertebrates (see Fig. 5.27). A small furrow extends from the edge of each upper lip to the nostril. The lower ends of the grooves may divide into long branches, break up into capillary networks, or end in nipple-like palps projecting downward from the upper lip. When the snout comes into contact with moist surfaces, fluid rapidly passes up the grooves by capillary action to the external nares, where ciliary action draws it into the nose and over the chemoreceptors of the vomeronasal organs (Brown, 1968; Dawley, 1987; Dawley and Bass, 1989). Nasolabial grooves are found in both sexes, but they are larger, better developed, and more elaborate in males (Dawley, 1992). They are thought to play a significant role in reproductive behavior by allowing males to track and identify females. Plethodontids frequently engage in nose-tapping, a behavior in which the snout is used to tap the substrate or other individuals. Plethodontid salamanders are the only nonmammalian vertebrates in which sexual dimorphism of the vomeronasal system has been documented.

Caecilians have an opening on each side of the head between the eye and nostril, through which a tentacle with both chemoreceptive and tactile functions can be extended. The tentacle, which is unique among vertebrates, contains a duct that opens to the exterior. Its primary function is to convey airborne chemoreceptive information to the vomeronasal organs. Development of the tentacle is thought to be an adaptation to caecilians' subterranean, burrowing existence, and the tentacle allows chemoreception during burrowing and swimming when the nostrils are closed. Tentacles appear to have evolved through modification of muscles and other structures associated with the eyes, which are degenerate (Billo and Wake, 1987; Schmidt and Wake, 1990).

In many caecilians, the paired tentacles can be protracted a considerable distance out of the head. In the East African caecilian *Scolecomorphus kirkii*, the eye is attached laterally to the base of the tentacle. As the tentacle protracts and retracts, the eye moves with it and can actually be protruded beyond the skull (O'Reilly et al., 1996). This is the only known vertebrate with highly mobile, protrusible eyes.

TASTE

Taste buds are primarily found scattered over the dorsal surface of the tongue, the floor of the mouth, the jaws, and the palate. Those on the dorsal surface of the tongue in frogs are in the form of epithelial disks (Jaeger and Hillman, 1976; Sato, 1976). Each taste bud consists of a cluster of gustatory (taste) cells opening via a taste pore.

Endocrine System

Because, in most cases, the endocrine organs are homologous in the vertebrates, the discussion in Chapter 4 included hormones and their respective actions for all groups. Only specific examples of hormonal action will be covered here and in the chapters on reptiles and mammals.

The morphological and physiological changes that occur during metamorphosis are the result of hormones secreted by a finely tuned integration of endocrine glands. The hypothalamus in the brain controls the release of pituitary hormones like thyroid-stimulating hormone, prolactin, and possibly a growth hormone—all secreted by the adenohypophysis (anterior pituitary gland)—which appear to control growth and development by regulating the activity of the thyroid gland. The thyroid gland, which secretes thyroxin and triiodothyronine, is considered to be the keystone of amphibian metamorphosis. Calcitonin, which lowers blood calcium levels, is produced in the ultimobranchial bodies, which are located near the larynx in amphibians. The ultimobranchial bodies conserve calcium to ensure an adequate supply for calcification during metamorphosis.

Changes during metamorphosis include regression of the gills, degeneration of the tail and tail muscles in anurans, development of limbs, formation of dermal glands, and reorganization of the intestinal tract (Duellman and Trueb, 1994). If the thyroid gland is removed from a tadpole, it will grow into an abnormally large, fat tadpole with lungs and reproductive organs, but it will never metamorphose into an adult. If thyroid extract is administered following the thyroidectomy, however, metamorphosis will take place. In adults, thyroid hormones help control the rate of metabolism, heart rate, and shedding of the skin. Molting and intermolt frequency are also under the control of adrenocorticotropic hormone (ACTH) and corticosterone produced by the adrenal glands.

Amphibians present the first evolutionary appearance of parathyroid glands, which develop from pharyngeal pouches in anurans and in many salamanders. Parathyroid hormone (parathormone) raises the calcium and phosphate levels in circulating blood by withdrawing these minerals from storage sites like bone. Seasonal differences in the parathyroid gland have been found in leopard frogs (*Lithobates* [*Rana*] *pipiens*), in which the glands degenerate during the winter (Cortelyou et al., 1960; Cortelyou and McWhinnie, 1967). Some paedomorphic salamanders lack parathyroid glands (Duellman and Trueb, 1994). Adrenal glands, which are diffuse in salamanders, appear as strips of golden yellow tissue partially embedded in the ventral surfaces of each kidney in anurans.

The hypothalamus and pituitary gland regulate reproductive behavior in both male and female amphibians. Estrogens and progesterone control the development of eggs and breeding behavior in females. Androgens, like testosterone, at least partially control the swelling of the thumb pads, the enlargement of the mental (chin) gland, changes in color pattern, the development of the dorsal crest in some salamanders, and the enlargement of the cloacal glands in males (Fig. 5.28). Stimuli from external social or environmental cues are transformed along a multistep pathway known as the hypothalamic-pituitary-gonadal axis into neural and endocrine information, ultimately affecting androgen production by the testes (Houck and Woodley, 1995). Typically, external cues provide stimulation that is converted into neural signals, which are integrated in several regions of the brain, including the hypothalamus. The hypothalamus produces gonadotropin-releasing hormone (GnRH), which, in turn, causes the pituitary to release two peptide hormones—follicle-stimulating hormone (FSH) and luteinizing hormone (LH)—which are carried by the circulatory system to the gonads. FSH prepares the Sertoli cells in the seminiferous tubules for spermatogenesis in the presence of androgens (male sex steroids), whose production by Leydig cells within the testis is stimulated by LH. Androgens most typically found in amphibians include testosterone (T) and dihydrotestosterone (DHT). These androgens diffuse within the testes and are also transported by proteins in the circulatory system to steroid-sensitive targets, including the brain. Circulating androgens may influence male reproductive behavior and also affect certain peripheral tissues, thus resulting in the development of secondary sexual characters.

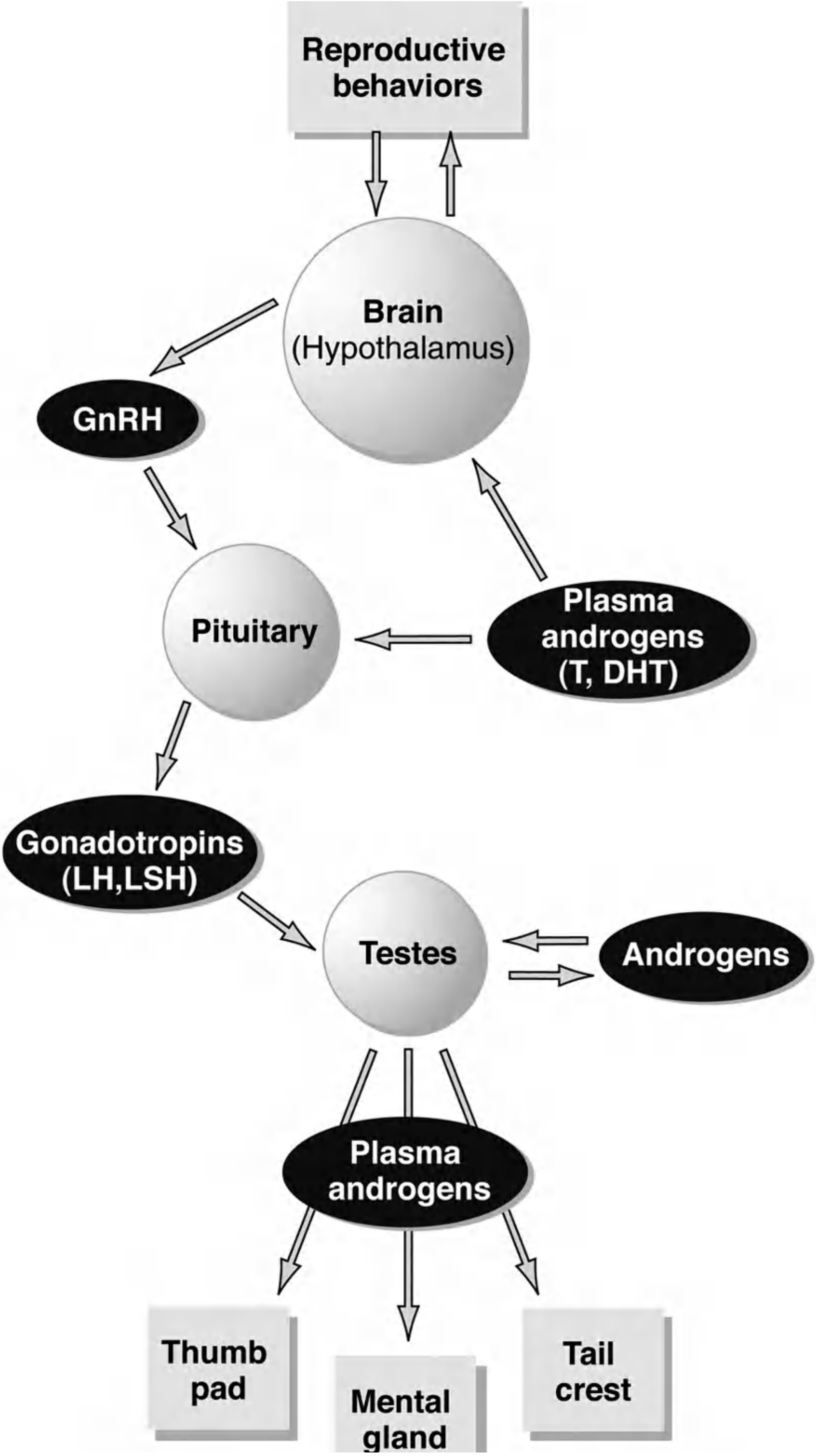

Reproductive behaviors
Brain
(Hypothalamus)
GnRH
Pituitary
Plasma androgens (T, DHT)
Gonadotropins (LH,LSH)
Testes
Androgens
Plasma androgens
Thumb pad
Mental gland
Tail crest

Figure 5.28. The hypothalamic-pituitary-gonad axis influences androgen production in male amphibians. Hormonal influences on androgen production by the testes are illustrated, as well as targets potentially affected by changes in androgen levels.

Diurnal rhythms of the melatonin level in the retina have been reported in amphibians, birds, and mammals (reviewed by Zachmann et al., 1992). Melatonin causes melanophores to aggregate.

Urogenital System

The pronephric kidney is functional during larval development, after which it is replaced by the opisthonephros, which serves as the functional kidney of most adult amphibians. In salamanders and anurans, the pronephric kidney consists of two to four tubules with nephrostomes that drain the coelomic cavities into a pronephric duct. In most other amphibians, the kidney is considerably shorter. Anuran kidneys are less than half the length of the coelom and are located posteriorly. In males, the anterior portion of the mesonephric duct becomes the epididymis and drains the testes through efferent tubules. Caecilians have a pronephric kidney consisting of 10 to 13 tubules and an opisthonephric kidney in which both anterior and posterior nephrostomes persist. The opisthonephros may extend most of the length of the coelom in these forms.

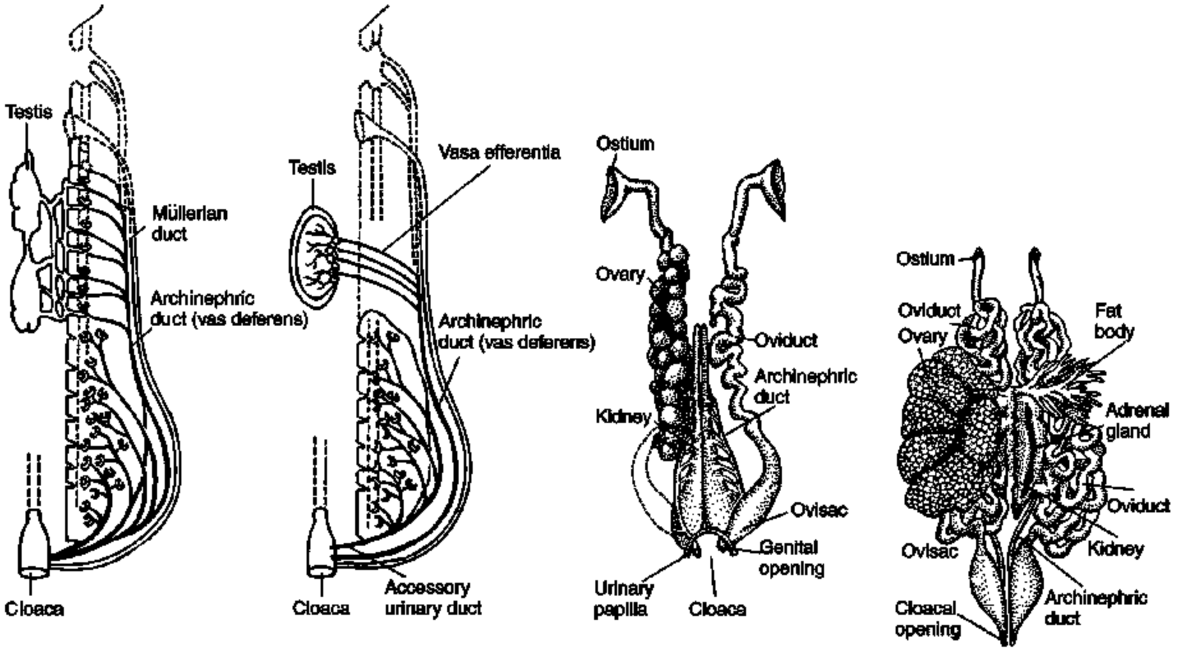
The bladder in all amphibians is a thin-walled evagination of the ventral wall of the cloaca. It receives and stores urine and participates in water and ion exchange processes. Glucose reabsorption from the urinary bladder in the freeze-tolerant wood frog (*Lithobates* [*Rana*] *sylvatica*) permits the recovery of sugar destined for excretion (Costanzo et al., 1997). Urine flows down the mesonephric duct (original pronephric duct) into the cloaca and then backs up into the bladder for storage. The bladder, along with the alimentary canal, mesonephric ducts, and oviducts, empties into the cloaca.

Reproductive System

Female Reproductive System

During embryonic development in female salamanders, each pronephric duct divides longitudinally into a duct, which becomes an oviduct, and an opisthonephric duct, which drains the kidney (Fig. 5.29c).

The ovary, a hollow sac with an enclosed lymphatic cavity, ranges in shape from short and compact in anurans to elongate in caecilians. Its surface contains germinal epithelium that gives rise to eggs, which are shed into the coelom. Oviducts are long and straight in caecilians, slightly convoluted in salamanders, and greatly convoluted in anurans (Fig. 5.29). The opening of the oviduct (ostium) is ciliated, and its walls contain smooth muscle. The lumen of the oviduct is lined with ciliated, glandular epithelium. The glandular lining of the oviducts secretes several jelly envelopes around each egg as peristaltic contractions of the smooth muscle carry the eggs through the oviducts. Caudal portions of the oviducts may enlarge to form **ovisacs**, where eggs are stored temporarily prior to oviposition. In those salamanders in which fertilization is internal and occurs as the eggs pass down the oviducts, the roof of the cloaca in females is modified into a **spermatheca**. This functions as a storage receptacle for spermatozoa prior to ovulation.



(a) Most adult male salamanders and frogs

(b) Some adult male salamanders and frogs

(c) Female salamander

(d) Female frog

Figure 5.29. Urogenital ducts of male and female amphibians: (*a*) most adult male salamanders and frogs; (*b*) some adult male salamanders and frogs; (*c*) female salamander; (*d*) female frog. Note the relatively straight oviducts in the female salamander as opposed to the highly convoluted oviducts in the frog.

Male Reproductive System

In some male salamanders, like *Necturus*, the mesonephric duct carries both urine and sperm. In many salamanders, however, including plethodontids, the mesonephric duct has lost its excretory function and carries only sperm (see Fig. 5.29b). A duct carrying only sperm is known as a **ductus deferens** or **vas deferens**.

In male anurans, a series of modified kidney tubules called **vasa efferentia** grow from the anterior tissue of the kidney to the testes (see Fig. 5.29b). The anterior part of the mesonephric duct, the vas deferens, functions primarily to transport spermatozoa, whereas the posterior part serves also for the elimination of urinary wastes. In some anurans, the lower portion of the mesonephric duct is modified into a seminal vesicle.

Testes, which serve as endocrine organs and produce the male sex hormone testosterone, are composed of vast numbers of seminiferous tubules. During the breeding season, when spermatogenesis activity is at its peak, the testes of all amphibians increase in size.

Fat bodies usually are associated with the gonads in both males and females, and both have a common embryological origin. According to Noble (1931), fat bodies are a source of nutrients for the gonads. They are largest just before hibernation, begin to shrink as ova and testes mature and enlarge, and are smallest just after the breeding season.

Using Bladders to Store Water

Large bladders in many amphibians allow them to store water in their bodies. The African bullfrog (*Pyxicephalus adspersus*), which weighs up to 900 g (2 lb.), inhabits the Kalahari Desert. When pools dry up, the bullfrog digs into the earth and survives in a protective cocoon made from layers of shed skin. The bullfrog’s large bladder allows for storage of water in amounts up to one-third of its body weight. The bullfrog can tolerate a loss of 45 percent of that original body weight. As water is lost, blood viscosity can thicken to four times its normal concentration. The bullfrog can wait in semidormancy for up to two years until rains begin filling the fleeting pools.

Crowe, 1995

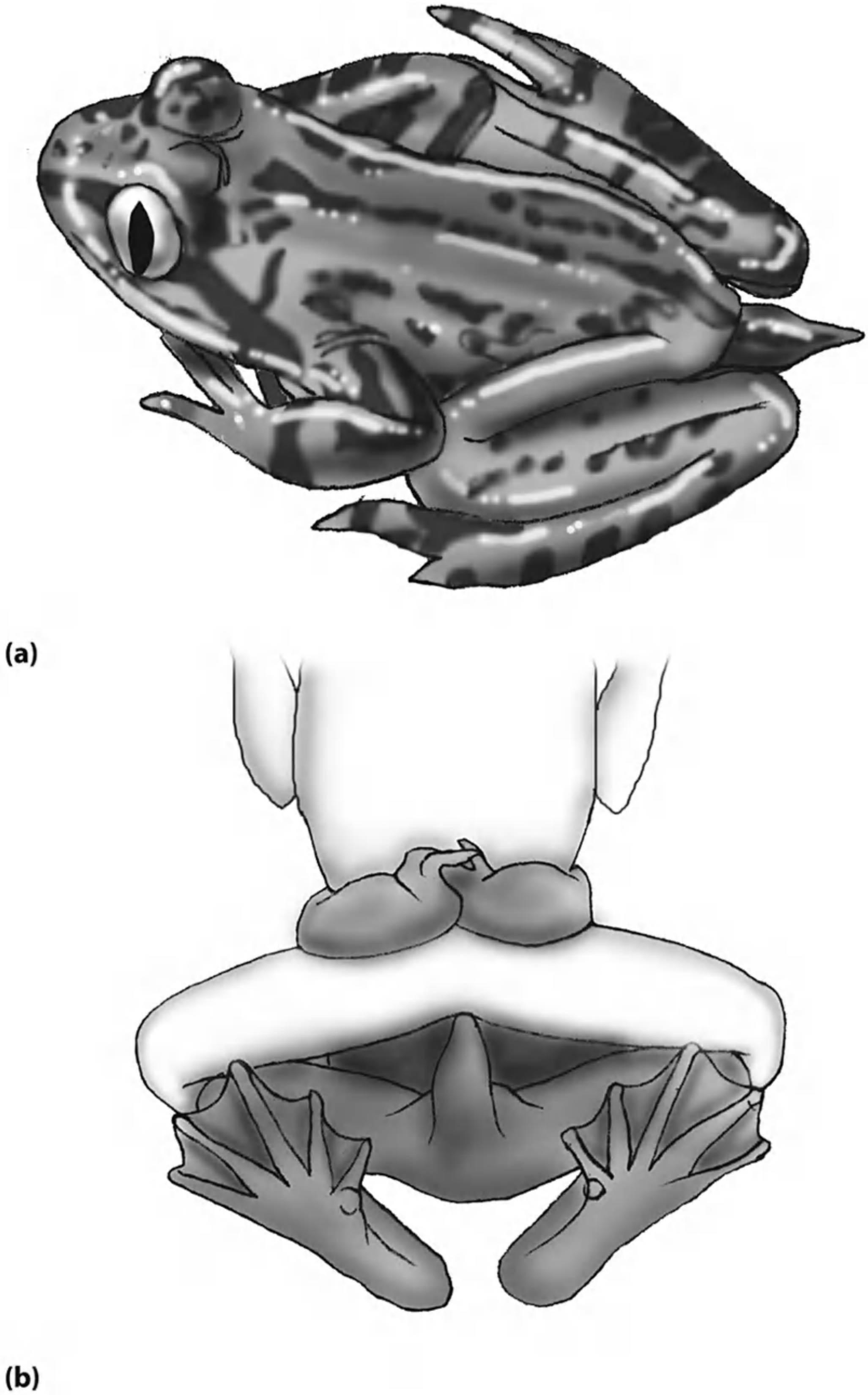


Figure 5.30. Male *Ascaphus truei*, the only anuran with an intromittent organ.

An intromittent organ that facilitates transfer of sperm from the male into the female's reproductive tract is present in caecilians and in one anuran (*Ascaphus*) (Fig. 5.30). In *Ascaphus*, the intromittent organ is a permanent tubular extension of the cloaca and resembles a tail, whereas male caecilians evert the cloaca to produce a temporary intromittent organ.

Male toads in the family Bufonidae possess rudimentary ovaries, known as Bidder's organs, in addition to functional testes. If testes are removed, Bidder's organ develops into a functional ovary, so that the result is complete sex reversal.

REPRODUCTION

Amphibian reproduction can be divided into three broad categories (Crump, 1974):

1. *Aquatic development:* Eggs deposited in water; larvae develop in water.
2. *Semiterrestrial development:* Eggs deposited out of water; larvae develop in water.
3. *Terrestrial development:* Eggs and young completely independent of standing water.

Precipitation and temperature are major climatic factors that affect breeding in amphibians. Photoperiod has little effect on regulation of sexual cycles in amphibians that are nocturnal or those that remain underground when inactive (Duellman and Trueb, 1994). Genetically controlled innate sexual rhythms, which would not be under the direct influence of environmental factors, may exist in some species.

Most North American amphibians have an annual cycle of breeding and become active with the increase in temperature in late winter and spring. Rainfall stimulates early breeders like spring peepers (*Pseudacris* [formerly *Hyla*] *crucifer*), wood frogs (*Lithobates* [*Rana*] *sylvatica*), and spotted salamanders (*Ambystoma maculatum*). Although most amphibians breed in late winter or spring, some, like the bullfrog (*Lithobates* [*Rana*] *catesbeiana*), may wait until June to deposit their 10,000 to 20,000 eggs. Others, like marbled salamanders (*Ambystoma opacum*), breed in late summer or early fall at dry pond sites. After breeding, females deposit their eggs in nest cavities under vegetation and logs and in crayfish holes. Female marbled salamanders stay with the eggs for as long as a month. Once the ponds start to fill and the nests are flooded, the eggs hatch. Even though most anurans have a primary breeding period, some may be stimulated to call, and even deposit additional eggs, later in the summer during periods of heavy rain.

Many amphibians may grow continuously throughout their lifetime (called indeterminate growth), and many can breed at 1 to 2 years of age (Duellman and Trueb, 1994). Ranid frogs, however, may remain as tadpoles for two or three years before metamorphosing. Newts may spend from four to eight years in a terrestrial juvenile stage known as an eft before returning to water and maturing. Some salamanders become sexually mature but retain some larval characters, a condition known as **paedomorphosis**. Paedomorphic forms are found in all families of salamanders and may require longer than a year before they are reproductively mature. Some hellbenders (*Cryptobranchus*) and amphiumas (*Amphiuma*) may require as long as five to six years to mature.

Salamanders recognize other members of their species by using visual and olfactory cues. Extensive courtship rituals involve nuzzling and rubbing the body of a potential mate. Sexual dimorphism is pronounced in some species like newts (*Triturus*), in which males develop large dorsal and caudal fins during the breeding season (Fig. 5.31).

A variety of courtship activities occur in anurans. Some of the most complex and elaborate mating behaviors have been recorded for many species of poison dart frogs (*Dendrobates*), including tactile interactions, specific postural displays, and species-specific calls (Silverstone, 1973; Wells, 1977). Some females guard their mates by remaining in or near their mates' territories, courting them frequently, and attacking any other females they encounter courting their mates (Summers, 1989). The spotted poison dart frog (*D. vanzolinii*) forms pair bonds, and both parents provide extended care of the young under natural conditions (Caldwell, 1997).

After touching a female, most male frogs and toads will tightly grasp her behind her forelimbs, a copulatory embrace known as **amplexus** (Fig. 5.32). Swollen glandular thumb pads of males aid in this process, and the pressure applied to the body of the female assists in expelling the eggs. Size and behavior are important sex recognition factors: females are usually larger than males of the same species and generally will be receptive to the male’s clasping efforts. If a male frog attempts to clasp another male, it will meet with resistance and an entirely different pattern of behavior.

(a) Female

(b) Male in nuptial dress

Figure 5.31. Sexual dimorphism in the newt *Triturus cristatus.* During the breeding season, males develop large dorsal and caudal fins.

(a)


(b)

Figure 5.32. (*a*) Male wood frog (*Rana sylvatica*) clasping the female in amplexus, which aids external fertilization. As the female releases eggs into the water, the male releases sperm over them. Note the eggs in a globular cluster. (*b*) Toads (*Bufo*) in amplexus. Note eggs in "string-of-pearls" formation.

Since most anurans breed at night, auditory rather than visual cues are most advantageous for attracting members of the opposite sex; thus, most male anurans have developed species-specific calls. Air passes through either a single median vocal pouch under the throat (see Fig. 5.18b, c) or paired pouches on either side of the head (see Fig. 5.18d). Ryan (1991) provided evidence that females show a preference for conspecific over heterospecific calls. The female auditory system decodes species-specific information contained in the male's advertisement calls (Capranica, 1976). For example, female coqui frogs hear the "co" in the "co-qui" call; males hear the "qui." Males of some species can alter the frequency of their calls, as well as determine the size of neighboring frogs by assessing the tones of their voices (Wagner, 1989a, 1989b). Because calling consumes energy that might otherwise be used for growth, some species reduce calling when food levels decrease (Ryan, 1991). In addition, calling is potentially dangerous because it marks the location of the calling male to possible predators.

The concave-eared torrent frog (*Odorrana tormota*) of China is the first known amphibian to use ultrasonic calls (Feng et al., 2006). Bursts above 20 kHz were in a range higher than the roar of the water splashing over rocks on the mountainside at Huangshan Hot Springs where the frogs live. The unusual recessed ears are thought to improve sensitivity to high pitches.

Underwater Mating Calls

The South American frog *Leptodactylus ocellatus* may have evolved an underwater mating call in response to airwave competition from another frog that uses the same frequency above water. Alejandro Purgue, a herpetologist at the University of Utah, documented the underwater calls using US Navy hydrophones and computer analysis. The underwater calls are thought to minimize competition with *Physalaemus cuvieri*, whose calls are in a similar range (250–500 Hz) but above water.

A population of the Chiricahua leopard frog (*Lithobates chiricahuensis*), known only from the Huachuca Mountains of southeastern Arizona, can be distinguished from other members of its species on the basis of morphology and mating-call characteristics. Males offer the mating call entirely underwater from a depth of more than a meter, making it completely inaudible in the air.

Weiss, 1990; Platz, 1993

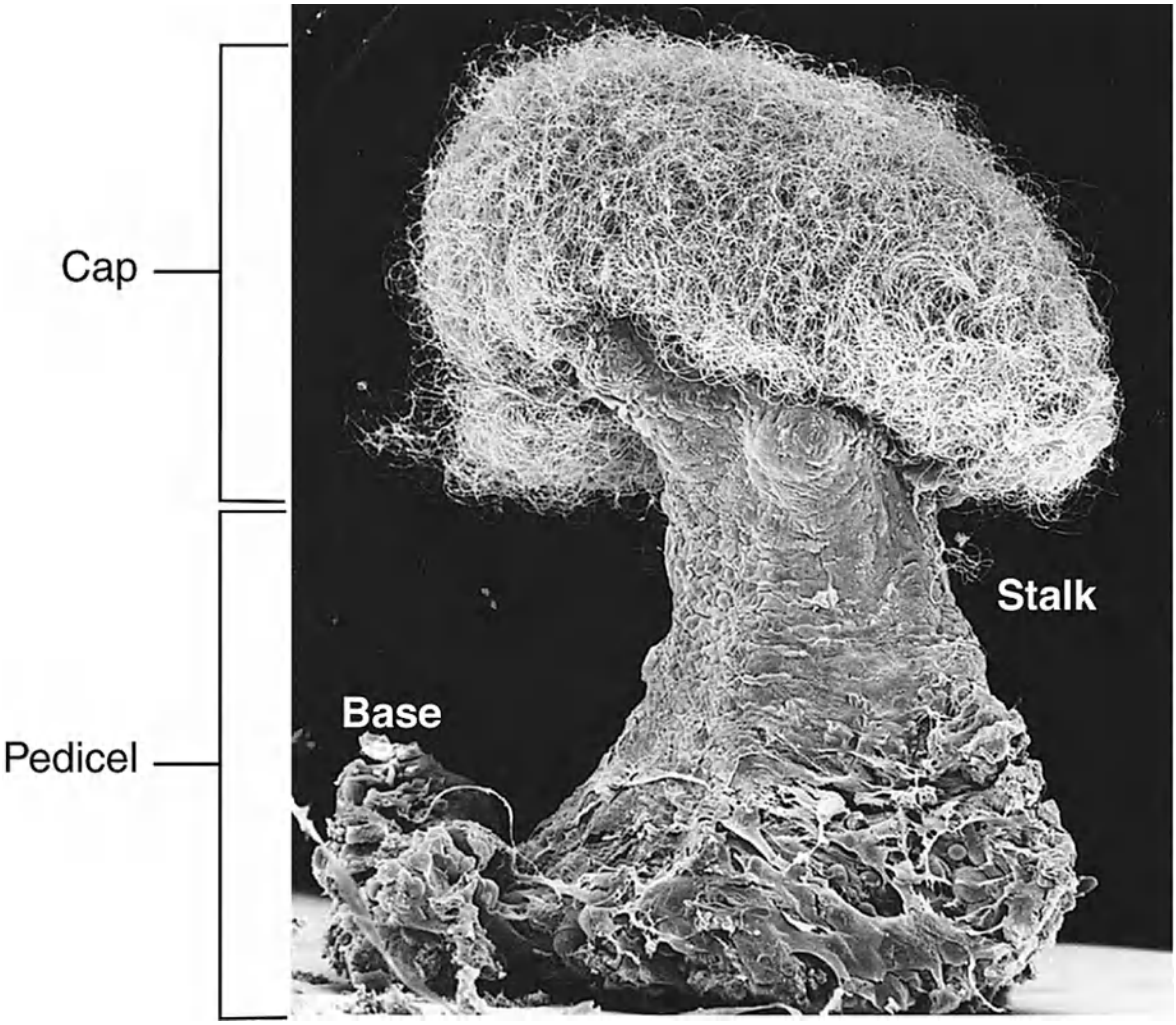


Figure 5.33. Salamander spermatophore. Whole spermatophore deposited by male *Ambystoma macrodactylum*. Sperm heads generally point outward, tails inward.

Red-backed salamanders (*Plethodon cinereus*) are completely terrestrial, and both mating and egg-laying occur in moist microhabitats. Males with high-quality territories achieve greater access to females than males with low-quality territories (Walls et al., 1989). In addition, feces of males with high-quality diets are attractive to females, and gravid females prefer to remain in areas near fecal pellets containing the remains of highly nutritious prey (Jaeger and Wise, 1991). In addition, males found near females are significantly larger than adult males found alone, and they are more aggressive when paired with smaller males. Large body size in males may positively affect both intra- and intersexual interactions and, ultimately, the mating success of male *P. cinereus* (Mathis, 1991b).

Approximately 90 percent of all salamanders use internal fertilization (Duellman and Trueb, 1994). A single male salamander may deposit packets of sperm, known as **spermatophores**, on submerged leaves and twigs (Fig. 5.33). The number of spermatophores produced varies widely, with one male spotted salamander (*Ambystoma maculatum*) depositing up to 81 spermatophores in a single evening with one female (Arnold, 1976). Newts of the genus *Triturus* deposit a few spermatophores each day for a few weeks, whereas members of the genus *Plethodon* are much more conservative and deposit one spermatophore each week for several weeks (Arnold, 1977). Because the breeding season for plethodontids may range from several months in temperate-zone species to the majority of the year in tropical species, and because plethodontids expend a great deal of energy per spermatophore in courtship activities and in defending a territory, it is evolutionarily advantageous for males not to expend all of their spermatophores on the first few females encountered.

Females grasp spermatophores with the lips of their cloacae and take the sperm packages inside their cloacae so that eggs can be fertilized as they pass out of the females' bodies. Some female salamanders may store sperm in specialized cloacal sacs (spermathecae) for months or years. Baylis (1939) reported fertilization of ova in *Salamandra salamandra* (Salamandridae) at least two years after the last possible mating.

In most anurans, males in amplexus deposit sperm on the eggs as the eggs are released by the female (see Fig. 5.32). However, internal fertilization occurs in a few genera (*Ascaphus*, *Nectophrynoides*, *Mertensophryne*, and *Eleutherodactylus*) (Townsend et al., 1981; Duellman and Trueb, 1994). The "tail" of the tailed frog, *Ascaphus*, is a posterior extension of the cloaca partially supported by paired rods. The "tail" serves as an intromittent organ for transferring sperm into the female (see Fig. 5.30). *Ascaphus* is the only known anuran to engage in copulation, internal fertilization that apparently ensures conception in the cold, fast-moving, turbulent streams of the Pacific Northwest where this frog resides.

All caecilians have internal fertilization (Duellman and Trueb, 1994). Some are oviparous with aquatic larvae; some are oviparous with embryos undergoing direct development into terrestrial young; still others are viviparous. The developing young of viviparous species have specialized teeth that are used to scrape the epithelial lining of the oviduct and obtain nutrients secreted by the oviducal cells (Wake, 1977). These teeth are shed after birth.

GROWTH AND DEVELOPMENT

Oviparous

Most amphibians deposit their eggs in water. Salamander eggs may be attached individually (Fig. 5.34d) or in small clusters to underwater vegetation (Fig. 5.34b, c) or to the undersides of partially or completely submerged rocks or boulders; they may be part of a globular gelatinous mass; or they may be part of a floating surface mass. Some terrestrial salamanders, like ensatina (*Ensatina*), the arboreal salamander (*Aneides*), and the woodland salamanders (*Plethodon* spp.), deposit their eggs in moist sites on land. Some caecilians (Rhinatrematidae, Ichthyophiidae) are oviparous and deposit their eggs in mud near water. The caecilian eggs hatch into free-swimming larvae.

Anurans exhibit a wider variety of larval development than any other group of vertebrates. Many anurans lay their eggs in water, either singly, in globular masses (see Fig. 5.34e), or in strings (see Fig. 5.34f). There are, however, many exceptions. Some tropical forms deposit their eggs on leaves overhanging water so that, as the eggs hatch, the larvae drop into the water. Some utilize the pools of water contained in bromeliads—epiphytic plants growing on trees in tropical forests. Some anurans encase their eggs in a frothy, protective foam mass consisting of air, sperm, eggs, cloacal secretions, and sometimes water. The outer surface of the mass dries and turns tacky (sometimes hard), protecting the eggs from physical harm, while the egg-filled interior remains liquid for as long as 10 days to enable the eggs to survive periods of drought. Other anurans possess dorsal pouches on their backs in which eggs are incubated (del Pino et al., 1975), or eggs may be attached in some other manner to the back of a parent, as in the Surinam toad (*Pipa pipa*), where they remain until hatching.

Changing Sex

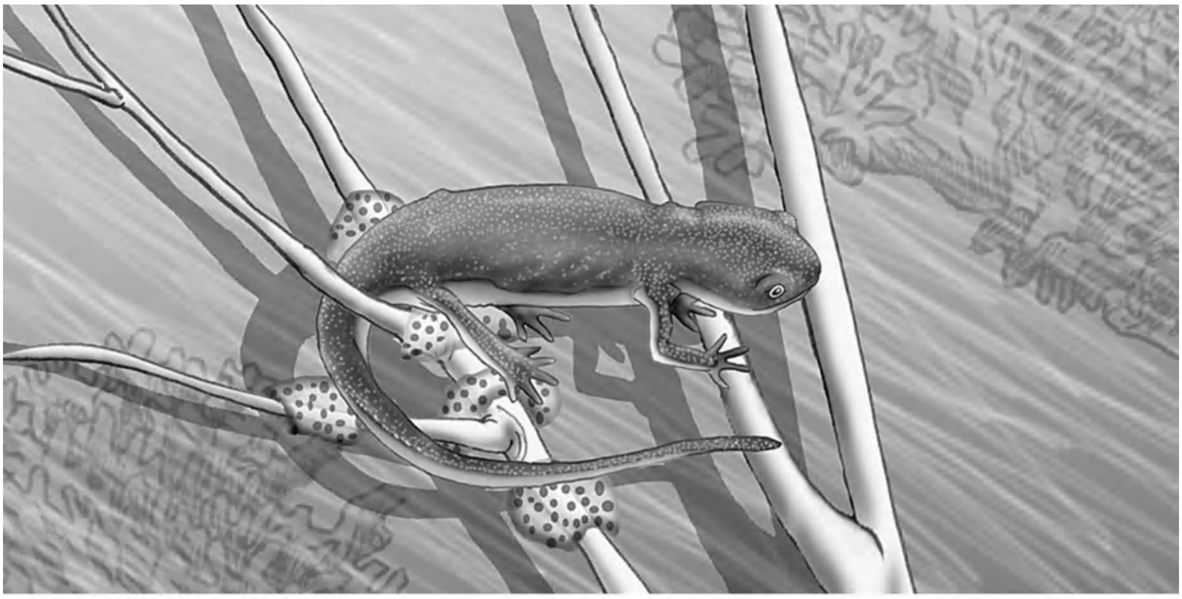
The ability to change sex exists in some fishes and amphibians. A few fish species switch sex apparently to maximize breeding in areas where breeding individuals of the opposite sex are not abundant. The only amphibian known to naturally change its sex and successfully breed is the African reed frog (*Hyperolius viridiflavus ommatostictus*). Male toads have a vestige of ovarian tissue (Bidder's organ) that will develop into functional ovaries if testicular tissue is surgically removed. Under experimental conditions, tadpoles of many species consistently develop into males after experimental exposure to the male hormone testosterone.

Grafe and Linsenmair, 1989

Nearly 800 species of anurans throughout the world (20 percent of the known species) have eliminated a free-living, feeding, tadpole stage. These frogs, which lay eggs that hatch into four-legged froglets, reproduce by **direct development** (Duellman, 1992). Eggs are deposited in moist sites, and in some cases, like certain species of whistling frogs (*Eleutherodactylus* sp.), they are guarded by the male parent. Whereas this method of reproduction provides the developing frogs with a food supply and protects them from aquatic predators, they are still susceptible to predation by ants and other invertebrates. The male Chilean rhinodermatid frog (*Rhinoderma darwinii*) incubates the eggs inside his vocal pouch until the young complete their metamorphosis and emerge as miniature adults. *Rheobatrachus silus* of Australia was a "gastric brooder" (Fig. 5.35). Adult females of this stream-dwelling species swallowed their eggs, hatching and protecting the development of the young in their stomachs. Soon after the offspring lost their tadpole-like tails, the mothers ejected the baby frogs out their mouths. Unfortunately, both the southern (*Rheobatrachus silus*) and northern (*Rheobatrachus vitellinus*) gastric brooding frogs are now extinct.

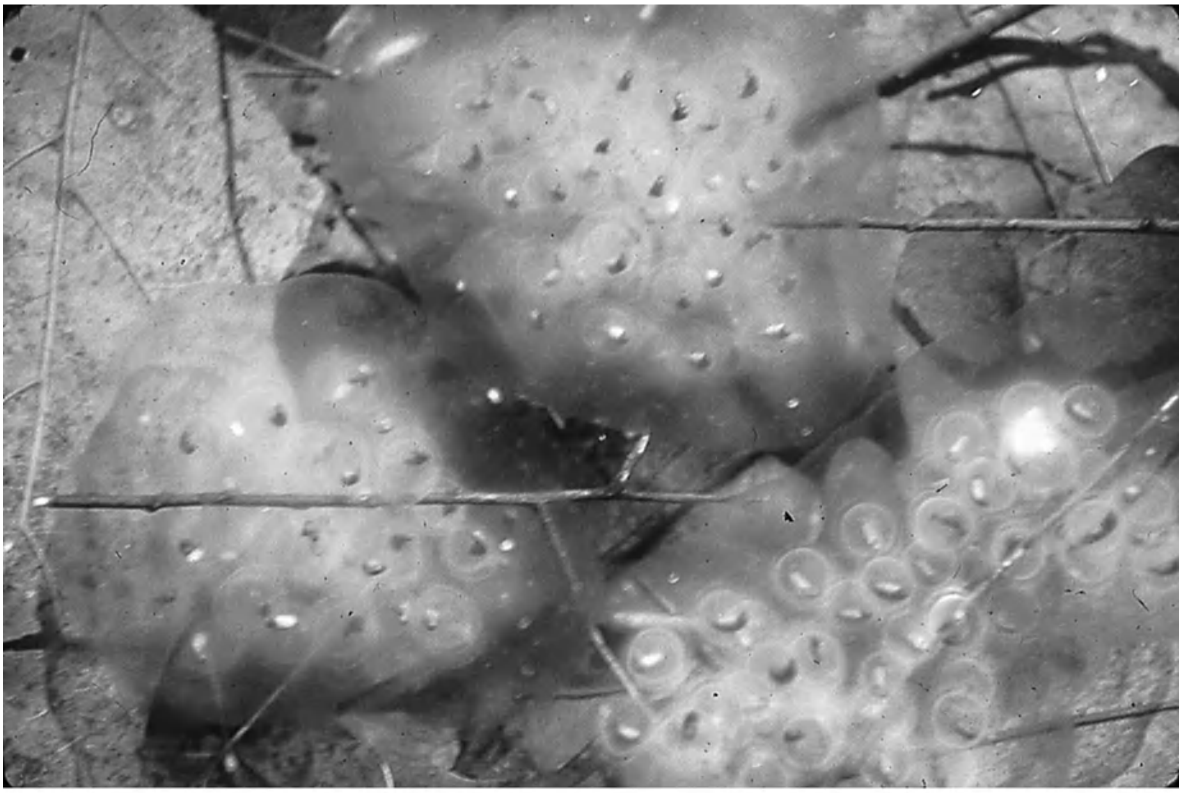
Viviparous

Four African toads in the genus *Nectophrynoides* (*N. liberiensis*, *N. occidentalis*, *N. tornieri*, and *N. viviparus*), the Kihansi spray toad (*Asperginus nectophrynoides*) of Tanzania, and one frog (*Eleutherodactylus jasperi*) are the only known anurans to give birth to live young. Female toads supplement yolk with secretions from their oviduct and give birth to newly metamorphosed toadlets (Wake, 1980b; Duellman, 1992). Some species of caecilians in the families Caeciliidae and Typhlonectidae are viviparous (Duellman and Trueb, 1994). In these species, fetuses have specialized teeth that are used for scraping the inner lining of the oviducts in order to release nutrients for ingestion. Among salamanders, this mode of reproduction occurs only in *Salamandra atra* and *Mertensiella luschani antelyana*. It may occur in montane populations of *Salamandra* and in females of *M. caucasica* subjected to prolonged drought (Duellman and Trueb, 1994).

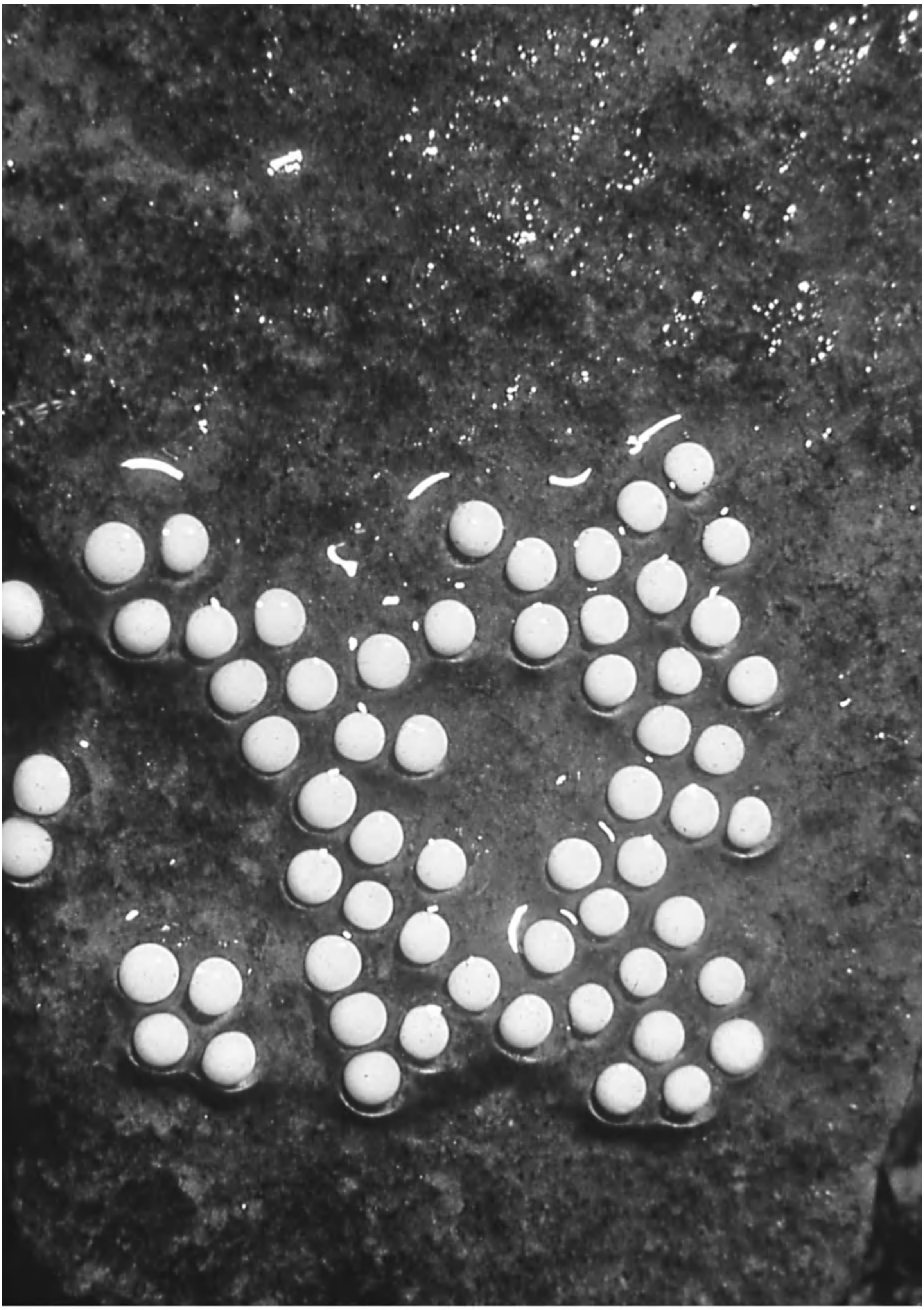


(a)

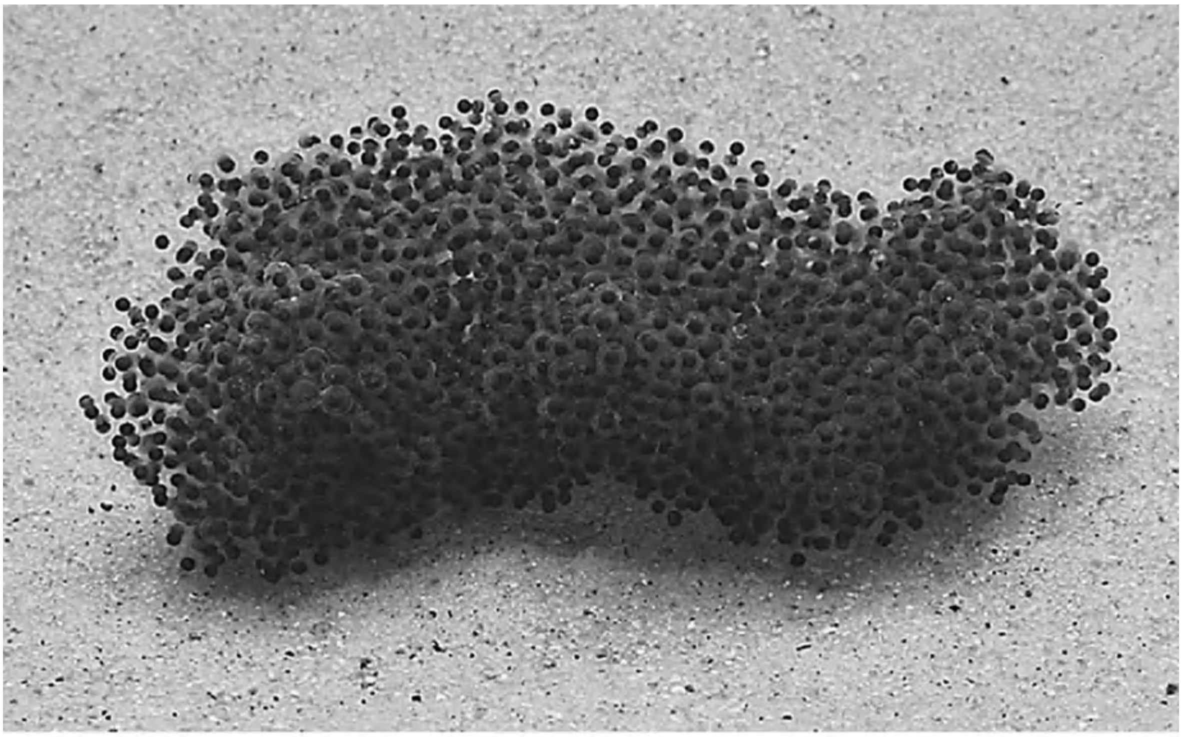
(b)



(c)



(d)



(e)

(f)

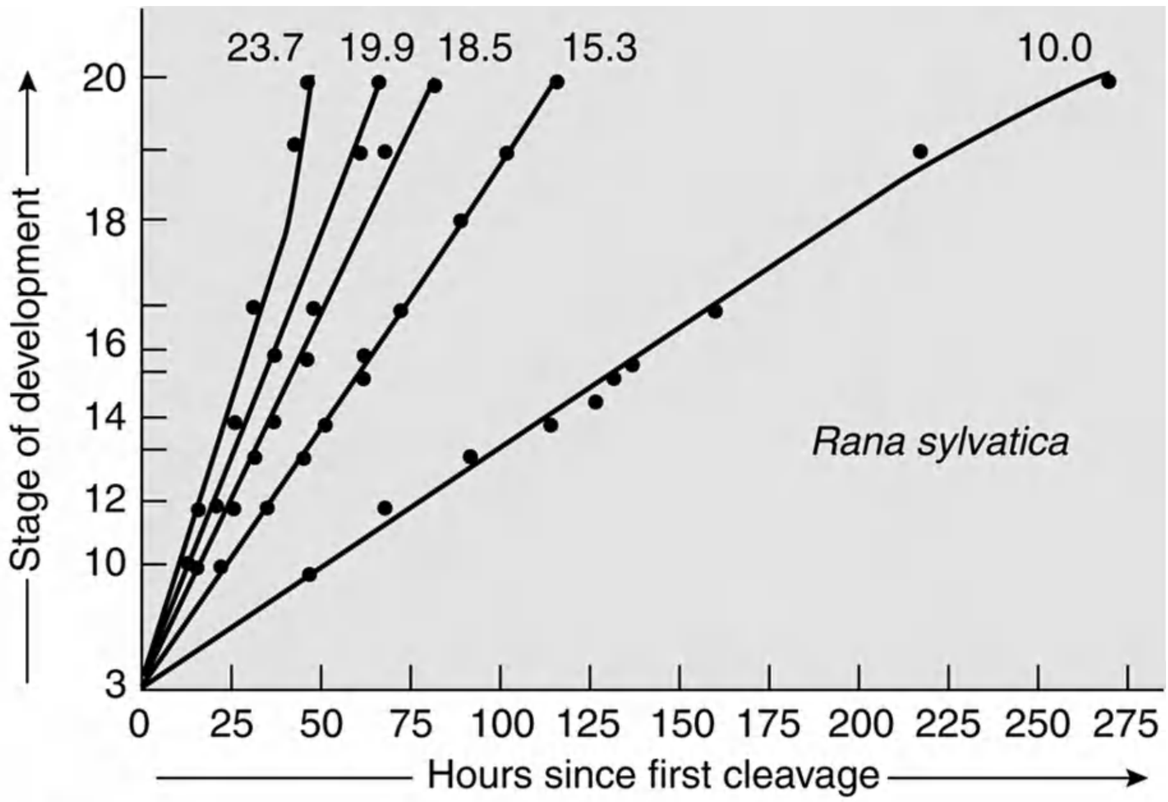
Figure 5.34. Egg deposition by amphibians. (*a*) An aquatic salamander, the California newt (*Taricha torosa*), laying her eggs in water. The clusters of eggs are usually attached to roots and stems. (*b*) A female eastern tiger salamander (*Ambystoma tigrinum*) attaching eggs to

submerged vegetation. (*c*) Egg mass of the spotted salamander (*Ambystoma maculatum*). (*d*) Eggs of the two-lined salamander (*Eurycea bislineata*). (*e*) Globular egg clusters of the leopard frog (*Rana pipiens*). (*f*) Egg strings of the common European toad (*Bufo bufo*).

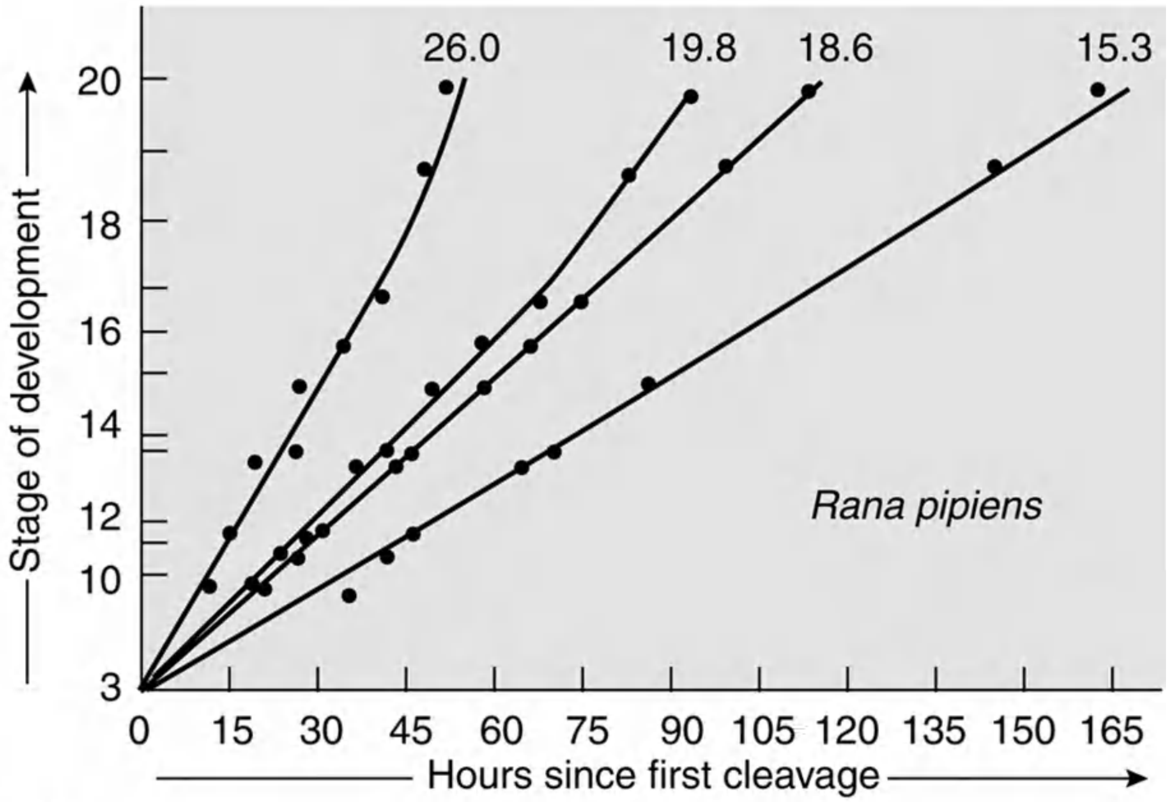
Figure 5.35. The gastric brooding frog *Rheobatrachus silus* of Australia. A froglet emerges from the mouth of its mother after having developed in her stomach for 37 days. During this time, the mother does not eat, and the secretion of acid and digestive enzymes from the stomach is suppressed. This species has not been seen for several years and may be extinct.

Duration of Embryonic Development

Embryonic development in amphibians ranges from one to two days to approximately nine months and is temperature-dependent (Fig. 5.36). The time from fertilization to hatching in salamanders ranges from about 13 days in some mole salamanders (*Ambystoma* spp.) to 275 days in the Pacific giant salamander (*Dicamptodon*) (Duellman and Trueb, 1986) (Table 5.1). The young of species that lay eggs early in the season (when environmental temperatures are cold) and species that live near the extremes of their ranges in both the Northern and Southern hemispheres develop more rapidly than those that spawn later under warmer conditions. Most anurans, on the other hand, develop faster than salamanders (Table 5.2). Some, like members of the genera *Anaxyrus* (*Bufo*), *Scaphiopus*, *Hyla*, and *Pseudacris*, which have aquatic eggs, may hatch in 1 to 2 days, whereas some ranids may require 40 or more days. Rates of development at the same temperature may show considerable variation among closely related species (Fig. 5.36). Most amphibians that undergo direct development in terrestrial eggs require between 15 and about 50 days to hatch, although an average of 107 days is required for *Pipa pipa* eggs (carried on the female's back) to hatch into froglets (Duellman and Trueb, 1994).


23.7
19.9
18.5
15.3
10.0
Stage of development
20
18
16
14
12
10
3
0
25
50
75
100
125
150
175
200
225
250
275
Hours since first cleavage
Rana sylvatica

(a)


26.0
19.8
18.6
15.3
Stage of development
20
18
16
14
12
10
3
0
15
30
45
60
75
90
105
120
135
150
165
Hours since first cleavage
Rana pipiens

(b)

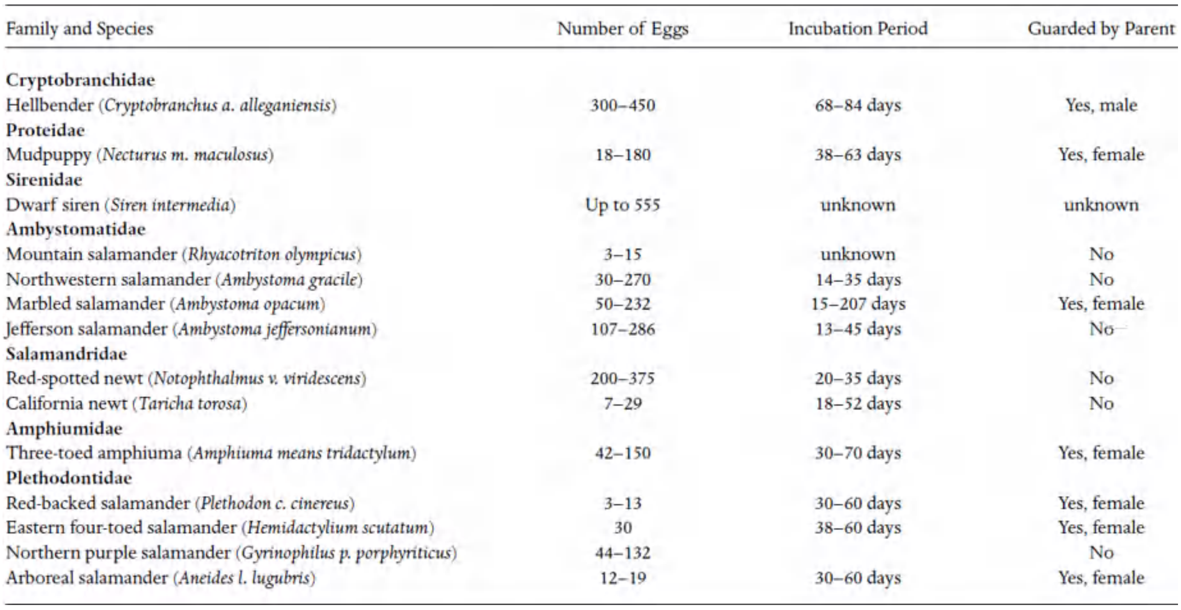
Figure 5.36. Rates of development in (*a*) the wood frog (*Rana sylvatica*) and (*b*) the leopard frog (*Rana pipiens*). The rate of development may show considerable variation among closely related species developing at the same temperature.

Three-day-old embryos of red-eyed tree frogs (*Agalychnis callidryas*) position their big, feathery, branching gills near the oxygen-rich egg surface. The part of an egg closest to the air typically carries twice the oxygen concentration of the deep interior squeezed among neighboring eggs. When researchers prodded embryos so their gills fell into the low-oxygen zone, most of the 3-day-olds twitched themselves back into place within 15 seconds (Rogge and Warkentin, 2008).

Hatching and Birth

Amphibian embryos produce hatching enzymes that assist in digesting the membrane enclosing them at the time of hatching. These enzymes are produced by frontal glands located primarily on the snout of the embryo. Only frogs in the genus *Eleutherodactylus* are known to possess an egg tooth with which they can cut through the egg capsule. The egg tooth is reabsorbed shortly after hatching.

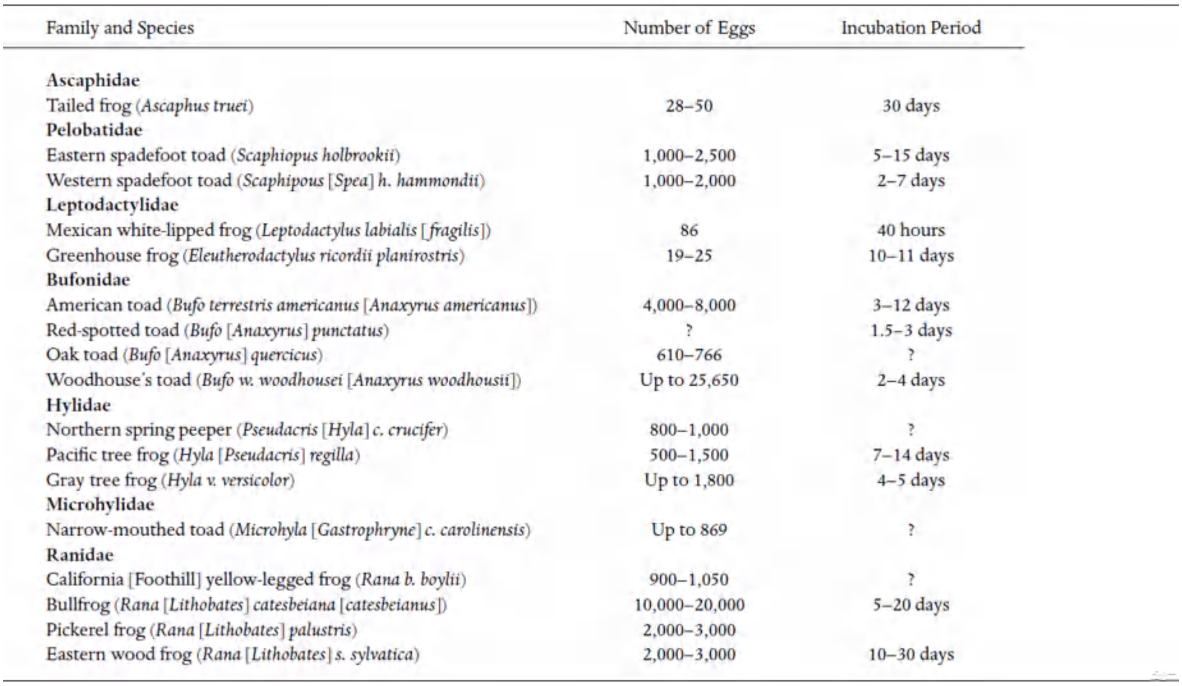
Table 5.1. Sample Salamander Reproduction Data



Family and Species	Number of Eggs	Incubation Period	Guarded by Parent
Cryptobranchidae			
Hellbender (*Cryptobranchus a. alleganiensis*)	300–450	68–84 days	Yes, male
Proteidae			
Mudpuppy (*Necturus m. maculosus*)	18–180	38–63 days	Yes, female
Sirenidae			
Dwarf siren (*Siren intermedia*)	Up to 555	unknown	unknown
Ambystomatidae			
Mountain salamander (*Rhyacotriton olympicus*)	3–15	unknown	No
Northwestern salamander (*Ambystoma gracile*)	30–270	14–35 days	No
Marbled salamander (*Ambystoma opacum*)	50–232	15–207 days	Yes, female
Jefferson salamander (*Ambystoma jeffersonianum*)	107–286	13–45 days	No
Salamandridae			
Red-spotted newt (*Notophthalmus v. viridescens*)	200–375	20–35 days	No
California newt (*Taricha torosa*)	7–29	18–52 days	No
Amphiumidae			
Three-toed amphiuma (*Amphiuma means tridactylum*)	42–150	30–70 days	Yes, female
Plethodontidae			
Red-backed salamander (*Plethodon c. cinereus*)	3–13	30–60 days	Yes, female
Eastern four-toed salamander (*Hemidactylium scutatum*)	30	38–60 days	Yes, female
Northern purple salamander (*Gyrinophilus p. porphyriticus*)	44–132		No
Arboreal salamander (*Aneides l. lugubris*)	12–19	30–60 days	Yes, female

Source: Data from Oliver, 1955.

Table 5.2. Sample Frog Reproduction Data



Family and Species	Number of Eggs	Incubation Period
Ascaphidae		
Tailed frog (*Ascaphus truei*)	28–50	30 days
Pelobatidae		
Eastern spadefoot toad (*Scaphiopus holbrookii*)	1,000–2,500	5–15 days
Western spadefoot toad (*Scaphipous* [*Spea*] *h. hammondii*)	1,000–2,000	2–7 days
Leptodactylidae		
Mexican white-lipped frog (*Leptodactylus labialis* [*fragilis*])	86	40 hours
Greenhouse frog (*Eleutherodactylus ricordii planirostris*)	19–25	10–11 days
Bufonidae		
American toad (*Bufo terrestris americanus* [*Anaxyrus americanus*])	4,000–8,000	3–12 days
Red-spotted toad (*Bufo* [*Anaxyrus*] *punctatus*)	?	1.5–3 days
Oak toad (*Bufo* [*Anaxyrus*] *quercicus*)	610–766	?
Woodhouse's toad (*Bufo w. woodhousei* [*Anaxyrus woodhousii*])	Up to 25,650	2–4 days
Hylidae		
Northern spring peeper (*Pseudacris* [*Hyla*] *c. crucifer*)	800–1,000	?
Pacific tree frog (*Hyla* [*Pseudacris*] *regilla*)	500–1,500	7–14 days
Gray tree frog (*Hyla v. versicolor*)	Up to 1,800	4–5 days
Microhylidae		
Narrow-mouthed toad (*Microhyla* [*Gastrophryne*] *c. carolinensis*)	Up to 869	?
Ranidae		
California [Foothill] yellow-legged frog (*Rana b. boylii*)	900–1,050	?
Bullfrog (*Rana* [*Lithobates*] *catesbeiana* [*catesbeianus*])	10,000–20,000	5–20 days
Pickerel frog (*Rana* [*Lithobates*] *palustris*)	2,000–3,000	
Eastern wood frog (*Rana* [*Lithobates*] *s. sylvatica*)	2,000–3,000	10–30 days

Source: Data from Oliver, 1955. Taxonomic data updated, 2019.

Red-eyed tree frog embryos can shorten their time in the egg by some 30 percent if attacked by snakes, wasps, or killer molds (Rogge and Warkentin, 2008). Predator-sensitive hatching has been documented in at least 17 other species of amphibians (as well as two species of fishes and a lizard), which can split open their eggs for an early escape in a crisis.

Parental Care

For many years, only a few amphibians were thought to exhibit parental care toward their eggs and/or offspring. In reality, however, parental care is exhibited by many species, especially those with terrestrial reproductive strategies. Extended parental care is more common in salamanders than in anurans and caecilians (Fig. 5.37). It may be provided by either sex and is shown in a variety of ways: guarding eggs against predators, moistening and/or aerating eggs, and transporting eggs and larvae. All instances involving the transport of eggs and/or larvae involve frogs. The duration of parental care for a given clutch of eggs in salamanders may extend from 5 to 6 weeks to as long as 275 days or more under certain conditions in *Dicamptodon* (Nussbaum, 1969). In anurans, parental care ranges from several days to as long as four months in *Gastrotheca riobambae*, which inhabits cool habitats in the Andes Mountains of South America (del Pino et al., 1975).

The benefit of parental care has been documented in various species of centrolenids that lay their eggs on vegetation above water. The benefit of egg attendance by male *Hyalinobatrachium orientale* varies with the season (Lehtinen et al. 2014). During the wet season, egg attendance decreases the risk of predation by arthropods, whereas during the dry season it decreases the risk of mortality from desiccation. During both seasons, egg attendance significantly increases offspring survivorship.

Some female caecilians also are known to guard their eggs. The East African caecilian, *Boulengerula taitanus*, is oviparous. Hatchlings have special teeth that enable them to peel the skin off their mothers (Kupfer et al., 2006). The hatchlings eat the skin, which is thicker than normal, swollen with fats and other nutrients. It is their only source of food during their first days.

Growth and Metamorphosis

Amphibian eggs that are deposited in water will hatch into gill-bearing larvae (salamanders) or tadpoles (anurans). In most terrestrial habitats, those eggs undergoing direct development will hatch into miniature adults. Morphological variation in salamander larvae and in tadpoles is related to their habitats (see Fig. 5.20) and/or to their methods of feeding (see page 127).

The larval stage in anurans may be as short as 7 to 10 days in spadefoot toads (*Scaphiopus*) or as long as 2 to 3 years in bullfrogs (*Lithobates* [*Rana*] *catesbeiana*). At the end of this time, most amphibian larvae undergo a process called **metamorphosis**—a dramatic change in their body shape as well as in their critical life support systems (Fig. 5.38). The role of hormones in controlling metamorphosis was discussed earlier in this chapter (see the section Endocrine System). During metamorphosis, lungs form so that atmospheric air can be used for respiration, and gills gradually are resorbed. The digestive system becomes adapted for a carnivorous diet. In anurans, the tail is resorbed and the limbs form. Fins that may be present on the tails of larval salamanders usually are lost. Shortly before the onset of metamorphic climax, when forelimbs and other adult features emerge, aquatic ranid tadpoles experience a deaf period of two to four days during which no auditory activity can be detected (Boatright-Horowitz and Simmons, 1997). Research suggests that a growing bit of cartilage important to adult hearing disables the tadpole’s hearing before the system matures.

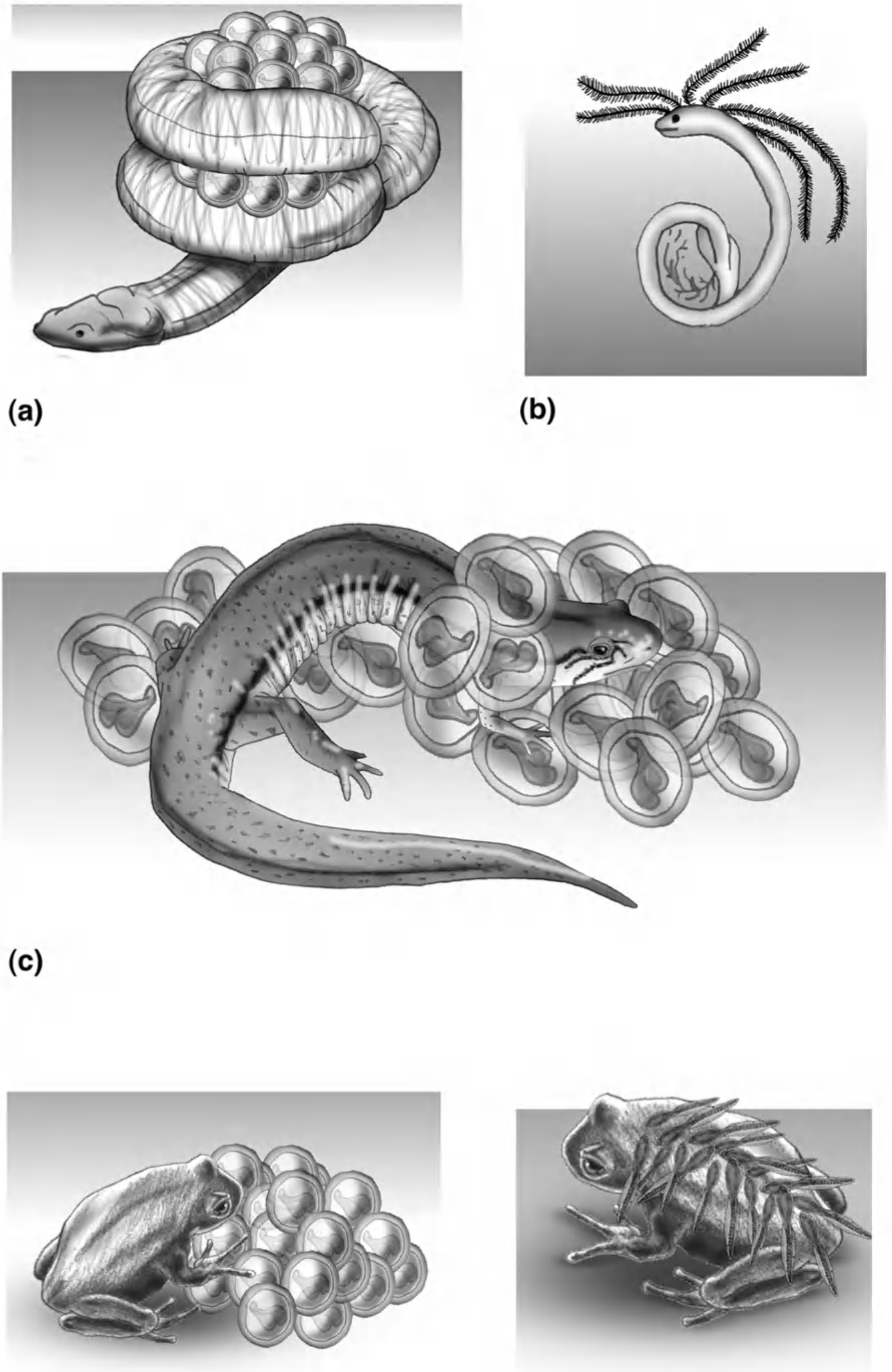

(a)
(b)
(c)
(d)
(e)

Figure 5.37. Parental care in amphibians. (*a*) Female *Ichthyophis glutinosa*, a caecilian, coiled up in a hole underground guarding her eggs. (*b*) An embryo of *Ichthyophis* nearly ready to hatch. Note gills, tail fin, and considerable amount of yolk. (*c*) Female *Desmognathus fuscus* brooding her eggs. (*d*) The dendrobatid frog *Colostethus subpunctatus* guarding its eggs and (*e*) transporting its tadpoles to water. The tadpoles attach to the back of the frog by a sticky mucus secreted by the skin of the female.

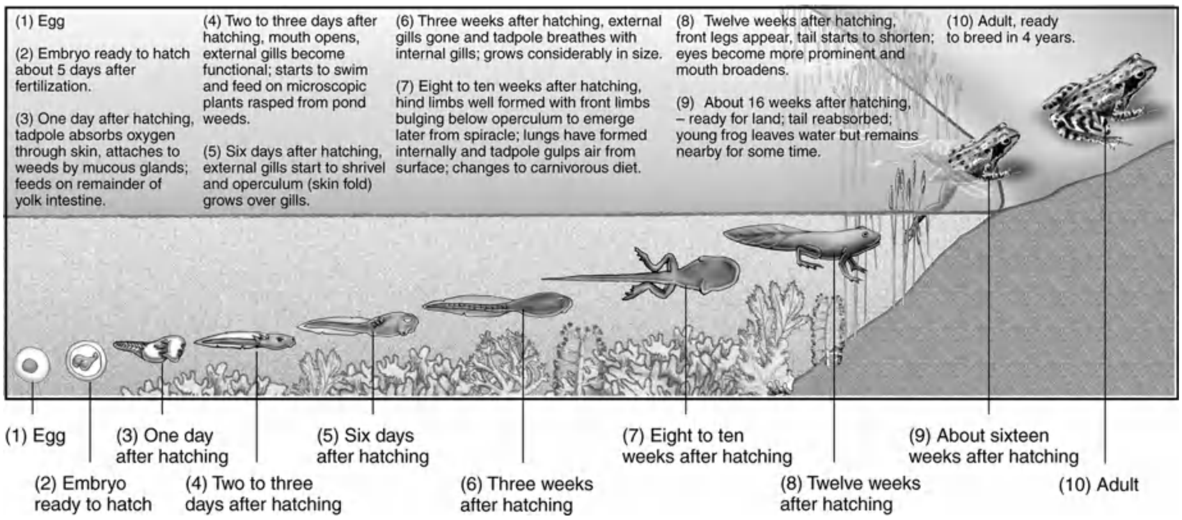


Figure 5.38. Lifecycle of the European common frog (*Rana temporaria*) showing stages of metamorphosis.

Some amphibians do not undergo complete metamorphosis, but retain some of their larval characteristics as adults. The attainment of sexual maturity with the retention of at least some larval morphology is known as **neoteny**. Reproduction by larval individuals is known as **paedogenesis**. Neotenic species include sirens (*Siren* spp.) and mudpuppies (*Necturus* spp.), both of which retain their external gills and never leave the water.

The eastern red-spotted newt (*Notophthalmus viridescens*) may metamorphose into an adult by passing through two "larval" stages. Eggs hatch into aquatic larvae. After several months, the aquatic larva metamorphoses into a terrestrial "larval," or juvenile, stage known as a **red eft**. This carnivorous stage develops lungs, leaves the pond, and lives a terrestrial existence for several years. After that time, it returns to water, develops fins on the dorsal and ventral surfaces of its tail, and lives the remainder of its adult life as a lung-breathing aquatic salamander.

Attainment of Sexual Maturity

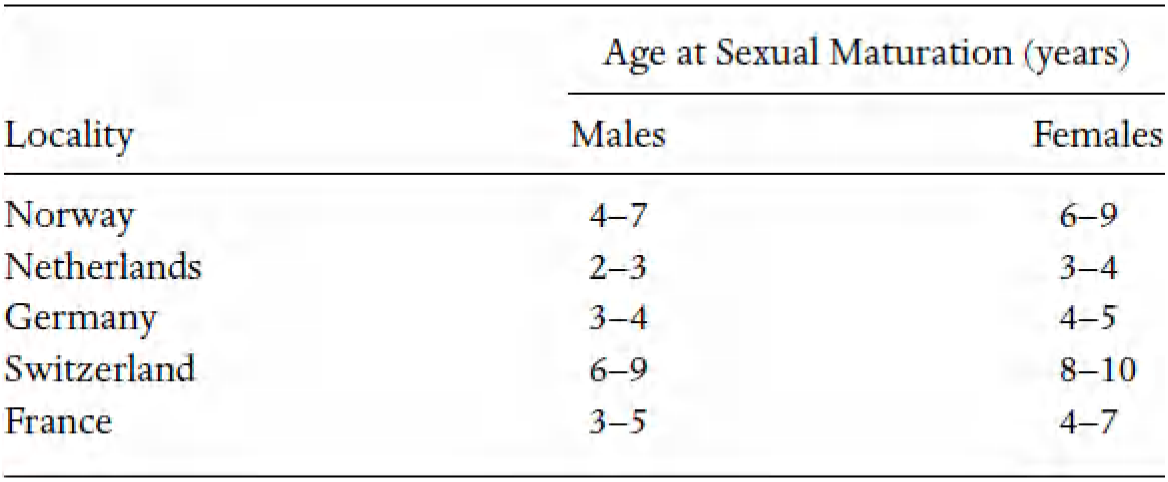
Most amphibians can breed the year following their birth. There can be, however, significant differences in the age of sexual maturation within the same species at different geographic sites (Table 5.3). Jorgensen (1992) noted: "The difference in age at sexual maturation among toads from various geographical locations may not arise entirely from different climatic environments, but may also be genetically fixed, determined by relationships between growth, body size, and sexual maturation that are established independently of particular climatic conditions."

The bullfrog (*Lithobates* [*Rana*] *catesbeiana*), which may spend one year as a tadpole in the southern portion of its range, may remain a tadpole for up to three years in the northern part. Thus, it might require four or five years for this species to become sexually mature. The European common frog (*Rana temporaria*) normally metamorphoses in about 16 weeks but does not become sexually mature for 4 years (see Fig. 5.38).

Longevity

While the maximum recorded longevity for most amphibians is generally between two and six years, some captive individuals have lived considerably longer. The olm (*Proteus anguinus*) holds the record for longevity among amphibians at 102 years. A Japanese giant salamander (*Andrias japonicus*) lived for 55 years. The mudpuppy (*Necturus maculosus*) has lived for 34 years, the spotted salamander (*Ambystoma maculatum*) has lived for 32 years, the hellbender (*Cryptobranchus alleganiensis*) has lived for 29 years, the two-toed amphiuma (*Amphiuma means*) has lived for 27 years, and the lesser siren (*Siren intermedia*) has lived for 25.7 years. Individuals of the tiger salamander (*Ambystoma tigrinum*), the eastern red-backed salamander (*Plethodon cinereus*), the eastern newt (*Notophthalmus viridescens*), the greater siren (*Siren lacertina*), and the Japanese fire belly newt (*Cynops pyrrhogaster*) have all lived for 25 years. The African bullfrog (*Pyxicephalus adspersus*) holds the anuran record with 45 years, followed by the common European toad (*Bufo bufo*) at 40 years, the American toad (*Anaxyrus* [*Bufo*] *americanus*) at 36 years, the African clawed frog (*Xenopus laevis*) at 30.3 years, the European frog (*Rana temporaria*) at 27 years, and the cane toad (*Rhinella marina*) at 24.8 years (Human Ageing Genomic Resources (HAGR), 2017).

Table 5.3. Age at Sexual Maturation in Populations of the Toad *Bufo bufo* from Different Sites in Europe



	Age at Sexual Maturation (years)	
Locality	Males	Females
Norway	4–7	6–9
Netherlands	2–3	3–4
Germany	3–4	4–5
Switzerland	6–9	8–10
France	3–5	4–7

Source: From Feder and Burggren, 1992. Copyright © 1992 University of Chicago Press, Chicago. Used by permission.

Review Questions and Topics

1. What adaptive advantage is gained by having two bones fuse into a single structure like the tibiofibula in anurans?
2. What adaptive advantages are there in having the limbs positioned beneath the body rather than out to the sides as in salamanders?
3. Why has the metameric arrangement of muscle, as seen in fishes, gradually been lost in higher vertebrates?
4. Compare and contrast the flow of blood through the heart of a shark with the flow through the heart of an adult anuran during a single circuit through the body.
5. Describe several different methods of gas exchange used by amphibians.
6. Describe the force-pump mechanism used by amphibians.
7. How is the length of the intestine correlated with herbivorous and carnivorous species? Why is this so?
8. What is the significance of having three semicircular canals in the inner ear, each lying in a different plane?
9. What is meant by sexual dimorphism? Give several examples.

10. Explain how environmental factors control the periodicity of breeding in ectotherms.

11. Define paedomorphosis.

12. Discuss several methods of egg deposition used by oviparous amphibians.

13. Give several advantages and several disadvantages of direct development in amphibians.

14. How do environmental factors like rainfall and temperature affect egg and larval development in amphibians?

15. Give some examples of evidence supporting either the lungfishes, rhipidistian, or coelacanth as the ancestor of the amphibians.

16. Discuss the problems faced by a vertebrate emerging from water to live on land. Have amphibians successfully solved all of the problems? If so, how?

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Vertebrate Internet Sites

1. Amphibia: Fossil Record

   www.ucmp.berkeley.edu/vertebrates/tetrapods/amphibfr.html

   Information on extinct amphibians.

2. Introduction to the Tetrapoda

   www.ucmp.berkeley.edu/vertebrates/tetrapods/tetraintro.html

   Information on tetrapod fossils, natural history, ecology, systematics, and morphology.

3. IUCN/SSC Amphibian Specialist Group (ASG)

   www.iucn-amphibians.org

   Formerly, the Declining Amphibians Task Force. Publishes bimonthly newsletter *Froglog*. Strives to conserve biological diversity by stimulating, developing, and executing practical programs to conserve amphibians and their habitats around the world.

4. FrogWatch USA

   www.aza.org/frogwatch

   FrogWatch USA is the Association of Zoos & Aquarium's (AZA) citizen science program and provides individuals, groups, and families opportunities to learn about wetlands in their communities by reporting on the calls of local frogs and toads. Long-term frog and toad volunteer monitoring program. Its goal is to engage the public in conservation, while helping to compile valuable information about frog and toad population distributions, population trends at individual wetlands, and yearly calling phenologies.

5. Terrestrial Vertebrates

   www.tolweb.org/Terrestrial_Vertebrates

   Characteristics, phylogenetic relationships, origin of stegocephalians, early evolution of limbs, conquest of land by vertebrates, bibliography, and web link.

6. North American Amphibian Monitoring Program

   www.pwrc.usgs.gov/naamp

   Information and links to information on the study and conservation efforts for amphibians. Supported by the US Geological Survey and the Patuxent Wildlife Research Center.

7. Animal Diversity Web, University of Michigan Museum of Zoology

   https://animaldiversity.org/accounts/Amphibia/classification

   Class Amphibia. Classification, information, pictures, specimens, and sounds.

6 | Evolution of Reptiles

There's an incomparable rush that comes from finding dinosaur bones. You know you're the first person to lay hands on a critter that lived 80 or 90 million years ago.

Jack Horner, 1988

INTRODUCTION

The class Reptilia is no longer recognized by phylogenetic systematists because it is not a monophyletic group. Traditionally, the class Reptilia included the turtles, tuatara, lizards, snakes, and crocodilians. Birds, which descend from the most recent common ancestor of reptiles, have traditionally been classified by themselves in the class Aves. Reptiles, therefore, are a paraphyletic group unless birds are included. Furthermore, based on shared derived characteristics, crocodilians and birds are more recently descended from a common ancestor than either is from any living reptilian lineage; thus, they are sister groups.

In phylogenetic systematics (cladistics), turtles, tuataras, lizards, snakes, crocodilians, and birds are placed in the monophyletic group Sauropsida. The Sauropsida include three groups: turtles (Testudomorpha); tuataras, lizards, and snakes (Lepidosauromorpha); and the crocodilians and birds (Archosauromorpha). In this method of classification, turtles are placed at the base of the tree. Evidence from 2 nuclear genes and analyses of mitochondrial DNA (mtDNA) and 22 additional nuclear genes join crocodilians with turtles and place squamates at the base of the tree (Hedges and Poling, 1999; Rieppel, 1999). Morphological and paleontological evidence for this phylogeny is unclear at the present time.

Considerable disagreement continues between proponents of evolutionary (traditional) taxonomy and cladistics. The classification used in this text, for the most part, will follow the cladistic method. Comparisons between the two classification methods will be presented at appropriate points. For ease of discussion, we will divide the reptiles (sauropsids) into three chapters: Evolution (this chapter); Morphology, Reproduction, and Development of Turtles, Tuataras, Lizards, and Snakes (Chapter 7); and Morphology, Reproduction, and Development of Crocodilians and Birds (Chapter 8).

EVOLUTION

The fossil record for reptiles is much more complete than the one for amphibians. Based on current evidence, all lineages of modern reptiles can be traced back to the Triassic period (Fig. 6.1). Disagreement, however, exists concerning origins and relationships prior to the Triassic and whether reptiles had a monophyletic, diphyletic, or even a polyphyletic origin. Molecular investigations, including comparative protein sequence studies of amniote (sauropsids and mammals) myoglobins and hemoglobins (Bishop and Friday, 1988), are shedding new light on reptilian relationships. A cladogram giving one interpretation of the relationships among the amniotes is presented in Fig. 6.2.

Dinosaur research—paleontological, anatomical, molecular—is advancing faster now than at any other time in history. Many areas of the world that have been virtually inaccessible have opened up over the last few decades. New technology—computed tomography (CT) scans, spectroscopy, and other methods—is helping greatly. Incredibly, about 50 new species of dinosaurs are being discovered a year—that's a new species *each week*, on average. Not a new bone or skeleton, but a totally new species (Brusatte, 2018).

Molecular studies have made significant discoveries in the past several decades. Evidence pointing to the existence of heme-containing compounds and/or hemoglobin breakdown products in extracts of trabecular tissues of the large theropod dinosaur *Tyrannosaurus rex* (*T. rex*) was reported by Schweitzer et al. (1997). In 2005, Mary Schweitzer, a paleontologist at North Carolina State University and Jack Horner, a paleontologist at the Burke Museum in Seattle, Washington, demineralized a *T. rex* bone. After dissolving away the minerals, what remained were structures that looked like millimeter-long blood vessels that flexed and stretched like real tissue when tugged by tiny tweezers (Schweitzer et al. 2005).

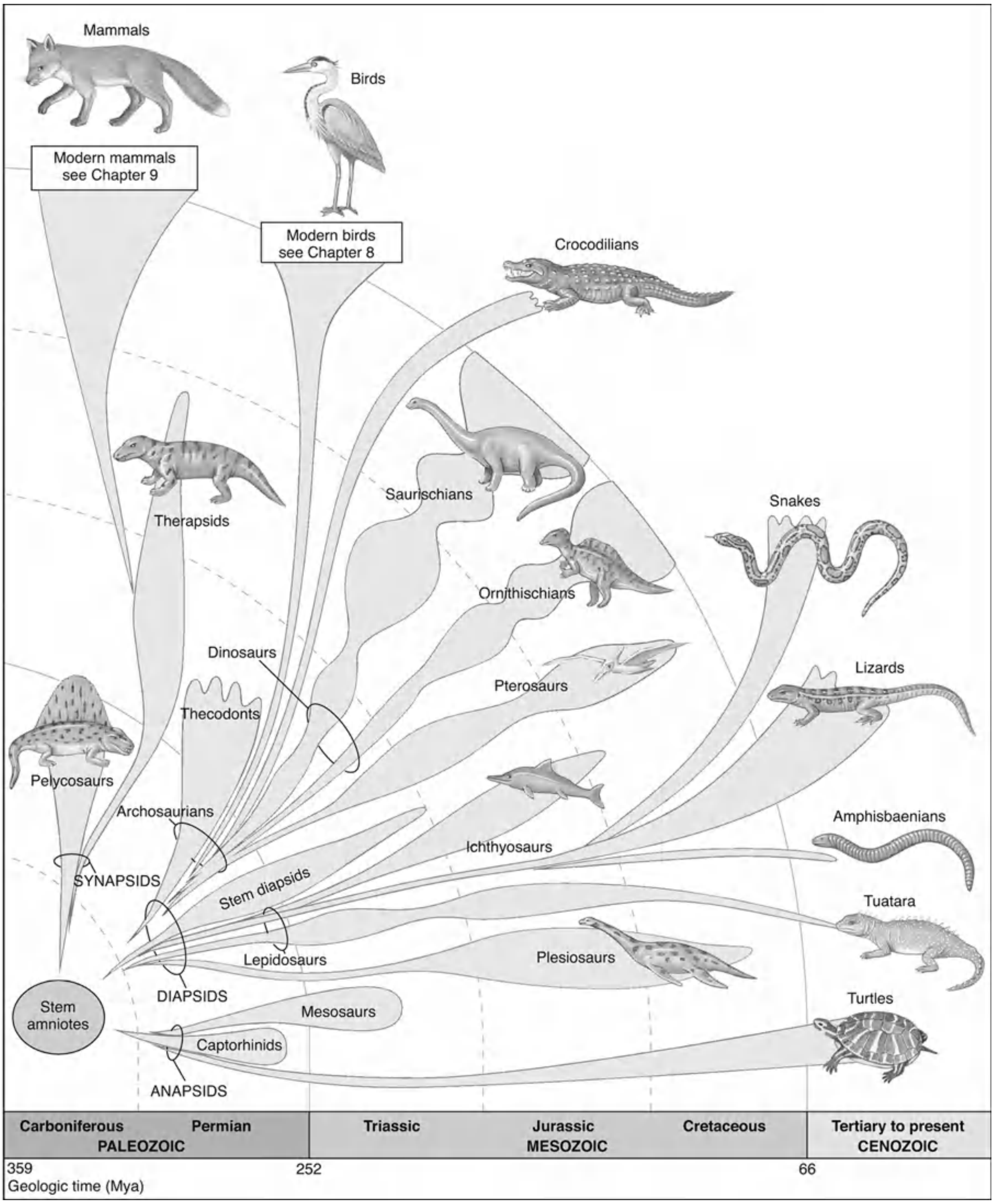


Figure 6.1. The evolutionary origin of amniotes. The evolution of an amniotic egg made reproduction on land possible, although this type of egg may well have developed before the earliest amniotes had ventured far onto land. The amniotes (reptiles, birds, and mammals) evolved from small, lizard-like forms known as captorhinids that retained the skull pattern of the early tetrapods. The mammal-like reptiles, which were the first to diverge from the primitive stock, possessed synapsid skulls. All other amniotes, except turtles, have a diapsid skull. Turtle skulls are of the anapsid type. The great Mesozoic radiation of reptiles may have been caused partly by the increased variety of ecological habitats available for the amniotes.

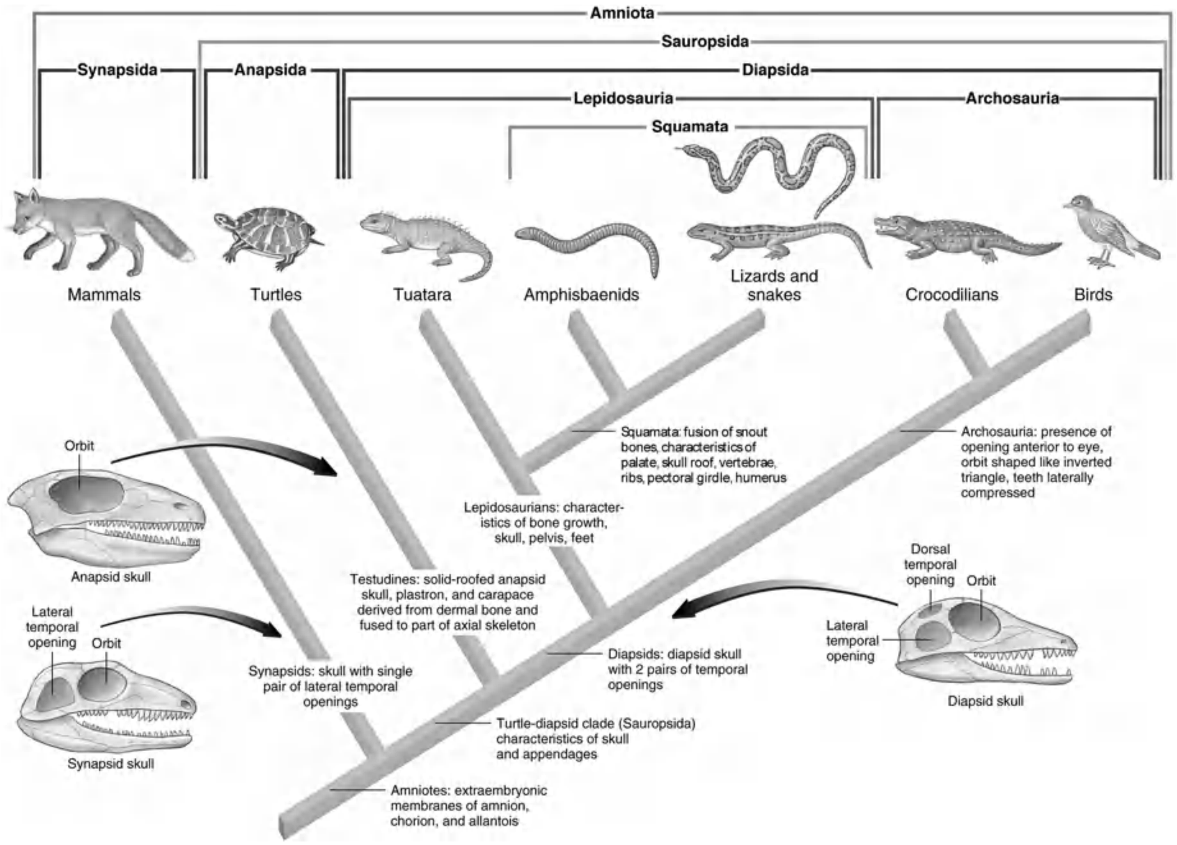


Figure 6.2. Cladogram of living amniotes showing monophyletic groups. Some of the shared derived characters (synapomorphies) are given. The skulls represent the ancestral condition of the three groups, because the skulls of modern diapsids and synapsids are often modified by a loss or fusion of skull bones that obscures the ancestral condition. The relationships shown in this cladogram are tentative and controversial, especially that between birds and mammals. Mammals are shown here as the outgroup, although some authorities support a sister-group relationship between birds and mammals based on molecular and physiological evidence.

In 2007, bits of protein (collagen) were obtained from connective tissues in a *T. rex* fossil found in Montana in 2003 and believed to be 68 million years old (Asara et al., 2007a). The researchers got the weights of six collagen fragments and were able to work out their amino acid sequences (Asara et al., 2007a; Schweitzer et al., 2007). At that time, this was the oldest such material ever found. Prior to this, the oldest sequenced protein (also collagen) came from a mammoth fossil that was 100,000 to 300,000 years old. The sequences resembled those of today's birds, supporting the wealth of fossil evidence that birds descend from extinct dinosaurs. In addition, Mary Schweitzer dissolved fragments of a leg bone of the *Tyrannosaurus* in acid and discovered blood vessels and structures that looked like whole cells inside the *T. rex* bone—the first observation of its kind (Asara et al., 2007b). Colleagues had never imagined that even a trace of still-soft dinosaur tissue could survive, and the results met with considerable skepticism at the time. Many doubted that dinosaur protein had been sequenced. The next question was whether protein and/or DNA might be lurking in that tissue.

In 2009, Schweitzer and her colleagues reported isolating intact protein fragments from 65-million-year-old and 80-million-year-old dinosaur fossils (Schweitzer et al., 2009). Once again, the claims were met with skepticism from biochemists and paleontologists who saw no way that fragile organic molecules could survive for tens of millions of years and wondered whether the samples were contaminated with modern proteins. Immunological and mass spectrometry evidence was presented in 2012 supporting evidence for the preservation of proteins comprising extant osteocytes in osteocytes recovered from two nonavian dinosaurs (Schweitzer et al., 2013). In 2017, Schweitzer and her colleagues reported that they did a complete makeover of their 2009 experiment to rule out any possible contamination (Schroeter et al., 2017). They took new samples from the same 80-million-year-old fossil of a duck-billed dinosaur called *Brachylophosaurus canadensis*. They reworked procedures for extracting would-be proteins from the bone, identified protein fragments with a more sensitive mass spectrometer, and compared the recovered protein sequences to those from many more living animals. Coauthor Elena Schroeter even went so far as to break down the mass spectrometer piece by piece, soak the whole thing in methanol to remove any possible contaminants, and reassemble the machine. Schweitzer said, “About the only thing that is the same [as the 2009 experiments] is the dinosaur.”

Schweitzer’s team identified three fragments of a protein called collagen 1 from their fossil. Collagen is the main protein in connective tissue and is abundant in bone. In each fragment, the mass spectrometer was able to identify 15 amino acids strung together. In their 2017 paper, Schweitzer’s team identified eight protein fragments, two of which were identical to those recovered in 2009, and six that were new. The three protein (collagen 1) fragments originally recovered in this new experiment most closely resembled the collagen found in living alligators and other reptiles. The new data show that *B. canadensis* collagen was a better match to that of birds.

In 2015, red blood cells and collagen fibers were discovered by researchers at the Imperial College in London in the fossilized remains of 75-million-year-old dinosaurs recovered from the Dinosaur Park Formation in Alberta, Canada (Bertazzo et al., 2015). In 2017, a team of researchers at the University of Toronto in Canada reported finding what they believe is collagen in a 195-million-year-old fossil rib from a large plant-eating dinosaur called *Lufengosaurus*, which lived in what is now southwestern China (Lee et al., 2017). The team's method, called Raman spectroscopy and synchrotron radiation-based Fourier transform infrared microspectroscopy (SR-FTIR), can probe the chemical makeup of a sample without the need to purify it first, which lowers the risk of contamination. The rib absorbed infrared light in wavelengths that match those of collagen from modern animals. Skeptics persist.

In 2016, researchers at the University of York in the United Kingdom managed to identify protein fragments from 3.8-million-year-old ostrich (Struthionidae) egg shells (Demarchi, et al., 2016). Most of their colleagues are in agreement with their findings.

The first definitive sexing of a dinosaur, from egg-laying tissue, was reported by Schweitzer et al. (2005). The egg-laying tissue, called medullary bone, was previously known only in living birds. Ovulating females rapidly create this mineral-rich tissue inside their legs and other bones as a storehouse for calcium for making eggshell. Schweitzer and her colleagues compared the fossilized leg bone of a roughly 70-million-year-old *T. rex* with modern ostrich bone, showing many similarities. Medullary bone was also found in a nearly 150-million-year-old tibia of the large predator *Allosaurus fragilis* from Utah where researchers found a layer of bone in which the tissue was disorganized and replete with traces of blood vessels, suggesting it had grown quickly (Lee and Werning, 2008). The same pattern turned up in a femur and tibia of an approximately 110-million-year-old *Tenontosaurus tilletti* from Montana. *Tenontosaurus* belongs to a major division of dinosaurs called the Ornithischia. This group split more than 230 Mya from the other major group of dinosaurs, the Saurischia. Because members of both groups had medullary bone, the tissue likely evolved in a common ancestor after that common ancestor split from the crocodilians.

By using the bright X-ray beam of the Stanford Synchrotron Radiation Lightsource, scientists have been able to identify very precisely the locations of chemical elements hidden within *Archaeopteryx*, a rare feathered dinosaur that perished some 150 Mya (Bergmann et al., 2010). From this, they created the first maps of the dinobird's chemistry, revealing half a dozen chemical elements that were actually part of the living animal itself. The chemical maps show that portions of the feathers are not merely impressions of long-decomposed organic material—as was previously believed—but are actual fossilized feathers that contain phosphorus and sulfur, elements that comprise modern bird feathers. Trace amounts of copper and zinc were also found in the dinobird's bones. These results provide a chemical link between dinosaurs and birds.

The Stanford Synchrotron has also been used to determine the color of a 150-million-year-old *Archaeopteryx* feather (Manning et al., 2013). The entire feather was scanned and found to be patterned: light in color with a black tip, rather than all black, as previously thought.

Ancestral Reptiles

An extensive fossil record documents the origin and early evolution of Amniota, and that record has played a key role in understanding phylogenetic relationships among the living amniotes. The oldest amniotes currently known date from the Carboniferous (Middle Pennsylvanian) locality known as Joggins, in Nova Scotia (Carroll, 1964). An earlier amniote from the Lower Carboniferous of Scotland, approximately 338 Mya (Smithson, 1989), was later shown to be only a close relative of amniotes (Smithson et al., 1993). Laurin and Reisz (1999) even suggested that it was more likely to be a stem-tetrapod or an early amphibian than a relative of amniotes. More recently, the same Scotland site yielded another Lower Carboniferous tetrapod, *Eucritta melanolimnetes*, which exhibits characters from three different types of primitive tetrapods: temnospondyls (relatives of living amphibians), anthracosaurs (amniotes and their close relatives), and baphetids (crocodile-like body with a unique keyhole-shaped orbit) (Clack, 1998). Since temnospondyls and anthracosaurs have previously been found at this site between Glasgow and Edinburgh, it has been hypothesized that at least three different lineages of early tetrapod may have independently evolved into medium-sized fish-eating animals. This is but one of numerous examples of parallel evolution in vertebrates.

The smallest of all known Lower Carboniferous tetrapods, *Casineria kiddi*, with an estimated snout-vent length of 85 mm, was reported from East Lothian, Scotland (Paton et al., 1999). *Casineria* shows a variety of adaptations to terrestrial life. For example, vertebrae are connected to each other to form a relatively stiff backbone, which would have served as a suspension bridge to hold up the animal's body. *Casineria* also possessed the earliest pentadactyl limb, which is clearly terrestrially adapted. The humerus had a constricted shaft and exhibited torsion between proximal and distal articulations, features associated with the maintenance of postural support and strong evidence of locomotion on land. The authors state that limbs described from most earlier Late Devonian animals, like *Ichthyostega* and *Acanthostega*, possessed more than five digits and belonged to arguably aquatic forms (Paton et al., 1999). *Pederpes*, however, was more advanced over its Devonian predecessors in having only five digits and having all of its toes pointed forward rather than sideways like those of its aquatic ancestors (Clack, 2002). Paton et al. (1999) note that the degree of terrestriality exhibited by *Casineria* indicates that the transition to land-dwelling may have taken place within a period of about 20 million years.

By the end of the Carboniferous (about 286 Mya), at least two phylogenetic lines of reptiles existed: the pelycosaurs (order Pelycosauria) and the more primitive captorhinids (suborder Captorhinomorpha of the order Cotylosauria). Both of these forms have been found together in deposits approximately 300 million years old in Nova Scotia. Because of their similarity, some investigators believe that they probably evolved from a common ancestor in the Early Carboniferous (Carroll, 1988). Romer's (1966) observation that the development of the amniote egg was so complex and so uniform among reptiles that it is not likely it could have evolved independently in two or more different groups of amphibians, lends additional weight to the belief that the origin of reptiles was monophyletic. Carroll (1988) noted that by the Upper Carboniferous, amniotes had diverged into three major lineages: synapsids gave rise to mammals, anapsids to turtles, and diapsids to all of the other reptilian groups, including birds.

Members of the order Anthracosauria (subclass Labyrinthodontia) most closely resemble the primitive captorhinomorphs. One group of these amphibians, the seymouriamorphs (suborder Seymouriamorpha), possessed a combination of amphibian and reptilian characteristics. The best-known genus of this group is *Seymouria*, discovered in Lower Permian deposits near Seymour, Texas (Fig. 6.3). Although *Seymouria* lived too recently to have been ancestral to the reptiles, it is thought to be an advanced member of a more primitive group of amphibians that did give rise to the original reptiles. *Seymouria* had a relatively short vertebral column, an amphibian-like skull, and well-developed limbs and girdles. The neural arches, however, were similar to those found in reptiles, and the dentition had a distinctly reptilian aspect with teeth set in shallow pits. *Seymouria* had a single occipital condyle, as did primitive amphibians and reptiles.

Seymouria appears to have been clearly capable of living on land and probably of supporting its body above the ground. *Seymouria* probably lived part of the time on land and part of the time in pools and swamps, where it fed on small fish as well as on aquatic and terrestrial invertebrates. Carroll (1969) believed that, although adults appeared to be adapted for life on dry land, they were phylogenetically, morphologically, and physiologically amphibian.

A fundamental difference between amphibians and reptiles involves the type of egg produced and the method of development of the young. Amphibians have an anamniotic embryo (one without an amnion) that must always be deposited in water or in a moist habitat. In most species of amphibians, fertilized eggs will develop into aquatic larvae. Numerous labyrinthodont amphibians are known to have had larval stages with external gills, as do many living amphibians (Carroll, 1969). Most reptiles, on the other hand, produce an egg sealed in a leathery shell that is much more resistant to desiccation (Fig. 6.4). Four extraembryonic membranes are present inside the leathery shell: a **chorion** (outer membrane surrounding the embryo that assists in gas exchange and in forming blood vessels); an **amnion** (inner membrane surrounding the embryo forming the amniotic cavity and containing amniotic fluid); a **yolk sac** (enclosing the yolk); and an **allantois** (forming a respiratory structure and storing nitrogenous waste). Reptiles lack a larval stage and, following hatching, develop directly into the adult form.

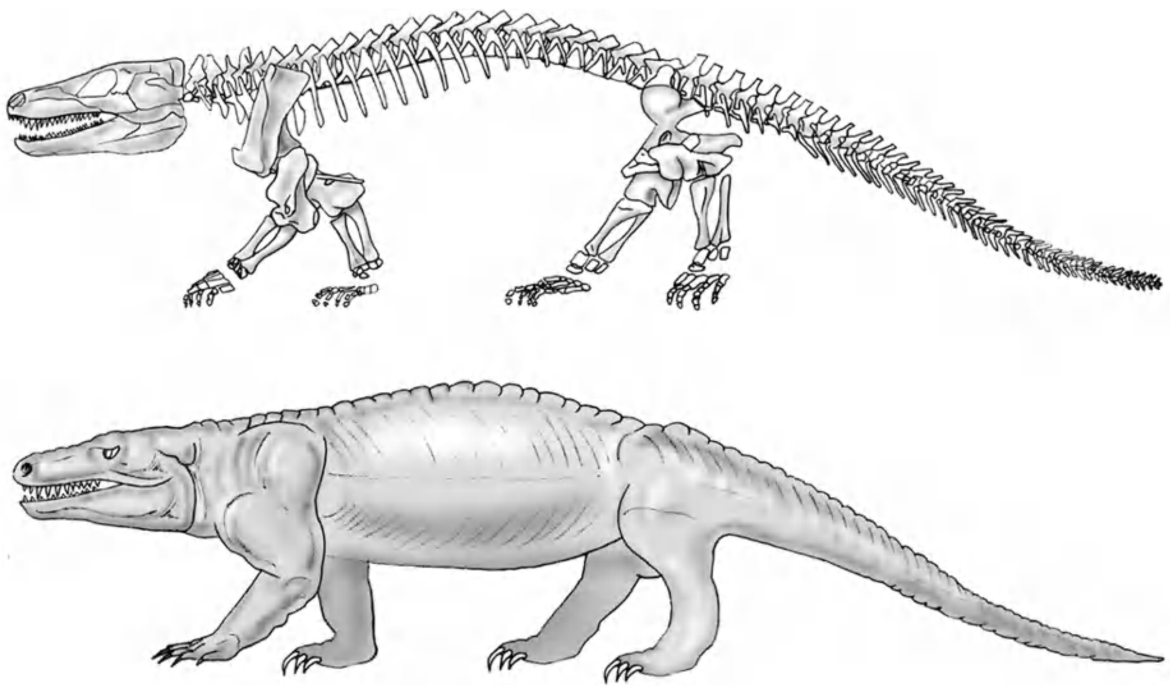


Figure 6.3. *Seymouria*, a primitive genus of reptile with well-developed limbs positioned beneath the body, providing better support. Estimated total length of the skeleton is approximately 80 cm (31 in.).

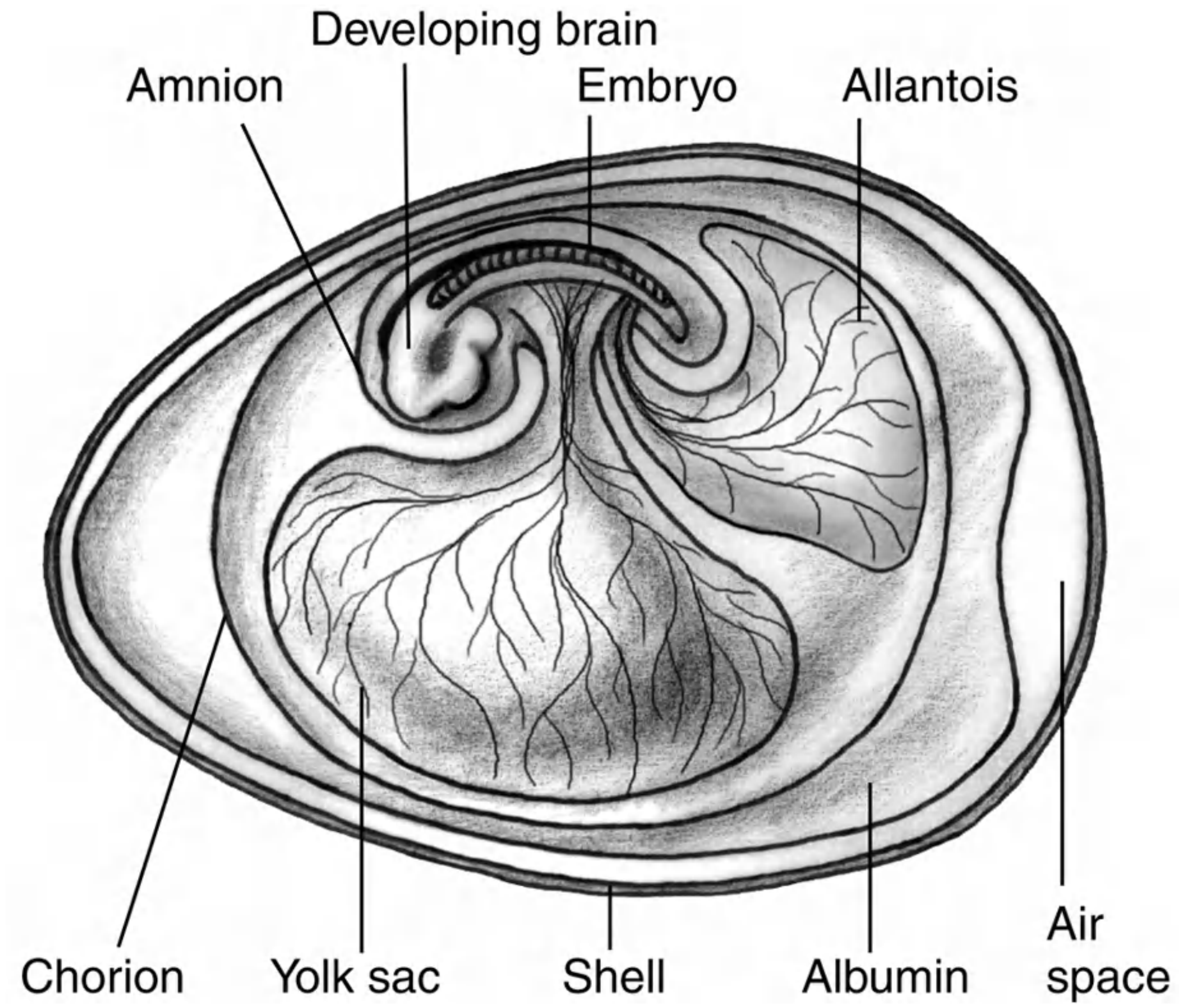


Figure 6.4. Generalized structure of the amniotic egg. Its membranes—chorion, amnion, yolk sac, and allantois—protect the embryo and provide it with metabolic support.

Unfortunately, little fossil evidence is available concerning eggs and early developmental stages of primitive reptiles because eggs do not generally fossilize well. The oldest fossil amniote egg was found in Early Permian deposits in Texas (Romer and Price, 1939). It was 59 mm in length and was probably deposited by a pelycosaur, the most common member of the fauna (Romer and Price, 1940).

How long young dinosaurs remained in their nest has been debated for many years. Some scientists have argued that the thigh bones of newly hatched dinosaurs were not formed well enough to support their weight. Geist and Jones (1996), however, examined the pelvic girdles of some living relatives of dinosaurs—crocodiles and birds. The pelvis starts out as soft cartilage and later becomes hard due to the deposit of minerals. Geist and Jones found that in animals that can walk immediately after birth—like crocodiles, emus, and ducks—the pelvis is bony by hatching time. But in animals that cannot walk immediately, the pelvis is not fully hardened at birth. Of the five dinosaur species for which embryos have been found, all had bony pelvises while they were still in the egg, implying that they could stand upright at birth.

Romer (1957) expressed the belief that the earliest reptiles were amphibious or semiaquatic, as were their immediate amphibian ancestors. The amniotic egg was developed by such semiaquatic animals, not by a group of animals in which the adults had already become terrestrial. Romer stated, “although the terrestrial egg-laying habit evolved at the beginning of reptilian evolution, adult reptiles at that stage were still essentially aquatic forms, and many remained aquatic or amphibious long after the amniote egg opened up to them the full potentialities of terrestrial existence. It was the egg which came ashore first; the adult followed.”

Tihen (1960) agreed with Romer regarding the origin of the amniote egg. He pointed out that the terrestrial egg probably developed in order to avoid “the necessity for an aquatic existence during the particularly vulnerable immature stages of the life history.” In addition, Tihen suggested that the development of the terrestrial egg occurred under “very humid, probably swampy and tropical, climatic conditions,” rather than during a period of drought. A generalization like “drought” during a portion of a geological period does not accurately indicate conditions on a regional and/or local level. Areas in close proximity to one another can have vastly different environmental conditions. In support of his theory, Tihen cited examples of modern amphibians living in areas where the water supply is intermittent and undependable. Rather than deposit their eggs on the fringes of the water, they deposit them “more positively within” the available bodies of water. Because most amphibians that deposit terrestrial eggs live in humid habitats, Tihen believed terrestrial eggs evolved as a device for escaping predation, *not* for avoiding desiccation. Furthermore, he noted that in the early stages of its evolution, the amniote egg must have been quite susceptible to desiccation and that only after the specializations that now protect it (extraembryonic membranes) had been developed could it have been deposited in even moderately dry surroundings.

Eggs and young of *Seymouria* are unknown. However, gilled larvae of a closely related seymouriamorph (*Discosauriscus*) have been discovered (Porter, 1972). The presence of gilled larvae indicates that these were definitely amphibians even though they were quite close to the reptilian phylogenetic line of development.

Were the earliest reptiles aquatic, coming onto land only to deposit their amniotic eggs as turtles do today, or were they primarily terrestrial animals? Did the amniotic egg evolve in response to drought conditions, or did it evolve as a means to protect the young from the dangers of aquatic predation? These questions continue to be the subject of much debate.

Dinosaur Nests and Eggs

Although the first publicized dinosaur nests and eggs were discovered in Mongolia in 1923 (Andrews, 1932; Brown and Schlaikjer, 1940; Norman, 1991), Carpenter et al. (1994) noted that dinosaur eggs have been known for thousands of years and that the first dinosaur egg shell in historical times can be traced back to 1859 in southern France (Buffetaut and LeLoewff, 1989). The Mongolian eggs were originally identified as being from *Protoceratops*, a small ceratopsian dinosaur, but later were reidentified as being from a theropod dinosaur in the family Oviraptoridae (Norell et al., 1994).

Over the past four decades, numerous discoveries of nesting sites, eggs, and embryos have greatly increased our knowledge of the evolution of reproductive behavior in nonavian dinosaurs. The first nest containing the remains of a baby dinosaur (*Mussaurus*) was reported in 1974 from Argentina (Bonaparte and Vince, 1974).

The best-known dinosaur nest (containing crushed egg shells as well as the skeletons of baby hadrosaurs) was discovered in 1978 in Montana (Horner, 1984; Horner and Gorman, 1988). The nest was approximately 1.8 m (6 ft.) in diameter and 0.9 m (3 ft.) deep and contained the fossilized remains of fifteen 1 m (3 ft.) long duck-billed dinosaurs (*Maiasaura*, meaning “good mother”). It provided evidence that, unlike most reptiles, these young had stayed in the nest while they were growing and that one or both parents had cared for them. The teeth were well worn, indicating that the young had been in the nest and had been eating there for some time. Analysis of the hatchlings’ bones revealed bone tissue that grows rapidly, the same way the bones of modern birds and mammals grow. The implications are that the young must have been developing rapidly and that they were probably homeothermic (Horner and Gorman, 1988).

Clusters of nests that were found indicate that female *Maiasaura* and *Orodromeus* laid their eggs and raised their young in colonies, as do some species of birds. The discovery of large fossil beds containing individuals of all ages led Bakker (1986), Horner and Gorman (1988), and Horner (1998, 1999) to conclude that some dinosaurs, including *Apatosaurus* (*Brontosaurus*) and *Maiasaura*, lived in large herds. Many of the bones of these dinosaurs were either unbroken or showed clean breaks, indicating they had been broken *after* fossilization. In 1979, a clutch of 19 eggs containing embryonic skeletons of *Troodon*, originally misidentified as *Orodromeus* (Moffat, 1997), was found in Montana. One was fully articulated and was the first such embryonic dinosaur skeleton ever unearthed (Horner and Gorman, 1988). Carpenter and Alf (1994) surveyed the global distribution of dinosaur eggs, nests, and young. More recently, numerous nests and eggs containing embryos have been recovered from exceptionally rich fossil sources in China (O'Brien, 1995), along the seashore in Spain (Sanz et al., 1995), and in Mongolia (Dashzeveg et al., 1995). The oldest dinosaur embryo, probably a theropod, was reported from 140-million-year-old Jurassic sediments from Lourinhã, Portugal (Holden, 1997).

In 1994, researchers from the American Museum of Natural History and the Mongolian Academy of Sciences announced the discovery of the fossilized remains of a 3 m carnivorous dinosaur (*Oviraptor*) nesting on its eggs like a brooding bird (Gibbons, 1994; Norell et al., 1994). This nest and its brood of unhatched young were discovered in the Gobi Desert of Mongolia and represent the first concrete proof that dinosaurs actively protected and cared for their young. A pair of shelled eggs, the first ever found within a dinosaur, were reported from an oviraptorosaurian (Sato et al., 2005).

Six exquisitely preserved titanosaur embryos, their articulated jaws, their peg-shaped teeth, and even their nostrils intact, were discovered in 1997 in Patagonia, Argentina (Chiappe et al. 2001). Each 30 cm (1 ft.) long embryo was curled up inside its cantaloupe-sized egg.

Thousands of sauropod dinosaur eggs were discovered at Auca Mahuevo in Patagonia, Argentina (Chiappe et al., 1998). The proportion of eggs containing embryonic remains was high at this Upper Cretaceous site—more than a dozen *in situ* eggs and nearly 40 egg fragments encasing embryonic remains. In addition, many specimens contained large patches of fossil skin casts, the first portions of integument ever reported for a nonavian dinosaur embryo.

The oldest known dinosaurian nesting site was reported by Reisz et al. (2012) from a Lower Jurassic site at Rooidraai, Golden Gate Highlands National Park, South Africa. The nesting site, yielding multiple *in situ* egg clusters of *Massospondylus*, predates other similar sites by more than 100 million years.

Dinosaurs used specific materials and techniques to build their nests (Tanaka et al., 2018). Different dinosaurs preferred different materials for nest-building: some used soil or plant materials to build organic-rich mound nests that relied on microbial decay for incubation, whereas others dug holes in the sand and relied on solar or potentially geothermal heat for incubation. Nest-building influenced how warm their eggs would be and may have affected the regions and environments in which they were able to live.

The discovery of the small ornithischian dinosaur *Psittacosaurus* sp. from Liaoning in China revealed a single adult clustered with 34 juveniles within an area of 0.5 m^2, providing strong evidence for post-hatching parental care in Dinosauria (Meng et al., 2004).

Ancient and Living Reptiles

Reptiles were the dominant terrestrial vertebrates during most of the Mesozoic era. There were terrestrial, aquatic, and aerial forms. There were quadrupedal and bipedal reptiles, as well as carnivorous and herbivorous forms. One group gave rise to the mammals in the Late Triassic. As many as 22 orders of reptiles have, at one time or another, inhabited the Earth, but their numbers have decreased until living representatives of only 4 orders remain. Living reptiles (and mammals) are thus the descendants of the great Mesozoic differentiation of the ancestral reptiles.

The traditional classification of reptiles is based on a single key character: the presence and position of **temporal fenestrae**, which are openings in the temporal region of the skull that accommodate the jaw musculature (Fig. 6.5). These criteria, using only Paleozoic taxa, yield three groups: Anapsida: turtles, captorhinomorphs, procolophonids, and pareiasaurs; Diapsida: dinosaurs, tuataras, lizards, snakes, crocodiles, and birds; and Synapsida: mammal-like reptiles.

Rieppel and deBraga (1996), however, adopted a more inclusive perspective by adding Mesozoic and extant taxa to the analysis. Their studies support diapsid affinities for turtles and require the reassessment of categorizing turtles as "primitive" reptiles in phylogenetic reconstructions. Platz and Conlon (1997) also concluded that turtles should be considered diapsids by determining the amino acid sequence of pancreatic polypeptide for a turtle and comparing it with published sequences for 14 additional tetrapod taxa. Other researchers (Lee, 1997; Wilkinson et al., 1997), however, question the analysis of the data presented by Rieppel and deBraga.

In the phylogenetic (cladistic) classification, anapsid turtles are placed in the Testudomorpha, whereas all of the diapsid forms (tuataras, lizards, and snakes) make up the Lepidosauromorpha (lepidosaurs), and crocodilians and birds compose the Archosauromorpha (archosaurs).

Turtles (Testudomorpha)

Turtles (see Figs. 1.4 and 6.2) are anapsid reptiles that lack fenestrae (openings) in the temporal regions of their skulls. Cotylosaurs, or stem reptiles (order Cotylosauria), first appeared in the Early Carboniferous and had anapsid skulls. One of the oldest known cotylosaur reptiles, *Hylonomus*, is a captorhinomorph—a group frequently cited as the possible primitive relatives of turtles. It lived 312 Mya in the Late Carboniferous and is the earliest unquestionable reptile. Fossils of *Hylonomus* have been found in the remains of fossilized club moss stumps in Joggins, Nova Scotia, Canada. Reisz and Laurin (1991), however, present new evidence showing that a group of primitive amniotes, the procolophonids (Fig. 6.6), were the closest sister group of turtles. If true, the origin of turtles may be as late as the Late Permian. Lee (1993), however, considered the evidence uniting captorhinid and procolophonoids with turtles to be weak and instead proposed the pareiasaurs as the nearest relatives of turtles. Pareiasaurs were large anapsid reptiles that flourished briefly during the Late Permian. They were ponderous, heavily armored herbivores. Cladistic analyses reveal that pareiasaurs shared 16 derived features with turtles.

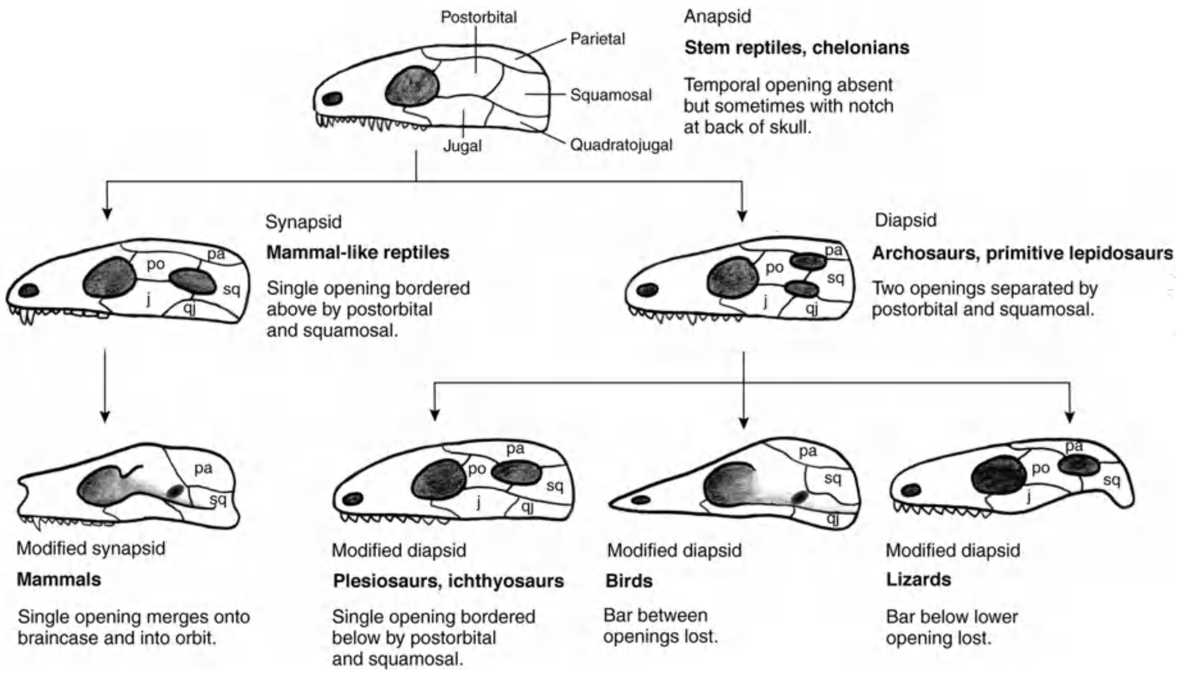


Figure 6.5. Phylogeny constructed by comparing temporal fenestrae of reptiles and their descendants.

The only living reptiles with anapsid skulls are the turtles (Testudomorpha), which first appeared in Triassic deposits (see Fig. 6.1). Their origin, however, is currently under debate. Although extensive morphological data from both extinct and extant data support the fact that turtles are most closely related to early diverging "parareptile" lineages that had no temporal fenestration, some recent molecular studies support a sister relationship between archosaurs and turtles. Researchers currently find it difficult to explain the different results of the molecular and morphological analyses. Molecular analyses include far more characters (thousands) than those based on morphological data (hundreds). However, because molecular data cannot be collected from fossil taxa, studies based on morphological data can better capture stem lineages that are phylogenetically informative (Pough et al., 2016).

Prior to 1995, the oldest turtle fossils, about 210 million years old, came from Thailand, Greenland, and Germany—all of which at that time (210 Mya) were part of the northern half of the supercontinent Pangaea. In 1995, turtle fossils were described from Argentina that were also 210 million years old, indicating that turtles had already spread over the planet by that time (Rougier et al., 1995). The Argentinian turtles were different from their northern contemporaries in that their shell extended over the neck (early turtles could not retract their necks), whereas other turtles had evolved external spines to protect their necks.

During the Late Triassic, some 220 Mya, a primitive turtle was preserved in sedimentary deposits in what is now southwestern China (Fig. 6.7). *Odontochelys semitestacea* is not only the oldest recognizable turtle, but its skull also shows that it is more primitive than other turtles because it retains a full complement of marginal teeth, rather than a beak, and also possesses free sacral ribs and a long tail (Li et al., 2008). It had a fully formed lower shell (plastron) but lacked a fully formed upper shell (carapace). Until 2018, it was the oldest undisputed stem turtle.

A newly discovered fossil turtle from southwestern China that lived 228 Mya is shedding light on how modern turtles developed turtle traits, namely a shell and a toothless beak (Li, et al., 2018). It was collected from sediments approximately 7.5 m below the horizon that contained the stem turtle *Odontochelys*. One of the coauthors, Olivier Rieppel, a paleontologist at Chicago's Field Museum, said: "The origin of turtles has been an unsolved problem in paleontology for many decades." Traits can evolve independently from each other and at a different rate, so that not every ancestral species has the same combination of these traits. Rather, some turtle relatives got partial shells while others got beaks, and eventually, the genetic mutations that create these traits occurred in the same animal. *Eorhynchochelys sinensis* had a beak, but its wide ribs had not grown to form a shell as in modern turtles. It was over 1.8 m (6 ft.) long, had a strange disclike body and a long tail, and the anterior part of its jaws developed into an odd beak. It is considered the earliest stem turtle with a beak and a rigid puboischiadic plate. A carapace and plastron are absent.

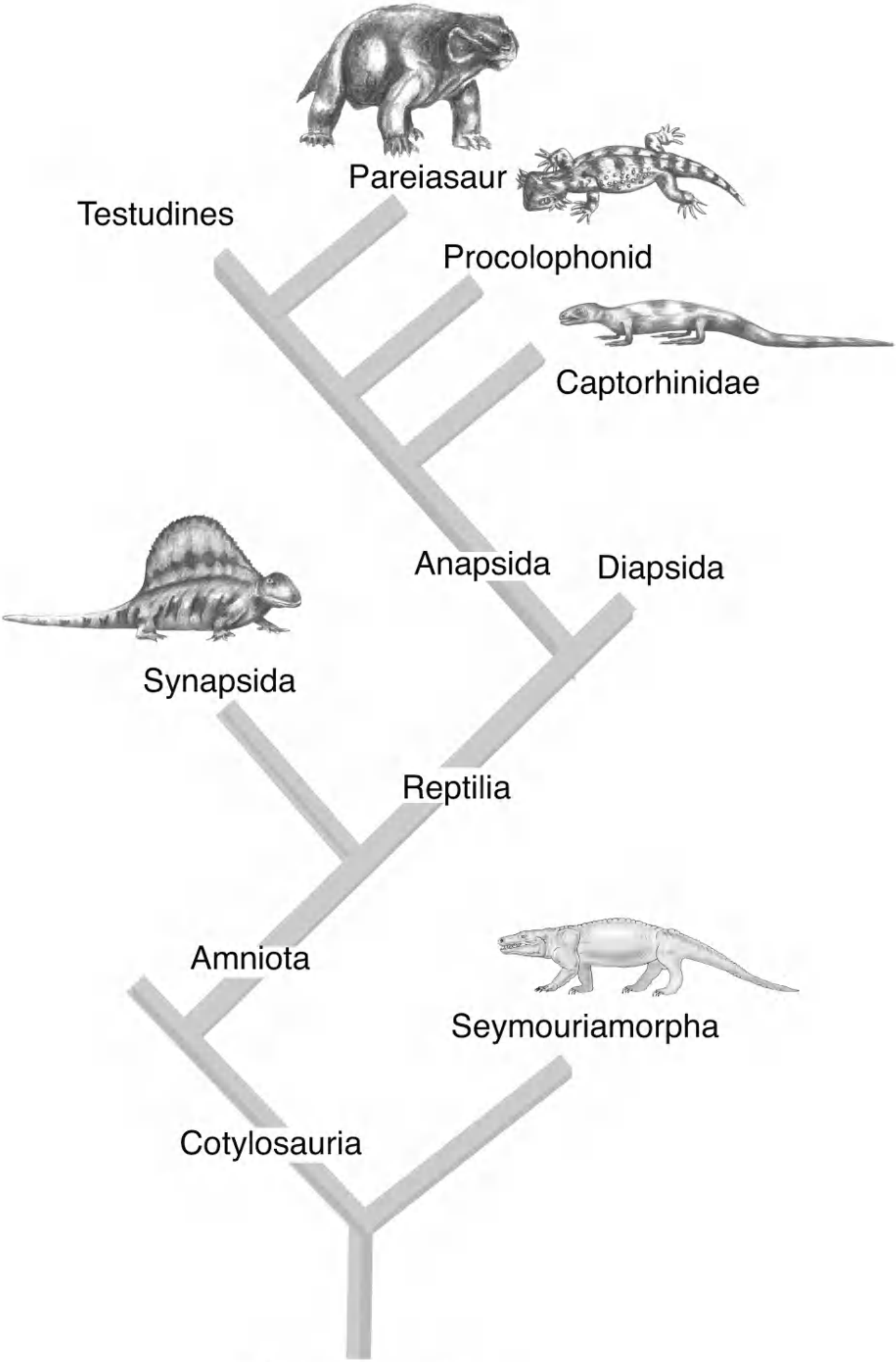
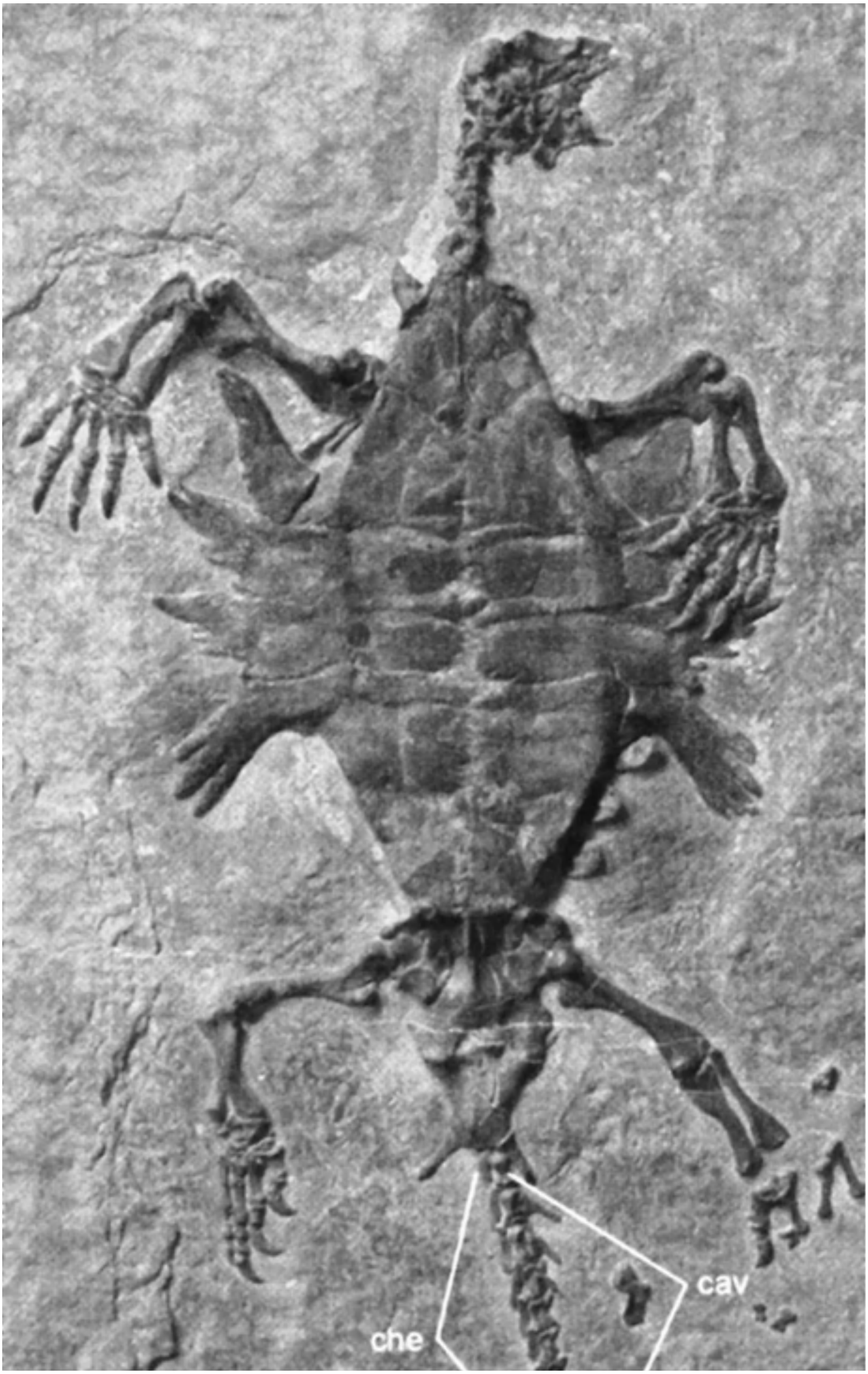

Pareiasaur
Testudines
Procolophonid
Captorhinidae
Anapsida
Diapsida
Synapsida
Reptilia
Amniota
Seymouriamorpha
Cotylosauria
Batrachosauria

Figure 6.6. Reisz and Laurin (1991) proposed the procolophonids as the closest sister group to turtles. Lee (1993), however, proposed the pareiasaurs as the nearest relatives.

The oldest known sea turtle, discovered in the 1940s in Colombia but not described until 2015, is *Desmatochelys padillai* (Cadena and Parham, 2015). Estimated to be more than 120 million years old, it superseded a record held by *Santanachelys gaffneyi* from the Early Cretaceous period of eastern Brazil (Hirayama, 1998). *Santanachelys* was primitive in the sense that the bones in its wrists, ankles, and digits had not become consolidated into rigid paddles. However, it possessed enormous salt glands around the eyes.

The fossilized remains of the largest turtle ever recorded (*Archelon*) were found along the south fork of the Cheyenne River in South Dakota (Fig. 6.8c). It was approximately 3.3 m long and 3.6 m across at the flippers.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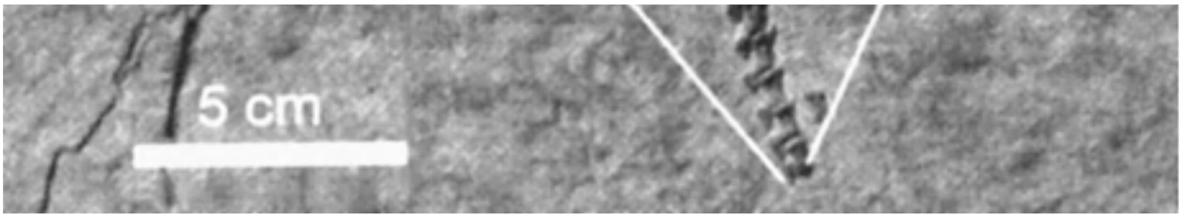


Figure 6.7. *Odontochelys semitestacea*, the oldest turtle fossil yet, has a fully formed lower shell, or plastron, but lacks a fully formed upper shell.

The oldest tortoise fossil is a 240-million-year-old fossil from Schwabisch Hall, Baden-Wurttemberg, Germany (Anonymous, 2015). Formerly, the oldest reptile with a shell was thought to be a 220-million-year-old tortoise fossil from China.

Ichthyosaurs, Plesiosaurs, Tuatara, Lizards, and Snakes (Lepidosauromorpha)

The Lepidosauromorpha include those reptiles having two pairs of temporal fenestrae (diapsid) separated by the postorbital and squamosal bones. Some species, however, have lost one or both temporal arches, so that the skull has a dorsal temporal opening but lacks a lower temporal fenestra (see Fig. 6.5). The earliest known diapsid fossil is the small, insectivorous, lizard-like *Petrolacosaurus* from the Upper Pennsylvanian of Kansas (Reisz, 1981). The lepidosaurs include two major extinct groups (ichthyosaurs and plesiosaurs) and one group (Squamata) containing three subgroups that survive today: Sphenodontia (tuataras), Lacertilia (lizards), and Serpentes (snakes).

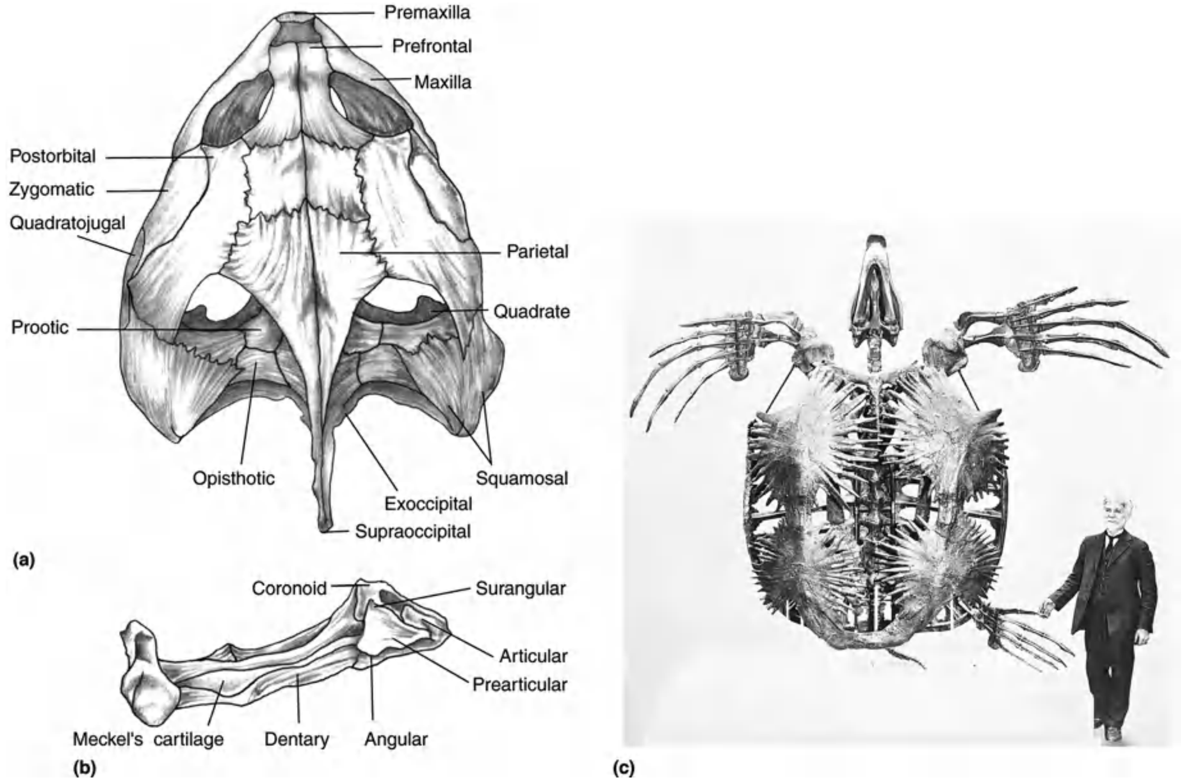


Figure 6.8. Snapping turtle (*Chelydra*) skull: (*a*) dorsal view of skull and (*b*) posteromedial view of lower jaw. (*c*) *Archelon*, the largest turtle ever found, from the Pierre shale on the south fork of the Cheyenne River approximately 56 km (35 mi.) southeast of the Black Hills of South Dakota. It was approximately 3.3 m (11 ft.) long and 3.6 m (12 ft.) across at the flippers.

ICHTHYOSAURIA

One extinct group, the Ichthyosauria (Fig. 6.9), comprised highly specialized marine lepidosauromorphs (more than 80 known species) that probably occupied the niche in nature now taken by dolphins and porpoises. Limbs were modified into paddle-like appendages, and a sharklike dorsal fin was present. Specimens of the oldest ichthyosaur, *Utatsusaurus hataii* from the Lower Triassic of Japan, show that this species retained features of terrestrial amniotes in both the skull and the postcranial skeleton, like the connection between the vertebral column and the pelvic girdle (Motani et al., 1998). Appendages were used primarily for steering, because an ichthyosaur swam by undulations of its body and tail. Other early ichthyosaurs included *Chaohusaurus* and *Grippia* from Canada, China, and Norway. These “fish lepidosauromorphs” became extinct near the end of the Cretaceous.

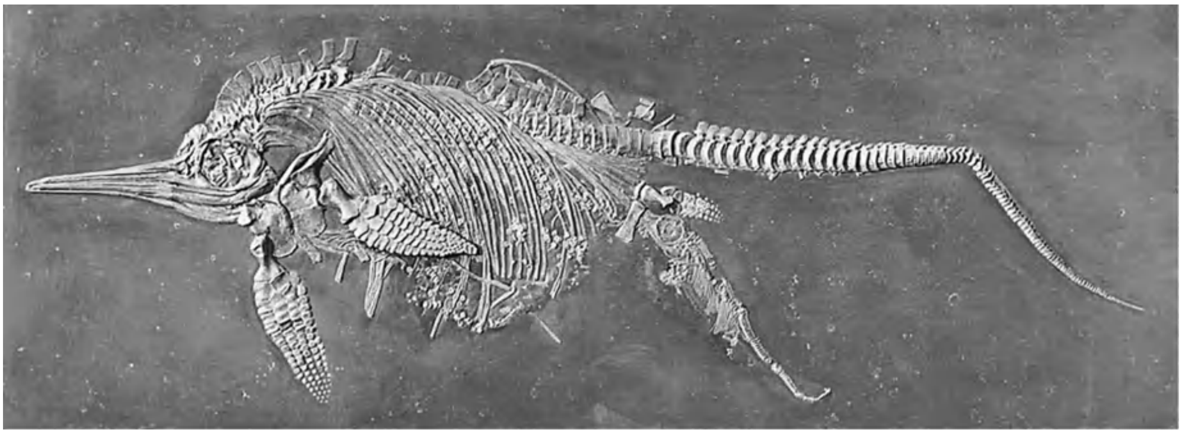


Figure 6.9. Complete fossil of an approximately 200-million-year-old female ichthyosaur that died while giving birth.

PLESIOSAURIA

Plesiosaurs (Fig. 6.10) formed a second extinct group of diapsids. The oldest plesiosaur fossil (*Rhaeticosaurus*), and the first Triassic plesiosaurian, was discovered in 2013 in a clay pit in Germany (Wintrich et al., 2017). Plesiosaurs were marine lepidosauromorphs that had broad, flattened forelimbs and hindlimbs that served as oars to row the body through the water. The trunk was dorsoventrally compressed, and the tail served as a rudder. Some had long necks and small heads, whereas others had short necks and long skulls. Nostrils were located high on the head, and the paddle-like limbs had additional phalanges. Like the Ichthyosauria, plesiosaurs became extinct near the end of the Cretaceous.

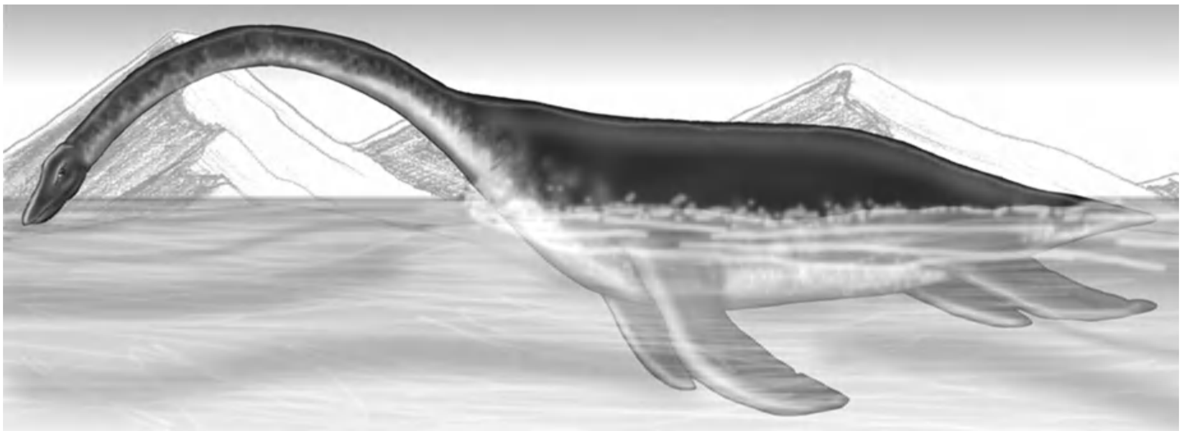


Figure 6.10. Plesiosaurs were marine diapsids that had flattened forelimbs and hindlimbs that served as “oars.” They became extinct near the end of the Cretaceous.

Figure 6.11. Tuatara (*Sphenodon punctatus*).

SPHENODONTIDAE

Tuataras (*Sphenodon* spp.) (Fig. 6.11) are relics from the Triassic that survive today on about 20 small islands in the Bay of Plenty and in Cook Strait north of Auckland, New Zealand. The two living species (*Sphenodon punctatus* and *S. guntheri*) have been called “living fossils” and are considered the most primitive of living reptiles. Fossil remains have been dated as far back as the Triassic (Carroll, 1988).

The tuatara has been found to undergo the fastest rate of molecular evolution of any vertebrate animal studied thus far (Hay et al., 2008). Researchers analyzed DNA samples taken from ancient tuatara bones and from living specimens. They found that, over the past 9,000 years, parts of the tuatara genetic code have changed 50 percent more quickly than those of any other vertebrate tested by the same method.

The tuatara’s teeth are attached to the summit of the jaws and are not replaced during the animal’s lifetime. The palate contains an additional row of teeth running parallel to the teeth on the maxilla. When the mouth is closed, teeth in the lower jaw fit between the two rows of teeth in the upper jaw. A parietal foramen for the pineal, or third eye, is present.

By day, the tuatara lives in a burrow, venturing forth after sunset to feed on snails, crickets, and even small vertebrates. Up to 14 eggs are deposited in the earth, where they remain for almost a year. Newly hatched tuataras are about 11 cm long, and it takes them several years to reach the maximum length of slightly more than 0.6 m. Tuataras have been known to survive more than 20 years. The long gestation and longevity are probably the result of the cold climate in this region of the world.

SQUAMATA

Lizards and snakes (see Figs. 1.4 and 6.2) are thought to have evolved from an eosuchian (order Eosuchia) ancestor, probably during the Triassic. Eosuchians were primitive lepidosaurs with a diapsid skull and slender limbs. Some taxonomists place a group of tropical and subtropical (mostly legless) reptiles known as amphisbaenians with the lizards; others classify them as a distinct group. Snakes, which arose from lizards during the Middle Jurassic-Lower Cretaceous (Caldwell et al., 2015), represent a group of highly modified legless lizards. These ancient snakes from about 170 Mya share features with fossil and modern snakes and with lizards. The previous oldest-known fossil snakes date from about 100-million-year-old sediments (Upper Cretaceous) and are both morphologically and phylogenetically diverse, indicating that snakes underwent a much earlier origin and adaptive radiation. Snakes are considered to be the most recently evolved group of reptiles (Romer, 1966; Carroll, 1988). Although all known snakes lack well-developed legs, the Cretaceous marine squamate *Pachyrhachis problematicus* possessed a well-developed pelvis and hindlimbs and is considered to be a primitive snake (Caldwell and Lee, 1997). The body was slender and elongated, and the head exhibited most of the derived features of modern snakes. A second limbed marine snake, *Haasiophis terrasanctus*, caused some researchers to consider a link between snakes and extinct marine lizards, like mosasaurs (Tchernoy et al., 2000). However, the two limbed snakes are advanced big-mouthed snakes, like pythons and boas, rather than primitive serpentine ancestors. The legs are too small in relation to the animal's body to have any function in moving the snake.

Vidal and Hedges (2004) collected genetic tissue samples from 19 families of lizards and 17 families of snakes—most of it shed skin. They concluded that snakes are not related to an extinct marine lizard known as the mosasaur and that, therefore, snakes likely evolved on land. Not everyone agrees.

A fossil found in Argentina revealed a two-legged creature that is one of the most primitive snakes known, adding fuel to the debate about whether snakes evolved on land or in the sea (Apesteguía and Zaher, 2006). The anatomy of *Najash rionegrina* and the location of the fossil show that the snake lived on land. It is the first time that scientists have found a snake with a sacrum, a bony feature supporting the pelvis. That feature was lost as snakes evolved from lizards. The authors stated that since this was the only known snake that had not lost the sacrum, it must be the most primitive one found to date.

Fossil evidence that snakes evolved from four-legged lizards is limited. A few snake fossils have nubby hind legs, but until now no one has found a fossil that so clearly connects snakes and lizards. A roughly 120-million-year-old fossil, four-legged snake (*Tetrapodophis amplectus*) from the Early Cretaceous Crato formation of Brazil was found in a German museum and may be the classic missing link between lizards and snakes (Martill et al., 2015). The snake has a serpentine body plan with an elongate trunk, short tail, and large ventral scales suggesting characteristic serpentine locomotion, yet retains small prehensile limbs. It lacks aquatic adaptations and instead exhibits features of fossorial snakes and lizards. It strengthens the theory that the ancestors of modern snakes may have evolved on land rather than at sea.

Fossils from northeastern Colombia have revealed the largest snake ever discovered: a behemoth that stretched 13 to 14 m (42–45 ft.) long and weighed more than 1,134 kg (2,500 lb.) (Head et al., 2009; Gugliotta, 2012). Named *Titanoboa cerrejonensis*, it would have been capable of eating something as large as a cow. While related to modern boa constrictors, it behaved more like an anaconda and spent almost all its time in the water. Among living snake species, the record holder is an individual python measured at about 9 m (30 ft.) long.

Thecodonts, Nonavian Dinosaurs, Pterosaurs, Crocodilians, and Birds (Archosauromorpha)

The diapsid archosaurs possess two fenestrae, each with an arch in the temporal region of their skull. The archosaurs include several extinct groups (thecodonts, most of the familiar dinosaurs, and the pterosaurs) and two living groups (crocodilians and birds). In discussing the evolution of dinosaurs, Sereno (1999) noted that the ascendancy of dinosaurs near the close of the Triassic appears to have been as accidental and opportunistic as their demise and replacement by therian mammals at the end of the Cretaceous.

THECODONTIA (= PROTEROSUCHIA)

One of the extinct groups of archosaurians, the Thecodontia, is considered to be ancestral to the dinosaurs, pterosaurs, and birds (Fig. 6.12). Thecodonts ranged in size from around 20 kg to as much as

80,000 kg. In many groups, limbs were positioned directly beneath the body—similar to the limb position in birds and mammals. In some groups, hindlimbs were much larger than forelimbs. Some bipedal species have left track pathways (Fig. 6.13) from which their running speed has been computed at up to 64 km per hour (Bakker, 1986). Researchers have also found the first evidence of a multispecies herd of dinosaurs moving together (Day et al., 2004).

Dinosaurs have traditionally been divided into the Saurischia and Ornithischia (see Fig. 6.14 and 6.16). Baron et al. (2017) have proposed a revision of the dinosaur family tree. The new study assesses kinship among 74 dinosaur species that span the family tree. The most notable revision grafts the theropod lizard-hipped lineage onto the branch containing all of the bird-hipped (ornithischian) dinosaurs, such as *Stegosaurus and Triceratops*. The team’s analysis indicates that members of both major groups share 21 anatomical traits, ranging from a distinctive ridge on their upper jaw to the fusion of particular bones in their feet. Needless to say, this proposal is creating much discussion among paleontologists (Brusatte, 2017).

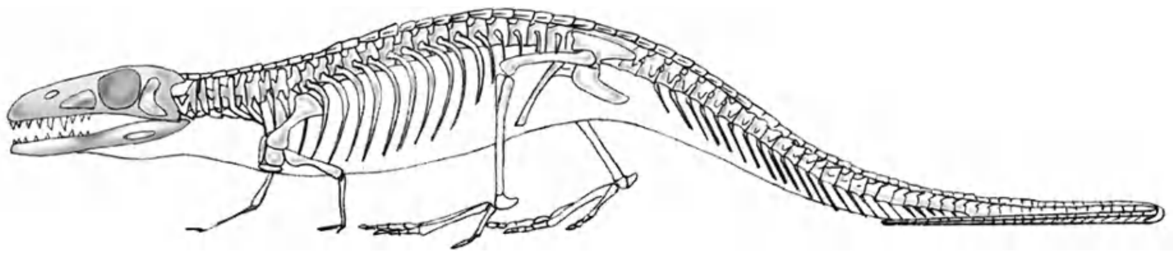


Figure 6.12. *Saltoposuchus*, a genus of primitive thecodont from Connecticut.

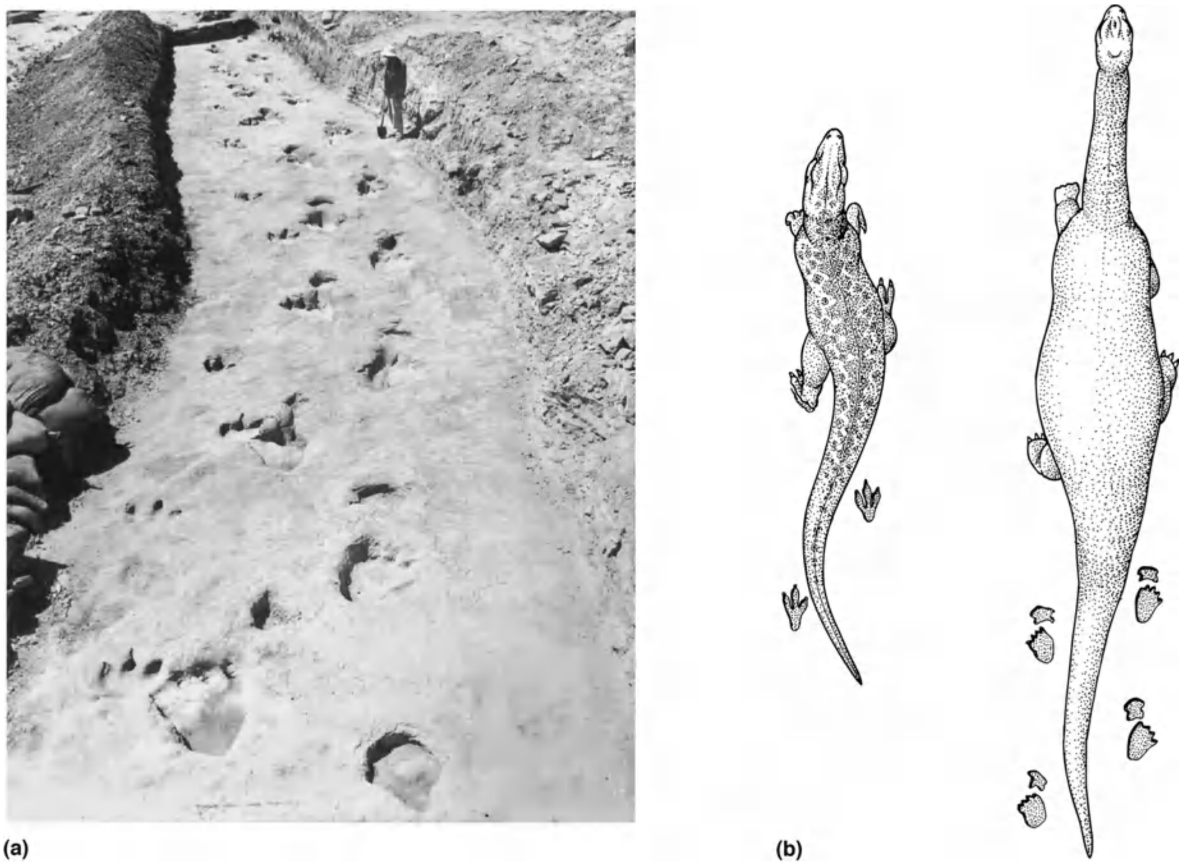


Figure 6.13. Dinosaur tracks. (*a*) Tracks from the Late Jurassic that were originally made in soft sand that later hardened to form rock. (*b*) The large tracks are those of a sauropod; the three-toed tracks are those of a smaller carnosaur, a bipedal carnivorous dinosaur.

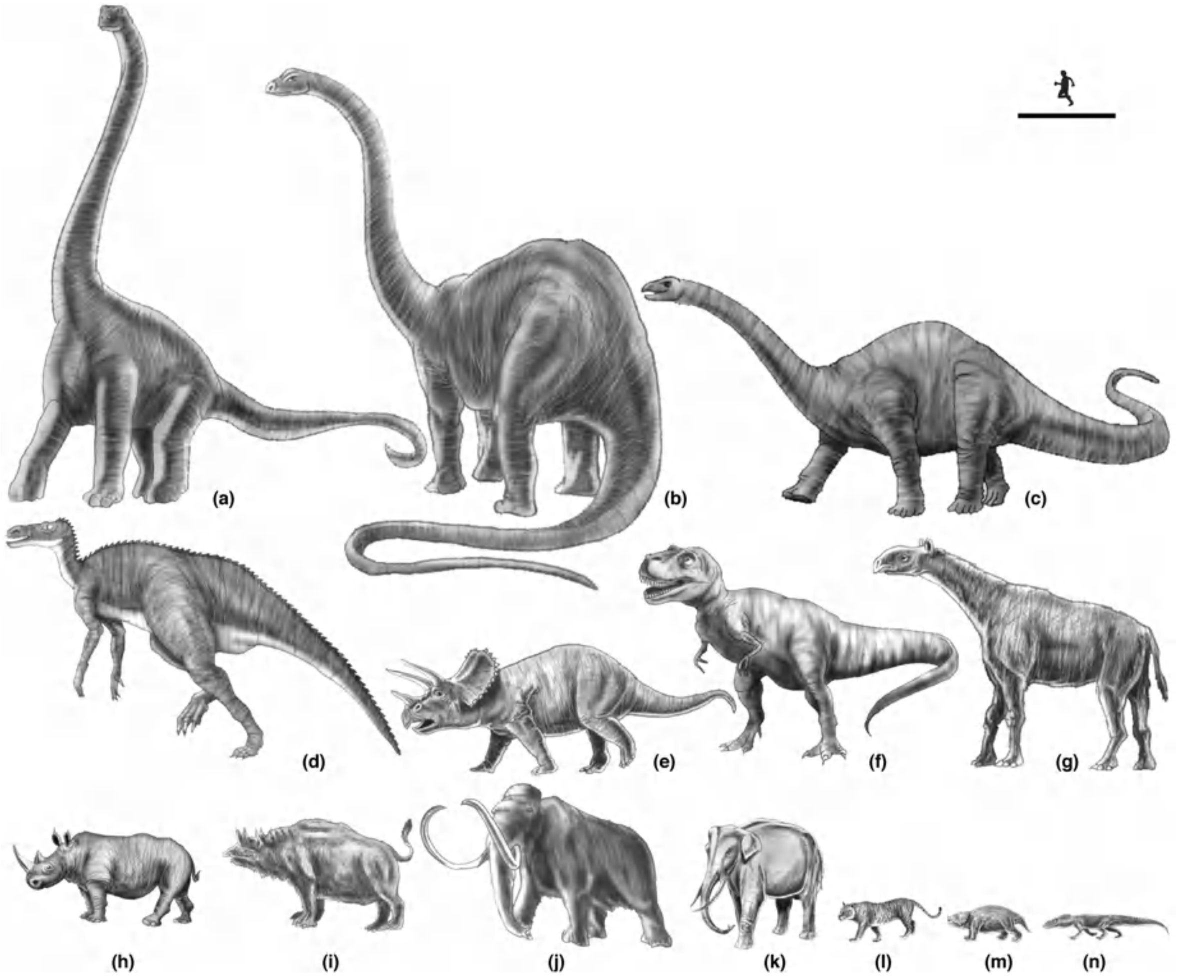


Figure 6.14. Size comparison of dinosaurs, mammals, and reptiles drawn to the same scale. Comparison of extinct taxa is based on the largest known specimens and masses from volumetric models. Comparison of extant and recent taxa is based on the sizes of large adult males. (*a*) titanosaur, 54–73 metric tons (60–80 US tons); (*b*) *Supersaurus*, 50 metric tons (55 US tons); (*c*) *Brachiosaurus* (= *Ultrasaurus*), 41 metric tons (45 US tons); (*d*) *Shantungosaurus*, 12 metric tons (13 US tons); (*e*) *Triceratops*, 5.4 metric tons (6 US tons); (*f*) *Tyrannosaurus*, 6.4 metric tons (7 US tons); (*g*) *Indricotherium*, 14.5 metric tons (16 US tons); (*h*) *Rhinoceros*, 1.8 metric tons (2 US tons); (*i*) *Megacerops*, 4.5 metric tons (5 US tons); (*j*) *Mammuthus*, 9 metric tons (10 US tons); (*k*) *Loxodonta*, 5.4 metric tons (6 US tons); (*l*) *Panthera*, 0.27 metric tons (0.3 US tons); (*m*) *Scutosaurus*, 0.9 metric tons (1 US ton); (*n*) *Megalania*, 0.9 metric tons (1 US ton). Human figure 1.62 m (5.3 ft.) tall. Scale bar = 4 m (13 ft.).

For 160 million years, dinosaurs diversified into between 500 and 1,000 known genera, though many of these are based on single (often partial) specimens. Since the mid-1990s, new dinosaur fossils are being discovered at the rate of about one each week (Brusatte, 2018). The finds since the 1960s may represent up to 50 percent of all dinosaurs currently known to have existed (Wang and Dodson, 2006). A sophisticated statistical analysis done by scientists at the University of Pennsylvania and Swarthmore College suggests that paleontologists have unearthed fewer than one-third of the various kinds of dinosaurs to be found.

Recent discoveries have unearthed genera like *Herrerasaurus* (Fig. 6.15) and *Eoraptor* in Argentina (Sereno and Novas, 1992; Sereno et al., 1993) that are two of the oldest dinosaurs ever discovered (232 million years old). However, they cannot currently be classified as belonging to either of these groups. The skulls have a unique heterodont dentition and do not exhibit any of the specializations of the Saurischia or Ornithischia. They are tentatively classed as “proto-dinosaurs.” Two prosauropod dinosaurs, primitive plant-eaters with long necks, from the Middle to Late Triassic (225–230 million years old) fauna of Madagascar (Flynn et al., 1999), may possibly represent the most primitive dinosaurs ever found.

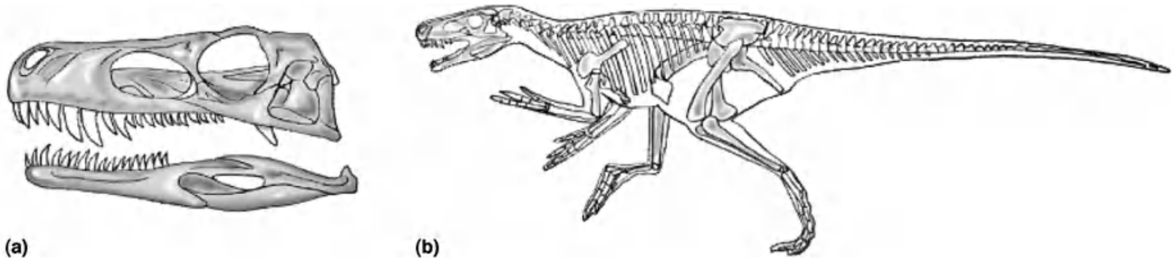


Figure 6.15. (*a*) Reconstruction of the skull of *Herrerasaurus ischigualastensis* from Argentina. (*b*) Skeletal reconstruction of *Herrerasaurus*.

What could be the oldest dinosaur ever found—or a member of the sister-taxon to Dinosauria—could push the appearance of dinosaurs back to 243 Mya (Nesbitt et al., 2012). At 2 to 3 m (6.5–10 ft.) long and no more than a meter tall, *Nyasasaurus parringtoni*, was discovered in the early 1930s in Tanzania's Ruhuhu Basin. Its weight was estimated at 20 to 60 kg (44–132 lb.). It lived during the Middle Triassic period, about 10 million to 15 million years earlier than the oldest confirmed dinosaurs. It possesses a unique combination of dinosaur character states and an elevated growth rate similar to that of definitive early dinosaurs. Additional material is needed before a determination can be made as to whether *Nyasasaurus* is definitely the oldest dinosaur ever found.

SAURISCHIA

Saurischians (Lat. *saur*, lizard, + *ischia*, hip) were one of the two main groups of dinosaurs that evolved during the Triassic from the Thecodontia. The members of these groups included both quadrupedal and bipedal herbivores and carnivores. They all possessed a triradiate ("lizard-hipped") pelvic girdle (see Fig. 6.16), with the ilium connected to the vertebral column by strong ribs. The pubis was located beneath the ilium and extended downward and forward. The ischium, also below the ilium, extended backward. The hip socket was formed at the junction of the three bones. Two types of dinosaurs—theropods and sauropodomorphs—had this type of hip structure. Norman (1991) noted that it seemed highly likely that modern birds were derived from one group of theropod dinosaurs. Even though the avian hip has a backwardly turned pubis, it is derived from the saurischian condition.

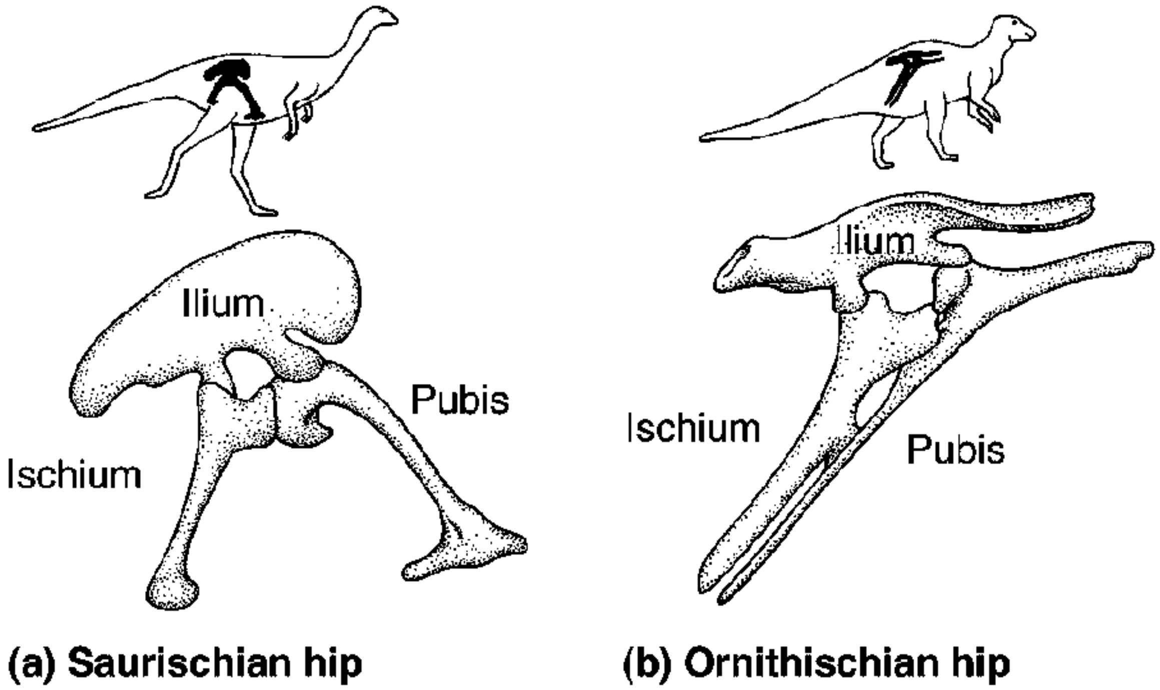


Figure 6.16. Dinosaur hips. (*a*) Saurischians possessed a pelvic girdle with three radiating bones. (*b*) Ornithischians had a hip with pubis and ischium bones lying parallel and next to each other.

THEROPODS

Theropods included birds and all of the carnivorous dinosaur genera like *Ornitholestes*, *Megalosaurus*, *Tyrannosaurus*, *Allosaurus*, *Ceratosaurus*, *Deinonychus*, *Struthiomimus*, *Utahraptor*, and *Afrovenator* (Sereno et al., 1994) (Fig. 6.17). Theropods are characterized by a sharply curved and very flexible neck; slender or lightly built arms; a rather short and compact chest; long, powerful hindlimbs ending in sharply clawed birdlike feet; a body balanced at the hip by a long, muscular tail; and a head equipped with large eyes and long jaws. Most were equipped with numerous serrated teeth (Abler, 1999), although some genera, like *Oviraptor*, *Struthiomimus*, and *Ornithomimus*, were toothless.

The Saurischia included the largest terrestrial carnivores that have ever lived, like *Giganotosaurus carolinii* from Argentina whose estimated length was between 13.7 and 14.3 m (45–47 ft.) and which may have weighed as much as 9,000 kg (19,700 lb.) (Coria and Salgado, 1995; Monastersky, 1997c), and *Tyrannosaurus*, with a length up to 16 m (52 ft.) head to tail, a height of approximately 5.8 m (19 ft.), and a weight of 6,500 to 9,000 kg (14,000–19,000 lb.) (Romer, 1966) (see Fig. 6.17). Coria and Salgado (1995) noted that these two enormous dinosaurs evolved independently—*Tyrannosaurus* in the Northern

Hemisphere, *Giganotosaurus* in the Southern Hemisphere; consequently, gigantism may have been linked to common environmental conditions of their ecosystems. In 2006, researchers reported the discovery of an even larger theropod, *Mapusaurus roseae*, from Patagonia in Argentina. An analysis of the bones showed that an adult exceeded 12 m (40 ft.) in length, slightly larger than *Giganotosaurus* and *Tyrannosaurus*. It had the longest known fibula, or shin bone, of any meat-eating dinosaur.

The largest land predator ever known, however, is *Spinosaurus aegyptiacus* which lived about 95 Mya in the massive river systems of what is now northern Africa. It weighed up to 18,000 kg (40,000 lb.), was approximately 15 m (50 ft.) long, and had narrow jaws containing at least two dozen sharp, piercing teeth. The narrow jaws were unique among predatory dinosaurs, as were its teeth—most carnivorous theropods had bladelike, serrated teeth, but these teeth were smooth and conical and resembled those of a crocodile. The nostrils are set high on the skull toward the eyes, allowing the animal to breathe with much of its head submerged. The barrel-shaped torso resembles dolphins and whales, and the density of its ribs and long bones is similar to that of the sea cow, an aquatic mammal. The short but heavily muscled hind legs, so oddly proportioned for walking, would have been perfect for paddling, particularly if the flat claws in its broad hind feet had been connected with webbing like a duck's, as the researchers suspect. It was a powerful swimmer with a propulsive tail similar to that of some fishes. The mega-predator also had a 2.1 m (7 ft.) tall sail on its back, likely used for display. It shows clear adaptations to life both on land and in the water, making it the first dinosaur known to swim. (The dinosaur-like marine reptiles called plesiosaurs and mosasaurs actually belonged to different orders.) The most recent bones were recovered from 97-year-old freshwater sediments in eastern Morocco (Ibrahim et al., 2014). Using CT scans, researchers discovered that *Spinosaurus* is the only dinosaur that evolved to lose the central cavity in its limb bones. This adaptation, which provides buoyancy control to allow an animal to submerge itself rather than float at the surface, can be seen today in aquatic animals such as the hippopotamus and penguin. The only other partially complete skeleton of *Spinosaurus* was discovered in 1912 in Egypt and was described by German paleontologist Ernst Stromer, who was astounded at its size but did not recognize it as being possibly aquatic. These bones were housed in Munich's state paleontology museum and were destroyed by bombing during World War II.

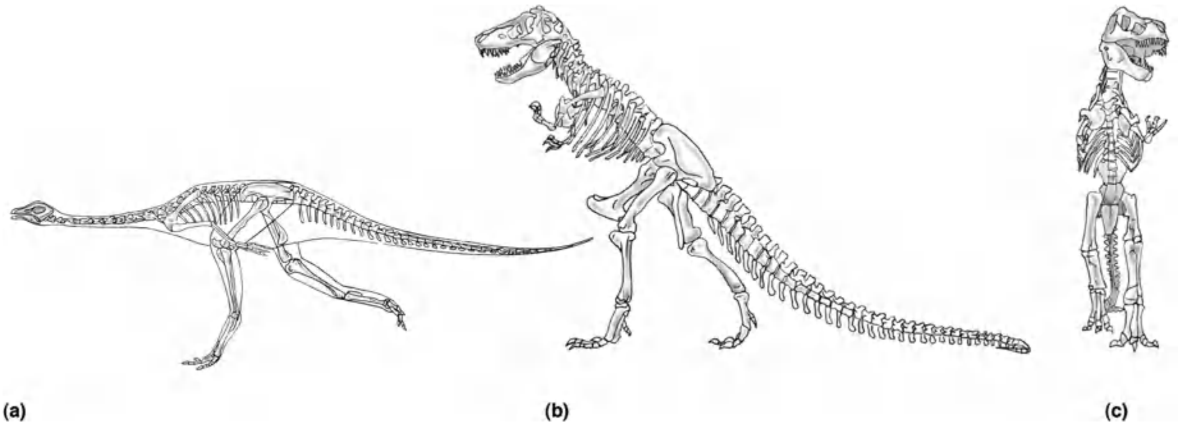


Figure 6.17. (*a*) A theropod: *Struthiomimus*. Theropods had flexible necks, slender arms, long, powerful hindlimbs, sharply curved, birdlike feet, and a body balanced at the hip by a long, muscular tail. Most had serrated teeth, but some were toothless. (*b*) Side view of *Tyrannosaurus* —members of this genus are among the largest dinosaurs that ever lived. (*c*) Front view of *Tyrannosaurus* showing orientation of pelvic girdle and hindlimbs.

Researchers have found the largest-ever dinosaur with full-fledged wings and feathers (Liu and Brusatte, 2015). The 125-million-year-old fossil, *Zhenyuanlong suni*, was found in China and was approximately 1.65 m (5.4 ft.) long. Although *Zhenyuanlong*'s wings had multiple layers of birdlike feathers, they were very short compared with those of most other winged dinosaurs, and thus it was probably unable to fly.

A 160-million-year-old dinosaur, *Yi qi*, discovered in northeastern China, had wings made of skin (similar to a bat or flying squirrel) rather than feathers (Xu et al., 2015). It weighed just under 400 grams and was closely related to the earliest birds. But, unlike any other bird or dinosaur, *Yi qi* had stiff rods projecting from each wrist that apparently supported the wings, as suggested by the remains of membranous material found between the rods. Researchers feel that it could fly, but it is unknown whether it was a glider or if was capable of powered flight.

An Extraordinary Fossil

The first theropod dinosaur ever to be found in Italy was a 24 cm (9.4 in.) theropod identified as *Scipionyx samniticus*. It represents a young dinosaur just hatched from its egg before it died. Fossilization normally preserves only hard body parts, like bones and teeth. However, this specimen is so well preserved that it displays the intestine, muscle fibers, and the cartilage that once housed its windpipe—details of soft anatomy never seen previously in any dinosaur. The exceptional quality of the preservation of the soft parts makes this one of the most important fossil vertebrates ever discovered.

Dal Sasso and Signore, 1998

Until recently, the fossil record of tyrannosaurids was restricted to the northern continents. Benson et al. (2010), however, reported an

Australian tyrannosauroid from the Early Cretaceous of Victoria, demonstrating that these extraordinarily successful predators were not restricted to Laurasia. Even though the remains are from an animal much smaller than *T. rex*, it shows that tyrannosauroids with the characteristic short arms and robust skulls probably had a global distribution in the Early Cretaceous.

Another huge dinosaur, *Carcharodontosaurus* (shark-toothed reptile), was discovered by Sereno in Morocco (Sinha, 1996). Its head was 1.6 m (5.2 ft.) long, just slightly larger than that of *T. rex*. The Moroccan bones represent the first major dinosaur fossils to be unearthed in Africa and are being used by paleogeographers and biogeographers in their quest to understand exactly when the continents split apart during the Jurassic (see Chapter 10).

Butler et al. (2010) identified the fossilized remains of the smallest dinosaur yet discovered in North America. *Fruitadens haagarorum* weighed less than 0.9 kg (2 lb.) and was about 71 cm (28 in.) long. It probably ate meat and plants. The smallest carnivorous dinosaur yet discovered in North America is the chicken-sized *Hesperonychus elizabethae* (Longrich and Currie, 2009). Weighing in at 1.8 to 2.25 kg (4–5 lb.), this small raptor lived 75 Mya in the swamps and forests of southern Alberta. It had an enlarged sickle-shaped claw on its second toe.

Some interesting revelations concerning dinosaurs have been discovered by using sophisticated equipment. For example, CT scanning utilizes an X-ray source moving in an arc around the body. X-rays are converted to electronic signals to produce a cross-sectional picture, called a CT scan. Formerly known as computerized axial tomography (CAT) scanning, this technique shows that both *Tyrannosaurus* and the smaller *Nanotyrannus* shared a trait still found in such diverse modern animals as crocodiles, elephants, and birds: a sophisticated system of air canals ramifying through their skulls. These large air pockets and tubes allowed dinosaurs to move air between their lungs and brain, presumably to help regulate the temperature of the brain. Such a need for temperature regulation has been cited as evidence by some researchers that these animals may have been homeothermic.

However, Hillenius (1994) used the absence of scroll-like turbinate bones in the nose as evidence that at least some of the dinosaurs were poikilothermic. CT scans of several theropod dinosaurs showed no evidence of respiratory turbinates in these active predators. Turbinate bones slow down the passage of incoming air so that it can be warmed and moistened. When the animal exhales, the turbinates recapture heat and moisture before it leaves the body. More than 99 percent of living mammals and birds have turbinate bones, but they are completely absent in living sauropsids. By using turbinate bones, Hillenius was able to trace endothermy back about 250 million years in the mammal lineage and 70 million years in birds. Although the absence of respiratory turbinates does not negate the possibility of other thermoregulatory strategies, these bones may represent an important anatomical clue to endothermy (Fischman, 1995a).

Figure 6.18. Transverse section of a *Tyrannosaurus rex* fibula revealing deposits of fast-growing bone rich in blood vessels and interrupted by rings that indicate regular pauses in growth.

Reptilian bones, and the bones of some Mesozoic birds (Chinsamy et al., 1994), generally grow in spurts, thus producing annual growth rings. In contrast, avian and mammalian bones form rapidly and produce fibrolamellar bone tissue in which the collagen (protein) fibers are haphazardly arranged and form a fibrous, or woven, bony matrix and no annual rings. Chinsamy (1995) conducted histological studies on the bones of a prosauropod and a theropod dinosaur. He found distinct reptilian-like growth rings, but also a type of fibrolamellar bone (Fig. 6.18). Thus, the bones showed both reptilian and mammalian characteristics. Studies of growth rings also indicate that some dinosaurs continued growing throughout their lives, whereas others stopped growing when they reached maturity, as is the case with mammals and birds. Erickson et al. (2001, 2004) found that *T. rex* and several smaller ancestors all stopped growing when they reached adult size, and that *T. rex* is the biggest because it grew the most during its teenage years. The growth curve for *T. rexes* was steepest between ages 14 and 18, when they added up to 4.6 pounds daily. *T. rexes* probably did not live more than about 30 years.

Chemical analyses of the bones of a 70-million-year-old *T. rex* by a research team from North Carolina State University revealed bone growth by an animal with a very narrow range of internal temperatures (Barrick and Showers, 1994). The researchers measured the ratio of two naturally occurring isotopes of oxygen that are part of the phosphate compounds normally found in bone. This ratio in bone varies with the temperature at which the bone formed. Bone from deep inside a homeothermic animal will have formed at nearly the same temperature as bone near its surface—the result of a metabolic process that keeps the entire body in a temperature range within which muscles can work at peak activity. Barrick and Showers interpreted their evidence as indicating that *T. rex*'s bones all formed at nearly the same temperature. The core body temperature and the temperature in the extremities varied by only 4°C (7°F) or less. Such a homeothermic animal could have been active at night when the temperature was cool and could have been active at high altitudes. Hence, they suggested that it was homeothermic. However, critics point out that, in the 70 million years that the bones lay in the ground, their oxygen isotope ratios could have been altered by groundwater and other substances, that bone tissue must be tested individually and not in groups, and that the animal's bulk alone could have meant that it retained more body heat than any of today's reptiles, all of which are smaller (Millard, 1995).

A Deadly Dinosaur

Utahraptor roamed the Colorado Plateau approximately 130 Mya. It stood approximately 2.5 m (8 ft.) tall, reached a length of about 6 m (20 ft.), and weighed about 900 kg (2,000 lb.). It has been nicknamed "super slasher"—the deadliest land creature the Earth has ever seen. *Utahraptor* was a swift runner, and it was armed with a 38 mm (1.5 in.) slashing claw that stood upright and apart from the other claws on each hind foot. The animal's forelegs were tipped with powerful claws suitable for grasping prey, while the dinosaur kicked its victim with its sickle-clawed hind feet. *Utahraptor* was described by its finders as a "Ginsu-knife-pawed kick-boxer" that could disembowel a much larger dinosaur with a single kick.

Kirkland et al., 1993

The growth rate of *Apatosaurus*, a sauropod that reached its full growth in 8 to 11 years, implies that sauropods deposited about 10.1 μm (micrometers) of bone tissue per day—about the same rate as living ducks, which deposit an average of 10.0 μm of bone per day (Stokstad, 1998). Ducks, however, reach their adult size in about 22 weeks, whereas dinosaurs maintained this growth rate for many years.

Ruben et al. (1997, 1999) examined the fossilized soft tissue of the Chinese theropod *Sinosauropteryx* and the Italian theropod *Scipionyx samniticus*. By using ultraviolet (UV) light, the researchers were able to distinguish the outlines of the intestines, liver, trachea, and muscles; they discovered that these two theropods had the same kind of compartmentalization of lungs, liver, and intestines as a crocodile—not a bird.

Theropods had two major cavities: the thoracic cavity containing the lungs and heart, and the abdominal cavity containing the liver, intestines, and other organs. These were completely separated from each other by a hepatic-piston diaphragm, as is the case in crocodiles. Most reptiles maintain a low resting metabolic rate and breathe by expanding their rib cages; they lack the power of a hepatic-piston diaphragm. Mammals and birds use both rib-based and diaphragm-driven respiration. The diaphragm system provides extra oxygen for sustained, intense activity.

The liver in *Scipionyx* extended from the top to the bottom of the abdominal cavity. A muscle located next to the pubic bone appeared similar to those in some modern reptiles that run from the pubis to the liver. It helps move the liver back and forth like a piston, causing the lungs to expand and contract. In *Scipionyx*, the diaphragm formed an airtight layer separating the liver and lungs.

Ruben et al. (1999) concluded that, although these theropods were basically poikilothermic, diaphragm-assisted lung ventilation was present, and their lungs might have been able to power periods of high metabolism and intense activity. This dual-metabolism hypothesis, which remains controversial, would have allowed highly active theropods to have had an economical resting metabolism with a capacity for bursts of activity.

Mass spectrometry studies of *T. rex* have revealed protein sequences that indicate their peptide bonds were remarkably stable (Asara et al., 2007b). Analyses of fibrous cortical and medullary tissues remaining after demineralization indicate that collagen 1, the main organic component of bone, has been preserved in low concentrations in these tissues (Schweitzer et al., 2007). The presence of protein in dinosaur bone may yield information about evolutionary relationships, as well as rates and patterns of molecular change and degradation.

A newly discovered dinosaur in Utah, called *Falcarius utahensis*, may show the transition from meat-eating to feathered, plant-eating dinosaurs (Kirkland et al., 2005). *Falcarius* appeared about 125 Mya and stood about 1.4 m (4.5 ft.) tall. It had the 10 cm (4 in.) long claws of a meat eater but tiny plant-eating teeth—a carnivore well on its way to becoming a vegetarian. Researchers do not know whether it was an omnivore, eating plants and meat, or whether it ate just plants.

Coprolites

Paleontologists have previously found numerous coprolites (fossil feces) from herbivorous dinosaurs. Assigning coprolites to theropods has been difficult because sites with dinosaur fossils often also contain skeletons of other carnivorous animals that could have produced bone-filled feces.

The first example of fossilized feces that clearly came from a carnivorous dinosaur was found in Saskatchewan, Canada. The whitish-green rock is so massive—44 cm (17 in.) long—that it must have come from a large theropod. The only large theropod known from these Saskatchewan deposits is *Tyrannosaurus rex*. The coprolite contains fragments of bone from a juvenile ornithischian dinosaur. It indicates that *T. rex*'s teeth were strong enough to crunch through bone, a topic of much debate in the past. The bone fragments indicate that tyrannosaurs repeatedly crushed mouthfuls of food before swallowing, unlike living reptiles that often swallow large pieces of prey.

Chin et al., 1998

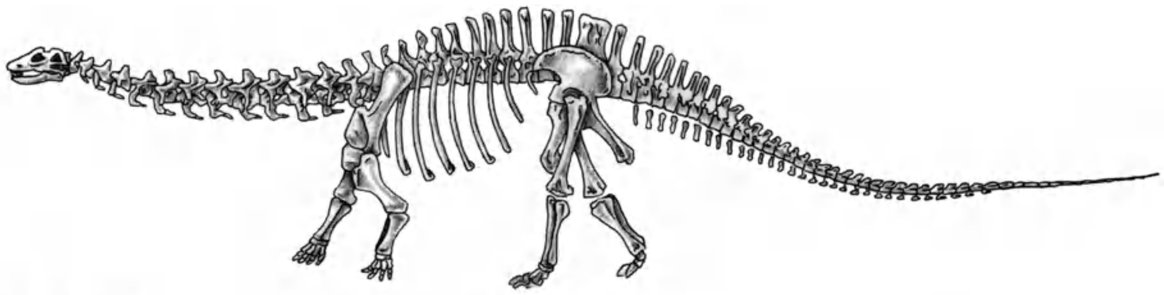
Fossils of a new theropod species, *Limusaurus inextricabilis*, reveal that some theropods had birdlike hand-bone arrangements (Xu et al., 2009). *L. inextricabilis* lived in China about 159 Mya and was probably a vegetarian. Unlike most theropods, which are vegetarians, this species had a beak and stomach stones—rocks swallowed to grind vegetation and aid digestion.

A fossil from the Liaoning, China, site, named *Microraptor*, is by far the smallest dinosaur yet discovered—about the size of a crow (Xu et al., 2000). *Microraptor* is surrounded by carbonized impressions that resemble the contour feathers covering the bodies of modern birds. Close to its thigh, the impressions appear to stick out from a central shaft, called a rhachis, which is a defining feature of true feathers. The claws are highly curved, and the feet resemble those of *Archaeopteryx*.

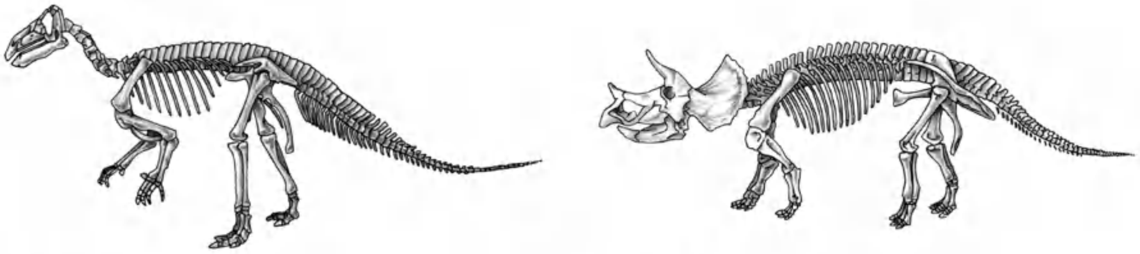
Birds were not the first to lay colored eggs. Using spectroscopic analysis of fossils to identify pigments in eggs of 15 species of dinosaurs and prehistoric birds, researchers found a wide range of hues and speckle patterns (Wiemann et al. 2018). As with modern birds, the dinosaurs' tinted shells likely camouflaged their eggs from predators, while distinctive speckling patterns may have helped parents distinguish their own eggs from those of dinosaurian nest parasites. The authors note that eggshell coloration likely had a single evolutionary origin in the theropods that gave rise to modern birds.

SAUROPODOMORPHS

Titanosauria was the most diverse and successful lineage of sauropod dinosaurs. Among sauropods, this lineage has the most disparate values of body mass, including the smallest and largest sauropods known. All **sauropodomorphs** were herbivorous (Fig. 6.19a) and included the largest quadrupeds that have ever existed—*Diplodocus*, *Apatosaurus* (*Brontosaurus*), *Brachiosaurus*, *Seismosaurus*, *Ultrasaurus*, *Argentinosaurus*, *Paralititan*, *Turiasaurus*, and *Dreadnoughtus*—with some forms reaching lengths of nearly 40 m (131 ft.) and estimated weights as great as 80,000 kg (175,000 lb.) (Colbert, 1962; Carroll, 1988; Norman, 1991; Appenzeller, 1994; Royo-Torres et al., 2006; Lacovara et al., 2014). The tallest of all dinosaurs, *Sauroposeidon*, was more than 18 m (59 ft.) tall and 30 m (98 ft.) long, and it weighed approximately 54,000 kg (118,000 lb.) (Wedel et al., 2000). The longest and heaviest animal to ever walk the Earth—*Patagotitan mayorum*—was discovered by a Patagonian shepherd in 2013 but was not described until 2017 (Carballido et al., 2017). It reached a length of 37 m (122 ft.) and an estimated weight of 63,000 kg (139,000 lb.). Limb bones of sauropods were thick, solid, and nearly vertical, and little bending occurred at the elbow and knee joints. Some, like *Supersaurus*, may even have had hollow bones (Monastersky, 1989a). This adaptation would reduce weight, yet the hollow bone might be stronger than solid bone. Paleontologists and computer scientists have recently joined forces in a new field of research called cyberpaleontology that uses computer-generated images to better understand the biomechanical movements of sauropods (Zimmer, 1997). By the end of the Cretaceous, all theropods and sauropods had become extinct.



(a) *Apatosaurus*



(b) *Iguanodon*

(c) *Triceratops*

Figure 6.19. (*a*) One of the largest sauropods: *Apatosaurus* (formerly known as *Brontosaurus*). All sauropods were herbivorous. (*b*) *Iguanodon*, a genus of ornithopod. Ornithopods were mostly small- to medium-sized reptiles that walked on their hind legs most of the time. Some may have lived in large herds. (*c*) *Triceratops*, a genus of ceratopsian. The frill may have served as an anchor site for powerful lower jaw muscles. It may also have played a role in agonistic and sexual behavior.

ORNITHISCHIA

Dinosaurs in the order Ornithischia (Lat. *ornithos*, bird, + *ischia*, hip) tended to have thin, pencil-shaped teeth, long, slender bodies, and whiplike tails. Ornithischians had a birdlike pelvis in which the pubis, instead of extending downward and forward, extended posteriorly alongside the ischium (see Fig. 6.16b). The pubis of some forms also developed an anterior projection. This arrangement is similar (convergent) to that of living birds, although no evidence exists that birds evolved from this group.

Ornithischians were either bipedal or quadrupedal herbivores. The lower jaw of all forms consisted of a small, horn-covered beak. Unusual features found in specific groups also included ducklike bills (hadrosaurs), overlapping plates of bony armor (ankylosaurs), rows of protective plates and spines down their backs and tails (stegosaurs), and parrot-like beaks along with bony frills (neck shields) and horns on their heads (ceratopsians). Although some ornithischians were larger than elephants, *Stegosaurus*, for example, was 6.5 m (21 ft.) in length and weighed at least 9,000 kg (19,700 lb.) (Feduccia and McCrady, 1991), they had relatively small brains for their size. By the end of the

Cretaceous period, all ornithischians, like saurischians, had become extinct.

Barreto et al. (1993) have shown that the cells within the growth plates (disks of cartilage near the ends of the bones) of *Maiasaurus*, an ornithischian, bear a striking resemblance to the cells of chicken growth plates and look very different from the growth plates of living reptiles and mammals. The plate zone boundary is very irregular, the cells (chondrocytes) are shorter and ovoid in shape, and all cell membranes are calcified. The researchers concluded that the similarity of the growth plates points to a common ancestor for dinosaurs and birds because it is too complex a morphological character to have evolved twice. In addition, this synapomorphy (shared derived anatomical character) supports the inclusion of birds along with reptiles in a group known as Dinosauria. The Dinosauria was first proposed in 1841 by Richard Owen, the first head of the British Museum of Natural History. Although it fell out of favor in the late nineteenth century, it was resurrected in the 1970s by Bakker and Galton, who argued that it should include not only the ornithischians and saurischians, but birds as well. However, not all paleontologists agree (Fischman, 1993b).

Five groups of ornithischians—ornithopods, ceratopsians, pachycephalosaurs, stegosaurs, and ankylosaurs—have been defined. Ornithopods were mostly small- to medium-sized genera like *Camptosaurus* and *Iguanodon* (see Fig. 6.19b), although hadrosaurs, or duck-billed dinosaurs, reached lengths of 13 m (42 ft.). Ornithopods walked on their hind legs most of the time. A duck-billed hadrosaur fossil from North Dakota was so well preserved that scientists were able to calculate its muscle mass and learn that it was more muscular than thought (Schmid, 2007). It also came complete with skin, ligaments, tendons, and possibly some internal organs. The fossil was found in 1999 and has been analyzed in the world's largest CT scanner, operated by the Boeing Company.

Dinosaurs in Antarctica

Early Jurassic tetrapods have been collected near the Beardmore Glacier in the Transantarctic Mountains in Antarctica, approximately 650 km (404 mi.) from the geographic South Pole. These fossils, which are similar to Early Jurassic fossils from other continents, indicate that no geographic or climatic barriers prevented dinosaurs from populating high southern latitudes during the Jurassic—a time when Antarctica sat 965 km (600 mi.) to the north of its current position and was able to support temperate forests. Fossils have included a large crested theropod (*Cryolophosaurus ellioti*), a sauropodomorph (*Glacialisaurus hammeri*), an ankylosaur (*Antarctopelta oliveroi*), an ornithopod (*Trinisaura santamartaensis*), a pterosaur, and a large tritylodont (synapsid). A 2016 expedition sponsored by the National Science Foundation and the US Antarctic Program included scientists from the United States, Australia, and South Africa. The expedition unearthed more than a ton of fossils on James Ross Island—most of which are between 71 million and 67 million years old—including remains of dinosaurs, plesiosaurs, mosasaurs, and birds.

Antarctica's location and climate have not always been as they are today. The changing positions of the continents (continental drift) and the resulting effects on vertebrate distribution are discussed in Chapter 10.

Hammer and Hickerson, 1994; National Science Foundation, 2004; Liberatore, 2016

Some ornithischians, especially the hadrosaurs, may have lived in large herds. In Massachusetts, John Ostrom found tracks of significant numbers of individuals moving in the same direction at the same time (Ostrom, 1972; Norman, 1991). A track site in Oxfordshire, United Kingdom, is extensive, containing more than 40 more-or-less continuous theropod and sauropod trackways preserved together on a single bedding plane with some trackways up to 180 m (590 ft.) in length (Day et al., 2004). These findings provide evidence for herding and possible migratory movements as socially integrated groups.

Ceratopsians were distinctive because of their parrot-like beaks and their horns and frills. The frills are thought to have served as anchor sites for powerful muscles that attached to the lower jaw and also were of great significance in agonistic (aggressive) and sexual behavior (Farlow, 1975). Because the frills contained networks of blood vessels, they may also have served to help regulate body temperature by cooling the blood before it returned to the interior of the body (Monastersky, 1989b). Ceratopsians included genera like *Protoceratops*, *Triceratops* (see Fig. 6.19c), and *Centrosaurus*. They also are thought to have lived in large herds.

Pachycephalosaurs are poorly known (Fig. 6.20a). They had "curiously domed and massively reinforced heads," with the bulge of the head being filled with solid bone. The head is thought to have been used as a battering device (Norman, 1991).

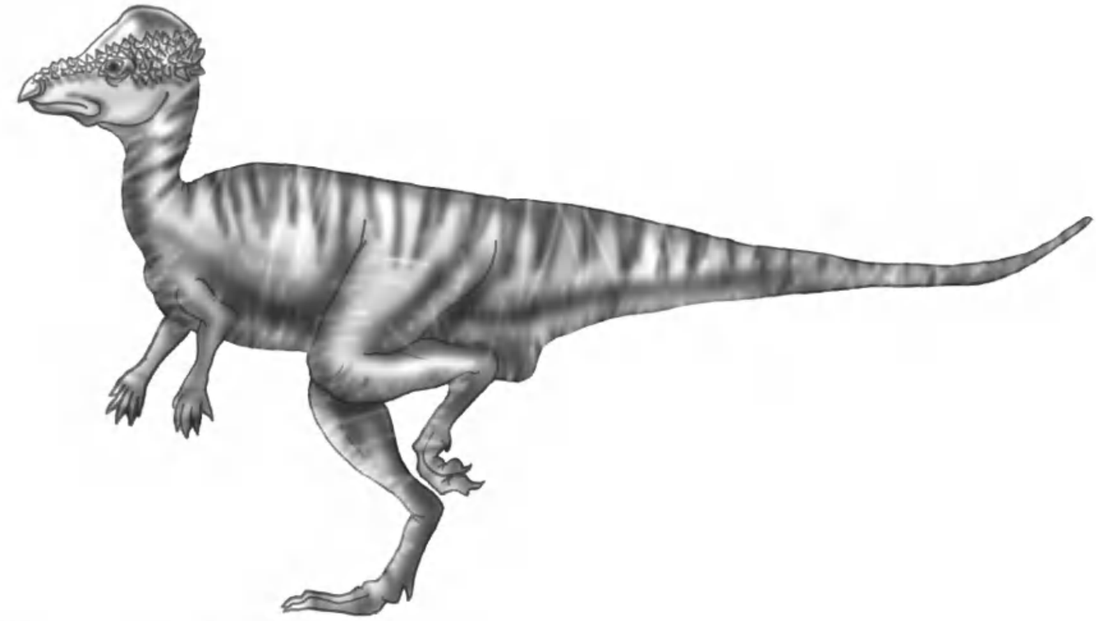
Stegosaurs were the plated dinosaurs (see Fig. 6.20b). The large plates and spines of such animals as *Stegosaurus* may have acted as panels to gain heat from the absorption of solar radiation and to lose heat by convection to wind currents, thereby regulating body temperature. They were light, honeycombed structures that seemed to be designed to allow large quantities of blood to pour through the plates and out onto the surface of the plates beneath the skin. These structures figure prominently in the debate over whether some dinosaurs were homeothermic or poikilothermic.

One *Stegosaurus* skeleton was so well preserved that researchers were able to confirm that dorsal plates were arranged in an alternating pattern rather than in matched pairs and that the animal had even more body armor than had been previously thought, including a disc-shaped plate near its hip and a web of ossicles—small, coin-sized bony plates—in its throat region. The size of the dorsal plates may indicate gender.

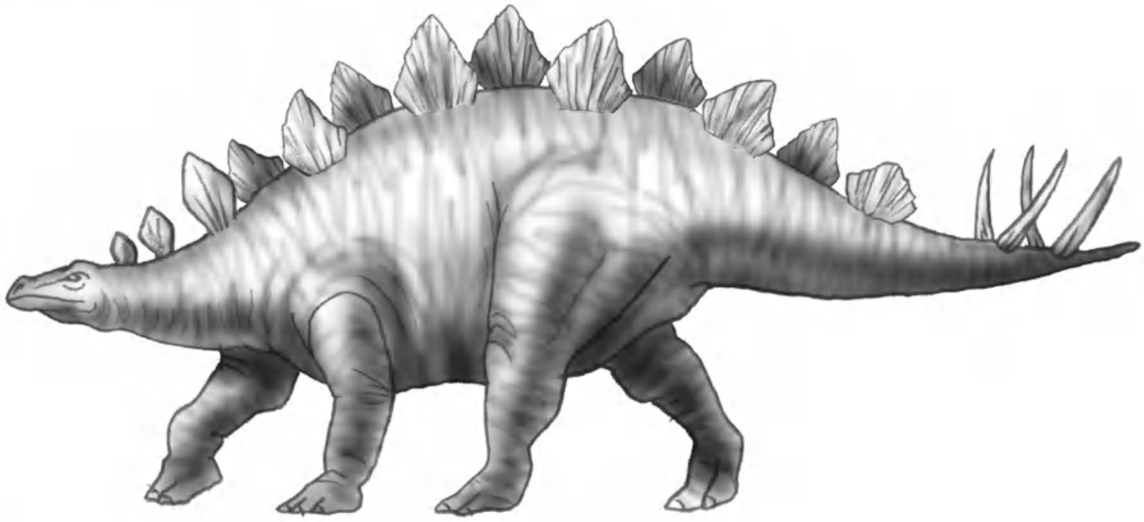
Investigations of dinosaur spinal canals show how dinosaurs may have stood and moved (Giffin, 1990, 1991). The varying thickness of the spinal cord (spinal quotient) is reflected in the varying width of the spinal canal, and the presence and relative size of neural bundles along the spinal cord provide information concerning the posture of a given species. Some dinosaurs carried themselves with their legs straight up and down—in a so-called improved posture—whereas others moved in a more lizard-like sprawl. The ratio of neural development between the limb and the torso region can show how an animal held its body. For example, stegosaurs possessed a smaller than expected spinal cord serving the front legs, an indication that the animal had a somewhat bowlegged, rather than an upright, posture.

The fifth group of ornithischians, the ankylosaurs, were heavily armored to provide protection from the larger carnivorous dinosaurs (see Fig. 6.20c). Some also had large, rounded clubs at the ends of their tails.

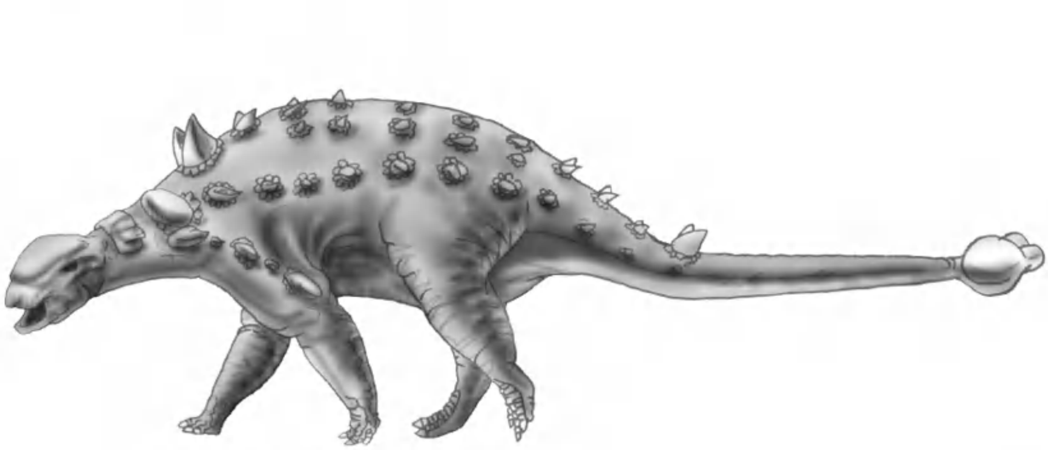
Bakker (1986) believed that all plant-eating dinosaurs constituted a single natural group—Phytosauria (“plant dinosaurs”)—which branched out from a single ancestor. In addition, Bakker believed that dinosaurs developed in a similar fashion to mammals—growing quickly and breeding early. The legs and muscles of many species were built for speed (with deep shoulder and hip sockets; the crests of the knee joints were massively developed to support the extensive muscles of the knee), so that they needed powerful hearts and lungs of high capacity. They had a mammal-like bone texture. The presence of densely packed Haversian systems in bone is only found in dinosaurs and mammals. On the basis of these characters, Bakker (1986) concluded that dinosaurs must have been homeothermic. As might be expected, considerable discussion and controversy have been generated by Bakker’s hypothesis. Studies of oxygen isotopes and infrared spectroscopy have been employed in an attempt to provide additional evidence concerning the possibility of endothermy in the dinosaurs.



(a) *Stegoceras*



(b) *Stegosaurus*



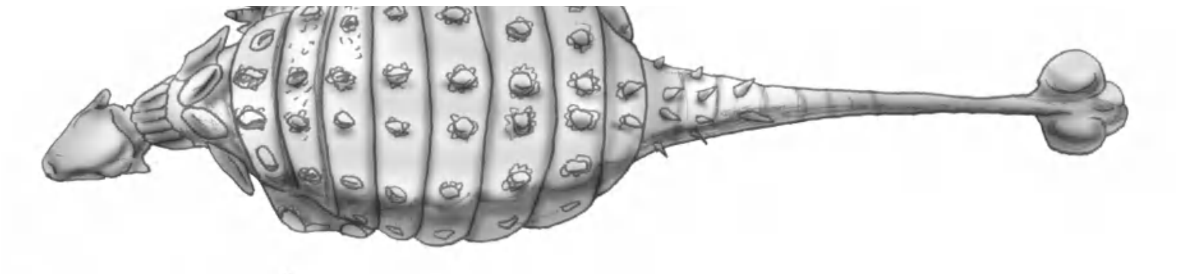


Figure 6.20. (*a*) *Stegoceras*, a pachycephalosaurid genus. These dinosaurs looked somewhat similar to the ornithopods except for their domed heads. (*b*) *Stegosaurus*. The large plates may have acted as solar panels to help control body temperature by collecting solar radiation for heat and also acting as radiators for cooling. (*c*) An *Ankylosaurus*: *top*, lateral view; *bottom*, dorsal view. The heavy armor provided protection from larger carnivorous dinosaurs.

PTEROSAURIA

Another extinct order of archosaurians—Pterosauria—included the first flying vertebrates (Fig. 6.21). They appeared about 230 Mya—around the same time as the earliest dinosaurs and more than 75 million years before *Archaeopteryx*. Many of the bones of pterosaurs were hollow and air-filled; their skull bones were thin and fused; their jaws were elongated and contained teeth; a large sternum was present; and their anterior appendages were modified into wings. The delicate, thin-walled bones that minimized a pterosaur's weight and enabled efficient flight did not usually leave intact fossils. It is now generally accepted that pterosaurs (pterodactyls) were fliers, but whether they had broad, batlike wings connected to both forelimbs and hindlimbs or narrow, stiff wings free of the legs has long been a subject of debate (Peters, 1995). The wings were membranous and had no feathers.

The discovery of well-preserved wing membranes on a long-tailed pterosaur (*Sordes pilosus*) from Kazakhstan shows that the hindlimbs were intimately involved in the flight apparatus (Unwin and Bakhurina, 1994) (Fig. 6.22a, b). The hindlimbs connected externally to the wing membrane and internally were connected by a uropatagium controlled by the fifth toe. Furthermore, the flight surface was nonhomogeneous with a stiffened outer half and a softer, more extensible inner portion. While some species had a wingspan approaching 10 m (33 ft.), *Nemicolopterus crypticus* was about the size of a sparrow and probably had a wingspan of just 25 cm (10 in.), making it the smallest known pterosaur (Wang et al., 2008).

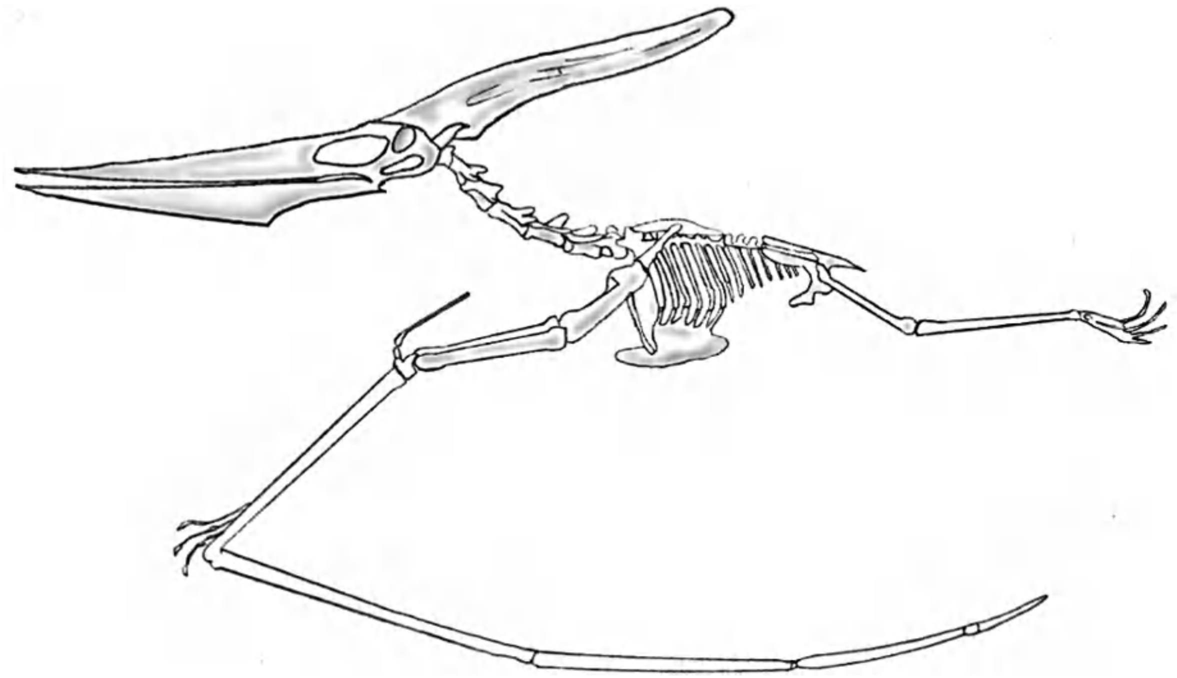


Figure 6.21. *Pteranodon*, a giant pterosaur from the Upper Cretaceous of Kansas. The wingspread was up to 6.7 m (22 ft.). The head, which was 3⅔ times the length of the body, was exceedingly light and strong.

The earliest known flying vertebrate, *Coelurosauravus jaekeli*, glided on a unique set of wings unlike any other known in living or extinct animals (Frey et al., 1997) (Fig. 6.23). The long, hollow bones that strengthened its wings formed directly in the skin itself, unlike the wing bones of birds and bats, which are converted front limbs.

The hip socket of pterosaurs was unlike that of birds in that it was shallow and had no central hole for a ligament (Boxer, 1987; Unwin, 1987). The femur extended outward and slightly upward from the pelvis, so that the animal presumably had a sprawling gait. The entire foot, rather than just the toes, contacted the ground during terrestrial locomotion (Clark et al., 1998).

Bakker (1986) presented evidence that if pterodactyls actively flapped their wings during flight, heat generated by their muscles would have warmed their body cores to temperatures higher than that of the air. In addition, the bodies of some pterodactyls were covered with a dense coat of long, hairlike scales, which presumably could have served to insulate the body.

The well-preserved skull and lower jaw of *Thalassodromeus sethi* was discovered in fine-grained sediments in northeastern Brazil (Kellner and de Almeida Campos, 2002). The 110-million-year-old fossil had an estimated wingspan of 4.5 m (15 ft.) and a skull with a hollow, bony crest whose surface was covered with many branching channels that once contained a network of blood vessels. Blood flowing from the brain through the crest would have lost heat as air rushed over the crest’s broad surface or gained heat in the morning sun. Thus, pterosaurs presumably used their cranial crests to regulate body temperature. The lower jaw also had a large number of blood vessels, which hints that the bill covering the jaw would have been riddled with nerves. The bladelike tip of the lower jaw and the streamlined shape of the upper one suggest that the pterosaur trolled its lower jaw across the water’s surface while it glided. As some seabirds like skimmers do today, the animal would have snapped its jaws shut when it sensed a fish inside them.

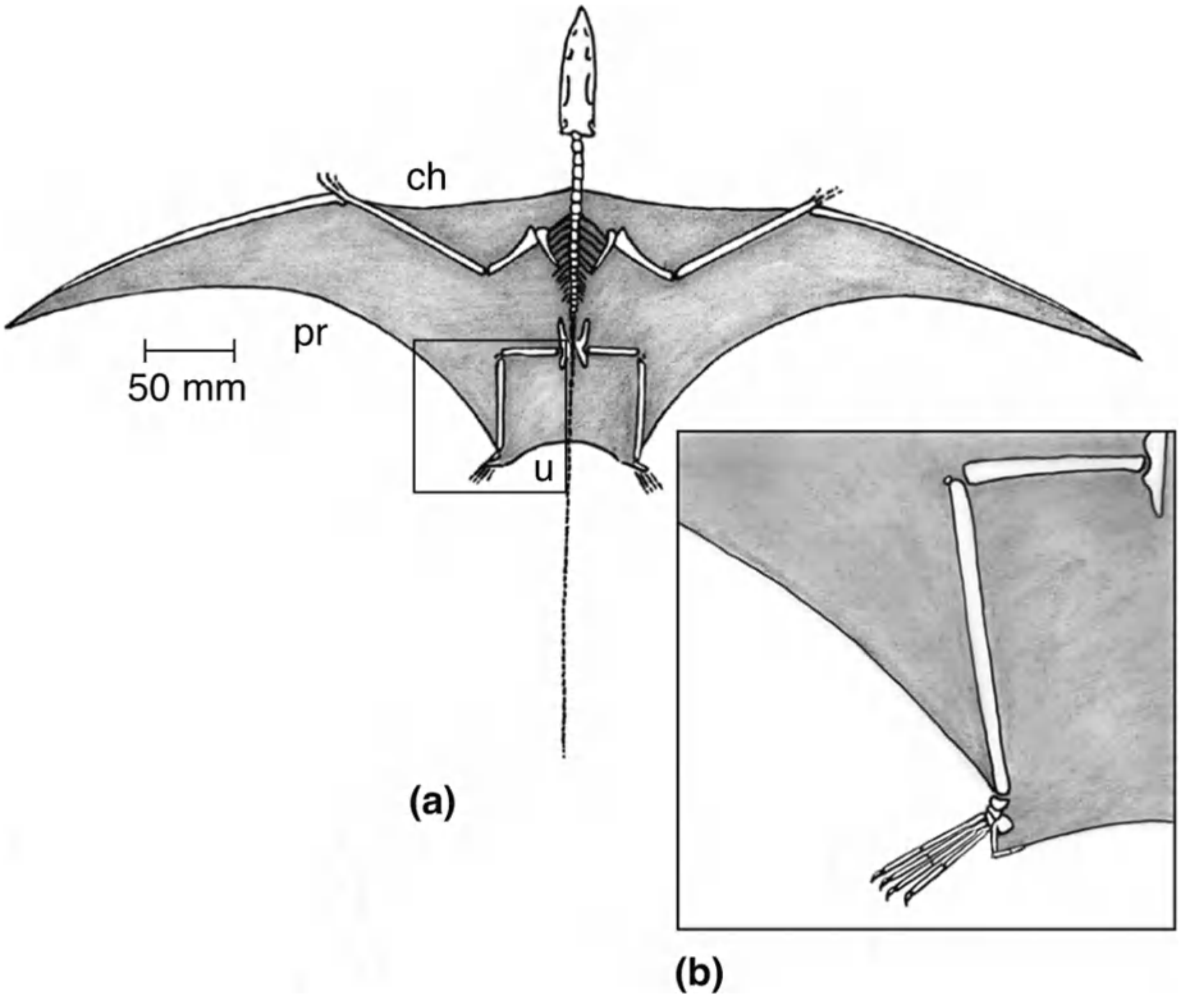


Figure 6.22. (*a*) Restoration of *Sordes pilosus*, a pterosaur, in dorsal view showing the relationship of the skeleton to the flight membranes. *Key*: pr, propatagium; ch, cheiropatagium; u, uropatagium. Scale bar = 50 mm. (*b*) The hindlimb of *Sordes pilosus* in "flight" position with the fifth metatarsal located dorsomedially to the foot, the first phalanx of the fifth toe directed laterally, and the second phalanx reflected medially to insert into the rear edge of the uropatagium.

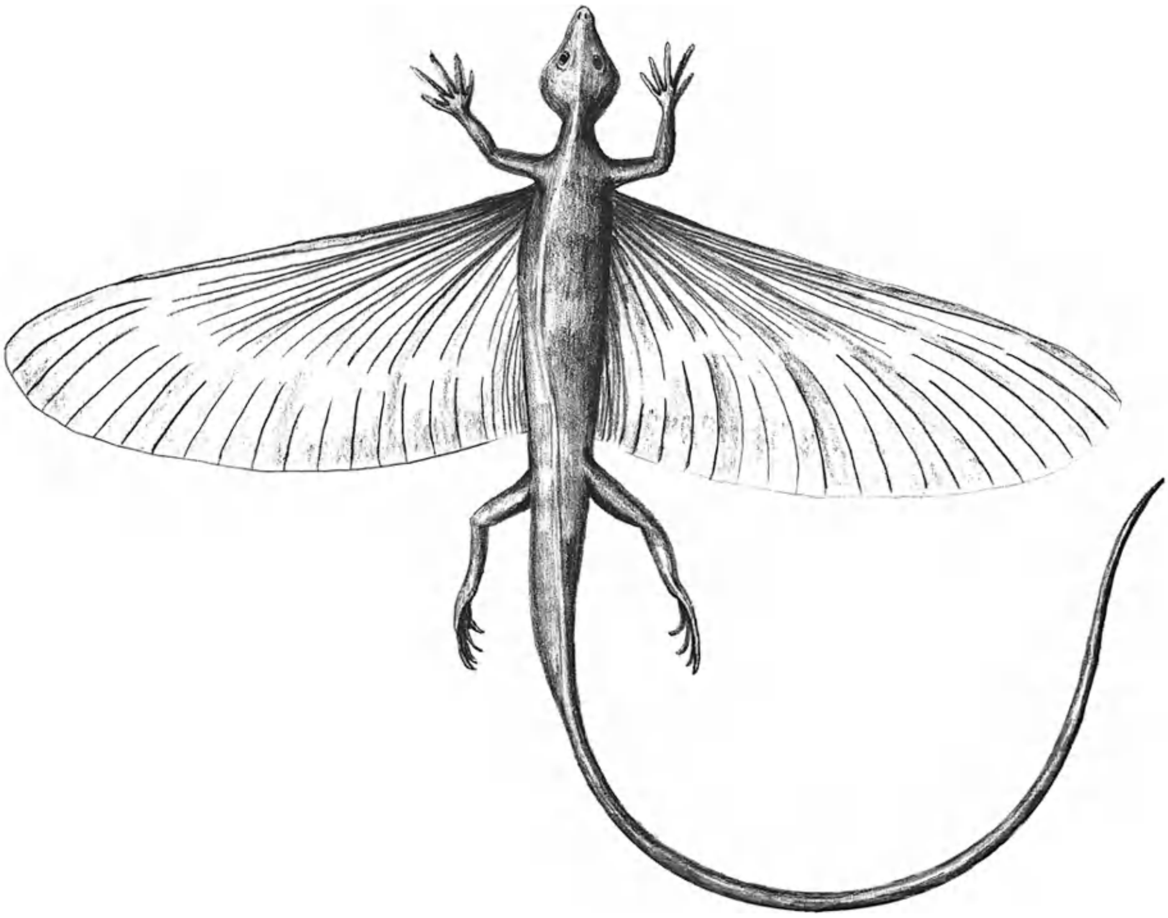


Figure 6.23. The earliest known flying vertebrate, *Coelurosauravus jaekeli*. Reconstruction in dorsal view. Note the numerous long rods for support of the lateral gliding membrane and the very long tail. Distal portions of the larger rods may have been curved backward as a result of tension produced by the intervening gliding membrane when the wing was spread. Reconstruction is based on a fossil with a snout-vent length of 18 cm (7 in.).

The discovery of *Darwinopterus modularis* from the Middle Jurassic of China provided an important transitional fossil between basal early pterosaurs, which were characterized by having long tails, short necks, and a separate nasal opening in the skull, and the more derived later group, the pterodactyloids, which had short tails, long necks, and nasal openings combined with another opening in the skull in front of the eye (antorbital fenestra) (Lu et al., 2009).

CT scans of the skull of *Rhamphorhynchus muensteri* show that it possessed a great sense of vision and its enlarged cortex served as a powerful computer to integrate sensor information and direct its muscles in flight.

Using CT scans of 155 bird specimens and a dozen species of pterosaurs, Mike Habib, a Johns Hopkins University biologist, found that they were greatly different in strength, size, and proportion. In birds, the hind legs were stronger than the front limbs, but in some pterosaurs the front limbs were several times stronger than the hind ones. Pterosaurs leapt into the air off all four limbs. They pitched forward at first, the legs kicked off first, then the arms took off. This "leapfrog" action allowed some of the ancient giants to get into the air in less than a second. Habib calculated that one 250 kg (550 lb.) pterosaur launched at a speed of 68 km (42 mi.) per hour (Borenstein, 2009).

Competition with birds is thought to be a primary reason for the extinction of the pterosaurs prior to the end of the Cretaceous period. They did not give rise to any other group of vertebrates.

CROCODILIA

The order Crocodilia, which includes the alligators, crocodiles, caimans, gavials, and their relatives, is thought to have arisen from thecodont stock (see Figs. 6.1 and 6.2). In 1986, the skull and jawbone of an extremely large fossil crocodilian (*Purussaurus*) were discovered in the Amazon region along the border between Peru and Brazil (Campbell and Frailey, 1991). This giant crocodilian had an estimated length of 12 m (39 ft.) and stood 2.5 m (8 ft.) tall. It is estimated to have weighed 10,000 to 12,000 kg (22,000–26,000 lb.), which would have made it even more massive than *T. rex*, the largest known terrestrial carnivore. In 2000, another large crocodile was reported (Sereno, 2001). Known as *Sarcosuchus imperator*, some of its conical teeth, vertebrae, and scutes had been previously discovered by French paleontologist Albert-Felix de Lapparent. This huge crocodilian ruled Africa's Middle Cretaceous rivers some 110 Mya. It had an estimated adult length of 12 m (40 ft.) and an estimated weight of at least 7,600 kg (17,000 lb.). Unlike any other crocodile, living or extinct, the skull of *Sarcosuchus* gets wider toward the front end, which is lined with a deadly row of enlarged incisors. The swollen end of the snout housed an enormous cavity under the nostrils, meaning this crocodile may have had an enhanced sense of smell and a most unusual call. Its eye sockets project upward for scanning the river's edge while submerged. It had a predicted bite force of over 8,000 kg (18,000 lb.). The highest bite force of any living animal is that of a 5 m (17 ft.) Australian saltwater crocodile, whose bite force was recorded at 1,678 kg (3,700 lb.).

The most primitive eosuchian crocodyliform (modern crocodilian) fossil was discovered in Australia (Salisbury et al., 2006). The new species, *Isisfordia duncani*, dates from between 95 and 98 Mya, around the time the group that contains today's species was beginning to diverge. It was relatively small at just 1.1 m (3.6 ft.) long. A possible plant-eating crocodyliform archosaur from the Cretaceous of China (*Chimaerasuchus paradoxus*) was reported by Wu et al. (1995). The presence of teeth possessing three longitudinal rows of cusps (multicuspid molariform) may make it the first known herbivorous member of the Crocodyliformes. The first trace and body fossil evidence of burrowing behavior in a dinosaur was reported with the discovery of *Oryctodromeus cubicularis*, where the remains of an adult and two juveniles were found in the expanded distal chamber of a sediment-filled burrow (Varricchio et al., 2007). Association of adult and young within a terminal chamber also provides definitive evidence of extensive parental care in the Dinosauria.

AVES

As early as 1868, Thomas Huxley and others had discussed a possible connection between dinosaurs and birds. Much of the current evidence, however, indicates that birds are a monophyletic group that arose from diapsid reptiles (theropods) during the Jurassic period. Birds still retain many traces of their reptilian ancestry (Norman, 1991) (Fig. 6.24). A cladogram of the Archosauria showing possible relationships of several archosaurian groups to modern birds is presented in Fig. 6.25.

Today, the origin of birds remains ornithology's longest-running debate. Some researchers are proponents of a dinosaur-bird link with the ancestral dinosaur being a theropod. These researchers include Philip Currie, a Canadian paleontologist and dinosaur curator who helped found the Royal Tyrrell Museum of Paleontology in Alberta, and who is now a professor at the University of Alberta in Edmonton, Canada; Mark Norell of the Peabody Museum of Natural History at Yale University; Luis Chiappe, Director of the Dinosaur Institute, Natural History Museum of Los Angeles; John Ostrom (deceased) former Curator at the Peabody Museum of Natural History at Yale University; Jacques Gauthier, Curator of Vertebrate Paleontology and Vertebrate Zoology at the Peabody Museum of Natural History at Yale University; and Paul Sereno, a University of Chicago paleontologist. Sereno has stated: "Everywhere we look, from their skeletal features to their behaviors to even the microstructure of their eggs, we see evidence that birds are descended from dinosaurs" (Morell, 1997e). In fact, paleontologists have identified some 200 anatomical features shared by birds and dinosaurs—

a far greater number than those linking birds to any other type of reptile, ancient or living (Monastersky, 1997b). Even the furcula (“wishbone”), whose absence in dinosaurs was considered powerful evidence barring them from bird ancestry, has now been found in several theropod dinosaurs (Norell et al., 1997).

Other researchers, like Alan Feduccia of the University of North Carolina and Larry Martin (deceased) of the University of Kansas, however, believe that dinosaurs and birds shared a common thecodont ancestor. Feduccia postulates that some as-yet-undiscovered, lightly built, tree-living reptile produced the avian line (Feduccia, 1980, 1996). Feduccia and other evolutionary biologists argue that dinosaurs and birds had a similar way of life that could account for a coincidental similarity of appearance—a process known as convergent evolution. Major elements of disagreement involve lung structure and ventilation, whether some theropods and early birds were ectothermic or endothermic, and the developmental patterns and homologies in the avian wing (hand) (Ruben et al., 1997; Gibbons, 1997d). Theropod hands retain only digits 1-2-3, whereas some researchers claim that birds supposedly have a 2-3-4 digital formula (Burke and Feduccia, 1997).

Jones et al. (2000) reported that an unusual gliding archosaur, *Longisquama insignis*, from the Late Triassic (220 Mya) bore a series of paired integumentary appendages that resembled avian feathers in many details, especially in the anatomy of the basal region. The latter is sufficiently similar to the calamus of modern feathers that each probably represents the culmination of virtually identical morphogenetic processes. Although the exact relationship of *Longisquama*, discovered in Kyrgyzstan in 1969, to birds is uncertain, the authors interpret the elongated integumentary appendages as nonavian feathers and suggest that they are probably homologous with avian feathers. If so, they antedate the feathers of *Archaeopteryx*, the first known bird from the Late Jurassic (145 Mya). They may provide insight into an evolutionary grade through which feathers passed almost 75 million years before *Archaeopteryx*.

Bird skulls are essentially reptilian with a single occipital condyle, only one auditory ossicle or middle ear bone (columella), and a lower jaw (mandible) composed of several bones. The lower jaw is hinged on a movable quadrate bone, as in snakes and some extinct reptiles. Most birds have flat processes on their ribs (uncinate processes), presumably to strengthen the thorax and prevent it from collapsing because of the force exerted by the powerful flight muscles as they contract with every beat of the wing during flight. The only other animals to possess uncinate processes are tuataras and crocodilians. In these lepidosaurs, uncinate processes provide support for muscle attachment and serve to strengthen the wall of the thoracic cavity. The ankle joint of birds is between two rows of tarsal bones (intratarsal), instead of being between the tibia and the tarsal bones as in the reptiles, and the foot retains the primitive phalangeal formula of 2-3-4-5 phalanges for the first four digits, similar to sauropsids. Scales are present on the legs and feet of birds. Only crocodilians, birds, and mammals have a four-chambered heart. Both reptiles and birds have nucleated erythrocytes, an egg tooth on the upper jaw at hatching, and the same general type of shelled telolecithal egg (having the yolk concentrated at one pole of the egg) with four extraembryonic membranes. Embryological development is also basically similar in both groups. Molecular evidence, including DNA sequences from four genes, provides strong statistical support for a bird-crocodilian relationship (Hedges, 1994).

The most obvious features that distinguish birds from modern reptiles are that birds are endothermic and possess feathers. As previously mentioned, however, evidence indicates that some, if not all, dinosaurs may have had high metabolic rates and also may have been endothermic (Bakker, 1986). Developmentally, feathers and reptilian scales are homologous structures. Feathers are produced by papillae in the skin, and their early development is quite similar to that of a scale. Romer (1966) noted that birds are structurally similar to reptiles and “are so close to the archosaurians that we are tempted to include them in that group.” Some taxonomists (Kemp, 1988; Gauthier et al., 1988a, b; Benton, 1990) place reptiles and birds in a single class, the Sauropsida. Others (Gardiner, 1982; Levtrup, 1985) have argued that Aves is the sister group (most closely related) of Mammalia, forming a larger clade, the Haemothermia.

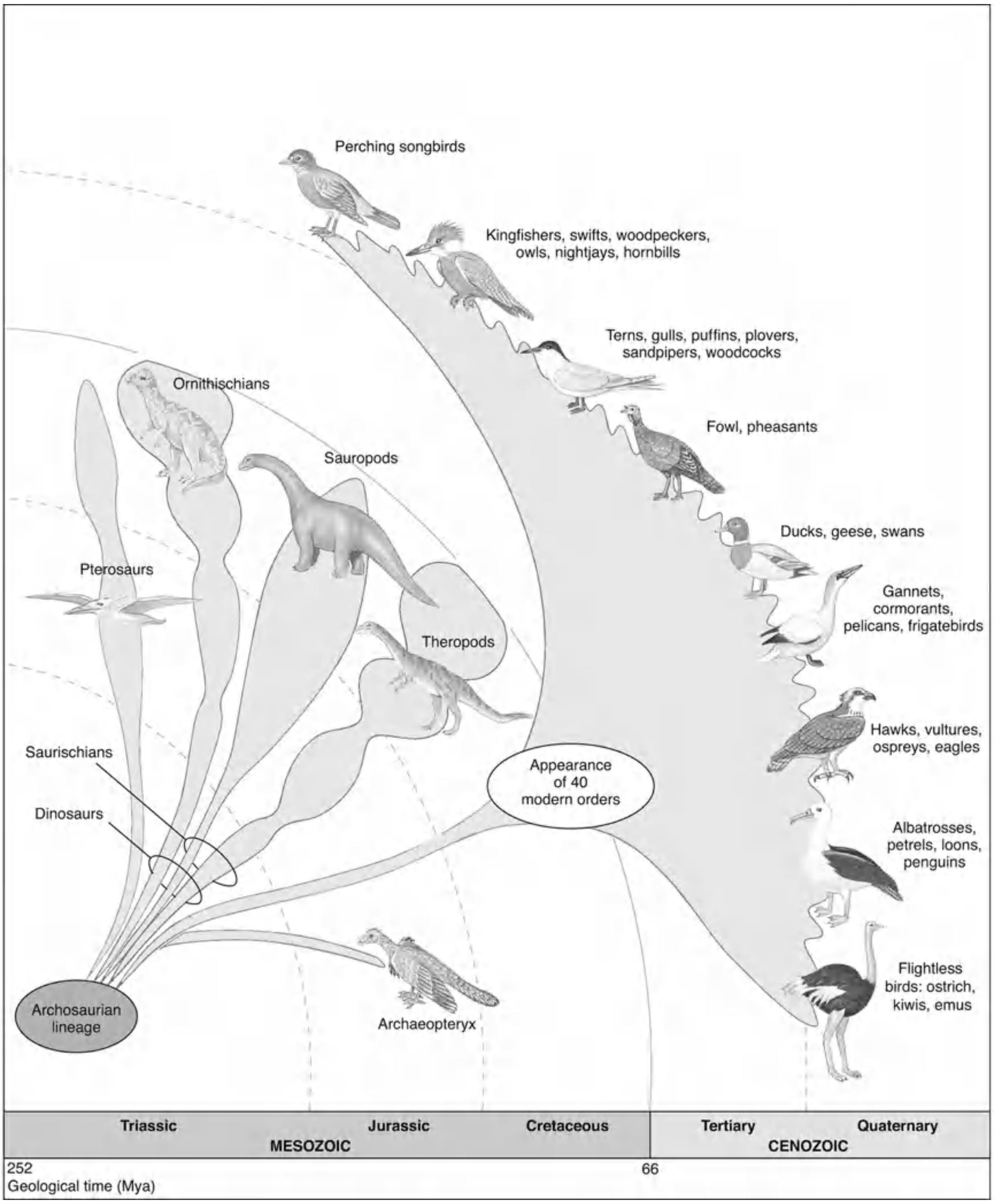


Figure 6.24. Evolution of modern birds. Nine of the largest of the 27 living orders of birds are shown. The earliest known bird, *Archaeopteryx lithographica*, lived in the Upper Jurassic, about 147 Mya. *Archaeopteryx* shares many specialized aspects of its skeleton with the smaller theropod dinosaurs and is considered by many researchers to have evolved within the theropod lineage. Evolution of modern bird orders occurred rapidly during the Cretaceous and Early Tertiary periods.

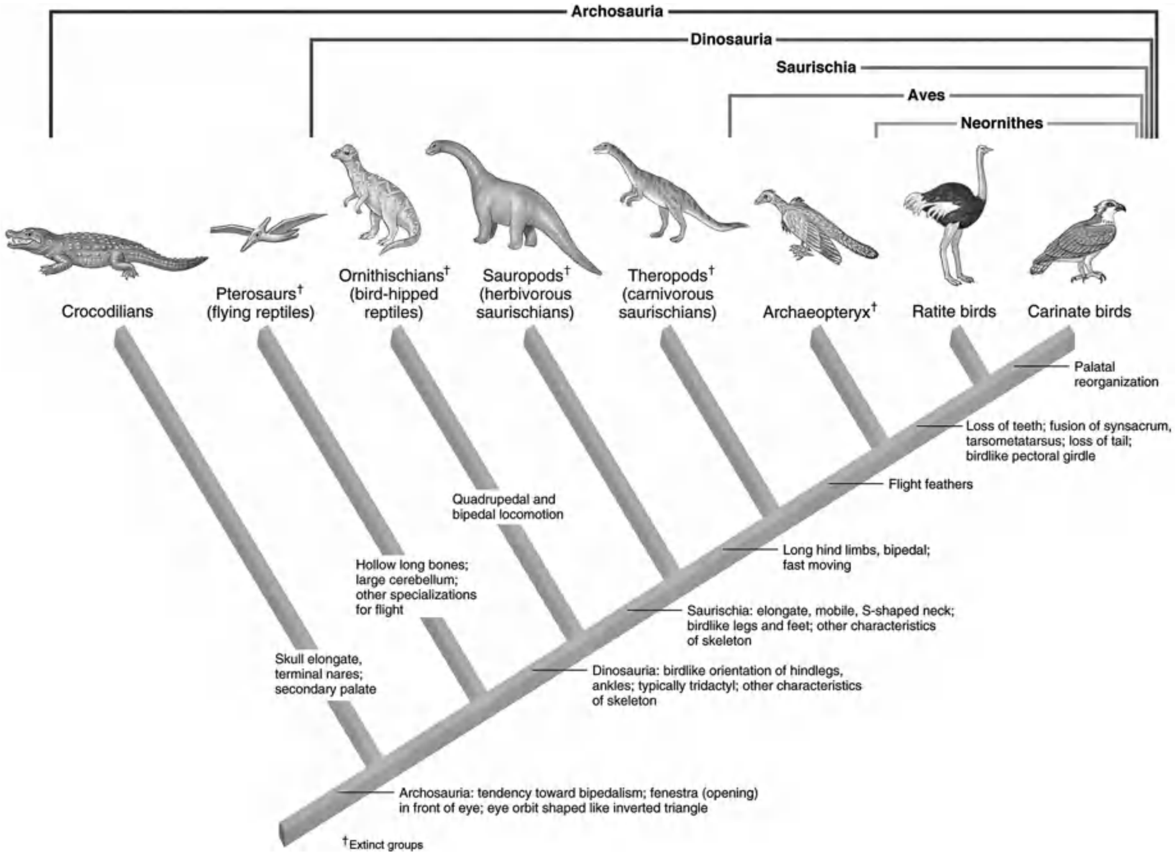


Figure 6.25. Cladogram of the Archosauria, showing the possible relationships of several archosaurian groups to modern birds. Shown are a few of the shared derived characters, mostly those related to flight, which were used to construct the genealogy.

Bakker (1986), another proponent of the dinosaur-bird link, claims that the traditional grouping that places birds in a class of their own and dinosaurs together with reptiles is “neither fair nor accurate.” He stated: “The small advanced predators like *Deinonychus* were so close to *Archaeopteryx* in nearly every detail that *Archaeopteryx* might be called a flying *Deinonychus*, and *Deinonychus* a flightless *Archaeopteryx*. There simply was no great anatomical gulf separating birds from dinosaurs. And that implies dinosaurs are not extinct. One great, advanced clan of them still survives in today’s ecosystem and the more than eight thousand species of modern bird are an eloquent testimony to the success in aerial form of the dinosaurs’ heritage.” Bakker further proposed to resurrect the name Dinosauria for a class that would include the dinosaurs, the therapsids, and the birds. He stated: “And let us squarely face the dinosaurness of birds and the birdness of the Dinosauria. When the Canada geese honk their way northward, we can say: ‘The dinosaurs are migrating, it must be spring!’”

Although reptiles have a common ancestry, the class Reptilia is not monophyletic. Based solely on shared derived characters, crocodilians and birds are living sister groups; they are descended from a common ancestor more recently than either is from any other living reptilian lineage (see Figs. 6.1 and 6.2). This is the reason cladists believe birds should be classified as reptiles, and crocodilians and birds should be placed in a separate clade, the Archosauria, which also includes the extinct dinosaurs. However, traditional evolutionary taxonomists point out that birds possess many unique morphological characteristics, whereas crocodilians have more features in common with reptiles. In this view, the morphological and ecological uniqueness of birds should be recognized by maintaining the traditional classification that places crocodilians in the Reptilia and birds in the Aves. This does not represent true evolutionary affinities and is, therefore, artificial systematics. However, the standard taxonomic practice in most texts is to classify crocodilians as reptiles. Keep in mind, however, that systematics is based on new techniques and discoveries and is continually being refined.

In October 1996, Pei-Ji Chen of the Nanjing Paleontology Institute in China showed photographs of two recently discovered "feathered" dinosaurs at the annual meeting of the Society of Vertebrate Paleontology (Monastersky, 1996b; Gibbons, 1996c, 1997b; Morell, 1997e). This is the first genus of dinosaur found with the fossilized impressions of feathers, as well as the first dinosaur where coloration has been determined. The 121-million-year-old fossils, known as *Sinosauropteryx prima*, could be the most graphic evidence yet that birds are descended from dinosaurs (Chen et al., 1998). Arrayed down the chicken-sized dinosaur's back, from the nape of its neck to the tip of its tail, is what appears to be an almost manelike row of feathers that have left their impression in the rock. The hollow filaments, up to 40 mm (1.6 in) long, resemble extremely simple two-branched feathers, called plumules, found on some modern birds like kiwis. The authors suggest that the fibers could either represent protofeathers that helped trap body heat, or they could have served as a colorful display for attracting mates. Luis Chiappe of the Natural History Museum of Los Angeles speculated that the "feathered" dinosaur may have developed feathers because it was on the road to warm-bloodedness, but had not gotten far. The first solid proof of pigmentation was found in the fossilized tail feathers of *Sinosauropteryx* (Zhang et al., 2010). The feathers seem to have russet-colored rings.

In life, the “feathered” dinosaur was about 90 cm (35 in.) long and had numerous serrated teeth in its mouth. It ran on its hindlimbs, holding its forelimbs in front of it. It appears closely related to a species of *Compsognathus*, a small dinosaur that ate insects and other small animals. One specimen has two oval shapes inside its abdomen—the first clear case of eggs found inside a dinosaur.

In April 1997, several researchers, including John Ostrom, Larry Martin, ornithologist Alan Brush, paleontologist Peter Wellnhofer, and photographer David Bubier, traveled to China to examine the fossil. Their conclusion was that the “feathers” were fibers either within the skin or above the skin (Monastersky, 1997a). If the fibers were within the skin, they could have been part of a ridge of collagen fibers similar to the frill of an iguana. If the fibers were above the skin, they could be bristles or protofeathers—structures that preceded the evolution of true feathers. Most researchers have disagreed with the identification of the structures as collagen or other structural fibers. The presence of pigment cells proved the structures were feathers, not collagen, as collagen does not contain pigment.

Liu et al. (2012) reviewed recent discoveries of fossils of feathered theropods and early birds from China during the previous decade and discusses the timing of the earliest known feathered dinosaurs.

Three theropod dinosaurs with feathers—*Protarchaeopteryx robusta*, *Caudipteryx zoui*, and *Sinornithosaurus millenii*—have been described from the Upper Jurassic/Lower Cretaceous formations of Liaoning, China (Padian, 1998; Qiang et al., 1998; Swisher et al., 1999; Xu et al., 1999). These turkey-sized animals had strong legs, stubby arms, and down-covered bodies. Although feathers covered the body of *Protarchaeopteryx*, no preserved evidence of wing feathers exists. *Caudipteryx*, or “tail feather,” has more plumage, including a generous tail fan. The postcranial skeleton of the dromaeosaurid *Sinornithosaurus* is remarkably similar to that of early birds. The structure of the shoulder girdle shows that terrestrial dromaeosaurid dinosaurs had attained the prerequisites for powered, flapping flight. The body was apparently covered by a layer of integumentary filaments generally reaching 40 mm (1.5 in.) in length that differ little from the external filaments of other theropod dinosaurs or even the plumule-like feathers of *Confuciusornis* from the same locality. These three theropod dinosaurs are thought to have been capable of running swiftly, flapping feathered wings, and fanning out impressive tail feathers, but were unable to actually fly.

Phylogenetic analysis indicates that all are more primitive than the earliest known bird, *Archaeopteryx*. These fossils are thought to represent stages in the evolution of birds from feathered, ground-living, bipedal dinosaurs.

The announcement of a turkey-sized animal that may have been the first flying dinosaur created much excitement in 1999 (Sloan, 1999). Fossils of the animal, named *Archaeoraptor liaoningensis*, came from the Liaoning, China, site. The shoulder girdle and breastbone resembled those of modern birds. In addition, it had hollow bones and a long, stiff tail. In January 2000, however, CT scans confirmed “anomalies” in the reconstruction of the fossil; the “feathered dinosaur” was a forgery—a composite combining the tail of a dinosaur with the body of a bird (Monastersky, 2000).

Although birds were once believed to have descended from the birdlike dinosaurs (Ornithischia), they are now thought to have branched from theropod ancestors (Ostrom, 1985, 1994; reviewed by Norman, 1991; Padian and Chiappe, 1998). A unique theropod skull discovered in Mongolia in 1965 from the Late Cretaceous shows a combination of theropod and primitive avian characters (Elzanowski and Wellnhofer, 1992). It has been named *Archaeornithoides deinosauriscus* and probably belongs to the closest of the known nonavian relatives of *Archaeopteryx* and other birds.

Through the use of CT scans, Bakker (1992) has found a number of similarities between carnivorous dinosaurs and birds. For example, members of the genus *Nanotyrannus*, a group of smaller dinosaurs related to those giant dinosaurs in the genus *Tyrannosaurus*, possessed cranial air canals that looked remarkably like those of *Troodon*, a small carnivorous dinosaur whose canals resembled those of modern birds. *Troodon*’s canals, along with its birdlike wrists and inner ear structure, have led some scientists to consider it to be the nearest known relative of modern birds. In addition, egg clutches and nests of *Troodon* indicate that two eggs were produced simultaneously at daily or longer intervals and that eggs were incubated using a combination of soil and direct body contact (Varricchio et al., 1997). *Troodon* egg shape, size, and microstructure suggest a more avian than crocodilian reproductive tract.

Mammal-Eating Dinosaur

While studying a specimen of *Compsognathus* from northeast China, researchers found the jawbone of a tiny mammal in the digestive tract of the dinosaur. This is the first evidence of a dinosaur preying on a mammal.

Monastersky, 1997a

Bakker (1992) speculated that approximately 140 to 160 Mya, birdlike innovations appeared and expressed themselves in both large and small dinosaurs. Suddenly a whole range of animals exhibited avian features. He stated: “Some of those creatures, perhaps including *Archaeopteryx*, actually *were* birds, while others stayed on the ground, keeping their birdness in terrestrial mode. The descendants of these bird-dinos—*Nanotyrannus*, *Troodon*, and others—would die out at the end of the Cretaceous, while the true birds would fly on into the evolutionary future.”

The relationship between birds and mammals also has generated considerable discussion. Comparative protein sequence studies of amniote myoglobin and hemoglobin by Bishop and Friday (1988) show that bird and mammal globins “frequently resemble one another biochemically more than would be expected on the majority view of their separate evolutionary histories.” The reasons for these similarities are not clear. Gardiner (1982) and Lovtrup (1985) presented cladistic arguments that mammals and birds are the nearest sister groups among living tetrapods. They noted about 20 characters shared by birds and mammals, but their arguments have been criticized by Kemp (1988) and others.

The fossil record has yielded few complete skeletons of birds. Because bird bones are fragile and many are hollow, they are easily broken and fragmented. As a result, much of the paleontological research on birds has been accomplished by studying fragments of bones, many of which may have been fragmented by carnivorous animals.

A remarkably well-preserved nestling bird dating from about 135 Mya was discovered in the Pyrenees of northern Spain (Sanz et al., 1997; Morell, 1997c). It is the earliest hatchling bird yet discovered and comes just 10 million years after *Archaeopteryx*, the first undisputed bird. The toothed skull of this nestling looks dinosaurian, but other features resemble those of modern birds. Postorbital bones found in small theropod dinosaurs but not in modern birds are still present in the nestling, but they show signs of breaking down.

A 90-million-year-old theropod dinosaur that folded up its front limbs as if they were wings was reported from Patagonia (Novas and Puerta, 1997; Morell, 1997c). *Unenlagia comahuensis* could have stretched its forelimbs out as if taking flight, but probably extended them for balance instead. Changes in arm and shoulder anatomy, coupled with its very birdlike pelvic girdle, suggest the kind of changes that dinosaurs would have undergone during their transition to birds.

Ancestral Birds

In 1861, the impression of a single feather was discovered in a German limestone quarry. This was the first evidence that birds existed in the Jurassic period, approximately 150 Mya. The next year, a fossilized pigeon-sized skeleton with imprints of feathers was discovered in the same quarry. A second skeleton was found in 1876, about 16 km (10 mi.) away (Fig. 6.26). At the present time, a total of 11 specimens have been recovered, with the latest, and presumably oldest at 150-million-years-old, having been discovered in 2010 (Rauhut et al., 2018). Although the first two skeletons originally were assigned to different genera, they later were classified in a single genus and species: *Archaeopteryx lithographica*. *Archaeopteryx* means “ancient wing,” and *lithographica* refers to the limestone that was used for lithographic plates during the nineteenth century.

In almost all of its structure, *Archaeopteryx* is intermediate between modern birds and thecodonts. The modified diapsid skull and hindlimbs are reptile-like; well-developed wing claws and a long, lizard-like tail are present, as are teeth set within sockets in both jaws. If clear imprints of feathers had not been present, the fossils very easily might have been classified as reptiles. In fact, the fifth specimen was classified as a small dinosaur for 20 years after its discovery in 1951 (Wellnhofer, 1990).

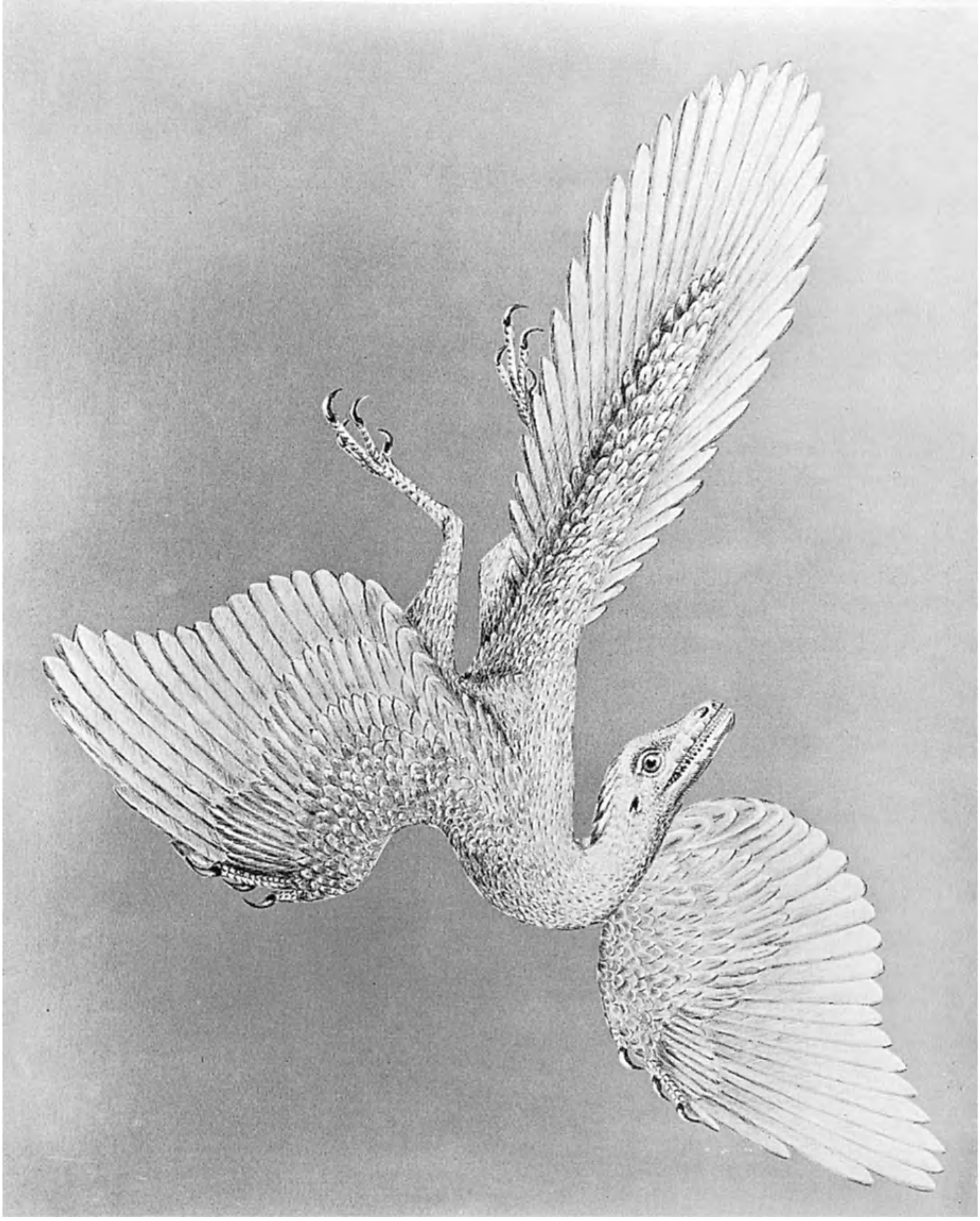


Figure 6.26. A restoration of the second specimen of *Archaeopteryx lithographica* to be discovered. Positions of the body parts correspond to the positions of the fossilized bones.

As late as the mid-1940s, some investigators still denied that *Archaeopteryx* was a bird. Lowe (1944), for example, suggested that *Archaeopteryx* was an arboreal, climbing dinosaur that should “take its place not at the bottom of the avian phylum [class] but at the top of the reptilian.” Recent studies of its bones and those of other fossils show that it was much less bird and far more dinosaur than had been believed (Erickson et al., 2009). Examining microscopic chips of bone, a team of scientists concluded that the bones were very dense and slow-growing, while those of birds are porous, light, and fast-growing. While a bird matures to full size in a few weeks, *Archaeopteryx* would be nearly as slow-growing as any other dinosaur, requiring at least two and a half years to reach full size.

The vertebral column of *Archaeopteryx* consists of cervical, thoracic, lumbar, sacral, and caudal vertebrae. The centra (body) of each vertebra is amphicoelous (biconcave). The presence of pneumatic foramina in the cervical and anterior thoracic vertebrae confirms the phylogenetic continuity between the pneumatic systems of some theropods like *Compsognathus*, *Allosaurus*, and *Ornithomimus* and living birds (Britt et al., 1998). Five of the sacral vertebrae are fused into a primitive synsacrum but no pygostyle (fused caudal vertebrae) is present. Although the structure of the pelvis is similar to that of ornithischian dinosaurs, the resemblances are thought to be due to parallel evolution (Carter, 1967). The bones of *Archaeopteryx* are solid, not pneumatic. Metacarpals are not fused, but metatarsals are partially fused; thus, no carpometacarpus (fused wrist and hand bones so characteristic of all birds except *Archaeopteryx*) exists (Vazquez, 1992). The two clavicles have fused to form a furcula, but no sternum has been found in any of the 10 specimens. Modern flying birds possess a broad-keeled sternum for the attachment of enlarged flight (pectoral) muscles. The lack of indications of well-developed pectoral muscles in *Archaeopteryx* suggests that its ability to fly would have been limited.

Studies of feather asymmetry in *Archaeopteryx* and extant birds have not resolved whether or not *Archaeopteryx* would have been capable of sustained flapping flight (Speakman and Thomson, 1994; Norberg, 1995). Gastral (abdominal) ribs, similar to those of its thecodont ancestors, were present. The feet were adapted for running and showed features intermediate between reptiles and birds: a reduced digit 1 (hallux), which was diverted to the rear; a fused metatarsus; a mesotarsal joint; and a claw curvature typical of perching and trunk-climbing birds (Feduccia, 1993). Contour feathers were well developed, and tail feathers arose from the lateral surfaces of the caudal vertebrae. Because the body appears to have been covered with feathers, Carter (1967) suggested that feathers may have evolved first as an insulating cover for the body and not for flight. If feathers had evolved for flight, they would be expected to be primarily on the wings, not covering the entire body in a primitive bird.

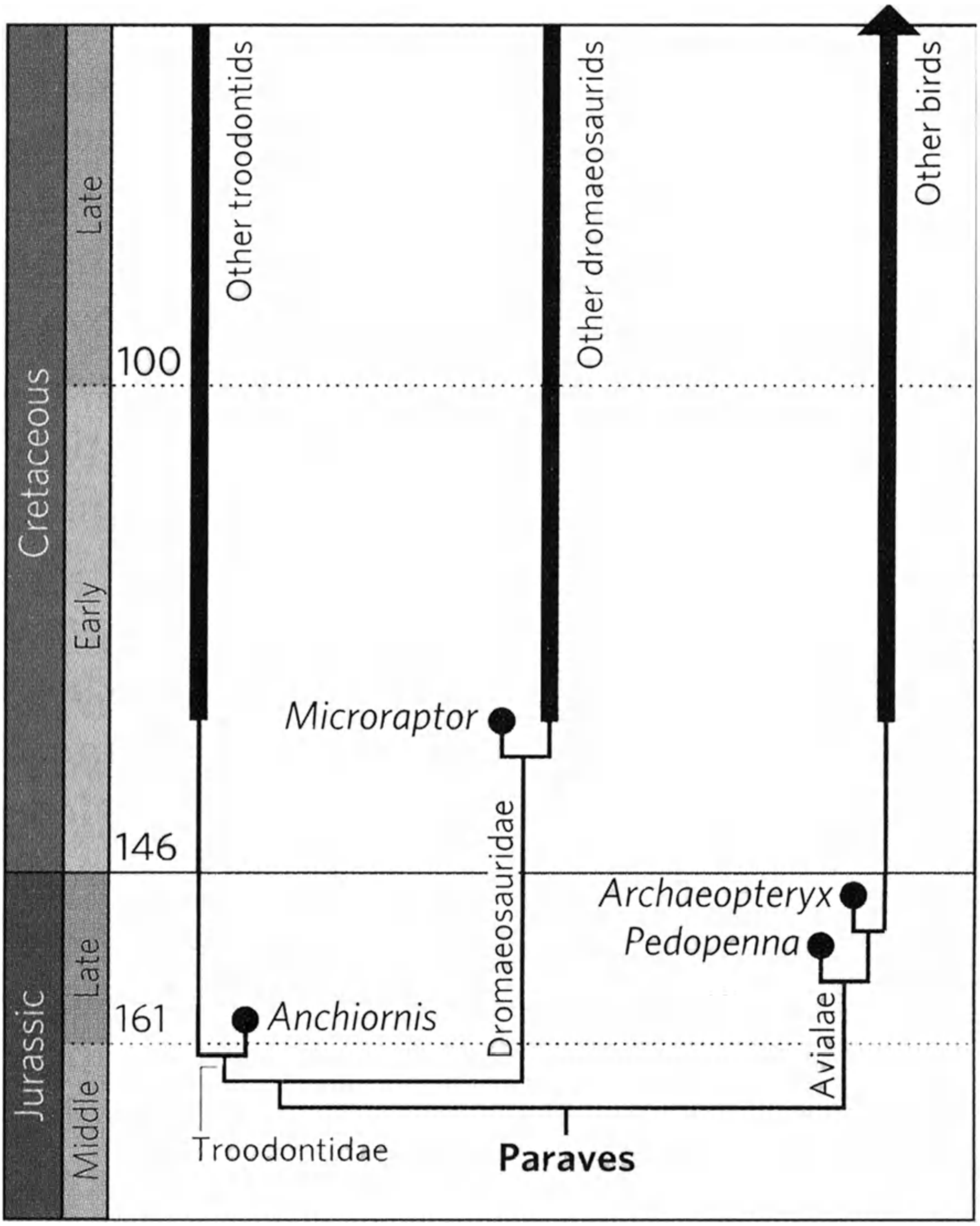


Figure 6.27. *Anchiornis* in context. *Anchiornis* is assigned to the family Troodontidae, which together with the closely related Dromaeosauridae and Avialae comprise the Paraves (itself a subgroup of the theropod dinosaurs). One significant aspect of *Anchiornis* is that it predates *Archaeopteryx*, the iconic “first bird,” by some 5 to 10 million years. Another is that it shows that basal members of all three of the Paraves groups—*Anchiornis*, *Microraptor*, and *Pedopenna*—had long, pennaceous feathers on their lower legs and feet, as well as on their hands and tail. The implication is that avian evolution conceivably went through a “four-wing” stage.

The first complete chemical analysis of feathers from *Archaeopteryx* revealed that they were patterned—light in color, with a dark edge and tip—rather than all black, as previously thought (Manning et al., 2013). Studies revealed the presence of trace-metals and organic sulfur, strongly suggesting that remnants of endogenous eumelanin pigment have been preserved.

In 2013, scientists discovered two well-preserved fossils in China of a previously unknown bird species that lived 130 Mya (Wang et al., 2015). Named *Archaeornithura meemannae*, the fossils pushed the earliest known modern bird back by about 5 million years.

The oldest known feathered dinosaur, *Anchiornis huxleyi*, was unearthed from 151- to 161-million-year-old sediments (1 million to 11 million years older than *Archaeopteryx*, the first known bird) in northeastern China (Hu et al., 2009) (Fig. 6.27). Two types of feathers adorned the dinosaur, which stood about 28 cm tall at the hip. One kind, known as "dino-fuzz," decorated the dinosaur's head and neck. The other type, similar in overall structure to the feathers of modern-day birds, consisted of small filaments that branched from a larger shaftlike filament. Feathers on the legs and feet appeared to have overlapped each other, creating aerodynamic surfaces that would have, in essence, given *Anchiornis* a wing on each of its four limbs (similar to *Microraptor gui* and others). With so many species having this arrangement, the four-winged configuration must have been an important phase in the evolutionary transition from dinosaurs to birds.

An even older feathered dinosaur—one that reestablishes *Archaeopteryx* as part of the bird lineage, even as it may simultaneously dethrone *Archaeopteryx* as the earliest known "bird"—was discovered in the Liaoning Province of northeastern China (Godefroit et al., 2013). A 50 cm (20 in.), chicken-sized fossil with small, sharp teeth, *Aurornis xui*, is estimated to be about 160 million years old, about 10 million years older than *Archaeopteryx*. The study authors believe that *Aurornis* represents the earliest known bird, but other scientists say it could be part of a group of birdlike dinosaurs that were developing feathers and birdlike features. The differences between birds and (nonavian) dinosaurs are very thin. Encased in sedimentary rock, *Aurornis* preserved traces of downy feathers along the animal's tail, neck, and chest, but the absence of larger feathers suggests it was not able to fly. Luis Chiappe, paleontologist at the Natural History Museum of Los Angeles, said, "You're looking at an animal that is either a very primitive bird or something very closely related to birds. I tend to think that it's not a bird, but that it's one of those true very close ancestors of birds." After a thorough examination of the fossil, researchers from Europe and China constructed a computer-generated family tree that puts both *Aurornis* and *Archaeopteryx* in the Avialae family—the group of dinosaurs whose only living representatives are birds.

The first Jurassic-Cretaceous birds from outside Germany were reported from northeastern China (Hou et al., 1995; Swisher et al., 1999). *Confuciusornis sanctus* has a primitive wing skeleton similar to that found in *Archaeopteryx*, including unfused carpal elements and long digits (Fig. 6.28). The pelvis and the climbing adaptations in the hands indicate a vertical, *Archaeopteryx*-like posture (Hou et al., 1996). The foot is similar to that of *Archaeopteryx*, with a reflexed hallux and large, recurved claws supposedly reflecting an arboreal lifestyle. The wings were well developed and a long, feathered tail was present. Teeth were absent. Contour feathers are thought to have covered the entire body. A second species, *C. dui*, is based on a remarkably well-preserved skeleton with feathers and, for the first time in the Mesozoic record, direct evidence of the shape of a horny beak (Hou et al., 1999).

A partial skeleton of a primitive bird, *Rahona ostromi*, was recovered from the Late Cretaceous of Madagascar (Forster et al., 1998). The skeleton exhibits a mosaic of theropod and derived avian features. For example, it possesses avian features like an avian antebrachium (forearm), feathered wings, a reversed hallux, and an avian-like synsacrum, but it retains characteristics that indicate a theropod ancestry, including a sickle-like claw on the second digit, a unique characteristic of certain theropod groups. Although it lived 80 million years after *Archaeopteryx*, phylogenetic analysis places *Rahona* with *Archaeopteryx*, making *Rahona* one of the most primitive birds yet discovered.

(a) Archaeopteryx lithographica **(b) Confuciusornis sanctus** **(c) Chaoyangia**

Figure 6.28. Restorations of Late Jurassic primitive birds: (*a*) *Archaeopteryx lithographica*; (*b*) *Confuciusornis sanctus*; (*c*) reconstruction of the *Chaoyangia* skeleton.

Fossils discovered in 1984, 1990, and 1994 in Spain (*Iberomesornis*, *Concornis*, *Noguerornis*, and *Eoalulavis*) and northeast China (*Sinornis*, *Cathayornis*, and *Boluochia*) date from the Early Cretaceous, between 130 and 120 Mya (Shipman, 1989; Wellnhofer, 1990; Monastersky, 1990a; Sereno, 1991; Zhou et al., 1992; Fischman, 1993a; Hou et al., 1996; Sanz et al., 1996). These fossils reveal unexpected diversity in early birds starting at about 135 Mya. They are intermediate both chronologically and anatomically between *Archaeopteryx* and modern birds. They represent the earliest known examples of birds with a toothless beak and modernized flying ability. The fossils resemble *Archaeopteryx* in having a primitive avian wing with an unfused carpometacarpus, a robust ischium with an anterodorsal ischial process, a posteriorly projecting pubis, a long bowed femur, partially fused metatarsals, and a reflexed hallux. The third metatarsal is the longest and the fifth metatarsal is present. Gastral ribs are present, and claws on the feet are long and curved in the Chinese specimens. However, they also show adaptations for flight, like a pygostyle to strengthen the tail, a collarbone strongly connected to the sternum, and a reduced first digit and enlarged second digit on the hand. These birds were known as Enantiornithes, or “opposite” birds; they were the dominant group of land birds during the Mesozoic. They are so named because three bones of their feet are partially fused from the top down, rather than from the bottom up as in modern birds (Fig. 6.29b, c).

This new clade of birds, the enantiornithine (opposite) birds, was proposed by Walker (1981). Opposite birds closely resemble

Archaeopteryx with their primitive pelvic region and toothed skull. However, instead of a long reptilian tail, caudal vertebrae were fused into a long pygostyle, and these birds were quite capable of flying. These were the dominant birds of the Mesozoic and included such genera as *Hesperornis*, *Sinornis*, *Ichthyornis*, and *Protopteryx* (see Fig. 6.29a). Unlike other known avian fossils, *Protopteryx* exhibits feathers with visible intermediacy between reptilian scales and true bird feathers (Zhang and Zhou, 2000). It also exhibits novel skeletal features clearly distinguishing early birds from the theropod dinosaurs.

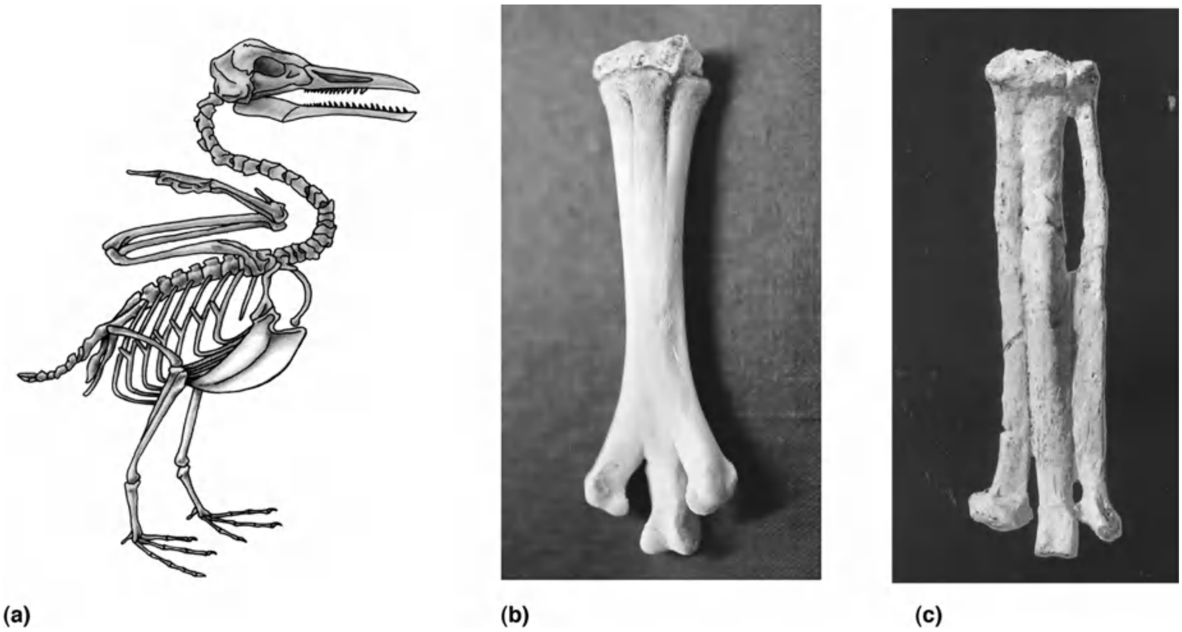


Figure 6.29. (*a*) Skeleton of the Upper Cretaceous bird *Ichthyornis*. Note the teeth and the well-developed keel on the sternum. (*b*) Modern birds have the foot bones fused from the bottom up; (*c*) in opposite birds, the fusion is top down.

An Early Cretaceous enantiornithine bird, *Pterygornis dapingfangensi*, from northeastern China, represents the oldest known example of fossilized remains showing bone fusion of its major parts (Wang et al., 2017). In order for birds to evolve from land- or tree-dwelling animals into creatures that could fly, many changes had to occur—they had to become lighter while maintaining a strong skeleton. One of the ways this occurred was through fusion of bones, such as fingers into wingtips, while many other bones were simply lost to evolution. Until the discovery of the 120-million-year-old *Pterygornis*, the consensus among scientists was that such changes did not occur until just before land-based dinosaurs became extinct. This new evidence suggests that the time frame will have to be pushed back approximately 40 million years.

An 80-million-year-old well-preserved fossil bird, *Apsaravis*, discovered in the Ukhaa Tolgod region of Mongolia, appears to have a mosaic of primitive and advanced traits (Norell and Clarke, 2001). Researchers have found 27 features that make *Apsaravis* an ornithurine and link it with modern birds (like its 10 fused sacral vertebrae) and 12 traits that were thought to be unique to Enantiornithes.

Until recently, many paleontologists thought that *Archaeopteryx* itself gave rise to opposite birds, which in turn evolved into modern birds. That view has faded, but Chiappe and others still hold that opposite and modern birds are closely related sister taxa, with a recent common ancestor that lived at about the time of *Archaeopteryx* or a bit earlier (Fig. 6.30).

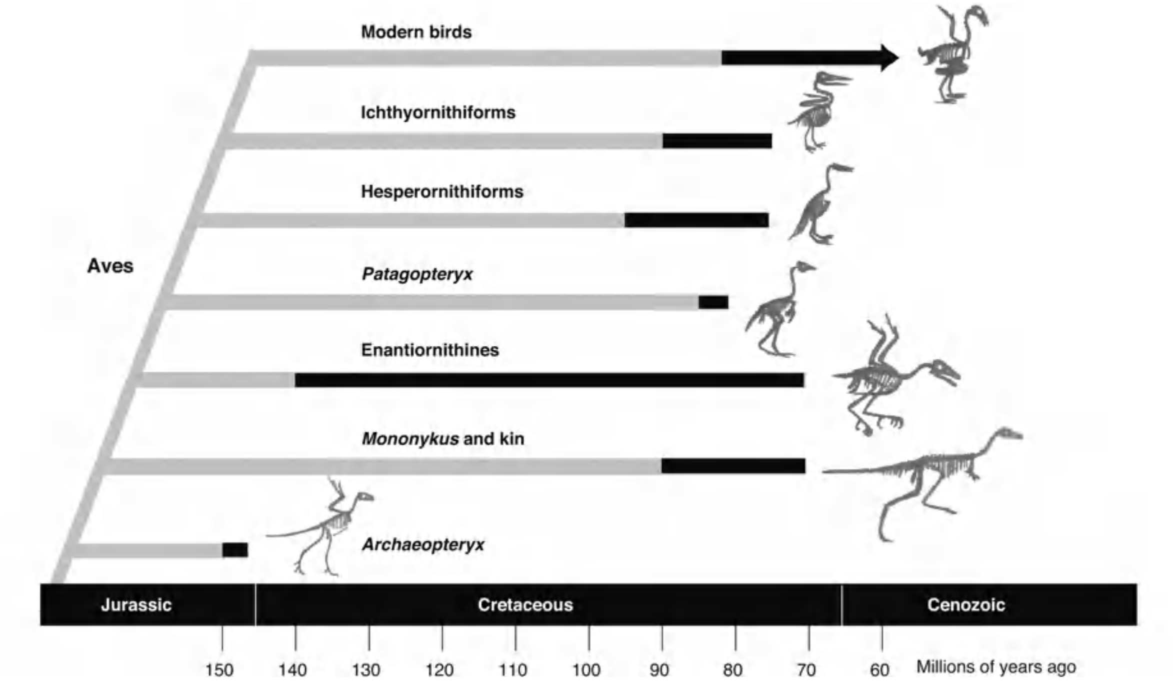


Figure 6.30. The fossil record reveals that living birds are just one branch on the avian family tree.

Hou et al. (1996) now challenge that view with fossils of sparrow-sized birds (*Liaoningornis*) from northeastern China's Liaoning Province. These specimens, taken from volcanic rock dated between 121 and 142 Mya, possess foot bones and a keeled sternum that resemble those of modern birds. The presence of a keeled sternum is the earliest evidence for this distinctly avian structure. The bones represent what may be the oldest modern-looking bird, or ornithurine. If the dating is confirmed, it provides evidence for a pre-*Archaeopteryx* or a rapid post-*Archaeopteryx* evolution in birds. It could cause *Archaeopteryx* and the enantiornithines to be moved off the evolutionary branch that leads to modern birds. It could even imply an earlier origin for all birds. Feduccia stated: "It shows that there was a dichotomy, and that *Archaeopteryx* and most of the other early birds were a side line of avian evolution" (Gibbons, 1996d). Feduccia and Martin believe birds had already diverged into two lineages by the time of *Archaeopteryx*, but that the fossil record is still missing. They noted that one lineage led to modern birds; the other led to *Archaeopteryx* and the opposite birds, which they view as sister taxa. They believe that both bird lineages must have descended from a much earlier ancestral bird.

The specimens of *Liaoningornis* come from the same fossil beds that yielded the magpie-sized primitive bird (*Confuciusornis*) and the controversial "feathered" dinosaur *Compsognathus prima*. These fossil beds are approximately 124 million years old, placing them within middle Early Cretaceous time (Swisher et al., 1999). The next oldest ornithurine bird is *Chaoyangia*, from the Early Cretaceous of China (see Fig. 6.28c). It possesses a keeled sternum as well as premaxillary teeth.

In 1986, the fossil remains of a crowlike bird were discovered in Triassic deposits in Texas (Chatterjee, 1991). It is 75 million years older than *Archaeopteryx* and tentatively has been placed in the genus *Protoavis* (Fig. 6.31). Chatterjee's discovery remains highly controversial due primarily to similarities he sees between the skull and neck bones of *Protoavis* and the bones of modern birds. These structural similarities include a lightly built and pneumatized skull, evidence of movable upper jaws as in modern birds, a temporal region similar to that in modern birds; heterocoelous (saddle-shaped) neck vertebrae, and a relatively large brain-case. No feather impressions have been found, nor has a carpometacarpus been found. Circumstances surrounding this specimen and its scrutiny by qualified scientists have resulted in considerable controversy (Chatterjee, 1991; Ostrom, 1991). Critics speculate that Chatterjee's poorly preserved specimen was completely disarticulated when it was found and that it is likely to be a collection of bones from several unrelated species of small dinosaurs rather than the bones of a single individual. Many of the crucial skull bones are mere fragments, providing ambiguous evidence for the supposedly birdlike features of the skull. However, some prominent avian paleontologists see *Protoavis* as important new evidence that birds arose as a distinct group before the theropod dinosaurs arose, and they strongly support Chatterjee's position that *Protoavis* has too many birdlike features to be written off as a misinterpretation of a poor specimen (Anderson, 1991; Zimmer, 1992). Whether *Protoavis* was a bird ancestor or a genuine "early bird" remains to be answered.

Figure 6.31. *Protoavis texensis* from the Triassic in Texas.

In 1993, a turkey-sized predator (*Mononykus*, meaning “one claw”) with a mouthful of sharp teeth and a long tail was reported from the Upper Cretaceous of the Gobi Desert of Mongolia (Perle et al., 1993; Dashzeveg et al., 1995). It looked like a modern flightless bird but had bone structure characteristic of both birds and theropod dinosaurs. For example, in *Archaeopteryx*, the fibula touches the ankle; in modern birds and *Mononykus*, it does not. Both modern birds and *Mononykus* have a keeled sternum. Some of *Mononykus*’s wristbones were fused together, providing another adaptation for flight. Some researchers are skeptical: should *Mononykus* be considered a primitive flightless bird? Zhou (1995) refutes the avian status of *Mononykus* by concluding that many of its resemblances to extant birds, like the large, ossified, keeled sternum and reduced fibula, are digging adaptations or adaptations for bipedalism. Chiappe et al. (1997), however, maintain that Zhou’s methodology and anatomical comparisons fail to support his claim. The controversy continues.

A Giant Bird

The 450 kg (992 lb.) elephant bird (*Aepyornis*) formerly inhabited Madagascar (see Fig. 6.32). When humans arrived on the island (probably less than 2,000 years ago), elephant birds were subjected to intense ecological pressures (forest destruction and hunting of the birds and their eggs) that led to their final extinction around the year 1000. However, their gigantic eggs (see Fig. 6.33), weighing more than 9 kg (20 lb.) and equal in size and weight to eight ostrich eggs, are still found.

Wetmore, 1967; Page and Morton, 1989

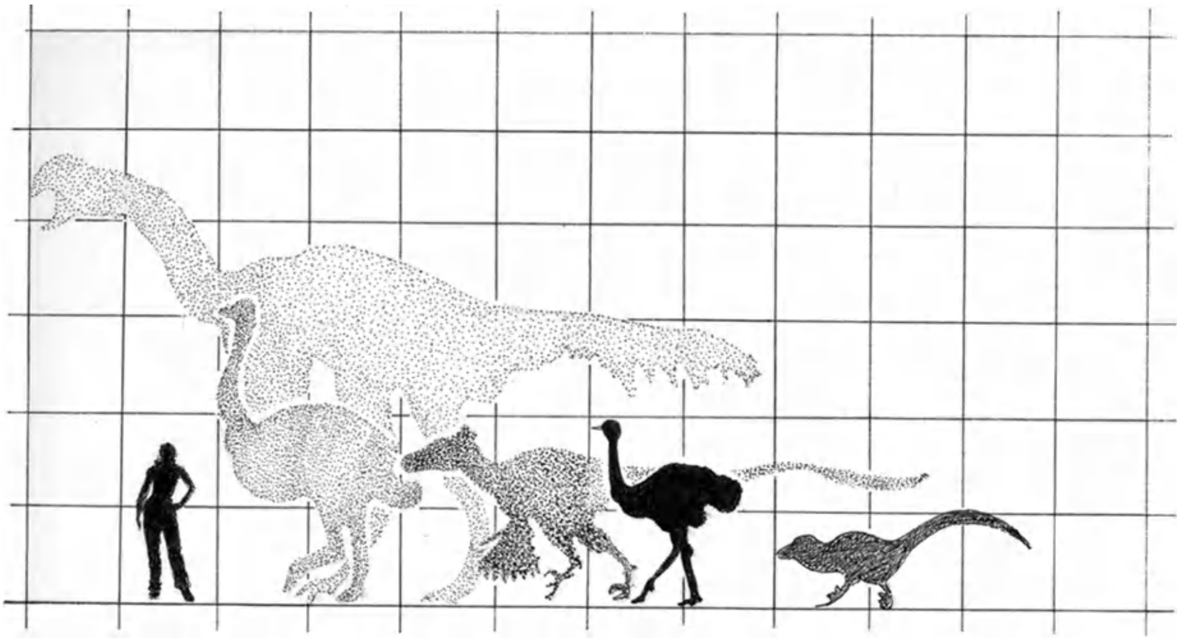


Figure 6.32. Size comparison of several giant birdlike dinosaurs and birds from various periods of geologic time, with modern human for scale. *From left*: *Gigantoraptor erlianensis*, an oviraptorosaurian dinosaur discovered in Inner Mongolia in 2005; the elephant bird, *Aepyornis maximus*, the world's largest bird with a height of more than 3 m (10 ft.) and weighing close to half a ton—400 kg (880 lb.); *Utahraptor ostrommaysorum*, the largest known member of the theropod dinosaur family Dromaeosauridae; *Struthio camelus*, an ostrich; and *Deinonychus antirrhopus*, a carnivorous dromaeosaurid dinosaur. Each grid segment = 1 square m.

In 2001, a juvenile duck-size theropod was discovered in China's Liaoning Province (Lemonick, 2001). Dating from 124 to 147 Mya, it has no fewer than three different types of feathers. The head sports a thick, fuzzy mat of short, hollow fibers, while the shoulders and torso have plumelike "sprays" of extremely thin fibers up to 5 cm (2 in.) long. The backs of its arms and legs are draped in multiple filaments arranged in a classic herringbone pattern around a central stem. Even the tail is covered with feathers, with a fan, or tuft, at the end. The find helps cement the dinosaur-bird connection, but it also casts new light on the mystery of why nature invented feathers in the first place. For the better part of a century, biologists have assumed that these specialized structures evolved for flight, but that is clearly not true. The feathers on this most recent dinosaur are not flightworthy, and the animals could not fly. They were too big, and they did not have wings. Thus, the original purpose of feathers might have been to keep dinosaurs warm and/or dry, to distract predators, or to attract mates.

A 0.9 m (3 ft.), 128-million-year-old fossil of a dromaeosaur that appears to have had full-fledged feathers was reported from China in 2002 (Norell and Clarke, 2001). Researchers said that the fossil reinforces the idea that at least some dinosaurs were warm-blooded creatures that needed feathers for insulation, not flight. The dinosaur appears to have had mature feathers identical to those of modern birds, including long, showy plumage on its tail and hind legs. Some of the feathers are more than 13 cm (5 in.) long. Hollow shafts and barbs that hold the feathers and their filaments are visible under magnification. Feathers also fringe the back of the forelimbs and hindlimbs, as well as the front and back of the hand. The dinosaur’s hollow bones were strikingly birdlike, and it had a killing talon on each foot. The dromaeosaur could not fly, but details suggest it would run toward its prey, then would silently glide in for the kill.

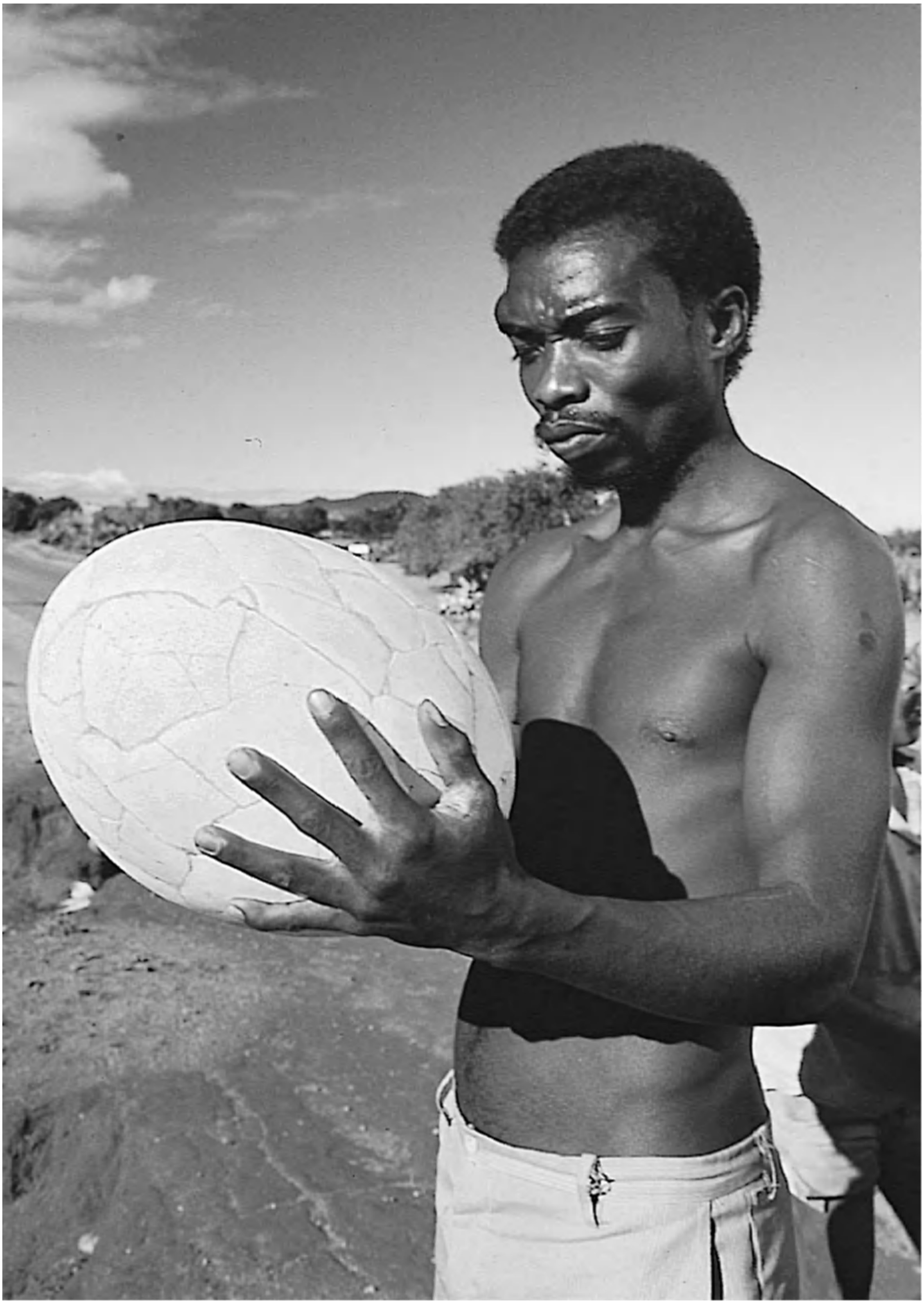


Figure 6.33. An elephant bird (*Aepyornis*) egg from Madagascar.

Modern Birds

Few modern orders of birds existed in the Late Cretaceous. The modern orders that did exist all belonged to what are termed “transitional shorebirds.” Bird fossils from the Cretaceous period (approximately 125 Mya) have yielded toothed birds with widely divergent skeletal structures that represent intermediate stages between *Archaeopteryx* and modern birds. These differences are indicative of the great radiation that took place in birds between the Jurassic and Cretaceous periods. The greatest radiation, however, occurred in the Cenozoic era. Most modern orders were fully differentiated by the Eocene epoch, but some made their first appearance in the fossil record of the Oligocene. The avian fauna during the Pleistocene was even richer than it is today. Feduccia (1995) hypothesized that birds endured massive Late Mesozoic extinctions, underwent a bottleneck at the Cretaceous-Tertiary boundary, and then experienced an explosive evolution in the Early Tertiary. He suggested that the explosive evolution that took place in the Early Tertiary produced all of the modern lineages within about 10 million years. If this is true, then former hypotheses attributing bird biogeography to drifting continents need to be reexamined (Cracraft, 1971, 1973, 1986; Sibley and Ahlquist, 1990; and others).

Joel Cracraft of the American Museum of Natural History continues to produce evidence that modern birds arose in the Southern Hemisphere (Pennisi, 2000b; Claramunt and Cracraft, 2015). Few fossils of modern birds exist prior to the mass extinction that occurred at the Cretaceous-Tertiary (K-T) boundary 65 Mya. Since most post-K-T fossils are found in the Northern Hemisphere, most researchers have assumed that modern birds arose on the giant continent called Laurasia, which included what is today North America, Europe, Asia, Greenland, and Iceland. Research combining fossil records with genetic and mtDNA data, however, indicates that some bird lineages date back to before the K-T boundary and that most bird lineages got their start on the great southern continent called Gondwanaland, which encompassed what is now Antarctica, South America, Australia, Africa, and India. The existence of land bridges facilitated the disjunct distribution of flightless species.

Origin of Flight

Theories concerning the origin of flight have been discussed and disputed since 1879–80, when two hypotheses—cursorial and arboreal—were proposed. The cursorial hypothesis supposes that the theropod ancestor was a cursorial, ground-dwelling form that held its arms out horizontally as it ran to capture insects and other food (Ostrom, 1974, 1985, 1994; Padian and Chiappe, 1998). The upward pressure of the air on the arms (held at a specific angle so that lift exceeded drag) is thought to have taken some of the weight off the feet. Some researchers conjecture that this would help the animal run faster, which would lead later to more continuous gliding flight, and finally to active flapping flight (Burgers and Chiappe, 1999). Others argue that it would slow the speed of running by removing the "traction" necessary for high speed. Frayed scales are thought to have gradually evolved into feathers for insulation. Those on the arms would increase the surface area and allow the theropods to take even more pressure off their feet. Albatrosses, geese, and swans today use a similar running-flapping method in order to get airborne but are forced to use longer takeoffs than other birds due to their relatively slow ground speed.

The arboreal hypothesis presupposes that the ancestors to birds were arboreal and that the arms and frayed scales served as parachute-like structures to aid the animal in jumping from branch to branch and to help break its falls. As feathered wings evolved, gliding from tree to tree or from tree to ground became possible. Only later would these ancestors evolve the ability to flap their wings and fly actively. Parachute-type structures and body modifications can be seen today in certain frogs, lizards, flying squirrels, and phalangers. Carter (1967), Bakker (1986), Norman (1991), and others have supported the climbing-and-gliding flier theory. Feduccia (1993) used claw geometry to conclude that *Archaeopteryx* appeared to have been a perching bird rather than a cursorial predator. The claws of both the foot and hand exhibit degrees of curvature typical of perching and trunk-climbing birds. Not all paleontologists agree (Morell, 1993b). Wellnhofer (1990) combined features of both the arboreal and cursorial theories into an arbocursorial, or climber-runner, theory.

The discovery of a small feathered dinosaur, *Microraptor gui*, in China from the Early Cretaceous period (125 Mya) revealed four "wings" (Xu et al., 2003; Chatterjee and Templin, 2007). Feathered flaps on the hind legs and feet, which served as the lower set of "wings" in flight, would have prevented it from running across the ground. Paleontologists say that *Microraptor gui*, which was about the size of a small hawk, was anatomically incapable of a wing-flapping takeoff from the ground. A computer simulation of the flight performance suggests that these biplane wings were adapted for undulatory gliding between trees, while the feathered feet helped with maneuverability. Modern raptors also have heavily feathered legs.

Turner et al. (2007) reported feather quill knobs in *Velociraptor mongoliensis*. The presence of quill knobs is a direct indicator of feathers of modern aspect (e.g., feathers composed of a rachis and vanes formed by barbs). The authors suggested that 14 secondaries were present in *Velociraptor*, which compares well with the 12 or more secondaries in *Archaeopteryx*. About 18 secondaries have been suggested for *Microraptor*.

Dial (2001; Dial et al. 2008) found that partridges routinely favor trees and other elevated spots for safety. Although these animals appear to fly up into trees, closer inspection revealed that in many cases they were actually running up—legs bent and body pitched toward the tree—while flapping their wings. Subsequent research revealed that wing-flapping assists in this vertical running by sticking the bird to the side of the tree, much as a spoiler helps to press a race car to a track. Although adult ground birds are generally perfectly capable of flying up into trees, their preference for running may stem from a time early in life when they could not yet fly: before a baby ground bird has the ability to launch itself into the air, the only means it has for getting off the ground is vertical running. When a juvenile is trying to evade a predator this way, the aid of even a partially formed wing can mean the difference between life and death. Perhaps a bird ancestor's proto-wing conferred the same benefit and therefore natural selection favored its development. Over time, wings evolved to the point of enabling not only vertical running but, when employed by an animal running across the ground, flight.

Review Questions and Topics

1. What is the significance of the extraembryonic membranes in reptiles and birds?
2. What adaptations did reptiles evolve that permitted them to live in xeric habitats?
3. What are the advantages and disadvantages of dinosaurs depositing their eggs in nests and caring for their young?
4. What advantages were gained by some dinosaurs growing to enormous size?

5. Why do reptilian bones generally grow in spurts and produce annual rings of growth, whereas bird and mammal bones do not form annual rings?
6. Which group is considered the most recently evolved group of reptiles—lizards, snakes, or crocodilians? Why?
7. Which characteristics are shared by reptiles and birds?
8. (a) List some of the reptile-like characteristics of *Archaeopteryx*. (b) List some of the birdlike characteristics of *Archaeopteryx*.
9. Discuss the two major theories concerning the origin of flight in birds.
10. Do you think that the fossil record will ever be complete? Why or why not?

Supplemental Reading

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Vertebrate Internet Sites

1. Fossil Secrets Revealed: X-Ray CT Scanning and Applications in Paleontology

www.researchgate.net/publication/316518116_FOSSIL_SECRET

High-resolution X-ray computed tomographic (X-ray CT) scanner-prepared visualizations of skull bones.

2. Testudines: Turtles, Tortoises, and Terrapins

   www.tolweb.org/Testudines

   Characteristics, fossil forms, phylogenetic relationships, ecology, physiology, and more.

3. Sea Turtle Evolution

   www.seaturtle-world.com/sea-turtle-evolution

   Sea turtle facts, types of sea turtles, sea turtle conservation, photos, videos, and many links.

4. Synapsida

   www.tolweb.org/Synapsida

   Characteristics, physiology, phylogenetic relationships, references, and links.

5. Introduction to the Pterosauria

   www.ucmp.berkeley.edu/diapsids/pterosauria.html

   Types, anatomy, physical characteristics, and links.

6. Fossil Record of the Aves

   www.ucmp.berkeley.edu/diapsids/birds/birdfr.html

   Description of fossil birds and links to other sites.

7. The Dino Directory: Natural History Museum

   www.nhm.ac.uk/discover/dino-directory.html

   Facts, figures, and images for more than 300 dinosaurs.

7 | Morphology, Reproduction, and Development of Turtles, Tuataras, Lizards, and Snakes (Testudines and Lepidosauria)

Reptiles and amphibians are sometimes thought of as primitive, dull and dimwitted. In fact, of course, they can be lethally fast, spectacularly beautiful, surprisingly affectionate, and very sophisticated.

Sir David Attenborough, 2015

INTRODUCTION

Reptiles, comprising more than 18,700 of the more than 66,800 species of vertebrates, include turtles (300 species), tuataras (2 species), lizards (4,675 species), snakes (3,000 species), crocodilians (26 species), and birds (10,711 species). With the evolution of internal fertilization and the amniote egg, reptiles became the first fully terrestrial vertebrates.

MORPHOLOGY

Integumentary System

Turtles and lepidosaurs possess scales that, unlike the scales of fishes, are formed mainly from epidermal layers. The dry, scaly epidermis, which may be six or more layers in thickness, serves primarily for protection and to reduce water loss. Some snakes utilize the broad, flat scales, known as scutes, on the undersides of their bellies to aid in locomotion. In turtles, the shell of dermal plates (Fig. 7.1a, b) is covered by horny, keratinized scales (also known as shields or scutes) (Fig. 7.1c, d). The embryonic origin and morphology of the integument in reptiles is discussed by Maderson (1985).

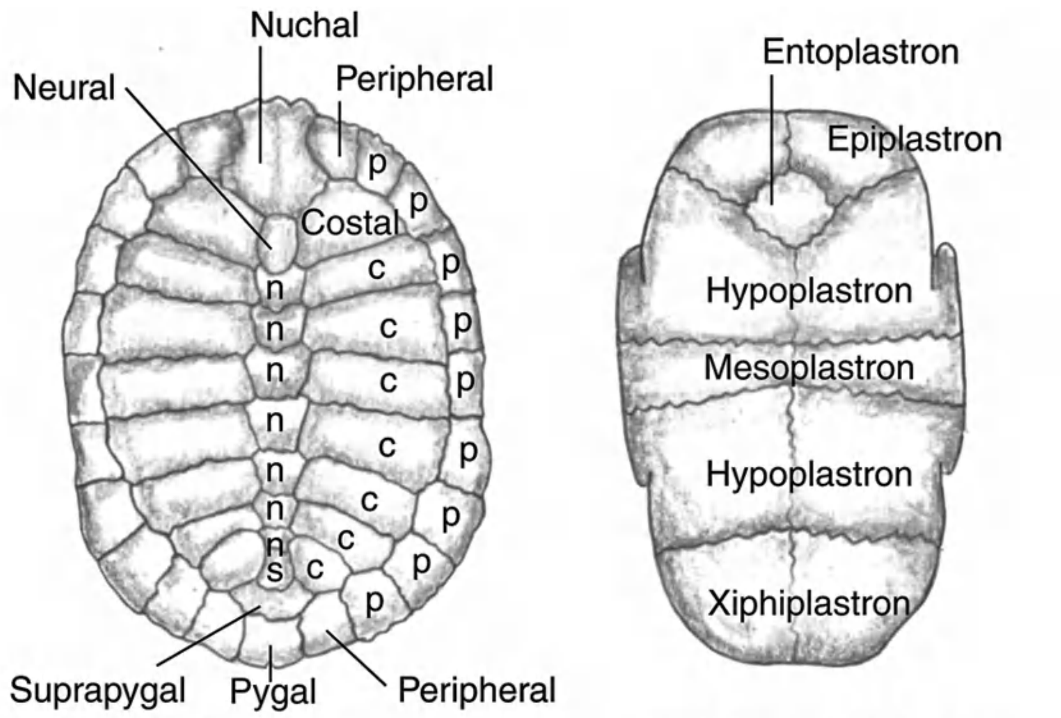
In squamates (snakes and lizards), the epidermis consists of a stratum corneum (outer tissue layer) and a stratum intermedium (middle tissue layer) above the stratum basale (basal cell layer) (Fig. 7.2a, b). In most lizards and snakes, a continual body covering of scales develops from the stratum corneum, with each scale projecting backward to overlap part of the one behind (Fig. 7.3). In turtles, however, each epidermal scale develops separately, so that the scales do not form a solid sheet. The number and arrangement of epidermal scales on the body is usually species-specific and is used extensively in classification.

The stratum corneum is sloughed and replaced either a few cells at a time or in patches, or it is shed at intervals in one piece, a process known as **ecdysis**. Healthy snakes usually shed their skins in one piece, whereas most lizards normally shed their skin in a number of pieces (Fig. 7.4). Old scales on some turtles peel off; in other species of turtles, the scales remain and give the shell a roughened texture.

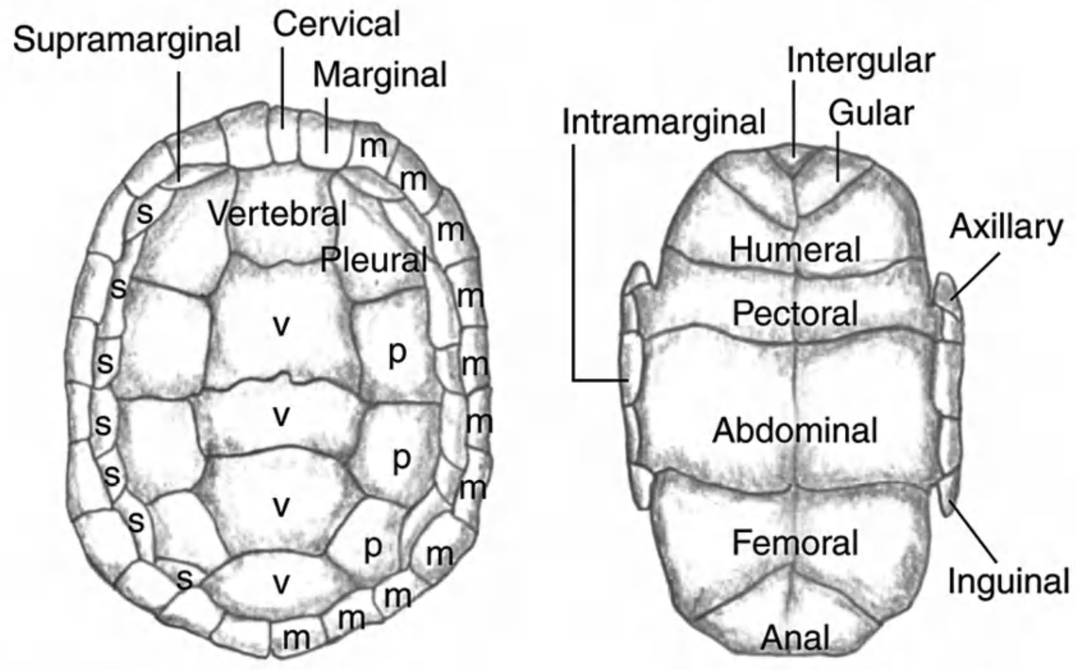
When ecdysis begins, the two epidermal layers separate simultaneously over the entire body, and the outer layer is removed (see Fig. 7.2). The stratum corneum is loosened primarily through the diffusion of lymph and white blood cells between the old and new layers. Shortly before shedding begins, the separation of the scales covering the eyes of snakes causes the eyes to become cloudy. As the outer layer of epidermis is removed, the inner layer becomes the new outer layer. Ecdysis normally begins in the head region and is initiated by an increase in blood pressure that causes the head to enlarge. This swelling causes the outermost layer of cells to loosen and rupture. Then, by means of the animal’s rubbing and crawling movements, the remainder of the outer layer is removed. After a week or so, the stratum germinativum will have produced enough new cells through mitosis to form a new inner tissue layer. Frequency of shedding varies with species, age, and the health of the animal.

Few integumentary glands are present in reptiles. Those that are present (musk, femoral, pre-anal, cloacal, and nuchodorsal) either secrete strong-smelling substances that may be obnoxious to potential predators or serve for species and sex recognition (pheromones) during breeding. No sweat glands are present.

Scales, claws, rattles, horny protuberances, and spines are all keratinized modifications of the epidermis. **Claws**, which first appeared in turtles and have persisted in birds and most mammals, are shed periodically in turtles and lepidosaurs; however, in birds and mammals, claws, nails, and hooves are worn down by abrasion.



(a) Bones of carapace **(b) Bones of plastron**



(c) Scales of carapace **(d) Scales of plastron**

Figure 7.1. Dermal bones forming the carapace (*a*) and plastron (*b*) of a turtle. Epidermal scales covering the carapace (*c*) and plastron (*d*) of a turtle.

Many lizards can climb vertical surfaces readily by using their sharp claws. Some climbing lizards, like geckos and anoles, utilize “dry” adhesion systems on their toes as additional aids when climbing on steep, smooth surfaces and overhangs (Cartmill, 1985; Autumn et al., 2002) (Fig. 7.5a, b). Autumn et al. (2002) have reported the first direct measurement of the adhesive function of the gecko’s feet. It has nothing to do with sticky toes, suction cups, or even a Velcro effect. The secret to the gecko’s grip hinges on a property of quantum mechanics known as the van der Waals forces. Named after the nineteenth-century Dutch physicist who first described them, the van der Waals forces occur when atoms come close to one another and—for a fleeting instant—display a weak electrical attraction. Although the forces are too weak to be felt by humans, when, for example, they press a palm to the wall, the gecko uses millions of microscopic pads to make contact with a surface. On the underside of each toe are approximately 20 broad, overlapping scales (lamellae) consisting of numerous minute setae composed of keratin (Ruibal and Ernst, 1965; Ernst and Ruibal, 1966). Up to 150,000 hairlike setae are located on the exposed surface of each lamella. The setae split into as many as 1,000 tinier hairlets, or bristles, each capped with a triangular pad, or endplate, whose shape has been likened to a hamburger flipper. These tips, called spatulae, are about the size of a small bacterium. As the gecko walks, it rolls these tiny hairs on the surface. When the spatulae are at the proper angle and proper pressure against the wall, they are so close together that they generate the same binding force that holds molecules together. To release the animal’s grip, the setae unroll or peel off. A single seta can lift an ant. If all the hairs worked simultaneously, they could theoretically hoist a 126 kg (280 lb.) man. Thanks to technology inspired by geckos, engineers have developed robots that can climb walls, created a glue, known as Geckel, that behaves like the adhesive on a Post-it Note but also works on wet surfaces, and even designed gecko-inspired climbing equipment.

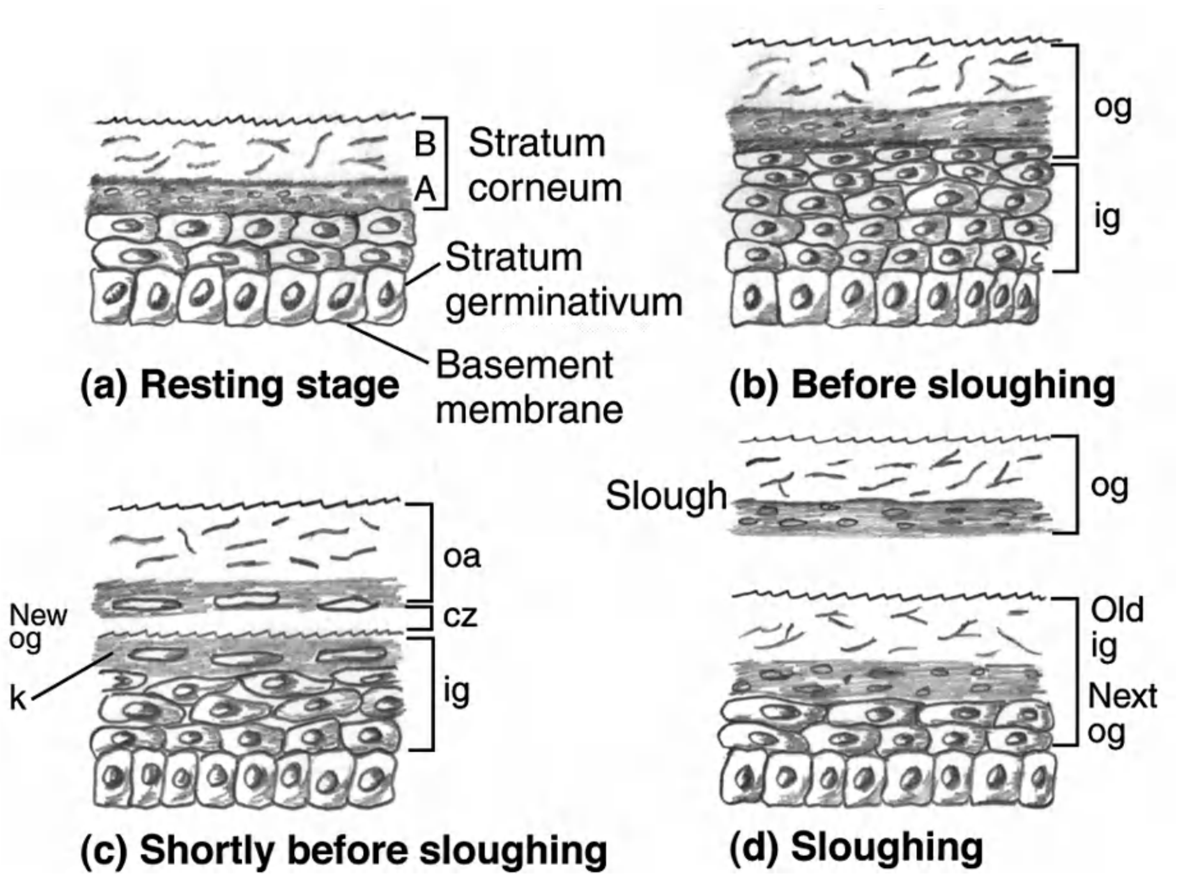


Figure 7.2. Simplified diagrams showing changes in the epidermis during the sloughing cycle of a snake. (*a*) Resting stage. (*b*) Before sloughing. The basal cells have divided to form a new, inner epidermal generation (ig). The snake's color is dulled. (*c*) Shortly before sloughing. A cleavage zone appears between the two generations; the superficial part of the inner generation is becoming keratinized (k), and a new serrated outer epidermal generation (og) is being formed. This stage probably coincides with the clearing of the skin. (*d*) Sloughing. The original outer generation is shed, and the old inner generation becomes the next outer generation.

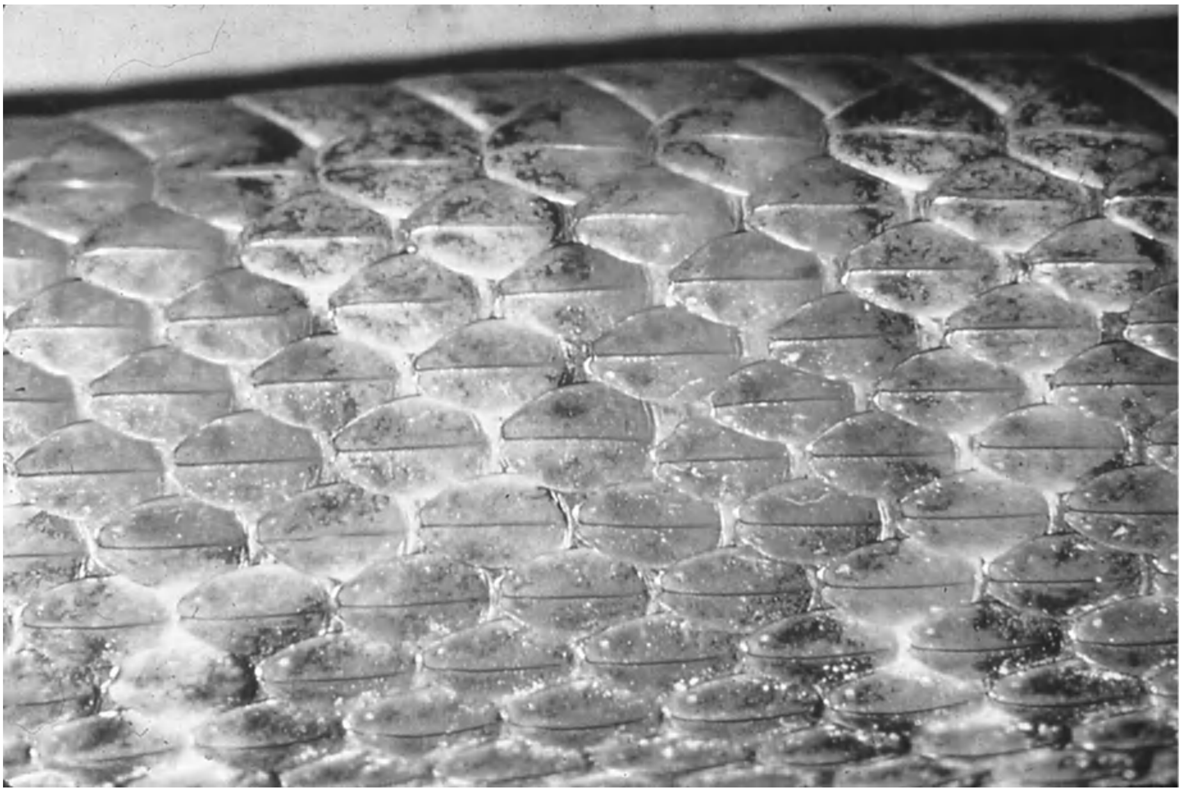


Figure 7.3. Epidermal scales of a corn snake, *Pantherophis* (formerly *Elaphe*) *guttata*. Note the keels on each dorsal scale.

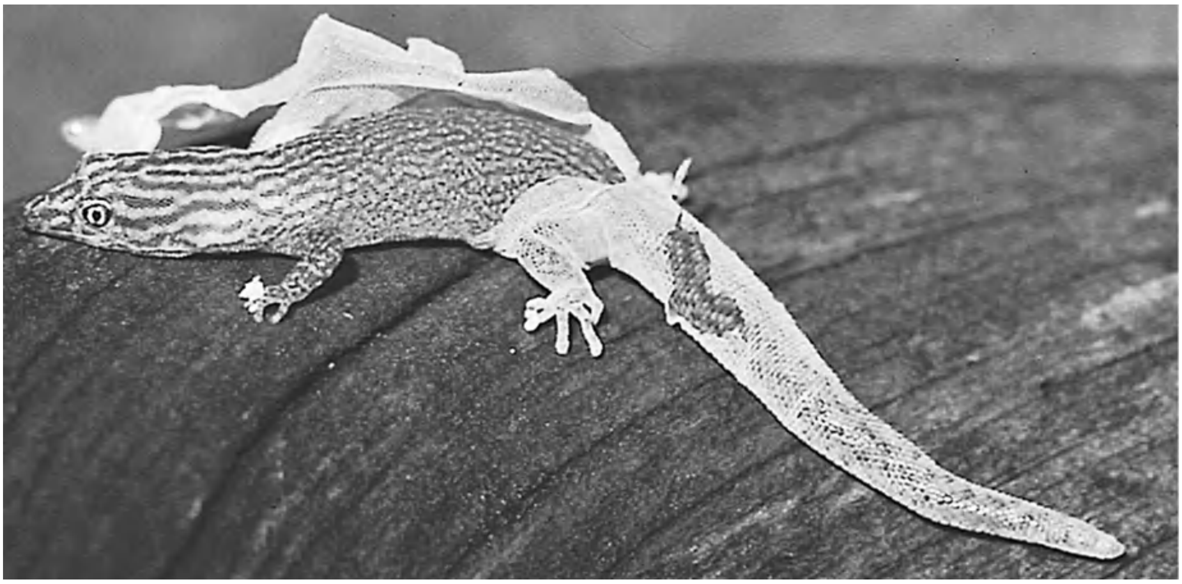


Figure 7.4. Ecdysis in a lizard. Most lizards shed their skin in pieces, whereas healthy snakes usually shed their skin in one piece.

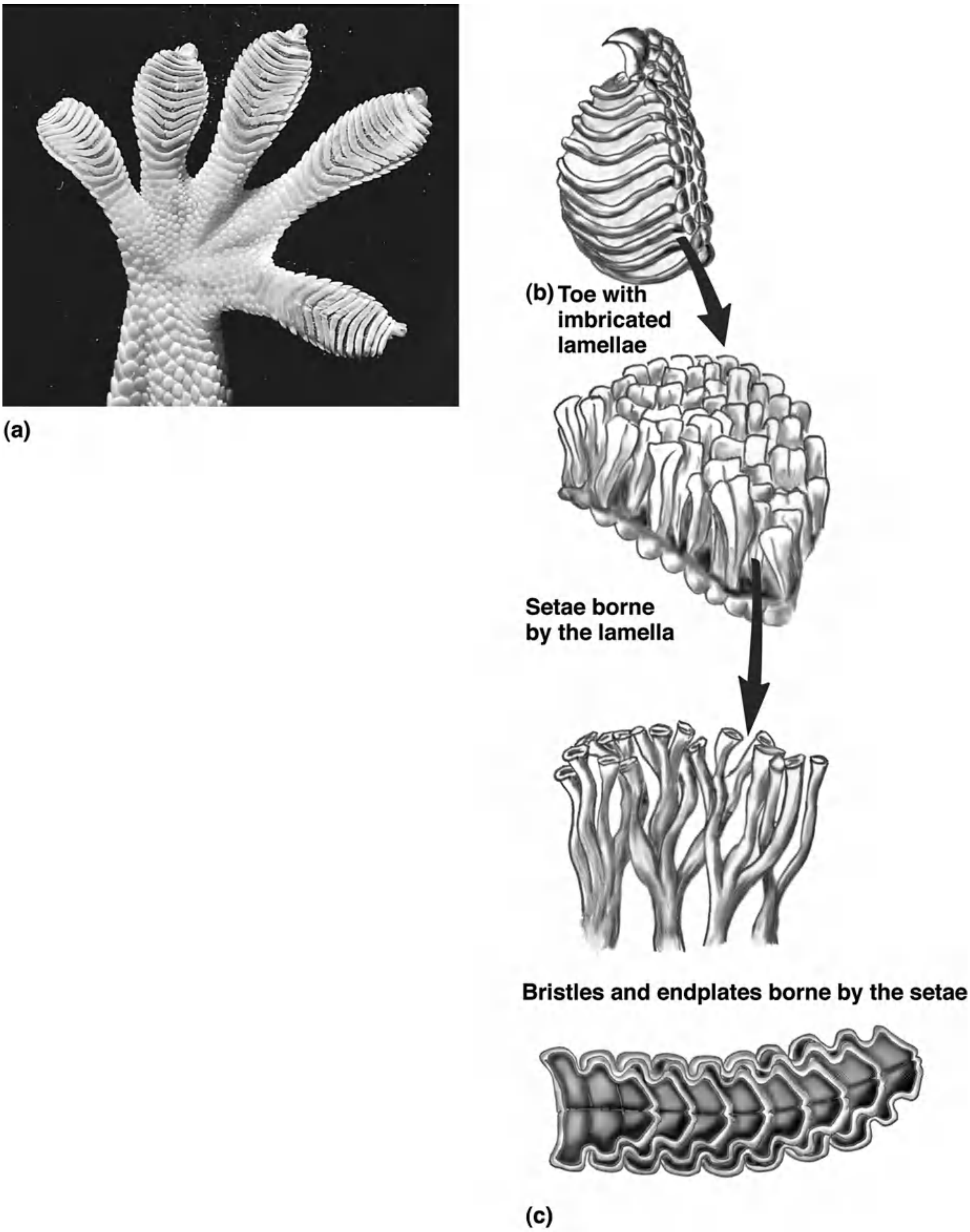


Figure 7.5. Modifications of the stratum corneum of lizards and snakes. (*a*) The toe pads of climbing lizards like geckos employ "dry" adhesion systems as additional aids when climbing on steep, smooth surfaces and overhangs. (*b*) The lamellae of the toes are composed of many setae, whose distal ends bear bristles and endplates. (*c*) One modification of the stratum corneum in reptiles is the rattlesnake's rattle, which consists of pieces of thickened skin left behind each time the snake sheds.

Hansen and Autumn (2005) discovered that the gecko's feet contain a self-cleaning adhesive. Unlike artificial adhesives, the millions of microscopic hairs embedded in a gecko's toes counteract the force of gravity, while at the same time repelling dirt. They calculated that a particle of dirt is too small to be attracted by the number of setae required to overcome the pull from any surface.

Rattlesnake **rattles** are modified portions of the stratum corneum that remain attached to the tip of the tail following each ecdysis (see Fig. 7.5c). The rattles interlock in such a way that they fit together more tightly dorsally than ventrally. The rapid oscillation of the tail and its horny appendage produces the characteristic buzzing sound of an agitated rattlesnake. Because lobes of the rattle often are broken off accidentally, and because snakes may shed their skins several times a year, the age of a rattlesnake cannot be determined accurately by simply counting the number of segments in the rattle.

The **horns** of the horned "toad" (a lizard) (*Phrynosoma* sp.) are bony projections of the occipital bone of the skull covered with scaly integument, whereas the hornlike processes on the head of the sidewinder rattlesnake (*Crotalus cerastes*) are exclusively integumental in origin. A horny sheath of stratum corneum covered the beaks of some extinct reptiles and continues to cover the beaks of living turtles.

The dermis of a reptile consists of a relatively loosely packed superficial layer and a much more densely packed deeper layer. As in other vertebrates, it consists of fat cells, nerve fibers, blood vessels, and chromatophores.

The skin of cotylosaurs (stem reptiles) was heavily armored with large bony dermal scales. Today, turtles are the most armored members of this group, with a shell consisting of large, bony, dermal plates (see Fig. 7.1a, b). The dorsal arched portion of the shell is the **carapace**; the ventral, flattened portion is the **plastron**. These are united by bony **lateral bridges**. Nuchal and costal plates of the carapace are fused with vertebrae, and each costal plate is united with a rib. Soft-shelled and leatherback sea turtles have leathery shells because the dense collagenous connective tissue of the dermis does not become ossified. A few lizards, like skinks and glass lizards, have similar, but smaller, bony dermal scales (osteoderms) that serve to reinforce their scales.

The dermis of reptiles has an abundance of **chromatophores**, which are responsible for elaborate color patterns. Although several speculative mechanisms for pigment pattern formation have been proposed, the actual mechanism of color pattern formation is not known. Some lizards, like chameleons, change their color in response to environmental stimuli by concentrating and dispersing pigment granules. Coloration may be protective (camouflage and warning patterns), may reflect dominant social status, may serve for sex recognition, or may be important in thermoregulation.

Color patterns of many snakes involve spots or stripes. Spotted patterns are usually thought to serve as camouflage and are most common in species that feign immobility when approached. Stripes, which make it hard to judge the speed of a moving object, are characteristic of species that flee when threatened. Brodie (1989) demonstrated a genetic link between behavior and pattern in newborn garter snakes (*Thamnophis ordinoides*) in which striped individuals tended to flee, whereas spotted individuals tended to remain motionless.

Skeletal System

Skeletal modifications for terrestrial life that originated in amphibians are developed further in reptiles. The skeleton shows numerous modifications for muscle attachment, varied dietary habits, and terrestrial locomotion. Reptiles can better support their body weight and, in many cases, can move with great speed. Papers discussing various aspects of the skeleton are included in Gans et al. (1969).

Adult reptilian skulls differ from those of amphibians in many ways (see Fig. 5.13). A single occipital condyle is present, the skull has a higher and narrower shape, a greater degree of ossification is present, and a reduction of bones through loss and/or fusion has occurred. A partial secondary palate is present in many turtles.

Quadrate and articular bones form in the skull from gill arch supports. The hyomandibular becomes the columella (stapes) in the middle ear, and the roof of the skull, palate, and lower jaw become ensheathed in dermal bones. The symphysis of the anterior ends of the two dentaries, the major tooth-bearing bones in the lower jaw, is a rigid suture in some turtles and some lizards, but in snakes and many lizards it is connected by ligaments. Independent movement of the upper jaw on the braincase is well developed in some snakes and allows for great distensibility of the mouth, an adaptation necessary for swallowing large prey. Some palatine bones, as well as the jaws, are connected so loosely to the skull that each half of the upper and lower jaws can move independently of each other (see discussion under Digestive System, pages **190–91**).

Amphibians and many reptiles swallow their food whole; thus, having internal nares in the anterior portion of the oral cavity presents no problem. Others (especially nonmammalian synapsids) tear, crush, and chew their food before swallowing. To avoid interrupting their breathing, it became necessary to get air into the pharynx posterior to the chewing mechanism.

Turtles developed a secondary palate below the primary palate. The secondary palate, which separates the nasal passages from the oral cavity, serves to increase the length of the nasal passages and permits an animal to breathe while processing food in its mouth. This latter adaptation (ability to breathe and chew food simultaneously) is seen as a link to the development of higher metabolic rates, leading to the origin of endothermy in Therapsida. Lepidosaurians (lizards, tuataras, and snakes) lack a secondary palate.

A feature seen for the first time in the evolution of vertebrates is the development of either one or two pairs of **fenestrae** (fossae) in the temporal region of the skull (see Figs. 6.2 and 6.5). These fenestrae provide additional surface area for stout muscles that originate from the temporal region of the skull and insert on the lower jaw, enabling it to close with increased pressure. Temporal fenestrae are major characters used in reptilian classification systems.

Stem reptiles (order Cotylosauria) lacked fossae, a condition referred to as **anapsid**. Today, the only living reptiles with anapsid skulls are turtles (order Chelonia). Extinct mammal-like reptiles (order Therapsida) developed a single pair of temporal fossae low on each side of the skull. This **synapsid** type of skull is found in extant mammals. **Diapsid** skulls have two pairs of fossae (superior and inferior) on each side of the skull. Diapsid skulls are characteristic of extinct archosaurs, surviving archosaurs (crocodilians), and the tuatara (*Sphenodon*). Lizards, snakes, and birds have modified diapsid skulls.

The reptilian vertebral column has undergone additional modifications and exhibits a wide range of types and arrangements of vertebrae. Snakes have the longest vertebral columns, with up to 500 vertebrae (Fig. 7.6). Most turtles and lepidosaurs have a variable number of cervical vertebrae. In addition, for the first time in the evolution of vertebrates, the first two cervical vertebrae have become modified to permit movements of the head in several directions. The first vertebra (atlas) is ringlike because most of its centrum has been detached. It articulates with the single occipital condyle on the skull. The second cervical vertebra (axis) has an anterior projection, known as the **dens** (or **odontoid process**), which rests on the floor of the atlas when the two vertebrae are articulated. It represents the detached centrum of the atlas. Cervical vertebrae of turtles are loosely articulated in order to allow the neck to be pulled back into the shell.

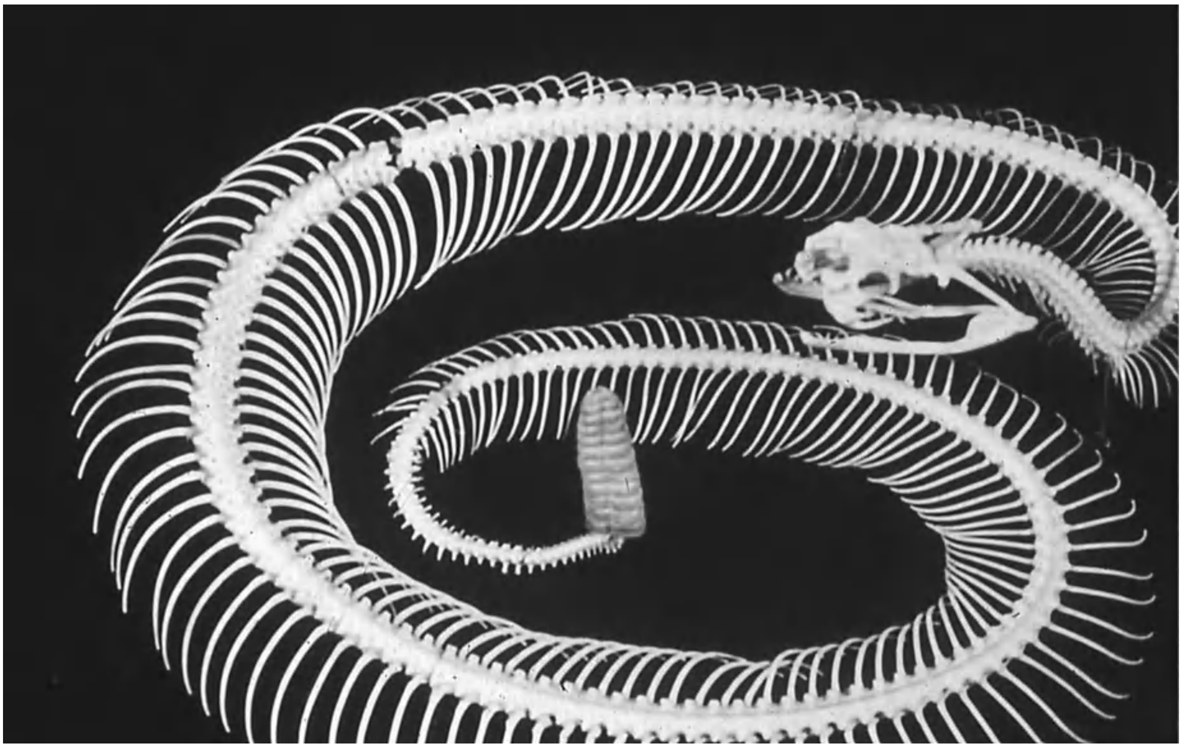


Figure 7.6. This rattlesnake skeleton has several hundred vertebrae and ribs. The large number of vertebrae gives the snake flexibility and allows it to bend and twist more than most vertebrates.

In most lizards, trunk vertebrae have differentiated into **thoracic** vertebrae that bear ribs, and **lumbar** vertebrae with ribs greatly reduced or are absent. The vertebral column of snakes and legless lizards is divided into two regions: a **precaudal** (anterior to the vent) series of vertebrae, which bear free ribs, and a **postcaudal** (posterior to the vent) series, with ribs either fused to the vertebrae or absent altogether. **Zygapophyses** (processes by which adjacent vertebrae articulate to one another) strengthen intervertebral joints. Most living reptiles possess two sacral vertebrae, which are usually fused to form a single bony complex, the **sacrum**, to support the pelvic girdle. The stronger sacrum provides the support necessary for raising the body off the ground as reptiles walk; some lizards and dinosaurs even adopted a bipedal mode of locomotion.

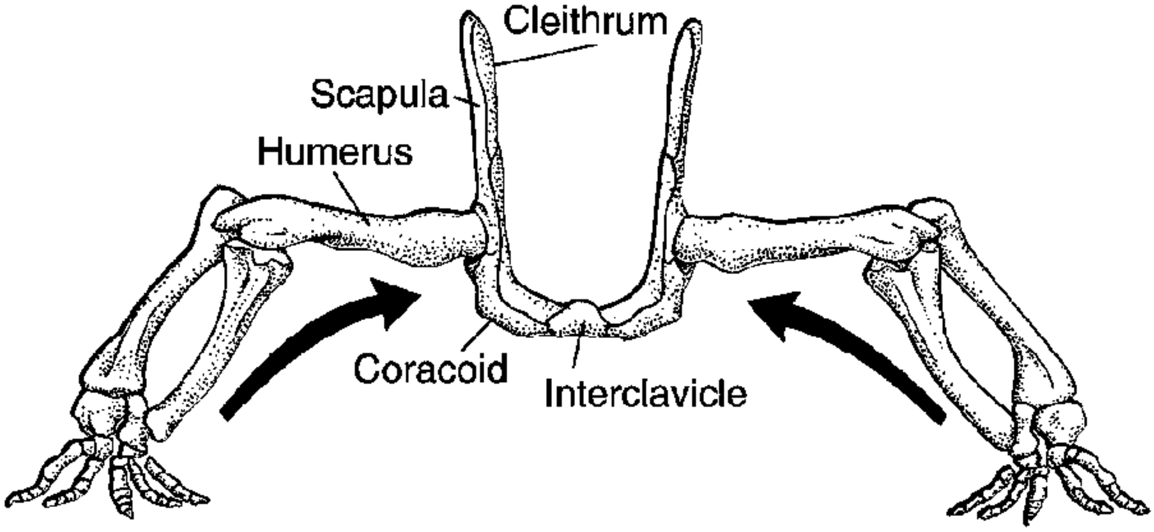
All reptiles have a distinct tail composed of many caudal vertebrae. A unique characteristic possessed by many lizards and a few snakes is the ability to break off their tails in order to avoid capture, a process known as **caudal autotomy**. This ability is possible because the centrum and part of the neural arch of each caudal vertebra are divided in half by an area of soft tissue. The plane of fracture occurs at this point, and most of the lost portion of the tail will regenerate. Caudal autotomy as a defense mechanism has been discussed by Dial and Fitzpatrick (1983) and Arnold (1988).

All vertebrae from cervical to caudal may have ribs. The ribs of turtles, as well as the neural arches of the dorsal, sacral, and first caudal vertebrae, are fused with the carapace. Posterior cervical and anterior dorsal ribs of tuataras each bear a curved cartilaginous **uncinate process**, which projects posteriorly to overlap the rib behind, presumably giving strength to the thoracic body wall. In "flying dragons" (family Agamidae), five to seven posterior trunk ribs are greatly elongated to support large, thin membranes, which allow these lizards to glide distances up to 60 m (197 ft.). A mostly cartilaginous sternum is present in some lizards, although it is absent in snakes, legless lizards, and turtles. When present, the sternum consists of a plate to which thoracic ribs attach.

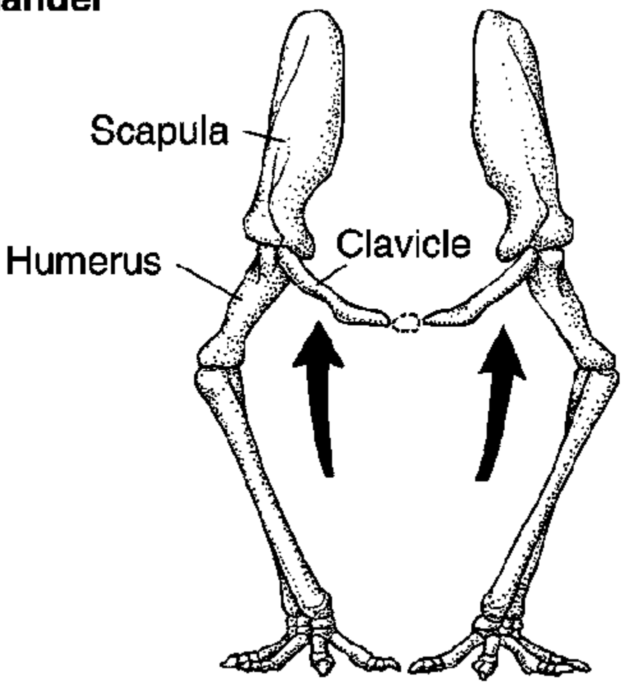
The limb structure shows considerable variation related to the burrowing, terrestrial, arboreal, or aquatic habits of these reptiles. Methods of locomotion include lateral undulation on both land and in water (swimming), as well as bipedal and quadrupedal gaits.

Most snakes and some lizards lack an appendicular skeleton. Clavicles are reduced or absent from the pectoral girdle in legless lizards, and the entire pectoral girdle is missing in snakes. In turtles, the clavicles are fused with the carapace.

Limbs are typically pentadactyl, with five digits normally present on both the front and rear feet. Elements of the anterior limb are similar to those in salamanders (Fig. 7.7a). In most reptiles, a rotation of the appendages toward the body causes the long axis of the humerus and femur to lie more nearly parallel to the body. A moderate bend at the elbow and knee allows the front limbs and hindlimbs to be directed somewhat vertically, and the elbow is directed **caudad** (toward the tail). Limbs oriented in this fashion can better support the weight of the body and serve as more efficient shock absorbers. In addition, by having the body moderately elevated above the ground, greater speed and agility are possible. Such reorientation was an essential step toward bipedalism in reptiles. Even with this reorientation, the position of the limbs among modern quadrupedal reptiles remains a sprawling one. Complete and more efficient elevation comes from the limb-girdle arrangement found in birds and mammals (Fig. 7.7b).



(a) Salamander



(b) Placental mammal

Figure 7.7. Evolution of limb structure. (*a*) Salamander. The sprawled posture of the salamander was typical of fossil amphibians as well as of most reptiles. (*b*) Placental mammal. This posture began to change in synapsids, so that in late therapsid reptiles the limbs were thought to be carried more beneath the body, resulting in better support and more rapid locomotion. As a result of the change in limb posture, the shoulder girdle also became modified. A sprawled posture brings a medially directed force toward the shoulder girdle, with medial elements playing a major role in resisting these forces. As limbs were brought under the body, these forces were directed less toward the midline and more in a vertical direction. This position of the limbs might account for the loss of some elements of the pectoral girdle in those phylogenetic lines in which the limb posture shifted.

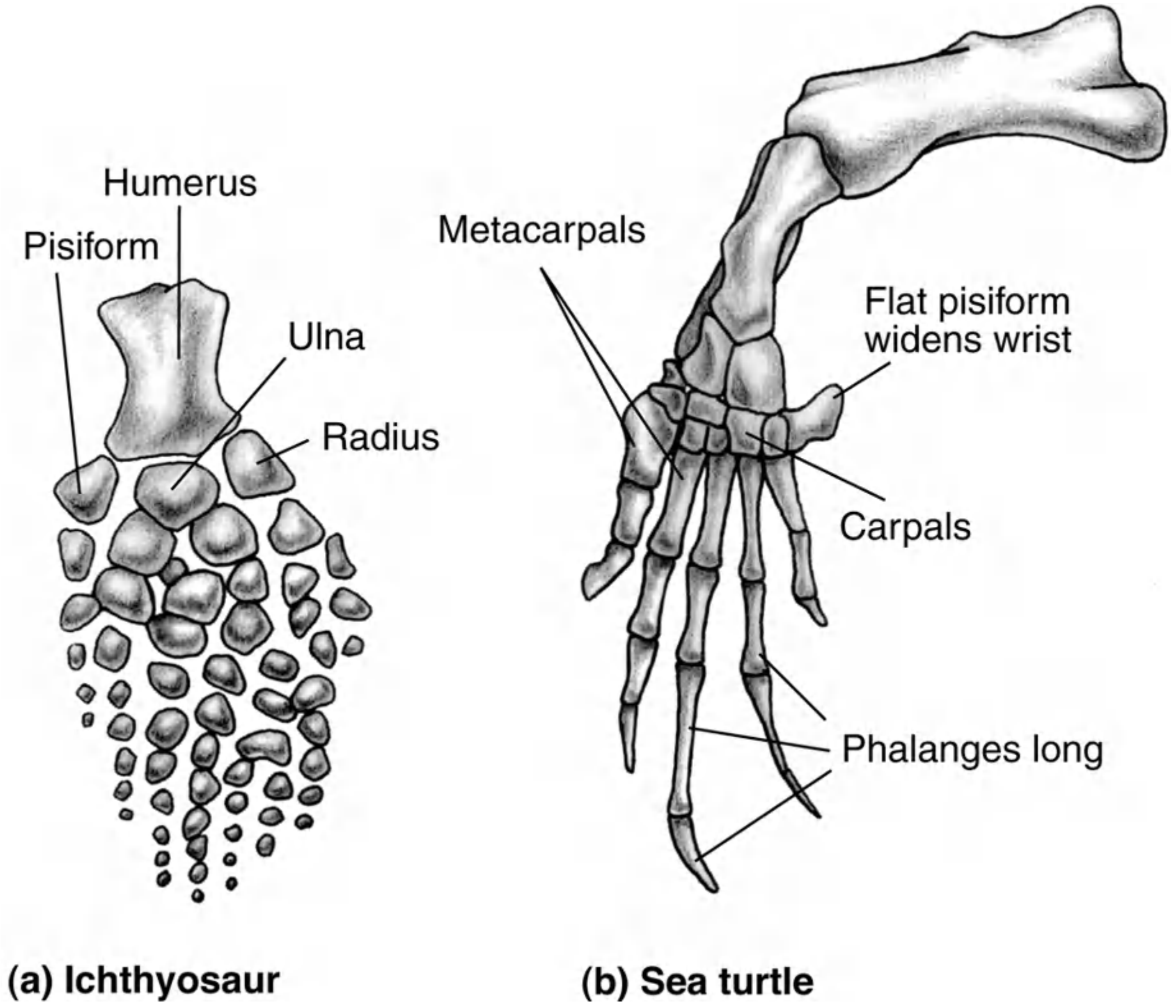


Figure 7.8. Front limb of (*a*) an ichthyosaur and (*b*) a sea turtle (*Chelonia*). The limbs are short and stout and often have an increased number of phalanges.

Modification of the front limb occurred in aquatic reptiles like ichthyosaurs, plesiosaurs, and sea turtles (Fig. 7.8). The short, stout appendages tend to become flattened and paddle-shaped, and in some, the number of phalanges is greatly increased. Aquatic and semiaquatic reptiles often have webbing between the toes.

Each half of the pelvic girdle consists of a pubis, ischium, and ilium. The ilium is braced against two sacral vertebrae and tends to become broader for the attachment of larger hindlimb muscles, particularly in dinosaurs and lizards that carry the trunk elevated well above the ground. In reptiles that have lost the hindlimbs, the pelvic girdle has been reduced (legless lizards) or lost (most snakes).

Bony elements in the posterior limbs of reptiles are similar to those in amphibians. The knee is directed anteriorly, and the ankle joint is located between two rows of tarsal bones rather than between the tarsals and the tibia and fibula. A **patella**, or kneecap, is present for the first time evolutionarily and occurs in certain lizards.

The order Squamata (lizards and snakes) is the only group of vertebrates in which there has been evolutionary losses of limbs and redevelopment of undulatory body movements. Snakes are thought to have evolved from lizards and to have lost both pairs of limbs as well as both girdles. Some primitive families like the Boidae, however, still possess vestigial pelvic girdles and/or rear legs (Fig. 7.9a, b). Different stages of reduction and loss of limbs are found in lizards. Some possess only vestiges of forelimbs, some have only hindlimbs, and others, like glass lizards (Anguidae), have lost all of their limbs.

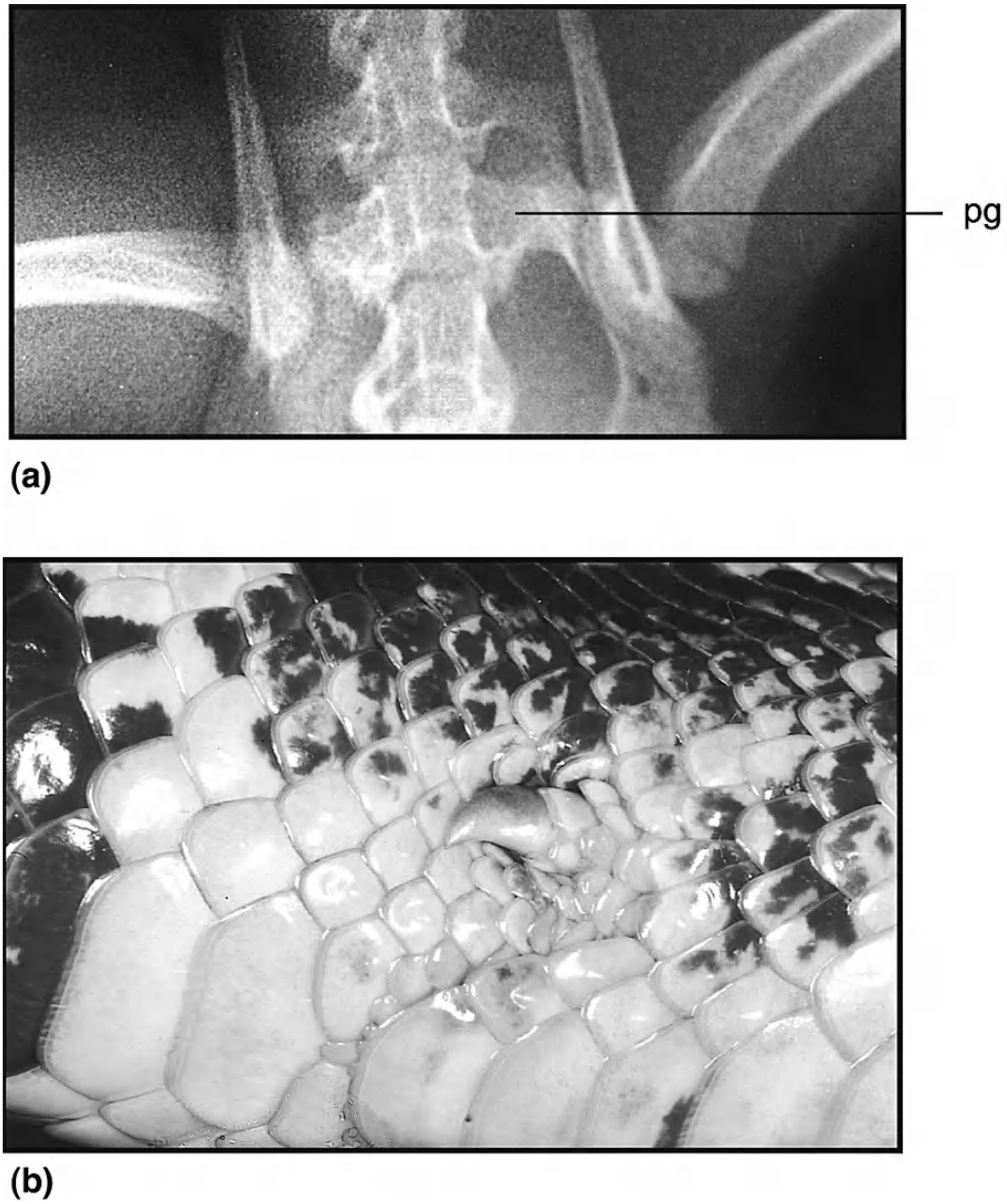


Figure 7.9. (*a*) The pelvic region of a boa constrictor, showing its vestigial pelvic girdle (*pg*). (*b*) The presence of a vestigial pelvic limb in boas, pythons, and a few other groups is associated with small claws or spurs located on either side of the vent. Male boas and pythons use their spurs, which are often longer than those of females, to stimulate females during courtship.

Most species that lack limbs (snakes, legless lizards) move by **horizontal undulations** (Fig. 7.10a). This method, in which all parts of the body move along the same wavy track, is efficient on the ground as well as in trees. Its effectiveness is diminished, however, when the substrate lacks fixed surfaces or when the fixed surfaces are too widely spaced. Under these latter conditions, most snakes use **concertina-**like movements in which the stationary portion of the body is bent into a series of *S*-shaped coils from which the moving anterior portion straightens and then bends again (Fig. 7.10b). The posterior coils press downward and backward against the substrate, relying on friction to prevent slipping. This method is used extensively by climbing and burrowing species like boids and rat snakes (*Elaphe*).

During **rectilinear** locomotion, the skin is drawn forward, the belly scales (scutes) make contact with the surface and provide stationary points, and then the body is pulled forward by the scutes (see Fig. 7.10c). Muscles that slant backward and downward from the ribs to the scutes cause the ventral skin, which fits loosely and is very distensible, to bunch at several regions so that the scutes overlap. Between these regions, the skin is stretched. Where scutes are bunched, they rest on the ground to support the animal's weight; where stretched, they are lifted off the ground. One by one, additional scutes are drawn into each bunched region from behind as others are stretched away anteriorly. Friction of the bunched scutes against the substrate prevents slipping. Muscles that slant backward and upward from the scutes to the ribs pull the body along within the skin. The body is held in a straight line and moves directly ahead. Rectilinear movement is slow and may be used by snakes and worm lizards (amphisbaenians) when stalking prey or moving in narrow tunnels.

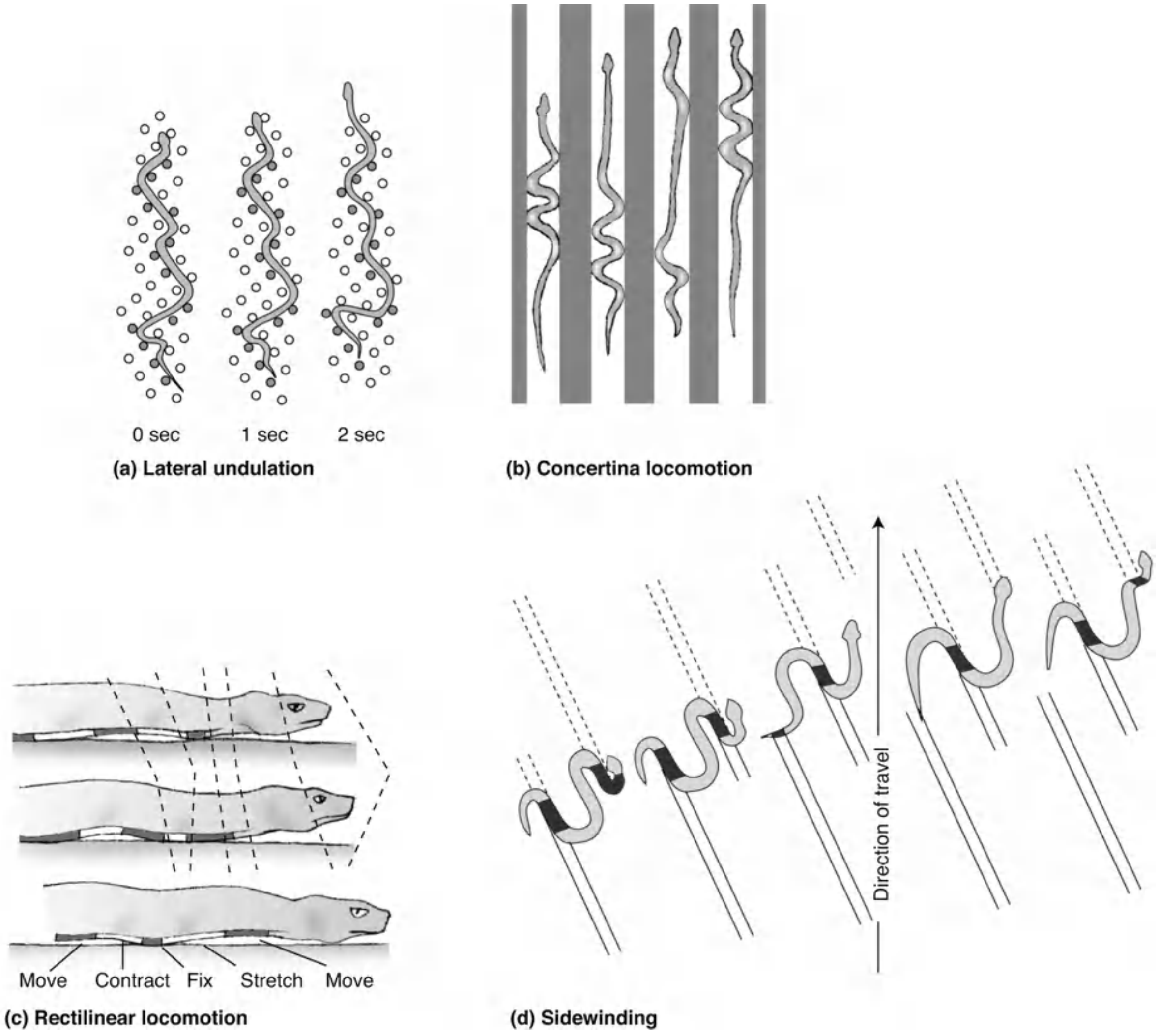


Figure 7.10. Snake locomotion: (*a*) lateral undulation, (*b*) concertina locomotion, (*c*) rectilinear locomotion, (*d*) sidewinding. Refer to the text for a discussion of each type.

Sidewinding is unique to snakes, especially desert species (see Fig. 7.10d). It provides for rapid travel over a smooth, unstable, and often hot substrate. The snake makes a series of tracks that are more or less straight lines, parallel to one another and angled to the direction of travel. Movement begins by the snake swinging its head, neck, and anterior body through an angle of 90° to 120° and placing its head on the ground in a new position. The remainder of the body is then lifted rapidly, section by section, from the old line of rest to the new position. The snake's body is in contact with two or three tracks at any given time that are constantly changing position. Parts of its body are within the tracks; other parts are arching between tracks and are held above the substrate. As each new track is made by anterior portions of the body, posterior segments are released from the previous track. The head normally starts swinging to a third track ahead of the snake's position before the tail comes to rest on the second. The body moves forward at an angle of about 60° to the direction of travel. Some snakes, like the African desert viper (*Bitis caudalis*), have modified the basic sidewinding locomotion and are able to jump short distances in order to reduce their contact with the intense heat of the desert floor.

Muscular System

The muscular system of reptiles has become more differentiated and better adapted to terrestrial life than that of amphibians. Muscles have become modified, not only to support the viscera and the weight of the body, but also to allow for various methods of locomotion. In addition, respiratory muscles have further differentiated and become better developed.

Epaxial muscles show less modification than hypaxial muscles, with some epaxial muscles losing their metamerism and differentiating into bundles. Besides their function of allowing side-to-side movement of the vertebral column, epaxial muscles take on new functions, including support and vertical bending, or arching, of the back. In turtles, epaxial muscles of the rigid trunk region are poorly developed, but those of the neck and tail are well developed.

The presence of ribs on most trunk vertebrae causes increased modification of the hypaxial muscles. Ribs form in the myosepta of the body wall muscles along most of the length of the vertebral column in snakes and legless lizards. The dissections of Mosauer (1935) and Gasc (1967) indicate the presence of as many as 20 discrete muscles on each side of a single snake vertebra. These muscles connect vertebra to vertebra, vertebra to rib, rib to rib, and both rib and vertebra to skin, as well as attach to longitudinal tendons that help form and control the curvatures of the body. In other reptiles, myosepta and ribs have become confined to the anterior portion of the trunk, now known as the **thorax**. Abdominal wall muscles lack segmentation, and they have differentiated into three layers: external oblique, internal oblique, and transversus abdominis. Hypaxial muscles of the thoracic body wall, known as **intercostal muscles**, assist in respiration by raising and lowering the rib cage.

The body of reptiles is suspended from the scapulae by muscles that show much more differentiation than those of amphibians. Muscles of the limbs and girdles consist of dorsal extensor and ventral flexor muscles. Increased specialization of the intrinsic muscles allows for more precise and powerful movement of the limbs as well as greater support for the body. In those forms utilizing quadrupedal locomotion, muscles attached to the humerus and femur must rotate these bones forward and backward, as well as hold the bones steady in a horizontal position at the appropriate angle to the horizontal so that the body can be held above the substrate.

Muscles of the first pharyngeal arch continue to operate the jaws, and muscles of the second arch are attached to the hyoid skeleton. Muscles of the remaining arches continue to be associated primarily with the pharynx and larynx.

Extrinsic integumentary muscles insert on the underside of the dermis and allow independent movement of the skin. This is the first group of vertebrates to have integumentary muscles capable of moving the skin.

It has long been thought that constrictor snakes kill their prey by suffocation. However, Boback et al., (2015) showed that when a snake cinches a loop or two around the upper body of its prey, it presses against its victim hard enough to starve organs of oxygenated blood. These results are the first to document the physiological response of prey to constriction and support the hypothesis that snake constriction induces rapid prey death due to circulatory arrest.

Cardiovascular System

Because reptiles are the first truly terrestrial vertebrates, many differences between the reptilian and amphibian cardiovascular systems are associated with the loss of functional gills and the need for efficient pulmonary circulation to bring blood to and from the lungs. Reptiles exhibit three different modes of circulation (Fig. 7.11). The ventricle of reptiles other than crocodilians is incompletely divided into dorsal and ventral chambers by a horizontal septum. A smaller vertical septum divides the ventricles into right and left chambers. The pulmonary trunk leaves the right ventricle. Both systemic trunks exit from the left ventricle in the Squamata (snakes and lizards); in turtles, however, one systemic trunk leaves the left ventricle and the other leaves the right ventricle. Because the interventricular septum is not complete, and because both atria open into the left ventricle, blood can flow from the left ventricle into the right ventricle.

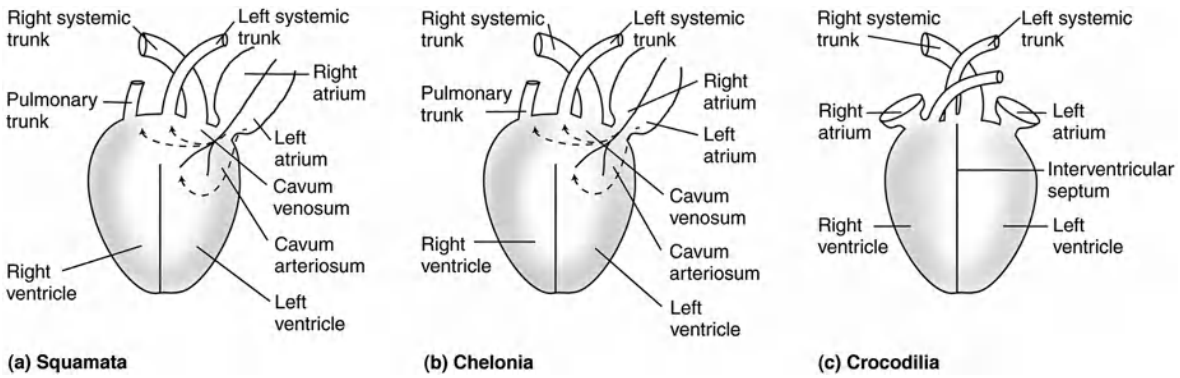
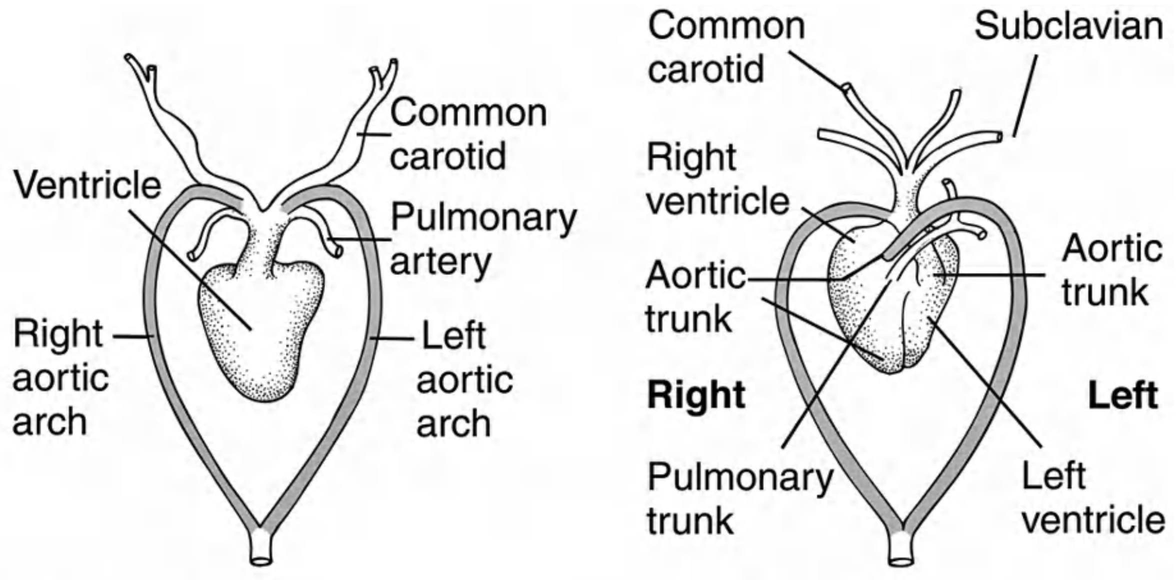


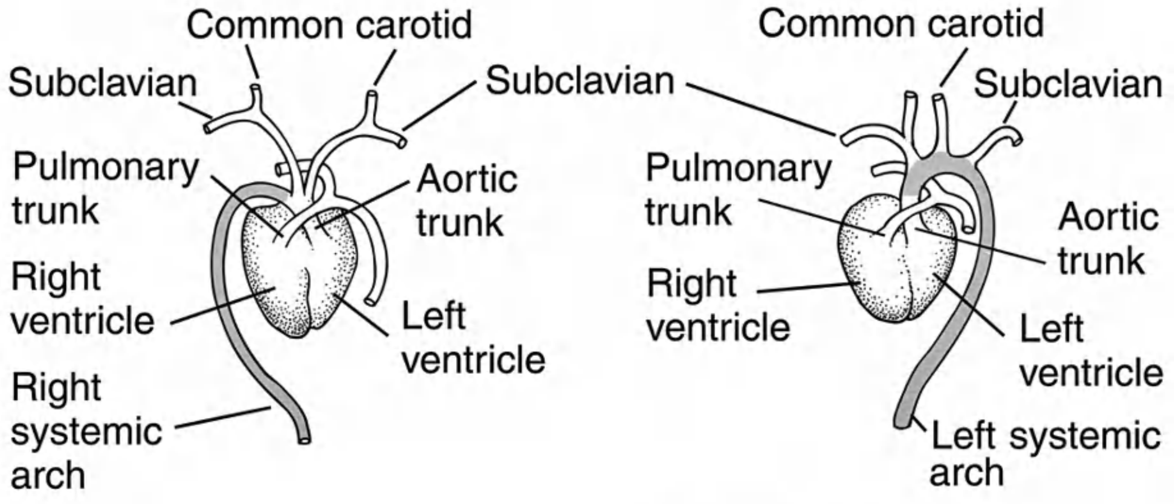
Figure 7.11. Diagrammatic representation of cardiac circulation in two lepidosaurs (*a*, *b*) and an archosaur (*c*). Note the complete separation of the ventricles in crocodilians.

The atrioventricular valve consists of two flaps that partially subdivide the left ventricle into a cavum arteriosum on the left and a cavum venosum on the right. When the atria contract, the cavum venosum becomes filled with deoxygenated blood from the right atrium and the cavum arteriosum becomes filled with oxygenated blood from the left atrium. Most of the deoxygenated blood in the cavum venosum flows into the right atrium. When the right ventricle contracts, the blood flows out through the pulmonary trunk, and in turtles through the right systemic trunk also. The oxygenated blood, together with some deoxygenated blood, is pumped out from the cavum arteriosum through the left systemic trunk (turtles) or both systemic trunks (Squamata).

Aortic arches III, IV, and the ventral part of VI remain in most adult turtles, lizards, and snakes, but their connections have been modified considerably (Fig. 7.12). The primitive ventral aorta splits into three channels: a pulmonary trunk and two aortic trunks. The pulmonary trunk leaves the right ventricle and carries blood to the lungs. One aortic trunk emerges from the left side of the ventricle and leads to the third aortic arch and to the fourth aortic arch on the right side of the body. A second aortic trunk emerges from the right side of the ventricle and leads to the fourth aortic arch on the left side of the body.



(a) Anuran **(b) Reptile**



(c) Bird **(d) Mammal**

Figure 7.12. Fate of the systemic arches in tetrapods. The systemic arches of both sides persist in adult anurans (*a*) and reptiles (*b*) Only the right systemic arch persists in birds (*c*), whereas only the left remains in mammals (*d*).

Because only one lung is functional in most snakes and legless lizards, the embryonic sixth aortic arch on the lungless side is lost. The third aortic arch on that side also disappears in most snakes. Most adult snakes, therefore, possess only a right pulmonary artery and a right common carotid artery.

The venous system shows little change from that of amphibians, although some modifications have occurred due to changes in the heart and kidneys and due to the elimination of cutaneous respiration. Due to the latter modification, reptiles have larger pulmonary veins and smaller cutaneous veins than amphibians.

Reptilian erythrocytes are oval and nucleated. They are smaller and more numerous than those of amphibians, ranging in length from about 15 to 23 μm. Leukocytes and thrombocytes make up the remaining cellular components of reptilian blood.

Respiratory System

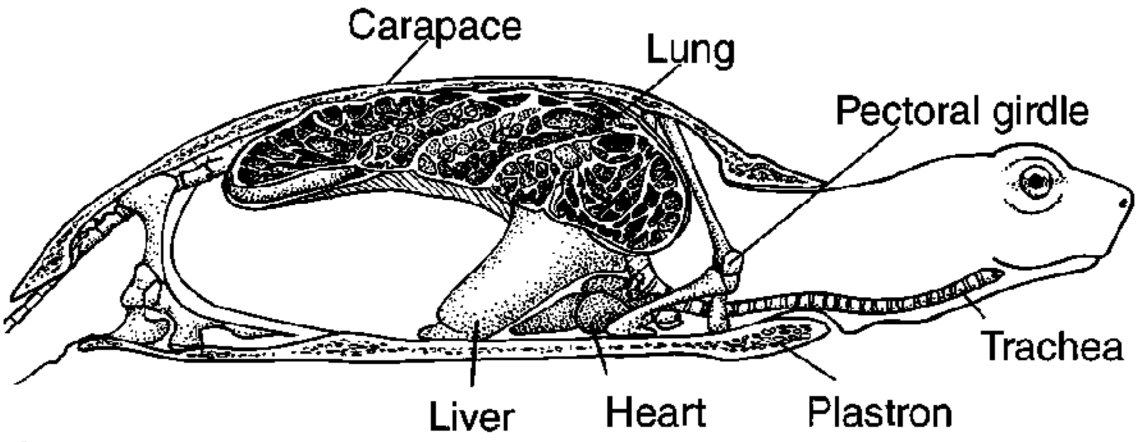
With the formation of a secondary palate in some reptiles, the anterior part of the respiratory tract begins to be separated from the anterior part of the digestive tract. The internal nares in these forms are located farther caudad and nearer the midline than in amphibians, and nasal passages are lengthened.

To keep the air passageway open while large prey is being slowly swallowed, snakes have a glottis that can be protruded. In most reptiles, the trachea is about as long as the neck; it is shortest in lizards. In some turtles, however, it is longer than the neck and convoluted.

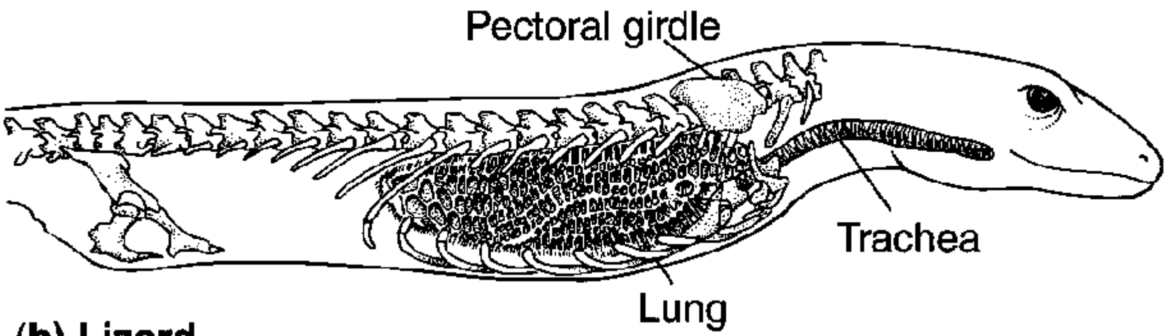
Although most reptiles are voiceless, some lizards and turtles possess vocal cords, but they produce few sounds discernible to the human ear. A few turtles make grunting noises, geckos “bark,” and many species of anoles emit distinctive squeaks, especially when being captured.

The lungs of most reptiles are located in the **pleuroperitoneal cavity** and are, in most cases, better developed than amphibian lungs. In turtles and most lizards, the lungs consist of numerous large chambers, each composed of many individual subchambers, called **faveoli** (Fig. 7.13a, b). Internal partitioning is best developed in legless lizards, with pockets of trapped air causing the lungs to be spongy. Lungs of snakes are elongate and may be paired or unpaired. In tuataras (*Sphenodon*), the lungs continue to exist as simple sacs similar to those in amphibians.

Reptiles may use a force-pump system similar to that of amphibians in order to get air into their lungs, or they may inspire air by active suction and expire by pressure. Most reptiles respire by expanding and compressing the pleuroperitoneal cavity through backward and forward movements of the ribs produced through contraction of intercostal muscles.



(a) Turtle



(b) Lizard

Figure 7.13. (*a*) Gas exchange in the turtle. Sagittal view showing the location of the lung and its relationship to other internal organs. Since turtle lungs are enclosed by a rigid, protective shell, the fixed rib cage cannot ventilate the lungs. To compensate, turtles have sheets of muscles within the shell that contract and relax to force air in and out of the lungs. Turtles can also alter the air pressure within their lungs by moving their limbs in and out of the shell. (*b*) Gas exchange in a lizard. The lungs, which are located in the thoracic cavity, are surrounded by ribs and are connected to the trachea. Compression and expansion of the rib cage force air in and out of the lungs. The internal lining of the lungs shows numerous faveoli, which give the lining a honeycomb appearance. The faveoli increase the respiratory surface area of the lung and function in gas exchange along with the capillaries that line their walls.

In a few snakes and lizards, the lungs are in separate **pleural cavities**. A tendinous transverse partition, the **oblique septum**, separates the pleural cavities from the coelom. Contraction of muscles tightens the septum, which lowers pressure within the lungs below that of the external atmosphere. Because turtles are encased in a rigid shell and the ribs are fused to the carapace, the ribs cannot function in gas exchange. Instead, specialized sheets of muscle contract and relax to move air in and out of the lungs (Gans and Hughes, 1967).

Reptiles depend almost entirely on lungs to aerate their blood. Some reptiles supplement gas exchange by utilizing gas exchange membranes in other areas of the body, including the pharynx (pharyngeal gas exchange), cloaca (cloacal gas exchange), and skin (cutaneous gas exchange).

Pharyngeal (buccopharyngeal) gas exchange is particularly well developed in soft-shelled turtles (Trionychidae) (Girgis, 1961; Dunson and Weymouth, 1965). It permits them to obtain dissolved oxygen from water and, hence, to stay underwater for long periods. Pharyngeal gas exchange also is known to occur in the Australian skink (Drummond, 1946).

Cloacal gas exchange may occur in many turtles in the families Chelydridae, Testudinidae, and Pelomedusidae. The accessory cloacal bladders have been proposed as auxiliary gas exchange structures, as water is pumped in and out of the vent when the turtles are submerged (Zug, 1993). Oxygen supposedly diffuses through the smooth and lightly vascularized walls of the bladders, and carbon dioxide passes out.

Cutaneous gas exchange has been reported in several turtles, including the soft-shelled turtle (*Apalone* sp.), musk turtles (*Sternotherus odoratus* and *S. minor*), mud turtles (*Kinosternon subrubrum*), snapping turtles (*Chelydra serpentina*), and pond sliders (*Trachemys scripta*) (Stone et al., 1992). Girgis (1961) reported that soft-shelled turtles obtain up to 70 percent of their oxygen by diffusion through the leathery skin covering their carapace and plastron.

Shallow-diving sea turtles are thought to make aerobic dives relying on their lungs' oxygen store. The leatherback is the largest sea turtle and the deepest diver, able to dive beyond 1,000 m (3,280 ft.) (Eckert et al., 1986). Increased hydrostatic pressure probably collapses their lungs during deeper dives (Berkson, 1967), so they may have to rely on blood and tissue stores of oxygen. The oxygen-carrying capacity of the leatherback's blood is twice that of shallow-diving sea turtles (Lutcavage et al., 1990). Their blood volume is slightly higher, but their lung volume is considerably smaller than in other sea turtles (Lutcavage et al., 1992).

Although one lung is rudimentary or absent in legless lizards and most snakes, both lungs are functional in primitive snakes like boas and pythons (family Boidae), where the left lung is about 30 to 80 percent as large as the right lung. In some snakes, like cobras, hognose snakes, and others that inflate their neck region as a defensive maneuver, a large saclike diverticulum of the left lung extends into the neck. Inflation of the sac causes the neck region to greatly expand.

Although the lung is the primary organ of gas exchange in the sea snake (*Pelamis platurus*), this species can take up oxygen through the skin at rates up to 33 percent of its total standard oxygen uptake and excrete carbon dioxide at rates up to 94 percent of its total rate (Graham, 1974). Specially adapted lungs that extend back to the cloaca and tightly sealing, valvular nostrils allow sea snakes to remain submerged for eight hours or more before surfacing (Cooke, 1991).

Some lizards, like the desert iguana (*Dipsosaurus dorsalis*), conserve a significant amount of water by exhaling air that is cooler than their body temperature (Murrish and Schmidt-Nielsen, 1970). The distal portion of the nasal passageways forms a slight depression in which fluid secreted from the nasal **salt gland** accumulates, which assists in humidifying incoming air. As the fluid becomes more concentrated, salts crystalize near the opening of the nares.

The chuckwalla (*Sauromalus*), a desert lizard from southwestern North America, often seeks refuge in rocky crevices. By inflating its lungs, it wedges its body in place and defies efforts to remove it from its safe haven. Studies have shown that *Sauromalus* “uses the primitive, anamniote, buccal pumping respiration for defense, and the derived, amniote, aspiration mechanism for respiration” (Deban and Theimer, 1991). Buccal pumping, unlike aspiration, can create greater-than-ambient pressures in the abdominal cavity.

Air sacs, which are diverticula of the lungs, extend among the viscera in some chameleons, often as far caudad as the pelvis (Orr, 1982). They serve to increase the air capacity and efficiency of the lungs in somewhat the same manner as the air sacs in birds.

Although five pharyngeal pouches develop in reptilian embryos, gills never develop, and adults never have open gill slits. The first pharyngeal pouch persists in adults as the Eustachian (auditory) tube and middle ear, and in reptiles and birds this temporarily opens to the outside during embryonic development. The other pouches become modified into other structures (thymus, parathyroid glands, and ultimobranchial body) or disappear during embryonic development.

Digestive System

The reptilian digestive tract exhibits numerous modifications as compared with that of amphibians. The jaws of most reptiles are covered by nonmuscular, immovable, thickened lips. The jaw margins of turtles, however, are covered with a shell of keratin and, together with the jaws, form a beak.

Oral Cavity

With the exception of turtles, some of which have serrations that simulate teeth on their horny beaks, all other groups of reptiles possess teeth. Although an evolutionary trend toward a reduction in the number of teeth and a restriction of the distribution of teeth is seen in the vertebrates, many reptiles still possess teeth on the palate as well as on the jaws.

Most reptiles have **homodont dentition**, although partial heterodonty is found in snakes and some lizards. Those with heterodont dentition (monitor lizards, *Varanus*; caiman lizards, *Dracaena*) have incisors, canine-like teeth, and molars. Tooth attachment is variable. In most lizards, the marginal teeth are attached to the biting edges of the jaws (**acrodont dentition**) (Fig. 7.14a); in other lizards, however, the jaw teeth are attached to the inner sides of the jawbone (**pleurodont dentition**) (Fig. 7.14b). Most snake teeth are recurved and either acrodont or pleurodont. The teeth of crocodilians are rooted in sockets (**thecodont dentition**) (Fig. 7.14c).

The right and left sides of many snakes' mandibles (as well as those of some lizards) are joined only by an elastic ligament so that the symphysis can stretch to accommodate large prey (Fig. 7.15a, b). Further expansion is possible because both halves of the lower jaw are suspended from the skull by a long, folding strut (the quadrate), which is divided into two hinged sections similar to a folding carpenter's rule. As large prey is engulfed, these joints swing outward on their flexible struts, greatly increasing the diameter of the throat region. Recurved teeth are present on the independently moving bones of the palate and jaws. By alternately engaging and disengaging the teeth on each side of the mouth, prey is gradually drawn into the oral cavity and passed to the pharynx and esophagus.

Figure 7.14. Three methods of tooth attachment in reptiles: (*a*) acrodont—attached to the rim of the jawbone; (*b*) pleurodont—attached to the side of the jawbone; (*c*) thecodont—rooted in sockets in the jawbone.

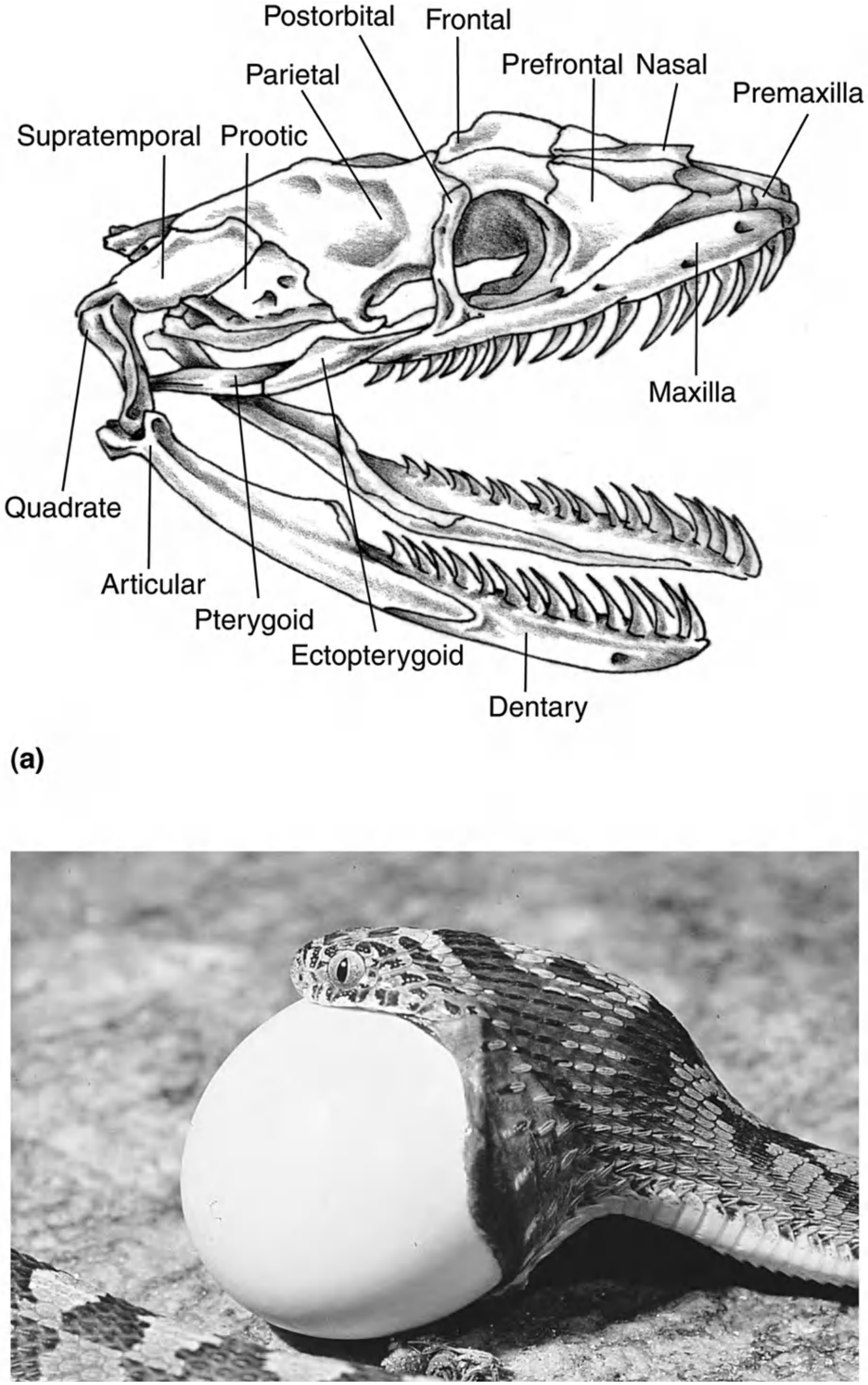

Postorbital
Frontal
Prefrontal
Nasal
Premaxilla
Parietal
Supratemporal
Prootic
Maxilla
Quadrate
Articular
Pterygoid
Ectopterygoid
Dentary
(a)

Figure 7.15. (*a*) Lateral view of python skull showing teeth and skull bones. The mouth of a snake is modified in order to accommodate large prey. The right and left sides of the mandible (lower jaw) are joined only by an elastic ligament so that the symphysis can stretch. In addition, both halves of the lower jaw are suspended from the skull by a long, folding strut, which is divided into two hinged sections. As large prey is engulfed, these joints swing outward on their flexible struts, thus increasing the diameter of the throat region. Recurved teeth securely hold the prey as upper and lower bones on one side of the jaw slide forward and backward alternately with bones of the other side. (*b*) Yellow rat snake (*Elaphe obsoleta quadrivittata*) swallowing an egg.

Living on Large Prey

Boa constrictors and pythons are sit-and-wait predators that eat infrequently and undergo long and unpredictable fasts of up to several months. When they do ingest prey, it may be extremely large (see Fig. 7.16). Pythons, for example, may consume between 50 and 160 percent of their own body weight at one time and digest and assimilate such an enormous meal in just a few days. The biggest prey on record is a 58.5 kg (128 lb.) antelope that was swallowed by an African rock python (Diamond, 1994). An Asian reticulated python consumed a 12.6 kg (27.5 lb.) goat and a 17.5 kg (38 lb.) goat at one sitting, and then downed a 32 kg (70 lb.) ibex a few days later.

Oxygen consumption in pythons increases up to 17-fold only 24 hours after feeding and is maintained for several days while the snake remains virtually motionless. Approximately 32 percent of the energy in the food consumed is used during digestion, as opposed to 10 to 23 percent in animals that feed regularly. During periods of fasting, the mucosal lining of the small intestine atrophies, resulting in significant energy savings.

Secor and Diamond, 1995; Cossins and Roberts, 1996

Threadsnakes (family Leptotyphlopidae) (see Fig. 1.7) grow 15 to 20 cm (6–8 in.) long, are a bit thicker than a strand of spaghetti, and weigh about 1 g (0.035 oz.). They feed upon insect larvae, pupae, and adults insects. These snakes have a unique feeding mechanism known as mandibular raking in which the anterior, tooth-bearing halves of the lower jaw rotate rapidly in and out of the mouth like a pair of swinging doors, dragging prey into the esophagus (Kley and Brainerd, 1999). This mechanism is made possible by the triple-jointed, extremely mobile lower jaw of threadsnakes that allows the transversely oriented mandibular tooth rows (the only teeth in the skull) to be rotated backward. The high-speed gulping is thought to minimize the time spent in insect nests. It is the only vertebrate feeding mechanism known in which prey is transported exclusively by movements of the lower jaw.

Tuataras (*Sphenodon* spp.) have only one set of teeth during their lifetime, a situation called **monophyodont dentition**. Most reptiles, however, have a constant and steady replacement of their teeth, which is called **polyphyodont dentition**. This occurs in a regular alternating pattern so that adjacent teeth are at different stages in their development (Edmund, 1969).

The only two venomous lizards in North America, the Gila monster (*Heloderma suspectum*) (Fig. 7.17) and the Mexican beaded lizard (*Heloderma horridum*), possess grooves on the anteromedial edges of their teeth. Venom from modified salivary glands flows upward along grooves in the teeth of the lower jaw and into the prey as the lizard “chews” its prey. The venom is primarily neurotoxic, affecting the nervous and respiratory systems of the prey.

Figure 7.16. The African rock python (*Python sebae*) may feed on mammals as large as this Thomson’s gazelle.

Figure 7.17. The Gila monster, one of only two venomous lizards in the world.

A drug derived from the saliva of the Gila monster is available to Type 2 diabetics. In May 2005, the Food and Drug Administration (FDA) approved Byetta, known chemically as exenatide, an antidiabetic peptide—the first in a new class of medications for Type 2 diabetes.

Many transitional forms exist between the complete absence of venom and the development of a venom-conducting apparatus. Three modifications occur in the teeth of venomous snakes. Less specialized venomous snakes lack hollow fangs but have one to three enlarged, grooved teeth at the backs of their upper jaws (maxillae). The normally weak venom from modified salivary glands flows into the prey as it is "chewed." These snakes, known as **opisthoglyphs**, occur in the family Colubridae. Rear-fanged snakes primarily inhabit tropical regions and include the mangrove snake (*Boiga dendrophila*), long-nosed tree snakes (e.g., *Dryophis oxybelis*), African vine snakes (*Thelotornis* spp.), African sand snakes (*Psammophis* spp.), and tree snakes (*Chrysopelea* spp.) of Malaysia and the East Indies. Lyre snakes (*Trimorphodon* sp.) of the southwestern United States and Mexico have a pair of enlarged, grooved rear fangs. Several other North American genera like black-headed snakes (*Tantilla* sp.), ground snakes (*Sonora* sp.), annulated snakes (*Leptodeira* sp.), night snakes (*Hypsiglena* sp.), shovel-nosed ground snakes (*Chionactis* sp.), and banded burrowing snakes (*Chilomeniscus* sp.) possess slightly to moderately enlarged posterior maxillary teeth that may or may not be grooved.

Some rear-fanged snakes are potentially dangerous to humans. The boomslang (*Dispholidus typus*) of Africa, a tree snake that can grow to a length of 1.5 m (5 ft.), causes multiple internal hemorrhages. It has been responsible for several human fatalities, including that of Dr. Karl Schmidt in 1957. Dr. Schmidt was curator emeritus of the Field Museum of Natural History in Chicago and an internationally known authority on reptiles. He died 24 hours after being bitten by an 83 cm (32 in.) specimen he was handling.

Proteroglyphs and **solenoglyphs** possess a pair of grooved or hollow elongated fangs attached to the maxillae in the front of their upper jaw. The fangs are each connected by a venom duct to a venom gland (Fig. 7.18). Both types of snakes use muscular contraction of the venom gland to inject the venom into the prey. Proteroglyphs, which have rigid fangs that fit into pockets in the outer gum of the lower jaw, include the cobras, coral snakes, and sea snakes (Elapidae). Solenoglyphs include the vipers and pit vipers (Viperidae). These snakes possess the most highly specialized fang mechanism. The maxilla rotates like a hinge on the anterior end of the prefrontal bone. The fangs are only connected to the maxilla. When the mouth is closed, the fangs fold back and lie along the upper jaw. When the mouth opens, the fangs swing down and forward.

Venom glands of snakes are modified labial salivary glands and are homologous with the parotid glands of mammals. Venom of elapids (Elapidae) is primarily neurotoxic, attacking nerve centers and causing paralysis of many parts of the body, including the respiratory center. Venom of the vipers and pit vipers (Viperidae and Crotalidae) is primarily a **hemolytic poison**, which breaks up formed elements (erythrocytes, leukocytes, and platelets) in the blood and attacks the lining of blood vessels.

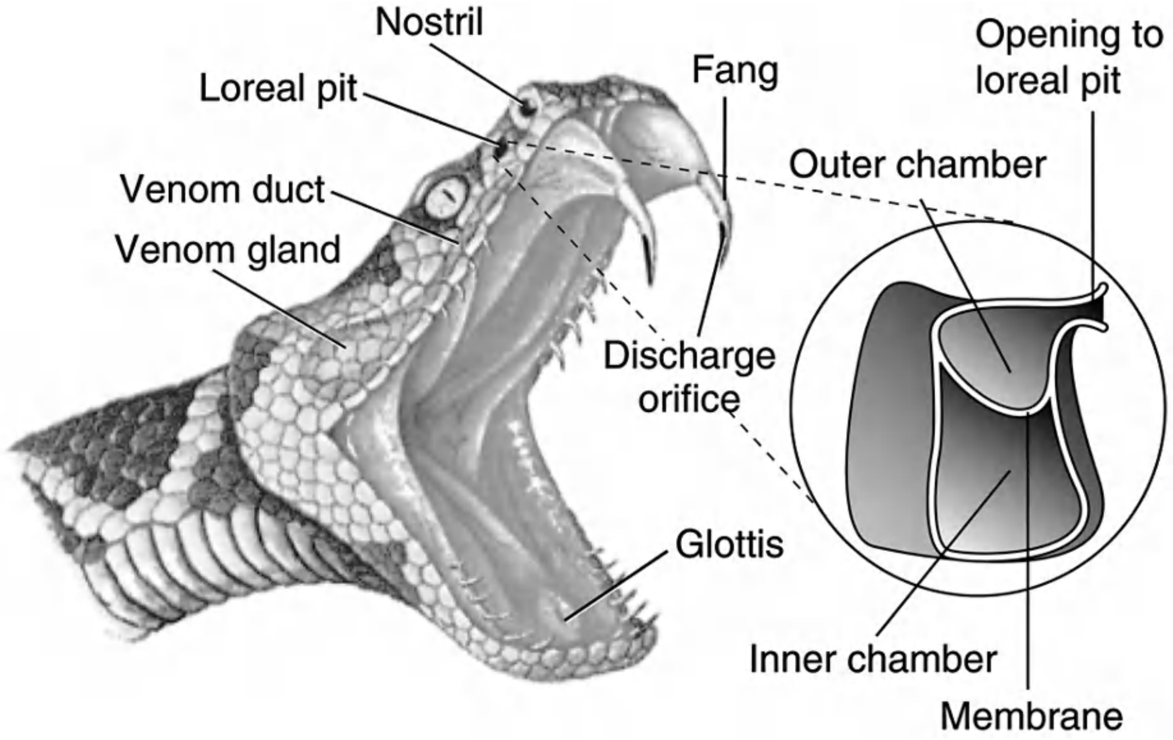


Figure 7.18. Head of a rattlesnake, a pit viper, showing the venom apparatus. The venom gland, a modified salivary gland, is connected by a duct to the hollow fang. Note the loreal pit containing the heat-sensing pit organ between the eye and nostril. The cutaway view of the pit organ shows the location of a deep membrane that divides the pit into inner and outer chambers. Heat-sensitive nerve endings are concentrated in the membrane.

In North America, the Centers for Disease Control and Prevention estimate 7,000 to 8,000 people receive venomous bites annually in the United States and about 5 (about 0.3 percent of all bites) of those people die (CDC, 2018). Venomous copperheads, cottonmouths, and even relatively small coral snakes are responsible for a portion of these, but most snakebite emergencies involve rattlesnakes. Even though fatalities are few, snakebites can cause lasting harm without killing. Permanent damage, like amputations and partial immobility of a joint near the site of the bite, may result.

Venom composition within some snake species has been found to show considerable geographical variation, presumably associated in some manner with local diets (Daltry et al., 1996). Because prey animals vary in their susceptibility to venom, geographical variation in venom composition may reflect natural selection for feeding on local prey. The venom from *Bothrops asper*, a pit viper in Costa Rica, differed depending on the population's geographical location. Snakes that lived on one side of a steep mountain range had markedly different venom profiles from those of snakes on the other side. In the same way a particular southern twang identifies a Texan, the composition of venom can reveal where a snake hails from.

Snake venom is full of proteins and smaller pieces of proteins called peptides. It is as thick as honey. Rattlesnake venom contains three main components: cytotoxic components that kill cells, hemotoxic components that affect blood, and neurotoxic components that attack nerves. Neurotoxic effects are the quickest acting and more life threatening (Tennesen, 2009). Toxins from the Brazilian arrowhead viper (*Bothrops jararaca*) have provided the key molecule for blood pressure-lowering drugs known as ACE (angiotensin-converting enzyme) inhibitors. The viper produces peptide inhibitors that bind to the active site of ACE in the same manner as natural substrates and reduce blood pressure. Created more than 30 years ago, **captopril** was the first drug based on a protein derived from snake venom.

Snake venoms, such as those from *Dendroaspis angusticeps*, *Micrurus corallinus*, *B. jararaca*, *Trimeresurus flavoviridis*, *Trimeresurus gramineus*, or *Agkistrodon halys blomhoffii* (and many others), represent one of the major sources of exogenous natriuretic peptides. These peptides are potent body fluid volume regulators and, therefore, also reduce blood pressure.

Other reptiles whose venoms have been repurposed as medicines for human use include the pygmy rattlesnake (**Eptifibatide**: antiplatelet for heart attack), the saw-scaled viper (**Tirofiban**: antiplatelet for heart attack), the lance-headed snake (**Batroxobin**: blood clotting), and the Gila monster (**Exenatide**: Type 2 diabetes control).

The reptilian tongue is better developed than that of amphibians and is quite variable in structure. In turtles, the tongue arises from the floor of the oral cavity and is nonprotrusible. In snakes and some lizards, however, the long, slender, forked tongue is flexible and moves with great speed (Fig. 7.19). It is best developed in African chameleons, which feed by projecting their highly extendable tongues (farther than their own body lengths) and capturing prey on their thickened stocky tips (tongue pads) (Fig. 7.20). Most lizards catch prey by using mainly surface tension—the stickiness created when a wet tongue contacts dry prey. But chameleons consume prey much too large for surface tension alone to handle. By dissecting tongues from several chameleon species, researchers found that two muscles form a pouch at the tip that acts as a suction cup (Herrel et al., 2000). Slow-motion film of chameleons capturing crickets, grasshoppers, and other lizards revealed that these muscles retract just before the tongue makes contact with the target.

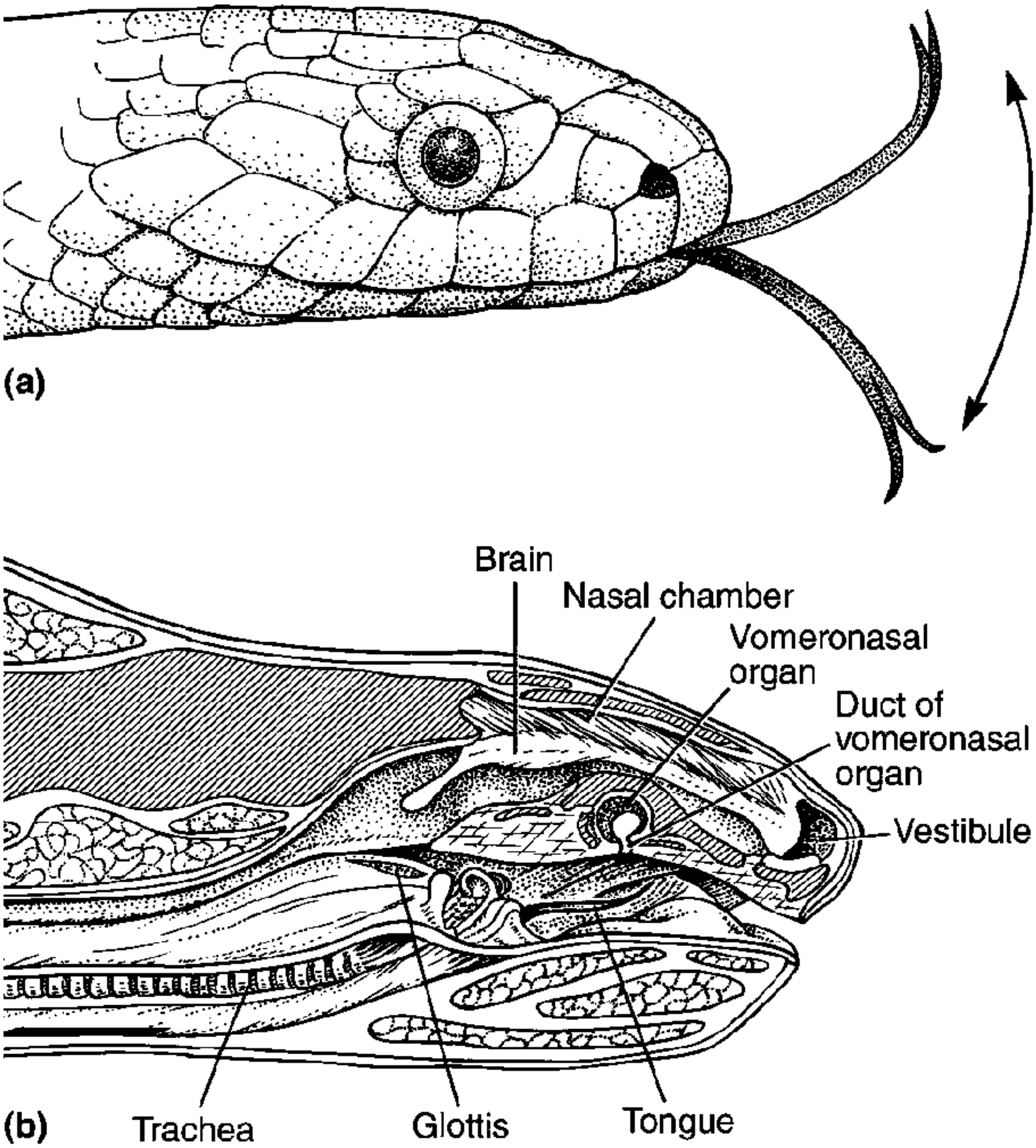


Figure 7.19. Tongue-flicking in snakes. (*a*) Snakes and lizards extend their tongues to sweep air in front of them. The tongue collects and transports airborne chemical particles into the mouth, where it deposits the particles onto the vomeronasal organ in the roof of the mouth. (*b*) Sagittal section of the head of a boa constrictor. The vomeronasal organ is a blind pocket with a lumen that opens directly into the mouth via a duct. The tip of the retracted tongue can be seen projecting from its sheath beneath the trachea.

Figure 7.20. A chameleon (*Chameleo chameleon*) using its tongue to capture prey. Note the prehensile tail.

In most species, the forked tongue samples environmental chemicals by means of **flicking**, a behavior in which the tongue is rapidly protruded, contacts the air, and is then retracted into the mouth (Burghardt, 1970; Chiszar et al., 1980). It does not function in the manipulation of food, but transfers chemicals in the air to chemoreceptors, thereby allowing the snake or lizard to follow pheromone and scent trails of mates and prey, respectively (Webb and Shine, 1992; Schwenk, 1994, 1995). Odor molecules on the tongue are delivered to the vomeronasal fenestrae in the palate; from there they make their way to the sensory epithelia of the paired vomeronasal (Jacobson's) organ (Burghardt, 1980; Halpern, 1983, 1992) (see Fig. 7.19). Vomeronasal organs are small, bulb-shaped structures that contain patches of sensory cells with nerves that connect to the olfactory lobe of the brain. These organs became highly specialized in the lineage leading to lizards and snakes. Vomeronasal organs are greatly reduced or absent in turtles.

The reason for the evolution of a forked tongue remains uncertain, although it may be related to the paired vomeronasal organs. A small notch at the anterior end of the upper jaw allows the tongue to be flicked in and out without the reptile having to open its mouth. The ability to simultaneously sample two points along a chemical gradient provides the basis for instantaneous assessment of a scent trail. Forked tongues have evolved at least twice, and possibly four times, among squamate reptiles. The brightly colored tongues of some African snakes serve as visible threats (Mertens, 1955; Pitman, 1974), and a skink (*Tiliqua scincoides*) threatens other members of its own species (conspecifics) by presenting its cobalt-blue tongue (Carpenter, 1978).

Esophagus

The esophagus of most reptiles is longer than that of amphibians and is clearly differentiated from the stomach. Longitudinal folds permit its expansion during the swallowing of large prey. Some egg-eating snakes have esophageal "teeth"—anterior vertebral processes that project into the esophagus—which form an egg shell-cutting apparatus (Fig. 7.21).

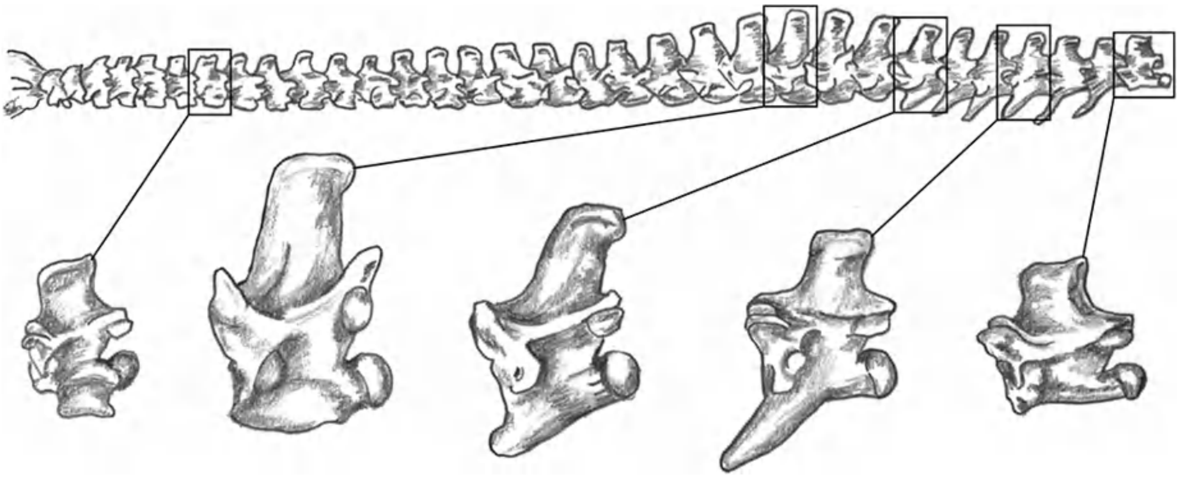


Figure 7.21. Morphology of vertebrae in the anterior vertebral column of the African egg-eating snake (*Dasypeltis scabra*). Anterior is to the left with the rear of the skull being shown. Note vertebrae with thickened hypapophyses (ventral processes) used for crushing egg shells and those with long, anteriorly directed hypapophyses that slit the egg membranes.

Stomach, Intestines, and Cloaca

The stomach is elongate in lizards and snakes, and a distinct large intestine is usually present (Fig. 7.22a, b). In some herbivorous lizards, a caecum is present near the junction of the small and large intestines. The caecum contains specific bacteria to assist in digesting the cellulose-containing plant material. In many reptiles, the cloaca has become partly subdivided so that the intestine and urogenital ducts open into separate compartments (coprodeum and urodeum, respectively), which then join in a common outlet, the vent.

Nervous System

In all vertebrates, larger animals tend to have smaller brains (in proportion to body size) than small animals. The brain of a shrew, for example, is equal to about 1/23 (4.3 percent) of the weight of the entire animal, whereas the human brain comprises approximately 1/48 (2.1 percent) of the total body weight. In a giant sauropod like *Apatosaurus*, the brain may have weighed only 1/100,000 (0.001 percent) of a total body weight of approximately 30,450 kg (67,130 lb.) (Bellairs, 1970). Figures for some weights of brain and body in a variety of vertebrates are presented in Table 7.1. Note that the brain weight differs little in three different-sized specimens of the green lizard (*Lacerta viridis*), an indication that the brain stops growing before the rest of the body (Bellairs, 1970).

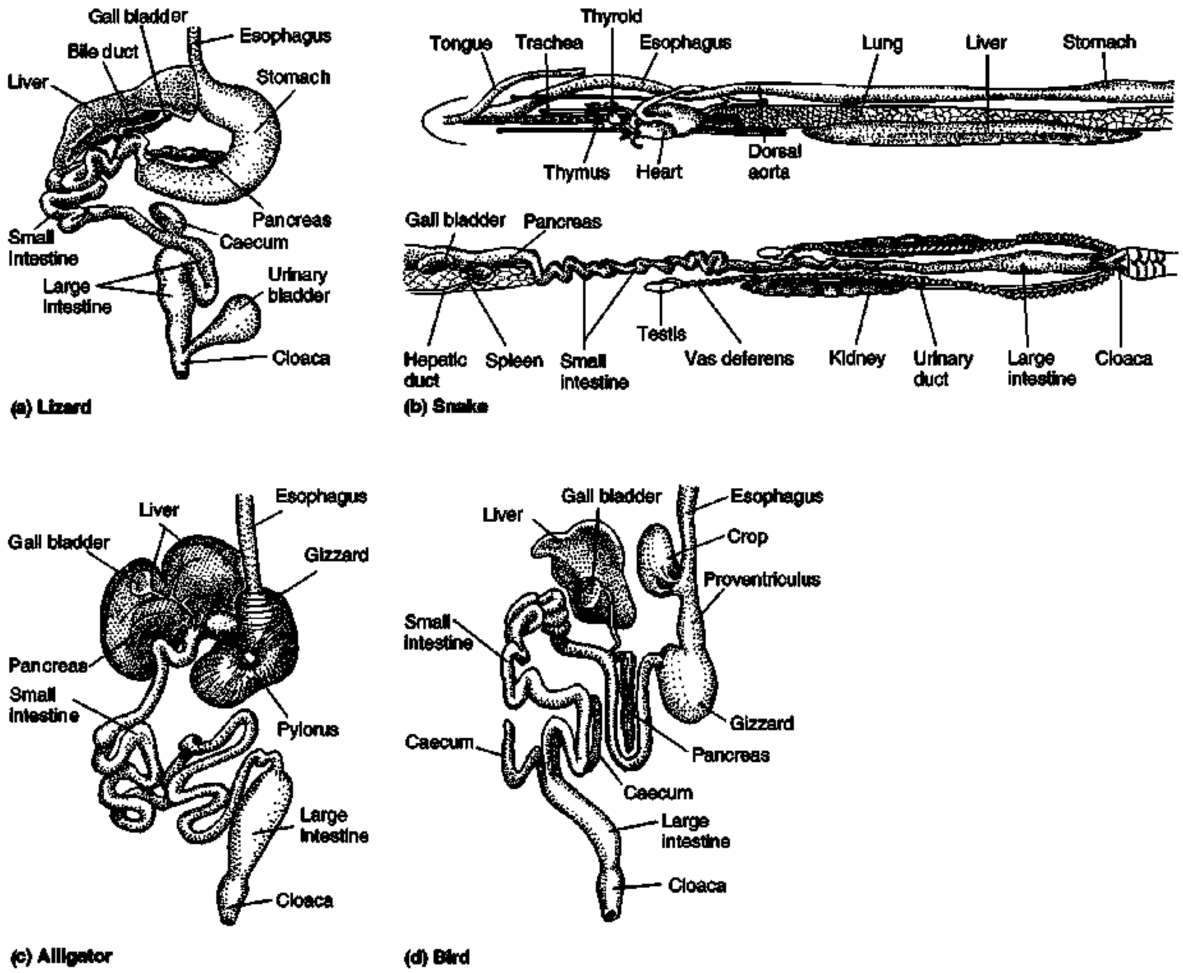


Figure 7.22. Ventral views of the alimentary canals in reptiles: (*a*) lizard (*Iguana*), (*b*) snake (*Natrix*), (*c*) alligator (*Alligator*), (*d*) bird (*Gallus*).

The brains of reptiles, particularly the cerebral hemispheres and cerebellum, are significantly advanced over those of fishes and amphibians. The cerebral hemispheres are considerably enlarged and bulge laterally, dorsally, and, to some extent, posteriorly over the diencephalon. The thalamus and hypothalamus have become more prominent and control the coordination of metabolic activities. The hypothalamus acts as a thermostat to control body temperature, a process known as **basking poikilothermy** (Fig. 7.24). If the hypothalamus becomes cooler than the preferred temperature range, nerve signals will induce the reptile to move to a warmer site; if the hypothalamus becomes warmer, the reptile will move to a cooler site. An increase of 10°C (18°F) within the biologically meaningful range of 0°C to 40°C (32°F–104°F) usually doubles or triples the rates at which physiological processes occur (Halliday and Adler, 1986).

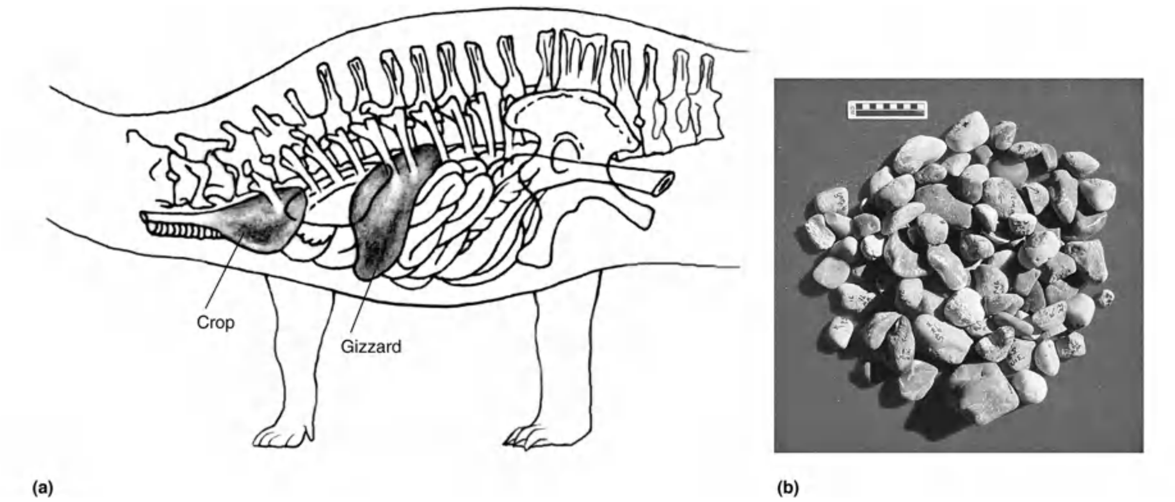
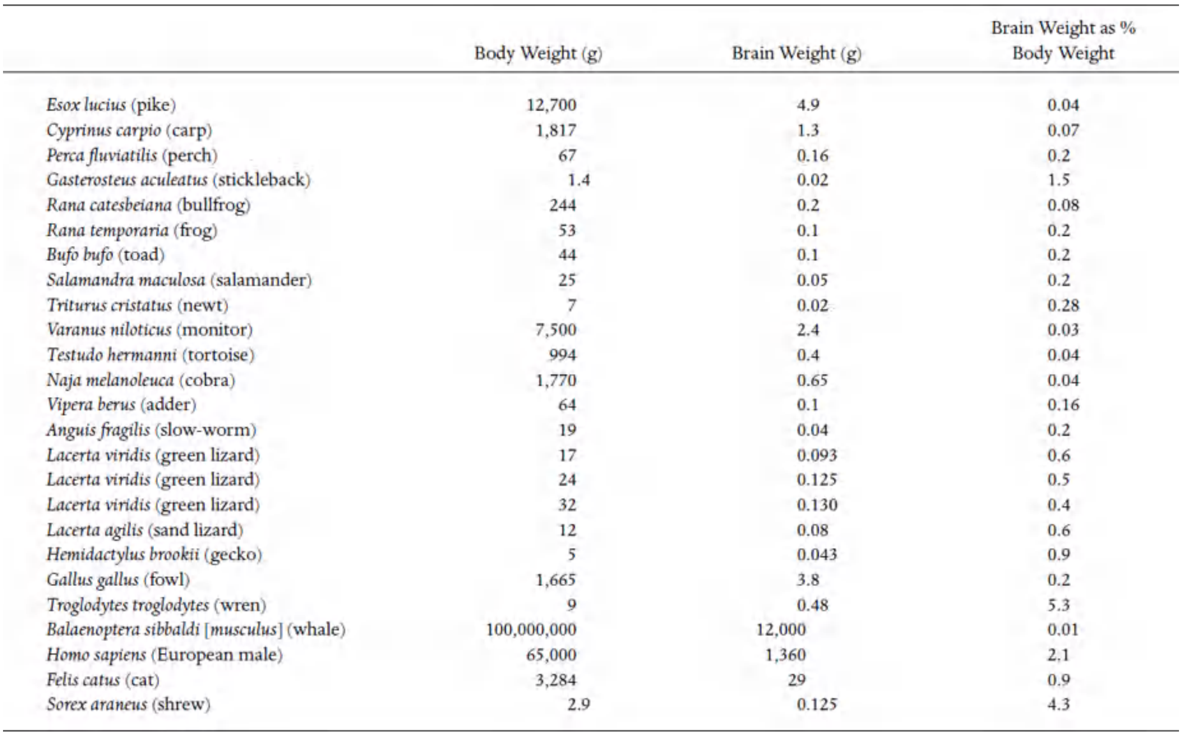


Figure 7.23. Stomach stones, or gastroliths (*inset*), were found in two main clusters in association with the *Seismosaurus* skeleton, suggesting that the creature's capacious digestive tract included a crop and a gizzard (*shaded areas*, *left*).

Table 7.1. Weights of Brain and Body in Representative Adult Vertebrates



	Body Weight (g)	Brain Weight (g)	Brain Weight as % Body Weight
Esox lucius (pike)	12,700	4.9	0.04
Cyprinus carpio (carp)	1,817	1.3	0.07
Perca fluviatilis (perch)	67	0.16	0.2
Gasterosteus aculeatus (stickleback)	1.4	0.02	1.5
Rana catesbeiana (bullfrog)	244	0.2	0.08
Rana temporaria (frog)	53	0.1	0.2
Bufo bufo (toad)	44	0.1	0.2
Salamandra maculosa (salamander)	25	0.05	0.2
Triturus cristatus (newt)	7	0.02	0.28
Varanus niloticus (monitor)	7,500	2.4	0.03
Testudo hermanni (tortoise)	994	0.4	0.04
Naja melanoleuca (cobra)	1,770	0.65	0.04
Vipera berus (adder)	64	0.1	0.16
Anguis fragilis (slow-worm)	19	0.04	0.2
Lacerta viridis (green lizard)	17	0.093	0.6
Lacerta viridis (green lizard)	24	0.125	0.5
Lacerta viridis (green lizard)	32	0.130	0.4
Lacerta agilis (sand lizard)	12	0.08	0.6
Hemidactylus brookii (gecko)	5	0.043	0.9
Gallus gallus (fowl)	1,665	3.8	0.2
Troglodytes troglodytes (wren)	9	0.48	5.3
Balaenoptera sibbaldi [*musculus*] (whale)	100,000,000	12,000	0.01
Homo sapiens (European male)	65,000	1,360	2.1
Felis catus (cat)	3,284	29	0.9
Sorex araneus (shrew)	2.9	0.125	4.3

Source: Data from Bellairs, 1970. © Universe Books, New York.

One or two outgrowths are present from the roof of the diencephalon. The anterior growth is the parapineal organ (parietal eye); the posterior is the pineal organ (epiphysis), which functions chiefly as an endocrine gland. A parapineal organ is prominent in *Sphenodon* and in many lizards, in which it serves as a photoreceptor.

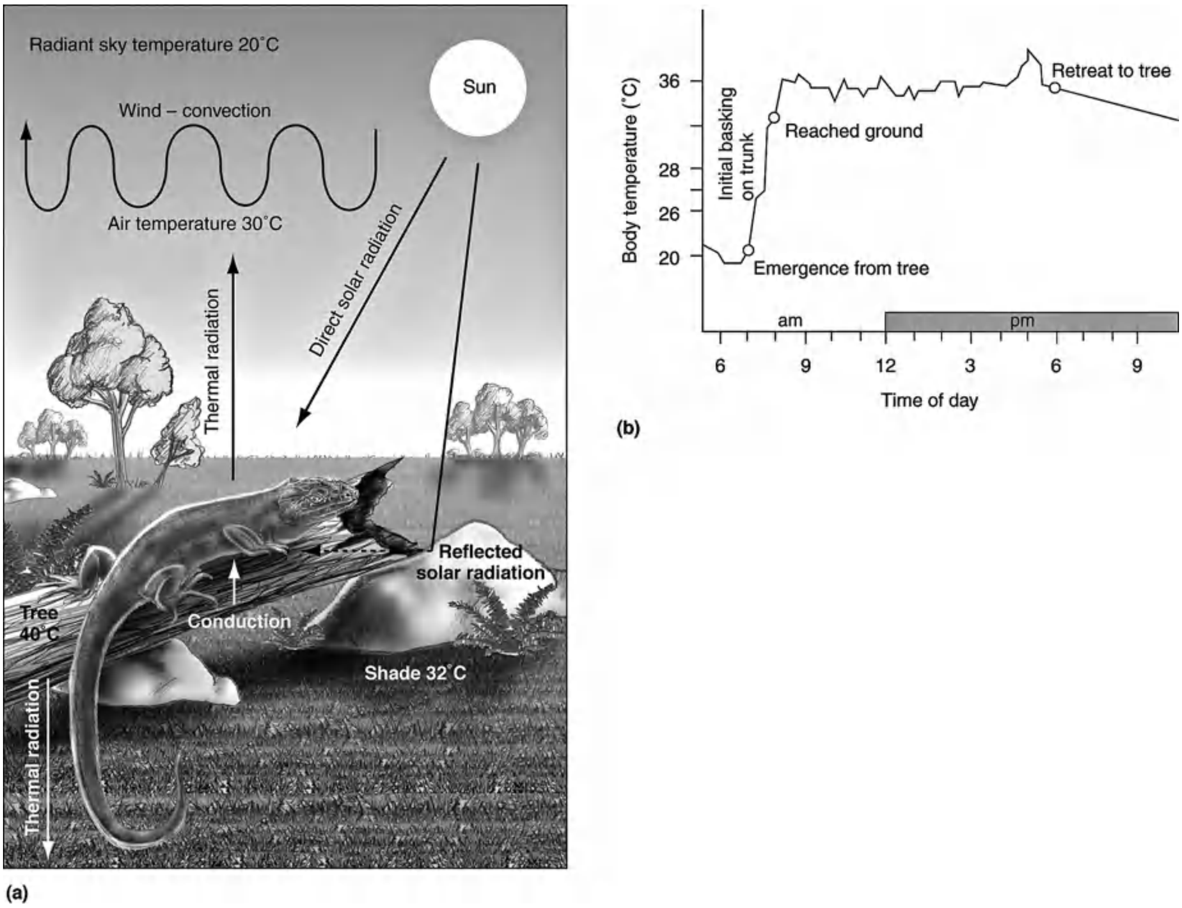


Figure 7.24. (*a*) Diagram showing the major avenues of heat exchange between reptiles and their environment. In regulating their body temperature, reptiles take advantage of the thermal diversity of their environment. (*b*) The body temperature of a lizard during the day is relatively high and constant, but it may fall when the lizard is in its retreat at night. These continuous records of core body temperature were gathered by a small temperature-sensitive radio transmitter swallowed by the lizard. The pulse rate of signals from the transmitter increases with the temperature.

Optic lobes and, for the first time evolutionarily in the vertebrates, distinct auditory lobes are present. The cerebellum, proportionately larger than in amphibians, is slightly larger in lizards, definitely larger in snakes, and best developed and most prominent in crocodilians and turtles. Cranial nerves have been discussed in Chapter 4.

The spinal cord is surrounded by two **meninges** (membranes): the dura mater and the leptomeninx. The spinal cord extends to the caudal end of the vertebral column in reptiles and, in most forms (except snakes and legless lizards), possesses cervical and lumbar enlargements in the two regions where large numbers of nerves that innervate the limbs exit the spinal cord. In turtles, the trunk region of the spinal cord is particularly slender because the thoracic and abdominal musculature is greatly reduced.

Sense Organs

CUTANEOUS RECEPTORS

Except for some vestiges of lateral-line organs in adult turtles (Feduccia and McCrady, 1991), lateral-line organs do not exist in reptiles. Cutaneous sense organs, however, are especially common in reptiles and occur in a variety of forms. Pain and temperature receptors are widely distributed. Pressure, tension, and stretching of the skin are monitored by intraepidermal and intradermal mechanoreceptors, some of which are present within the hinges that lie between the scales of lizards and snakes.

Some snakes have receptors in the form of pits that open onto the general body surface between epidermal scales. A single pair of specialized pits housing infrared receptors are found on the heads of crotalid snakes (family Viperidae) and on boas and pythons (see Fig. 7.18). The venomous viperids, which include such North American snakes as rattlesnakes, copperheads, and water moccasins, are often referred to as “pit vipers” because of this feature. These specific receptors, called **loreal pits**, are located between the eye and the nostril and are highly specialized heat-sensing structures. They are deep, directed forward, and covered by a thin transparent membrane. In adult snakes, the pits are about 5 mm (1/4 in.) deep and several millimeters in diameter; the inner cavity of the pit is larger than the external opening. Loreal pits in boas are slitlike and less obvious. Both types of pits are thermal receptors that respond to radiant heat. Studies of pit vipers have shown the loreal pits can detect temperature changes of 0.003°C (Bullock and Diecke, 1956). Thus, they can detect the presence of objects, including homeothermic animals on which the snakes prey, even if the object is only slightly warmer than the environment. Because of this extreme sensitivity, these snakes, which are at least partly nocturnal, can locate and strike accurately at objects in the dark. They prey on small mammals that are primarily nocturnal and whose temperatures usually differ from those of their surroundings.

Insights from Gastroliths

The discovery of approximately 240 gastroliths—“stomach stones” that certain animals ingest as an aid to grinding food—in and near a fossilized skeleton of a *Seismosaurus* dinosaur in New Mexico has provided possible clues concerning its digestive tract (see Fig. 7.23). Stones discovered within the *Seismosaurus*’s rib cage were arranged in two distinct clusters: a larger group near the base of the neck, and a smaller group near the pelvic region. This arrangement suggests that the herbivorous *Seismosaurus* might have had a crop and a gizzard. Researchers hypothesize that the swallowed food passed from the crop into the gizzard, where it was ground by the gastroliths, to a gastrolith-free stomach, where it was subjected to enzymatic action. The processed food then passed into the gizzard for additional grinding before finally moving into the intestine. Some living reptiles, particularly crocodilians, use grinding stones.

Based on feeding experiments with ostriches and comparative data for relative gastrolith mass in birds, Wings and Sander (2007) argued against the presence of a gastric mill in sauropods. Gastrolith clusters of some derived theropod dinosaurs (oviraptorosaurs and ornithomimosaurs) compared well with those of birds, suggesting that the gastric mill evolved in the avian stem lineage.

In 1997, each of 12 skeletons of an ornithomimid dinosaur from China contained a preserved gastrolith mass inside its ribcage. The presence of gastroliths indicates that these nonavian toothless theropods may have had gizzards and been herbivores like modern herbivorous birds that use grit to grind up plant matter. The gastroliths found in these dinosaurs were mainly composed of grains of silicate, with no bony elements or insect remains as might be expected if the dinosaur were insectivorous or omnivorous.

Monastersky, 1990b; Gillette, 1995; Kobayashi et al., 1999

EARS

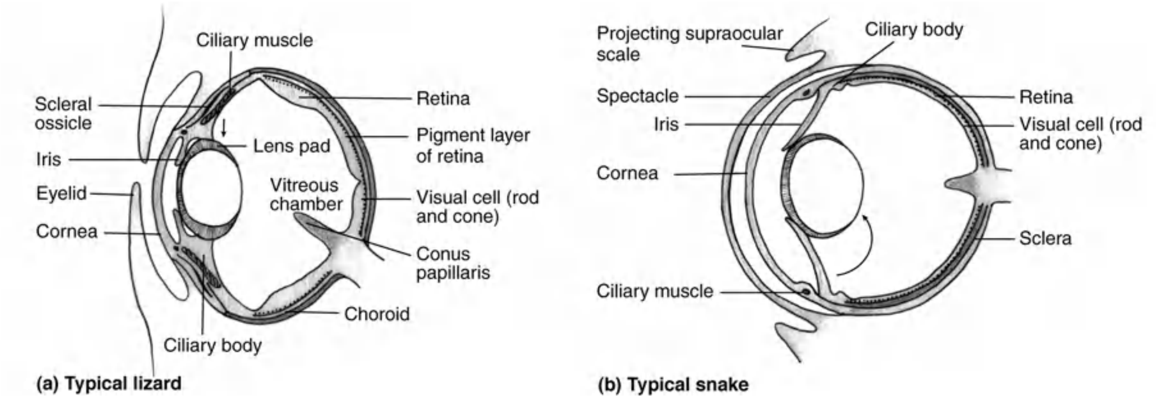
The reptilian ear serves as an organ of both equilibrium and hearing. Some lizards have no eardrum and no middle ear cavity. In snakes, a tympanic membrane, middle ear cavity, and Eustachian tube are missing entirely, although the semicircular canals and simple cochleae are present. A **cochlea**, an organ for detecting sound, has developed from the lagena of more primitive vertebrates. Sound waves are transmitted from the tympanic membrane to the cochlea via the columella in the middle ear cavity.

The distal end of the columella in snakes, which would articulate with the tympanum in other reptiles, articulates with the quadrate bone. Because snakes have no external ear openings, many have thought that snakes could not hear airborne vibrations (sound waves). Wever and Vernon (1960) demonstrated clearly that some colubrid snakes (e.g., *Pituophis melanoleucus*, *Thamnophis sirtalis*, and *Nerodia* [*Natrix*] *sipedon*) can hear aerial sounds and are moderately sensitive to frequencies in the range of 100 to 700 Hz. They concluded that the quadrate bone acts as a receiving surface for the aerial sounds and have noted that its removal produces moderate reduction in the inner ear response to sound. Hearing apparently is possible because the muscle and fiber layers over the distal end of the columella continue to transmit sound pressures to it. In working with species of the families Colubridae, Crotalidae, and Boidae, Hartline (1971) reported a more restricted frequency range, from about 150 to 600 Hz. Vibrations also may be conducted from the ground to the membranous labyrinth by way of the bones of the jaws.

In most reptiles other than snakes, the tympanic membrane is visible on the surface of the head. It is typically found at the inner boundary of a cavity (external auditory meatus). In aquatic turtles, the tympanic membrane is thin and transparent, whereas in other turtles it is covered with scales. Studies of turtles (Wever and Vernon, 1956a, 1956b) indicate that their hearing is similar in range and sensitivity to that of snakes. The tympanic membrane of some iguanian lizards (*Holbrookia* and some *Phrynosoma*) is covered with scaly skin. In most burrowing lizards, the middle ear has degenerated and the tympanic membrane is vestigial or absent. In some lizards, the cavity of the middle ear also has been lost. These groups are probably insensitive to airborne sounds, but they can likely detect ground vibrations.

EYES

In snakes, some lizards, and a few turtles, the upper and lower eyelids are permanently united in a “closed” position and are transparent, forming a **spectacle** that resembles a cornea (Fig. 7.25). The lids fuse together during embryonic development. The stratum corneum on the outer surface of the eyelids is shed each time the animal molts. The lower lid is the larger, and its upward movement is primarily what closes the eye. A third eyelid, more or less transparent, is called a **nictitating membrane** and is located medial to the eye in turtles (Fig. 7.26) and some lizards; it is absent in snakes. The nictitating membrane serves to cleanse and lubricate the cornea by rapidly sweeping back over its surface.



(a) Typical lizard **(b) Typical snake**

Figure 7.25. Transverse section of (*a*) a typical lizard eye and (*b*) a typical snake eye. In the lizard, contraction of the ciliary muscles forces the ciliary bodies against the lens pad and squeezes the lens. In the snake, the ciliary muscles have shifted into the iris and those near its roots press the iris against the vitreous body; this raises the intravitreous pressure and pushes the whole lens forward.

Figure 7.26. Head of an eastern box turtle (*Terrapene carolina*) showing a small portion of the nictitating membrane in the medial corner of the eye.

Lacrimal glands are present in many reptiles (absent in snakes) and secrete a watery fluid (tears) to keep the surface of the eye moist and clean. Although poorly developed in some reptiles, the lacrimal gland is enormous in marine turtles, where it plays an important role in osmotic regulation by controlling the excretion of salt.

Focusing of the eyes in reptiles occurs in two ways. In most snakes, increased pressure in the posterior chamber of the eye pushes the lens forward for focusing. This pressure is the result of the contraction of muscles at the root of the iris, which puts pressure on the vitreous humor. This, in turn, forces the lens forward (Gans and Parsons, 1970). In reptiles other than snakes, lens shape is changed by the contraction of radial muscles in the ciliary body encircling the lens. The lens is flattened for focusing on distant objects, and its curvature is increased for focusing on near objects.

Great variation exists with respect to the presence of photoreceptor cells (rods, cones) in the eyes of reptiles. **Rods** are responsible for vision at low illumination levels, while **cones** are used for color vision at higher light levels. Cones are lost in burrowing snakes, like blind snakes (*Typhlops*), and only tiny rods are present. Many diurnal lizards and snakes in the family Colubridae have lost the rods and are virtually blind at night. Both rods and cones are always present in the retinas of tuataras and turtles.

Colored oil droplets (yellow, orange, and red) are found between the inner and outer segments of cone photoreceptor cells on the retinas of lizards and turtles (Bowmaker, 1986; Robinson, 1994). The color in the droplets absorbs particular wavelengths of light, thereby narrowing the spectral sensitivity of the four visual pigment proteins while expanding the waveband of color sensitivity. The result is a tetrachromatic (four-color) visual system that extends from near-ultraviolet (350 nm) to infrared (750 nm) in turtles. Thus, turtles appear to have good color vision.

Chameleon eyes move independently until they lock onto prey. In addition, the eyelids make an aperture in front of the cornea that moves with the eye and serves as an iris to control the amount of light entering the eye (Land, 1995). Most remarkable, however, is that the lens, which is slightly convex, has negative refractive power (it causes light rays to diverge rather than converge) (Ott and Schaeffel, 1995). This is the only known example of a lens with negative power occurring in a vertebrate. Such an unusual optical design might have evolved to further extend the range of accommodation or to maximize the relative retinal image size. When retinal image sizes in a variety of vertebrate eyes were compared, chameleons were found to have the largest images.

Many lizards have a vestigial “eye” in the top of their head. The parapineal organ (parietal body) serves as this third, or **parietal**, eye. It lies beneath a single, translucent epidermal scale in the midline of the head and consists of a cornea, a lens, and retina-like receptor cells. In most lizards, it has the structure of a degenerate eye, but it is well developed in tuataras (*Sphenodon*). This medial eye is used to regulate body temperature by regulating the duration of exposure of the body to the sun. It is also partly responsible for the daily and annual body rhythms necessary for survival.

NOSE

Nasal passages of reptiles are longer than those of amphibians. The internal nares normally open into the anterior portion of the oral cavity except in turtles, which have a partial secondary palate that allows the nasal passageways to open farther posteriorly.

In snakes and some lizards, **vomeronasal** (Jacobson's) **organs** are well developed. These tubular organs lose their connection with the nasal canal and open into the anterior roof of the oral cavity (Fig. 7.27). Here, there are moist chemoreceptive depressions that monitor the odoriferous chemicals that accumulate on the tongue from the air. Vomeronasal organs are vestigial or absent in turtles.

TASTE

Although the sense of taste in reptiles is poorer than that of fishes and amphibians, it still plays a role in the recognition of prey, enemies, or potential mates. Taste buds are found primarily in the lining of the pharynx, with few, if any, located on the tongue. Turtles can probably taste objects held in the mouth.

Endocrine System

The endocrine system has been discussed in Chapter 4. Only those hormones that have specific and unique functions in reptiles are included here. Hormones secreted by the thyroid glands assist in regulating the metabolism of reptiles. They also play an important role in ecdysis (shedding). Parathyroid glands produce parathormone, which helps regulate levels of calcium and phosphate in the blood. Regulation of calcium is important, not only for homeostasis, but also for the proper formation of the calcareous shell enclosing some reptilian embryos.

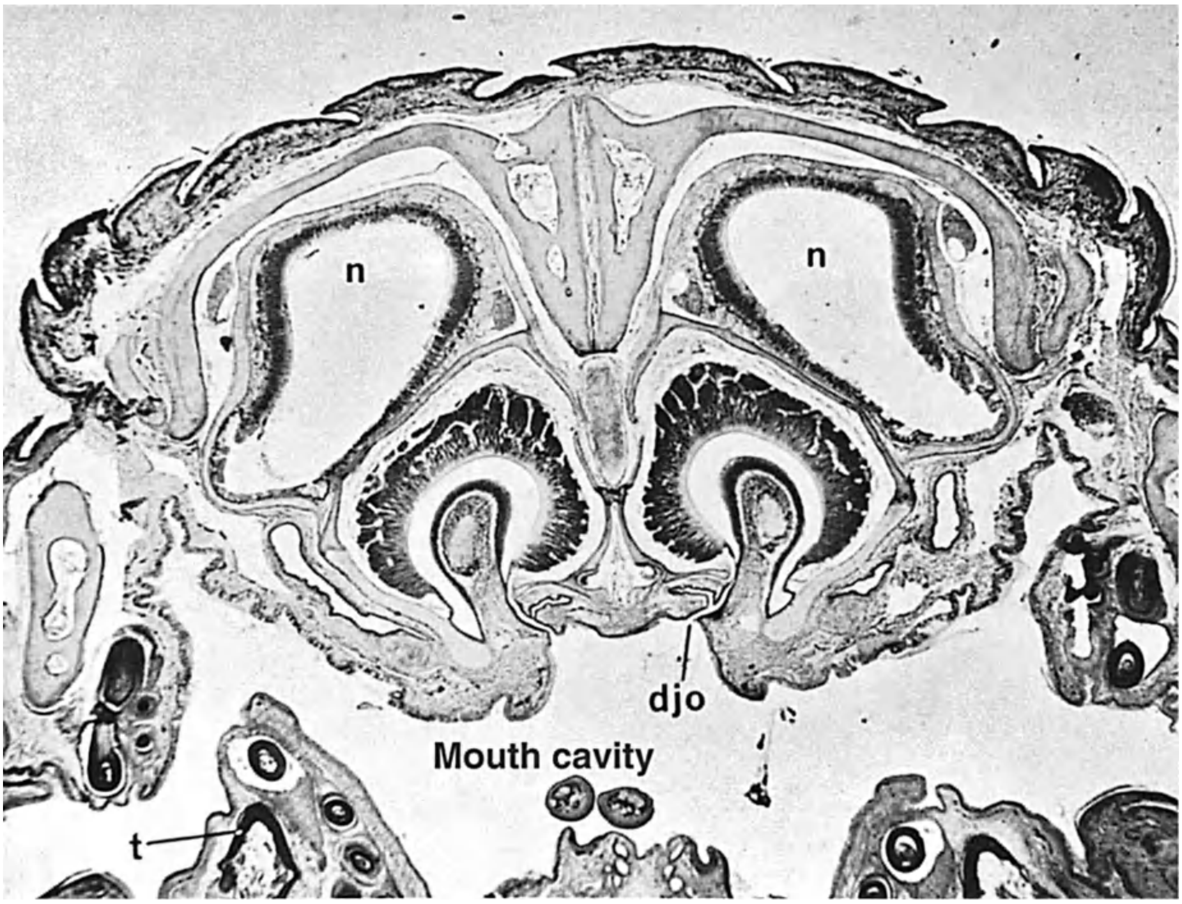


Figure 7.27. Transverse section through the head of a lizard (*Lacerta*) showing the crescent-shaped vomeronasal (Jacobson's) organs and their connections to the mouth cavity via ducts (*djo*). The larger openings (*n*) above the paired vomeronasal organs are the nasal passages, which are completely independent of the vomeronasal organs.

Testosterone, estrogen, and progesterone regulate reproductive behavior. Studies of the red-sided garter snake (*Thamnophis sirtalis parietalis*) show that the testosterone levels in males peak in late summer—more than eight months before the breeding season, as females are not receptive to mating until spring (Fackelmann, 1991).

Melatonin, secreted by the pineal gland, is responsible for the daily (and possibly seasonal) hypothermia in various lizard species, including the European green lizard (*Lacerta viridis*) (Rismiller and Heldmaier, 1987). These lizards display a pronounced rhythm in body temperature selection with daily voluntary hypothermia in fall, preceding winter dormancy. Because light inhibits the synthesis of melatonin, increasing amounts are produced as photoperiod (day length) shortens in the fall.

Urogenital System

The reptilian kidney is designed for a terrestrial environment in which the excretory and reproductive tracts become separated. A pronephros develops in the embryo, but it apparently never functions as an excretory organ. The structure of the functional embryonic kidney, the opisthonephros, is essentially the same as the adult kidneys of fishes and amphibians. It continues to function for a short time after hatching—as late as the first hibernation in some lizards and the first molt in some snakes.

During the time that the opisthonephros is functioning, the **metanephros** is in the process of development (see Fig. 3.16d). The metanephros replaces the **mesonephros** and becomes the adult kidney. Thus, reptiles are the first vertebrates evolutionarily to have a true metanephros as a functioning kidney. As the metanephros begins to function, the mesonephros slowly ceases functioning, so that, during later stages of embryonic development, both kidneys function simultaneously. Soon, only remnants of the mesonephros remain. As long as the mesonephros is functioning, the metanephric duct serves as an accessory urinary duct. When the mesonephros involutes, the metanephric duct becomes the sole urinary duct (ureter).

The more compact metanephric kidney contains renal corpuscles, proximal and distal convoluted tubules, and collecting tubules. Two or more renal arteries bring blood to the kidney to be filtered. No trace of segmentation is evident in the metanephric tubules, and no nephrostomes are present.

Filtration pressures of ectothermic vertebrates, which are much lower than those of endotherms primarily due to lower blood pressures in ectotherms, may decrease even more because of low body temperatures. Hibernation, for example, causes depressed cardiac function and a drop in blood pressure. In some parts of their range, painted turtles (*Chrysemys picta*) may spend as long as six to seven months in ice-covered bodies of water. Herbert and Jackson (1985) reported a reduction in systolic blood pressure in the painted turtle from 28.9 mm Hg at 20°C (68°F) to 7.7 mm Hg at 3°C (37°F) during submergence. The lower blood pressure in the renal arterioles during hibernation may limit or eliminate glomerular filtration.

Most reptilian kidneys are lobulate, with each lobe consisting of clusters of many tubules. In snakes and legless lizards, kidneys are elongated to conform to the slender body. In most reptiles, the ureters empty into a cloaca. A urinary bladder is present in tuataras, turtles, and many lizards, but lacking in snakes and crocodilians. When present, the bladder is an evagination of the ventral wall of the cloaca. Urine backs up into the reptilian bladder from the cloaca. In a few male reptiles, however, the ureters continue to empty into the mesonephric ducts, which carry sperm.

Turtles and many lizards have large bladders. Some turtles also have two highly vascularized, thin-walled accessory cloacal bladders that may function as water reservoirs in dry environments (C. B. Jorgensen, 1998). This function depends on copious water intake when water becomes available and discontinued voiding of urine in the absence of water. In females, this excess water helps moisten the soil when the female is excavating a nest for her eggs.

The cloaca in reptiles is divided into three chambers: a coprodeum, a urodeum, and a proctodeum. The **coprodeum** receives the terminal portion of the large intestine. The **urodeum** contains the openings of the excretory and genital ducts. The **proctodeum** is a short chamber enclosed by a sphincter muscle at the vent.

Nitrogenous waste excretions of reptiles may be in the form of ammonia, urea, or uric acid. Aquatic and semiaquatic forms are more likely to excrete ammonia, whereas terrestrial forms, which must conserve water, generally excrete uric acid, a concentrated waste product that is inert and insoluble in water. Some reptiles also have extrarenal salt excretion mechanisms that are active only when the osmotic concentration of the plasma becomes high. In the orbit of each eye, marine turtles have a salt-excreting lacrimal gland. A nasal gland performs a similar function in marine iguanas and some desert-dwelling lizards (Templeton, 1966). Sea snakes have a salt-excreting gland in their palate.

In female snakes and lizards, the paired ovaries are saccular with hollow lymph-filled cavities (lacunae) and are basically similar to those found in amphibians (Fig. 7.28a). In turtles and crocodilians, the ovaries are solid structures, similar to the ovaries of birds and mammals. The number of ova maturing at any one time in a reptile is less than in most amphibians—usually fewer than 100.

Reptilian oviducts are similar to those of amphibians (see Fig. 7.28a). They form from embryonic Müllerian ducts and are lined with glands that secrete albumen around the ovum. The posterior portions of the oviducts, known as uteri, contain specialized shell glands that secrete the egg shell (which is porous enough to allow for respiratory gas exchange) over the outer layers of the eggs. The two uteri enter the cloaca independently. In some snakes and lizards, special vaginal tubules known as **spermathecae** store sperm over the winter. Some lizards, some snakes, and all crocodilians retain only the right oviduct as a functional oviduct in adults; the left remains rudimentary.

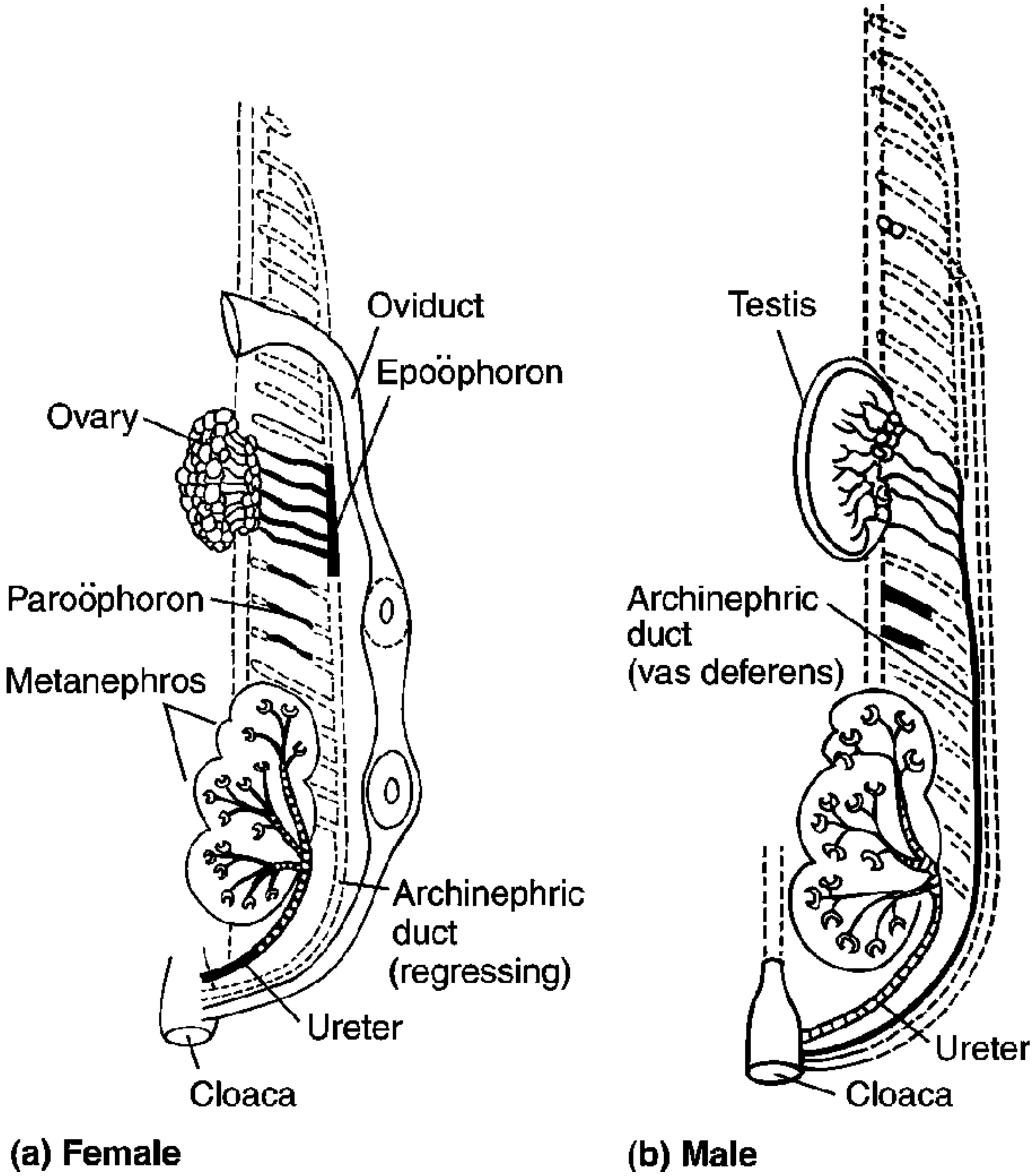


Figure 7.28. Comparison of female (*a*) and male (*b*) urogenital systems in reptiles (and birds).

The paired testes of males are suspended in the abdominal cavity (see Fig. 7.28b) and undergo marked seasonal fluctuations in size. Although mesonephric kidneys disappear during early development, mesonephric ducts of males remain. The portion closest to the testis forms the highly coiled **epididymis**. The remainder becomes known as the **ductus deferens** (vas deferens) and empties into the cloaca. Thus, a complete separation of excretory and reproductive tracts occurs anterior to the cloaca.

Fertilization, which is internal in all reptiles, occurs in the upper portion of the oviducts. With the development of internal fertilization, intromittent (or copulatory) organs evolved in males to introduce sperm into the female reproductive tract. Although present in a few fishes, amphibians, and birds, intromittent organs are characteristic of mammals and all male reptiles except tuataras (*Sphenodon*).

Two types of intromittent organs are present in reptiles. Paired structures known as **hemipenes** evolved in male squamates (lizards and snakes) and lie concealed in long sacs opening to the outside of the body on each side of the cloacal aperture (Fig. 7.29). Hemipenes lack specific erectile tissue; they are erected when they are turned inside out and everted like the fingers of a glove. This eversion is accomplished by muscle action and by filling of blood sinuses within the hemipenes. When everted, the hemipenes protrude through the vent. The shape of hemipenes is extremely variable and is used in squamate taxonomy. A groove on the surface of each hemipenis (sulcus spermaticus) conducts sperm into the cloaca of the female. Normally, only one hemipenis is inserted. Homologous structures, although much smaller, are present in females.

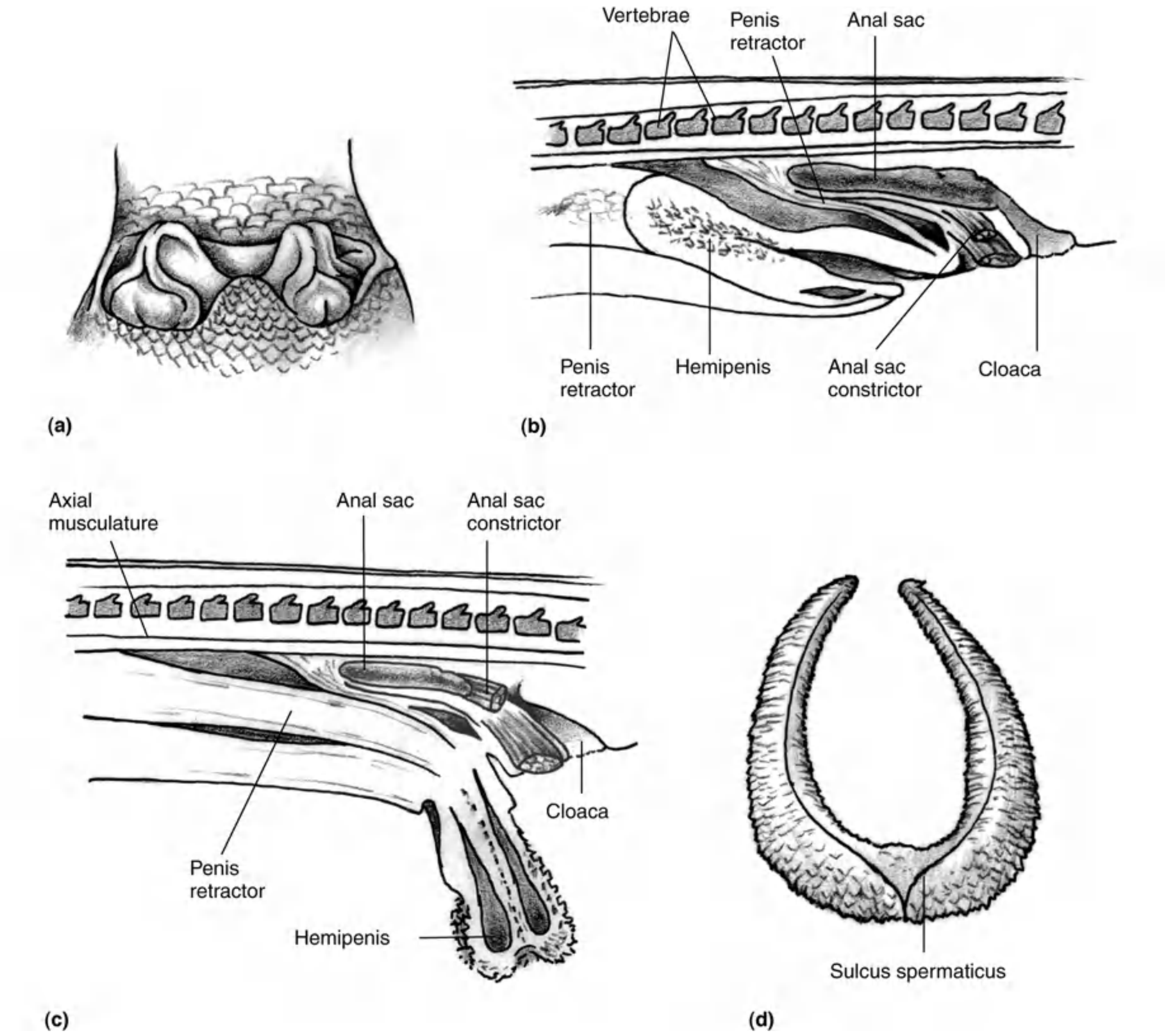


Figure 7.29. Lizards and snakes have paired hemipenes, but usually only one is used during copulation. (*a*) The hemipenes of a lizard. (*b*) The hemipenis is pulled back into the body by the retractor muscle (sagittal view). (*c*) When erect, the hemipenis's internal sinuses become engorged with blood and it pops through the vent (sagittal view). During copulation, the male inserts his hemipenis into the cloaca of the female. Sperm travel down the sulcus spermaticus into the female. (*d*) One of the two hemipenes from the rattlesnake *Crotalus atrox* is shown everted. This single hemipenis is divided, which gives it a horseshoe shape. Note the divided sulcus spermaticus that runs along each arched branch of the hemipenis.

Male turtles and crocodilians possess an unpaired **penis** (Fig. 7.30). The penis consists of the corpus cavernosum (spongy erectile tissue), which contains blood sinuses. The corpus cavernosum also bears a sulcus spermaticus for the passage of both sperm and urine. A rudimentary penis, the **clitoris**, develops in females.

REPRODUCTION

One of the most important evolutionary developments for long-term adaptation to terrestrial life was the development of the amniotic egg in reptiles (see discussion in Chapter 6; Fig. 6.4). The parchment-like shell (hard shell in crocodilians) allows for the exchange of gases, whereas the four extraembryonic membranes assist in forming blood vessels (chorion), surround the embryo and enclose the amniotic fluid (amnion), enclose the yolk (yolk sac), and serve as a respiratory organ and a repository for nitrogenous wastes (allantois). The adaptive value of the amniotic egg is to provide an internal aquatic environment for the development of young on land.

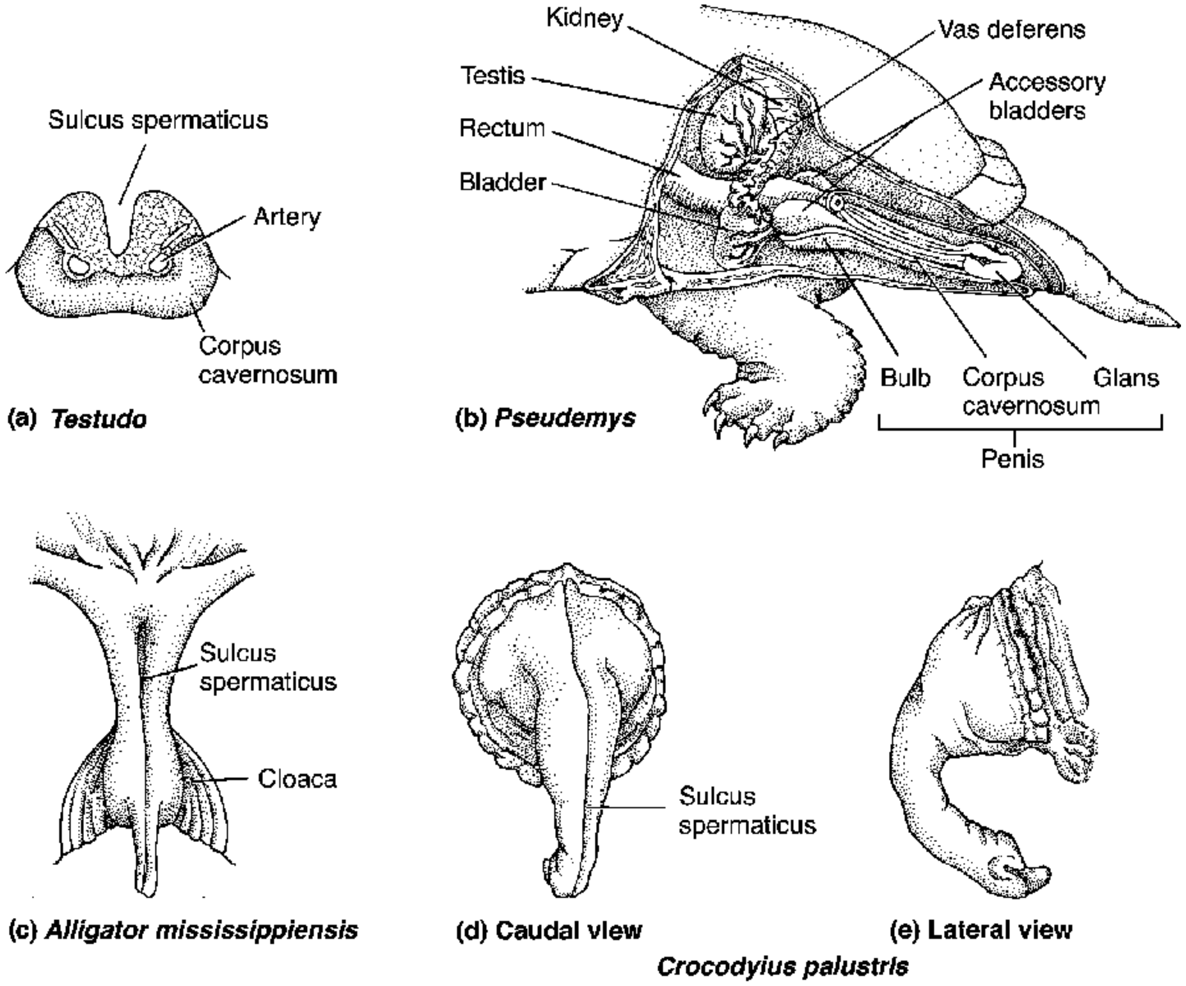


Figure 7.30. Penes of reptiles. (*a*) Turtle, *Testudo*: cross section of the penis within the cloaca. (*b*) Turtle, *Pseudemys*: sagittal section of the penis. (*c*) Alligator, *Alligator mississippiensis* penis. Caudal (*d*) and lateral (*e*) views of the penis of the crocodile, *Crocodylus palustris*.

Reptilian reproductive behavior is influenced primarily by temperature and photoperiod, with precipitation appearing to play only a minor role in initiating the breeding cycle. Some tropical lizards and crocodiles, however, manage to breed, lay eggs, and/or have their young during or following the rainy season—a possible adaptation to seasonally abundant food supplies. In temperate regions, reptiles usually breed within four to eight weeks following their emergence from hibernation and produce a single clutch of eggs annually, whereas in many tropical regions breeding may take place throughout the year.

Vision and olfaction are the most important senses used by most reptiles in seeking a suitable mate. During the breeding season, the musk glands of some turtles (e.g., *Sternotherus*) enlarge and may secrete pheromones. Lizards, which are primarily diurnal and live at fairly high densities, use primarily visual cues for attracting members of the opposite sex. Many lizards and snakes use pheromones for species and sex recognition, identification of eggs, and recognition of individuals. Some, like male broad-headed skinks (*Eumeces laticeps*), follow female conspecific odor trails (Cooper and Vitt, 1986). Chemical trailing of conspecifics also occurs widely in snakes.

Courtship behavior of most reptiles is poorly known. Although all turtles are oviparous (egg-laying) and lay their eggs on land, aquatic species mate in the water and appear to rely almost entirely on visual means for species and sex recognition. Males swim onto the backs of females and grip their carapaces with their long claws. Terrestrial and semiaquatic turtles mate on land and use visual and olfactory cues for sex recognition. Courtship behavior usually involves head-bobbing by the male, an action that gives an obvious visual signal but that also may be sending scent through the air. Lizards depend primarily on visual clues like brightly colored patches of skin, conspicuous head crests, and bobbing of the head and body. Both sexes of some anoles like *Anolis carolinensis* and *A. sagrei* possess an orange-red or pink flap of tissue beneath their chin (Fig. 7.31). This flap, known as a **dewlap**, can be voluntarily extended and retracted. It plays an important role in both courtship and territorial defense. Snakes also appear to use mainly visual and olfactory cues for sex and species recognition. Courtship in most species involves tactile stimulation of the female and olfactory stimulation of the male. Many species entwine their bodies around each other prior to copulation.

Lipids extracted from the skin of female red-sided garter snakes (*Thamnophis sirtalis parietalis*) are attractive to sexually active courting males (Mason et al., 1989) (Fig. 7.32). The lipids contain a female sex attractant pheromone, which consists of a series of long-chain methyl ketones (Mason et al., 1989). Females of related groups of snakes have some of the same methyl ketones as well as variations of the compound forming the pheromone. When extracts of lipids from male skins are added to female extracts, male courtship stops, suggesting that males emit specific chemical cues that identify them as males. One chemical in the male lipid, squalene, caused a significant reduction in courting behavior and is important in the male sex recognition pheromone.

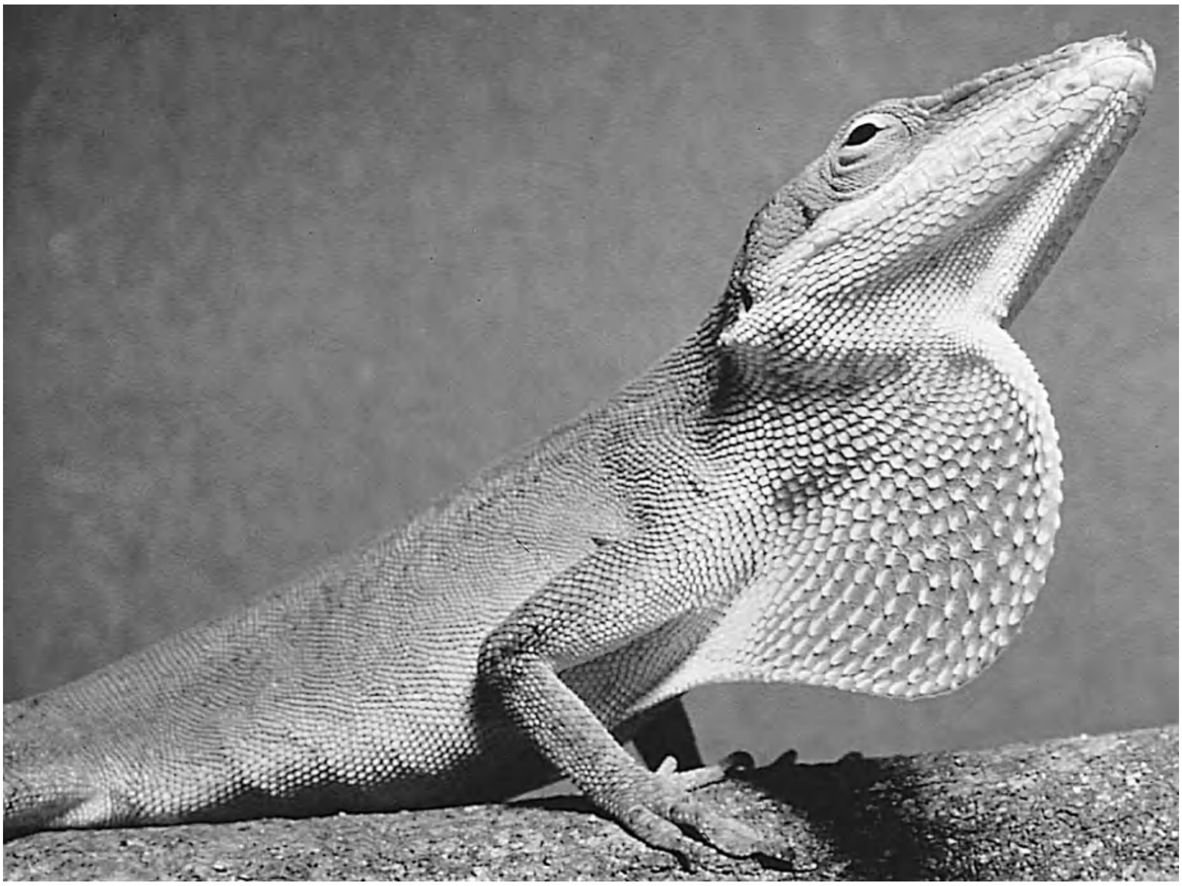


Figure 7.31. Male anoles (*Anolis carolinensis*) of the southeastern United States possess an orange-red flap of tissue beneath their chins known as a dewlap. The dewlap, which can be voluntarily extended and retracted, plays an important role in courtship and territorial defense.

Lipids stored in abdominal fat bodies can play an important role in the reproductive cycle of lizards (Derickson, 1974, 1976). In seasons during which lipid storage is reduced, egg production also is reduced greatly (Ballinger, 1977). Lipids in the fat bodies are depleted immediately upon emerging from hibernation and are not restored until after reproduction is completed. Seasonal changes in lipid composition during the reproductive cycle in fence lizards (*Sceloporus*) were reported by Ballinger et al. (1992). For example, the fatty acid triacylglycerol made up 88 percent of total lipids in fat bodies early in the reproductive season but declined to 66 percent following egg production.

Although most lizards and snakes are oviparous, a few, like most boas (Boidae), pit vipers (Crotalidae), some skinks (Scincidae), night lizards (Xantusiidae), and garter and ribbon snakes (*Thamnophis*), are viviparous (live bearers). Viviparity provides additional protection for the developing young. In garter snakes (*Thamnophis sirtalis*), the developing young are attached to the reproductive tract of the female. The placenta serves as a respiratory organ and also facilitates the transfer of amino acids from the mother to the embryo (Clark et al., 1955). Viviparity, however, elicits a substantial cost to the female in reducing mobility (rendering her less able to evade predators and catch food) and energetics.

Figure 7.32. Lipids extracted from the skin of female red-sided garter snakes (*Thamnophis sirtalis parietalis*) are attractive to sexually active courting males. The snake whose head is farthest to the left is the female.

Multiple copulations are reported in Swedish adders (*Vipera berus*) (Madsen et al., 1992). In this species, females averaged 3.7 copulations (range 1–8) per season, usually with different males. Multiple matings enhanced the genetic diversity of the offspring and significantly reduced the proportions of young that were born dead. Because female snakes can store sperm for months before ovulation, collecting sperm from numerous males creates a “competition” within the female’s body in which the best-performing and most competitive sperm have the best chance to fertilize eggs. If sperm that are more successful in fertilizing ova are also more effective in producing viable offspring, then the increase in the average viability of offspring would be correlated with multiple matings. However, multiple matings in Swedish adders did not result in increases in the size of offspring, litter size, or total litter mass, nor did females have higher fertility.

Female sand lizards (*Lacerta agilis*) copulate with virtually every male that courts them. Thus, they often mate with close relatives. However, they actively select, via intrauterine sperm competition, the sperm from distantly related males (Olsson et al., 1996). Even if they are unable to avoid mating with close relatives, females “choose” not to use sperm from these matings.

A Volcanic Nest

In a study of land iguanas (*Conolophus subcristatus*) on Fernandina Island in the Galápagos, Dagmar Werner found that, following mating, 95 percent of the females migrated into the caldera of a volcano to nest, a trip of up to 6 km (3.5 mi.), involving an initial climb of 1,400 m (4,600 ft.) to the crater rim, followed by a 900 m (2,950 ft.) descent to the caldera floor. Prior to descending, several thousand females circle the crater at the rim searching for the descent access, adding approximately 9 km (5.5 mi.) to their journey. This is the longest distance known to be walked by any species of lizard to its nesting grounds. On average, the time spent between leaving the mating area and nesting was 30 days. The journey to reach the rim required between 4 and 10 days.

Each female lays between 8 and 23 eggs in a fumarole crevice with soft earth at least 40 cm (16 in.) deep. The eggs are heated by hot vapor and remain between 32°C and 34°C (90°F and 93°F) both day and night. Incubation requires three to four months, during which time the eggs are unattended. After nesting, females slowly return to the proximity of the mating area.

Werner, 1982, 1983

Most reptiles have one breeding cycle per year, which for most temperate species begins upon their emergence from hibernation. Some, however, may not breed for several years at a time. Female tuataras (*Sphenodon*) breed only once every four or five years and take two or three years to develop eggs. After mating, eggs are held in the oviduct for another seven months before they are deposited. Twelve to 16 months later, the eggs finally hatch. The 10 cm (4 in.) babies spend a few days in their underground nest before pushing up through the soil.

Some all-female species and some populations of vertebrates reproduce by **parthenogenesis**, a process in which a new individual develops from an unfertilized egg. In some species, parthenogenesis is **facultative**, occurring only when this mode of reproduction is necessary as a last resort for producing offspring. In a few species, however, reproduction is exclusively parthenogenic.

Parthenogenesis may evolve only in populations devoid of the parental bisexual individuals because such species would prevent newly formed unisexuals from establishing clones, due to either hybridization or competition. Parthenogenesis has its advantages, the most obvious being higher potential population growth because all individuals (rather than half) can produce eggs. This doubles the intrinsic rate of increase (r-strategist) and increases the ability of one individual to establish a new colony. Thus, parthenogenic species hypothetically can invade and occupy habitats faster than bisexuals.

Parthenogenesis, known in fishes, amphibians, and reptiles, occurs most commonly in lizards. Thirteen parthenogenic species occur in the genus *Cnemidophorus* in the United States. The desert grassland whiptail lizard (*C. uniparens*) is one such species. It is a single clone in which the chromosomes of each lizard duplicate just before the oocyte divides, producing the homozygous diploid condition as well as genetically complete and identical eggs. The first ever instance of parthenogenesis in the Komodo dragon was reported in 2006 at London’s Chester Zoo (Bryner, 2006).

Only one species of snake is known to have obligate parthenogenesis. It is a member of the Scolecophidia, or blindsnakes, called the Brahminy blindsnake or flowerpot snake (*Ramphotyphlops braminus*). This tiny egg-laying species is made up only of females and is extremely widespread, primarily thanks to the ability of just a single individual to colonize new areas.

GROWTH AND DEVELOPMENT

Prenatal Development

Turtles and most lizards and snakes are oviparous reptiles that deposit their eggs on land (Fig. 7.33). No aquatic larval stage exists.

Reptiles were the first group of vertebrates to have colonized the terrestrial environment successfully. They solved the problem of having to return to water to reproduce by evolving the amniote egg with its leathery shell and four extraembryonic membranes (amnion, chorion, yolk sac, and allantois) (see Fig. 6.4). The **amnion** completely surrounds the embryo and contains the amniotic fluid in which the embryo floats. During later stages of development, it forms part of the chorioamnionic connection where the amnion and chorion remain united (Ewert, 1985). The **chorion** is the outermost membrane and assists primarily in gas exchange through the shell. The **yolk sac**, which is attached to the digestive tract, contains the yolk, which serves as the embryo's source of nutrients (a carryover from anamniotes), whereas the **allantois** functions as the primary organ for mid- to advanced embryonic respiratory gas exchange and as a receptacle for the embryo's metabolic wastes. It is the last extraembryonic membrane to form. As the embryo develops, the allantois expands and fuses with the chorion to form the chorioallantoic membrane, which lines the entire shell membrane with blood vessels and provides a rich vascular network.

Courtship in a Unisex Lizard

Captive whiptail lizards, although all female, go through the motions of courtship and mounting behavior. One female acts as a receptive (gravid) female; the other takes the male role of mounting the receptive female, slipping her tail under her partner, and assuming the stereotypical male copulatory position. Every 10 to 14 days, the two females switch roles. The lizard that has just ovulated has a surge of progesterone, which causes her to act like a male; after a week or so her ovaries become larger and secrete estrogen, and she reassumes the female's part. Individual lizards are more likely to ovulate when they are with a malelike female. Thus, "pseudosexual" behavior apparently serves to maximize the number of eggs produced.

Crews and Young, 1991

(a)

(b)

Figure 7.33. (*a*) A female loggerhead sea turtle (*Caretta caretta*) depositing her eggs on a tropical beach. (*b*) Female black racer (*Coluber constrictor*) depositing her eggs.

Figure 7.34. Hatching kingsnakes (*Lampropeltis getula*). Most snakes are oviparous and lay leathery-shelled eggs.

Amniotic eggs are characteristic of reptiles, birds, monotremes, and, in modified form, therian mammals. The development of the amniotic egg was such a remarkable event in the evolution of terrestrial vertebrates that it serves as a major characteristic separating fishes and amphibians—**anamniotes**—from the reptiles, birds, and mammals—**amniotes**.

Most reptilian eggs are enclosed in a leathery shell to prevent desiccation (Fig. 7.34). They may be buried in sand, mud, or soil, or deposited in decaying vegetation or rotting logs. Most adult female sea turtles breed on one- to three-year cycles (reviewed by Ehrhart, 1981) and only return to land for periods of several hours to deposit their eggs in nests excavated on sandy beaches (see Fig. 7.33a). The sand heated by the sun incubates the eggs.

Many oviparous lizards and snakes retain eggs in utero until about halfway through their embryonic development (Shine, 1983). One such lizard, *Sphenomorphus fragilis*, exhibits extreme egg retention (Greer and Parker, 1979). The female lays thinly shelled eggs that "hatch" almost immediately after being laid. Greer and Parker (1979) concluded that *S. fragilis* was "effectively a live-bearer but that it has retained the egg shell of its presumed oviparous ancestor, albeit in a greatly thinned condition.”

The smooth green snake (*Opheodrys vernalis*) is one of the northernmost oviparous snakes in North America. The time between egg-laying and hatching in this species has been shown to be as short as four days (Blanchard, 1933).

Parthenogenesis in Snakes

Facultative parthenogenesis has been recorded in snakes on several occasions. A captive 14-year-old female timber rattlesnake (*Crotalus horridus*) that had never been with a male gave birth to a litter of young. A female garter snake (*Thamnophis elegans*) caught as a young adult in 1983 lived only with females for the next year and was kept completely isolated from snakes after that. She produced four litters between 1988 and 1994. Two clutches of baby snakes were born to an aquatic Australian Arafura filesnake (*Acrochordus arafurae*) in 1988 and 1991 that had been isolated from all males since 1983. Other confirmed parthenogenic species include the Burmese python (*Python bivittatus*), rainbow boa (*Epicrates maurus*), boa constrictor (*Boa constrictor*), both captive and wild cottonmouths (*Agkistrodon piscivorus*) and copperheads (*Agkistrodon contortrix*), captive eastern diamondback (*Crotalus adamanteus*), timber (*C. horridus*), and Aruba Island (*C. unicolor*) rattlesnakes, and four species of garter snakes (*Thamnophis couchii*, *T. elegans*, *T. marcianus*, and *T. atratus*). Allen et al. (2018) recorded parthenogenesis for the first time in elapid snakes.

Dubach and Sajewicz, 1997; Schuett et al., 1997; Durso, 2014; Allen et al., 2018

Viviparity has evolved at least 55 times among lizards and 35 times among snakes (Blackburn, 1982, 1985). Young are retained within the female for their entire gestation period. All North American rattlesnakes are viviparous, as are the well-known garter snakes (*Thamnophis sirtalis*) of North America and two species of horned lizards (*Phrynosoma douglassi* and *P. orbiculare*). Viviparity in reptiles serves to protect eggs from predators and to speed development of those species living in cool montane regions, as well as those species living near the extremes of their ranges in both the Northern and Southern hemispheres.

Charland and Gregory (1990) have shown that the body temperature maintained by gravid prairie rattlesnakes (*Crotalus viridis*) is far more constant than in nongravid females. Regulation of body temperature is accomplished by moving between locations of higher and lower environmental temperature and by influencing rates of heat gain and loss by making subtle changes in basking posture or orientation that alter the surface area exposed to the sun. Adaptive strategies of temperature regulation can result in an increased rate of development and better control of the time of birth.

Two species of lizards—*Sceloporus aeneus* (Iguanidae) and *Lacerta vivipara* (Lacertidae)—have been shown to exhibit both modes (oviparity and viviparity) of reproduction. Viviparity is the usual mode of reproduction for *L. vivipara* in its range from Russia to Scandinavia and northern France (Heulin et al., 1991). However, in the warmer, extreme southwestern part of its range in France and northwest Spain, it is oviparous. Studies of embryonic development and birth dates found one main advantage of viviparity to be that embryos developed more rapidly at high maternal temperatures than at low soil temperatures (Heulin et al., 1991). The difference in birth dates between oviparous and viviparous forms did not exceed one week when oviparous eggs were artificially incubated at temperatures close to the body temperatures of pregnant viviparous females. However, oviparous eggs incubated under lower outdoor temperatures hatched approximately one month after viviparous females gave birth to their young. The evolutionary origins of viviparity in reptiles have been discussed by Blackburn (1982, 1985), Packard et al. (1991), and Guillette (1991).

Duration of Embryonic Development

Reptile eggs require incubation periods ranging from 5 weeks to 16 months. Most turtle eggs hatch between 8 and 16 weeks from the time they are deposited. Lizard eggs require 5 to 12 weeks to hatch, whereas the incubation period for snake eggs ranges from 8 to 12 weeks (see Fig. 7.34). Female tuataras retain fertilized eggs within the oviduct for approximately 7 months before laying them, and eggs hatch 12 to 16 months after being deposited in an underground nest.

Hatching and Birth

The young of oviparous reptiles develop a **caruncle** (egg tooth) prior to hatching. In these reptiles, it usually is located on the premaxillary bone. Just prior to hatching, the egg tooth is used to crack, or “pip,” the shell. The pressure exerted by the young inside the egg, together with the increasing movements of the embryo, causes the weakened shell to crack enough to allow the young reptile to emerge. The egg tooth is reabsorbed shortly after birth.

In many species of reptiles, sex is determined by incubation temperature of the egg during the middle third of incubation (reviewed by Bull, 1983; Janzen and Paukstis, 1991a), which is the time when gonads differentiate (Wibbels et al., 1991). Three patterns of temperature-dependent sex determination (TSD) have been identified: Type A: males produced at high temperatures, females at low temperatures (most crocodilians and some lizards); Type B: females produced at high temperatures, males at low temperatures (many turtles); and Type C: females produced at high and low temperatures with males produced at intermediate temperatures (three crocodiles, one lizard, and three turtle species) (Bull, 1980, 1983; Brooks et al., 1991; Ewert and Nelson, 1991; Etchberger et al., 1992). For example, nest temperatures greater than 33°C (91°F) have been found to produce a greater percentage of male alligators (Ferguson and Joanen, 1982). The underlying molecular and physiological basis of TSD is unknown (Janzen and Paukstis, 1991a).

The possible adaptive significance of environmental sex determination (ESD) mechanisms in reptiles was investigated by Janzen and Paukstis (1991b). They concluded that comparison of sex-determining mechanisms (hydric, thermal) with sexual dimorphism in adult body size did not support the sexual dimorphism hypothesis that posthatching growth correlates with both incubation temperature and offspring sex. No relationship existed between the type of ESD and patterns of sexual dimorphism in adult body size. They noted, however, that evidence for the possible adaptive significance of ESD in leopard geckos (*Eublepharis macularius*) had previously been reported by Gutzke and Crews (1988). Female geckos incubated at warm temperatures apparently are later functionally sterile, whereas females incubated at cool temperatures are fertile and sexually receptive when courted by males.

Wibbels et al. (1991) reported a female to male ratio of 2.1:1 for immature loggerhead sea turtles (*Caretta caretta*) inhabiting the Atlantic coastal waters of Florida. Shepherd (1989) reported that nest temperatures of 29°C (84°F) and below produced male loggerheads, whereas temperatures above 31°C (88°F) produced females. Sex-biased ratios may be of importance in managing or manipulating populations of endangered species. For example, researchers working with the endangered Kemp’s ridley sea turtle (*Lepidochelys kempii*) along Mexico’s Gulf Coast plan to repopulate native waters with egg-laying females.

Until recently, sexing turtles younger than 2 years of age has been difficult. At about 2 years of age, radioimmunoassay for testosterone can reveal the gender with 90 percent accuracy. Most recently, scientists at the University of Tennessee at Memphis have developed a promising alternative based on genetic fingerprinting techniques (Demas et al., 1990). After fragmenting DNA extracted from a small blood sample, researchers apply a genetic probe that selectively binds to gender-specific DNA fragments. The technique can determine sex even in hatchlings. It has been used successfully in Kemp's ridley sea turtles and green sea turtles (*Chelonia mydas*).

The choice of nest sites by female diamondback terrapins (*Malaclemys terrapin*) alters the incubation temperature and, consequently, the sex of the young that hatch (Roosenburg, 1996). Terrapins have a large variation in egg size between clutches, but little variation within clutches. Egg mass, the primary determinant of hatchling mass, can cause as much as a three-year difference in reaching the size of first reproduction in females, but may not affect age or size of first reproduction in males. In addition, nesting females apparently can discriminate among nesting sites (sun-open versus sun-edge habitats). Nest temperature can be adjusted by adjusting the depth of the nest—a difference of 2 to 3 cm (1 in.) can drastically change the temperature at which the eggs incubate. Larger females deposit their eggs in open nest sites that receive lots of sunlight, whereas smaller, younger terrapins lay their eggs in cooler sites. The warmer eggs, which are also larger and have more yolk, hatch into females that can start laying their own eggs earlier.

Incubation temperature may have long-term effects on posthatching survival, growth rates, behavior, and environmental preferences of some reptiles (Lang, 1987; Burger, 1989; Webb and Cooper-Preston, 1989; Van Damme et al., 1992). To determine behavioral differences as a function of incubation temperature, pine snake (*Pituophis melanoleucus*) eggs were incubated at temperatures of 21°C, 23°C, 26°C, 28°C, 30°C, and 32°C (70°F, 73°F, 79°F, 86°F, and 90°F). Hatchlings from medium-temperature incubation, 26°C or 28°C (79°F or 82°F), performed all behavioral and physiological tests better than hatchlings from eggs incubated at low temperatures, 21°C or 23°C (70°F or 73°F). Hatchlings from eggs incubated at high temperatures, 30°C or 32°C (86°F or 90°F), performed some behavioral tests less well than medium-temperature, 26°C to 28°C (79°F to 82°F), hatchlings. Physiological and behavioral activities like shedding time, drinking speeds, and movement were monitored, with some of the behavioral differences persisting for at least 24 weeks following hatching.

Van Damme et al. (1992) incubated eggs of the lacertid lizard, *Podarcis muralis*, at temperatures ranging from 24°C to 35°C (75°F to 95°F). Although embryos incubated at 32°C and 35°C (90°F to 95°F) hatched about 10 days earlier than those incubated at 28°C (82°F), and more than five weeks before those incubated at 24°C (75°F), hatching success was highest at 24°C and 28°C (75°F to 82°F). Neonates incubated at low temperatures had larger snout-vent lengths and body masses, grew faster, and had higher sprint speeds than hatchlings incubated at higher temperatures.

Oxygen availability to embryos is critical to their development. Low oxygen concentrations extended the incubation period of mud turtles (*Kinosternon subrubrum*), snapping turtles (*Chelydra serpentina*), and painted turtles (*Chrysemys picta*) and killed many embryos prior to hatching (Ewert, 1985). Turtle eggs incubated at higher than atmospheric oxygen (30 percent oxygen), however, did not show an increase in growth rate.

Scientific attention has been increasing concerning the ecological and evolutionary effects of climate change on species with TSD (Mitchell and Janzen, 2010; Escobedo-Galvan, 2013; Refsnider and Janzen, 2016). Organisms become adapted to their environment by evolving through natural selection, a process that generally transpires over many generations. Currently, anthropogenically driven environmental changes are occurring in orders of magnitude faster than they did prior to human influence, which could potentially outpace the ability of some organisms to adapt. Opinions vary as to whether the effect on TSD species will be the imbalance of sex ratios (which, in turn, would threaten population viability) or whether TSD species could shift sex ratio in response to thermal fluctuations, specifically reversing the sex ratio or balance sex ratios. Additional information is needed before it will be possible to predict the effects of climate change on TSD species.

Parental Care

Numerous lizards and snakes care for their eggs, but parental care of offspring is rare in reptiles (reviewed by Shine, 1988; Branch, 1989). Some female skinks (*Eumeces* spp.) brood their eggs and even retrieve them if necessary, but no apparent association exists between maternal females and their offspring following hatching (Vitt and Cooper, 1989). Egg-guarding has been observed in several species of snakes, including the king cobra (*Ophiophagus hannah*), some members of the genus *Elaphe*, and the Texas thread snake (*Leptotyphlops dulcis*). All species of pythons brood their eggs, but only female Indian pythons (*Python molurus*) coil around their eggs—they reportedly can increase their body temperature from 5.5°C to 7.5°C (42°F to 45°F) during incubation by contracting their body muscles (shivering thermogenesis) (Fig. 7.35) (Halliday and Adler, 1986). The number of contractions increases as the ambient temperature decreases so that the temperature within the clutch of eggs is maintained at 32°C to 33°C (90°F to 91°F), which may be as much as 7.5°C (13.5°F) above that of the surrounding air. Shivering thermogenesis has also been reported in a brooding Burmese python (*Python molurus bivittatus*) in the Everglades (Snow et al., 2010). Nest temperatures were maintained both warmer and cooler than ambient temperatures. Female mud snakes (*Farancia abacura*) also have been known to coil around their eggs, but it is not known if they can increase their body temperatures.

Growth

Reptiles hatch or are born as miniature adults (see Fig. 7.34); development is completed inside the egg or inside the female's body. At hatching or birth, they are capable of moving about on their own, feeding, and defending themselves.

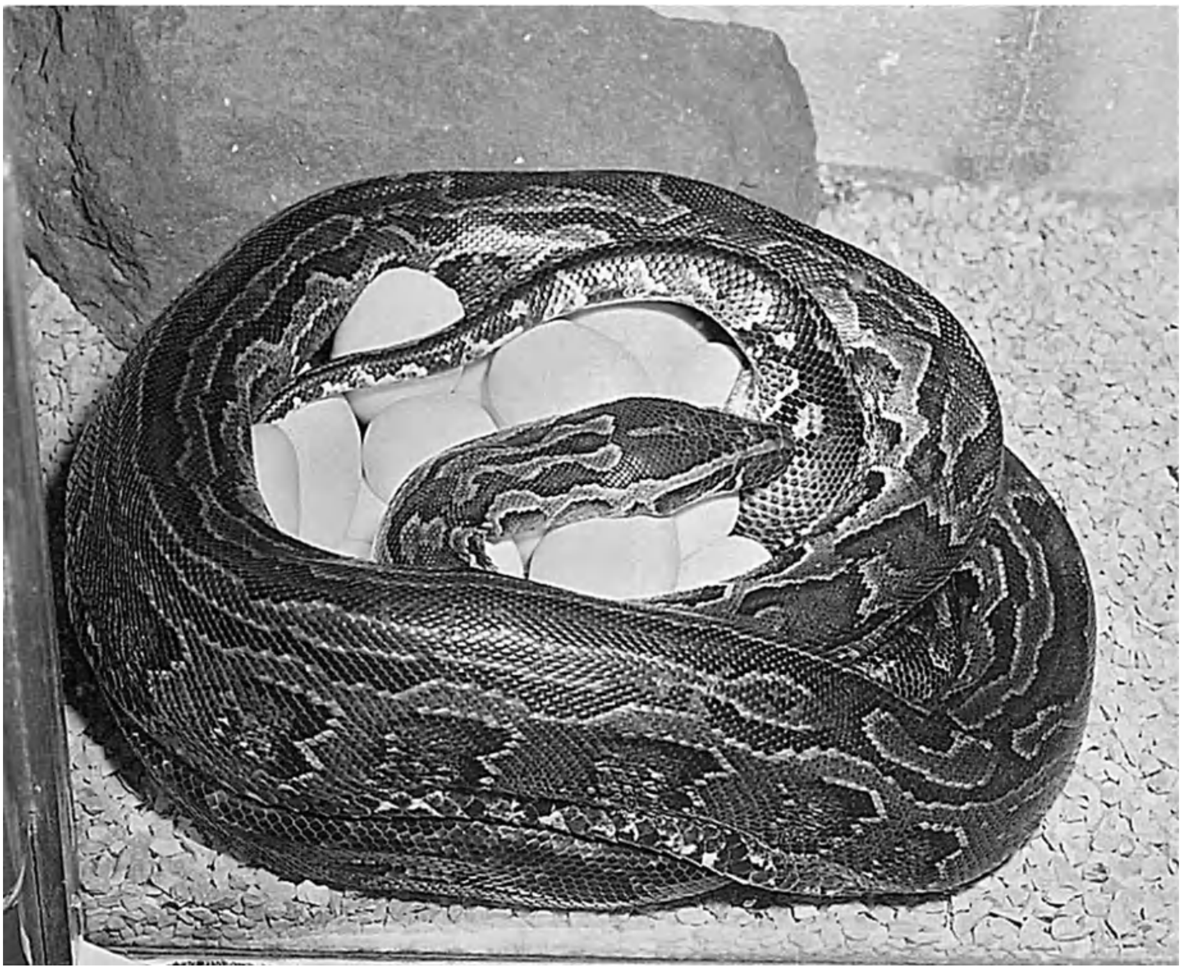


Figure 7.35. Python (*Python sebae*) coiled around a clutch of eggs and contracting her muscles at a regular rate, thus raising the temperature of her body by as much as 7.5°C (13°F) and warming the clutch of eggs.

The Madagascan chameleon (*Furcifer labordi*) has an *annual* lifecycle. Individuals hatch in November, grow at astonishing rates, reach maturity by January, battle fiercely over mates, breed, and lay their eggs by February, and then die. For the next nine months, the entire species is represented by eggs. This is the shortest lifespan ever recorded for a four-legged vertebrate.

Attainment of Sexual Maturity

Reptiles continue to grow throughout their lives. As with amphibians, most appear to reach sexual maturity after they have reached a certain size rather than a specific age. Many of the smaller lizards and snakes can breed in the year following their birth. Female utas (*Uta stansburiana*) become sexually mature at 4 months of age. Most snakes reach sexual maturity after 2 to 3 years, and most turtles can breed when

3 to 5 years of age, but female Galápagos tortoises (*Geochelone gigantea*) and female tuataras (*Sphenodon*) require approximately 11 years to reach maturity (Grubb, 1971; Bourne and Coe, 1978; Castanet et al., 1988). The age at which a species reaches maturity is a compromise among many variables, with the “goal” of maximizing an individual’s contribution to the next generation. One way of achieving this goal is to mature and reproduce quickly; however, smaller adults are more susceptible to predation and small body size reduces the number and/or size of offspring that can be produced. Maturing later and at a larger body size permits the production of more and/or larger offspring but increases the probability of death prior to reproducing and may yield a smaller total lifetime output of offspring.

The Asiatic reticulated python (*Python reticulatus*) holds the world’s record for length of a snake, with the longest ever measured at 10 m (33 ft.). Weighing in at 249 kg (550 lb.), the aptly named giant anaconda (*Eunectes murinus*) is the largest snake in the world considering its length-to-weight ratio. This species, also known as the green anaconda, averages about 5 m (17 ft.) in length, though some individuals grow to as long as 9 m (30 ft.). The longest snake in captivity, according to the Guinness Book of World Records, is 17-year-old Medusa, a reticulated python, born on October 13, 2004, who lives in Missouri and measures 7.67 m (25 ft., 2 in.) in length and weighs well over 136 kg (300 lb.).

Longevity

Galápagos tortoises have been known to survive for more than 175 years and the tuatara for 77 years (Goin et al., 1978) (Table 7.2). A Galápagos tortoise named Harriet left her native Galápagos Islands in 1835 aboard the HMS *Beagle*, escorted by naturalist Charles Darwin, and spent 169 years living in Australia (Woodall, 2005) (Fig. 7.36). Harriet was born about five years before the *Beagle*’s departure. She spent the last two decades of her life living at Australia Zoo in Queensland. Harriet passed away peacefully in June 2006 at the age of 176.

Table 7.2. Longevity of Some Species of Reptiles

Species	Maximum Age (years)
Testudines	

Species	Maximum Age (years)
Testudinidae (*Testudo radiata*)	189
Emydidae (*Terrapene carolina*)	138
Chelydridae (*Macroclemys temmincki*)	70.3
Trionychidae (*Trionyx triunguis*)	50.6
Pelomedusidae (*Pelusios subniger*)	47
Chelidae (*Chelidona longcollis*)	37
Cheloniidae (*Caretta caretta*)	37
Sphenodonta	
Sphenodontidae (*Sphenodon punctatus*)	90
Squamata	
Varanidae (*Varanus komodoensis*)	62
Anguinidae (*Anguis fragilis*)	54
Iguanidae (*Cyclura nubila*)	47.6
Scincidae (*Oligosoma otagense*)	44
Gekkonidae (*Woodworthia maculatus*)	37
Helodermatidae (*Heloderma suspectum*)	28.9
Cordylidae (*Cordylus giganteus*)	24.9
Agamidae (*Hydrosaurus samboinensis*)	24.4

Species	Maximum Age (years)
Serpentes	
Pythonidae (*Python regius*)	47.5
Boidae (*Boa constrictor*)	40.4
Colubridae (*Elaphe obsoleta*)	33.9
Colubridae (*Pituophis catenifer*)	33.8
Viperidae (*Crotalus lepidus*)	33.6
Colubridae (*Lampropeltis getula*)	33.3
Boidae (*Eunectes murinus*)	31.8
Viperidae (*Crotalus horridus*)	30.2
Viperidae (*Agkistrodon contortrix*)	29.8
Elapidae (*Naja melanoleuca*)	29.1

Source: From Goin et al., 1978. Copyright by D. H. Freeman and Company, New York. Used with permission. Supplemented (2019) by data from various sources.

Jonathan is a Seychelles giant tortoise (*Aldabrachelys gigantea hololissa*) who lives on the grounds of Plantation House, the official residence of the Governor, and belongs to the government of Saint Helena. Jonathan is thought to be the oldest currently living terrestrial animal known, although his age was "estimated" when he was brought to the island of St. Helena, a British Overseas Territory in the South Atlantic Ocean in 1882 (Kettle, 2014). His age was estimated by the fact that he was "fully mature." *Fully mature* means at least 50 years old, giving him a hatching date no later than 1832. If correct, Jonathan was approximately 186 years old in 2018. He is blind from cataracts and has lost his sense of smell, but has retained excellent hearing. In January 2016, the BBC reported that Jonathan had been given a new diet intended to keep him healthy and extend his life. The all-time verified record holder for the world’s oldest tortoise, according to *Guinness World Records*, is Tu’i Malila, who died in Tonga in 1965 at the age of 189. This tortoise was born in 1777.

Figure 7.36. Harriet, a Galápagos tortoise, was born about 1835 in the Galápagos Islands but spent most of her life in Australia. She passed away in June 2006, at the age of 176.

Several species of snakes, including boas and cobras, have survived for more than 25 years. At 62 years, the Komodo dragon (*Varanus*) holds the record among lizards.

Review Questions and Topics

1. Describe the process of ecdysis in reptiles. Why is it necessary?
2. How does ecdysis differ in turtles, lizards, snakes, and crocodilians?
3. Integumentary glands, which are abundant in amphibians, are sparse in reptiles. What is the adaptive significance of this modification?
4. List several modifications of the stratum corneum in reptiles.
5. Describe the four methods of locomotion used by snakes. In what situations would each be used?
6. How does the crocodilian heart differ from the hearts of other reptiles?
7. List four methods of gas exchange used by reptiles.
8. Discuss the adaptations of a snake's jaws that allow it to engulf large prey.

9. How do opisthoglyphs differ from proteroglyphs? From solenoglyphs? Discuss the poison-conducting apparatus of each.
10. What is the function of the tongue in snakes? Explain how it accomplishes this function.
11. How does body temperature regulate physiological processes in reptiles? How does it affect growth?
12. Differentiate between the two types of intromittent organs found in reptiles. Discuss the structure and function of each.
13. Differentiate between determinate and indeterminate growth. Give examples.
14. Why is internal fertilization a necessity for amniotes?
15. What is the evolutionary significance of the amniotic egg?
16. List several advantages of viviparity in reptiles.
17. Discuss environmental sex determination and its possible adaptive significance in managing endangered species populations.

Supplemental Reading

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Vertebrate Internet Sites

1. Snake Anatomy

   www.reptilesmagazine.com/Reptile-Care-For-Beginners/Snake-Anatomy

   Series of articles by veterinarian Dr. Douglas Mader. External anatomy, respiratory system, cardiovascular system, immune system, and gastrointestinal tract anatomy. Photographs and drawings.

2. Best Reptile Sites Directory

   www.bestreptilesites.com

   Many reptile and amphibian websites checked for quality. Health and care, organizations and zoos, photography, reptile supplies, shelters and sanctuaries, webcams, and more.

3. Sea Turtle Status

   www.seaturtlestatus.org

   This ever-growing international group of scientists, conservationists, artists, and concerned citizens works together to further global sea turtle and marine conservation. Get the “State of the World’s Sea Turtles” report, read articles, watch videos, and view interactive maps of turtle nesting beaches.

4. 2019 Amphibians and Reptiles—Internet Resources

   www.soinc.org/sites/default/files/uploaded_files/19_HERPETOLOGY_INTERNET_Resources.pdf

   Field guides, organizations, websites, fact sheets, and more.

5. Guidelines for Use of Live Amphibians and Reptiles in Field and Laboratory Research.

   www.asih.org/sites/default/files/documents/resources/guidelinesherpsresearch2004.pdf

   Guidelines compiled by the Herpetological Animal Care and Use Committee of the American Society of Ichthyologists and Herpetologists.

8 | Morphology, Reproduction, and Development of Crocodilians and Birds (Archosaurs)

There is nothing in which the birds differ more from man than the way in which they can build and yet leave a landscape as it was before.

Robert Lynd, 1923

INTRODUCTION

Archosaurs are a group of diapsid amniotes whose living representatives consist of crocodilians and birds. This group also includes the dinosaurs, the pterosaurs (flying reptiles), and several groups of extinct forms.

MORPHOLOGY

Integumentary System

Crocodilians have heavily armored bodies with long snouts and powerful tails. Each epidermal scale develops separately, so that the scales do not form a solid sheet. The epidermal scales wear away and are gradually replaced. The dorsal armor is formed by heavy plates of bone, called **osteoderms**, that lie within the dermis, underneath the epidermal scales.

In some species, osteoderms also occur on the ventral surface of the body. Otherwise, the dermis is thick and relatively soft.

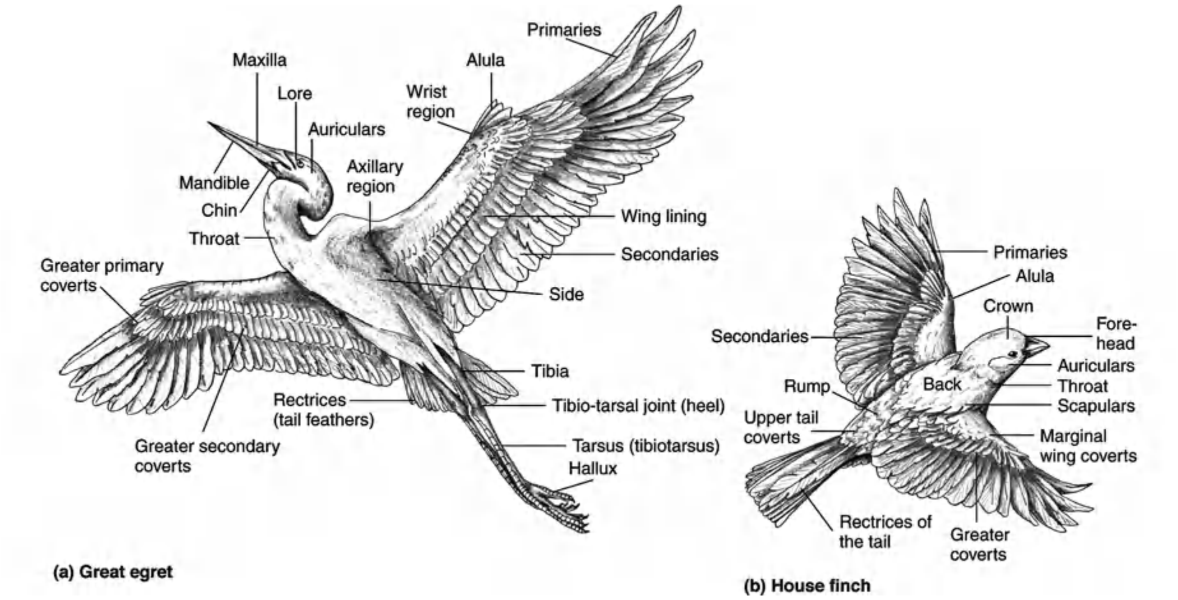
Feathers are modified reptilian scales and distinguish birds from all other animals. They are derived from the keratinized stratum corneum portion of the epidermis. Typical epidermal scales, which occur chiefly on the legs and at the base of the beak (Figs. 8.1 and 8.2), are homologous to those found on other reptiles. The claws and horny covering of the beak are also modifications of the keratinized stratum corneum.

The lightweight feathers help to insulate the body and form the resistant, yet flexible, flight surfaces of the wings and tails of many birds. Feathers are highly diversified keratinized structures that are specialized in form, color, and arrangement. A large bird like a whistling swan (*Cygnus columbianus*) may have more than 25,000 feathers on its body, whereas a ruby-throated hummingbird (*Archilochus colubris*) may have less than 1,000, with those from each part of the body being characteristically unique in form. There is no significant sexual variation in the number of feathers. Counts for individuals of the same species often vary by less than 1 percent (Wetmore, 1936; Trainer, 1947; Brodkorb, 1951). Despite their individual lightness, the combined weight of the feathers often exceeds the weight of the entire skeleton.

A typical feather consists of a long, tapering central **shaft** composed of two main parts: the hollow cylindrical basal portion known as the **calamus** (quill) and a solid, squarish portion, the **rachis**. A row of small parallel branches, or **barbs** (which are set at an angle, inclined toward the tip of the feather), collectively form the **vane** on each side of the rachis. Barbs possess yet smaller branches known as **barbules**, which are inclined toward the tip of the barb. Barbules have **hamuli (hooklets)**, which interlock with the barbules of adjacent barbs to stiffen the vane.

Five basic types of feathers can be distinguished: contour feathers, semiplumes, down feathers (plumules), bristles, and filoplumes (see Fig. 8.2).

Contour feathers (see Fig. 8.2a) are those that form the contour or outline of the body of the bird. A typical contour feather has a large, firm vane and a downy base. On most birds, these feathers do not arise randomly over the body of the bird. Rather, **feather follicles** arise from definite tracts known as **pterylae** (Fig. 8.3). Bare patches between pterylae are known as **apteria**. A few birds, like penguins, kiwis, ostriches, and South American screamers, lack feather tracts and feathers arise randomly over the body. Feather tracts vary in shape and extent in different species and are important in deducing taxonomic relationships. Feathers on the wing and tail have become highly developed for flight and/or display. Feathers borne on the modified hand of the bird and located between the wrist and the tip of the wing are known as **primaries**; those on the forearm, between the wrist and the elbow, are **secondaries** (see Fig. 8.1). Tail feathers are collectively known as **rectrices**. Small feathers that overlie the bases of the flight feathers (primaries and secondaries) and several rows of small feathers between the bases of the flight feathers and the leading edge of the wing are known as **coverts** (see Fig. 8.1).



(a) Great egret

(b) House finch

Figure 8.1. External anatomy of a bird: (*a*) great egret (*Ardea alba*), ventral view; (*b*) house finch (*Carpodacus mexicanus*), dorsal view.

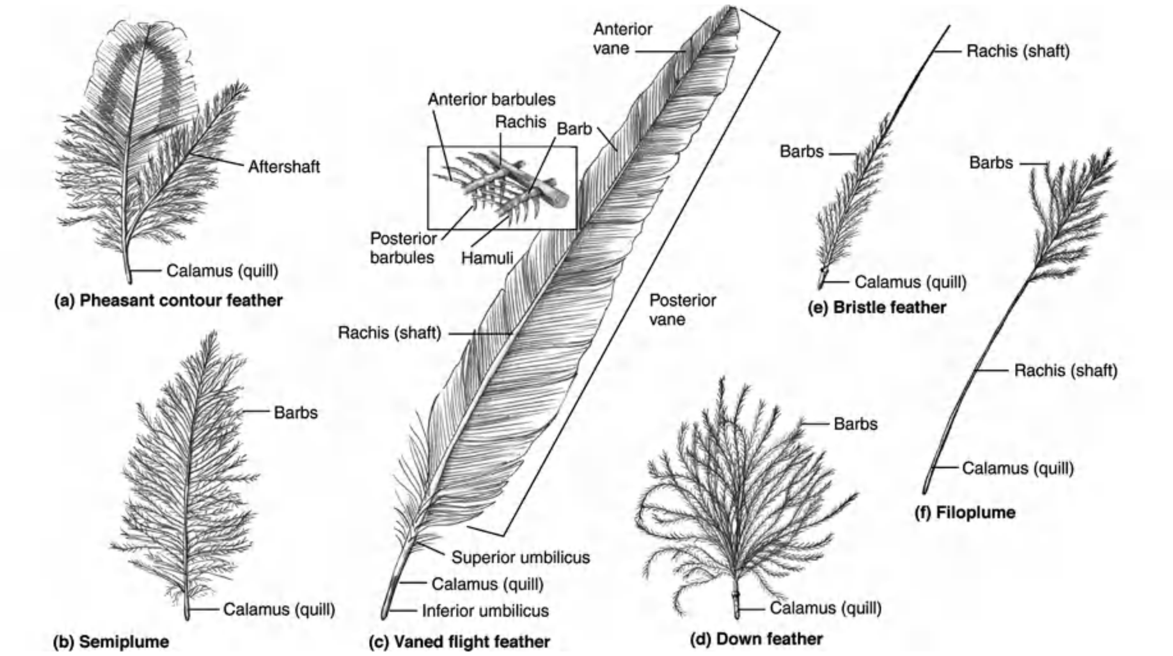


Figure 8.2. Basic feather types: (*a*) contour feather, (*b*) semiplume, (*c*) flight feather, (*d*) down feather, (*e*) bristle feather, (*f*) filoplume. *Inset*: Detail of the vane of a flight feather.

Semiplumes (see Fig. 8.2b) are loosely webbed contour feathers. Each possesses a definite rachis but no hamuli and, thus, no firm vane. Semiplumes are found most often at the margins of pterylae. They help insulate the body and increase the buoyancy of waterbirds.

Down feathers (see Fig. 8.2d) are small, fluffy feathers lying beneath and between the contour feathers. They are fluffy because their barbs do not interlock along any portion of the rachis. They usually are not confined to the pterylae, but are widely distributed over the body. The principal function of down feathers is to provide insulation. Newly hatched birds lack contour feathers and are covered at hatching by a coat of natal (newborn) down.

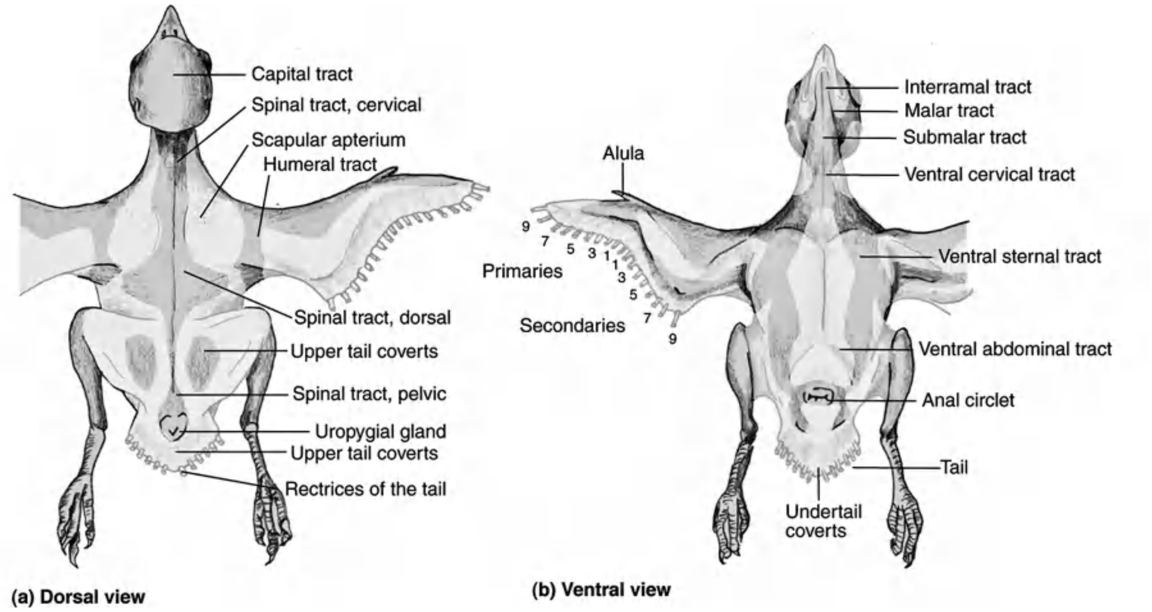


Figure 8.3. Feather tracts (pterylae) in a typical passerine: (*a*) dorsal view; (*b*) ventral view.

Powder down feathers are highly modified down feathers that grow continuously from the base and disintegrate at the tip. As the barbs disintegrate, they give off a fine, talclike powder composed of minute scalelike particles of keratin. The powder may be used in preening and may serve to protect the feathers from moisture. In some species, the powder may affect the color of the plumage.

Bristles (see Fig. 8.2e) are modified, usually vaneless, feathers that consist of only a shaft. They normally are found around the mouth, nostrils, and eyes. Those around the nostrils probably serve to filter incoming air, whereas those around the mouth help swifts and other aerial insect eaters to trap insects. Others may have a sensory function.

Filoplumes (see Fig. 8.2f) are specialized, hairlike feathers. They generally lack vanes and consist mainly of a threadlike shaft. They are usually scattered over the skin between contour feathers and may serve both decorative and sensory functions. The long, colorful feathers of a peacock are examples of filoplumes.

Erector muscles known as **arrectores plumarum** originate in the dermis and insert on the wall of each feather follicle. Along with extrinsic integumentary muscles, the arrectores plumarum muscles enable a bird to fluff its feathers for display and/or to alter their insulating properties by either trapping a layer of air between the feathers and the skin or flattening the feather to reduce insulation when temperatures are high.

Poisonous Birds

Five species of pitohuis (*Pitohui*) endemic to New Guinea and the ifrita (*Ifrita kowaldi*) contain one of nature's most powerful toxins and are the world's only known poisonous birds. Bioassays have shown that the feathers and skin are most toxic, with striated muscle, heart, liver, stomach, intestines, and uropygial glands containing lesser concentrations. These tissues contain the steroidal alkaloid homobatrachotoxin—the same nerve agent that is secreted by poison dart frogs (*Phyllobates*) of Central and South America. Batrachotoxins depolarize nerve and muscle cells by activating sodium channels and also irritate sensory neurons in and around the mouth. Extracts from these birds are capable of killing a mouse within just a few minutes. In humans, the alkaloid causes numbness, burning, and sneezing on contact.

Data presented by Dumbacher et al. (2008) reveal that toxicity is not ancestral: instead, it has evolved several times in this particular group of birds, and it has evolved convergently in five of the six *Pitohui* species—the single exception is the white-bellied pitohui (*P. incertus*), which lacks batrachotoxins in its skin and plumage.

Dumbacher et al., 1992, 2000, 2008

Feathers are subjected continually to wear and deterioration. Thus, they must be replaced periodically by a process known as **molting**, which is closely synchronized with reproductive cycles and the seasons of the year. Following their breeding and nesting activities, most adult birds undergo a single annual molt called a **postnuptial** molt. The males of some species, however, also undergo a partial molt prior to breeding (a **prenuptial** molt), during which they may acquire their colorful breeding plumage. Most migratory species complete their postnuptial molt prior to the beginning of fall migration. Changing day length (photoperiod) is primarily responsible for initiating the molting process.

The early development of a feather is similar to that of a scale (Fig. 8.4). Vascularized tissue in the dermis first forms a cone-shaped structure known as a **papilla**. Then the thin, over-lying epidermal layer sinks inward and forms a cylindrical pit, known as the **feather follicle**, out of which the papilla develops into a feather. During molting, new feathers develop from the same reactivated dermal papilla that gave rise to the previous feathers. Incoming feathers, in many cases, push the old feathers out of the follicles.

Molting is an orderly process in most birds, although the timing of molt varies greatly among species. A complete molt usually begins with the innermost primaries of the wings. Next, the remaining primaries drop out in succession as their predecessors are replaced. At any one time, only a small gap between primaries is present and the bird retains its power of flight. When molting of the primaries is partially completed, molting of secondaries begins. This is followed by the tracts of other feathers on the body. Tail feathers are usually molted a few at a time so that the tail can remain useful as an organ of flight. Some birds (mainly aquatic and semiaquatic species that can elude predators for several weeks without resorting to flight) lose all of their flight feathers at once. These include ducks, geese, and swans (Anatidae), most rails (Rallidae), and many alcids (Alcidae).

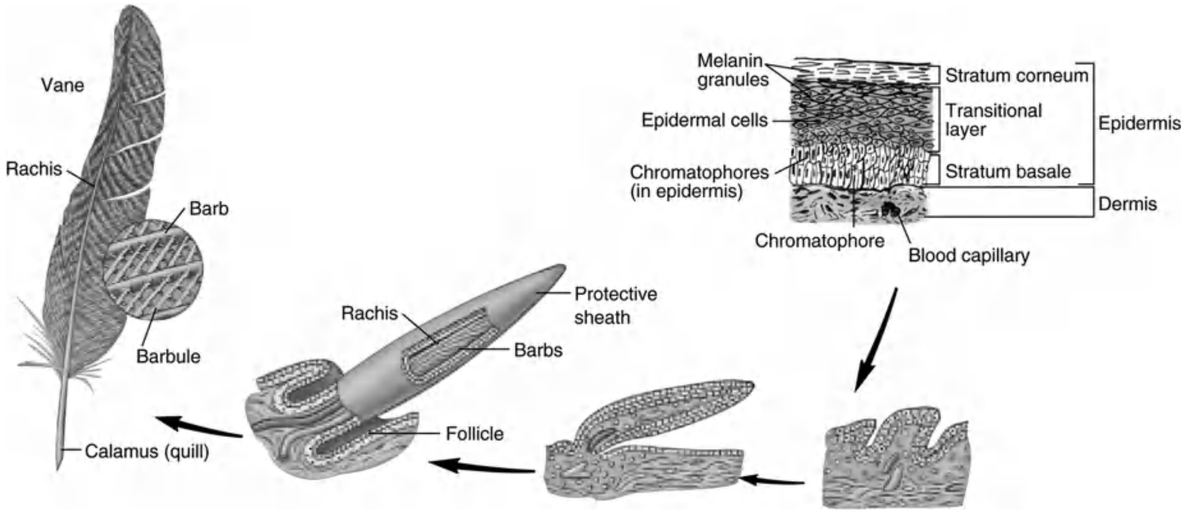


Figure 8.4. Section of skin showing the stratum basale and the keratinized surface layer, the stratum corneum. Cells moving out of the basal layer first spend time in the transitional layer before reaching the surface. This middle transitional layer is equivalent to the stratum spinosum and stratum granulosum layers of mammals.

Birds are among the most colorful of all animals, with colors being produced by a variety of pigments and structural features of the feathers. Melanins produce black, grays, and browns; carotenoids produce intense reds and yellows; and porphyrins are responsible for a range of reds, browns, and greens. Complex patterns of reflection and refraction in the cell membranes of the barbs and barbules of each feather produce metallic blues, greens, and iridescent colors. Much of the color is modified by abrasion and oxidation. Coloration is important for concealment from predators, for identifying members of the same or related species, and for controlling the absorption of radiant energy. Seasonal changes in color are accomplished through molting or wearing off the tips of feathers.

In peacocks, the outer covering of the barbules is a very regular structure built of tiny rods of melanin connected by keratin (Zi et al., 2003). Different colored barbs vary in how these matrices are arranged. Depending on how closely the rods are spaced and how many layers of rods are stacked up, the barbule could appear as anything from yellow to green to blue to brown. Thus, in peacock feathers, it is the precise structural array of melanin rods in keratin that creates different colors, with one array reflecting back yellow light, for example, and a different arrangement reflecting back blue light.

Owl feathers confer the advantage of silent flight, both at frequencies audible to the human ear and at ultrasonic levels (Thorpe and Griffin, 1962). By reducing their own noise, owls can both make maximal use of their acute hearing and silently approach their prey. Three structural adaptations that tend to reduce flight noise were identified in barn owls by Graham (1934). First, a very prominent, stiff, comblike fringe is present along the leading edges of the flight feathers, particularly the outer primaries. This fringe reduces turbulence in air flow and hence cuts noise production. Second, the primaries and secondaries along the trailing edge of the wing have a soft, hairlike fringe, which probably reduces turbulence where air streams flowing over the top and bottom of the wing meet. Third, the downy upper surfaces of the primaries, secondaries, and coverts must reduce noise that would otherwise be produced when these feathers move over each other during the normal wingbeat. This downy appearance is produced by extremely elongated extensions of the barbules (Fig. 8.5).

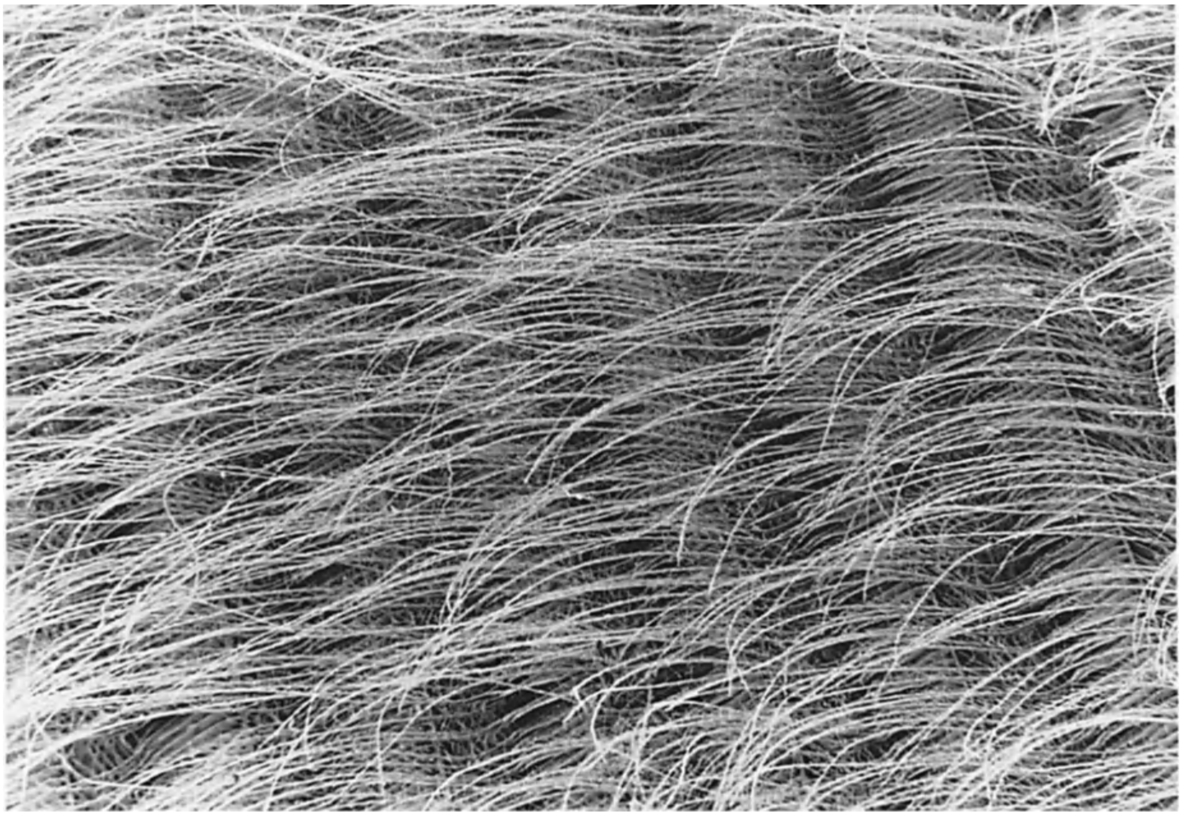


Figure 8.5. Barn owl feathers. Long, hairlike extensions of the barbules seen in this highly magnified scanning electron micrograph enable the barn owl to fly silently. These structures are responsible for the soft, downy feel of the barn owl’s plumage.

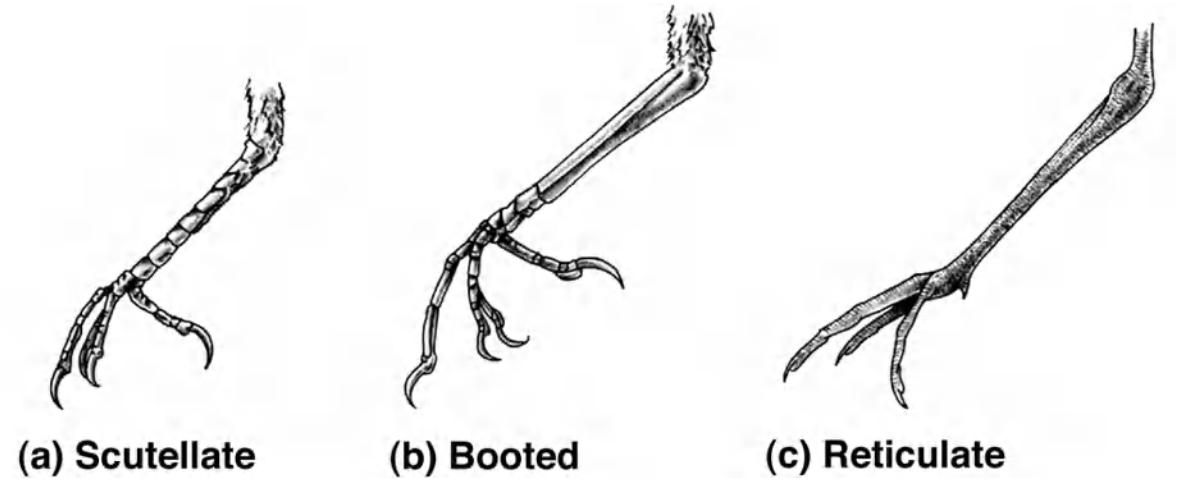


Figure 8.6. Examples of the three major types of horny sheaths on the avian tarsometatarsus: (*a*) scutellate (flycatcher); (*b*) booted (robin, other thrushes); (*c*) reticulate (plover).

Owls and ptarmigans have lower legs and feet that are completely feathered, whereas other species, like rough-legged hawks, have feathers on their lower legs but not on their feet. Most birds, however, have featherless lower legs and feet that are covered with horny scales (Fig. 8.6). When these scales overlap one another on the anterior surface of the leg (tarsometatarsus), as they do in finches and sparrows, they are said to be *scutellate* (Fig. 8.6a). Individual scales are not present in the smooth appearance of the *booted* tarsometatarsus of thrushes (Fig. 8.6b). In geese and many shorebirds, the tarsometatarsus is broken up into many small, irregular, nonoverlapping scales and is referred to as being *reticulate* (Fig. 8.6c).

Figure 8.7. Baby hoatzins of South American rain forests have claws on their wings that enable them to clamber about the limbs of their streamside nesting bushes. At any sign of an aerial predator, a baby hoatzin drops into the water beneath the nest. As soon as the danger has passed, it uses its claws to scramble out of the water and away from other predators lurking there.

The stratum corneum at the ends of the digits in birds is modified into claws (see Fig. 8.6). All birds possess claws on their feet. Ostriches, geese, some swifts, and others may also possess sharp claws at the ends of one or two digits of the wings. Hoatzins (*Opisthocomus hoatzin*) are chicken-sized birds that live along sluggish tropical rivers in South America. Young hoatzins use two reptile-like claws on each wing to provide increased grasping ability for climbing about in trees (Fig. 8.7). If frightened, young hoatzins may drop out of the nest into the water. They are able to swim underwater before they can fly. They return to the nest by using their claws and crawling up the trunk and limbs in lizard-like fashion. These claws are lost when the birds mature and become capable of flight. Fossilized remains of the earliest known bird (*Archaeopteryx*) have revealed the presence of three claws on each wing (see Fig. 6.26).

Birds have fewer epidermal glands than any other vertebrate group. One of these glands, the **uropygial gland**, is best developed in aquatic birds (see Fig. 8.3). Located dorsally at the base of the tail, this gland exudes an oily secretion of semisolid fatty substances that contain precursors of vitamin D. Birds rub their beaks against these glands or squeeze the nipple of the gland with their beaks and distribute the oil over their feathers as they preen. Some of the oil may be swallowed for its essential vitamin D. The presence or absence of this gland has been used in some taxonomic classifications; it is absent in some woodpeckers, pigeons, parrots, and ostriches, and in some other birds. Some birds also have small oil glands lining their outer ear canal and the area around the exit from the cloaca. Sweat glands are absent.

As in other vertebrates, the dermis is richly vascularized and supplies oxygen and nutrients to the epidermis. It consists of blood vessels, lymphatic vessels, nerve endings, and sense organs. It is attached to underlying tissues by means of the basement membrane.

Skeletal System

Crocodilians possess a complete secondary palate below the primary palate (Fig. 8.8). The evolution of a secondary palate allows the air passageways to be separated from the oral cavity. Teeth are set into sockets in the jaws, a situation known as **thecodont** dentition (see Fig. 7.14c). The vertebral column of crocodilians consists of cervical, thoracic, lumbar, sacral, and caudal vertebrae. Posterior cervical and anterior thoracic ribs each bear a curved cartilaginous **uncinate process**, which projects posteriorly to overlap the rib behind, presumably giving strength to the thoracic body wall. A sternum is present and consists of a plate to which the ribs attach.

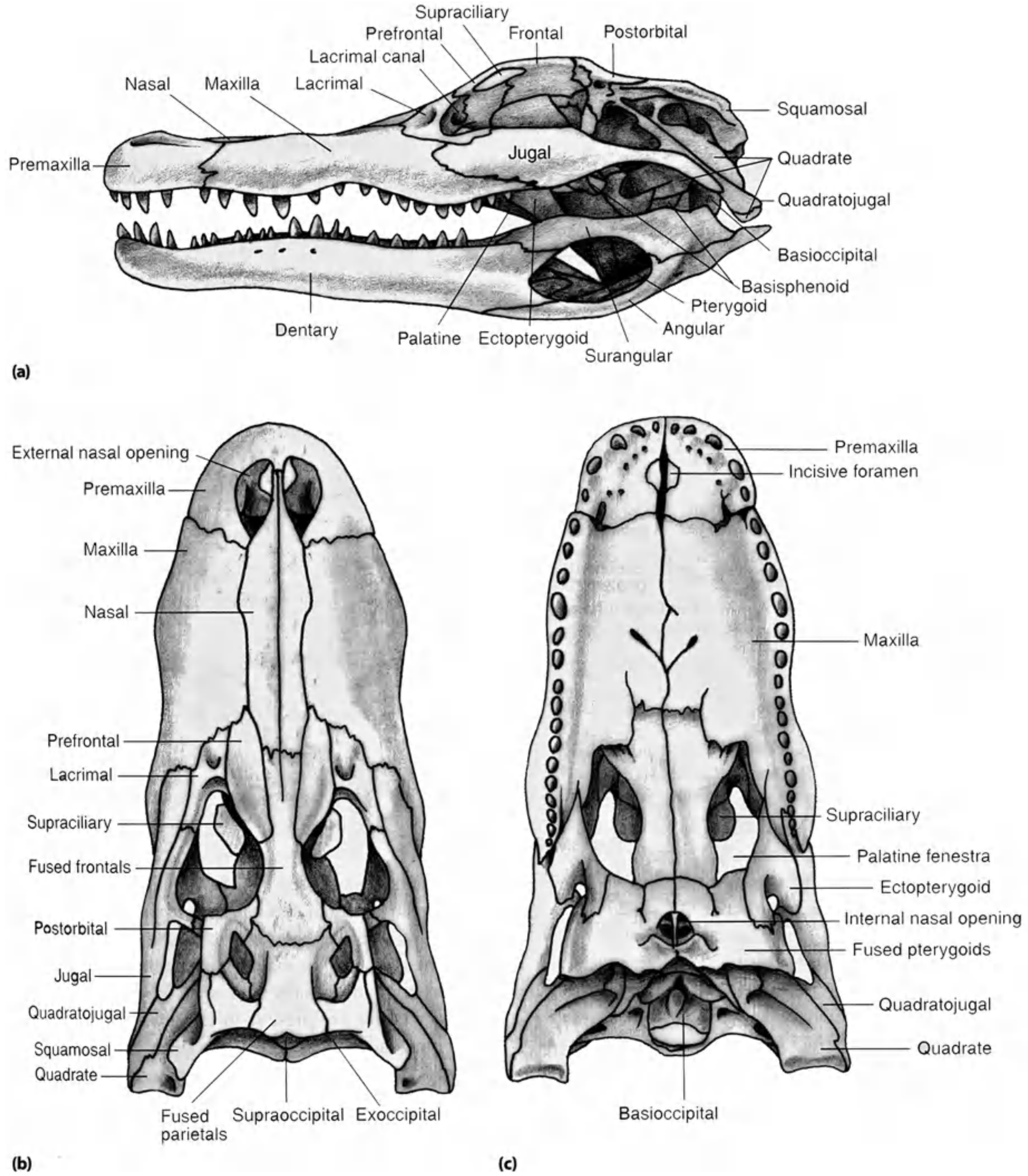


Figure 8.8. Skull of American alligator (*Alligator mississippiensis*): (*a*) lateral view; (*b*) dorsal view; (*c*) ventral view.

Bite Force

Scientists at Florida State University have established that the Australian saltwater crocodile has the most powerful bite ever measured among living species. For 11 years, biology professor Gregory Erickson and his colleagues measured the bite force of every known species of alligator and crocodile, placing a bite-force device between the back teeth. A 5 m (17 ft.) Australian saltwater crocodile took top honors with a bite force of 1,678 kg (3,700 lb.), beating a 1,351.7 kg (2,980 lb.) value for a 4 m (13 ft.) wild American alligator. Human bite force checks in at 102 kg (225 lb.).

Erickson et al., 2012; Handwerk, 2012

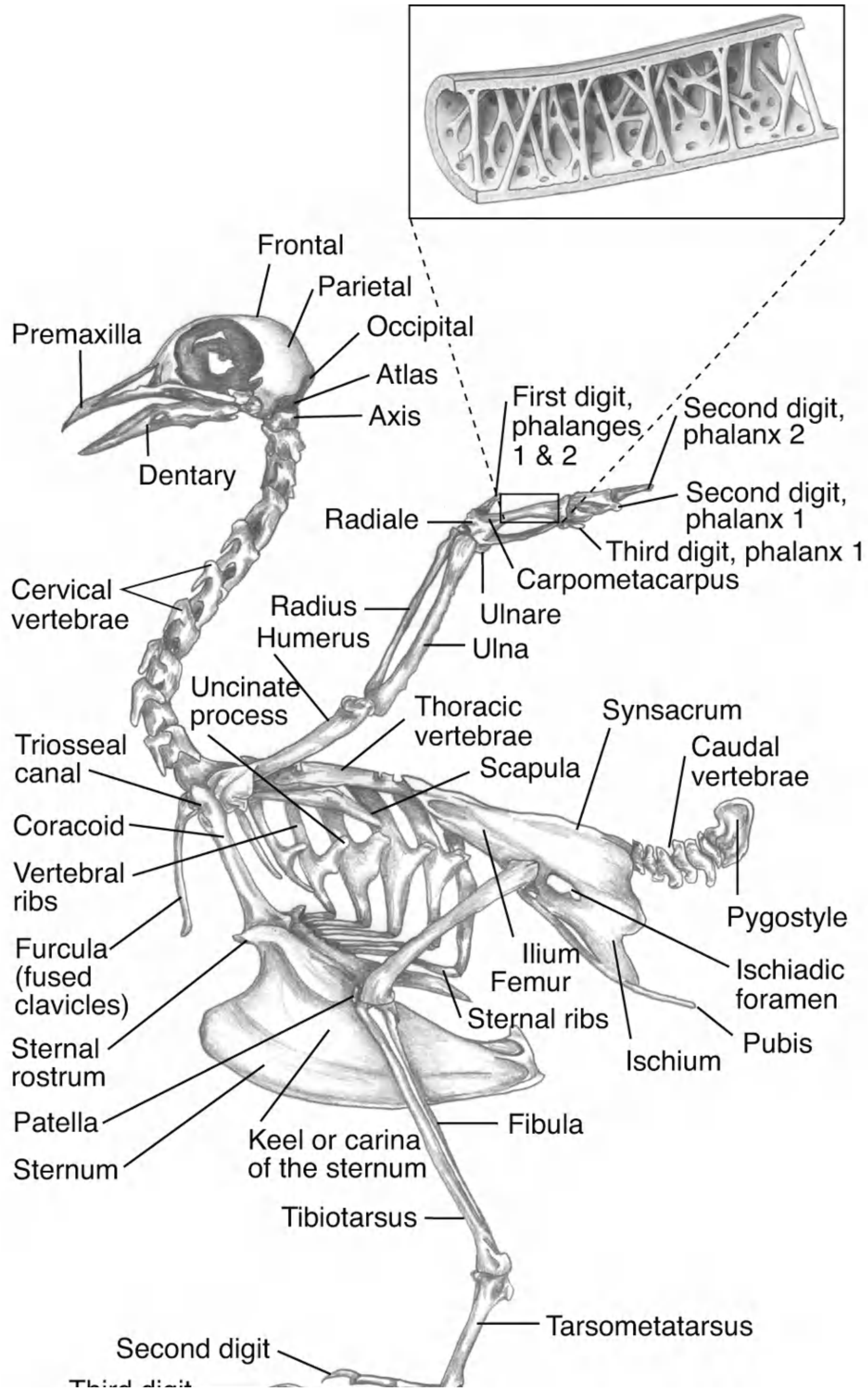

Frontal
Parietal
Premaxilla
Occipital
Atlas
Axis
Dentary
First digit, phalanges 1 & 2
Second digit, phalanx 2
Second digit, phalanx 1
Radiale
Third digit, phalanx 1
Carpometacarpus
Cervical vertebrae
Radius
Ulnare
Humerus
Ulna
Uncinate process
Thoracic vertebrae
Synsacrum
Caudal vertebrae
Triosseal canal
Scapula
Coracoid
Vertebral ribs
Pygostyle
Furcula (fused clavicles)
Ilium
Femur
Ischiadic foramen
Sternal ribs
Sternal rostrum
Ischium
Pubis
Patella
Fibula
Sternum
Keel or carina of the sternum
Tibiotarsus
Tarsometatarsus
Second digit

Figure 8.9. Lateral view of the skeleton of the rock dove (*Columba livia*). Note the many fused bones along the axial skeleton (the skull, spinal column, and pelvis). The fused bones provide a strong, stable central platform for the flight muscles. The bird skeleton is extremely light (see inset). In some birds, the skeleton weighs less than the feathers. *Inset*: Hollow bone of a bird showing the stiffening struts and air spaces that replace bone marrow. Such "pneumatized" bones are remarkably light and strong.

The legs of crocodilians are sprawled during normal walking; however, when moving rapidly, the legs hold the body off the ground in a semi-erect attitude. In water, crocodilians fold the limbs against the body and use lateral undulations of the body and tail to swim. Webbing is present between the toes.

The avian skeleton is specialized for both lightness and strength (Fig. 8.9). Many bones that form the structural framework of the skeleton are paper-thin. In most birds, resorption of the marrow and its replacement by stiffening struts, air spaces, and extensions of the air sac system further strengthen the bone while decreasing its weight (Fig. 8.10). In addition, the fusion of many of the main bones provides strength.

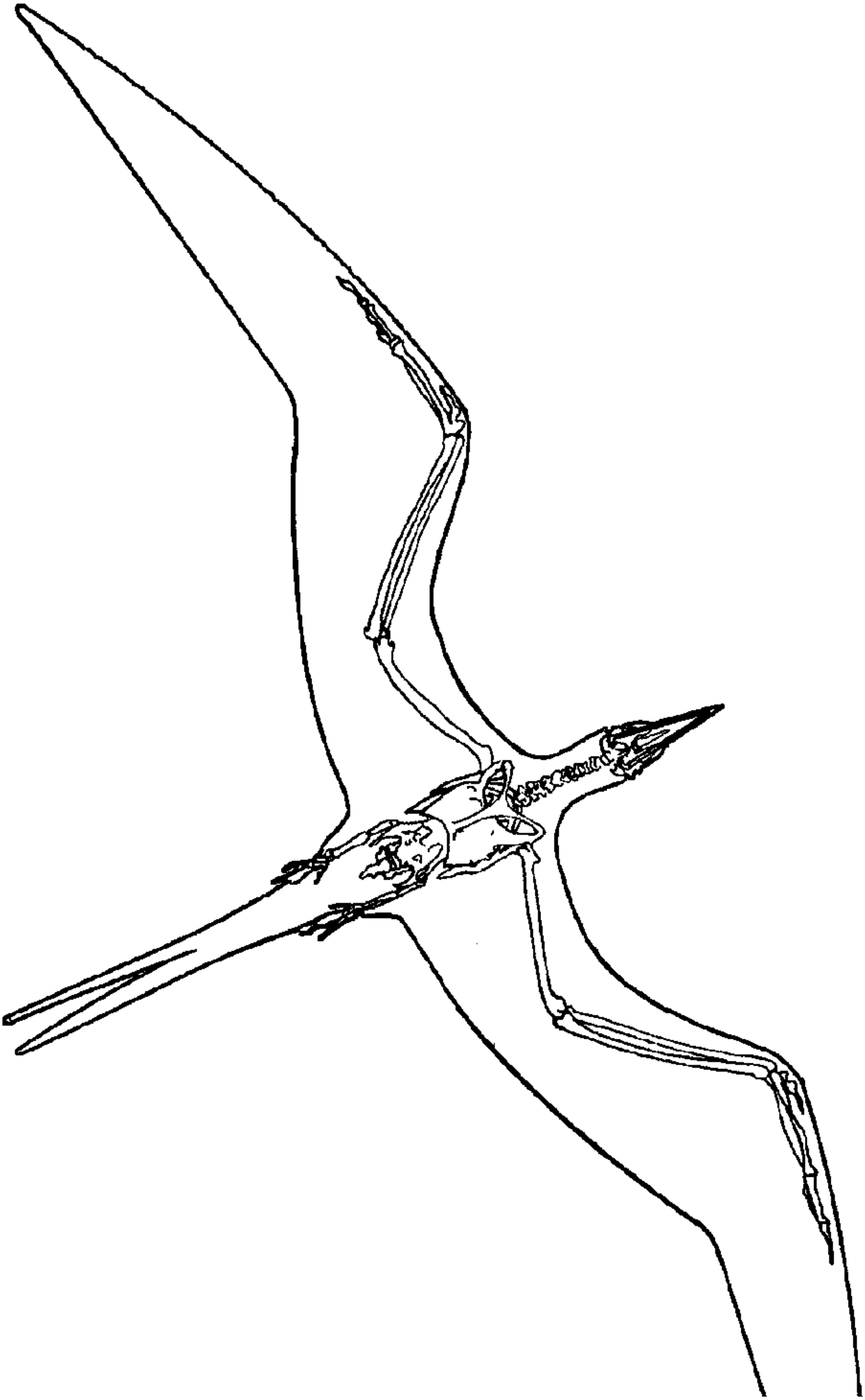
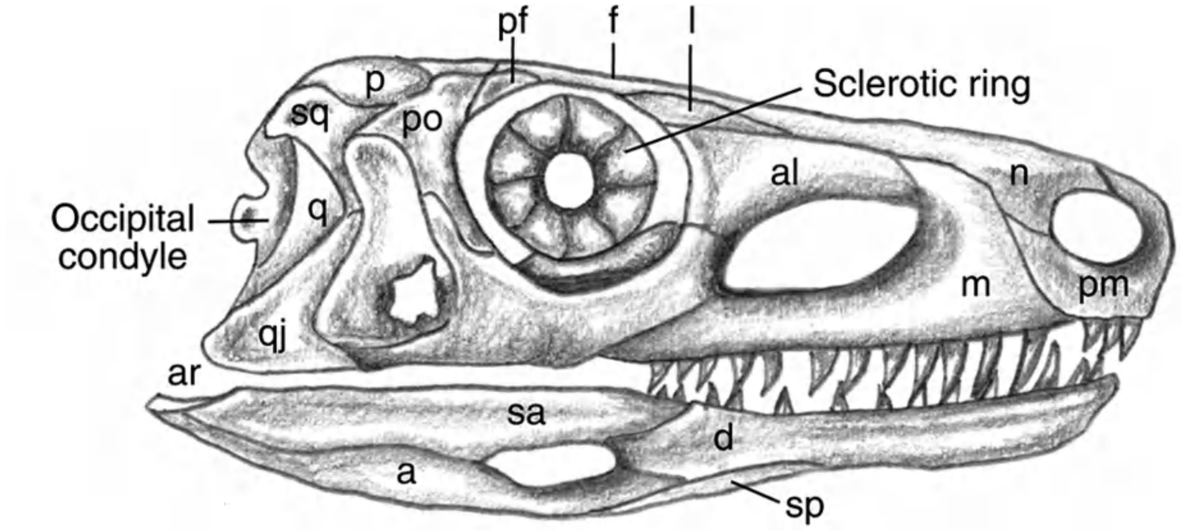


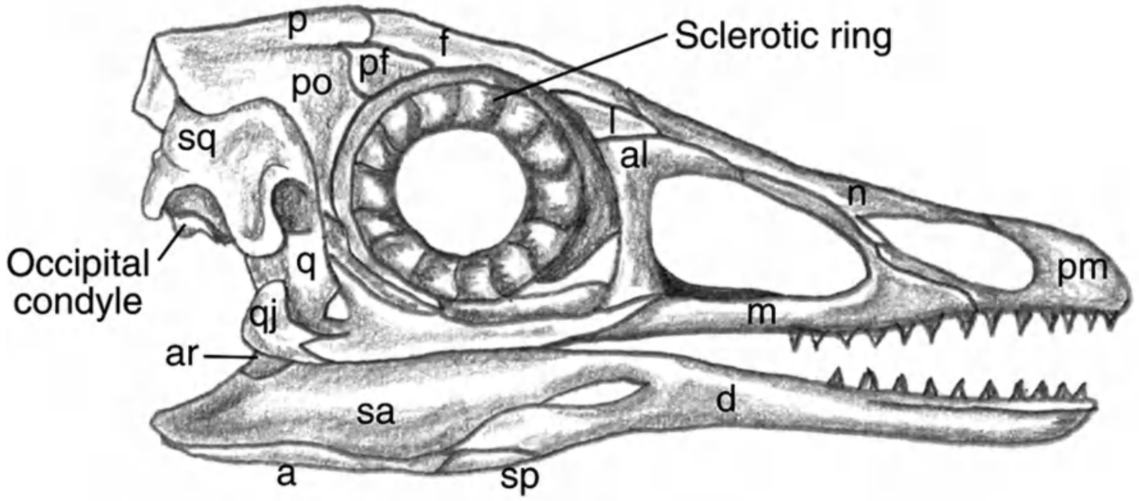
Figure 8.10. The frigatebird (*Fregata magnificens*) has a 2.1 m (7 ft.) wing span, but its skeleton weighs only 113 g (4 oz.)—less than the weight of its feathers. The skeleton is shown against the outline of the bird.

The bird skull (see Fig. 8.9) exhibits many features of the diapsid reptilian skull like a single occipital condyle and an incomplete secondary palate. Unlike the case for reptiles, the major bones making up the braincase in adult birds are very thin and usually are fused completely. Quadrate and articular bones are present in the jaws of birds. The freely movable quadrate bone suspends the mandible from the cranium. In adult birds, few if any remnants of Meckel's cartilage remain within the mandible: it has ossified or become totally ensheathed by membrane bones. The hyomandibular cartilage becomes the columella of the middle ear. This quadrate-articular-columella arrangement is essentially similar to the reptilian condition. However, the brain of a bird is larger than that of a comparable-sized reptile. The orbits are also large. An anterior **sclerotic ring** consisting of 10 to 18 overlapping platelike bones develops in the sclera of the eye (Fig. 8.11). Its function is to reinforce the huge eyeball.

A beak (bill) is formed primarily by the elongation of the premaxillary and dentary bones (see Figs. 8.9 and 8.11). The upper beak, supported by the maxilla and other bones of the skull, is composed of a bony framework covered by a tough layer of keratin. Unlike the jaws of mammals, the upper jaw of all birds is slightly mobile, because the pterygoid, quadrate, and zygomatic bones that support the maxilla can slide forward or backward. Birds depend on their beaks not only to obtain food (Fig. 8.12), but also to preen their feathers, build their nests, perform courtship displays, and defend themselves from predators or rivals. The bill of the toco toucan (*Ramphastos toco*) accounts for 30 to 40 percent of the toucan's surface area and is used to dispense body heat (Fig. 8.13). By controlling the amount of blood flowing through their supersized, uninsulated beaks, toucans can regulate their body temperature (Tattersall, et al., 2009).



(a) ***Euparkeria***



(b) ***Archaeopteryx lithographica***

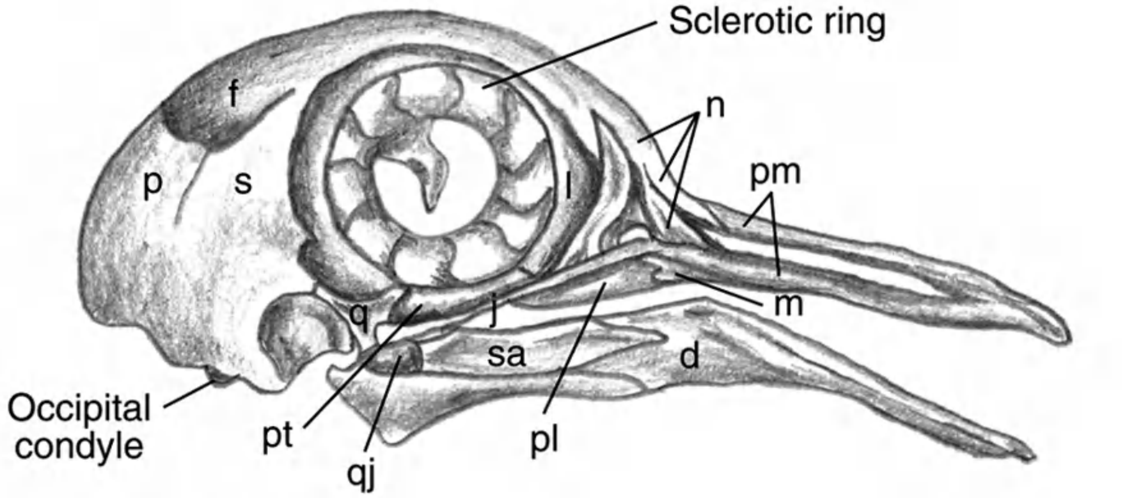


Figure 8.11. Skulls of (*a*) a pseudosuchian reptile (*Euparkeria*); (*b*) *Archaeopteryx lithographica*; and (*c*) a modern bird (*Columba*) in lateral view. The sclerotic ring within the orbit of the skull is shared by birds and their reptilian ancestors. In birds, the sclerotic ring reinforces the huge eyeball. *Key*: a, angular; ar, articular; d, dentary; f, frontal; j, jugal; l, lacrimal; m, maxilla; n, nasal; p, parietal; pl, palatine; pm, premaxilla; po, postorbital; q, quadrate; qj, quadratojugal; sq, squamosal.

Birds have cervical, thoracic, lumbar, sacral, and caudal vertebrae. Those vertebrae that are connected to the sternum by ribs and that do not fuse with the synsacrum sometimes are known as dorsal vertebrae. The highly flexible neck may consist of as many as 25 vertebrae with saddle-shaped ends, called **heterocoelous** vertebrae. The anterior two cervical vertebrae are modified as the atlas and axis.

Most birds have two sacral vertebrae. These are fused with the last thoracic, the first few caudal, and all of the lumbar vertebrae to form one structure, the **synsacrum** (see Fig. 8.9). The synsacrum, along with the pelvic girdle to which it is more or less fused, forms a rigid framework both for flight and for the bipedal gait of birds. Thoracic vertebrae anterior to the synsacrum also usually fuse together, so that there is little flexibility in the vertebral column behind the neck.

Usually 10 to 15 caudal vertebrae are present in birds. These vertebrae are the remnants of an ancestral reptilian tail. The first six or seven vertebrae posterior to the sacrum are free, whereas the remaining vertebrae (usually four to seven) fuse together to form a **pygostyle**—the skeleton within the tail (see Fig. 8.9).

The ribs of birds are ossified. Thoracic ribs have flat uncinate processes, each of which overlaps the next most posterior rib and provides added support to the rib cage and attachment sites for muscles (see Fig. 8.9). The ossified sternum articulates with the pectoral girdle and the ribs. In **carinate** (flying) birds, and also in penguins (which are powerful swimmers), the sternum has a midventral **keel**, or **carina**, for the attachment of the large flight muscles (see Fig. 8.9). In general, **ratites** (flightless birds) like ostriches and emus lack a keeled sternum.

Each pectoral girdle is formed by the clavicle, coracoid, and scapula. Coracoids have become prominent in most birds, and they function in bracing the pectoral girdle against the sternum. In most carinate birds, the two clavicles unite in the midline with the interclavicle to form the **furcula**, or wishbone (see Fig. 8.9). In ratites and some carinate birds, including some parrots and pigeons, clavicles are absent or rudimentary.

The skeleton of the anterior appendage consists of the humerus, radius, ulna, carpals, metacarpals, and phalanges; it has been modified for flight through the loss and fusion of bones. Pectoral muscles insert chiefly on the humerus and provide the power for flight, while air moving over the convex surface of the wings provides the necessary lift. Three distal carpal bones usually fuse with three metacarpals to form a rigid **carpometacarpus**. Three digits are usually present, but the number of phalanges in each has been reduced. The anterior appendages of penguins have been further modified as paddles for life in the sea by becoming flattened, shortened, and stout, whereas the appendages of soaring birds like herring gulls (*Larus argentatus*) have lengthened and become lighter to maximize their efficiency for soaring flight.

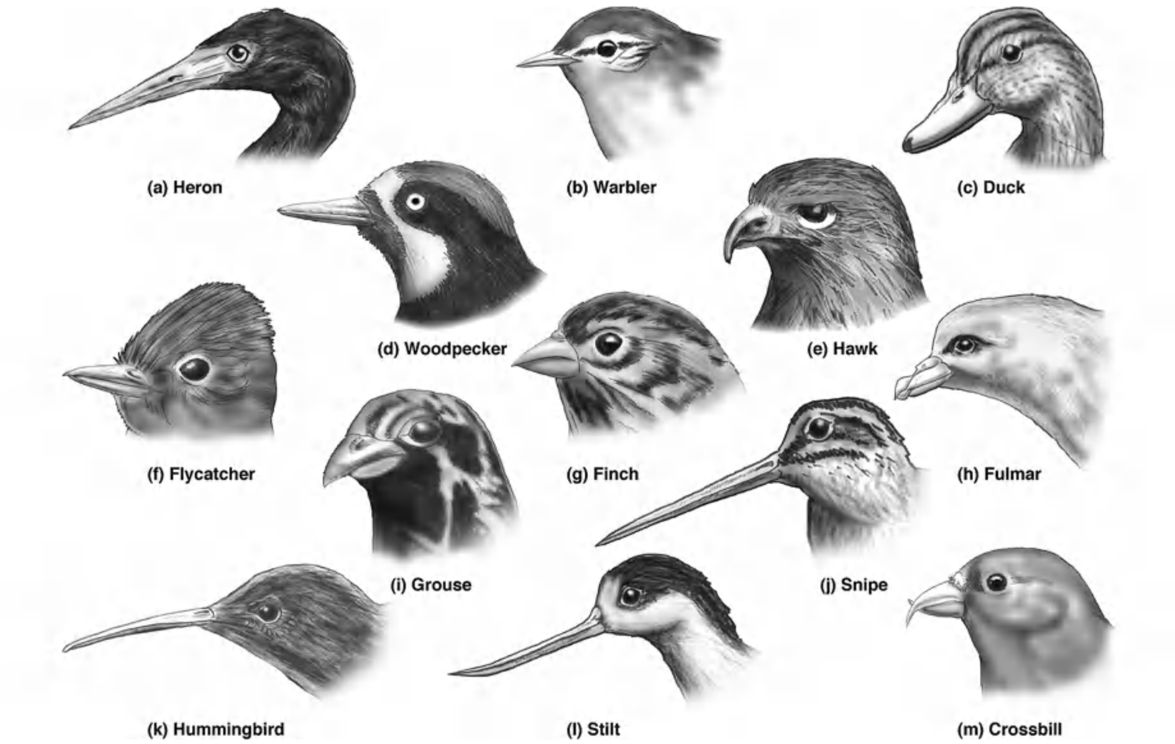


Figure 8.12. Specialized feeding methods and bill modifications that reflect the adaptations to the ecological niches of various birds: (*a*) heron, (*b*) warbler, (*c*) duck, (*d*) woodpecker, (*e*) hawk, (*f*) flycatcher, (*g*) finch, (*h*) fulmar, (*i*) grouse, (*j*) snipe, (*k*) hummingbird, (*l*) stilt, (*m*) crossbill.

The pelvic girdle is formed by the fusion of the pubis, ischium, ilium, and synsacrum. The ilium, which is braced against both lumbar and sacral vertebrae, is broad and expanded for the attachment of the appendicular muscles, which are highly developed for bipedal locomotion. Pubic bones are reduced to long splinters projecting toward the tail. A pubic symphysis is absent in most birds (*Archaeopteryx* and ostriches are exceptions).

The legs of birds contain the same bones as those of reptiles. In birds, however, the tibia fuses with the proximal row of tarsals to form a **tibiotarsus**, and the metatarsals fuse with the distal row of tarsals to form a **tarsometatarsus** (see Fig. 8.9). The joints between the tibiotarsus and tarsometatarsus, and those between the tarsometatarsus and the toes, allow flexion to occur. In some birds, like parrots, the fibula may be reduced to a splinter. A patella is present and protects the knee joint.

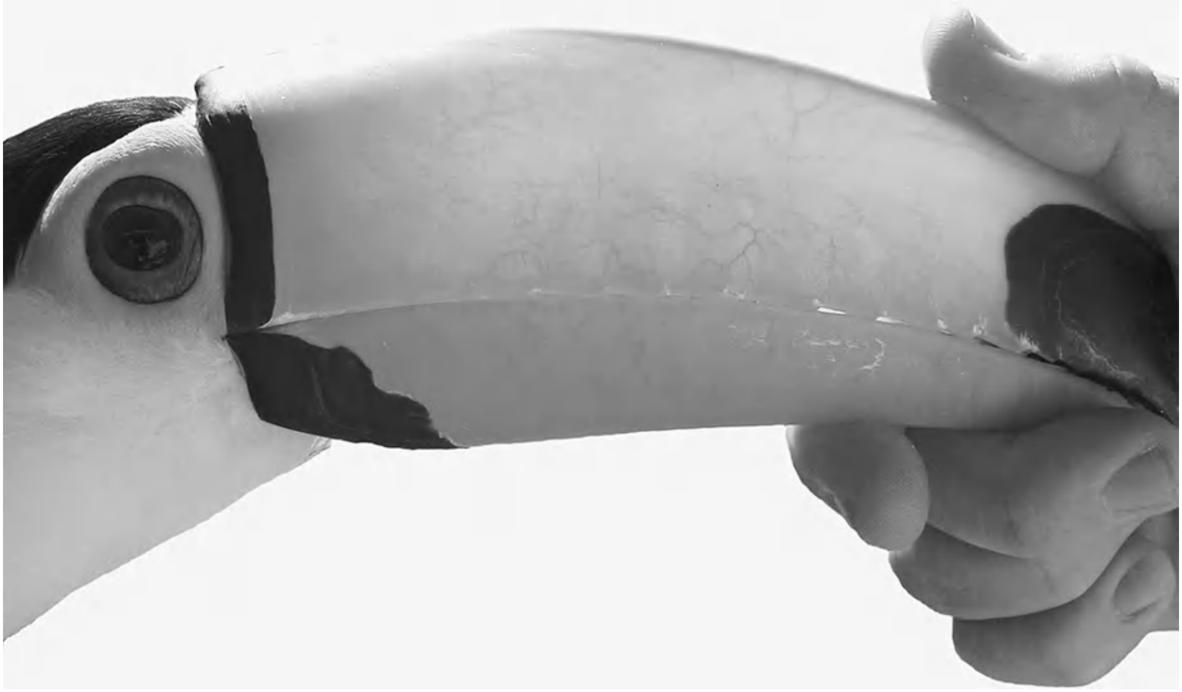


Figure 8.13. An adult toco toucan. The vast array of blood vessels in the uninsulated bill allows the toucan to radiate excess heat.

Ostriches are the only living two-toed (didactyl) birds. The feet of all other birds have either three or four functional toes and show a wide variety of modifications (Fig. 8.14). Aquatic birds—ducks, geese, gulls, and others—have feet that either are webbed or have lobed toes to assist in swimming. (The term *semipalmate* is frequently used in describing the degree of webbing on shorebirds and other aquatic birds. It means "half-webbed" and refers to the condition of having the front three toes joined by a web along only the basal half [or less] of their length.) Grebes have flattened claws that are incorporated into a paddle-like foot. Some marsh birds have elongated toes designed to support them as they walk on water plants or mudflats. Gallinaceous birds, like quail, grouse, turkeys, and pheasants, have strong feet and legs adapted for running. Their strong claws are used for scratching the ground in search of food. Hawks and owls, which seize their prey with powerful feet, have long, sharp claws called talons. Perching birds, including most songbirds, have a long, backward-pointing hind toe (hallux) that helps the bird secure a foothold on a branch or other perch. The feet of woodpeckers are adapted for climbing and, except for the three-toed woodpecker (*Picoides tridactylus*), consist of two toes facing forward and two facing rearward (zygodactylous).

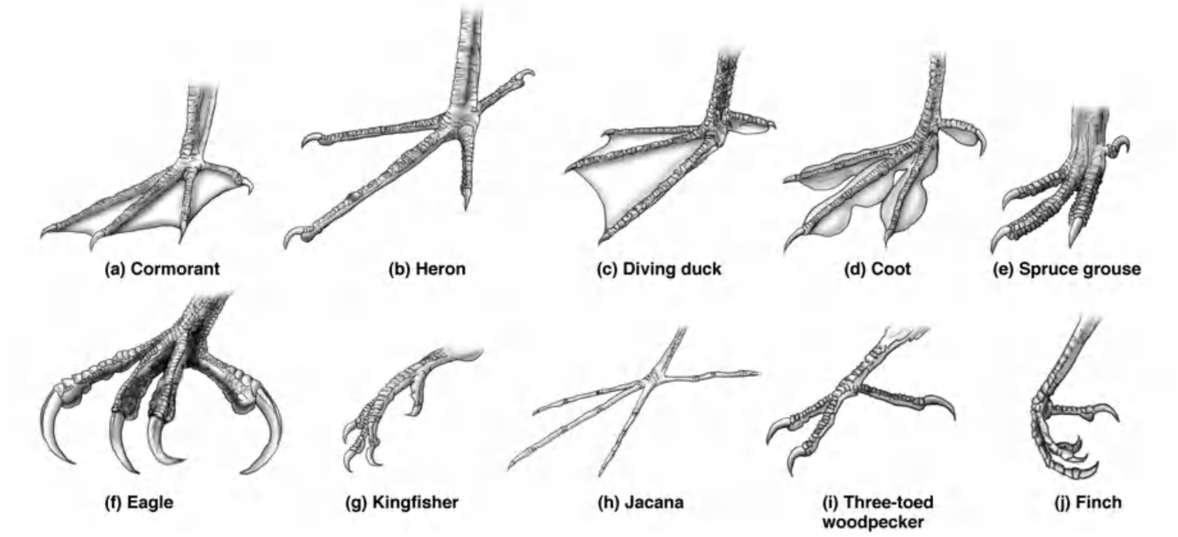


Figure 8.14. Selected examples of avian feet: (*a*) cormorant, (*b*) heron, (*c*) diving duck, (*d*) coot, (*e*) spruce grouse, (*f*) eagle, (*g*)≈kingfisher, (*h*) jacana, (*i*) three-toed woodpecker, (*j*) finch. Note the extensive webbing in the aquatic birds (*a*, *c*) and the lobing in the coot (*d*), a shorebird.

Penguins are the most specialized of all birds for swimming underwater. Their wings are short, narrowed, and flattened—all adaptations for underwater "flying," and their legs are attached more posteriorly on the body. The modified feathers are scalelike, which provides a smooth surface on the fusiform body. Their solid bones reduce buoyancy. Diving behavior and physiology have been discussed by Kooyman and Ponganis (1990).

Muscular System

The musculature of crocodilians has become well differentiated into individual powerful muscles. The limb muscles are especially well developed. Although crocodilians usually use a sprawling gait, their limb muscles allow them to raise their body off the ground and travel rapidly for short distances.

The jaws of both alligators and crocodiles are hinged on the bottom; the top jaw is simply an extension of the skull. The muscles responsible for opening the jaws (depressor mandibulae and several dorsal neck muscles) are relatively small and have very little mechanical advantage; thus, it is possible to keep a crocodilian's mouth shut by holding its jaws. Two large pterygoid muscles, however, can generate tremendous power and force when closing the jaws.

The epaxial musculature of birds (Fig. 8.15) is basically similar to that described for lepidosaurs, although many birds have lost their muscular metamerism and developed muscle bundles. Because the vertebral column in the trunk region is more or less rigid, epaxial muscles in this region are poorly developed; those in the neck and tail region, though, are much better developed. Differentiation of the abdominal wall muscles is greatly reduced, and metamerism is no longer evident. External and internal intercostal muscles are present to assist in breathing.

Two “color” types of skeletal muscle tissue occur in birds: red and white. Red muscle fibers are smaller in diameter, have a richer blood supply, and contain more nuclei and mitochondria than white fibers. In addition to hemoglobin, red muscle also contains the protein myoglobin. Myoglobin, which is found in the flight muscles of many birds, accounts for the designations of “dark” meat and “white” meat. Myoglobin stores oxygen that can then be released to the muscle as required. Because myoglobin has a higher affinity for oxygen than blood hemoglobin, it automatically loads up from this latter source. Some muscles may be composed of red fibers in one species and white fibers in another, depending on their function. White muscle is designed for short bursts of intense activity, like a turkey taking off and flying a short distance. Red muscle is designed for sustained activity. Even in the same species, the type of muscle fiber in a given muscle may vary (e.g., breast muscle in a wild turkey [red] versus a domestic turkey [white]).

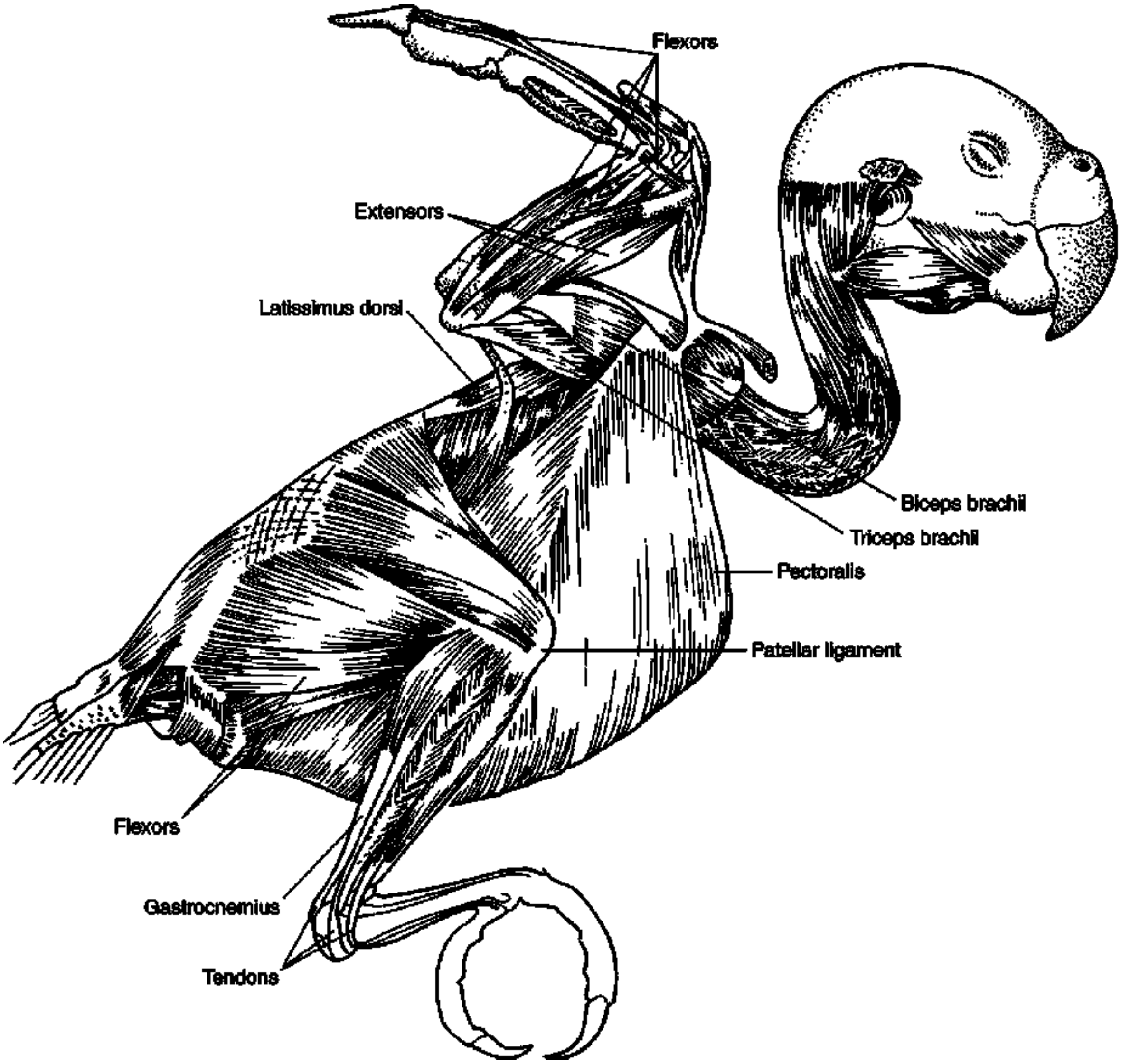


Figure 8.15. Superficial musculature of a parakeet.

Appendicular muscles of birds are highly modified for flight as well as for perching, grasping, walking, hopping, and swimming. The largest and most powerful muscles in carinate birds are the **extrinsic** (originating *outside* the part on which they act) muscles of the wings (see Fig. 8.15). These pectoral, or breast, muscles (pectoralis and supracoracoideus) are attached primarily to the keeled sternum as well as to the coracoid and furcula. The avian pectoralis muscle is proportionately the most massive paired muscle found in any tetrapod; it can occupy as much as 25 percent of a bird's total body mass (Greenwalt, 1962). Contraction of the pectoralis muscles pulls the wing downward and forward to provide lift (see Fig. 8.16). Elevation of the wings is brought about primarily by contraction of the supracoracoideus, which also originates on the ventral side of the sternum but whose tendon passes through the foramen triosseum (an opening formed by the clavicles, coracoids, and scapulae) to insert on the humerus. This pulley-like action pulls the humerus upward. This unusual arrangement permits the primary abductor and adductor muscles of the wings to originate and insert on the same bones. The **intrinsic** (originating *on* the part on which they act, i.e., the wing) musculature of the wings is reduced. On the other hand, the musculature of the hindlimbs is well developed. Specialized muscles are necessary in the legs and feet of raptors, passerines, and aquatic species to allow for the diverse uses of their legs. Perching birds, for example, have long tendons that extend from muscles on the proximal part of the leg and insert on the digits on the distal end. This arrangement has a double purpose. The bird's energy expenditure is reduced because the muscles do not have to shorten as much as they would if they were extrinsic muscles. In addition, whenever the bird is perching, bending of the leg causes the tendons to tighten, effectively "locking" the toes around the perch.

Among the most important features of the thermal physiology of flight are the greatly increased heat production generated by the flight muscles and the increased oxygen uptake. For example, the metabolic rate of Costa's hummingbird (*Calypte costae*) during hovering flight was seven times the standard rate (Lasiewski, 1963). The flight metabolism of rock doves (*Columba livia*) exceeded that during rest by a factor of 8.2 (LeFebvre, 1964). Similar increments in oxygen uptake during flight have been recorded in budgerigars (*Melopsittacus undulatus*) and in the laughing gull (*Larus atricilla*) by Tucker (1966, 1972). For very short periods of flight, the oxygen uptakes of the evening grosbeak (*Coccothraustes vespertinus*), ring-billed gull (*Larus delawarensis*), and black duck (*Anas rubripes*) were 12 to 13 times the resting values (Berger et al., 1970). Metabolic rates vary with the flight speed. Some of the heat produced during flight is stored in the bird; elevations of body temperature of 1.5°C to 2.6°C have been described after flight (Dawson and Hudson, 1970). Most of the excess heat is lost by evaporative cooling (Tucker, 1968).

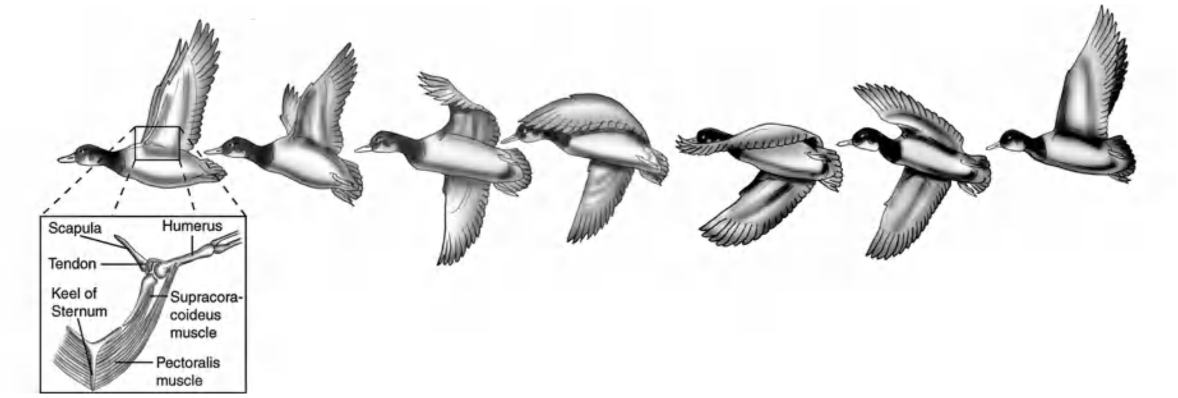


Figure 8.16. In strong fliers like ducks, normal flapping flight is accomplished by the fully extended wings sweeping downward and forward. The primary feathers at the wing tips provide thrust. The upbeat occurs by bending the wing and bringing it upward and backward. The wing is then extended and ready for the next downbeat. The detail shows the frontal view of the pectoral girdle and attached wing muscles. Flight muscles are arranged to keep the center of gravity low in the body. Thus, both major flight muscles are anchored on the keel of the sternum. Contraction of the pectoralis muscles pulls the wing downward and forward to provide lift. The upstroke is due to the contraction of the supracoracoideus muscle, which is also attached to the sternal keel. The tendon of the supracoracoideus passes through a foramen to insert on the humerus. This pulley-like system pulls the humerus upward. In chickens and most other birds that fly weakly or not at all, the flight muscles are white and produce adenosine triphosphate (ATP) anaerobically. In good fliers, the muscles, which contain numerous mitochondria, are red and aerobic.

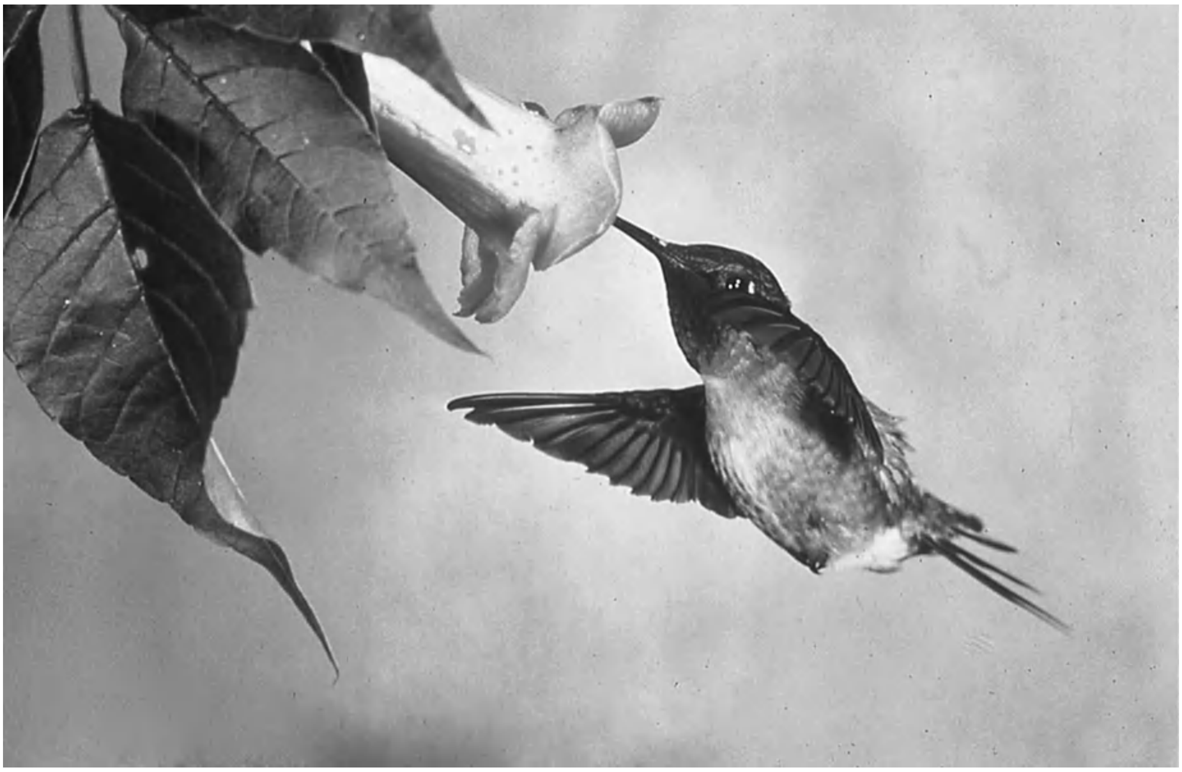


Figure 8.17. Wingbeat frequencies up to 80 to 100 per second have been recorded in a hovering hummingbird.

Branchiomeric muscles serve much the same function as they do in reptiles. They operate the jaws, the hyoid skeleton and its derivatives, as well as the pharynx and the larynx.

Both extrinsic and intrinsic integumentary muscles are present in birds. Extrinsic muscles permit independent movement of the skin. Intrinsic muscles are mostly smooth muscles that attach to the feather follicles (arrectores plumarum). These muscles are used to ruffle the feathers for insulation, for display, or as an emotional response to danger.

Cardiovascular System

The crocodilian heart possesses a complete interventricular septum oriented in a vertical position (see Fig. 7.11c). Not only are the ventricles totally separated from each other, but the right atrium opens into the right ventricle, and the left atrium opens into the left ventricle. The pulmonary trunk and one systemic trunk leave the right ventricle and one systemic trunk leaves the left ventricle. While underwater and/or in response to changing hormone levels, crocodilians have the ability to shunt blood that has just come from the body back for another circuit instead of sending it to the lungs (which become less useful during a dive, as their oxygen is depleted) to reload oxygen.

Both crocodilian and avian erythrocytes and thrombocytes are nucleated and usually oval in shape. All five types of leukocytes (neutrophils, eosinophils, basophils, monocytes, and lymphocytes) and thrombocytes are present.

Antibacterial activity of plasma has been reported in the American alligator (*Alligator mississippiensis*), the saltwater crocodile (*Crocodylus porosus*), the freshwater crocodile (*Crocodylus johnstoni*), and the Siamese crocodile (*Crocodylus siamensis*) (Merchant et al., 2005; Merchant and Britton, 2006; Kommanee et al., 2012; Bishop et al., 2015). Recent lab tests show that tiny amounts of alligator blood extract—some scientists call it alligacin—have been shown to kill up to 23 types of bacteria, including Methicillin-resistant *Staphylococcus aureus*, which can trigger skin infections, sinusitis, and food poisoning, and *Pseudomonas aeruginosa*, which can cause inflammation and sepsis. It also helps fight HIV (Fong, 2008). Previous experiments have revealed that alligator blood extract cripples many human pathogens, including *E. coli*, the herpes simplex virus, and some strains of the yeast *Candida albicans*. The serum’s antimicrobial power derives from protein bits called peptides, which were identified in the matrix via a novel technique called bioprospecting particle-assisted proteomes. The antibacterial activity of plasma from the Siamese crocodile exhibited substantial antibacterial activities against the pathogenic bacteria *Staphylococcus aureus*, *Salmonella typhi*, *Escherichia coli*, *Vibrio cholerae*, *Pseudomonas aeruginosa*, and *Staphylococcus epidermidis*.

The Beak of the Crossbill

Crossbills (*Loxia*) have remarkable beaks (see Fig. 8.12m). The lower mandible twists to either the right or left of, and crosses over, the upper one. This unique beak serves as an adaptation for extracting and handling seeds from conifer cones, allowing crossbills access to parts of the cone that other birds cannot reach. Conifer cones vary in structure depending on ripeness. Cone scales are initially closed, but as the cone matures, the scales have wide gaps between them. Cone scales must be separated so that crossbills can extract seeds with their tongue. On closed cones, crossbills create gaps between the scales by biting between the scales with their crossed and pointed mandibles. The lower mandible curves slightly laterally, to either the left or right, whereas the upper mandible is directed more straight ahead. To create a gap between cone scales, the decurved and pointed upper bill slides between the scales in a biting motion. After an initial gap is created, the jaws spread sideways (the lower jaw is abducted laterally in the direction that its tip points). Lateral spread of the jaws widens and deepens the gap between the scales. When the seed is exposed, the tongue is protruded and its spoon-shaped tip carries the loose seed to the bill to be husked. Lateral mobility of the lower mandible probably evolved because it increased the rate with which seeds could be extracted from partly open cones. It provides increased access to seeds in cones whose scales are spread apart. Crossed mandibles further expand the time during which conifer seeds can be used, especially from closed cones.

Crossbills have evolved larger bills, and associated musculature and body mass, to provide the power necessary to separate cone scales. This specialization, however, may cause high mortality during conifer cone failures due to their ineffectiveness in handling nonconifer seeds because of their narrow mandibles (which reduce the efficiency with which large seeds can be handled), a lowered horny palate, and a large body mass.

Benkman found that small-billed crossbills, like white-winged crossbills (*Loxia leucoptera*), forage more efficaciously on small conifer cones, like tamarack and spruce, with thin and relatively short cone scales, whereas large-billed crossbills, like red crossbills (*Loxia curvirostra*), forage more efficiently on large conifer cones, like pines and black spruce, with thicker cone scales. White-winged crossbills rely less on powerful lateral abduction of their mandibles in separating adjacent cone scales to expose seeds.

Based on bill depth and palate structure, Benkman found that each taxon of red crossbill in North America is adapted to a particular species of conifer, a “key conifer.” The adaptive value of bill size differences among red crossbill populations shows morphological diversification in bill characteristics in response to adaptive peaks represented by their main food: seeds in conifer cones.

Nestlings have uncrossed bills. Crossing over starts at about the age of 27 days (one week after fledging) and is complete by about 45 days, when young birds are able to feed effectively on cones.

Robbins, 1932; Griscom, 1937; Benkman, 1987, 1988a, 1988b, 1993

Birds have two atria and two ventricles that are completely separated (Fig. 8.18). The sinus venosus is reduced and largely incorporated into the wall of the right atrium during embryonic development. It always is retained in adult birds, however, as a discrete structure delineated externally from the right atrium by a sulcus (groove) and internally by the retention of its valves (Feduccia and McCrady, 1991). Deoxygenated blood, carried by the two precaval veins, postcaval vein, and coronary veins, empties into the right atrium through the sinus venosus. It then flows into the right ventricle and is pumped to the lungs via the pulmonary trunk and the pulmonary arteries. Oxygenated blood returns to the left atrium via the pulmonary veins and then passes to the left ventricle, which pumps the blood through the right aortic arch (the only half of the fourth aortic arch remaining in birds) and then through the body. This makes possible a double circulation, with completely separated pulmonary and systemic streams. The backflow of blood is prevented by four valves: the tricuspid (between the right atrium and the right ventricle), the pulmonary semilunar (at the entrance to the pulmonary trunk), the bicuspid (between the left atrium and the left ventricle), and the aortic semilunar (at the entrance to the aorta).

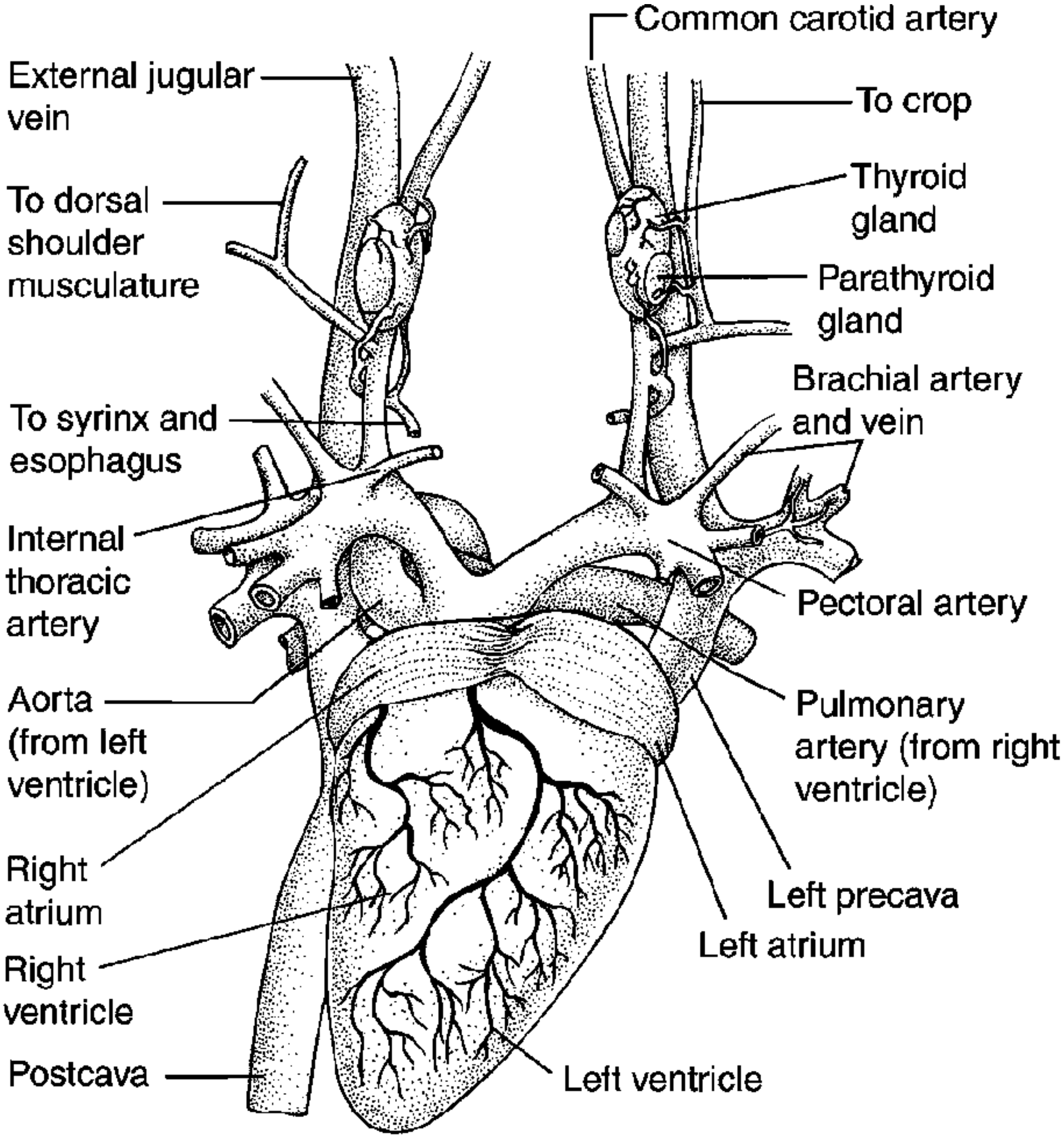


Figure 8.18. Ventral view of the four-chambered avian heart and major blood vessels.

Table 8.1. Heart Size and Body Weight

	Body Weight (g)	Heart Weight/Body Weight (%)
Goose	4,405	0.8
Duck	1,685	0.74
Chicken	3,120	0.44

	Body Weight (g)	Heart Weight/Body Weight (%)
Ptarmigan	258	1.05
Hummingbird	–	2.4
Coturnix (quail)	119	0.90
Pigeon	458	1.02

Source: From Sturkie, 1976. Copyright © Springer-Verlag, New York.

The size of the heart (Table 8.1) and the rate of the heartbeat vary with the size and lifestyle of the bird: larger birds generally have relatively smaller and slower-beating hearts than smaller birds. The heart rate of a turkey, for example, may be less than 100 beats per minute, a hen chicken about 300 beats per minute, and a sparrow nearly 500 beats per minute (Young, 1962).

A pulmonary trunk emerges from the right ventricle and leads to what in early vertebrates was originally the sixth aortic arch. A single aortic trunk emerges from the left ventricle and leads to derivatives of the third and right fourth aortic arches. The left fourth aortic arch is absent in birds. The unpaired dorsal aorta gives off branches to the body wall, the viscera, and the appendages before continuing into the tail as the caudal artery.

Hummingbird Flight

Hummingbirds typically hover to feed more than 100 times a day, consuming about 20 percent of their daylight hours with this expensive aerobic activity (see Fig. 8.17). Hover-feeding usually lasts less than a minute. Hummingbird heart rates are about 500 beats per minute at rest and may increase to about 1,300 per minute during hovering flight. Wingbeat frequencies up to 80 to 100 per second have been recorded. Unlike most other birds, lift during hovering is generated in both up- and downstrokes in the wingbeat cycle. The main flight muscles—the pectoralis and the supracoracoideus—are highly developed and constitute about 30 percent of the body mass. Some hummingbirds, like the ruby-throated hummingbird (*Archilochus colubris*), fly nonstop for several hundred kilometers across the Gulf of Mexico during their annual migration, a trip that may require about 20 hours to complete.

Suarez, 1992

The venous channels of birds are much like those of crocodilians. Internal jugular veins and subclavian veins join to form precaval veins anterior to the heart. All blood from the hindlimbs now bypasses the kidneys and goes directly into the postcaval vein, which is the chief vessel draining the trunk. The renal portal system is reduced to draining the tail. Postcardinal veins are absent.

Heat exchange in the legs is important, especially for birds that stand or swim in cold water. Blood flowing to these thin-skinned peripheral surfaces passes through a **heat exchanger** in order to reduce heat loss. Heat energy from the arterial blood warms the cold venous blood returning to the heart. Arteriovenous **retia mirabilia** are located near the junctions of the legs with the body. In these *retia*, small arterioles going to the legs run alongside small veins in which blood is flowing in the opposite direction, and heat energy is exchanged between them. After leaving the *retia*, arterial blood is at approximately the same low temperature as the legs. In this manner, the legs lose much less heat energy than they otherwise would, and heat energy is retained by the body core in the blood of the veins. Through this heat exchanging mechanism, energy loss is minimal. Because blood flows in opposite directions in the two opposing streams, this type of heat exchanger is known as a **countercurrent heat exchanger**.

Respiratory System

The nostrils of crocodilians are located at the tip of the snout and are closed by valves during diving. Due to the presence of a complete secondary palate, the internal nares are located at the rear of the oral cavity (Fig. 8.19). The internal nares can be closed off from the throat by fleshy folds on the back of the tongue and palate so that crocodilians can continue to breathe while holding prey in their mouth. The trachea is longer than the neck and convoluted. The lungs, each of which is located in a separate pleural cavity, consist of numerous large chambers, each composed of many individual subchambers (alveoli). Internal partitioning is well developed in crocodilians, with pockets of trapped air causing the lungs to be spongy.

The back-and-forth movements of the liver in crocodilians act as a piston on the lungs (Fig. 8.20). Inhalation occurs when the rib cage expands and the liver is pulled back; exhalation takes place when the rib cage relaxes and the forward-moving liver compresses the lungs. The lungs and air sacs of birds move air in only one direction during both inspiration and expiration through most of the tubular gas-exchanging bronchi (parabronchi), whereas in the lungs of mammals, air moves tidally through bronchi, which terminate in small cul-de-sac chambers where blood vessels exchange carbon dioxide for oxygen. Air then exits the lungs via the same pathway. Recent research shows that air also flows unidirectionally through parabronchi in the lungs of the American alligator (Farmer and Sanders, 2010). The primary bronchi each split into two branches shortly after the point where air enters each lung. Air moves through the first branch in each lung in the same direction whether the alligator is inhaling or exhaling. This finding could mean that this mode of breathing is far older than scientists suspected and may have helped archosaurs, the common forebearers of birds, alligators, and dinosaurs, rise to a dominant ecological niche millions of years ago. One carnivorous dinosaur, *Aerosteon riocoloradensis*, has been discovered that shows the presence of air sacs along with pneumatic hollowing of the furcula and ilium. Respiration was apparently similar to that of a bird (Sereno et al., 2008).

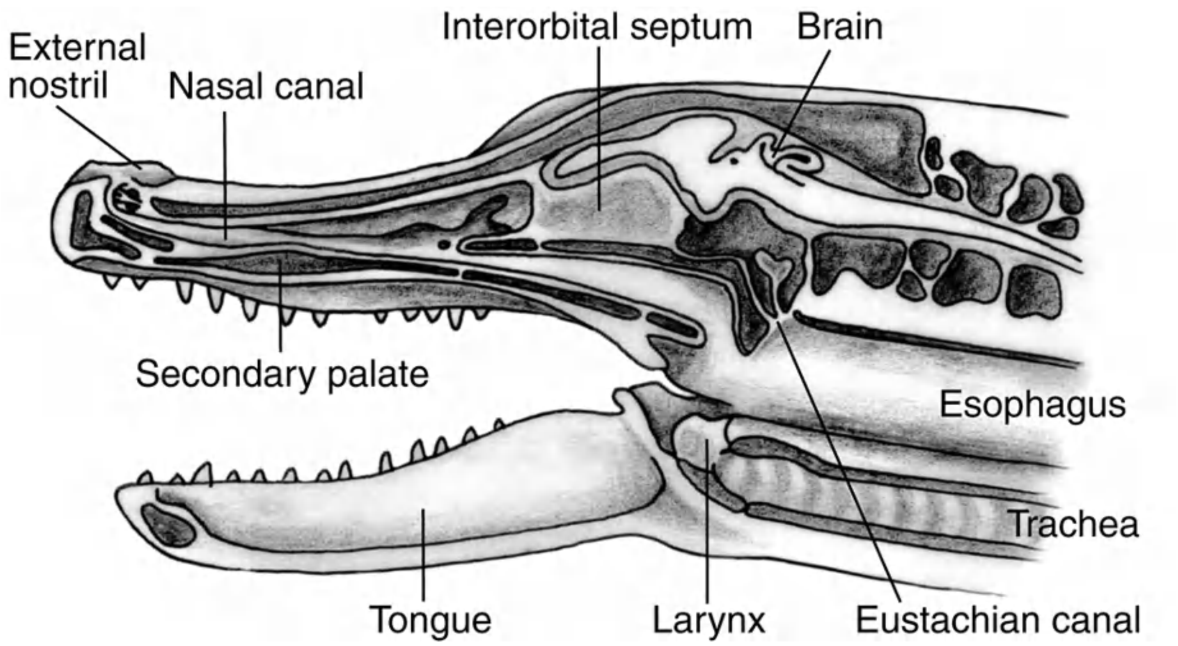
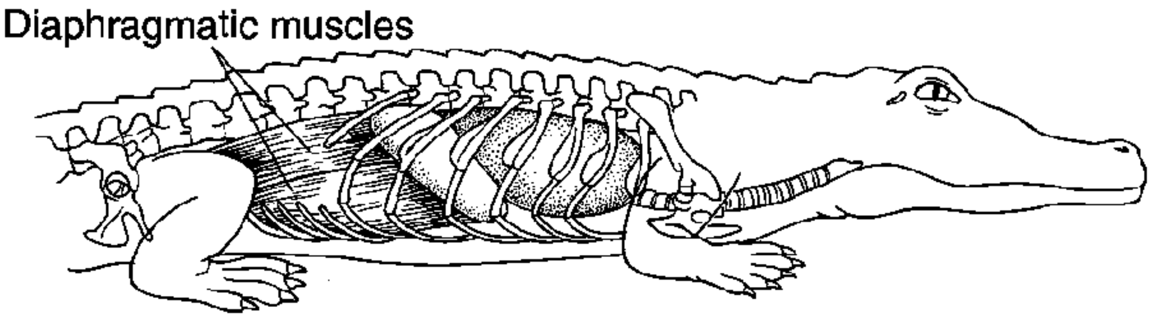


Figure 8.19. Midsagittal section of the head of the alligator, *Alligator mississippiensis*, showing the right nasal canal running above the bony palate and opening far back into the pharynx opposite the glottis.

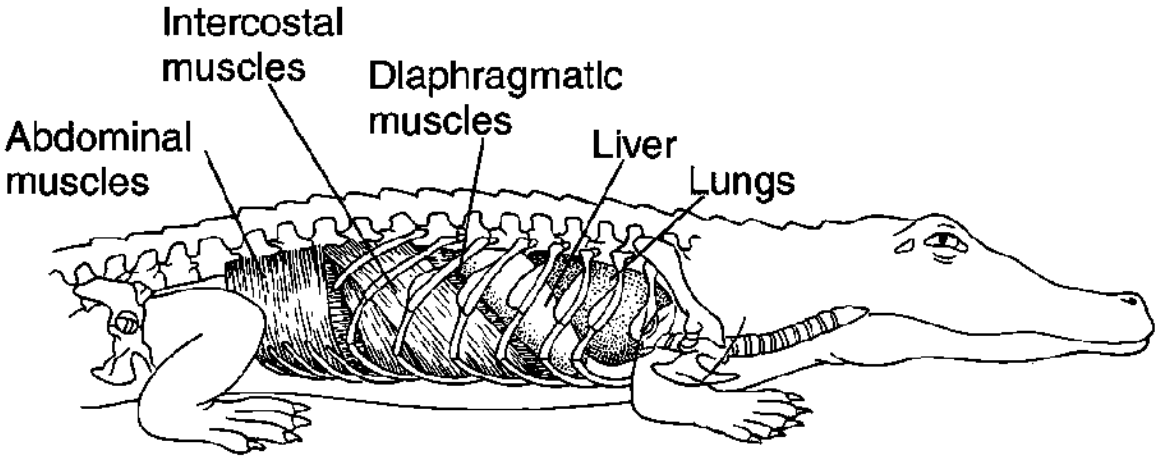
Crocodilians are the most vocal of reptiles, using a wide variety of vocalizations for both close-range and long-range communication. For example, adults bellow during the mating season. Young crocodilians emit sounds from within the nest that attract the mother, who assists the newborn in exiting the eggs and the nest. Even after hatching, the young produce "alarm cries" that summon the adults.

In birds, air enters through the external nares, flows through nasal canals above the secondary palate, and exits through internal nares located near the rear of the oral cavity. Air then flows through the glottis and into the trachea. The glottis is surrounded by a series of cartilages that form the larynx. The larynx, however, is not a sound-producing organ; it serves to modulate tones that originate in the **syrinx**, the special voice box unique to birds (Fig. 8.21). It is an enlargement and modification of the lower end of the trachea. The syrinx contains a pair of semilunar membranes with muscles that alter the pitch of the sound. Contraction of the muscles as air is expelled from the lungs alters the membranes and produces the songs and calls characteristic of different species. A series of cartilaginous or bony rings, most of which are complete, supports the trachea. The trachea bifurcates (splits) to form two bronchi that then lead to the lungs. The syrinx is located at the bronchial bifurcation.

In some birds, the trachea is essentially straight, but in at least 60 species—including the trumpeter swan (see Fig. 8.21)—it consists of coils and loops instead of taking a direct route between the throat and the lungs. This trait is found in six avian orders and has probably evolved several times (Whitfield, 1999). In some species, only males possess elongated tracheae, whereas in others, both sexes do. The elongated trachea serves as a resonator, producing a deeper, more baritone sound.



(a) Inhalation



(b) Exhalation

Figure 8.20. Gas exchange in the crocodile. Crocodiles use their rib cage as well as piston-like back-and-forth movements of the liver to move air into and out of the lungs. (*a*) During inhalation, the rib cage expands and the liver is pulled back, enabling the crocodile to inhale fresh air into its lungs. (*b*) During exhalation, the lungs are compressed by the rib cage and the forward-moving liver, allowing the crocodile to exhale spent air.

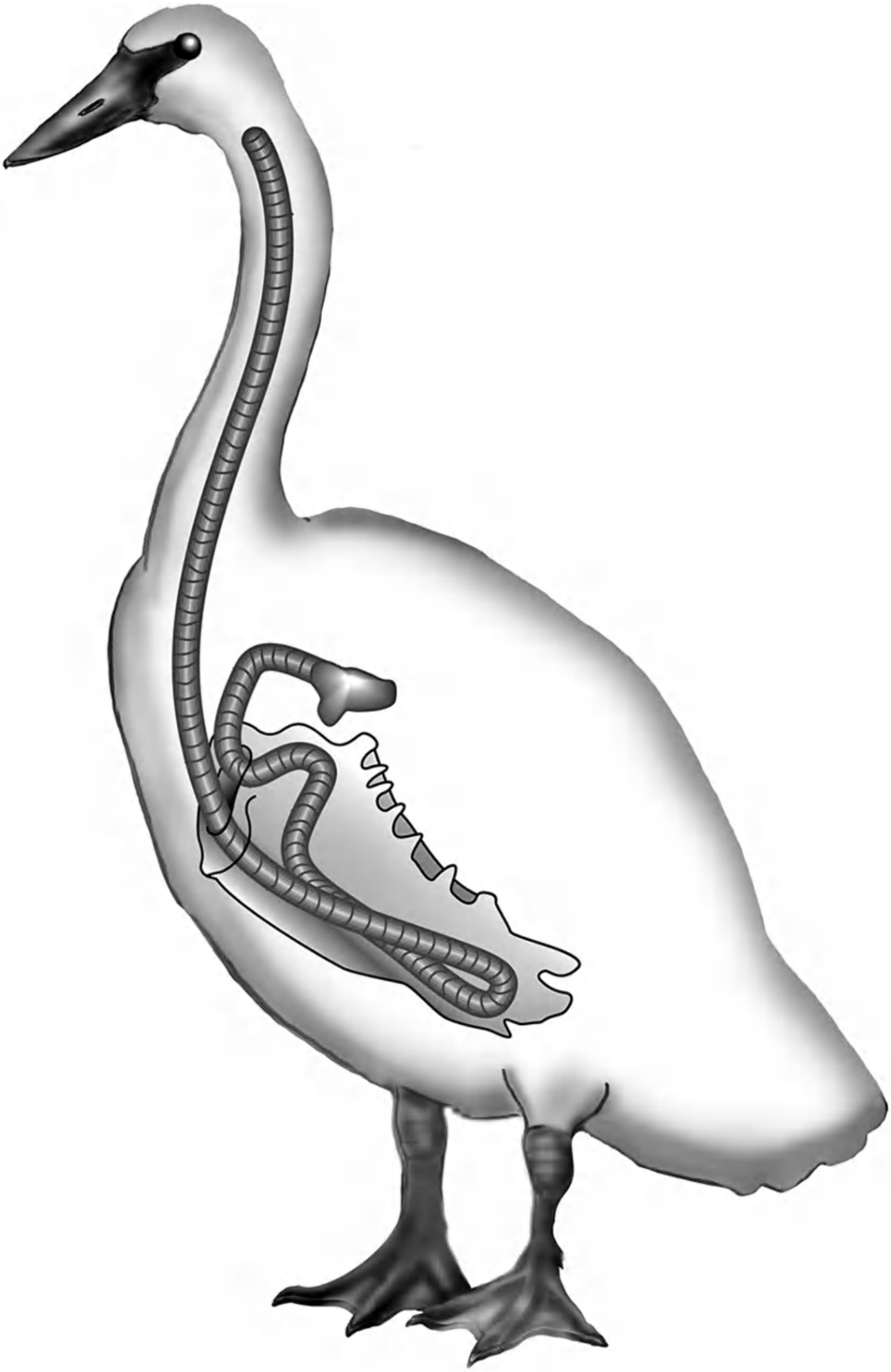


Figure 8.21. The long, coiled trachea of the trumpeter swan (*Olor buccinator*).

Birds have no muscular diaphragm as exists in mammals, and the thoracic and abdominal cavities are functionally continuous. The lungs are located in **pleural cavities**. An oblique septum extends caudally from the pericardium to the lateral body wall as a mostly membranous partition that separates the pleural cavities from the rest of the coelom. This membranous "diaphragm" participates in the operation of the suction pump by which the lungs are inflated, though it functions differently from the muscular mammalian diaphragm. Contraction of the external intercostal muscles causes the ribs to move outward and the sternum to move downward. This tightens the septum, which lowers the pressure around and within the lungs to below atmospheric pressure. Air then can be drawn into the air sacs after traversing the lungs on its way. During expiration, air is forced through the lungs on its way back to the trachea.

Bird lungs are highly modified: 7 to 12 diverticula (air sacs) of the lungs invade many parts of the body (Fig. 8.22 a, b). These air sacs are thin-walled, distensible diverticula derived from the primary or secondary bronchi. They lie between layers of pectoral muscle, project among the viscera, and even penetrate the marrow cavity of some bones. They may occupy as much as 80 percent of the total body cavity. Anatomically and functionally, air sacs form two groups: a posterior, or caudal, group that includes the large abdominal sacs and an anterior, or cranial, group that consists of several somewhat smaller sacs. Most air sacs are paired, but some may be united across the midline. Paired air sacs usually occur near the base of the neck (cervical), near the heart (anterior thoracic), within the oblique septum (posterior thoracic), and among the viscera (abdominal). An air sac that may or may not be united across the midline is usually located dorsal to the furcula (interclavicular). Some birds also possess air sacs between the layers of pectoral muscle (axillary). Diverticula of these air sacs may invade almost any part of the skeleton, most frequently the humerus, femur, and vertebrae.

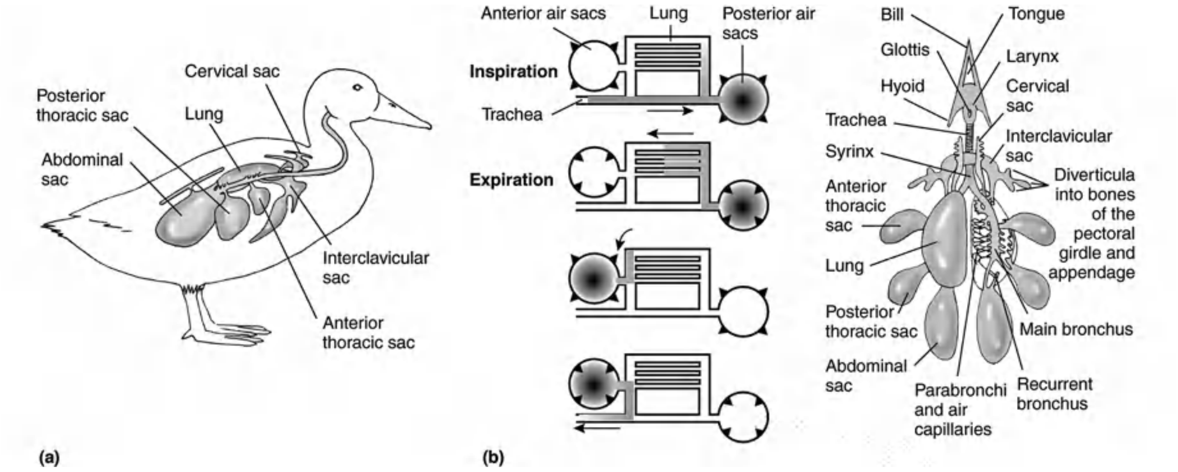


Figure 8.22. The ventilatory system in a mallard duck. (*a*) The vocal organ is the syrinx, which is located at the point where the two bronchi join to form the trachea. (*b*) Movement of a single volume of air through the bird's respiratory system. One of the most distinctive features of the avian ventilation system is the presence of numerous air sacs that are connected to the bronchial passages and the lungs. Major air sacs are shown in the diagram; additional air sacs that enter into the bones are not shown. Most of the inhaled air goes directly into the posterior sacs. As the ventilatory cycle continues, air from the posterior sacs passes through the lungs and into the anterior sacs. This mechanism provides a continuous flow of air through the lungs, in contrast to all other tetrapods, in which the air is moved into and out of only the lungs, which serve as blind sacs. Two full respiratory cycles are required to move the air through the system.

The lung volume of a typical bird is only about half that of a mammal of the same size, but with the air sacs, the total potential volume of the respiratory system is some three times as great as that of a mammal. Air sacs are not designed to function directly in gas exchange. They contain no alveoli or respiratory epithelia with any network of capillaries necessary for gas exchange. However, they do play an important accessory role in ventilation. During inspiration, incoming air flows through the bronchioles and mainly into the posterior air sacs (see Fig. 8.22 b). Some air also goes into the lungs. The air that first reaches the posterior sacs is air that was left in the trachea after the previous inhalation, so that it contains more carbon dioxide than does fresh air. On exhalation, the sacs decrease in size, and air from the posterior sacs flows into the lungs, which contain parabronchi (tubes) rather than alveolar sacs. On the next inhalation, the mass of air moves from the lungs into the anterior sacs. On the following exhalation, it is discharged from the air sacs into the trachea and, finally, to the outside. The bellows action of the air sacs provides a continuous, unidirectional flow through the bird's lungs.

The duct system within the bird lung is unique. All of the air ducts are open-ended and interconnecting (parabronchi), and none terminate blindly within the lung. This makes possible a steady flow of oxygen-rich air, permitting cross-current gaseous exchange and increased efficiency. The bellows action of the air sacs causes the air to be constantly and completely replaced. Bird lungs, therefore, contain only fresh air, in contrast to the lungs of other vertebrates, in which there is always residual unexpired air partly depleted of its oxygen content.

Contraction of the intercostal and abdominal muscles maintains an adequate flow of air over the respiratory epithelia when a bird is at rest. During flight, however, alternate contraction and relaxation of pectoral muscles provide additional force for the bellows action. Inspiration is coordinated with the upstroke of the wings and expiration with downstroke. A more rapid respiratory rate is required during flight because of an increased oxygen demand. In addition, in black-billed magpies (*Pica pica*), the respiratory pattern changes as the wingbeat pattern changes from high-amplitude rapid flaps to low-amplitude slower flaps with interspersed brief glides (Boggs et al., 1997). Breath cycle times were longer when associated with low-amplitude, longer duration wingbeats and shorter when associated with high-amplitude, shorter wingbeats. In the absence of sweat glands, an increase in the respiratory rate effectively increases heat loss. Thus, air sacs also aid in thermoregulation by helping dissipate excess internal heat energy produced by the muscular action of flight activity.

Birds, as well as small mammals, normally exhale air that is well below body temperature. Murrish and Schmidt-Nielsen (1970) noted: “The cooling of the exhaled air is due to heat exchange in the nasal passageways; it is merely the reverse process of the heating of air that takes place during inhalation. During inhalation, the air is heated and humidified and the walls of the passageways are thus cooled by convection and evaporation; on exhalation the returning warm air gives up heat to these cool surfaces and water vapor condenses.”

Dehydration is probably the most important physiological constraint for migrating birds. Studies of blackcaps (*Sylvia atricapilla*) migrating across the Sahara Desert suggest they “go to ground” during the day to minimize evaporative water loss at high altitudes (Izhaki and Maitav, 1998). Although a majority of the birds migrating in fall had accumulated sufficient fat to enable them to traverse the Sahara in a single flight, they would probably lose at least 12 percent of their initial mass through dehydration by the time they reached their southern destination. Therefore, most birds probably use intermittent migration with stopovers at sites where food and water are available. By resting during the day, when evaporative water loss is highest, and flying at night, the majority of small migrants can successfully navigate the (at minimum) 1,200 km (750 mi.) Sahara crossing.

The Deep Dives of Penguins

Penguins have solid bones that reduce buoyancy; tightly packed, scalelike feathers; and narrow, flattened wings for underwater "flight." King and emperor penguins are amazing divers—they can dive to depths of 304 m (1,000 ft.) and 534 m (17,500 ft.) for as long as 7.5 and 15.8 minutes, respectively. The abdominal temperature of king penguins may fall to as low as 11°C (52 °F) during sustained deep diving. The slower metabolism of cooler tissues resulting from physiological adjustments associated with diving could partially explain why penguins and possibly marine mammals can dive for such long duration.

Such dives are also longer than the penguin's oxygen stores should allow. Emperor penguins surface from some of their dives with almost no oxygen left in their bodies. Their blood-oxygen level—the lowest ever recorded in a healthy, conscious bird or mammal—is less than a quarter of the level at which people black out. Researchers believe that the penguins probably also share some of the same adaptations to a low-oxygen lifestyle as diving mammals. That adaptation involves two special proteins in brain tissue: neuroglobin and cytoglobin. Comparisons of these two proteins in the brains of active divers like otters and certain dolphin species show twice the levels as in terrestrial species. It is likely that the proteins secure traces of oxygen and mobilize them to sustain brain activity.

Ancel et al., 1992; Kooyman et al., 1992; Harding, 1993; Kooyman and Kooyman, 1995; Handrich et al., 1997; Ponganis et al., 2007; Williams et al., 2008

In the humid tropics, evaporative cooling is relatively ineffective in small birds like variable seedeaters (*Sporophila aurita*). They employ an elevated body temperature (hyperthermia) to cope with heat (Weathers, 1997). They can survive body temperatures between 46.8°C and 47.0°C (116°F and 116.6°F), among the highest recorded for birds. Tolerance of hyperthermia is advantageous for this species because it allows them to maintain an unusually high body temperature to ambient air temperature gradient in hot environments, and thus they are able to dissipate heat passively. The main response of these birds to heat stress in the field is to avoid it behaviorally rather than to overcome it physiologically.

Digestive System

Crocodilians possess homodont dentition with the teeth rooted in sockets (thecodont dentition) and confined to the jaws. Teeth are continually replaced during the animal's lifetime (polyphyodont dentition). A nonprotrusible tongue is present that assists in moving food within the oral cavity. The crocodilian stomach (see Fig. 7.22c) is similar to the stomach of grain-eating birds, with the posterior portion being modified into a muscular gizzard-like compartment that grinds food against ingested small stones that have been deliberately swallowed. Gastric juices are added in the thin-walled glandular region of the stomach that lies in front of the gizzard. The small intestine consists of duodenum, jejunum, and ileum regions. A pancreas, located near the junction of the stomach and duodenum, secretes pancreatic juice into the duodenum in order to facilitate digestion and to neutralize the acidic chyme from the stomach. A cloaca leads to the vent. Whereas the vent is a transverse slit in turtles and lepidosaurs, it is oriented longitudinally in crocodilians.

All living birds lack teeth. The horny "egg tooth" developed by young birds (when within the egg) is a temporary, epidermal, toothlike scale located dorsally (externally) on the upper jaw. It functions in helping to crack the egg shell for hatching and is either resorbed or shed after hatching.

The tongue of birds is nonmuscular and exhibits great diversity in form and structure. Most bird tongues are short, narrow, and triangular with few taste buds. Woodpeckers use their long, specialized tongue as a probe to obtain insects between cracks in tree bark or in holes they excavate. When retracted, the woodpecker's tongue actually wraps around inside the back of the head (Fig. 8.23).

A complex system of tactile sensors is present on the tongue, so that birds can make fine distinctions in food items based on the feel of the food to the tongue and hard palate. Well-developed salivary glands are present in most birds, but are reduced or absent in most aquatic birds (ducks are the only prominent exception) (Worden, 1964). Both unicellular and multicellular oral glands are more numerous than in amphibians and reptiles, and these secrete mostly mucus. The salivary secretions of swifts (Apodidae) and crested swifts (Hemiprocnidae) are used in nest construction, and in one species of cave swiftlet (*Collocalia inexpectata*), the entire nest is composed of saliva. These salivary secretions are the source of "bird's nest soup," which is a million-dollar-a-year industry in Indonesia.

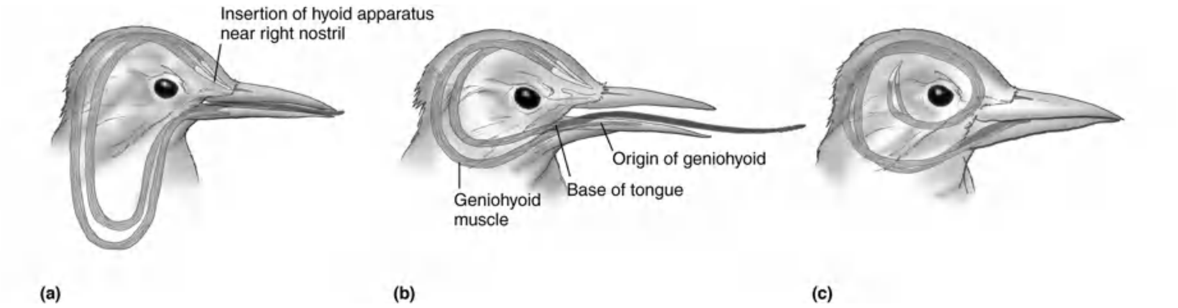


Figure 8.23. Woodpeckers have an exceptionally large and unusual hyoid apparatus to support their long tongues, which are used to probe into deep crevices of trees in search of insects. To allow the long tongue to be extended and retracted from the mouth, the ceratobranchial and epibranchial horns of the hyoid apparatus wrap completely around the back of the skull and attach near the bones at the base of the upper mandible. (*a*) When the tongue is not extended, retractor muscles (*crosshatched*) of the hyoid horns insert far forward. (*b*) When the retractor muscle contracts and draws the hyoid horns forward, the loop of the tongue is raised and the tongue is shot far beyond the tip of the bill. (*c*) When fully contracted, the hyoid horns end at or in front of the eyes in the cavity of the upper mandible, or (as seen here) are even wound around the eye.

The esophagus conducts food from the pharynx to the stomach (see Fig. 7.22d). A portion of the lower part of the esophagus in some birds is modified to form a membranous diverticulum known as a **crop**. A crop occurs primarily in grain-eating birds and is used for the temporary storage of seeds. This permits small birds to feed intensely in short bouts on the ground and then retreat to the safety of a branch for leisurely digestion. In some birds, enzymes may be secreted in the crop for preliminary digestion. In predatory birds, the lower portion of the esophagus may be dilated to form a temporary crop that is used to store partially digested food until it can be regurgitated to nestling young. In some species, the crop is greatly expanded.

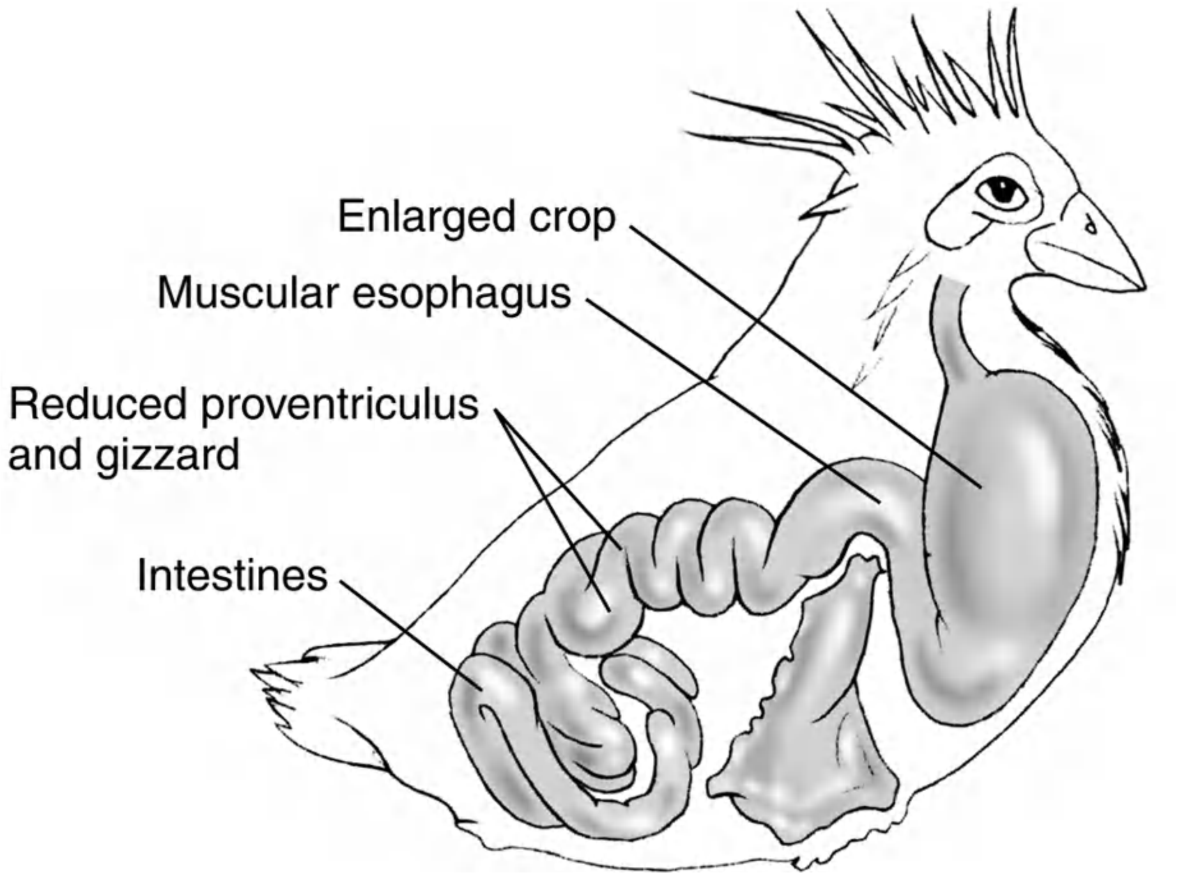


Figure 8.24. The hoatzin (*Opisthocomus hoazin*) is a true ruminant, feeding almost entirely on leafy foliage and fermenting the ingested leaves with a stomach that functions much like the stomach of a cow. Like cows, hoatzins are foregut fermenters. A series of chambers near the anterior end of the intestinal tract house bacteria that break down the leaves and their indigestible cellulose fibers into simpler digestible carbohydrates. Two such fermentation chambers are located within the hoatzin's large crop. Further fermentation occurs as the fermented mash of leaves passes through an enlarged lower esophagus area. The crop and esophagus are both quite muscular in the hoatzin, contracting to grind the leaf mash much as a cow "chews its cud" to aid fermentation. In the hoatzin, the proventriculus and gizzard areas of the true stomach are relatively small and of secondary importance in digestion.

The South American hoatzin (*Opisthocomus hoazin*) possesses an unusually large and muscular crop (Grajal et al., 1989) (Fig. 8.24). Leaves constitute more than 80 percent of its diet, and it is the only bird known to digest food in the same way as cows, sheep, and other ruminants—by using bacteria to break down the fibrous plant material in a special chamber before the plant material reaches the stomach. Ruminants have a prestomach compartment known as a rumen (see Chapter 9), whereas the crop and lower esophagus of hoatzins, both of which are quite muscular, are used to extract volatile fatty acids from the cellulose of tender young plants and to break down indigestible cellulose fibers into simpler digestible carbohydrates before they reach the small intestine. The crop and esophagus contract to grind the leaf mash much as a cow “chews its cud” to assist in fermentation; therefore, the proventriculus and gizzard are small.

Tool Use among Reptiles

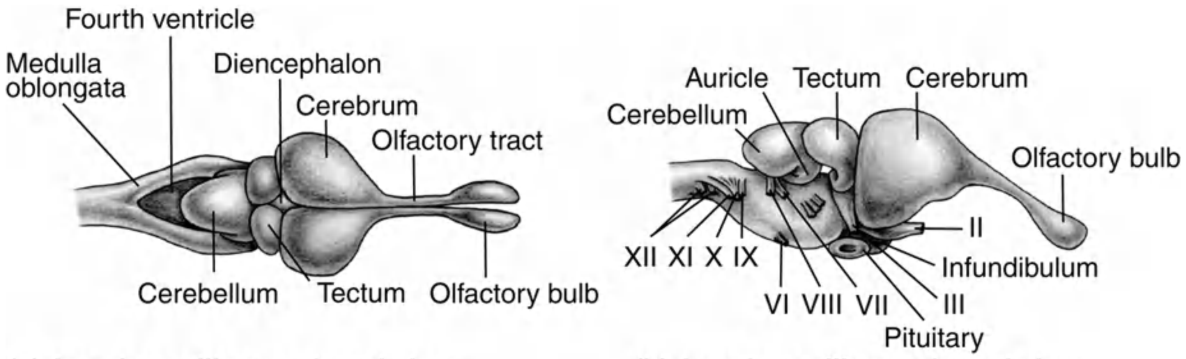
In what could be the first example of tool use among reptiles, researchers have discovered that both alligators and crocodiles use twigs and sticks to attract nest-building birds. The behavior was first noticed in 2007 when mugger crocodiles (*Crocodylus palustris*) at a zoo in India balanced small sticks on their snouts near a rookery where egrets compete for sticks to build their nests. The same strategy was observed in alligators in Louisiana that displayed sticks much more frequently near egret rookeries and during the nest-building season when demand for twigs was high. Multiple attacks have been observed after alligators lured birds with sticks. The authors note that this is the first case of a predator not just using objects as lures, but also taking into account the seasonality of prey behavior.

Dinets, et al., 2015

The crop is modified in some birds (pigeons, doves, emperor penguins, and flamingos) to produce “pigeon’s milk,” the initial food fed to nestlings. In these species, the hormone prolactin stimulates glandular cells lining the crop in both parents to release fatty secretions. This substance then is regurgitated, mixed with partially digested food, and fed to nestlings. The milk is thick and curdlike and consists of 65 to 81 percent water, 13 to 19 percent protein, 7 to 13 percent fat, 1 to 2 percent mineral matter, and vitamins A, B, and B_2 (Skutch, 1991). The proteins contain a large variety of amino acids, whereas the mineral component is largely sodium, with a small amount of calcium and phosphorus. There are no sugars or other carbohydrates in crop milk. Initially, nestlings receive only crop milk, but later the milk is mixed with increasing amounts of other foods. The prolactin that stimulates secretion of “pigeon’s milk” is the same hormone that causes lactation in mammals.

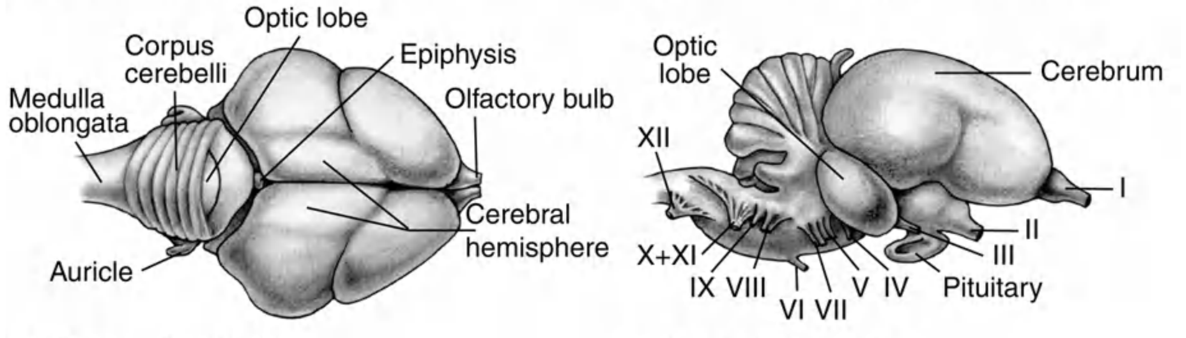
The stomach is well differentiated from the esophagus. In many birds, especially those that feed on seeds and grain, the stomach is divided into two regions: a glandular **proventriculus**, which secretes gastric juice, and a thick, muscular **gizzard**, which often contains grit and pebbles (see Fig. 7.22d). The gizzard serves a grinding function in the absence of teeth.

Piersma and Gill (1998) examined bar-tailed godwits (*Limosa lapponica baueri*) that died after colliding with a radar dome in Alaska just after taking off on a trans-Pacific flight of 11,000 km (6,800 mi.). The birds had relative fat loads (subcutaneous and intraperitoneal) making up approximately 55 percent of their fresh body mass, among the highest ever recorded in birds. These birds also had very small gizzards, livers, kidneys, and guts as compared with northbound godwits from New Zealand. The authors suggested that upon departure, long-distance migrants “dispense” with parts of their body not directly necessary during flight and rebuild these organs after arriving at their destination.



(a) American alligator, dorsal view

(b) American alligator, lateral view



(c) Goose, dorsal view

(d) Goose, lateral view

Figure 8.25. Dorsal (*a*) and lateral (*b*) views of the brain of an American alligator (*Alligator mississippiensis*). Dorsal (*c*) and lateral (*d*) views of the brain of a goose (*Anser*). Compare the size of the cerebrum with Fig. 5.22 (amphibian).

The long, convoluted small intestine consists of a short duodenum and a long, coiled ileum (see Fig. 7.22d). In some birds, the large intestine is divided into a colon and a rectum. Most birds have paired caeca at the juncture of the small and large intestines that apparently have a major digestive function. These caeca are large in ostriches, gallinaceous birds, many ducks, and shorebirds and, in species like the sage grouse (*Centrocercus urophasianus*), may be responsible for one-third to one-half of the absorption of glucose and certain amino acids (Obst, 1991). Caeca are vestigial and probably nonfunctional in herons, gulls, and passerines. They are absent in woodpeckers, hummingbirds, and other species. The absence or presence of caeca and their degree of development are taxonomically useful. The rectum is usually a short, straight tube, but in some species, it may be long and coiled. The rectum and cloaca empty via the vent.

Nervous System

The cerebral hemispheres of the crocodilian brain are enlarged and partially cover the diencephalon (Fig. 8.25a, b). Although a pineal organ is present in turtles, lizards, and snakes, it is absent in crocodilians

(Wurtman et al., 1968). Both optic lobes and auditory lobes are present. The cerebellum is prominent and well developed.

Alligators locate their prey in the swamps by using nerve-packed bumps (dome pressure receptors) on their jaws so sensitive that they can detect ripples from a single drop of water (Soares, 2002). Hundreds of such bumps, known as integumentary sense organs (ISOs), cover the face like a beard (Fig. 8.26). The nerve endings in each bump feed through the bone and lead to the trigeminal nerve, the largest cranial nerve in the alligator’s skull.

Figure 8.26. Hundreds of nerve-packed bumps on the face of an American alligator are used to help locate prey.

In birds, the olfactory portion of the brain has become greatly reduced in size, so that most birds, with the exception of some carrion eaters and some seabirds, have a poor sense of smell (see Fig. 8.25 c, d). Vomeronasal organs are absent. Cerebral hemispheres are better developed than in most reptiles and are much like those of crocodilians.

Optic lobes are greatly enlarged and well developed, and a pineal gland is present. The cerebellum is large and may overlie part of the medulla and the midbrain. It is highly developed in flying birds but is relatively small in some flightless species.

Adult canaries and zebra finches generate a fresh supply of brain cells to replace those lost with age in forebrain regions that control song learning and song production (Alvarez-Buylla et al., 1990). Newly formed cells are known as projection neurons; these link two related structures in the bird’s cerebral song-control center. Thus, adult avian brains possess considerable potential for self-repair as neurons age and gradually deteriorate.

During a short sensitive period just after hatching, young birds of many precocial species form an attachment, called **imprinting**, to the first moving object they see—normally their mother. As early as 1935, Konrad Lorenz found that young goslings separated from their mother shortly after hatching imprinted on other moving objects, including humans (Fig. 8.27a). Early social experience plays a major role in survival and subsequent sexual preferences. Lorenz emphasized that, in some birds, the preference of an individual to mate with a member of its own species is subject to its imprinting shortly after hatching. Altricial birds imprint much later.

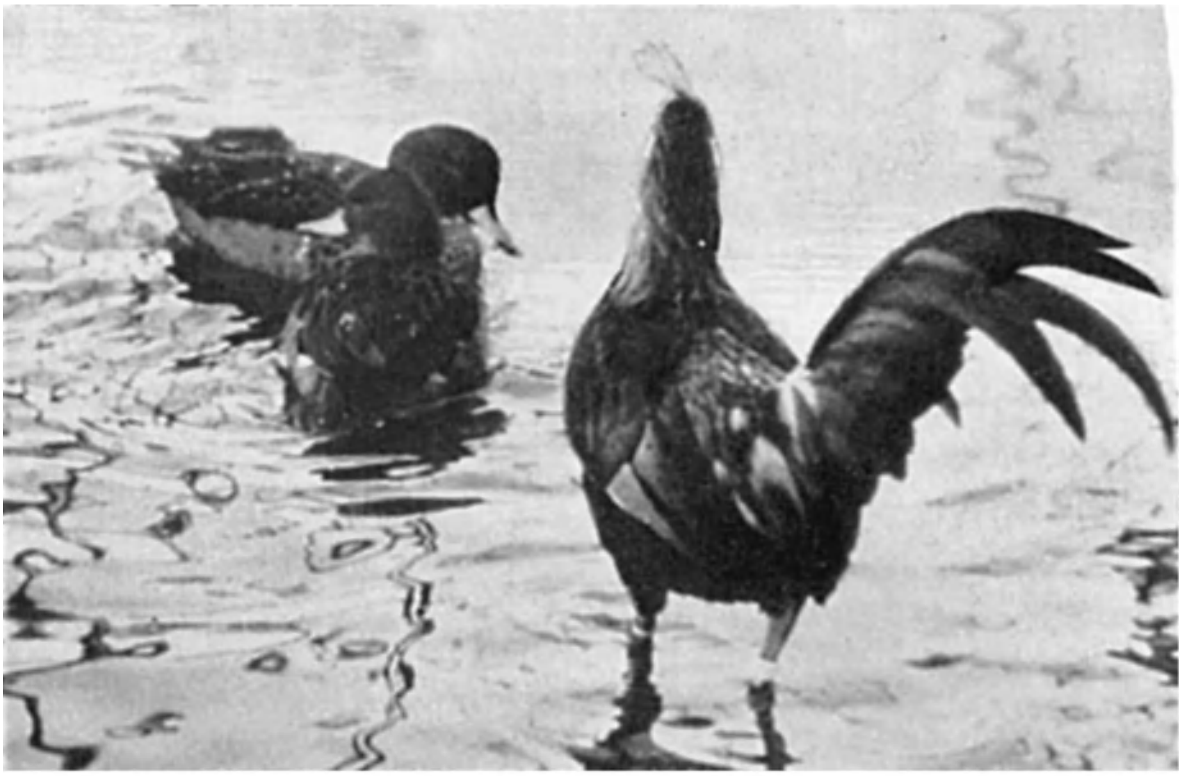
When young birds of a variety of species are foster-reared through the time of fledging, they will subsequently direct their sexual preferences toward the foster species (see Fig. 8.27b). Even large amounts of postfledging exposure to their own species may not reverse their preference for their foster species. Sexual imprinting has critical implications for captive breeding programs, including those involving the hand-rearing of young by human caretakers, and those involving foster-rearing of chicks by parents of closely related species. For example, extreme care is taken so that young California condors (*Gymnogyps californianus*) being raised in captivity do not imprint on humans. They are provided food by means of a mitt in the shape of the head of an adult California condor. Caretakers of young whooping cranes (*Grus americana*) drape themselves in loose-fitting sheetlike material to prevent young birds from imprinting on them.

Cranial nerves have been discussed in Chapter 4. Some researchers believe that birds possess only 11 cranial nerves and that the “accessory nerve” is only a caudal extension of the vagus (X) nerve.

In some birds, the spinal cord is surrounded by two meninges: a dura mater and a leptomeninx. In a few birds, the leptomeninx differentiates into a weblike **arachnoid layer** and an inner **pia mater**. Because the embryonic vertebral column elongates more rapidly than the spinal cord, the cord is somewhat shorter than the backbone. All birds have enlargements of the spinal cord, with the cervical enlargement being most pronounced in carinate birds due to the great development of muscles and nerves needed to operate the wings.

Many diurnal birds migrate at night, but do not appear to suffer unduly from sleep loss. Migrating Swainson’s thrushes (*Catharus ustulatus*) spend just 5 percent of their daylight hours—when they rest from flying—with their eyes closed (Fuchs, 2006). Brain waves revealed that the birds’ repeated eye closures, which usually lasted 12 seconds, did coincide with true sleep. Thrushes, like many other birds, sometimes sleep with only one eye shut. Brain wave recordings confirmed that when one eye is closed, only the opposite brain hemisphere is dozing. This so-called unihemispheric sleep helps birds react quickly to signs of trouble. Similar results have been found in white-crowned sparrows.

(a)



(b)

Figure 8.27. Imprinting in young birds. During a critical period in a young bird's life, an object becomes fixed (imprinted) in the bird's brain for life. The critical period for imprinting is most likely to occur 13 to 16 hours after birth. (*a*) Imprinted goslings following Konrad Lorenz on land. (*b*) An imprinted rooster wading out to meet a mallard duck to which it was exposed during its critical imprinting period. As the rooster matured and its sexual behavior developed, it sought out ducks and not birds of its own kind.

Sense Organs

EYES

Eyesight is well developed in crocodilians with social signals often involving combinations of visual, olfactory, and acoustic cues.

Birds have the best vision and are the most visually dependent of all vertebrates. Many adaptive responses to their environment and their survival depend on precise visual discrimination. Such behaviors as foraging (including the striking of prey with talons), avoiding branches when flying through thickets, landing on branches, defense of a territory and the nest, the selection of mates, orientation, homing, flying in formation in flocks, and navigation depend on a well-developed and highly sensitive visual system.

The eyes of most birds are asymmetrical rather than being spherical as is the mammalian eye (see Fig. 1.20). The flattened back of a bird's eye forms a much more even "screen" on which the entire image is in focus, not blurring toward the periphery. The exact shape of the eye varies with the species and is characterized by a change in shape of the cornea. This resultant loss of strength in the cornea is compensated for by a ring of bony plates, the sclerotic ossicles (see Fig. 8.11).

The Germination of Ingested Seeds

Seed germination may be affected by passage through a bird's digestive system. Studies conducted on white-eyed bulbuls (*Pycnonotus xanthopygos*) and Eurasian blackbirds (*Turdus merula*) revealed that, in most cases, seed ingestion had no consistent influence on germination, although certain seeds ingested by blackbirds showed substantially higher germination percentages than those ingested by bulbuls. Blackbirds retain seeds longer, which may cause greater seed coat abrasion and better germination.

On the Canary Islands, the fruit-eating lizard *Gallotia atlantica* is preyed on by the great gray shrike (*Lanius excubitor*). Seeds of the only fleshy-fruited plant on the island (*Lycium intricatum*) (Solanaceae) in the lizard's digestive tract are ingested by the shrike when the lizard is consumed. The seeds in the shrike pellets had a higher germination rate (64 percent) than those from lizard droppings (50 percent) or directly from the plant (54 percent), showing that their experience in passing through two vectors had increased their potential for immediate germination. Where seed transfer involves increased mobility and range, predation can also play a biogeographically significant role in dispersal.

Barnea et al., 1991; Nogales et al., 1998

The eyes of a bird are so large that they may equal or exceed the weight of the brain. Ostrich eyes are among the largest of all land vertebrates, with an axial length of 50 mm as compared with 24 mm for the human eye. They are the most widely separated eyes of all birds; therefore, ostriches have a surprisingly small binocular field (Martin, 1993; Martin and Katzir, 1995). The binocular retinal visual field spans only 20° as compared with 140° in humans.

The eyes of most birds have very limited mobility. The extrinsic eyeball muscles that rotate the eyeball in its socket are reduced in size and are poorly developed. The lack of eyeball movement in birds is compensated for by an increase in neck mobility, so that a bird must move the entire head to change the direction of its gaze. While foraging for food, birds use visual control of their bill position to make highly accurate pecks. The eyes of owls are immovably fixed in their orbits; however, some owls are able to rotate their heads through an arc of almost 270°.

The position of the eyes in the head differs among species. In some, like owls and birds of prey, the eyes are positioned toward the front of the head. In others, including many ground-feeding birds like doves, the eyes are positioned on the side of the head. These two different designs serve different functions. Birds that hunt fast-moving prey must track their prey during the chase. To be successful, they need accurate perceptions of speed and distance. These are achieved through binocular (or stereoscopic) vision—that is, both eyes are locked onto the object simultaneously. Owls have a binocular field of 60 to 70° and hawks up to 50° or more, whereas most granivorous birds have binocular fields of considerably less than 25° (Van Tyne and Berger, 1961; Zeigler and Bischof, 1993).

Birds with laterally positioned eyes have a very large field of view—more than 300° in pigeons—but gain this advantage at the cost of having a much-reduced field of binocular vision (Hockey, 1997). A wide field of view is, however, of great value in detecting approaching danger.

In birds, unlike primitive vertebrates, the lens of the eye is elastic and resilient, and its shape is altered by ciliary muscles located at the base of suspensory ligaments. Birds can change their focal distance very rapidly. Accommodation occurs via adjustment of the lens and via changes in the curvature of the cornea. In addition, in order to catch their fish prey, species like kingfishers, gannets, herons, and ospreys must compensate for the refraction of light at the air-water interface and visual distortion caused by ripples (Fig. 8.28) (Katzir, 1993, 1994). As the bird moves from air to water, refraction increases by some 20 diopters (Hockey, 1997). Humans wear glasses to correct for a deficiency of 1 diopter; glasses needed to correct for 20 diopters would probably require a neck brace. Rapid accommodation can be accomplished because bird lenses are much softer than those of mammals, and their shape can be changed more easily by the ciliary body and zonular fibers attaching to them. In addition, birds can also change the shape of their cornea by drawing the edges backward, thus increasing the curvature in the middle. Sivak (1986) noted that the avian eye generally has the most effective accommodative mechanism among terrestrial vertebrates. Lacrimal glands are present but are usually poorly developed.

Figure 8.28. Pied kingfisher returning from a successful dive with a captured fish (from a 16 mm film taken at 64 frames per second).

Many birds, including hummingbirds, pigeons, zebra finches, starlings, and kestrels, can perceive ultraviolet and polarized light (Delius and Emmerton, 1979; Goldsmith, 1980; Hockey, 1997; Hunt et al., 1997; Goldsmith, 2006). The pattern of light polarization in the sky changes during the day as the sun's position moves. Especially on overcast days, the ability to detect polarized light may aid migrating birds that use the sun as a compass. Those birds that have had their visual pigments characterized have been found to have four spectrally distinct classes of cones in their retinas and can distinguish colors ranging from ultraviolet (approximately 300 nm) to red (approximately 750 nm) (Bowmaker, 1986; Hunt et al., 1998). For comparison, humans have three distinctive cone types and can distinguish wavelengths between approximately 400 nm and 700 nm. Birds that appear to be monochromatic in the human visible spectrum may be dichromatic in the ultraviolet. This has significant implications for both intra- and interspecific analyses of sexually selected traits (Bennett and Cuthill, 1994; Bennett et al., 1996, 1997). For example, male blue tit (*Parus caeruleus*) crests tend to be brighter than those of females, particularly in the ultraviolet (Andersson et al., 1997; Hunt et al., 1998). All females tested chose the male with the brightest crest, an indication that ultraviolet plumage reflections are important in intersexual signaling. Electrophysiological studies of bird species from 10 different families have revealed that these birds have cones that are maximally sensitive at 370 nm, well within the ultraviolet region (Chen et al., 1984).

Using Ultraviolet to Find Prey

Unlike humans, kestrels can see in the ultraviolet light range. They use this ability to detect voles, their primary prey. Voles communicate with one another by laying highways through grass and vegetation, which they mark with urine and feces. Vole waste products are strong absorbers of ultraviolet light, much stronger than the background absorption of vegetation. To a human's eye, the difference between a vole highway and any other patch of grass is not discernible; however, a kestrel sees every field as streaked with the marks of vole activity. Both laboratory and field experiments have shown that kestrels take a far greater interest in an environment daubed with ultraviolet-absorbing vole excrement than one without. This ability to see and use vole scent marks to assess vole numbers enables kestrels to "screen" large areas in a relatively short time in order to rapidly detect areas of vole abundance.

Viitala et al., 1995

The mammalian retina is richly supplied with blood vessels, but the space occupied by these vessels limits the number of rods and cones that can be accommodated. There is no blood supply to the avian retina; rather, nutrition is provided via a small, blood-rich structure known as the pecten. The pecten is anchored to a small area of the retina called the optic disk, the region where the photosensitive cells come together and leave the eye via the optic nerve en route to the brain. The optic disk contains no rods or cones, so that bird vision is not impaired. The central fovea acts as a small magnifying glass and projects a slightly enlarged image onto the retina. Some birds that pursue prey at high speed, like hawks, swallows, and kingfishers, have two foveae on their retinas: a lateral fovea for vision to the side of the head and a temporal fovea that gives these birds better forward binocular vision (Proctor and Lynch, 1993).

The cones of birds contain oil droplets between their inner and outer segments (Robinson, 1994). Five types of avian cone droplets—transparent, colorless or clear, pale, yellow, and red—have been identified (Goldsmith et al., 1984; Stavenga and Wilts, 2014). The colored droplets, which are absent from the rods, contain high concentrations of carotenoids dissolved in lipids. The oil may be brightly colored (ranging from deep red through orange to yellow) to transparent. The types of oil droplets vary considerably; some birds (like pigeons) have up to 50 percent red and orange droplets, whereas other species have only about 10 percent. This may be related to their habits and activity patterns. Nocturnal species have only a few colored droplets, whereas birds active at twilight, like swallows and swifts, have low percentages of red and yellow droplets. Penguins, which hunt underwater, also have but a few colored droplets (Bowmaker and Martin, 1985), whereas gulls and terns have high percentages of red droplets.

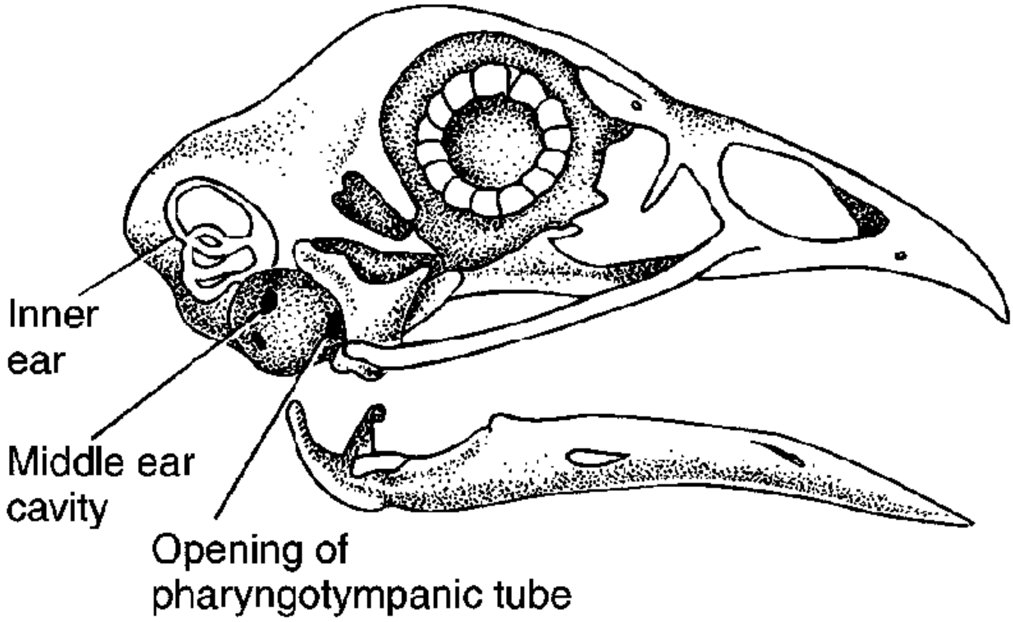
The oil droplets do not produce a color image per se, but they filter the light, in the same way as photographic filters do, before it is absorbed and detected by the photosensitive visual pigments. Thus, yellow droplets would remove much of the blue from the background by enhancing contrast between an object and a blue sky. Red droplets would remove much of the green, which would help birds searching for insects in a forest. Color vision can guide behavior in feeding and in a variety of social interactions like sexual recognition, courtship, and mating. Oil droplets may also act as lenses focusing light onto the outer segment of the photoreceptors, thus enhancing the amount of light striking the visual pigments (Young and Martin, 1984).

Gondo and Ando (1995) examined the retinas of 30 avian species with different ecological habits and found that diurnal birds had red, yellow, orange, and pale green oil droplets, whereas nocturnal birds had only pale green oil droplets. Their findings suggested that each colored oil droplet has specific advantage for visual perception, and that each bird has the retina that best matches its natural environment and feeding behavior in each habitat.

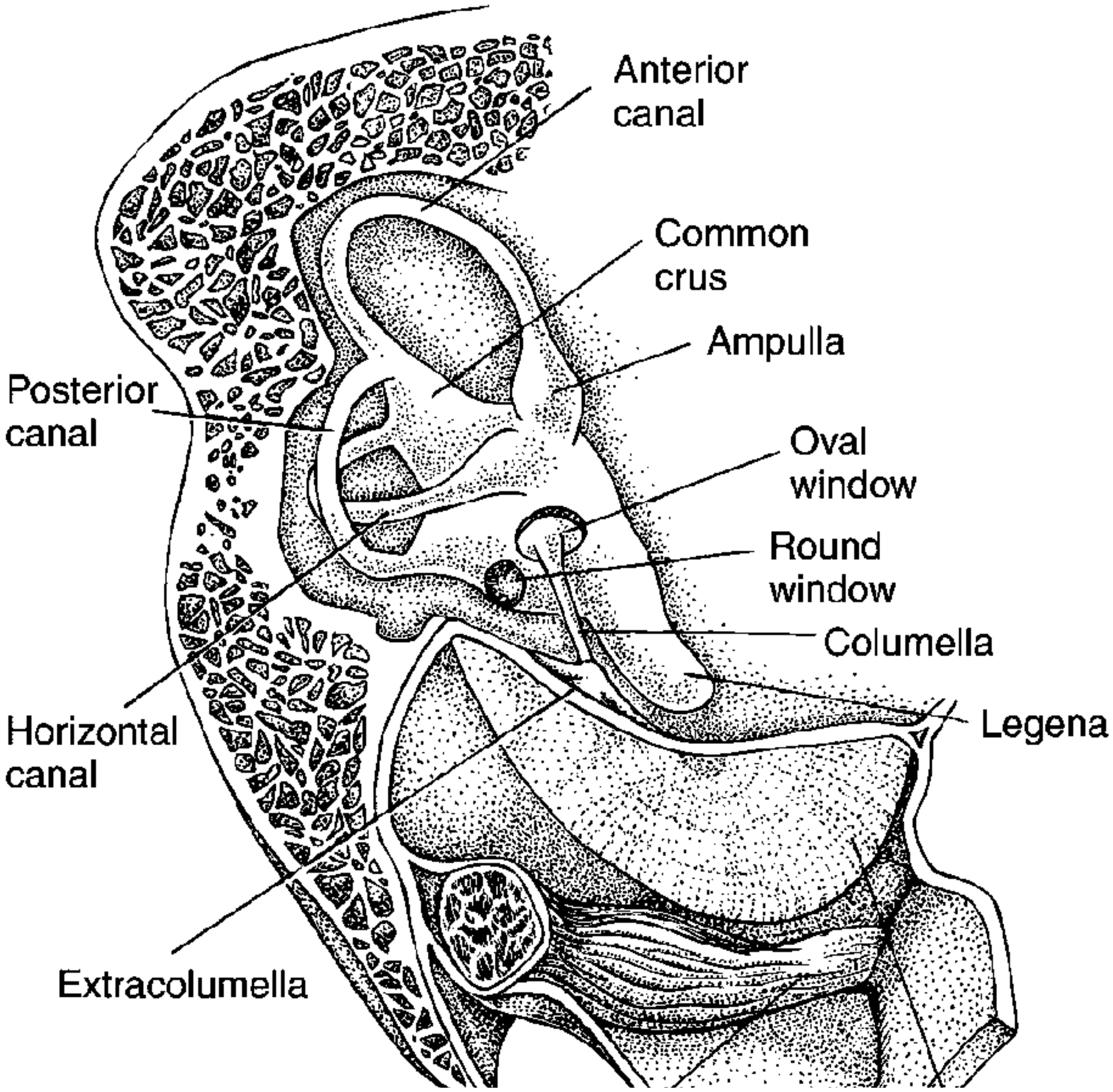
EARS

Hearing acuity is good in crocodilians, and vocalizations are used in a variety of social contexts, including territorial bellowing during the breeding season, aggressive warnings to intruders, and signals given by neonates in the nest to elicit nest-opening behavior by attending adults. A tympanic membrane is present in crocodilians, as it is in all reptiles. A special muscle allows crocodilians to close the ear cavity when submerging in water. The middle ear is well developed, with two Eustachian tubes joining just before connecting to the pharynx and opening into it by a single median orifice. The cochlear duct, which is straight in turtles, lizards, and snakes, forms a simple spiral in crocodilians.

Hearing is keen in birds and is next to sight in importance (Fig. 8.29). Pinnae (external ear flaps) are absent. The "ears" of owls are just tufts of feathers. The eardrum (tympanum), which is located at the inner end of the external auditory meatus, transmits vibrations to the columella, which in turn transmits vibrations across the middle ear cavity to the oval window in the lateral wall of the inner ear. An auditory (Eustachian) tube connects the middle ear cavity with the pharynx. The membranous labyrinth of the inner ear consists of a cochlea and a spiral organ, which convert the vibrations of the tympanum and columella into nerve impulses that are sent to the brain via the cochlear nerve, a branch of the auditory cranial nerve (VIII). The inner ear also houses the organs of balance and equilibrium (utriculus, sacculus, and semicircular canals).


Inner ear
Middle ear cavity
Opening of pharyngotympanic tube

(a)


Anterior canal
Common crus
Ampulla
Posterior canal
Oval window
Round window
Columella
Legena
Horizontal canal
Extracolumella

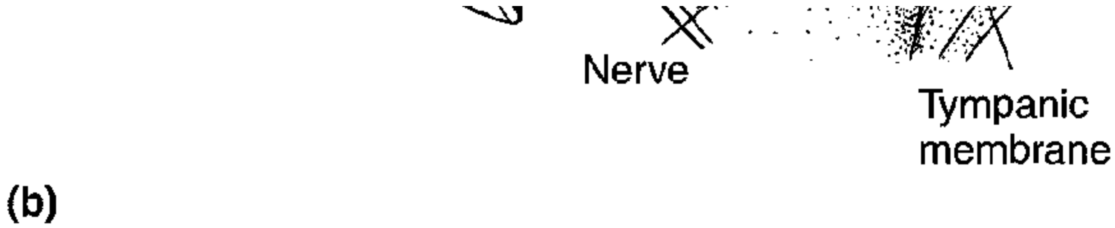


Figure 8.29. Hearing in birds. (*a*) Lateral view of a bird skull, showing the location of auditory and equilibrium organs. (*b*) The organs of equilibrium (vestibular apparatus) in a chicken.

Hearing is extremely well developed in owls, which use sounds coming from their prey to determine its location. Barn owls, for example, can locate prey in total darkness, using only their sense of hearing, with an error of less than 1° in both the vertical and the horizontal planes. For such accuracy, owls depend on frequencies of about 5,000 Hz, which provide better directional capabilities than lower frequencies (Payne, 1971). Many owls possess a facial ruff of stiffened feathers that acts as a parabolic sound reflector, focusing sounds on the external auditory meatus and amplifying them by 10 dB (Konishi, 1973) (Fig. 8.30). In addition, the right and left external ear openings, as well as the external ear canals, are asymmetrical, an adaptation that allows these birds to quickly locate sounds by tilting their head. This difference in size and shape allows the two ears to receive sound stimuli from many directions.

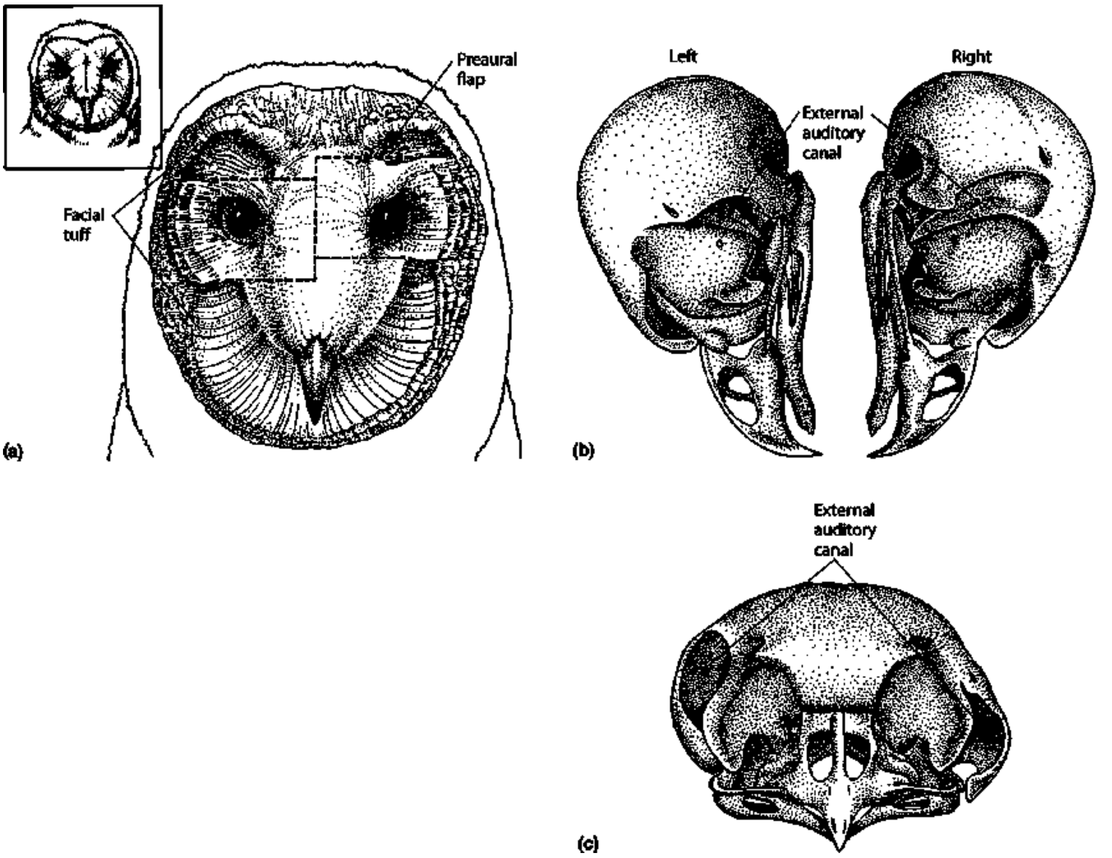


Figure 8.30. Auditory acuity in owls. (*a*) Facial disk feathers of a barn owl in the normal position (*inset*) have been removed to reveal the auditory feathers arranged in tightly packed parabolic rims encircling the face and external orifice of the ear. This facial ruff of feathers collects and directs sounds to the external auditory canal of the ear. Note the asymmetrical positioning of the preaural flaps of feathers (*dashed lines*). (*b*) Left and right sides of the skull of a Tengmalm's owl (*Aegolius funereus*) showing slight differences in the size of the external auditory canal. (*c*) Anterior view of Tengmalm's owl showing the asymmetry of the otic areas.

Several birds use **echolocation**, including oilbirds (*Steatornis caripensis*) of South America and cave swiftlets (*Collocalia*) of Southeast Asia, both of which live and nest in deep caves. Oilbirds use a sonar system much like that of bats, except their sounds have a frequency of only about 7,000 Hz—well within the range of human hearing (Griffin, 1953, 1954).

Infrasound—sound frequencies below those that humans can hear—may be important in navigating and determining direction in birds. The **lagena**, a specialized portion of the cochlea, may be the area responsive to low frequencies.

Natural infrasound is generated by events such as earthquakes, pounding ocean waves, volcanoes, and severe storms. Homing pigeons can detect extremely low frequencies—as low as 0.05 Hz (Kreithen and Quine, 1979). Before supersonic flights were discontinued, the infrasound noise from Concorde jets could interfere with the ability of racing pigeons to find their way home (Hagstrum, 2000).

In April 2014, a research team was tracking a population of golden-winged warblers (*Vermivora chrysoptera*) in the mountains of eastern Tennessee (Streby et al., 2015). Golden-winged warblers winter in Central and South America before returning to the Great Lakes and Appalachian Mountains to breed. The research team found that the birds left their breeding grounds and flew south to the Gulf of Mexico one to two days ahead of the arrival of powerful supercell storms. Their report stated that when the birds made their exit, the storm was still 402 to 901 km (250–560 mi.) away, and local cues to inclement weather—changes in atmospheric pressure, temperature, and wind speed—were largely absent. Streby said: "The warblers in our study flew at least 1,500 km (932 mi.) total to avoid a severe weather system. They then came right back home after the storm passed." This was the first study to show this type of storm avoidance in birds during their breeding season after they had established their breeding territory. Infrasound seemed to be a logical explanation.

NOSE

The sense of smell is well developed in crocodilians with social signals often involving combinations of olfactory, visual, and acoustic cues. Smell is also used to locate food from a distance. The presence of a secondary palate in crocodilians permits the internal nares to be located at the rear of the oral cavity. Vomeronasal organs are absent.

Table 8.2. Comparison of the Number of Taste Buds in Various Animals

Animal	Number of Taste Buds
Chicken	24
Pigeon	37
Bullfinch	46
Starling	200
Duck	200

Animal	Number of Taste Buds
Parrot	350
Japanese quail	62
Snake	0
Kitten	473
Bat	800
Human	9,000
Pig	15,000
Goat	15,000
Rabbit	17,000
Calf	25,000
Catfish	100,000

Source: From Kare and Rogers, Jr., 1976. Copyright © Springer-Verlag, New York. Used with permission.

Olfactory mechanisms are less developed in birds than in other vertebrates; thus, most birds, with the exception of carrion eaters like vultures and some seabirds like petrels, are believed to have a poor sense of smell. Vomeronasal organs are absent.

Experimental studies in sub-Antarctic waters have shown that many procellariiform seabirds like white-chinned petrels and prions may use a naturally occurring scented compound, dimethyl sulfide (DMS), as an orientation cue (Nevitt et al., 1995). DMS is produced by phytoplankton in response to zooplankton grazing. Zooplankton are, in turn, eaten by seabirds. The petrels and prions responding to DMS often forage at night, when olfactory cues might be especially valuable, whereas albatrosses often forage by locating aggregations of seals, whales, and other visibly conspicuous seabirds. Black-browed albatrosses were not attracted to DMS.

TASTE

Taste buds are less abundant in birds than in most other groups of vertebrates (Table 8.2). Only a few taste buds are present; they occur primarily on the palate, pharynx, and epiglottis. The abundance and location of taste buds in crocodilians is not known.

Endocrine System

The endocrine system in vertebrates was discussed in Chapter 4. As noted, certain parental behavior patterns are brought about by the effects of prolactin. These behaviors include such activities as nest-building, incubation of eggs, and protection of the young. As discussed previously, prolactin promotes a secretion from the crop of pigeons, doves, emperor penguins, and flamingos that is fed to the young by regurgitation. This nutritive secretion is known as "pigeon's milk."

The size of the thyroid in birds is influenced by age, sex, climatic conditions, diet, activity, and species (Ringer, 1976). Female chickens (*Gallus domesticus*) have a greater thyroid weight than males. Early investigators reported that the thyroid weight of chickens and pigeons (*Columba livia*) was greater in the winter than in the summer. However, two studies on ducks in the Mediterranean region (Rosenberg et al., 1967; Astier et al., 1970) have shown greater thyroid weight and activity in the summer (June) than in the cold months. In southern France, for example, Astier et al. (1970) reported a definite annual rhythm of thyroid function in male Pekin ducks, with maximum iodine uptake occurring in June. June is the time of maximum photoperiod, the seasonal decrease of testicular activity, and the onset of the annual molt. Lowest thyroid function was in January and February.

Corticosterone is the primary glucocorticoid and hormone of stress in birds (Wingfield et al., 1983; Wingfield, 1984, 1985a, 1985b; Astheimer et al., 1995). It is released rapidly into the bloodstream in response to a variety of stressors. A rise in corticosterone in the bloodstream promotes glucogenesis and leads to an increase in glucose levels. This additional energy store helps an individual meet increased energy demands that occur during periods of extreme stress like storms, attacks by predators, or food shortage.

In studies of white-crowned sparrows (*Zonotrichia leucophrys gambelii*), Wingfield et al. (1996) found that long days resulted in the well-known increase in body mass and fat store, indicative of preparations for migration. In females, treatment with low temperatures resulted in a reduction in the premigratory increase in fat and body mass when transferred to long days. This was accompanied by an increase in plasma levels of corticosterone during the early stages of photostimulation. Temperature did not affect photoinduced testicular development or length of the cloacal protuberance (an androgen-dependent copulatory organ) in males or ovarian follicle development in females. Temperature regimes had no effect on fattening or body mass in males despite an early increase in plasma corticosterone at low temperature. In addition, temperature treatments—low, 5°C (41°F), moderate, 20°C (68°F), and high, 30°C (86°F)—had no effect on plasma levels of thyroid hormones in males, but low temperatures did inhibit thyroid secretion in females, thus impairing preparations for migration in females but not males. The sexual dimorphism in this response may be related to sexual selection in which males arrive on the breeding grounds ahead of females regardless of local weather conditions.

Increased levels of testosterone initiate the process of spermatogenesis in males and, together with the lack of estrogen, causes the development of secondary sex characteristics like brightly colored breeding plumage. Estrogens and progesterone regulate female reproductive activity.

The emerging evolutionary perspective of androgen action has been greatly influenced by studies of birds (Wingfield et al., 1990). The role of testosterone in male-male aggression has revealed that, during the mating season, male-male aggression related to territorial defense can result in rapid and profound elevations in plasma levels of testosterone. These surges far surpass any daily variation that might normally occur in plasma testosterone levels, and therefore the response is easily distinguished. This dramatic hormonal response to social interactions has been termed the “challenge response” by Wingfield and colleagues. Wingfield observed that the challenge response is most likely to be observed in monogamous birds in which the male contributes heavily toward parental care. In contrast, species that are polygynous and lack male parental care usually do not exhibit hormonal changes in response to male-male aggression. More broadly, the challenge response also comprises other social interactions, including male-female mating behaviors.

Regulation of calcium levels by the parathyroid glands is important for the proper formation of the calcareous shell enclosing bird embryos. If insufficient calcium is present, parathormone will cause it to be released from storage in the bones. Interference with this system by chlorinated hydrocarbon chemicals, like dichlorodiphenyltrichloroethane (DDT), caused thinning of egg shells in some species by reducing calcium availability. In some birds, the **ultimobranchial bodies** produce calcitonin, a hormone that lowers blood calcium levels. The pineal gland's role in avian thermoregulation has been discussed by Heldmaier (1991). Barnwell (1960) reported circadian rhythms in oxygen consumption in developing chicken embryos.

Urogenital System

A pronephric developmental stage is present early in embryonic growth of both crocodilians and birds but is supplanted by the mesonephros, which serves as the functional embryonic kidney. The mesonephros reaches its peak of development about halfway through embryonic life. When the metanephros begins to function, the mesonephros gradually ceases functioning. The metanephric kidney consists of many convoluted tubules and collecting tubules, with each kidney being drained by a pair of ureters. Mesonephric ducts remain as sperm ducts in male birds, but they involute in females and remain only as short, blind **Gartner's ducts** embedded in the mesentery of the oviducts.

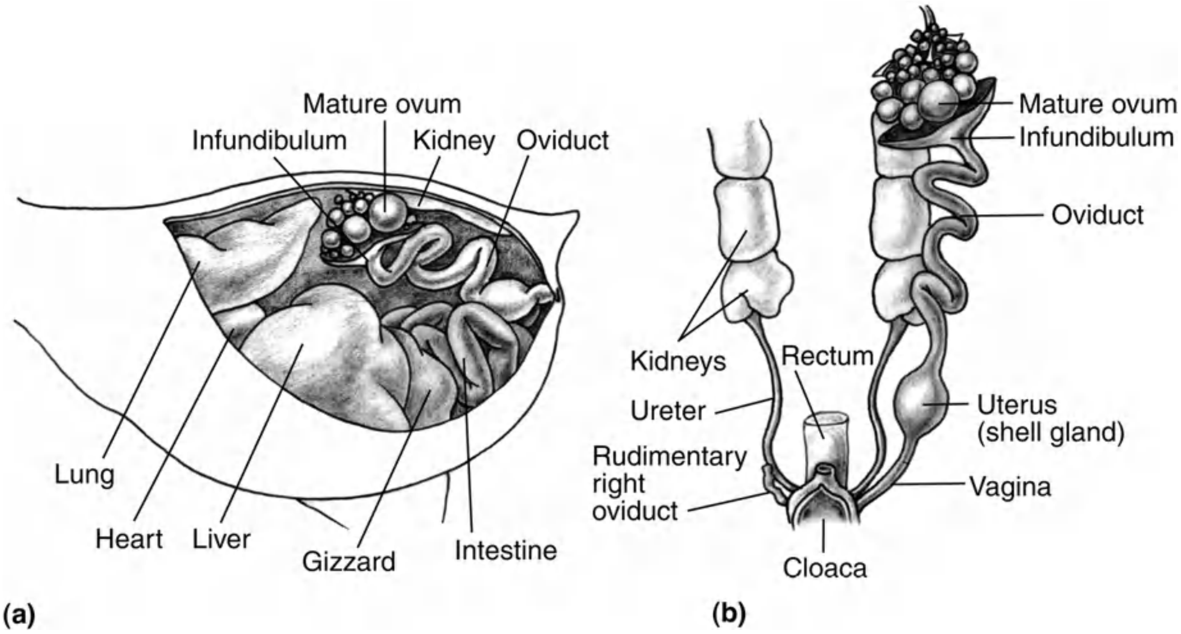


Figure 8.31. (*a*) Reproductive tract of the chicken in relation to other organs in the body cavity. The single functional ovary and oviduct are on the hen's left side; an undeveloped ovary and an oviduct are sometimes found on the right side, having degenerated in the embryo. (*b*) Both the ovary and oviduct are involved in the formation of the egg. The shell is formed in the uterus, which is also called the shell gland.

The avian kidney, like that of reptiles, consists of lobes; each lobe is composed of clusters of many tubules. The kidneys lie in a retroperitoneal position flattened against the sacrum and ilium. In most birds, the ureters empty into the **urodeum**, the middle of the three compartments forming the cloaca. Only ostriches possess a urinary bladder.

Birds produce a semisolid and hypertonic urine, with uric acid as the main nitrogenous excretory product. Urine excreted by the kidneys is concentrated during its passage through the renal tubules, and additional water reabsorption takes place in the **coprodeum**, where the urine is mixed with the feces.

The urogenital anatomy of a female bird is basically similar to that found in most reptiles (Fig. 8.31). Histologically and ultrastructurally, it is comparable to that of a crocodilian (Palmer and Guillette, 1992). Both birds and crocodilians have separate regions, which may be homologous, for formation of the egg shell membrane and the calcareous layer.

The ovaries of birds consist of many fluid-filled cavities. In most, only the left ovary is functional; if present, the right ovary is rudimentary. Most birds also possess only a single (left) oviduct; the other remains rudimentary. Although the right ovary and oviduct are formed in the embryonic stages, they usually do not persist in adult life. The presence of only one ovary and oviduct is thought to be an evolutionary adaptation to lighten the body for flight.

Fertilization occurs in the upper region of the oviduct. Glands lining the oviduct secrete albumen around the ovum, and the caudal portion of the oviduct becomes modified as a thick-walled shell gland. A short, muscular terminal segment (vagina) empties into the urodeum portion of the cloaca. The vagina secretes mucus that seals the pores of the shell and then expels the egg.

The male reproductive system is also similar to that of reptiles. Two testes are present, in contrast to the single ovary and oviduct in females. Opisthonephric ducts empty into the urodeum. Unpaired copulatory organs (penis in males; clitoris in females) develop from the ventral wall of the proctodeum and are present in swans, ducks, ostriches, and a few other birds.

REPRODUCTION

Female alligators and crocodiles construct nests of vegetation that may be 1 to 2 m (3–6 ft.) in diameter and 45 to 90 cm (18–36 in.) high (Fig. 8.32). Oval, hard-shelled eggs are laid in the center and covered by vegetation. Heat generated by the decaying vegetation provides the warmth needed for incubation.

Increasing daylength in late winter appears to be the primary factor initiating gonadal development in temperate-zone breeding birds, whose gonads undergo seasonal regression in late summer and fall. Associated hormonal changes cause development of the nuptial plumage, courtship behavior, breeding, and the migration of many species that spend the winter months in warm climates and then fly to non-tropical areas to breed and raise young.

For the first time, biologists have documented a second breeding season during the annual cycle of five songbird species—yellow-billed cuckoos, orchard orioles, hooded orioles, yellow-breasted chats, and Cassin’s vireos—which spend summers in temperate North America and winters in tropical Central and South America. These species squeeze in a second breeding season during a stopover in western Mexico on their southward migration (Rohwer et al., 2009). Migratory double-breeding has been observed in two Old World bird species on their northward migration, but this is the first documented observation of “migratory double breeders” in the New World, and the first anywhere for the southward migration.

Figure 8.32. Female saltwater crocodile (*Crocodylus acutus*) guarding her nest made of vegetation. The eggs are deposited in the center of the nest and are incubated by heat generated by the decaying vegetation.

Climatic conditions greatly affect breeding efforts and clutch size. Breeding success in some species, especially aquatic feeders, is related to rainfall. Breeding success is high in years with abundant rainfall, but falls during periods of drought (Maddock and Baxter, 1991). Many birds produce only a single brood annually, although some passerines like bluebirds (*Sialia sialis*), robins (*Turdus migratorius*), starlings (*Sturnus vulgaris*), and sparrows may produce two and even three broods during the summer months under optimal conditions. Clutch size usually numbers between two and five chicks, although albatrosses, shearwaters, petrels, tropic birds, most penguins, some auks, some nightjars, and others lay only a single egg each year. Loons, gannets, boobies, hummingbirds, whooping cranes, some penguins, most pigeons, and many tropical passerine birds lay just two eggs every year (Van Tyne and Berger, 1961). Some birds, however, breed much less frequently. For example, the California condor (*Gymnogyps californianus*) lays only a single egg every other year.

Breeding in most species begins the year following birth, but some take longer to mature. Bald eagles (*Haliaeetus leucocephalus*), for example, require 3 years to mature, and puffins require 4 to 5 years. The California condor does not mature for approximately 9 years, and albatrosses take as long as 10 years to reach adulthood.

Sexual dimorphism among birds involves primarily visual and auditory differences, since birds are primarily diurnal and live at fairly high densities. Some species, like the American avocet (*Recurvirostra americana*), have permanent morphological differences (Fig. 8.33a): the bills of females curve upward more than those of males. Males of many species, like wood ducks (*Aix sponsa*) (Fig. 8.33b), develop brightly colored feathers or patches of skin as part of their breeding plumage. Other examples of sexual dimorphism include the red shoulder patches of male red-winged blackbirds (*Agelaius phoeniceus*); the black hood of the male hooded warbler (*Wilsonia citrina*); the orange tail patches of male American redstarts (*Setophaga ruticilla*); and the distinctive black-below, white-above color pattern of male bobolinks (*Dolichonyx oryzivorus*). Female swallows (*Hirundo rustica*) use two criteria in choosing a mate: the size and shape of a potential partner's tail. Female swallows prefer mates with long, perfectly forked tails. Males with elongated symmetrical tails mate earlier and enjoy larger annual reproductive success (Moller, 1992). Female house finches (*Carpodacus mexicanus*) prefer the most colorful males (Hill, 1990).

The ability of birds to see in ultraviolet light may be an important factor in courtship. For example, female starlings (*Sturnus vulgaris*) ranked males in a different and nonrandom order in the absence of ultraviolet light, but plumage reflectance in the human visible spectrum did not predict choice (Bennett et al., 1997). Thus, nocturnal variation in ultraviolet reflectance is important in avian mate assessment; the prevailing light environment may have profound effects on observed mating preferences.

(a)

(b)

Figure 8.33. Sexual dimorphism in birds: (*a*) American avocets (*Recurvirostra americana*). Bill curvature differs between sexes: bills of females (*bottom*) turn upward more than those of males (*top*). (*b*) Wood ducks (*Aix sponsa*). Highly colored iridescent male is on the left.

The species-specific songs and calls evolved by many birds identify the male's territory and attract members of the opposite sex for breeding. The same is true of actions like the "drumming" performed by male grouse. Female great reed warblers (*Acrocephalus arundinaceus*) base their mate choice on the quality of the male's territory and on the range of his song repertoire (Hasselquist et al., 1996). In addition, some male birds like rollers and falcons put on spectacular aerial displays to impress prospective mates. Others, like weaver-birds (*Ploceidae*), build a basket-like nest to attract a female.

Postural displays, as well as the display of colored, highly specialized breeding plumage, are important aspects of courtship in many species (Fig. 8.34). Evidence that vocal stimulation controls endocrine state and follicular growth in ring doves (*Streptopelia risoria*) was presented by Cheng (1992), who showed that female ring doves affect their own endocrine state by cooing. Females prevented from performing the nest-coo showed little or no growth of ovarian follicles. While male courtship stimulates females to begin nest-cooing, the female's own nest-coos stimulate her hypothalamus to respond. Vocalizations also accelerate ovulation in several species, including white-crowned sparrows (*Zonotrichia leucophrys gambelii*) (Cheng, 1992).

Figure 8.34. Courtship behavior of the albatross (*Diomedea immutabilis*). Unpaired birds perform “sky call,” one of a number of positions assumed in their frenetic dance that includes bill touching, wing flaring, and “moo” and “aww” sounds. Once a bond is established, pairs spend the next year at sea, returning then to copulate and raise a chick.

Breeding strategies among birds range from monogamy to polygamy with indiscriminate breeding (promiscuity) by both males and females occurring in some species. The mating of a male with more than one female is thought to enhance the male’s genetic fitness by increasing the number of his offspring and their genetic variability, whereas polygamous females are thought to be seeking the best-quality genes for their offspring. A male that mates with more than one female is **polygynous (polygyny)**. A female that mates with more than one male is referred to as **polyandrous (polyandry)**.

In many species of birds, males and females jointly build a nest, incubate the eggs, and feed the young. Following the successful fledging of their young, male and female often separate. Some, however, like swans and Canada geese (*Branta canadensis*), pair for life and will remain together after breeding. Males guard incubating females, assist in caring for the young, and migrate with their mates.

Formerly, researchers believed that approximately 94 percent of all bird species were monogamous (Stone, 1991). The loon (*Gavia immer*), some gulls, and the Florida scrub jay (*Aphelocoma coerulescens*) are among birds known to be monogamous (Quinn et al., 1999). However, extra-pair copulations (EPCs) have been found to be widespread in so-called monogamous birds and can result in extra-pair fertilizations (Mennill et al., 2002; and others). In some studies, DNA analyses of a variety of species have shown that "30 percent of baby birds in a nest are not the offspring of the caretaking male" (Stone, 1991). Almost all songbirds have been found to be quite promiscuous. For example, research shows that 50 percent of the eggs in the typical American robin's (*Turdus migratorius*) nest have a different father (Quinn et al., 1999). The evolutionary significance of EPCs is thought to be an attempt by females to increase genetic diversity for their offspring.

Studies of the indigo bunting (*Passerina cyanea*) revealed that more than 30 percent of all offspring were of extra-pair paternity (Westneat, 1987). One study showed that 55 percent of the young from 86 percent of the nests of reed buntings (*Emberiza schoeniclus*) were not the offspring of the territorial male (Dixon et al., 1994). Male reed buntings appeared to adjust their brood care in proportion to their likelihood of paternity and fed illegitimate broods less than broods they fathered. Estimated frequencies of polygynous mating among American redstarts (*Setophaga ruticilla*) in New Hampshire were 16, 5, and 8 percent in 1988, 1989, and 1990, respectively (Secunda and Sherry, 1991).

EPCs, therefore, are not unusual among North American passerines as a facultative or opportunistic reproductive strategy. Females may be as promiscuous as males, because they are the ones that often enter an adjoining male's territory for an extra-pair copulation. Males develop counterstrategies to prevent EPCs by females, including frequent copulations and guarding of females in order to ensure paternity.

In some species, like Smith's longspur (*Calcarius pictus*), a small Canadian subarctic bunting, females averaged 350 copulations per clutch and copulated with two or more males, while males typically mated with one to several females (Briskie, 1992). Multiple matings and the lack of territorial behavior in males are thought to be adaptations to sperm competition.

Figure 8.35. Male prairie chicken in a courtship display (lekking).

Most studies of fertilization have looked at the fertilization success of two males after a single copulation from each (Birkhead, 1988). In spotted sandpipers (*Actitis macularia*), however, the mating procedure usually involves repeated copulations by one male, followed by the laying of a clutch of eggs; then repeated copulations by a second male, followed by the laying of a second clutch. Oring et al. (1992) concluded that stored sperm from former mates was still the primary source of fertilizations for these second clutches. Because old males precede younger males to the breeding grounds, early pairing gives older males a reproductive advantage through additional fertilizations from sperm stored by females, thereby increasing their fitness.

Lekking

In approximately 200 species of birds, males assemble in a small area (a lek) during the breeding season for communal courtship display and mating (lekking). Females pass through this group of small territories and choose a male for copulation. The prairie chicken (*Tympanuchus cupido*) (see Fig. 8.35), sage grouse (*Centrocercus urophasianus*), and sharp-tailed grouse (*Tympanuchus phasianellus*) of the western United States are well-known lekking species. Three hypotheses have been proposed to explain why males aggregate: the hotspot model (clusters form near places females frequently visit), the hotshot model (individuals cluster around attractive males to increase their chances of being noticed), and the female-preference model (males cluster because females like to visit groups, where they can choose a mate quickly and safely).

Tests of each hypothesis have found support in some species, but not others. Gibson et al. (2003) proposed an additional theory: male grouse join leks in order to avoid predation.

Long-tailed manakins (*Pipridae*) are lek-mating Central American birds that engage in a unique behavior not typical of other lekking species. Manakins cooperate in multiyear male-male partnerships in which an alpha male is responsible for virtually all mating and the beta male assists in courtship displays. Alpha and beta males are not usually related. Beta males forgo reproduction for many years in order to maintain this unusual form of male-male cooperation. Benefits for beta males include rare copulations, future ascendancy to alpha status, and female lek fidelity.

The African topi, a majestic antelope that lives in East Africa, is one of the few mammals with a mating system based on a “lek.” In an antelope lek, both male and female topi gather in a specific area, and females receptive to mating will pick out a mate. Once the choice is made, the female will fight to exhaustion to protect her rights.

Gibson et al., 2002

A few species, like the spotted sandpiper (*Actitis macularia*), red phalarope (*Phalaropus fulicarius*), and Wilson’s phalarope (*Steganopus tricolor*), reverse sex roles: females are aggressive and play the more active role in courtship, while males provide most or all of the care for the young (Oring, 1995). Some species are polyandrous, a condition in which dominant females mate with multiple males, each of which tend a clutch of eggs. Males have higher prolactin levels (prolactin promotes incubation) than females and low testosterone levels. Female sandpipers are able to store sperm for up to 31 days before using it to fertilize eggs (Oring, 1995).

Some female birds, including the domestic chicken (*Gallus domesticus*), pheasant (*Phasianus colchicus*), pigeon (*Columba livia*), mallard (*Anas platyrhynchos*), and domestic goose (*Anser anser*), can store sperm for periods ranging up to 52 days (Birkhead, 1988). Sperm storage allows sperm of previous mates to compete with sperm from more recent copulations; however, at least in domestic birds, sperm from the most recent copulation has the greatest probability of fertilizing eggs (Birkhead, 1988). Sperm are stored in sperm storage tubules at the uterovaginal junction of the oviduct (Bakst, 1987). The number of sperm storage tubules ranges from 500 to 20,000, depending on the species (Birkhead and Moller, 1992). Sperm size among species of birds varies considerably, primarily due to variation in the length of the sperm’s tail (Briskie and Montgomerie, 1992).

Young Seychelles warblers (*Acrocephalus sechellensis*) often remain in their natal territories and help their parents raise later offspring. Helpers are mostly adult daughters and, on high-quality territories where food is plentiful, they increase their parents’ reproductive success. On low-quality territories, however, these helpers decrease their parents' reproductive success through competition for limited food. Biased hatchling sex ratios are caused by biased reproduction (Komdeur et al., 1997). Breeding pairs without helpers on low-quality territories produce 77 percent sons, whereas pairs without helpers on high-quality territories produce 13 percent sons. Breeding pairs that were transferred from low-quality to high-quality territories switched from the production of male to female eggs. Breeding pairs occupying high-quality territories switched from producing female eggs when less than two helpers were present, to producing male eggs when at least two helpers were present in the territory. These are the largest skews in hatchling sex ratios and adaptive modifications that have ever been recorded in a bird species (Gowaty, 1997).

GROWTH AND DEVELOPMENT

Prenatal Development

Crocodilians lay eggs in which the embryos and the four extraembryonic membranes are enclosed in a leathery shell; all birds lay eggs with hard, calcified shells. Egg size and shape vary greatly among different species of birds. The largest known egg, which measured 34 by 24 cm (13 by 9.5 in.) and had a capacity of 9 liters (2.4 gal.), was that of the extinct elephant bird (*Aepyornis maximus*) of Madagascar (Faaborg, 1988). The smallest known egg belongs to the Jamaican vervain hummingbird (*Mellisuga minima*); the egg measures only 1 by 0.65 cm (0.4 by 0.26 in.) and has a mass of 0.5 g (0.02 oz.), or about 1/50,000 of an elephant bird egg.

Finding Calcium for Eggshells

Female birds need calcium to produce thick, protective egg shells, but those whose diets are restricted to seeds and insects have trouble getting enough calcium from these sources. Therefore, during egg-laying, they seek out calcium supplements, foraging for bits of bone, seashells, and other items rich in the mineral.

The first known instance of a bird hoarding a substance for its mineral, rather than caloric, content was reported in the red-cockaded woodpecker (*Picoides borealis*). Several days before and during egg-laying, birds would land near a bone they spotted on the ground, consume flakes of it, and then carry larger fragments to a nearby tree and wedge them into the bark. They were observed retrieving the fragments on several occasions during the egg-laying period.

Repasky et al., 1991

Bird eggs can be classified into three basic shapes: oval, elliptical, and pyriform (Fig. 8.36). Oval eggs, which are round on both ends but widest in the middle, are produced by most birds. Grebes, hummingbirds, and some raptors, however, produce eggs in which the curvatures of each end are about the same (elliptical). Pyriform, or pear-shaped, eggs have one large end and one smaller end and are characteristic of most shore birds and many passerines. The pyriform eggs of murres (*Uria lomvia*) roll in tight circles on the rock ledges where the birds nest, thus making it less likely they will fall into the sea.

Although most birds deposit their eggs in nests constructed of plant materials, mud, or even salivary secretions (Fig. 8.37), some lay their eggs directly on the ground with little or no nesting material. Killdeer (*Charadrius vociferus*), for example, lay their well-camouflaged eggs among stones or gravel. Royal terns (*Sterna maxima*) deposit their single egg in a depression in the sand (Fig. 8.38). The fairy, or white, tern (*Gygis alba*) of the Pacific and southern Atlantic oceans lays a single egg on a rock or on a horizontal branch with no nesting material whatever. Auks (*Alcidae*) and sheathbills (*Chionis alba*) lay their eggs on rock ledges and in rock crevices. Some birds, like burrowing owls (*Speotyto cunicularia*), fairy penguins (*Eudyptula minor*) (Fig. 8.39), and sooty shearwaters (*Puffinus griseus*) (see Chapter 14 for a discussion of an interesting commensal relationship between shearwaters and tuataras), nest in underground burrows or in holes in banks (e.g., bank swallow, *Riparia riparia*; kingfisher, *Megaceryle alcyon*); some are cavity nesters (purple martins, *Progne subis*; bluebirds, *Sialia* spp.; and woodpeckers, *Picidae*); some nest in chimneys (chimney swift, *Chaetura pelagica*); and some have nests that float on the water (grebes, Podicipedidae). African social weavers (*Philetairus socius*) construct elaborate nests by weaving grass and plant fibers. Bahama parrots (*Amazona leucocephala bahamensis*) nest in limestone solution cavities beneath the ground, a habit unique among New World psittacines (Gnam, 1991).

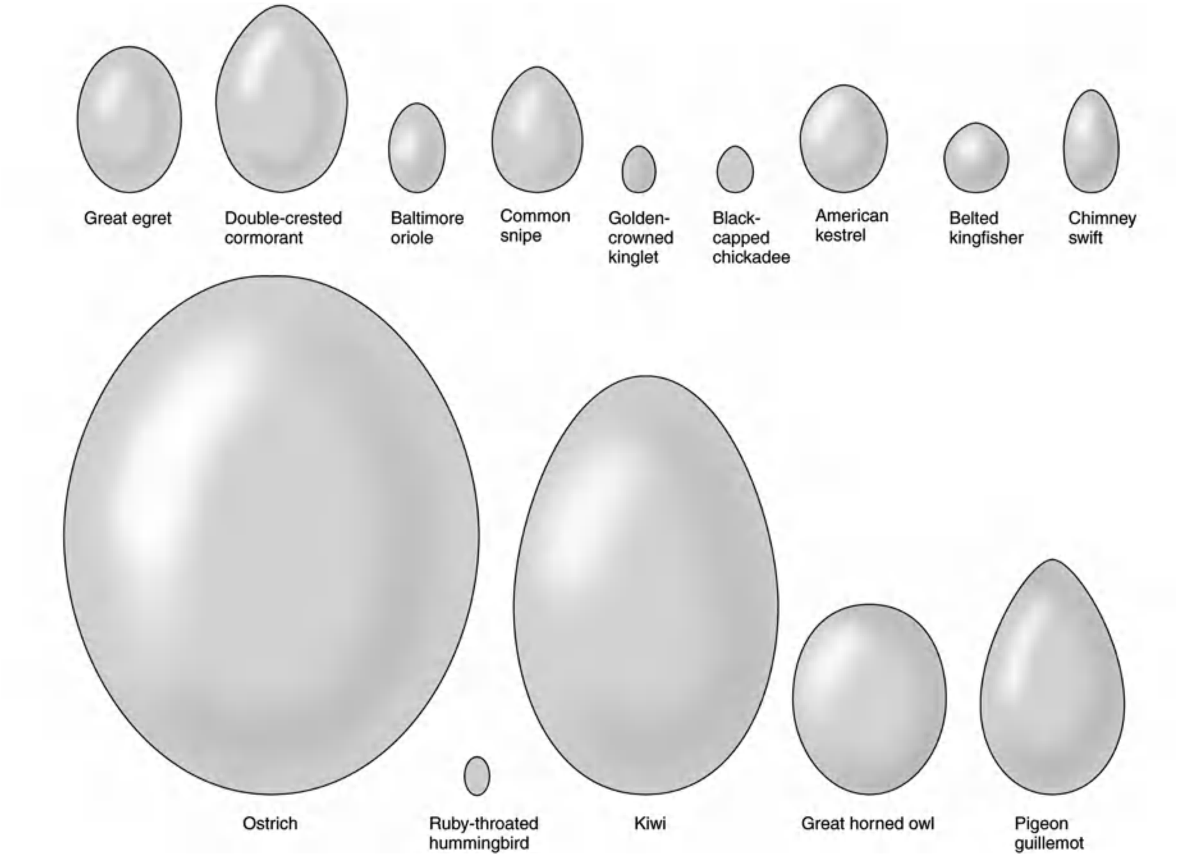


Figure 8.36. Bird eggs vary greatly in size and shape. The three basic shapes are oval (round on both ends but widest in the middle—e.g., egret); elliptical (curvature of each end is about the same—e.g., hummingbird); and pyriform (one large end and one smaller end—e.g., snipe).

Megapodes, or brush-turkeys, of Australia and the East Indies, are mound builders (Fig. 8.40). They construct mounds of decaying vegetation or volcanic ash somewhat resembling those of the American alligator and deposit their eggs in the center. Eggs are incubated by solar, geothermal, or microbial-generated heat. The Australian brush-turkey (*Alectura lathami*) constructs a mound of decomposing vegetation with an average volume of approximately 12.7 m^3 and a weight of about 6,800 kg (Seymour and Bradford, 1992). The rate of heat production is more than 20 times the heat production of a resting adult.

Some birds, like the brown-headed cowbird (*Molothrus ater*) and Old World cuckoos (*Cuculus*), are parasites. Females never build a nest; rather, they deposit one or more eggs in the nest of another species when that female is away from her nest (see Parasitism in Chapter 14; see also Hatching, below).

Prehatching vocalizations by the young beginning just prior to hatching are common in precocial and some altricial birds (Evans, 1988;

Bugden and Evans, 1991). Altricial American white pelican (*Pelecanus erythrorhynchos*) embryos that are close to hatching emit harsh squawks from inside the egg if their temperature begins to drop. This is a frequent occurrence with terminal eggs in clutches from altricial species that hatch asynchronously, because the parent is spending an increasing amount of time obtaining food for the first hatchlings and less time incubating the unhatched eggs (Evans, 1990a). Hatching of pelican embryos is significantly retarded by moderate chilling (Evans, 1990b). The squawking gets the attention of the parents and usually results in a parent resettling over the nest and resuming incubation (Evans, 1992). Thus, late-stage embryos influence their own incubation temperature by communicating with their parents (Evans, 1990c, 1990d).

Conditions occurring at the time of breeding (like changes in food abundance and population density) are known to affect clutch size. In addition, studies of zebra finches (*Taeniopygia guttata*) and great tits (*Parus major*) show that environmental factors affecting the food intake by nestling females (e.g., the ability of parents to locate food, the quality of the territory, the timing of food abundance) may permanently influence the mechanisms controlling the clutch sizes of nestlings when they reach adulthood (Haywood and Perrins, 1992).

(a)

Figure 8.37. Diversity of nests and nest sites in birds. (*a*) The terrestrial ground nest of the lesser prairie chicken (*Tympanuchus pallidicinctus*). (*b*) The mud and pebble nests of the house martin (*Delichon urbicum*).

Ornithologists have long suspected that the order of egg-laying can influence a bird's size and survival (Badyaev et al., 2002). Studies of two groups of house finches native to desert regions of the Southwest led the authors to suggest that the first few birds hatched get bigger doses of sex hormones from the mother. Higher hormone levels may play some role in the birds' size. Or it is possible that the early hatchlings, ahead in terms of growth, are stronger competitors when food is delivered to the nest.

Figure 8.38. Royal terns (*Sterna maxima*) deposit their single egg in a depression in the sand. Tern eggs are in the foreground.

Figure 8.39. Nesting burrow of the fairy penguin (*Eudyptula minor*) taken on Phillip's Island, Australia.

Figure 8.40. Megapodes (brush-turkeys) deposit their eggs in mounds of soil and debris. The eggs are incubated by the heat generated by the decomposing vegetation.

Birds in the Northern Hemisphere lay more eggs than their counterparts in the Southern Hemisphere (Martin, et al., 2000; Pennisi, 2001). Bird populations on opposite sides of the equator, in Arizona and in Argentina, were studied. Researchers also analyzed 182 species, comparing birds from Europe and North America with those from New Zealand, Australia, and South Africa. For example, wrens in Arizona averaged 5.8 chicks per nest, while their southern counterparts averaged just 3.7. It has been suggested that since northern birds sometimes live just one season, they invest more in reproduction by laying more eggs the one chance they have. Southern birds hedge their reproductive potential, producing fewer eggs at one time but breeding more than once.

Three factors have been proposed to affect this pattern: seasonality of resources, nest predation, and length of the breeding season (Griebeler et al., 2010). This study suggested that increasing seasonality of resources from the tropics to the poles by itself or in combination with a decreasing predation rate and length of the breeding season can generate the latitudinal gradient in clutch size.

Duration of Embryonic Development

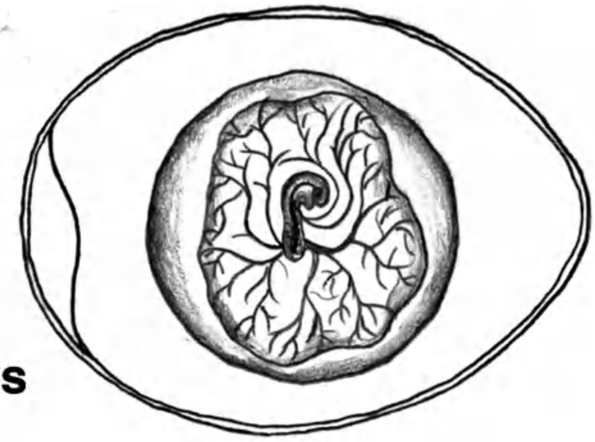
American alligator eggs hatch in about 9 or 10 weeks. Temperature-dependent sex determination occurs in all species that have been examined. Incubation of bird eggs ranges from approximately 10 or 11 days in some passerine birds to 11 or 12 weeks in the royal albatross (*Diomedea epomophora*). Incubation in domestic chickens requires approximately 21 days (Fig. 8.41). In most species, incubation is carried out by one or both parents. In the megapodes, however, decaying vegetation generates the heat necessary for incubation.

Prinzinger and Hinninger (1992) reported a diurnal (circadian) rhythm of energy metabolism present as early as the fourth day of incubation in pigeon (*Columba livia*) embryos. Nighttime values of oxygen consumption were significantly below those for daytime. The mean difference between the daytime value and the value for the following night was 17 percent. Data supporting diurnal rhythms in chicken (*Gallus domesticus*) embryos (Barnwell, 1960) and herring gull (*Larus argentatus*) embryos (Drent, 1970) have also been reported.

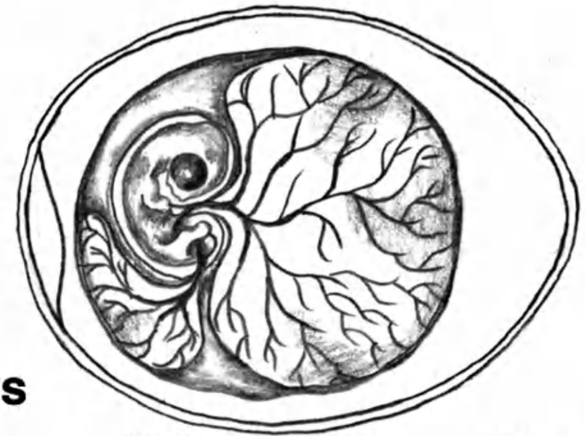
Hatching

At the end of the incubation period, young crocodilians begin to emit gruntlike sounds from within the nest of vegetation. In addition to alerting a nearby parent, some researchers have suggested that young within the eggs use vocalizations to communicate with one another, perhaps to synchronize hatching.

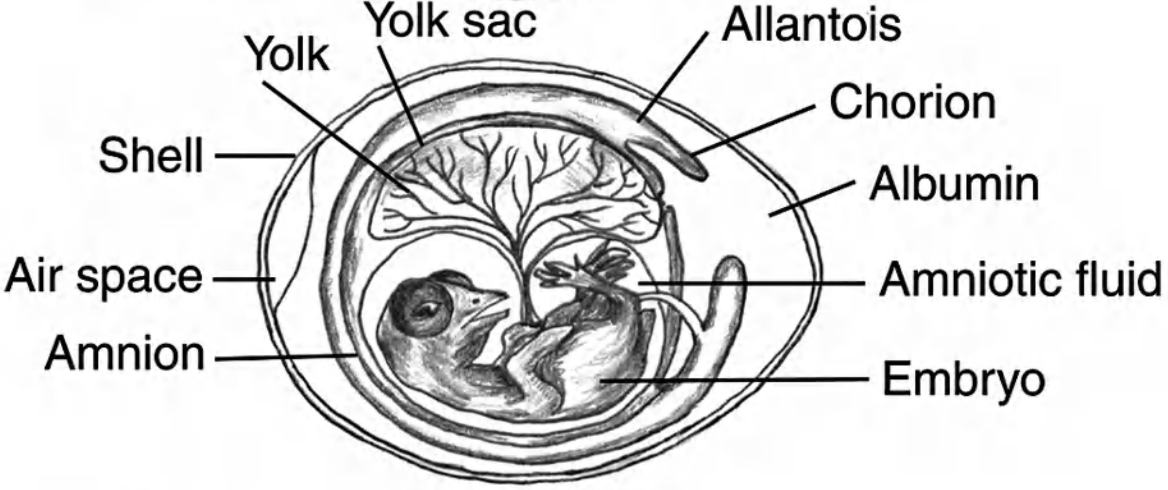
Evaporative water loss from eggs has been found to affect hatching success (Walsberg and Schmidt, 1992). Mourning dove embryos incubated under either arid or humid conditions developed normally up to, and including, pipping; however, only 50 percent of the embryos incubated under humid conditions hatched as opposed to approximately 85 percent incubated under arid conditions and 90 percent at an intermediate relative humidity. Increased mortality of those under humid conditions apparently was caused by the lack of sufficient space inside the egg for the embryo to maneuver in order to break the shell. This lack of space presumably was caused by decreased evaporative water loss.



3 days



5 days



11 days

Figure 8.41. The fetus of a domestic chicken exhibits rapid changes in development. The chorion is the outer boundary of structures derived from the true egg shell. The shell and thick layer of albumen (a protein) surround the developing chick. Shown here are embryos at 3, 5, 11, and 19 days after incubation begins. Hatching requires approximately 21 days in this species.

In birds, pipping of the shell may begin 10 hours or more before hatching due to the random movement of the embryo (Faaborg, 1988). At some point, the movement becomes much more active. Strong thrusts of the beak into the shell are accompanied by movements of the entire body produced by pushing with the feet. During this time, the embryo rotates within the shell, a process that causes a ring of cracks to form near the blunt end of the egg. The full-term embryo possesses a horny knob, or egg tooth, on its upper mandible and hatching muscles on the back of its head (Fig. 8.42) that are responsible for the vigorous forward thrust of the head during pipping. Both the egg tooth and the hatching muscles are lost or regress shortly after hatching. Continued movement and thrusting by the embryo eventually cause the end of the shell to break free and allow the baby bird’s emergence from the egg. The entire hatching process may last from several hours to several days.

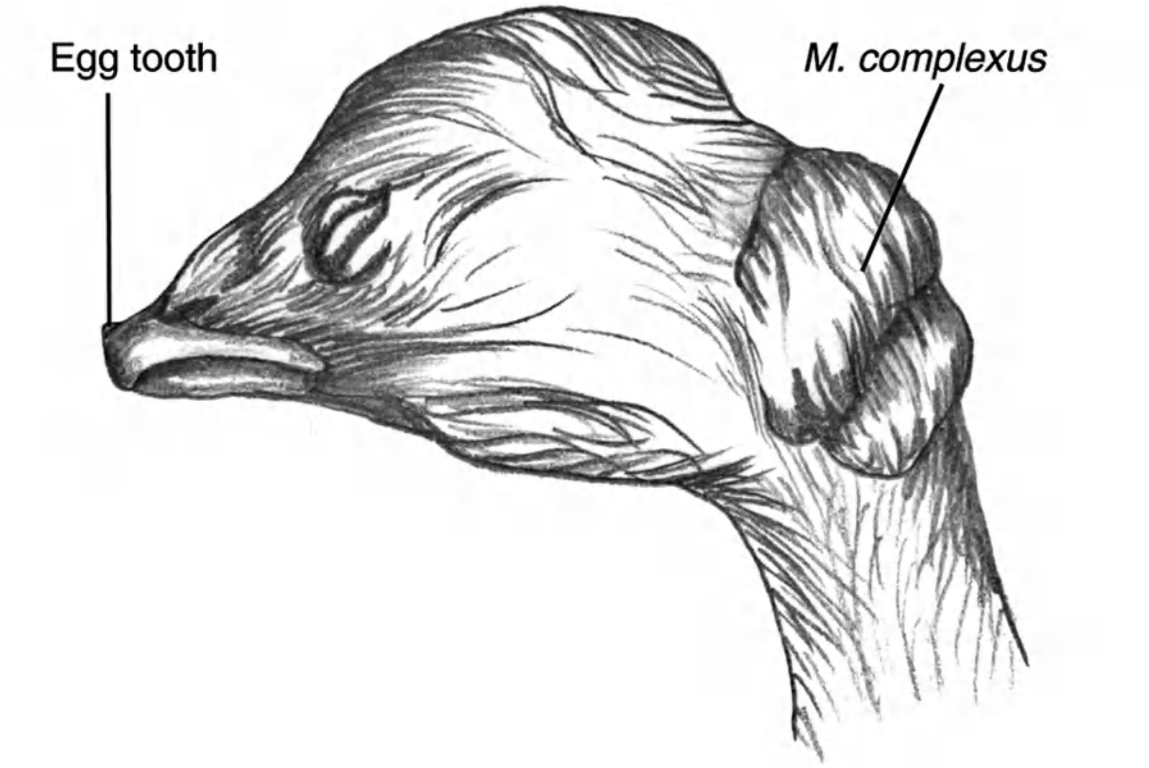


Figure 8.42. The hatching muscle in a chicken on the day of hatching. This muscle is primarily responsible for the vigorous forward thrusting movements of the head that result in pipping of the shell.

The eggs of parasitic birds, like cowbirds and cuckoos, generally have a shorter gestation period than the eggs of their hosts and usually are the first to hatch. In addition, McMaster and Sealy (1998), who analyzed cowbird eggs laid in nests of yellow warblers, concluded that cowbirds hatch before many hosts by prolonging incubation of smaller eggs and, possibly, hatching early in response to stimuli from host eggs. Because the cowbird egg is roughly twice the size of warbler eggs, it keeps the incubating parent from making optimal contact with those eggs, thus adding about a day and a half to the normal 11-day incubation of yellow warblers. Newly hatched parasitic nestlings often push one or more of the host's eggs out of the nest (Fig. 8.43) and consume much of the food delivered to the nest by the parents. Nestling common cuckoos (*Cuculus canorus*) stimulate their adoptive parents to provide adequate food by possessing a rapid begging call that sounds remarkably like a whole brood of host chicks (Davies et al., 1998).

Parental Care

Female crocodilians often remain in the vicinity of their nests during the incubation period. Hatching young emit grunting noises that attract the female who assists the young in escaping from the nest by pulling the nest apart with her front feet and mouth. Both male and female crocodilians may pick newly hatched young up in their mouth, one at a time, and gently carry them to a nearby source of water (Fig. 8.44). Females also respond to alarm cries from the young.

Most birds are well known for providing parental care. Depending on the species, either one or both parents incubate the eggs and feed the young. Male barn swallows (*Hirundo rustica*) in North America assist in incubating the eggs, but male incubation has never been recorded in European populations of this species (Smith and Montgomerie, 1992).

Figure 8.43. Newly hatched parasitic cuckoo nestling that is in the act of rolling the eggs of its host out of the nest.

Male emperor penguins (*Aptenodytes forsteri*) incubate the single egg for approximately 120 days, often under severe conditions of high winds and temperatures of –30°C (–22°F). They fast during the entire incubation period (Ancel et al., 1992) and are relieved by the female near hatching time. Once the female takes her place on the nest, satellite monitoring has revealed males walking up to 296 km (184 mi.) to open water to forage, whereas males swimming in light pack ice traveled as far as 895 km (555 mi.) from the breeding colony.

In some species, like bluebirds (*Sialia* spp.) and parakeets (*Melopsittacus* spp.), fathers feed female nestlings more often than male nestlings—in some cases, twice as frequently—whereas mother bluebirds feed sons and daughters equally (Fackelmann, 1992). The reason for this behavior is unknown. There is no difference in metabolic rates between male and female nestlings. Some researchers believe that daughters are fed preferentially in order to instill high standards for selecting a mate. Those females that have been favored as nestlings might look for more generous mates that can provide plenty of food for a hungry brood.

Some birds do not care for their young. Megapodes construct a mound nest in which eggs are incubated, but provide no parental care for their newborn. Only the parasitic species, like European cuckoos (*Cuculus canorus*) and cowbirds (*Molothrus ater*), neither build a nest nor care for their young.

Incubating birds are known to retrieve eggs displaced from their nests. Waterfowl accomplish this by rolling the egg with their bills. Two incubating mallards are known to have moved their eggs to drier nest sites 30 cm (12 in.) and 55 cm (21 in.) away from their initial nest site (Fleskes, 1991). One new site was 15 cm (6 in.) above the original site, so that the female had to roll the eggs uphill.

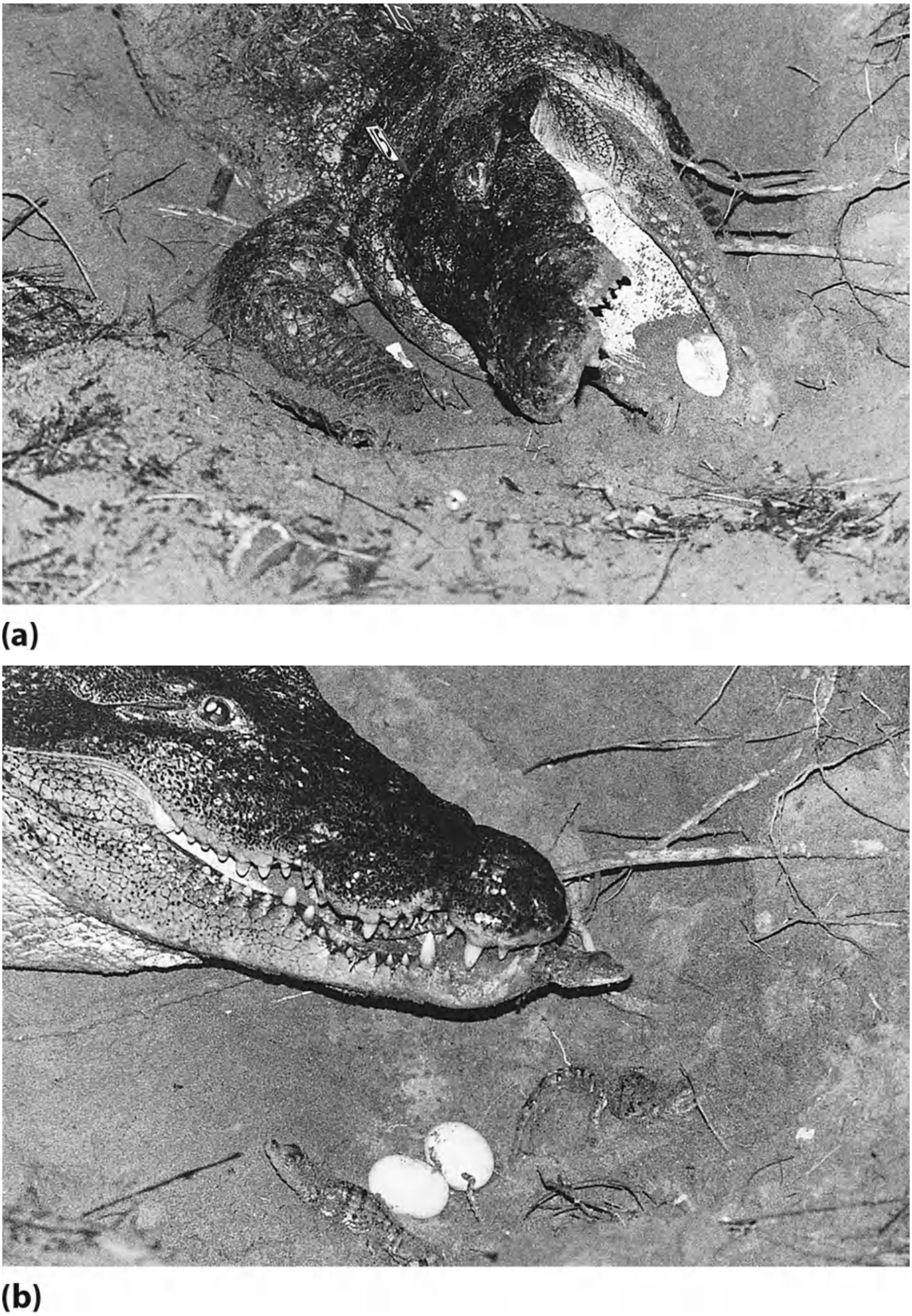


Figure 8.44. Male parent crocodile at the nest with a hatchling in his jaws. The male was observed transporting the young, one at a time, in his mouth to the nearby water.

Growth

Neither crocodilians nor birds have a larval stage; they hatch into miniature adult forms. Many birds hatch with their eyes sealed and their bodies naked. These **altricial** species require extensive parental care before they can fend for themselves (see Fig. 1.24a). They soon develop a covering of down feathers and, later, contour feathers to aid in thermoregulation. It may take several years for individuals of some species, like bald eagles, to acquire their adult plumage. Most species must also learn to fly. The young of other birds, like ducks, geese, shorebirds, and gamebirds, have their eyes open, are covered with a thick coat of natal down at the time of hatching, and require a lesser degree of parental care than altricial species. The **precocial** young of aquatic birds begin swimming with their parents shortly after birth. Even though the young can thermoregulate well and obtain their own food, the parents still are involved in such activities as brooding and protecting their chicks from predators. The most precocial birds are the megapodes of Australia, whose young require no parental care. Table 8.3 compares characteristics of precocial and altricial species of birds.

Table 8.3. A Comparison of the Characteristics of Precocial and Altricial Birds

Precocial	Altricial
Large eggs	Small eggs
Much yolk	Minimal yolk
Large clutch size	Small clutch size
Delayed incubation	Immediate incubation
Long incubation period	Short incubation period
Short nest period	Long nest period
Large chick	Small chick
Much down	Little or no down

Precocial	Altricial
Great attrition of young	Less attrition of young
Short ectothermic period	Long ectothermic period
Partially dependent on adults	Totally dependent on adults
Slow growth rate	Rapid growth rate
Do not remove shells from nest site	Remove shells from nest site

Source: From Alcorn, 1991. Copyright © Stackpole Books, Harrisburg, Pennsylvania.

Most young birds assume a series of distinct subadult plumages as they mature. The natal down coat that precocial chicks are born with and altricial chicks develop in the first weeks of life is replaced gradually by the **juvenal plumage** through a **postnatal molt**. The juvenal plumage, which includes the flight feathers, is usually retained until late in the first summer. The **postjuvenal molt** is a partial molt in which the juvenal plumage (except for the flight feathers) is replaced by the first winter plumage. The first **nuptial (breeding) plumage** is usually completed by mid-spring of the next year. Birds like gulls or eagles may require up to five years to mature and attain their adult plumage. Thereafter, winter plumages alternate with nuptial plumages.

Attainment of Sexual Maturity

Breeding may not occur in crocodilians for 10 or more years, although Bellairs (1970) noted that the American alligator (*Alligator mississippiensis*) is one of the more rapidly growing species and matures when it is about 6 years old. Most passerine birds can breed the spring following their hatching. Larger birds, like gulls and eagles, may require three or more years to mature. The California condor requires at least five years to mature, whereas the royal albatross may not begin breeding until it is approximately 8 years of age.

Longevity

Among birds, parrots live longer than any other species. The average life span for cockatoos is 65 years, for macaws it is 60 years, and for Amazon and African gray parrots it is 50 years.

As of August, 2017, the 20 longest surviving species of birds in the Patuxent Bird Banding Laboratory database were as follows:

1. Laysan albatross (*Phoebastria immutabilis*)—66 years and 0 months
2. Black-footed albatross (*Diomedea nigripes*)—53 years and 11 months
3. Gray-headed albatross (*Thalassarche chrysostoma*)—47 years and 2 months
4. Great frigatebird (*Fregata minor*)—43 years and 0 months
5. Bald eagle (*Haliaeetus leucocephalus*)—38 years and 0 months
6. Sandhill crane (*Grus canadensis*)—36 years and 7 months
7. White tern (*Gygis alba*)—35 years and 11 months
8. Wandering albatross (*Diomedea exulans*)—35 years and 7 months
9. Sooty tern (*Onychoprion fuscatus*)—35 years and 4 months
10. Common murre (*Uria aalge*)—34 years and 8 months
11. Arctic tern (*Sterna paradisaea*)—34 years and 0 months
12. Black-browed albatross (*Diomedea melanophris*)—34 years and 0 months
13. Western gull (*Larus occidentalis*)—33 years and 11 months
14. Canada goose (*Branta Canadensis*)—33 years and 3 months
15. Red-tailed tropicbird (*Phaethon rubricauda*)—32 years and 8 months
16. Atlantic puffin (*Fratercula arctica*)—31 years and 11 months
17. Golden eagle (*Aquila chrysaetos*)—31 years and 8 months
18. Southern giant petrel (*Macronectes giganteus*)—31 years and 7 months
19. Rhinoceros auklet (*Cerorhinca monocerata*)—31 years and 1 month

20. Bonin petrel (*Pterodroma hypoleuca*)—30 years and 9 months

Table 8.4 lists the current longevity records of the American alligator and some additional species of birds. A banded Leach's storm-petrel (*Oceanodroma leucorhoa*) with an estimated minimum age of 31 years was recorded by Klimkiewicz and Futcher (1989). Banded great horned owls have lived more than 28 years (Nero, 1992). Swans, geese, and some ducks often survive 20 or more years (Klimkiewicz and Futcher, 1989). Birds like condors and ostriches probably live no more than 15 or 20 years. A banded broad-tailed hummingbird (*Selasphorus platycercus*) lived more than 12 years. Banded jays have survived for 17 years. Records of the Bird Banding Laboratory come only from wild birds; other records may come from either wild or captive individuals.

Table 8.4. Longevity of the American Alligator and Some North American and Central Pacific Species of Wild Birds

Species	Maximum Age (years)
Alligatoridae	
American alligator (*Alligator mississippiensis*)	77
Fregatidae	
Great frigatebird (*Fregata minor*)	43
Magnificent frigatebird (*Fregata magnificens*)	34
Diomedeidae	
Laysan albatross (*Phoebastria immutabilis*)	65
Black-footed albatross (*Diomedea* [*Phoebastria*] *nigripes*)	42.1
Wandering albatross (*Diomedea exulans*)	50

Species	Maximum Age (years)
Black-browed albatross (*Diomedea* [*Thalassarche*] *melanophrys*)	43.7
Phaethontidae	
Red-tailed tropicbird (*Phaethon rubricauda*)	32.7
Ardeidae	
Great blue heron (*Ardea herodias*)	24.5
Anatidae	
Canada goose (*Branta canadensis*)	42
Mallard (*Anas platyrhynchos*)	29.1
Accipitridae	
Bald eagle (*Haliaeetus leucocephalus*)	48
Golden eagle (*Aquila chrysaetos*)	48
Peregrine falcon (*Falco peregrinus*)	25
Osprey (*Pandion haliaetus*)	32
Vulturidae [Cathartidae]	
Black vulture (*Coragyps atratus*)	25.5
Laridae	
Herring gull (*Larus argentatus*)	49

Species	Maximum Age (years)
White tern (*Gygis alba*)	35.9
Sooty tern (*Sterna fuscata*)	35.8
Arctic tern (*Sterna paradisaea*)	34
Caspian tern (*Sterna caspia*)	30
Alcidae	
Atlantic puffin (*Fratercula arctica*)	40.8
Columbidae	
Mourning dove (*Zenaida macroura*)	31
Trochilidae	
Ruby-throated hummingbird (*Archilochus colubris*)	9.1
Tytonidae	
Barn owl (*Tyto alba*)	34
Picidae	
Yellow-shafted flicker (*Colaptes auratus*)	12.5
Hirundinidae	
Barn swallow (*Hirundo rustica*)	16
Corvidae	
Common crow (*Corvus brachyrhynchos*)	20

Species	Maximum Age (years)
Blue jay (*Cyanocitta cristata*)	26.2
Paridae	
Black-capped chickadee (*Parus atricapillus*)	12.4
Turdidae	
American robin (*Turdus migratorius*)	17
Sturnidae	
Starling (*Sturnus vulgaris*)	22.9
Icteridae	
Brown-headed cowbird (*Molothrus ater*)	16.9
Red-winged blackbird (*Agelaius phoeniceus*)	20
Common grackle (*Quiscalus quiscula*)	29.1
Emberizidae	
Northern cardinal (*Cardinalis cardinalis*)	18.5
Song sparrow (*Melospiza melodia*)	11.3

Sources: Data from Bellairs, 1970; Carey and Judge, 2000; Lutmerding and Love, 2018.

Review Questions and Topics

1. Describe the six major types of feathers and give the function of each.
2. Compare the early development of a feather with that of a reptilian scale.

3. Discuss the modifications of the bird skeleton that allow it to be lightweight yet strong.
4. What is the functional advantage of a synsacrum?
5. Differentiate between red skeletal muscle and white skeletal muscle.
6. How does the heart of a bird differ from the heart of a shark?
7. Explain how the countercurrent heat exchanger works in the leg of a bird.
8. Explain the process of ventilation in a bird. What are the functions of the air sacs?
9. Why do so few birds live as grazers on leaves and grass?
10. List several types of nest sites used by birds. Give an example of a bird using each type of site.
11. What is the adaptive significance of prehatching vocalizations in birds?
12. Discuss adaptations used by oviparous vertebrates to escape from the membrane or shell enclosing them at hatching.
13. Give several examples of parental care in reptiles.
14. Differentiate between an altricial species and a precocial species. Give several examples of each found in birds.

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Vertebrate Internet Sites

1. Introduction to the Aves

   www.ucmp.berkeley.edu/diapsids/birds/birdintro.html

Introduction to birds with links to fossil record, life history and ecology, systematics, and morphology.

2. Digimorph—*Alligator mississippiensis*, American Alligator

   www.digimorph.org/specimens/Alligator_mississippiensis/adult

   State-of-the-art high resolution X-ray computed tomographic (X-ray CT) scanned images from the NSF Digital Library at the University of Texas at Austin. Viewer can manipulate the images—roll, pitch, yaw; cutaway images; slice movies, etc.

3. Birdsource

   www.birdsource.org

   Maintained by the National Audubon Society and Cornell Laboratory of Ornithology, Birdsource features terrific interactive maps describing where and when to find anything with feathers. It also sponsors the Great Backyard Bird Count and other research projects in which users can participate.

4. Project FeederWatch

   www.birds.cornell.edu/pfw

   Project FeederWatch began more than 30 years ago. Regular citizens count and identify the birds that arrive at their feeders from November until early April and then send the data to Cornell University or Bird Studies Canada, where scientists track the health and habits of North American birds. To participate, go to the website and order the kit. There are also helpful pictures to aid in the identification of the birds at your feeder.

9 | Mammals

When it comes to conserving wildlife and the environment, it's more important to be outspoken, than unspoken.

Paul Oxton, 2017

INTRODUCTION

Descendants of synapsid reptiles, mammals are vertebrates with hair and mammary glands. Additional characteristics distinguishing mammals from other vertebrates include a lower jaw composed solely of a dentary bone articulating with the squamosal bone, two sets of teeth (deciduous and permanent), three middle ear bones (ossicles), a pinna to funnel sound waves into the ear canal, marrow within the bones, loss of the right fourth aortic arch, non-nucleated red blood cells, and a muscular diaphragm separating the thoracic and abdominal cavities. In addition, most mammals have sweat glands, heterodont dentition, and extensive development of the cerebral cortex. Approximately 5,700 species of mammals currently inhabit the world.

EVOLUTION

Fossil evidence indicates that mammals arose from a synapsid reptilian ancestor (Fig. 9.1). The subclass Synapsida appeared during the Lower Pennsylvanian more than 300 Mya and became extinct about the end of the Triassic period, some 190 Mya. The earliest synapsid, *Archaeothyris*, was a pelycosaur found in the Joggins fossil cliffs in Nova Scotia, Canada (Reisz, 1972). This is the same locality in which the early reptile *Hylonomus* (which resembles *Archaeothyris*) was found. The climate of Nova Scotia some 300 Mya was warm and moist, and much of the land was covered by forests dominated by giant lycopods. A cladogram of the synapsids emphasizing mammalian characteristics is presented in Fig. 9.2.

Synapsids were quadrupedal reptiles (see Fig. 9.2) that possessed a single temporal fossa whose upper border was formed by the postorbital and squamosal bones (see Fig. 6.5). Some researchers feel that a chain of small bones (articular, quadrate, angular) that formed the hinge attaching jaw and skull in mammal ancestors began moving back along the skull in synapsids. These bones were beginning to do double duty: hinging the jaw and likely picking up higher-frequency sounds (perhaps made by insects). They also were destined to join with the columella (stapes) already in the ear to become part of the middle ear in all mammals, a process that would result in a shift in jaw articulation from articular-quadrate to dentary-squamosal. The quadrate became the incus, the articular became the malleus, and the angular became a bony ring, the tympanic, which holds the tympanum (eardrum) (Fig. 9.3). When sound waves strike the tympanum, vibrations are transmitted via the malleus, incus, and stapes to the inner ear.

Brain growth in early mammals could have triggered the migration of these skull bones. Paleontologist Timothy Rowe of the University of Texas at Austin followed brain growth and ossicle position in opossum embryos (Fischman, 1995b). Whereas the ossicles reached their maximum size three weeks after conception, the brains continued to enlarge for another nine weeks, putting pressure on the ear ossicles. The ossicles, whose movement away from the jaw was caused by the expansion of the skull to hold the bigger brain, were pushed backward until they reached the adult position.

As early synapsids increased in size, they adapted by developing proportionately larger heads, longer jaws, and more advanced jaw muscles. Teeth differentiated into incisors, canines, and grinding cheek teeth (molars). Of all the synapsids, therapsids (order Therapsida) are considered to be the line that branched to the mammals (see Fig. 9.2). Therapsids date back to the early Permian, 280 Mya (Novacek, 1992); fossils of Middle and Late Permian and Triassic age are known from all continents. The temporal fossae of all therapsids were much larger than in pelycosaurs, indicating an increase in size of the jaw-closing musculature (Kemp, 1982). Associated with this was the presence of a single large canine in each jaw, sharply distinct from both incisors and postcanine teeth. The skull is also more robust than in advanced pelycosaurs. Broom's (1910) classic paper demonstrated that the therapsids were closely related to the pelycosaurs, and this affinity has never been questioned.

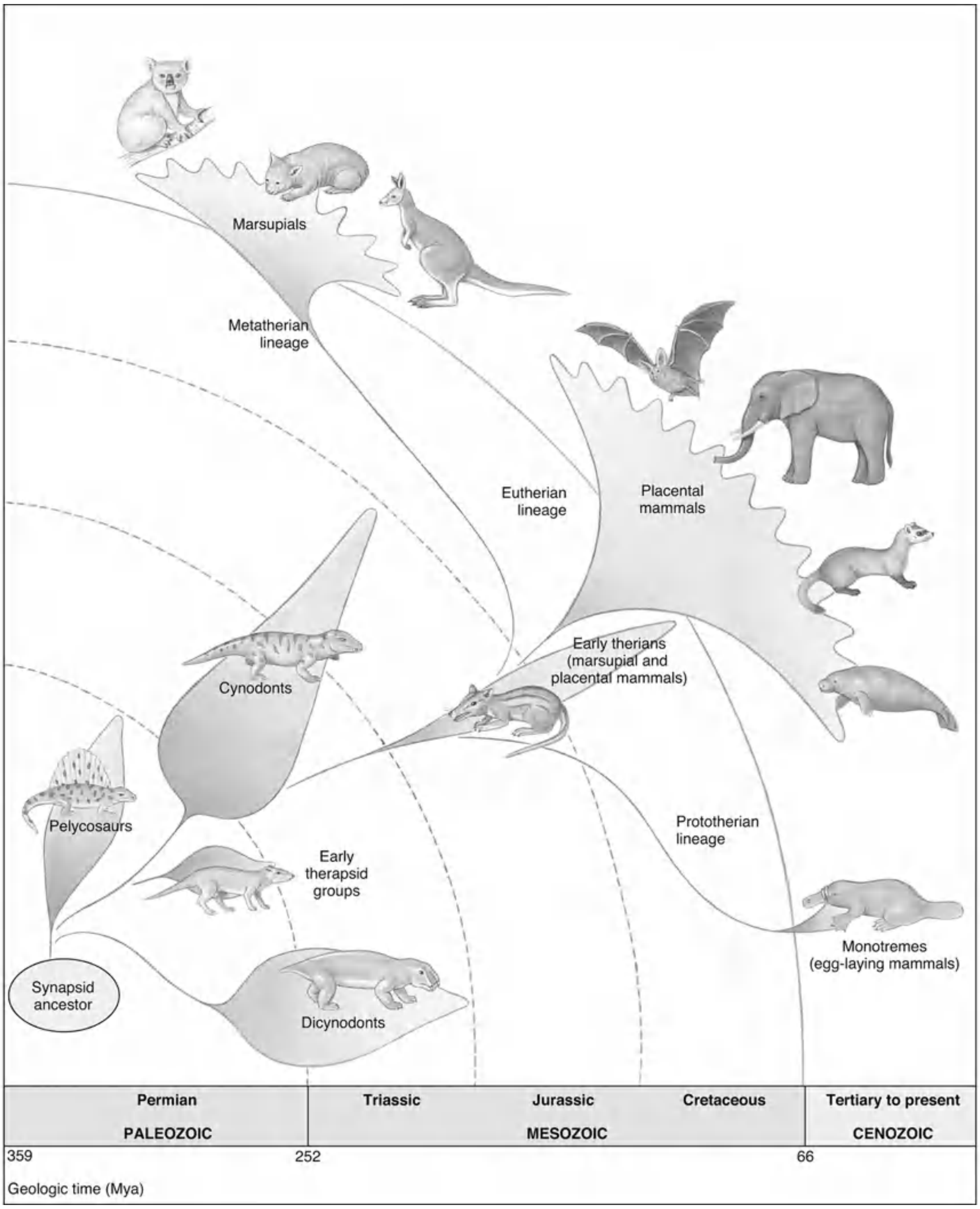


Figure 9.1. Evolution of major synapsid groups. Synapsids are characterized by a single temporal opening on each side of the skull. Pelycosaurs (early mammal-like amniotes of the Permian) and their successors, the therapsids, gradually evolved changes in their jaws, teeth, and body form that presaged several mammalian characteristics. One group of therapsids, the cynodonts, gave rise to the therians (true mammals) in the Triassic. Current fossil evidence indicates that all three groups of living mammals—monotremes, marsupials, and placentals—are derived from the same lineage. The great radiation of modern placental mammals occurred during the Cretaceous and Tertiary periods.

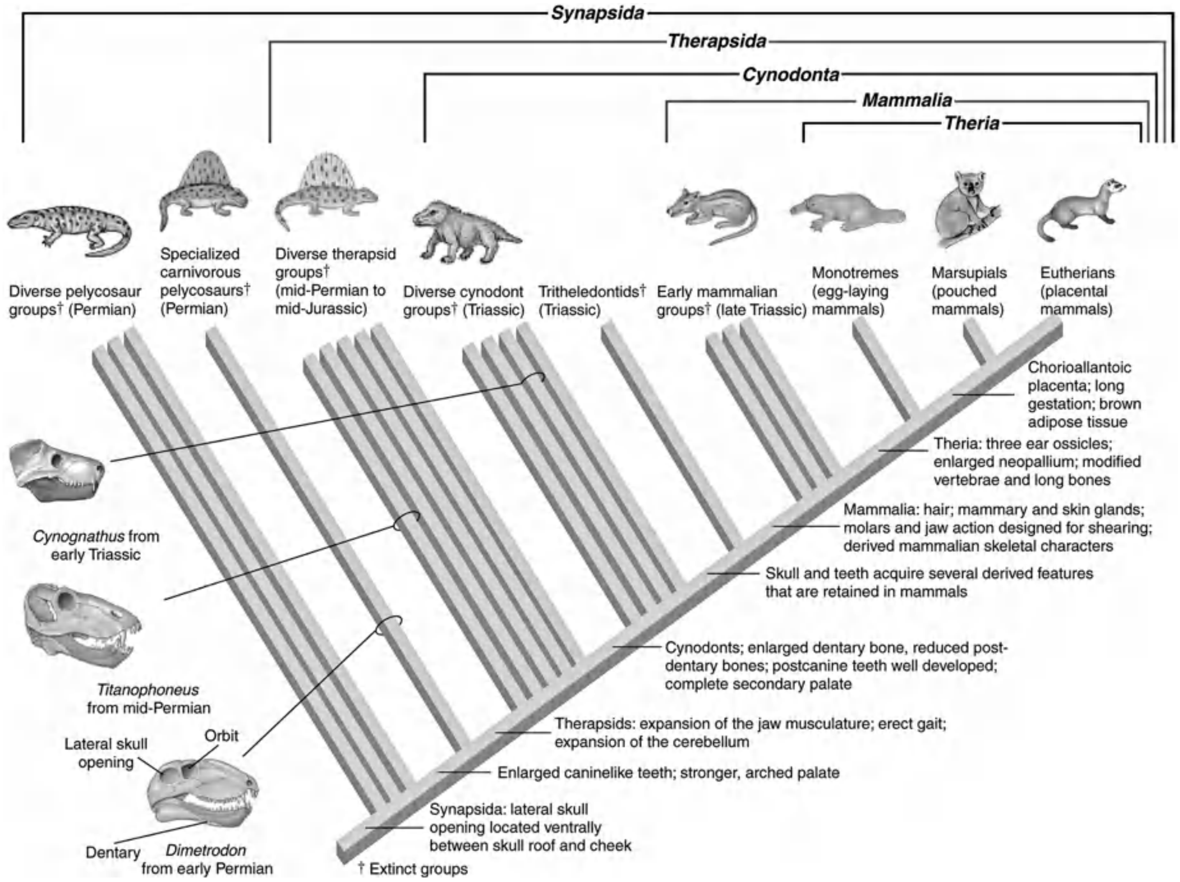


Figure 9.2. Cladogram of the synapsids emphasizing the origins of important mammalian characteristics, which are shown to the right of the cladogram. The skulls show the progressive increase in size of the dentary relative to other bones in the lower jaw.

There were five major groups of mammal-like reptiles: dinocephalians (primitive carnivorous therapsids), gorgonopsians (advanced carnivorous therapsids), anomodonts (herbivorous therapsids), therocephalians (advanced carnivorous therapsids), and cynodonts (advanced carnivorous therapsids). Of these, cynodonts are most closely associated with the lineage that evolved into modern mammals.

Cynognathus was a typical advanced cynodont (Fig. 9.4a). The known members of this genus were the size of a large dog and had powerful jaw muscles (masseter and temporalis). The dentary bone formed most of the lower jaw, in contrast to the typical reptilian mandible, which consisted of several bones. Heterodont dentition was present; instead of swallowing food whole as reptiles do, *Cynognathus* had cheek teeth that were adapted for cutting and crushing food. A well-developed secondary palate and two occipital condyles were present. Although the articulation of the mandible to the skull was still reptilian (articular-quadrate), the articular bone of the lower jaw and the quadrate bone of the skull had decreased in size. Thus, *Cynognathus* had not yet attained the most widely accepted character separating mammals from reptiles—a functional joint between the dentary and squamosal bones.

The limbs of therapsids like *Cynognathus* had evolved from the primitive sprawling position to a position where the long bones of the limbs were parallel to the body and almost beneath the trunk, thus making support and locomotion easier (see Fig. 9.4b, c). The elbow was directed posteriorly and the knee anteriorly. This resulted in changes in bone shape and associated musculature.

It is unknown whether *Cynognathus* possessed hair or whether it was warm-blooded. Cynodonts probably did have a high metabolic rate and a more advanced, mammal-like temperature physiology (Kemp, 1982). Regardless of whether or not *Cynognathus* was a direct ancestor of mammals, it definitely appears to have been closely associated with the lineage that was evolving into mammals.

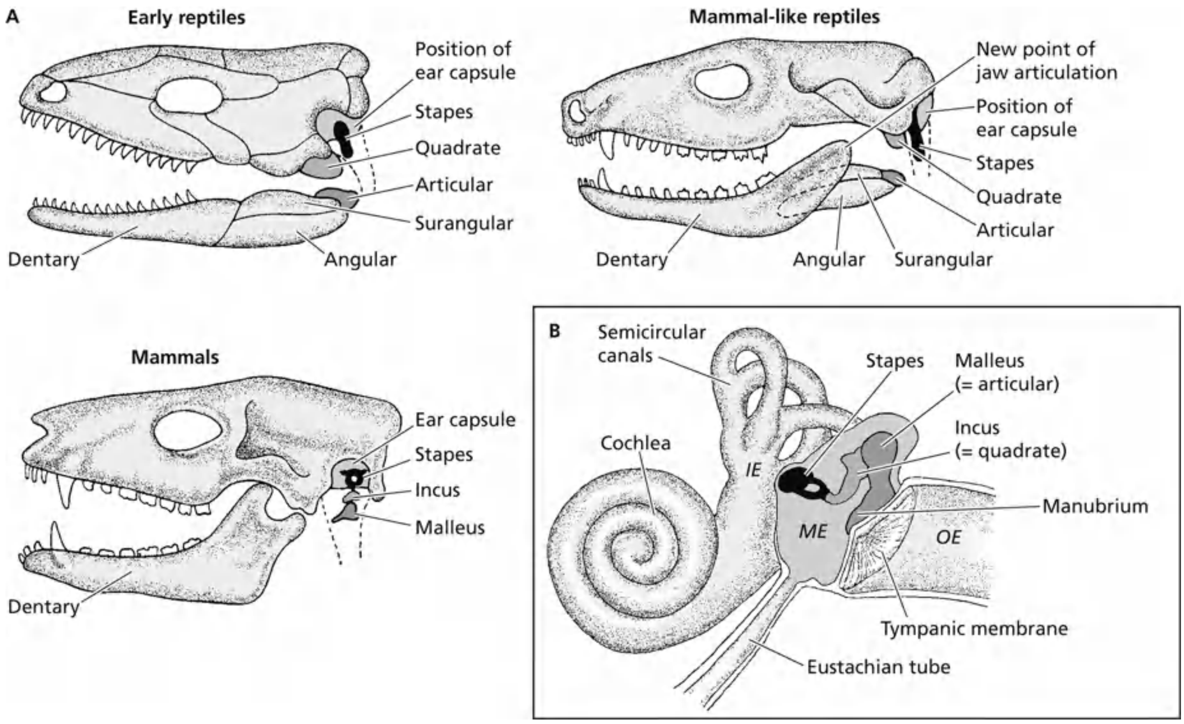
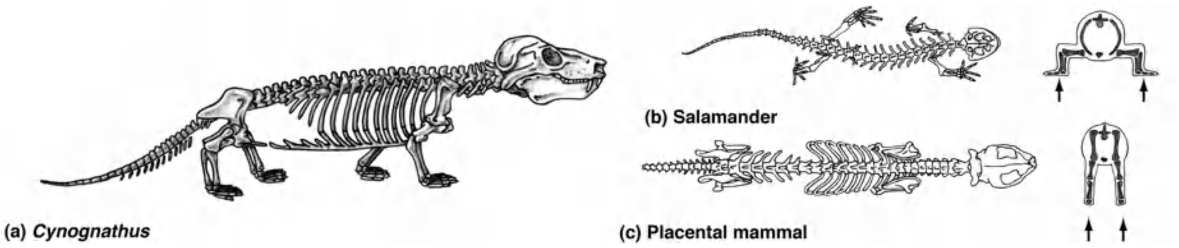


Figure 9.3. Phylogeny of the jaw articulation and ear ossicles. Stylized lateral views somewhat distorted for two-dimensional representation (e.g., stapes is medial, not posterior to quadrate).



(a) *Cynognathus*

(b) Salamander

(c) Placental mammal

Figure 9.4. (*a*) *Cynognathus*, an advanced cynodont, was about the size of a large dog. Powerful jaw muscles and heterodont dentition allowed the cutting and crushing of food. A well-developed secondary palate and two occipital condyles were present. Evolution of posture: (*b*) The sprawled posture of the salamander was typical of fossil amphibians as well as of most reptiles. (*c*) Placental mammals. This posture began to change in synapsids, so that in late therapsid reptiles the limbs were thought to be carried more beneath the body, resulting in better support and more rapid locomotion.

The discovery of a possible new therapsid, *Chronoperates paradoxus*, from the Late Paleocene indicates that "therapsids and mammals were contemporaries for at least the first two thirds of mammalian history" (Fox et al., 1992). *Chronoperates* is thought to have branched from a primitive cynodont and survived as a relict into the Paleocene. Prior to this discovery, therapsids were thought to have become extinct by the mid-Jurassic. The recent Paleocene fossil extends the existence of therapsids by 100 million years and has generated considerable discussion (Sues, 1992).

Controversy continues as to whether mammals had a monophyletic origin (Hopson and Crompton, 1969; Moss, 1969; Hopson, 1970; Parrington, 1973; Crompton and Jenkins, 1979; Futuyma, 1986) or a polyphyletic origin (Simpson, 1945; Romer, 1966; Kermack, 1967; Marshall, 1979; Kermack et al., 1981). Kemp (1982) noted that all of the various groups of mammals can be traced to a single, hypothetical ancestor that had itself achieved the mammalian organization. He pointed out that mammals share such a range of derived characters with the advanced cynodonts that a relationship between the two seems beyond question.

Carroll (1988) considered it difficult to establish interrelationships among the remaining, nontherian mammals (monotremes, triconodonts, and multituberculates) of the Mesozoic. The entire assemblage, including the monotremes, was placed within the subclass Prototheria. However, as Carroll noted, it is presently impossible to establish that the Prototheria is a natural group. Aside from spiny anteaters (echidnas) and the platypus, all living mammals are included in a single monophyletic assemblage, the Theria (marsupial and placental mammals).

Which of the cynodonts are most closely related to mammals is still open to question. There are three possible candidates: a small, advanced carnivore (*Probainognathus*), another group of small carnivorous forms (the tritheledontids), or the tritylodontids, which possess the greatest number and range of mammalian characters of any of the cynodonts (Kemp, 1982).

Ruta et al. (2013) compared 150 distinct skeletal features in 52 species of cynodonts and two early mammal species. They concluded that, in the end, the probainognathians became the most diverse and most varied in adaptation of all cynodont clades and that they gave rise to the first mammals some 25 million years after the mass extinction.

Probainognathus was a small animal with a slender zygomatic arch. The dentary had possibly just made contact with the squamosal, forming the mammalian secondary jaw hinge alongside the reptilian hinge. Canine teeth were present.

Aleodon is a genus of Probainognathus cynodont, a taxon which evolved in the Triassic period, co-existed with dinosaur precursors and other archosaurs, and is thought by many to have eventually given rise to mammals. *Aleodon* was first described using fossils from Tanzania and Namibia and was known only from Africa until Martinelli et al., (2017a) described a new species (*Aleodon cromptoni*) from Rio Grande do Sul in southern Brazil. As part of an ongoing study into the evolutionary relationships between cynodonts and the earliest mammals in South America, Martinelli et al. (2017b) examined the skulls, jaws, and teeth of two new species (*Bonacynodon schultzi* and *Santacruzgnathus abdalai*) from Middle-Late Triassic fossil specimens from Rio do Sul, Brazil. These specimens strengthen the correlation between probainognathians from that epoch in South America and in Africa. The shape and dentition of *S. abdalai*'s teeth are reminiscent of those present in early mammals.

Diarthrognathus, the best-known of the tritheledontids, possessed the nonmammalian articular-quadrate joint as well as the mammalian dentary-squamosal joint. Postorbital and prefrontal bones were absent, the zygomatic arch was slender, and the teeth were covered with enamel. Dentition indicates that these were highly specialized herbivores, whereas early mammals were carnivorous (Carroll, 1988).

Tritylodontids, which possessed multirooted teeth, had also lost the prefrontal and postorbital bones. They possessed acoelous (flattened centra on both anterior and posterior surfaces) vertebrae. The large acromion process of the scapula permitted the development of a large supraspinatus muscle. The humerus had become slender, and the forelimb now operated in a more erect manner. The pubis had turned posteriorly, and the ischium was reduced and horizontal. The musculature and locomotion were virtually fully mammalian.

Even though the tritylodontids possessed the greatest number and range of mammalian characters, Hopson and Barghusen (1986) and Shubin et al. (1991) presented data supporting the cynodont-tritheledont phylogeny. The decision as to which groups should be included as mammals still is open to conjecture and cannot be answered definitively until additional evidence clarifies the relationships among several key groups. The “answer” ultimately depends on the definition one uses to define a mammal.

Diphyodonty (having two sets of teeth during life) is considered a basic characteristic of the class Mammalia. Parrington (1971) has shown fairly conclusively that diphyodonty occurred in *Eozostrodon* specimens examined from the Triassic. *Eozostrodon*, believed to be an early triconodont (primitive mammal), was similar to a small shrew, with a skull length of 2 to 3 cm (0.75–1.25 in.) and a presacral length of approximately 10 cm (4 in.) . Many features of the skull were mammalian, including tooth structure, the presence of diphyodont dentition, and the form of the lower jaw. However, the articular bone still formed a jaw hinge with the small quadrate bone lying in a pocket in the squamosal. Thus, the postdentary bones had not formed a set of ear ossicles independent of the lower jaw, as occurs in modern mammals. Parrington (1967) and Crompton and Jenkins (1968) independently concluded, from the similarity of the molar teeth, that *Kuehneotherium*, a therian, and *Eozostrodon* were closely related. The molar teeth of *Eozostrodon* appear to be the basic type from which all therian molars have evolved.

During the Triassic, each group of advanced synapsids gave rise to a different group of animals (symmetrodonts, pantotheres, multituberculates, triconodonts) that we can call mammals. The transition from primitive reptile to primitive mammal occurred between the end of the Pennsylvanian period and the close of the Triassic. Prior to 2014, the earliest known mammal fossils were from the Late Triassic of Europe. However, Bi et al. (2014) described three new small squirrel-like species that place a poorly understood Mesozoic group of animals firmly in the mammal family tree. It supports the idea that mammals originated at least 208 Mya in the late Triassic, much earlier than some previous research suggests. The three new species—*Shenshou lui*, *Xianshou linglong*, and *Xianshou songae*—were described from six nearly complete 160-million-year-old fossils found in China. After studying the fossil teeth and bones, the research team found that the animals fit within a branch of the mammalian family tree that includes all mammals living today. The animals, which researchers have placed in a new group, or clade, called Euharamiyida, likely looked similar to small squirrels. They weighed between 28 to 283 g (1–10 oz.) and had tails and feet that indicate that they were tree dwellers. The overall morphology seen in the new specimens is mammalian, including the presence of a typical mammalian ear with three ear bones. Though the fossils are only about 160 million years old, previously discovered haramiyids trace back even farther—to more than 200 Mya, so that the common ancestors of these animals and modern mammals must be at least that old, or older.

Synapsids were diverse during the Permian but were greatly reduced after the end-Permian extinction. The few groups that survived into the Triassic were mostly small and retained a sprawling gait. However, the dicynodont *Lisowicia bojani*, from the Late Triassic of Poland, was a gigantic synapsid with seemingly upright cursorial limbs that reached a length of more than 4.5 m (14.75 ft.), a height of 2.6 m (8.5 ft.), and a body mass of almost 9,000 kg (20,000 lb.) (Sulej and Niedzwiedzki, 2019). It was as large as some coexisting dinosaurs and appears to have had an erect gait—like modern mammals. It was the largest nondinosaurian terrestrial tetrapod from the Triassic and shows that megaherbivore radiation was not solely restricted to dinosaurs.

The Symmetrodonta and Pantotheria were both Jurassic mammals and are probably more closely related to each other than to the other groups. Symmetrodonts had the cusps of their molar teeth arranged in a symmetrical triangle, with the base of the triangle external in the upper jaw and internal in the lower. Pantotheres had molars that were three-cusped, with the cusps arranged in an asymmetrical triangle. The Multituberculata were probably among the earliest herbivorous mammals, although they also probably included insectivorous and omnivorous forms. Ranging from the size of a small mouse to as large as a woodchuck, multituberculates appeared in the Upper Triassic and persisted into the Eocene. Some researchers feel they are most closely related to monotremes; others consider them closer to therians (Monastersky, 1996d). Triconodonts were Jurassic mammals that were probably carnivorous; their molars typically had three sharp conical cusps arranged in a row along the long axis of the tooth. The main cusp of the lower molars occluded between the main cusp and the anterior accessory cusp of the corresponding upper molar. This shearing dentition may indicate that they preyed on other vertebrates.

Hadrocodium wui was reported by Luo et al. (2001) from the Lower Lufeng Formation of Yunnan, China. Based on the analysis of 90 cranial and dental characters, and supported by a large number of shared derived characters, the authors indicate that it is a new lineage of mammaliaforms and should be considered a sister taxon to the clade of triconodontids and extant Mammalia. With an estimated adult body weight of only 2 g (0.07 oz.), the fossil insectivore from the Early Jurassic (195 Mya) is distinguishable from all other nonmammalian mammaliaforms and mammals from the Late Triassic and Jurassic. Overwhelming evidence points to the divergence of monotremes (the egg-laying platypus and echidna) and therian mammals (marsupials and placentals that give birth to live young) from a unique common ancestor. Anatomical and phylogenetic analyses reveal that *Hadrocodium* diverged before the appearance of the most recent common ancestor of monotremes and therians. Strictly speaking, it is not a mammal, but is a member of the Mammaliaformes—a broader grouping comprising mammals and some of their closest fossil allies. The authors suggest that *Hadrocodium* is the nearest fossil relative of mammals.

During the Jurassic and Cretaceous, a variety of mammals evolved. Analyses by Rowe (1999) indicate that the last common ancestor of living mammals probably lived in the Early or Middle Jurassic. Thus, Mammalia is 20 to 40 million years older than once believed. Until recently, the earliest details of mammalian history were unknown due to a lack of fossils.

In 1999, Ji et al. (1999) described one of the world's oldest complete mammal fossils (*Jeholodens jenkinsi*) (Fig. 9.5), dating back at least 20 million years. The fossil is a close relative to the common ancestor of all mammals alive today, from monotremes to opossums to humans. The incredibly complete fossil comes from the same Late Jurassic/Early Cretaceous deposit of Liaoning, China, which has yielded feathered dinosaurs and one other complete mammal skeleton. Although the teeth identify it as a triconodont, skeletal characteristics largely support the sister-group relationship of multituberculates with therian mammals. The rat-sized animal walked on mammalian front legs and splayed reptilian hind legs (Zimmer, 1999). The elbows point back, whereas the knees point to the side. The limb structure indicates it was probably a ground-dwelling animal, thus indicating that mammals arose as terrestrial forms and only later did their therian descendants take to the trees.

Figure 9.5. The ancestor of all modern mammals may have resembled this reconstruction of *Jeholodens jenkinsi*, a 120-million-year-old mammal from China.

(a)

(b)

Figure 9.6. Monotremes—the only egg-laying mammals: (*a*) duck-billed platypus; (*b*) echidna. The platypus raises its young in a nest; the echidna, or spiny anteater, places them in a pouch on her abdomen.

Living mammals are classified into 26 orders. The Monotremata contains the only egg-laying mammals (duck-billed platypus and two species of echidnas, or spiny anteaters) (Fig. 9.6). All other mammals are viviparous. Currently, all monotremes are restricted to the Australian continent. However, Pascual et al. (1992) reported the first discovery of monotremes in South America. Australia did not completely separate from East Antarctica until between the middle Eocene and early Oligocene (45–38 Mya), and South America maintained an archipelagic connection to West Antarctica until the late Oligocene (~35 Mya). Phylogenetic studies have suggested that at least one order of marsupials or its descendants spanned the three unified continents before the early Tertiary. A comparable distribution now characterizes monotremes.

Figure 9.7. *Castorocauda lustrasimilis*, a mammal from the Middle Jurassic, is the most primitive mammal to be preserved with fur. It is the earliest swimming mammal that has been discovered.

The Jurassic and Early Cretaceous were times of “experimentation” for mammals. Dinosaurs were still abundant. Primitive hooved mammals and even some early primates had evolved. Birds were able to fly. The discovery of a furry, beaver-like animal that lived 164 Mya shows that the ecological role of mammals in the time of the dinosaurs was far greater than previously thought (Ji et al., 2006). The animal, *Castorocauda lustrasimilis*, was discovered in the Inner Mongolia region of China (Fig. 9.7). It is the earliest swimming mammal to have been found and is the most primitive mammal to be preserved with fur. It is the first evidence that some ancient mammals were semiaquatic. *Castorocauda* had a flat, scaly tail like a beaver, vertebrae like an otter, and teeth like a seal. It swam in lakes and fed on fish.

Figure 9.8. The mouse-sized primate *Shoshonius cooperi* was discovered in North American deposits aged 50 million years old.

A tiny, squirrel-like creature, *Volaticotherium antiquus*, glided through the air 130 to 164 Mya, more than 75 million years earlier than scientists had documented that ability in a mammal (Meng et al., 2006). Discovered in Mongolia in 2005, it is clearly older than the 51-million-year-old bat that used to be the oldest evidence of flying or gliding in a mammal. It may have even preceded the earliest known bird, *Archaeopteryx*, which flew about 150 Mya. It is much younger than flying reptiles called pterosaurs, which are dated from 230 Mya. The creature weighed about 0.45 kg (1 lb.) and was similar in shape to today’s flying squirrels. It stretched a furry membrane between its limbs to provide an airfoil for gliding after it jumped from a tree. It steered with a long, stiff tail that acted as a rudder. It is one of the oldest in the fossil record to show fur, and it was so different from any other known mammal that the researchers had to create a new genus, family, and order for it. It serves as yet another example that early mammals were a lot more varied than scientists have traditionally envisioned.

The fossilized remains of a 130-million-year-old opossum-size mammal, *Repenomamus robustus*, were reported from Yixian, China (Hu et al., 2005). The mammal's last meal had been a juvenile dinosaur. Its limbs, fingers, and teeth were lodged within the mammal's rib cage, where its stomach had been. This is the first direct evidence that some of the early mammals were carnivorous and fed on small vertebrates, including young dinosaurs.

The Late Cretaceous was a time of change. Dinosaurs and most other reptiles became extinct. The extinction of Mesozoic reptiles left empty niches that were exploited by the more efficient mammals. Mammals began to "inherit the Earth." The advantages of homeothermy, viviparity, and the expansion of the brain allowed mammals to spread over most of the land surface of the Earth, to develop flight, and to reinvade the aquatic environment.

At the time of the dinosaurs' demise, most mammals were small, about the size of shrews and cats. The longstanding idea has been that once the dinosaurs were gone, mammals were suddenly free to exploit new food sources and habitats, and as a result they produced a burst of new species. A recent study says that happened to some extent, but that the new species largely led to evolutionary dead ends (Bininda-Emonds et al., 2007).

In contrast, no such explosion of species was found among the ancestors of modern-day mammals like rodents, cats, horses, elephants, and humans. Instead, researchers discovered an initial burst between 100 and 85 Mya, with another between about 55 and 35 Mya. The timing of that first period of development generally agrees with the conclusions of some previous studies of mammal DNA, which argue for a much earlier origin of some mammal lineages than does the fossil record. The second burst did show up in the fossil record.

A study of maximum body size revealed that within 25 million years of the dinosaurs' extinction—fast, in geologic terms—overall, land mammals had reached a maximum size and then leveled off (Smith et al., 2010). There was remarkable congruence in the rate, trajectory, and upper limit across continents and orders, despite differences in geographical and climatic history, turnover of lineages, and ecological variation. The largest land mammal ever was a rhinoceros-like creature, minus the horn, that stood 5.5 m (18 ft.) tall, weighed roughly 15,000 kg (33,000 lb.), and grazed in forests in what is now Eurasia. The researchers' analysis suggests that, although the primary driver for the evolution of giant mammals was diversification to fill ecological niches, environmental temperature and land area may have ultimately constrained the maximum size achieved.

The Saltville Deposits

Saltville, a small town with extensive saline deposits along the Holston River in southwestern Virginia, has been the site of major paleontological investigations since 1964. Large Pleistocene mammals known from this site include Jefferson's ground sloth (*Megalonyx jeffersonii*), the giant short-faced bear (*Arctodus*), the mastodon (*Mammut americanum*), the woolly mammoth (*Mammuthus primigenius*), the horse (*Equus* sp.), the caribou (*Rangifer tarandus*), the stag-moose (*Cervalces scotti*), and the musk ox (*Bootherium bombifrons*). Thomas Jefferson mentioned the "salines opened on the North Holston" in his 1787 book, *Notes on the State of Virginia*, giving them as the source of a mastodon tooth sent to him. Jefferson's reference makes the Saltville Valley one of the earliest localities on record for fossils of large mammals that lived in North America during the Pleistocene.

France et al., 2007; Moxley, 2016

Primate Evolution

Two families of primates of modern aspect are known from the Early Eocene of North America, Europe, and Asia: Adapidae and Omomyidae. Adapids are generally larger and, in some aspects, more lemur-like, while omomyids are smaller and more tarsier-like. Both families are frequently mentioned as possible stem groups having given rise to Anthropoidea. The oldest North American adapid is *Cantius torresi* from Wyoming.

Teilhardina (Omomyidae) was an early marmoset-like primate that lived in Europe, North America, and Asia in the Early Eocene epoch, about 56–47 Mya. Eight species are currently recognized. In North America, the discovery of mouse-sized primates *Shoshonius cooperi* and *Carpolestes simpsoni* in Wyoming deposits 50 million to 55 million years old (see Fig. 9.8), as well as *Teilhardina magnoliana* in 55.8-million-year-old rocks from the Gulf Coastal Plain in Mississippi, have altered estimates of when early primate groups first evolved. The oldest primates currently known from Europe (*T. belgica*) and Asia (*T. asiatica*) are slightly older than *T. brandti* from Wyoming. *T. magnoliana* is the most basal member of this genus currently known from either North America or Europe and is older than all other North American and European primates. Anatomical features of four nearly complete fossil skulls of *Shoshonius* indicate that it was a primitive form of tarsier—a tree-dwelling primate today found only in the forests of Southwest Asia. *Carpolestes* belonged to a group of small, long-tailed primates that lived just before the evolution of creatures with traits characteristic of modern primates: relatively large brains, grasping hands and feet with nails instead of claws, forward-facing eyes to enhance vision, and limbs capable of leaping. A 45-million-year-old fossil from eastern China, *Eosimias*, displays several anthropoid characteristics like small incisors, large canines, and the presence of distinctive premolars and molars. The back corner of its lower jaw was rounded along the bottom, as is the jaw of humans and other higher primates.

Scientists had assumed the evolutionary parting of tarsiers and simians had occurred about 40 Mya. Prior to the discovery of *Shoshonius* in the mid-1980s, *Eosimias* in 1994, *Carpolestes* in 2002, and *Teilhardina magnoliana* in 2008, the oldest well-documented anthropoids were found in Egypt in 1995 in 36-million-year-old rocks, suggesting that such creatures arose in Africa; however, the *Eosimias* fossils indicated an earlier origin, possibly in Asia. It now appears that *Shoshonius*, *Carpolestes*, *Teilhardina*, and modern tarsiers evolved from a common ancestor that split off from the forerunners of simians—monkeys, apes, and humans—sometime before 55 Mya. The discovery of a near-complete 55-million-year-old fossil of a tiny creature in China in 2002 has bolstered the idea that the anthropoid group of primates had appeared by at least 55 Mya. *Archicebus achilles* is thought to be the earliest-discovered ancestor of tarsiers, showing that even at this early time, the tarsier and anthropoid groups had split apart. *Archicebus* has several anthropoid-like features, including relatively small eyes and a short heel bone. It is considered to be the earliest known primate. The fossil, which was encased in rock, took 10 years of painstaking work to describe in detail.

Beard (2008) stated: “Undoubted primates first appear almost synchronously in the fossil records of Asia, Europe, and North America. This temporal pattern has complicated efforts to reconstruct the early dispersal history of primates in relation to global climate change and eustatic fluctuations in sea level.” Studies by Beard (2008) indicate that the earliest North American primates inhabited coastal regions of the continent for thousands of years before they were able to colonize the Rocky Mountain interior.

Beard et al., 1991; Bower, 1995; Simons, 1995; Culotta, 1995b; Bloch and Boyer, 2002; Ni et al., 2003; Smith et al., 2006; Beard, 2008; Ni et al., 2013

Relationships among fossil and extant mammals are being investigated and clarified through new systematic methods and techniques such as X-ray computed tomography (CT) (Rowe et al., 2011; 2016), a growing molecular database, and continuing paleontological discoveries. Cladistics and powerful computer programs have permitted the analyses of diverse anatomical characters and nucleotide sequences, while molecular techniques have produced data through protein-sequencing, direct comparisons of DNA sequences from selected genes, and immunological comparisons. For example, Springer et al. (1997) found that the sequence of nucleotides of five genes differed from animal to animal. Of the mammals studied, the most closely related turned out to be elephants, aardvarks, manatees, golden moles, elephant shrews, and hyraxes (small, rabbit-like animals of Africa and Asia). Far less similar were the animals that had been considered relatives of golden moles—shrews, common moles, and hedgehogs. The genetic evidence also showed that elephant shrews, thought to be most closely related to rabbits and rodents, are nearer to aardvarks and elephants. Based on the genetic differences observed, Springer et al. (1997) estimated that the common ancestor of all these mammals lived about 80 Mya, probably in Africa, since that is where the earliest fossils of members of these six groups have been found. Embryological studies of the renal, reproductive, and respiratory systems of the elephant confirm that it evolved from an aquatic mammal and that elephants share a common ancestor with sea cows (Sirenia) (Gaeth et al., 1999). Virtual three-dimensional "casts" of the fossilized skulls of animals that preceded the first mammals suggest that brain areas involved in smell, or olfaction, catalyzed brain growth in the evolutionary branch that gave rise to mammals (Rowe et al, 2011).

The Number of Mammalian Genera

John Alroy at the University of Arizona has compiled a massive database showing an "equilibrium" of mammalian diversity in North America. After the Cretaceous-Tertiary extinctions 65 Mya, the number of mammalian genera shot up to a high of about 130 genera 55 Mya. Thereafter, the number of genera waxed and waned, sinking to as low as 60 and rising to as high as 120, presumably in response to climate change and immigration. These fluctuations lasted millions of years, but diversity over time always averaged an equilibrium of about 90 genera. This equilibrium may represent the ecological carrying capacity for North America, and resource (e.g., food) availability may be enforcing the limit. When diversity is low, species tend to fare better because they face less competition from other species. As diversity increases, speciation declines and extinction rates go up. The result is a continuous turnover of genera but the maintenance of a relatively stable mammalian diversity over time.

Culotta, 1994

Molecular, paleontological, and morphological studies have suggested that the cetaceans (whales, dolphins, and porpoises) and artiodactyls (even-toed ungulates, including pigs, hippopotamuses, camels, and ruminants) form a clade or monophyletic group, that is, they have a common ancestor that is not shared by any other group of mammals. Molecular data presented by Shimamura et al. (1997) and reviewed by Milinkovitch and Thewissen (1997) confirm this close relationship and also propose that cetaceans, ruminants, and hippopotamuses form a monophyletic group within the Artiodactyla.

For years, the hippopotamus has been the leading candidate for the closest land relative to cetaceans because of its similar DNA and whalelike features. The 48-million-year-old *Indohyus* discovered in the Kashmir region of India is considered to possibly be the missing evolutionary link between whales and land animals (Thewissen et al., 2007). The key finding connecting *Indohyus* to the whale is its thickened ear bone, something only seen in cetaceans. An examination of its teeth show that the land-dwelling creature spent a lot of time in the water and may have fed there, like hippos and whales. Also, the specific positioning and shape of certain molars connects *Indohyus* to the earliest whales, which are about 50 million years old. The earliest whales lost their legs and the ability to walk on land about 40 Mya. *Indohyus* looks like a tiny antlerless deer about the size of a raccoon. It most resembles the current African mousedeer, which has a ratlike nose and jumps in the water and hides when danger approaches.

Until recently, the oldest known hippo ancestor dated from 20 Mya. In 2015, the molars and lower jaw of a new species, *Epirigenys lokonensis*, were discovered at Lokone in northern Kenya (Lihoreau et al., 2015). *E. lokonensis* is about the size of a sheep; it and the hippo both came from an anthracothere forefather which migrated from Asia to Africa about 35 Mya. These fossils, which have been shown to be a hippopotamoid displaying a functionally intermediate combination of characters, improve our understanding of the anthracothere-hippopotamid relationship in Africa and push back the evolutionary history of hippopotamids in Africa to the Paleogene. They confirm that cetaceans are the hippo's closest living cousins.

MORPHOLOGY

Integumentary System

The presence of a lightweight, waterproof epidermal layer has been important in allowing mammals to successfully colonize a variety of terrestrial environments. Some mammals, like beavers and rats, have epidermal scales on parts of their bodies (feet, tail), but only the armadillo has **dermal scales (plates)** beneath the epidermal scales (see Fig. 1.10). These dermal scales form the protective armor covering of the armadillo.

The mammalian epidermis, which is composed of keratinized stratified squamous epithelium, is differentiated into distinct layers (Fig. 9.9). The deepest layer is the **stratum basale (germinativum)** and, as in other vertebrates, is the area of active mitosis. As new cells form, older cells are pushed toward the surface and become successively part of the **stratum spinosum**, the **stratum granulosum**, often the **stratum lucidum**, and finally, the surface **stratum corneum**. **Keratin**, which is impermeable to water and gases, is produced by **keratinocytes**, the most abundant of the epidermal cells. **Melanocytes** (melanophores) produce the pigment melanin, which is primarily responsible for skin color and for protecting keratinocytes and the underlying dermis from excessive ultraviolet (UV) radiation.

The epidermis gives rise to hair, various glands, nails, scales, hooves, baleen, and (together with the dermis) horns. Hair is one of the most characteristic epidermal specializations in mammals. It represents a new development, not a modification of horny scales, in the way feathers are. Anatomical, developmental, neurological, and paleontological data have been used to support the hypothesis that mammalian hair arose from highly specialized sensory **mechanoreceptors** (receptors that detect mechanical deformation of the receptor itself) found in early synapsids.

Two kinds of hair are present. The outer, coarser, and usually longer hairs, which serve a primarily protective function, are **guard hairs**. The inner, finer, and usually shorter hairs constitute the **underfur**, which serves to insulate the body. Vibrissae, bristles, and quills are specialized modifications of guard hairs. Specialized hairs around the mouth (mystacial vibrissae) and eyes (superciliary vibrissae) often serve as tactile organs and are sensitive to touch. Each vibrissa is attached beneath the skin to a capsule that loosely surrounds it. In the capsule is a jelly-like layer of fatty tissue that can stimulate the capsule membrane, to which up to 150 nerve fibers may be attached.

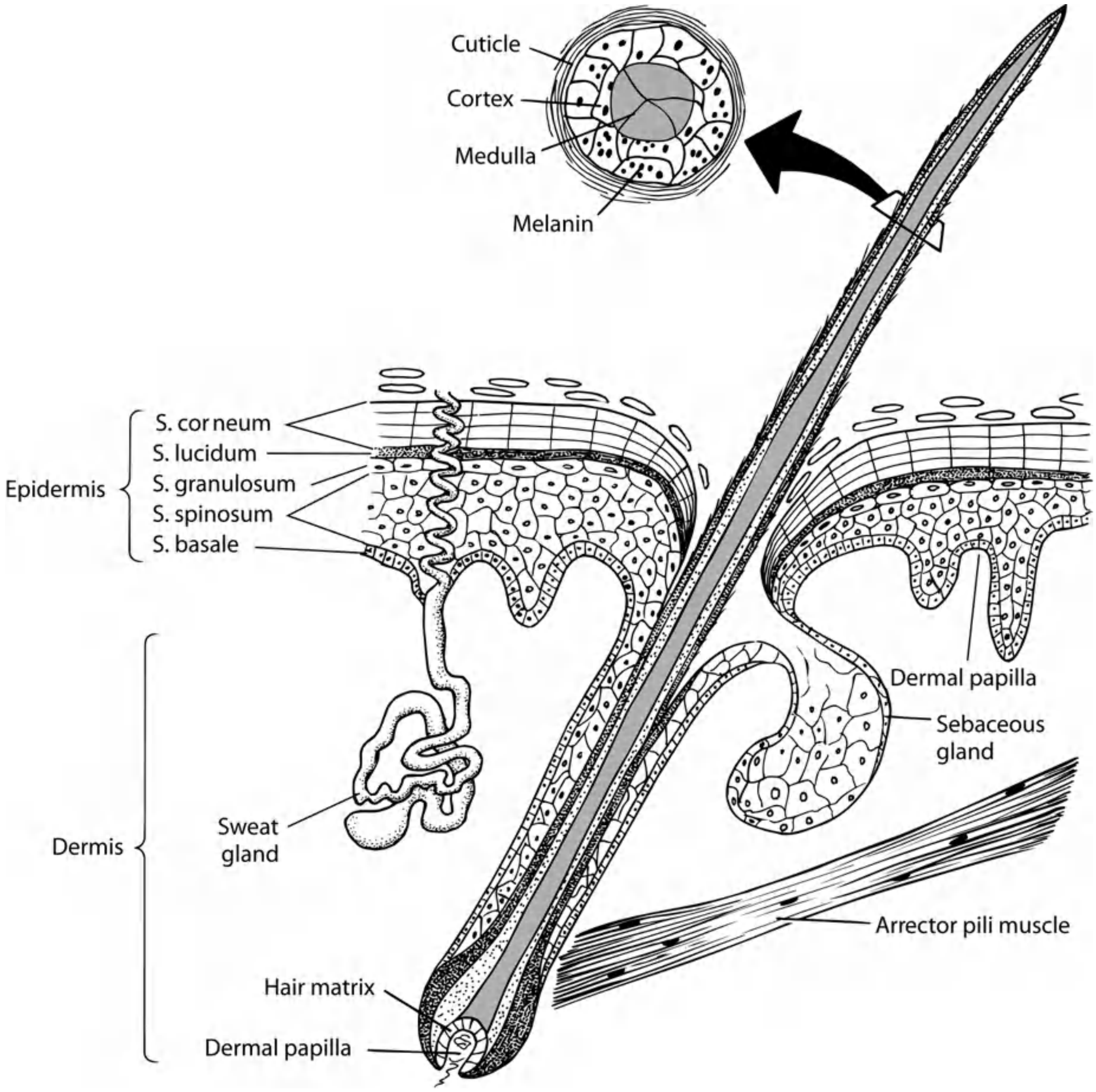


Figure 9.9. Section of mammalian skin showing the structure of a hair and glands. Sebaceous glands produce sebum, which lubricates the hair and skin. Sweat (sudoriferous) glands secrete either a watery sweat that cools the body as it evaporates or a milky secretion that may play a role in sexual attraction.

Hair is present in at least some stage of development in all mammals. Intraspecific variation occurs, especially in the guard hairs and in the scales along the hair shaft. There is little or no sexual or seasonal difference in hair structure.

Hair completely covers the bodies of most species, although it may be restricted to specific areas in others. For example, the naked mole rat (*Heterocephalus glaber*) of Ethiopia, Somalia, and Kenya has only a few pale-colored hairs scattered over the body, vibrissae on the lips, and fringes of hairs on its tail and between the toes of its hind feet (Sherman et al., 1992). In some adult whales, hair may be almost entirely absent, with only a few vibrissae being present around the lips. In some whales, hair may be present only in the young. At the other end of the spectrum, sea otter fur contains about 100,000 hairs per cm^2—the densest fur of any mammal (Love, 1992; Kruuk, 1995).

Compensating for poor eyesight and murky water, Florida manatees (*Trichechus manatus*) have an acute sense of touch (Reep and Sarko, 2009). Their mastery of the tactile world comes from their thick, bristly vibrissae (Fig. 9.10). Unlike normal hair fibers, each vibrissa is a finely calibrated sensory device, its follicle surrounded by a blood-filled pocket or blood sinus. The manatee has 2,000 facial vibrissae of varying thickness, 600 of them in the so-called oral disk, a circular region between its mouth and nose that the manatee uses much like an elephant's trunk to grasp or explore objects. Each facial vibrissa is linked with 50 to 200 nerve fibers. An additional 3,000 vibrissae are spaced less densely over the rest of the body.

Dolphin Swimming

Dolphins are among the sea's fastest swimmers, capable of pacing ships traveling 48 km (30 mi.) per hour or more. Japanese scientists have uncovered one of the secrets of the animal's speed: shedding skin. Dolphins shed their skin every two hours. By using computer models, researchers showed that the flaking skin helps break up tiny drag-inducing whirlpools of water called vortices that form around the swimming dolphin and slow it down.

Nagamine et al., 2004

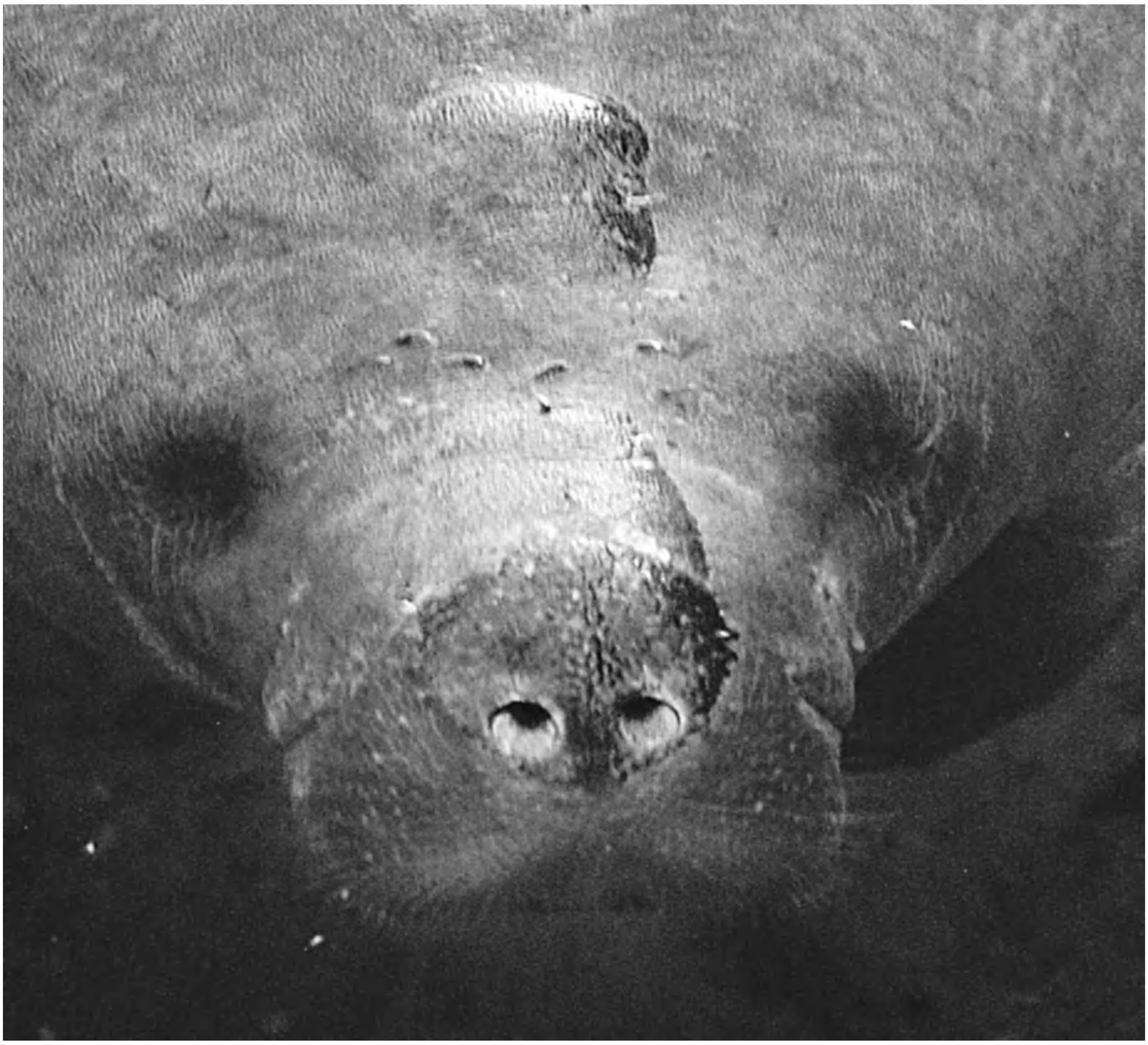


Figure 9.10. Each of the Florida manatee's vibrissae is an acute tactile sensory structure.

An individual hair first appears as a hair primordium. The primordium is a downward-projecting growth from the stratum basale. A dermal papilla forms at the base of the indentation. As epidermal cells continue to proliferate, the hair primordium grows deeper into the dermis and is nourished by blood vessels of the papilla. The hair primordium finally surrounds the dermal papilla as an inflated balloon would surround a finger pushed into it. When the bulb at the base of the primordium is differentiated sufficiently, cells begin to appear and a hair shaft begins to rise in the follicle. The hair thus is forced out of the skin by growth from below.

A typical hair consists of a **shaft** and a **root** (see Fig. 9.9). The shaft lies free within the follicle and projects above the surface of the skin. In general, the shaft points posteriorly in order to minimize friction with the environment. The root is that portion deep within the follicle where the hair has not yet separated from the surrounding epidermal cells of the follicle wall. The swelling at the base of the hair containing the dermal papilla is known as the **bulb**. It is an area of rapid mitosis, which is constantly contributing new cells that make the hair longer.

The shaft of a typical hair consists of an inner **medulla** (which contains most of the pigments that determine the appearance of the hair), a surrounding **cortex** (which forms the main bulk of the hair and is usually transparent, but may contain pigments), and an outer **cuticle**. Hair color is determined by the distribution and density of melanin and xanthophyll granules in the keratinized cells and by the number of air vacuoles in the medulla of the hair. Gray and white hairs result from large numbers of air vacuoles and little melanin.

The thin cuticle is devoid of pigment and is composed of **cuticular scales** that completely surround the hair shaft. Scale patterns vary so greatly that their arrangement is often characteristic of a species and has been used to identify loose hairs from animal dens and scats (feces). Large hairs generally contain air spaces that add greatly to the insulating properties of the hair. In cross section, hairs may be round, oval, or flattened. Circular hairs are usually straight or only slightly curved, whereas flattened hairs are curly.

The **arrector pili** (see Fig. 9.9), a small smooth muscle, inserts on the wall of the hair follicle in the dermis of many mammals. When the arrector pili muscles contract, the follicles and hair shafts are drawn toward a vertical position. The skin around the base of each hair is pulled into a tiny mound, causing (in humans) “goose bumps” or “goose flesh,” a vestigial physiological response no longer capable of serving an insulating function. In most mammals, however, the action of the arrector pili muscles allows a layer of air to be trapped between the skin and the fur to provide increased insulation for both heat gain and heat loss. When frightened or alarmed, some mammals show aggression by erecting their hair.

Hairs, like feathers, are nonliving, keratinized structures that are constantly subjected to wear and must be replaced. In many mammals, hair replacement is seasonal; some molt their fur annually, usually in the fall. Snowshoe, or varying, hares (*Lepus americanus*) and short-tailed weasels (*Mustela erminea*) are examples of mammals that molt twice a year, in the spring and fall; still others molt irregularly. The replacement of specialized hairs like eyelashes and vibrissae occurs on a continual basis and varies with each individual.

Some species undergo dramatic changes in appearance when they molt. Short-tailed weasels, for example, remain brown throughout the year in the southern part of their range. In the northern part of their range, however, they turn white in winter and are much less conspicuous on snow-covered terrain. This change results from a molt in which the new hairs contain no pigment. Several hares, including the snowshoe hare (Fig. 9.11), weasels, the Arctic fox (*Alopex lagopus*), and collared lemmings (*Dicrostonyx* sp.) are among 20 or more color-changing species of birds and mammals around the world that exhibit similar seasonal changes. Mills et al. (2018) mapped global patterns of seasonal coat color change across eight species including hares, weasels, and foxes.

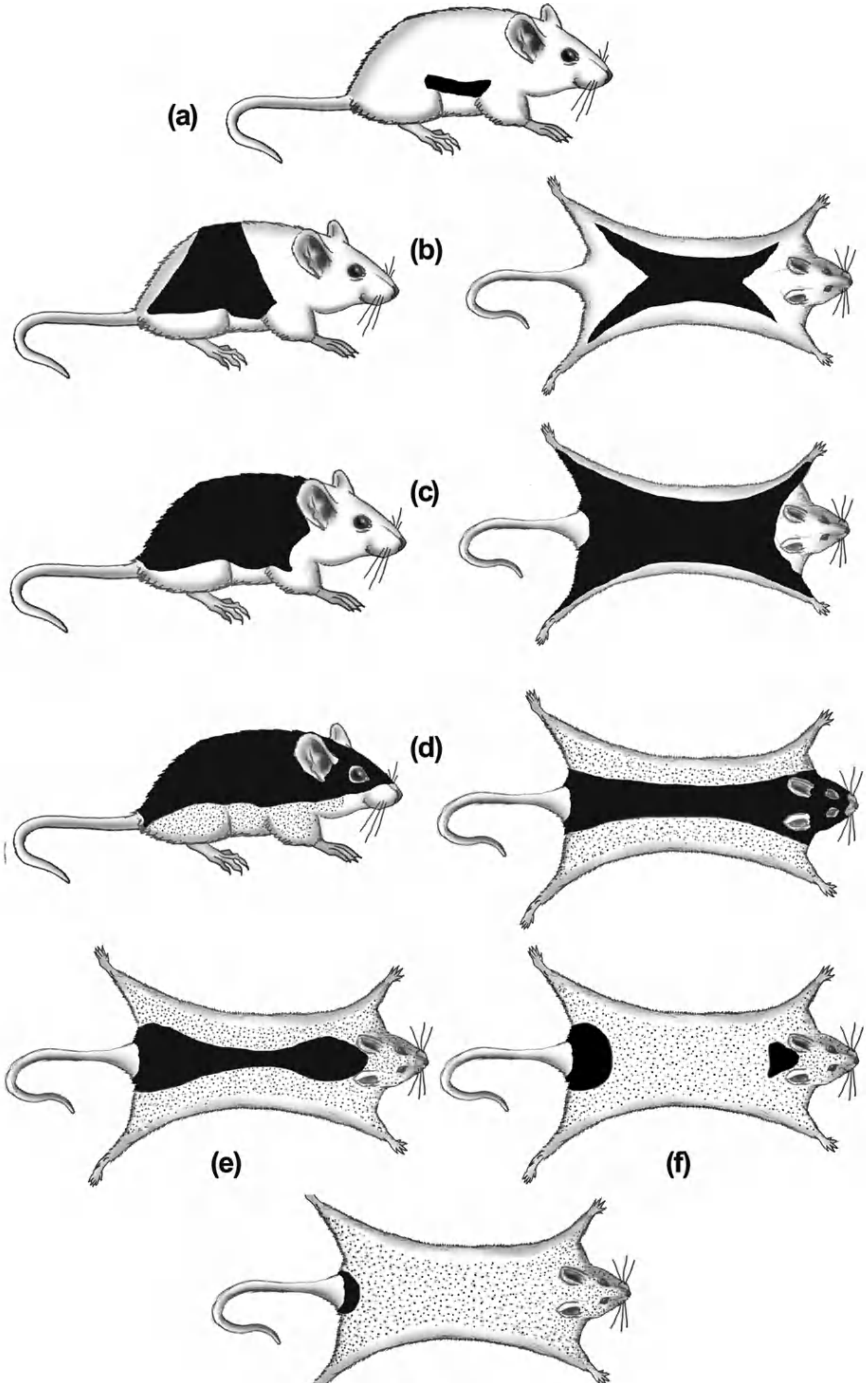
Snow cover is predicted to become rarer as climate change results in warmer temperatures. In a study of snowshoe hares (*Lepus americanus*) in western Montana, Mills et al. (2013) showed that annual average duration of snowpack is forecast to decrease by 29 to 35 days by midcentury and 40 to 69 days by the end of the century. Seasonal coat color polyphenism creating camouflage against snow is a direct and potentially severe type of seasonal mismatch if crypsis becomes compromised by the animal being white when snow is absent. Currently, the average hare is mismatched only about a week out of the year. When hare deaths were tracked, researchers were able to show that when hares are mismatched with the color of their background, they experienced weekly survival decreases up to 7 percent (Zimova et al., 2016). The study found that populations of snowshoe hares have plasticity in the rate of the spring white-to-brown molt, but not in either the initiation dates of color change or the rate of the fall brown-to-white molt.

Gigliotti et al. (2017) compared the physiological characteristics of snowshoe hares from Canada’s Yukon with those in Pennsylvania. They found that Pennsylvania hares produce relatively light-duty winter fur coats. The underfur was 58 percent less dense than those of their northern counterparts, while their guard hairs were 32 percent less dense and 20 percent shorter. Temperature sensors indicated that Pennsylvania hares produced less body heat than hares from the Yukon, which suggests that they have slower metabolism. Several hares in the study did not change color from brown to white in winter. The authors speculated that (1) the hares may have kept their summer coat because they did not need the insulation or (2) there may be some reduced predation risk for hares that retain a brown coat in an environment where persistent snow cover is unpredictable. If the duration of snow cover decreases due to climate change, the authors predict that the range of the hare will contract northward. If they cannot adapt fast enough, snowshoe hares may become extirpated from Pennsylvania.

Photoperiod (day length), in conjunction with melatonin produced by the pineal gland, initiates changes in the central nervous system and in the endocrine glands that induce molting. Molting is a gradual process in which old hairs are not lost until new hairs have almost fully formed. The sequence of hair replacement and the molting pattern is species-specific (Fig. 9.12).

(a)

Figure 9.11. Snowshoe, or varying, hare (*Lepus americanus*) in (*a*) brown summer pelage and (*b*) white winter pelage. In winter, extra hair growth on the hind feet provides the hare with better support in the snow. Snowshoe hares inhabit the northern coniferous forests and serve as important food for lynxes, foxes, and other carnivores.


(a)
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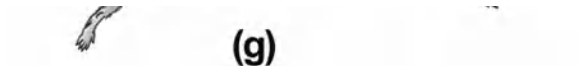


Figure 9.12. Sequence of postjuvenal molt on the dorsum in the golden mouse (*Ochrotomys nuttalli*). Shaded portions represent areas of active hair replacement. Stippled areas represent adult pelage.

The color of a mammal is the result of either the color of the skin due to capillaries and pigments, the color of the fur (pelage), or both. Hair color is determined by the amount and distribution of pigments in addition to the structure of the hair. Two pigments, melanin and xanthophyll, are normally found in mammalian hairs and are deposited while the hair is growing in the follicle. Melanin may be present in the medulla and/or cortex of a hair and produces black or brown hair. Xanthophyll occurs only in the medulla and results in reddish or yellowish colors. Color patterns are caused by genetically controlled variations in the amounts and distribution of pigments present in the hair.

Two color phases may be expressed in different individuals of the same species. This phenomenon is termed **dichromatism**. The occurrence of these color phases (which is genetically controlled) often consists of a black phase (melanistic form), as well as the normal wild type in the same population. Black gray squirrels (*Sciurus carolinensis*) and black fox squirrels (*Sciurus niger*) often have melanistic individuals and normal-colored individuals occurring in the same litter. The darker phase sometimes is more prevalent in the northern part of the range of the species. As many as 12 color phases are known in the fox squirrel (*Sciurus niger*).

Whereas one function of hair is to serve as a tactile organ, other major functions are to protect the body from the elements, to provide insulation, to aid in concealment, to serve as a warning mechanism, to assist with communication, and even to assist in locomotion. Air trapped under the hair also can modify the buoyancy of some aquatic mammals like river otters (*Lutra canadensis*); hair on the dorsoventrally flattened tails of flying squirrels (*Glaucomys*) assists in gliding by helping the tail serve as a rudder (Fig. 9.13); water shrews (*Sorex palustris*) and muskrats (*Ondatra zibethicus*) have a fringe of hairs along the outer edge of each foot, which assists their movements in water by providing a greater surface area. Quills of the porcupine (*Erethizon dorsatum*) and scales (modified hairs) of the pangolin (*Manis tricuspis*) serve for protection. In certain situations, hair may be used to show aggression. Some prey species have developed elaborate displays that may often be warning signals directed to other prey. For example, the white rump patch of white-tailed deer (*Odocoileus virginianus*) is normally covered by the tail and is only slightly visible, but when the deer is alarmed, the tail is raised and the exposed white rump patch serves as a warning to other nearby deer (Fig. 9.14). In other species, the prey display may be aimed instead at the predator in an apparent attempt to deter further pursuit (Hasson, 1991).

Figure 9.13. The nocturnal northern flying squirrel (*Glaucomys sabrinus*) has excellent night vision. When the gliding skin (patagium) is spread, the undersurface is nearly trebled, and glides of 40 to 50 m (130–165 ft.) are possible. Special muscles adjust the position of the patagium during flight, thus providing good maneuverability.

Claws, **nails**, and **hooves** are hard, keratinized modifications of the stratum corneum at the ends of digits. Most mammals possess claws, but these structures have evolved into nails in most primates and into hooves in ungulates. None of these structures is shed; they must be worn down by friction.

Several unique epidermal derivatives occur in some mammals. For example, pangolins are covered with epidermal scales that are composed of fused bundles of hair. Hairs also grow between these scales. The scales covering the tails of rodents are also epidermal in origin. Large plates of **baleen** (often known as whalebone), which develop from cornified oral epithelium, are suspended from the palate in toothless whales (Mysticeti). The frayed edges of these sheets serve to strain plankton from water in the oral cavity (Fig. 9.15).

Four types of structures that adorn the heads of some mammals—true horns, rhinoceros horns, antlers, and giraffe horns—play roles in reproductive behavior, defense, and offense. **True horns**, characteristic of most members of the bovine family (cattle, most antelope, sheep, and goats) (Fig. 9.16a–d), consist of a permanent bony dermal core covered by a permanent horny epidermal sheath. True horns, which generally are not branched and usually are never shed, occur in both sexes but are typically larger in males. Horns grow from the base, and the dermal core increases in girth as the animal ages (Figs. 9.16a, 9.17a). The growth rings that are formed are somewhat similar to those of a tree and are useful in determining age. Pronghorn antelopes (Fig. 9.16d) possess true horns, but they are forked; the horny covering (but not the bony core) is shed annually.

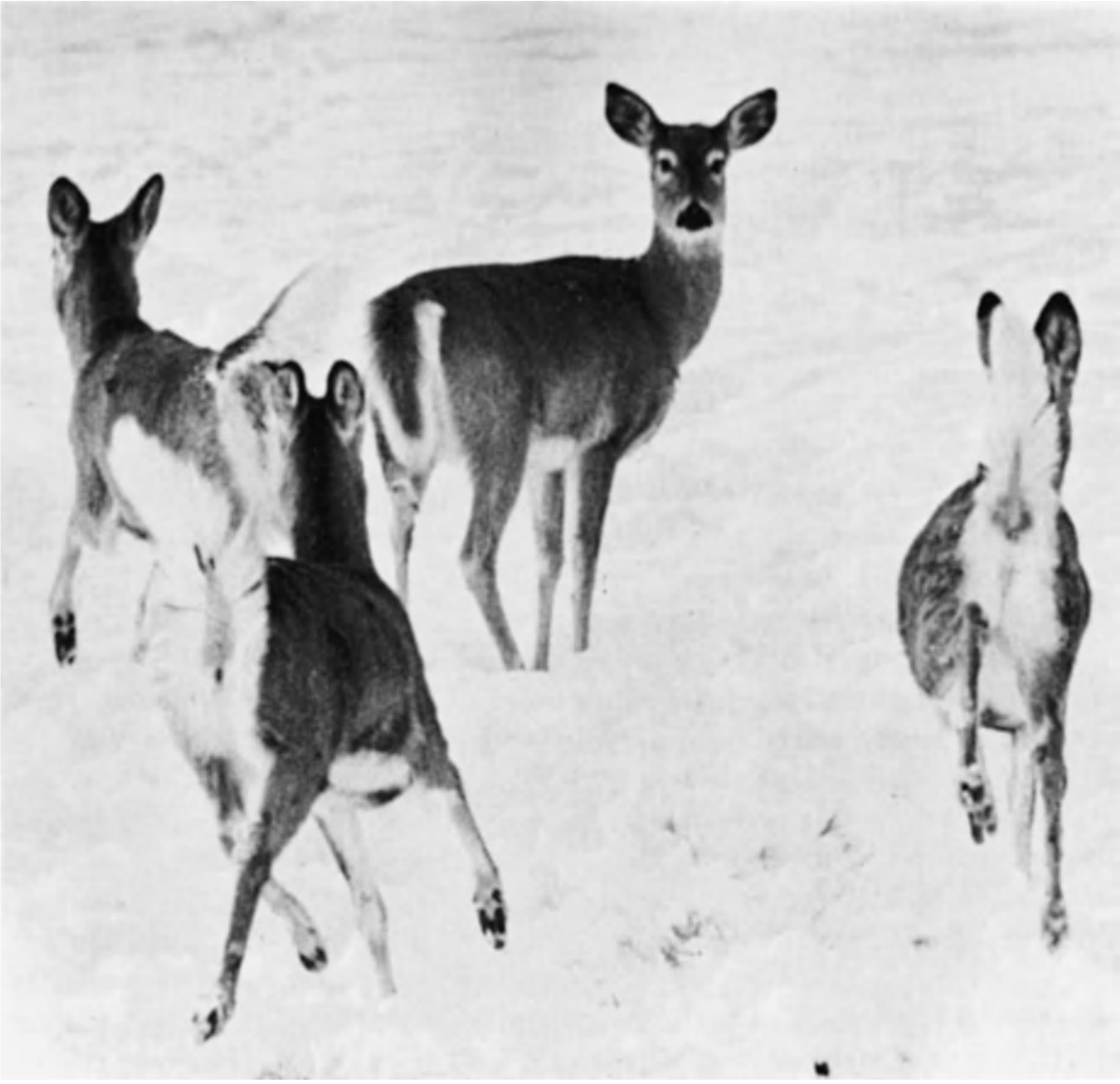


Figure 9.14. Alarmed white-tailed deer (*Odocoileus virginianus*) lift their tails high in the air and expose the conspicuous white underside as a means of alerting other members of the herd or perhaps as a signal to a potential predator that it has been seen.

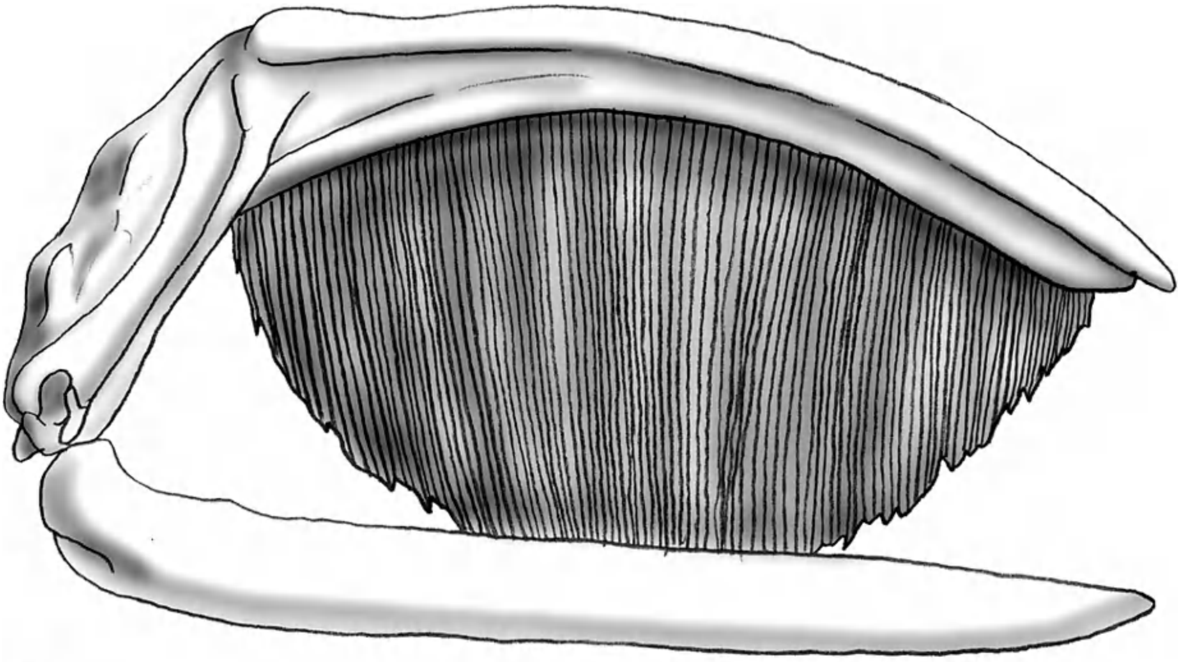
Vibrissae in Seals

Extremely well-developed vibrissae (specialized hairs around the mouth and eyes) are found in the ringed seal (*Phoca hispida saimensis*), which lives in perpetually murky water around Finland. The innervations of the vibrissae are more than 10 times as great (1,200–1,600 fibers) as those normally found in mammals. The seals are thought to maneuver and locate food by echolocation; however, their low-frequency clicks do not reflect well. The sensitive vibrissae may aid echolocation by serving as antennae for monitoring the returning echoes. In addition to spatial orientation, the vibrissae may also provide the seals with information about the diving speed and changes in swimming orientation. Harbor seals (*Phoca vitulina*) also use their vibrissae as a hydrodynamic receptor system to detect minute water movements, allowing them to gain information about aquatic prey, predators, or conspecifics. The vibrissae have been found to be superbly sensitive detectors of motion in the swirling wake left by swimming fish.

Hyvärinen, 1989; Dehnhardt et al., 1998, 2001

Rhinoceros horns (see Fig. 9.16e), are not true horns; they are composed of tightly packed, keratinized filaments similar to hairs but which differ in that they possess gas spaces and lack a cuticle (Ryder, 1962). Each fiber is separately visible, and there is no bony core. Rhinoceros horns occur on the snouts of both sexes and never are shed. Indian rhinoceroses (*Rhinoceros*) have one horn; African rhinoceroses (*Diceros*) have two horns. These horns grow throughout the animal’s life and will regrow if removed.

Antlers are branched structures composed of solid, dead dermal bone and are characteristic of members of the deer family (Cervidae) (Figs. 9.17b and 9.18). Antlers, which are secondary sex characteristics, are affected by annual fluctuations in secretion of sex hormones, primarily testosterone. Photoperiod is the primary stimulus for antler replacement (Goss, 1983). Increasing photoperiod stimulates the **adenohypophysis** (anterior pituitary gland), which in turn stimulates the production of testosterone. Antlers normally begin growing in spring, reach their full growth during summer, and are shed in mid-winter (Fig. 9.19a–e). They are renewed annually by apical growth centers; thus, they grow by adding new material at the extremities. While forming, antlers are covered with a layer of skin, or “**velvet**.” Blood in the arteries of the velvet supplies the growing antlers, which are innervated by branches of the trigeminal nerve. When the antler reaches its full growth, the velvet is shed or rubbed off, and the bare, dead, branched bone remains. Antlers usually occur only on males and are shed annually. In caribou, also known as reindeer (*Rangifer tarandus*), antlers occur on both sexes, although those of males are larger and more branched. The only members of the family Cervidae that do not possess antlers are the Chinese water deer (*Hydropotes inermis*) and the musk deer (*Moschus* sp.), both of which have evolved tusks (Fig. 9.20). A complete discussion of the anatomy, evolution, and function of antlers may be found in Goss (1983).



(a)

(b)

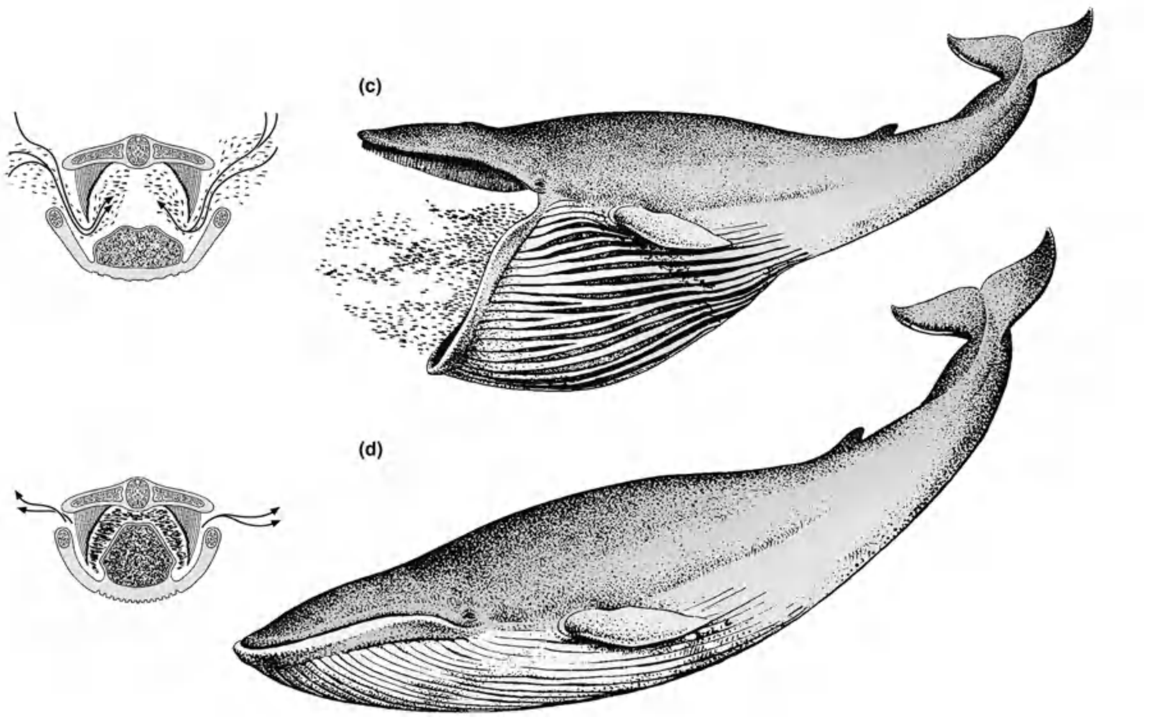


Figure 9.15. Baleen. The lining of the mouth in some whales includes an epithelium with the ability to form keratinized structures. Groups of outgrowing epithelia become keratinized and frilly to form the baleen. (*a*) Skull of the Atlantic right whale (*Eubalaena*); length of the skull is approximately 4 m (13 ft.). Note the baleen plates attached to the maxilla. (*b*) Lateral view into the partly opened mouth of a gray whale (*Eschrichtius robustus*) showing the plates of baleen hanging from the palate. Gulping (lunge feeding) in baleen whales: As the mouth opens, huge amounts of water pour in along with great quantities of plankton and nekton as the throat grooves (*c*) allow for expansion of the oral cavity. (*d*) This water is then expelled through the filter-like baleen as the throat contracts, trapping the food that is scraped off by the tongue and swallowed.

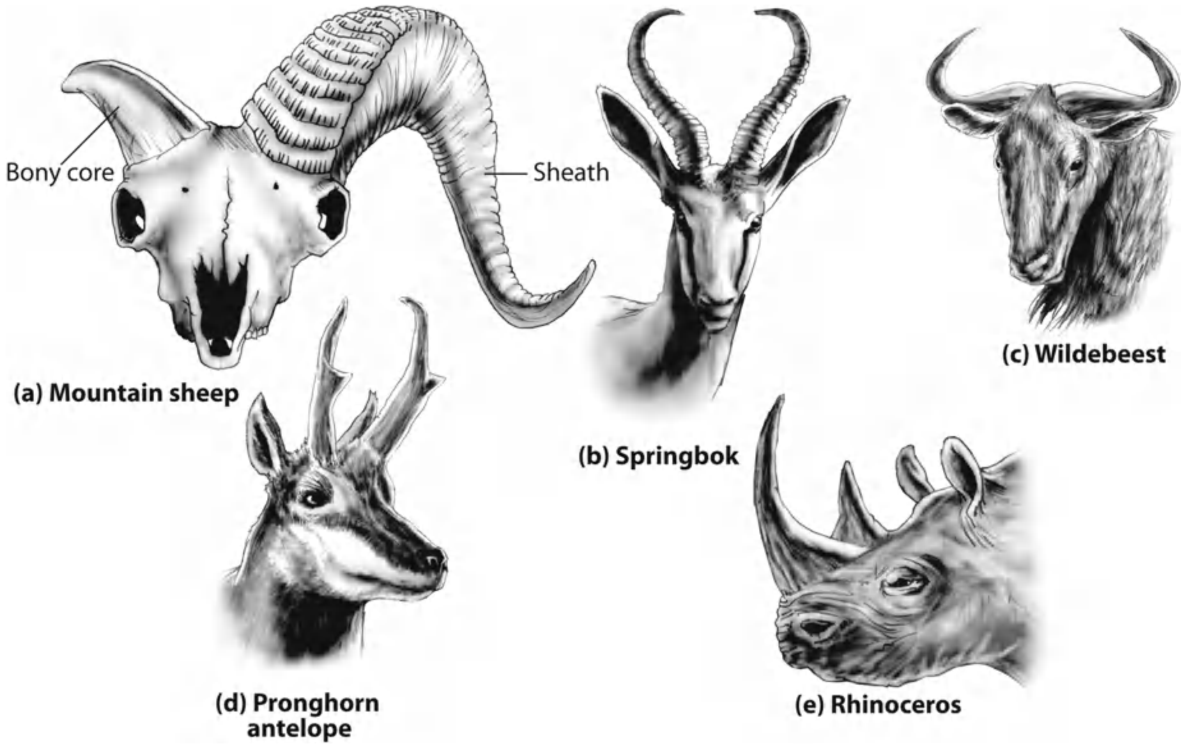


Figure 9.16. True horns consist of a bony core covered by an epidermal sheath and, in most species, are permanent structures: (*a*) mountain sheep with the cornified covering of the horn removed on one side to reveal the bony core; (*b*) springbok; (*c*) wildebeest; (*d*) pronghorn antelope, the only horned animal with horns that are deciduous and are periodically shed; (*e*) rhinoceros horns are solid structures composed of compacted keratinized fibers.

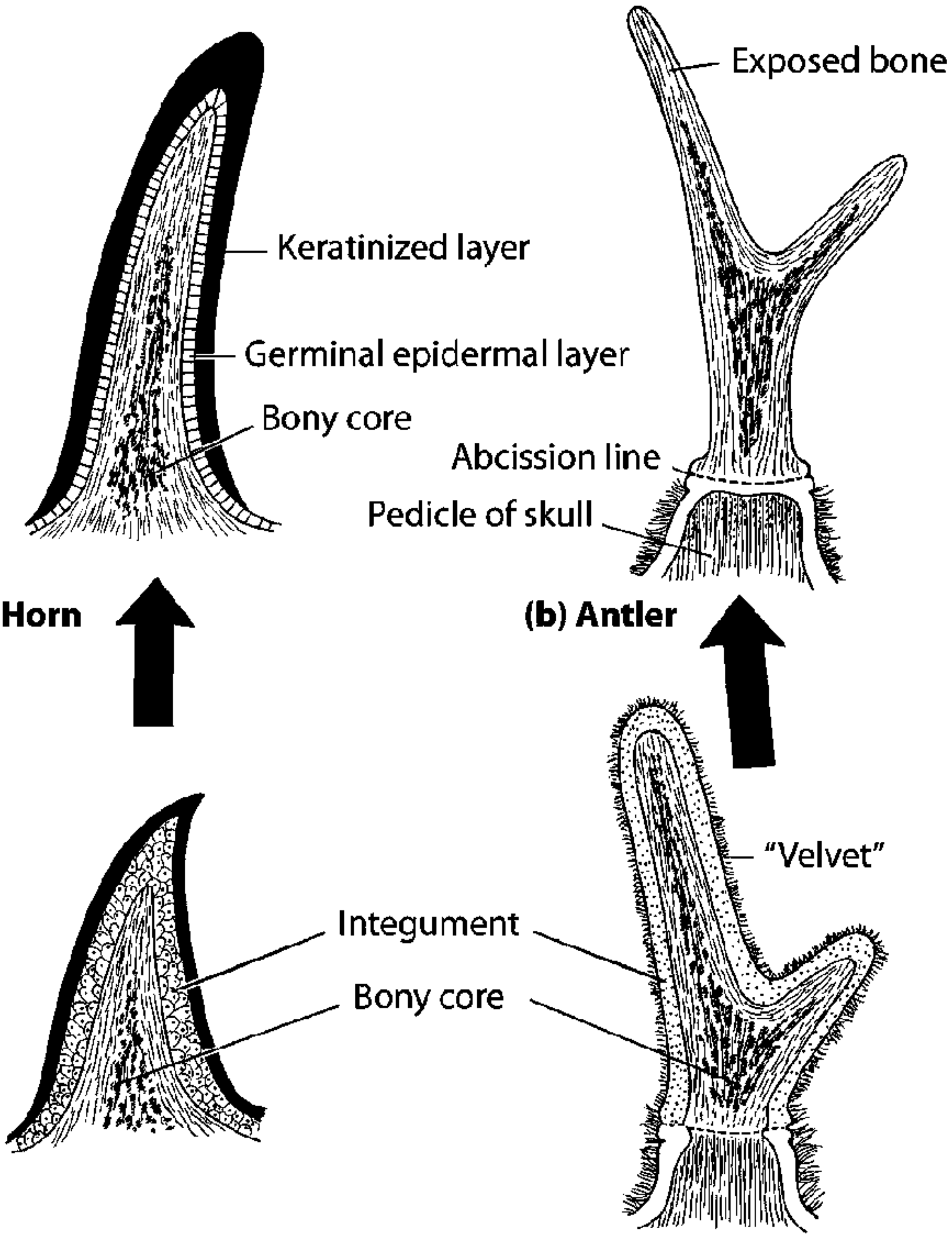


Figure 9.17. Horns and antlers. (*a*) Horns are bony outgrowths of the skull beneath the integument; the integument forms a keratinized (cornified) sheath. Horns occur in bovids of both sexes and are usually retained year-round. (*b*) Antlers are also bony outgrowths of the skull beneath the integument. The integument, or skin, which is referred to as "velvet" because of its appearance, gradually dries and falls off, leaving the bone of the antlers exposed. Antlers are found only in members of the deer family (Cervidae) and, except for caribou (reindeer), they are normally present only in males. Antlers are shed and replaced annually.

Figure 9.18. The massive antlers of the extinct giant Irish elk weighed more than its entire internal skeleton.

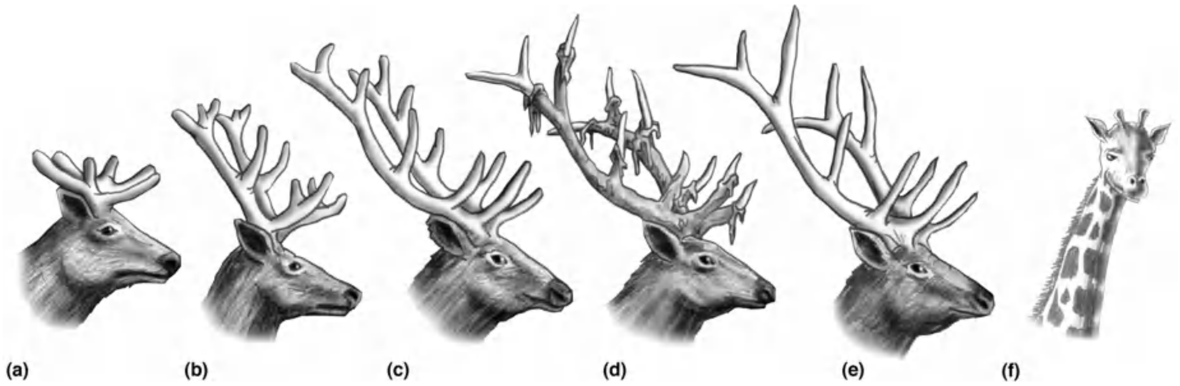


Figure 9.19. Annual growth of elk antlers: (*a*, *b*) New antlers begin to grow in April. (*c*) By May, antlers are nearly fully formed, even though they are still covered by the living integument (velvet). (*d*) By late summer, the velvet has begun to dry and peel off. (*e*) Fully formed bony antlers are in place. Antlers are normally shed in March and early April. (*f*) Giraffe horns are small, ossified knobs covered by the integument.

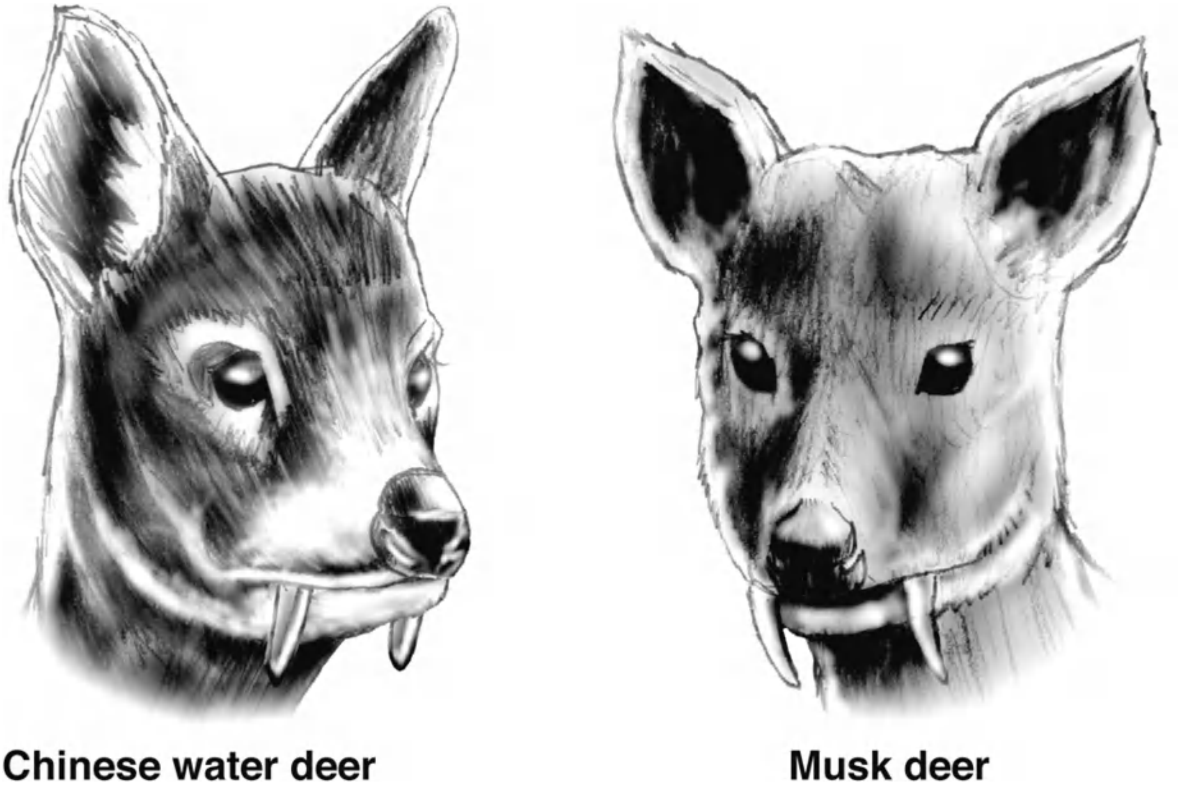


Figure 9.20. The Chinese water deer (*Hydropotes inermis*) (*left*) and the musk deer (*Moschus*) (*right*) are the only members of the family Cervidae that do not possess antlers. These two species, however, have evolved tusks.

Giraffe horns occur on giraffes (*Giraffa camelopardalis*) (see Fig. 9.19f) and okapi (*Okapi johnstoni*). These stubby “stunted” horns remain covered by living skin (velvet) throughout life and never are shed.

Multicellular skin glands are more abundant and diverse in mammals than in any other vertebrate group. They serve many functions, from sensing changes in the environment to providing milk for the young. Glands like the mammary and sweat glands are unique to mammals.

Sudoriferous (sweat) glands are long, slender, coiled tubes of epidermal cells that extend deep into the dermis and often into the subcutaneous layer (see Fig. 9.9). Their secretion is watery and contains fatty substances, salts, and pigments. Sweat assists in thermoregulation and also helps eliminate wastes, like urea and various salts, from the body. Sweat glands, which occur in most mammals, are absent in moles, sloths, scaly anteaters, elephants, and many marine forms. They may be distributed widely over the body or restricted to certain regions like the soles of the feet (mice, cats), the face (some bats), or the ventral surface of the body (wandering shrew).

Mammary glands (Fig. 9.21), one of the distinguishing characteristics of mammals, are modified sudoriferous (sweat) glands that produce milk for the nourishment of the young. They consist of numerous lobules, each of which is a cluster of secretory alveoli in which milk is produced. The alveoli may empty into a common duct that opens directly to the surface through a raised epidermal papilla, or nipple (Fig. 9.21, inset). Alveolar ducts can also open into a common chamber, known as a cistern, with a long collar of epidermis, called the teat (Fig. 9.21, inset). Secretion of milk is mainly due to the hormone prolactin, produced by the anterior lobe of the pituitary gland. The distribution and number of mammary glands vary with species, with the number ranging from a single pair to as many as 12 pairs. In general, the number of teats is equal to the maximum litter size or twice the average litter size (Diamond, 1988b). Teats occur in locations appropriate to the habits of the species—thoracic (bats, primates, elephants, manatees), abdominal (many rodents, carnivores), or inguinal (ungulates) (Fig. 9.21a, b). Nutria (*Myocastor coypus*) have nipples high on their sides so that the young can nurse while swimming. Monotremes (duck-billed platypus and echidna) lack true mammary glands and nipples. Glands resembling modified sweat glands produce a nutritious secretion that is lapped off tufts of hairs. In many cetaceans (whales, dolphins, porpoises) and seals, the nipples may be retracted into slits on either side of the vent when they are not in use (Fig. 9.21c). This improves hydrodynamics during swimming and keeps the nipples warm. The nipples descend when the pup nudges its mother's belly.

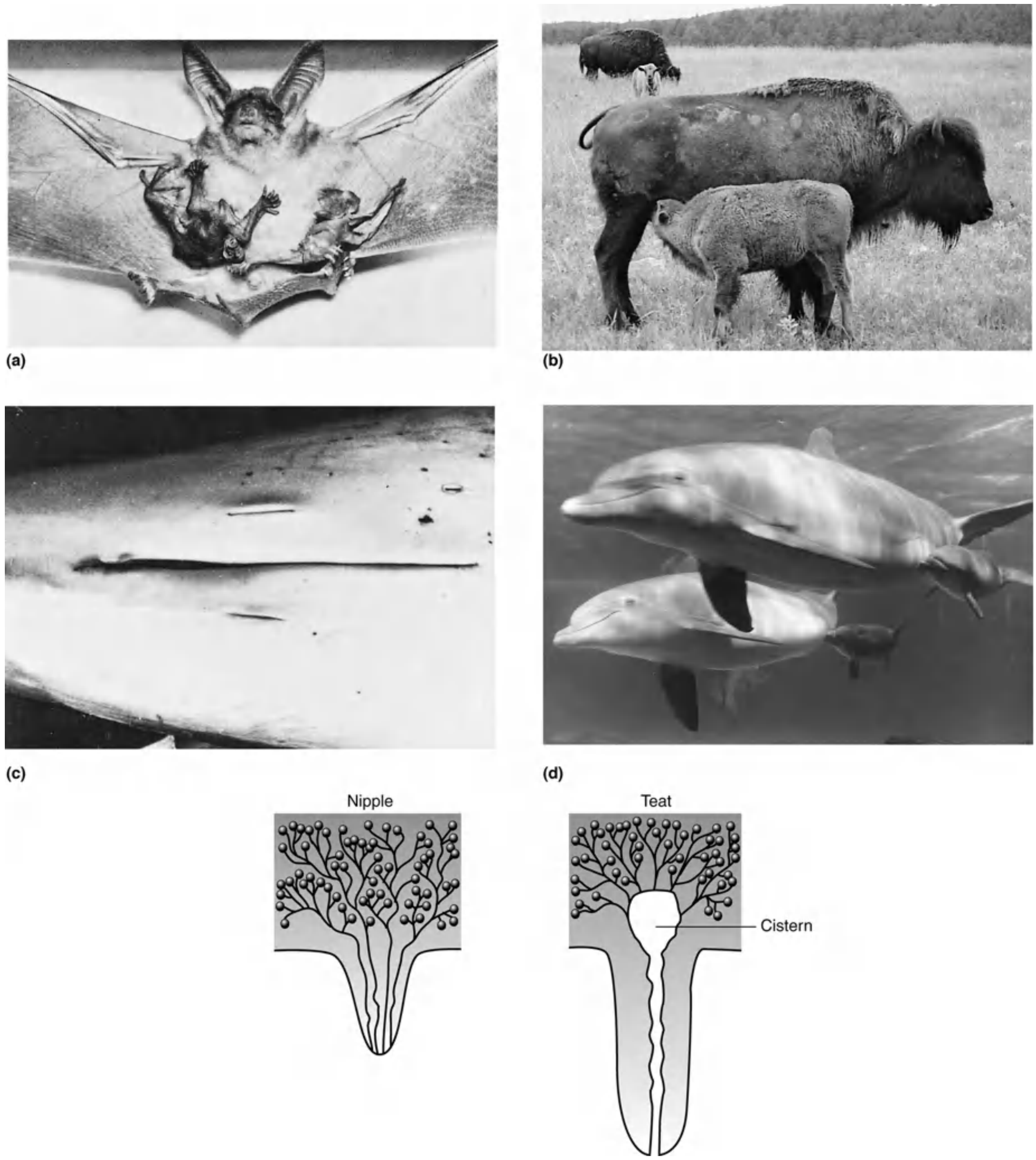


Figure 9.21. The mammary gland and milk are characters of major importance in the class Mammalia. (*a*) Young pallid bats (*Antrozous pallidus*) are naked and helpless when born. (*b*) American bison (*Bison bison*). (*c*) In cetaceans, the nipples of the female (when not in use) are retracted within slits situated on either side of the vent, as seen on the undersurface of this female harbor porpoise (*Phocoena phocoena*). (*d*) Nursing bottlenose dolphins (*Tursiops truncatus*). *Inset*: nipple and teat.

Sebaceous, or **oil**, **glands** are normally associated with hair follicles (see Fig. 9.9). Their secretion, **sebum**, is emptied into the follicle to lubricate the hair and surrounding skin and to act as an antibacterial agent. Many marine mammals possess little hair and lack sebaceous glands.

Scent glands, which may be modified sudoriferous or sebaceous glands, are numerous and widely distributed on the bodies of most mammals. They are most highly developed in those mammals that have the keenest sense of smell and may be used to mark an individual's territory, to attract members of the opposite sex, or for defensive purposes. Glandular secretions that elicit a specific reaction from other individuals of the same species are known as **pheromones** (see Chapter 13).

The function of scent glands varies, depending on the sex and physiological state of the species. Perianal glands of skunks secrete a defensive spray consisting of several major components that may cause severe irritation and temporary blindness (Andersen and Bernstein, 1975). Major volatile components differ in the secretions of the striped skunk (*Mephitis mephitis*) and the spotted skunk (*Spilogale putorius*) (Wood, 1990; Wood et al., 1991). The release of scent during times of stress has also been reported in the house shrew, mice, rats, woodchucks, mink, weasels, and the black-tailed deer, among others. Territorial marking is practiced by many species, including short-tailed shrews, muskrats, beaver, social rabbits, canids, antelope, and deer. Deer have glands anterior to the eye (preorbital), on the medial side of the tarsal joint (tarsal), on the outside of the metatarsus (metatarsal), and between the main digits (interdigital) (Fig. 9.22). Many bats have scent glands in the skin of the face and head.

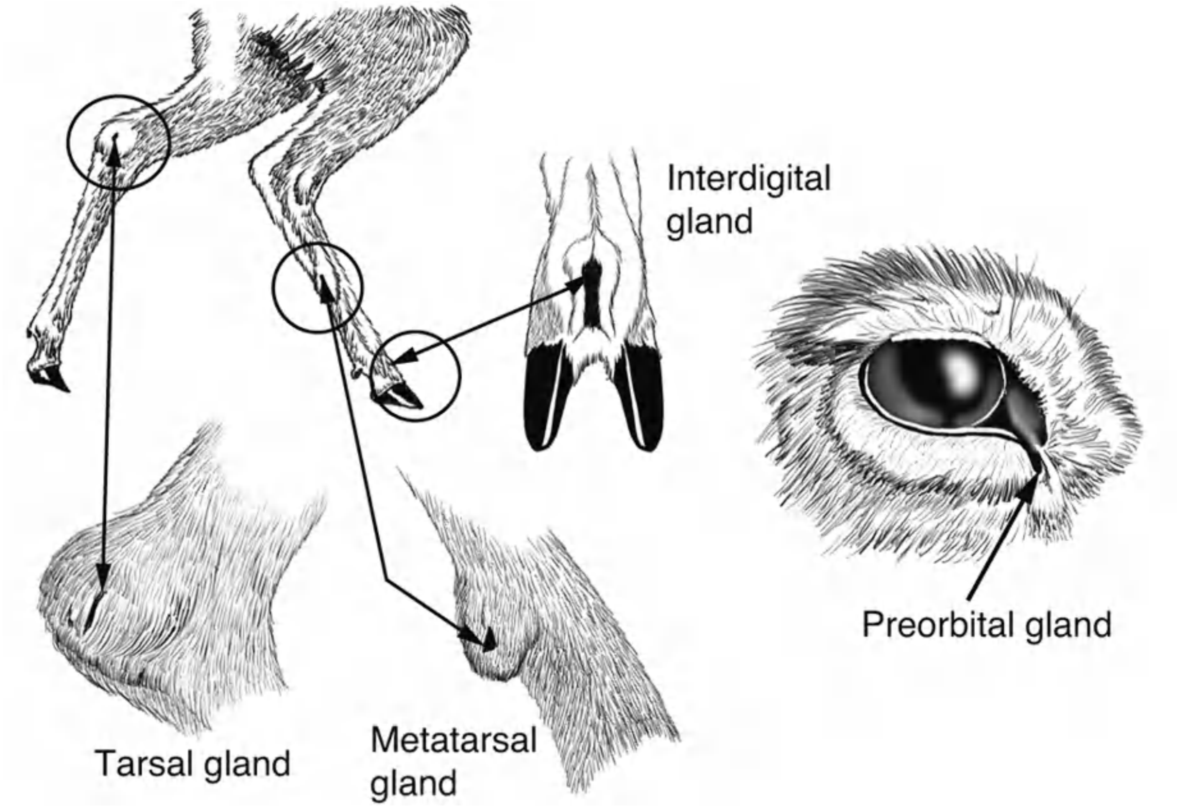


Figure 9.22. Scent glands of white-tailed deer (*Odocoileus virginianus*).

Because the epidermis lacks blood vessels and nerves, it must be supplied by the highly vascularized dermis. The mammalian dermis contains vast networks of blood vessels, lymphatic vessels, free nerve endings, and encapsulated sense organs sensitive to touch and pressure. Beneath the dermis is a subcutaneous layer that in many mammals has a substantial fat component, which serves as protection, as an insulating layer, and as an emergency energy source. In many marine mammals, the subcutaneous layer serves to minimize heat loss in the water and provide buoyancy; however, it may also serve as an energy reservoir to provide nourishment during long periods of fasting. Some of the larger whales are insulated by a layer of fat that may reach 0.6 m in thickness (Riedman, 1990).

Skeletal System

Axial Skeleton (Skull, Auditory Ossicles, Hyoid, Ribs, Sternum)

The skeleton of mammals supports the body, provides protection for important organs, and serves as a point of attachment for skeletal muscles (Fig. 9.23). The mammalian line of evolution, however, has resulted in significant modifications of skeletal elements. Because of loss and/or fusion, the number of bones in the skull and lower jaw of mammals is less than in other vertebrates (Fig. 9.24). The axial skeleton has become stronger and more rigid, most of the skeleton has completely ossified, and skeletal growth is generally restricted to immature mammals.

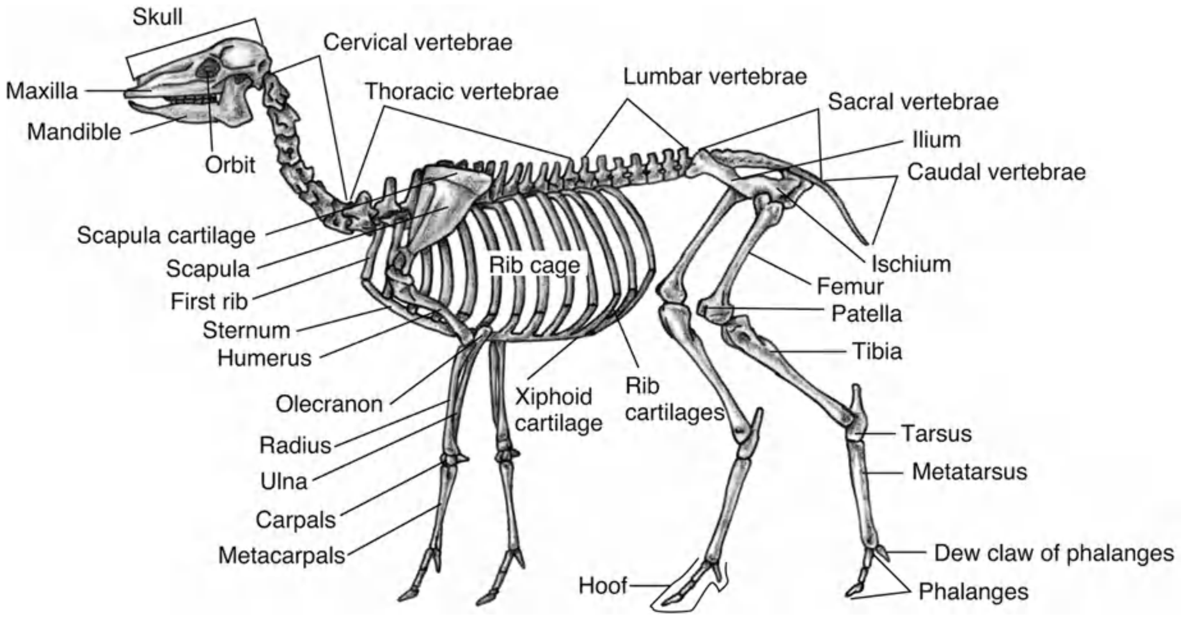


Figure 9.23. The skeletal structure of a white-tailed deer (*Odocoileus virginianus*). The mammalian skeleton provides support and protection for internal organs and serves as a point of attachment for muscles.

The mammalian skull, which inherited its basic characteristics from its synapsid reptilian ancestor, includes a single pair of temporal fenestrae bounded ventrally by the zygomatic arches (Fig. 9.25). One of the most remarkable modifications of bones in the history of vertebrate evolution is the transformation and change of articulating elements between the jaw and skull in reptiles to auditory elements in mammals (Rowe, 1996). In mammals, the posterior portion of the palatoquadrate cartilage ossifies as the quadrate bone. It becomes enclosed by the developing middle ear cavity, separates from the remainder of the palatoquadrate cartilage, and becomes the **incus** of the middle ear. Intermediate evolutionary steps can be seen in mammal-like reptiles. Dermal bones ensheathe the anterior portion of the palatoquadrate. Meckel's cartilage totally ossifies in adult mammals. The posterior tip of Meckel's cartilage—the **articular—**projects into the middle ear cavity, separates from the rest of Meckel's cartilage, and becomes the **malleus**. The malleus and the incus (homologous to the quadrate) still articulate with one another, but the joint is now in the middle ear instead of at the tip of the jaw. The reptilian stapes (columella) was already present in the middle ear. These three ear ossicles conduct vibrations from the eardrum to the inner ear. The dentary, the only remaining dermal bone in the lower jaw, articulates directly with the squamosal and/or temporal bone. Jarvik (1980) cited several problems with the long-held theory of evolution of mammalian ear ossicles, and he proposed a new theory in which the malleus and incus evolve from portions of the hyoid arch. This theory, however, has never been widely accepted.

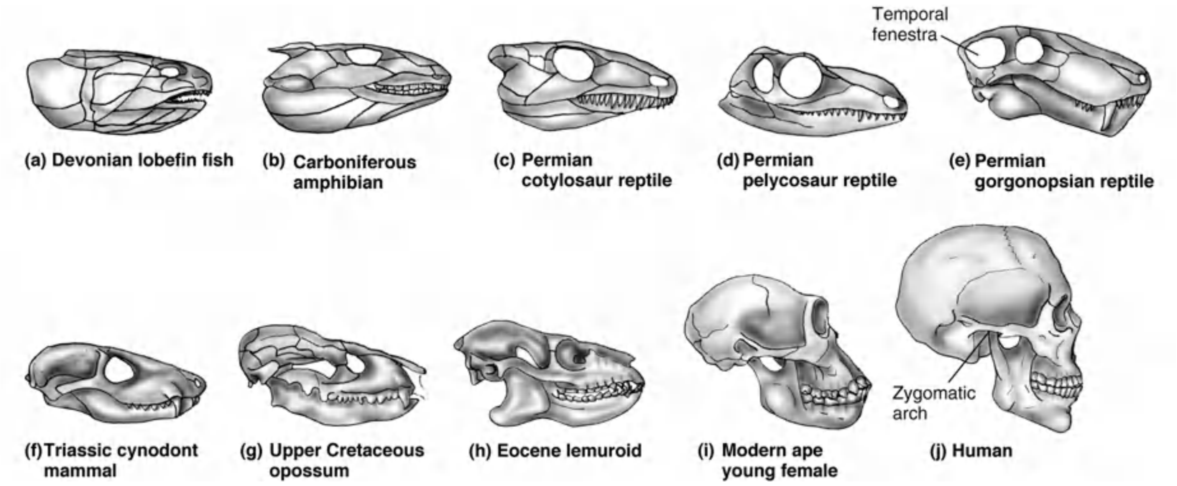


Figure 9.24. Evolution of the vertebrate skull from fish to human.

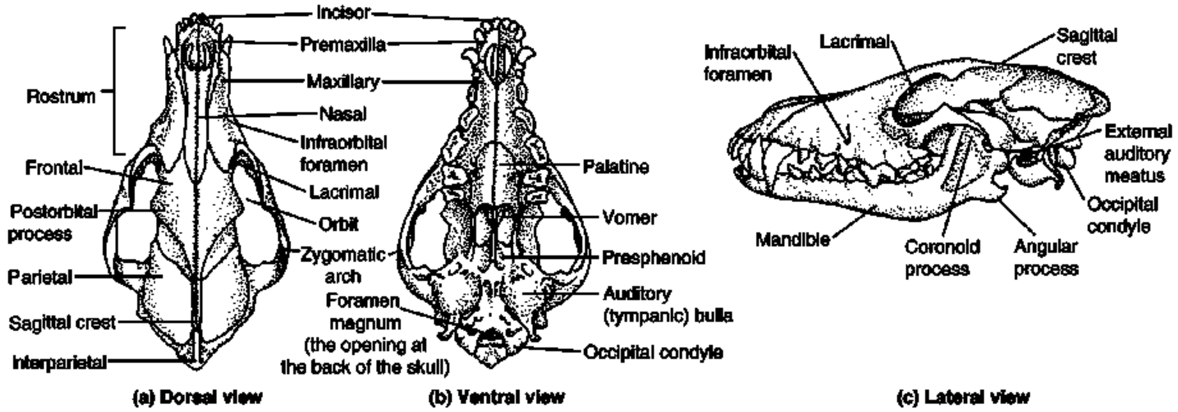


Figure 9.25. Skull and mandible of the coyote (*Canis latrans*): (*a*) dorsal view, (*b*) ventral view, (*c*) lateral view.

Most mammals possess a zygomatic arch, which assists in protecting the eye and provides the origin for the masseter muscle (see Fig. 9.25). The zygomatic arch is incomplete in some insectivores, anteaters, and some other less derived mammals. It is absent in whales and some insectivores.

Mammals possess a complete secondary palate, which serves to separate the nasal passages from the oral cavity, allowing mammals to continue breathing while chewing food and to strengthen the skull when chewing. The caudal portion fails to ossify and forms a “soft” palate.

The hyobranchial skeleton shows considerable variation, and precise homologies are unclear. Basically, it consists of a **hyoid apparatus** associated with the posterior portion of the tongue and a **larynx** comprising the upper end of the trachea.

Felid Anal Scent Glands

Chemical cues secreted from felid anal scent glands, by which cats recognize their own species, are being used as the basis for a new cat phylogeny. Comparative analysis of the lipid components of this chemical cocktail from 16 felid species produced strikingly consistent results, indicating a strong phylogenetic signal from these compounds. Relationships between many cat species can now be established with more confidence, allowing systematists to focus more closely on remaining problem areas.

Bininda-Emonds et al., 2001

The mammalian vertebral column is made up of a series of intersegmentally arranged, acoelous vertebrae: cervical, thoracic, lumbar, sacral, and caudal (Fig. 9.27). Zygapophyses (articulating processes) overlap adjacent vertebrae to give additional firmness to the backbone and limit the amount of flexion and torsion to which it can be subjected.

Most mammals possess seven cervical vertebrae (see Figs. 9.23 and 9.27). The only exceptions are xenarthrans (formerly called edentates)—anteaters, armadillos, and sloths—with six, eight, or nine, and manatees with six. In some mammals, like cetaceans, some rodents, and armadillos, cervical vertebrae are shortened and more or less fused together. The first two cervical vertebrae in all mammals, the atlas and axis, are specialized for articulation and movement of the skull (see Fig. 9.27). The ring-shaped atlas has no centrum and wide transverse processes; anteriorly, it has two concave surfaces that articulate with the occipital condyles of the skull. The axis has a centrum that is elongated anteriorly as the **dens** (odontoid process) and a large neural spine that overlaps the atlas. The dens represents the original centrum of the atlas. When the atlas and axis are articulated, the dens occupies its original position even though it has become a functional part of the axis. The atlas-occipital condyle articulation permits the typical vertical (up-and-down) movement of the head, whereas the atlas-axis articulation allows lateral (side-to-side) movements of the head.

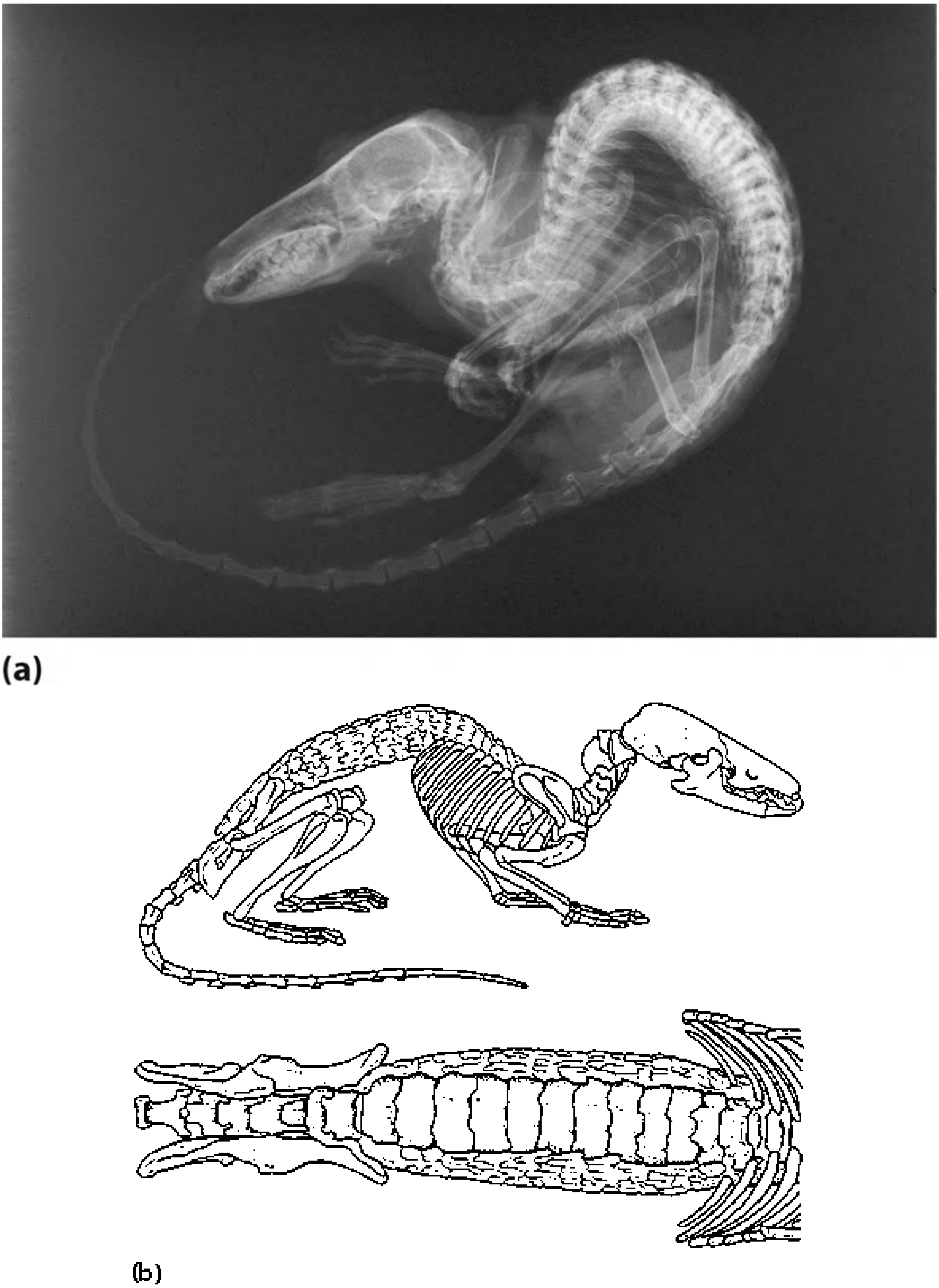


Figure 9.26. (*a*) An X-ray image of the body of the armored shrew (*Scutisorex somereni*) of Congo (formerly Zaire), Rwanda, and Uganda. These shrews have 11 (rather than 5) lumbar vertebrae, giving them extra bending points and a remarkably strong vertebral column. (*b*) Vertebrae of the armored shrew are particularly sturdy due to the presence of many lateral, dorsal, and ventral interlocking spines (apophyses) forming a basket-like structure unlike that in any other mammal.

Thoracic and lumbar vertebrae vary in number and structure. Most thoracic vertebrae have short centra, tall posteriorly directed neural spines, and small zygapophyses. These vertebrae also articulate with the ribs. Lumbar vertebrae vary in number from 2 (in some monotremes) to as many as 21 (in cetaceans). Typical lumbar vertebrae are large and stout with prominent, broad neural spines and long, forward-projecting transverse processes. No ribs articulate with lumbar vertebrae. Whereas the number of thoracic and lumbar vertebrae varies from species to species, and even occasionally within one species, the total number of thoracic and lumbar vertebrae is constant in a given species and even in higher taxonomic groups.

The Hero Shrew's Vertebral Column

The armored, or hero, shrew (*Scutisorex somereni*) of Congo (formerly Zaire), Rwanda, and Uganda has a remarkably strong vertebral column. Its strength is derived, in part, from a backbone equipped with extra joints for flexibility. Whereas most shrews have 5 lumbar vertebrae, hero shrews have 11, giving them extra bending points (see Figs. 9.26 a, b). In addition, the shape and size of individual vertebrae, together with an increased number of articular facets, make them unique among mammals. Vertebrae are three times wider than those of other shrews and have interlocking, finger-like projections that create sturdy links between neighboring vertebrae.

In discussing the extraordinary strength of this shrew, Allen (1917) noted:

> Whenever [the natives] have a chance they take great delight in showing its resistance to weight and pressure. After the usual hubbub of various invocations, a full-grown man weighing some 160 pounds steps barefooted upon the shrew. Steadily trying to balance himself upon one leg, he continues to vociferate several minutes. The poor creature seems certainly to be doomed. But as soon as his tormentor jumps off, the shrew after a few shivering movements tries to escape, none the worse for this mad experience… . The strength of the vertebral column, together with the strong convex curve behind the shoulder … evidently protects the heart and other viscera from being crushed.

Allen, 1917; Pennisi, 1996

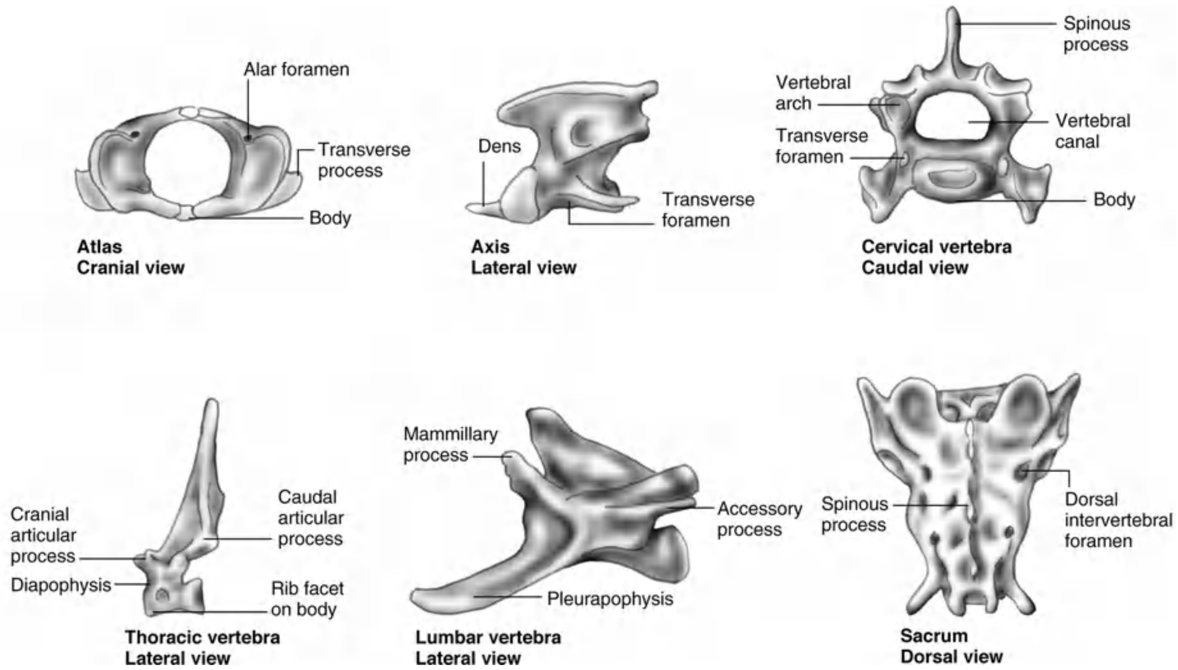


Figure 9.27. Representative vertebrae from a cat (*Felis*). For those shown in the lateral view, cranial is toward the left.

Most mammals have three to five sacral vertebrae that are fused to form the sacrum, which serves as a point of attachment for the pelvic girdle. There is no sacrum in whales due to the absence of hindlimbs and a pelvic girdle. The number of sacral vertebrae may range up to 13 in some xenarthrans.

Mammals still have remnants of an ancestral reptilian tail and have 3 to 50 caudal (tail) vertebrae (see Fig. 9.23). In apes and humans, the 3 to 5 caudal vertebrae are called coccygeal vertebrae because some or all usually fuse to form a **coccyx**. Caudal autotomy (the ability to break off the tail) is known to occur in a few rodents.

Most mammals possess 12 to 15 pairs of ribs (see Fig. 9.23). Most are composed of a dorsal (vertebral) portion and a ventral (sternal) portion. The latter remains as a **costal cartilage** in mammals. The costal cartilages connect, either directly or indirectly, with the sternum to form a rib cage that functions in protection as well as in respiration. Floating ribs lack a sternal connection.

The mammalian sternum articulates with the ribs and anteriorly with the pectoral girdle. In all mammals except cetaceans and sirenians, the sternum consists of bony segments known as **sternebrae**. The sternum assists in strengthening the body wall, helps protect the thoracic viscera, serves as a point of attachment for pectoral and limb muscles, and, in some amniotes, aids in ventilating the lungs.

Appendicular Skeleton (Pectoral and Pelvic Girdles and Appendages)

The pectoral girdles of most mammals, other than monotremes, consist of either a pair of clavicles and scapulae or just a pair of scapulae. A clavicle is present in those mammals whose front limbs move in several planes; it is absent in those where the forelimbs move in only one plane, like deer and horses. When present, the clavicle braces the scapula against the sternum. Some marsupials, insectivores, bats, rodents, and higher primates, including humans, have a clavicle. It is lacking in cetaceans, ungulates, and some carnivores. In other carnivores, like cats, the clavicle has been reduced to a slender bony splinter that fails to articulate with either the sternum or the scapula.

The efficiency of mammalian limbs has been increased by bringing the limbs to a vertical position and, at the same time, rotating them. Hindlimbs are rotated forward, so that knees and feet point anteriorly; forelimbs are rotated backward so that elbows point to the rear. An additional 180° rotation at the wrist is necessary to allow the front feet to also point forward. The rotation at the wrist resulted in the crossing of the radius and ulna in the forearm.

The anterior appendage contains the same six skeletal elements as in all tetrapods (humerus, radius and ulna, carpals, metacarpals, and phalanges) (see Fig. 9.23). The shape, length, and number of skeletal elements in the appendages have evolved as primitive mammals developed specialized locomotory techniques (Fig. 9.28a). Further modifications have occurred in association with the occupation of subterranean, arboreal, aquatic, and aerial habitats. For example, the humerus of moles, echidnas, and other burrowing mammals is short and stout and has expanded areas for attachment of large muscles used for digging. In ungulates, the shaft of the ulna may fuse with the radius during embryonic development; in other mammals, like bats, it may fail to develop fully. The front limb of bats has been modified into a wing for flight. Metacarpals and phalanges of the last four digits have become elongated to support the wing membrane. Although bats typically hang by their feet upside down, the thumb remains free and is sometimes used when crawling.

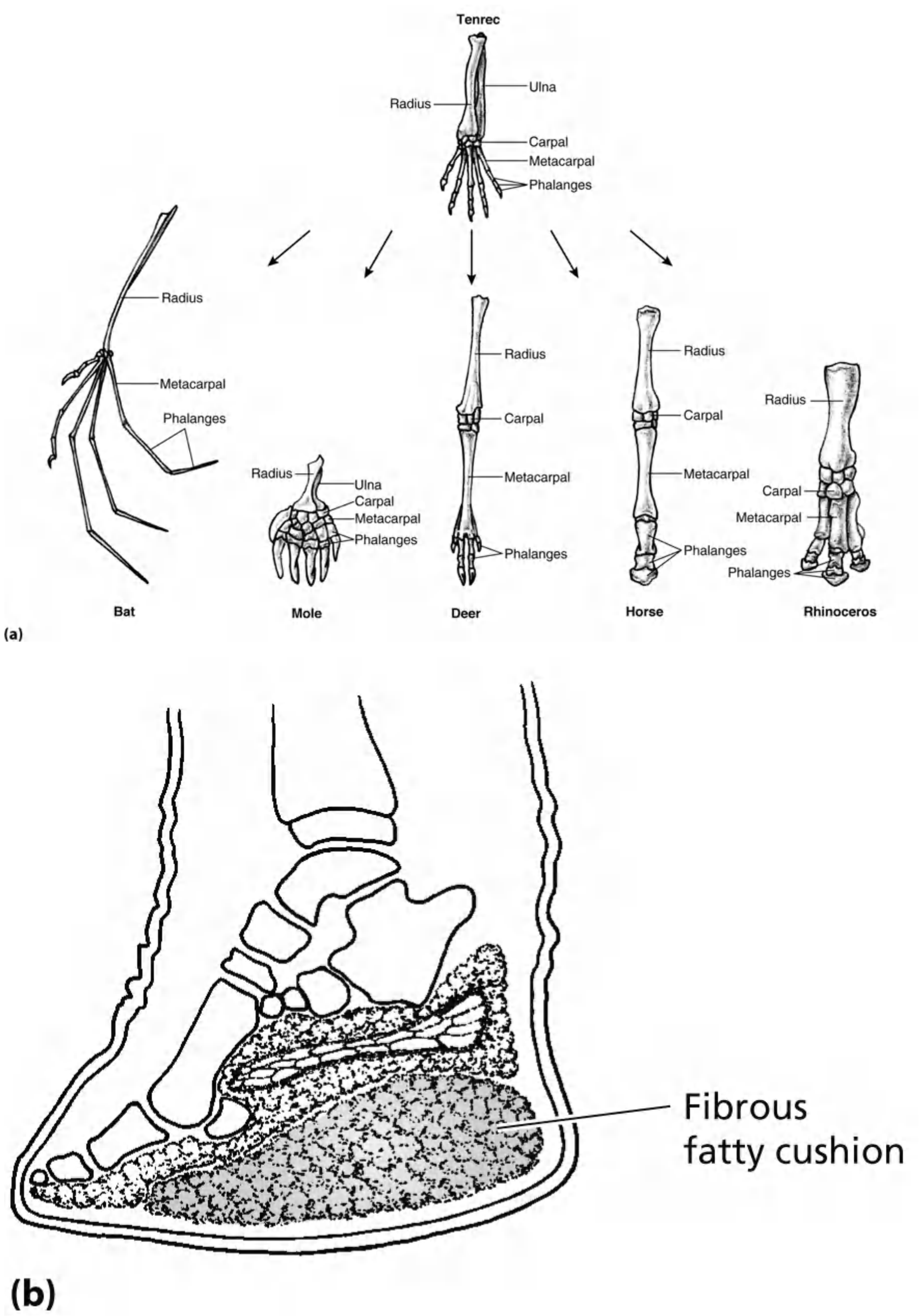
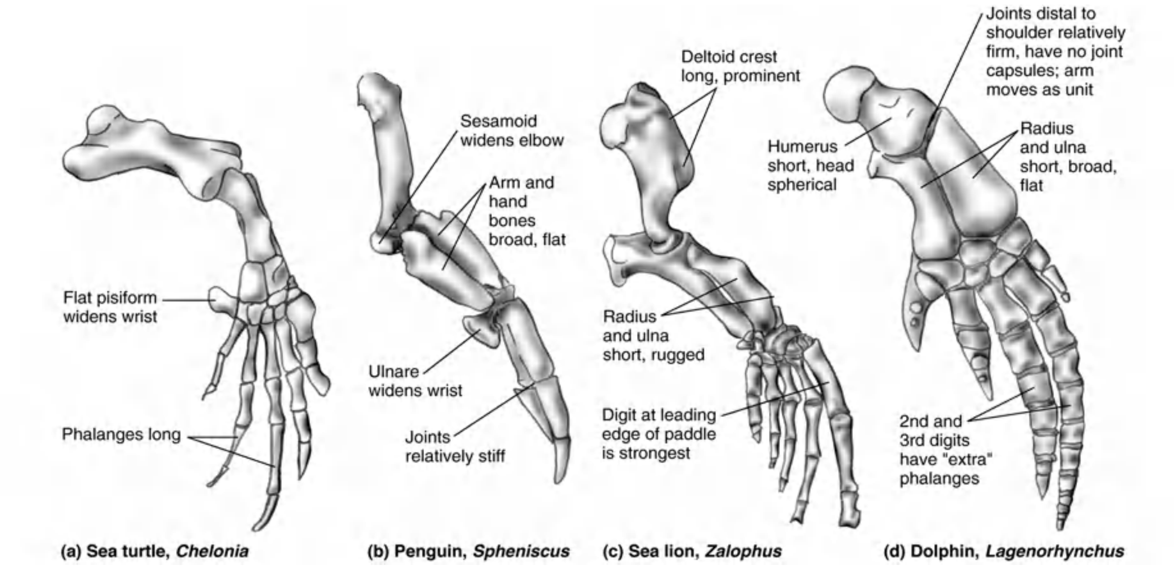


Figure 9.28. (*a*) Adaptive radiation of the forelimbs of mammals. The forelimb of a tenrec (*top*) is used as an example of a primitive form. Although not drawn to scale, portions of the forelimbs of a bat, mole, deer, horse, and rhinoceros show various modifications by the fusion of parts, the loss of parts, or changes in the proportion of parts of the limb. (*b*) Forefoot of an

African elephant. Although elephants are functionally plantigrade, they actually walk on their toes (digitigrade). A cushion of fibrous, fatty connective tissue helps to cushion the bones of the feet and to distribute the massive weight of the animal over a broader area.

The broad feet of elephants have the phalanges embedded in a matrix of elastic tissue to help cushion the bones of the feet and to distribute the weight of the animal over a broader area (Fig. 9.28b).

The front limbs of cetaceans, sirenians, seals, and sea lions are modified for life in the sea and superficially resemble the modified appendages of sea turtles and penguins (convergence) (Fig. 9.29). Appendages become flattened, short, and stout and may have a greatly increased number of phalanges. Insectivores and primates have tended to remain **pentadactyl** (five fingers, five toes) and usually have five carpals and five metacarpals.



(a) Sea turtle, *Chelonia* **(b) Penguin, *Spheniscus*** **(c) Sea lion, *Zalophus*** **(d) Dolphin, *Lagenorhynchus***

Figure 9.29. Dorsolateral views of the right forelimb skeletons of some aquatic vertebrates that use the pectoral appendage for propulsion: (*a*) sea turtle (*Chelonia*), (*b*) penguin (*Spheniscus*), (*c*) sea lion (*Zalophus*), (*d*) dolphin (*Lagenorhynchus*).

Front limbs of many mammals have been modified for grasping, with the thumb developing into an opposable structure capable of touching each of the other digits (Fig. 9.30). The evolution of an opposable thumb was accomplished by the development of a unique joint known as a **saddle joint** at the base of the thumb and by the development of strong skeletal muscles to operate the thumb. In those primates that swing from branch to branch (brachiation), the large clavicle is firmly attached to the sternum. In some forms of monkeys that are almost exclusively arboreal, like spider monkeys (*Ateles*) and woolly spider monkeys (*Brachyteles*), the thumb is rudimentary or has been lost altogether, an evolutionary modification that facilitates movement through the canopy (Fig 9.30).

Pandas possess a pseudothumb (see Fig. 9.31) (Catton, 1990). This is, functionally, a sixth digit formed by a wristbone, the radial sesamoid, and lies beneath a pad on the animal's forepaw. Muscles that normally attach to the thumb attach to the radial sesamoid and enable the panda to grip and manipulate bamboo efficiently.

Adhesive devices have been identified on the thumbs of five genera of vespertilionid bats (*Thyroptera*, *Glischropus*, *Tylonycteris*, *Pipistrellus*, and *Myzopoda*) (Thewissen and Etnier, 1995). These pads may adhere by suction, dry adhesion, or gluing.

World's Fastest Flying Animal

Until now, most experts believed that birds from the swift family held the world speed record for horizontal flight. The common swift, for example, can fly as fast as 97 km (60 mi.) per hour. Recent research, however, using tiny radio transmitters temporarily attached to several bats and a mobile receiver installed on a small airplane revealed that Brazilian free-tailed bats (*Molossus brasiliensis*) can achieve horizontal speeds approaching 161 km (100 mi.) per hour. Measurements indicated that tail winds did not assist the bats, which weigh about 12 grams (0.4 oz.) each.

McCracken et al., 2016

The Vertebrae of the Queen Naked Mole Rat

In naked mole rat (*Heterocephalus glaber*) colonies, the queen has an elongated body. The elongation is caused by a lengthening of individual vertebrae after a female becomes a breeder—a phenomenon unique among mammals. The average litter numbers 12 pups, but it can reach 28, the largest known for any mammal.

Sherman et al., 1992

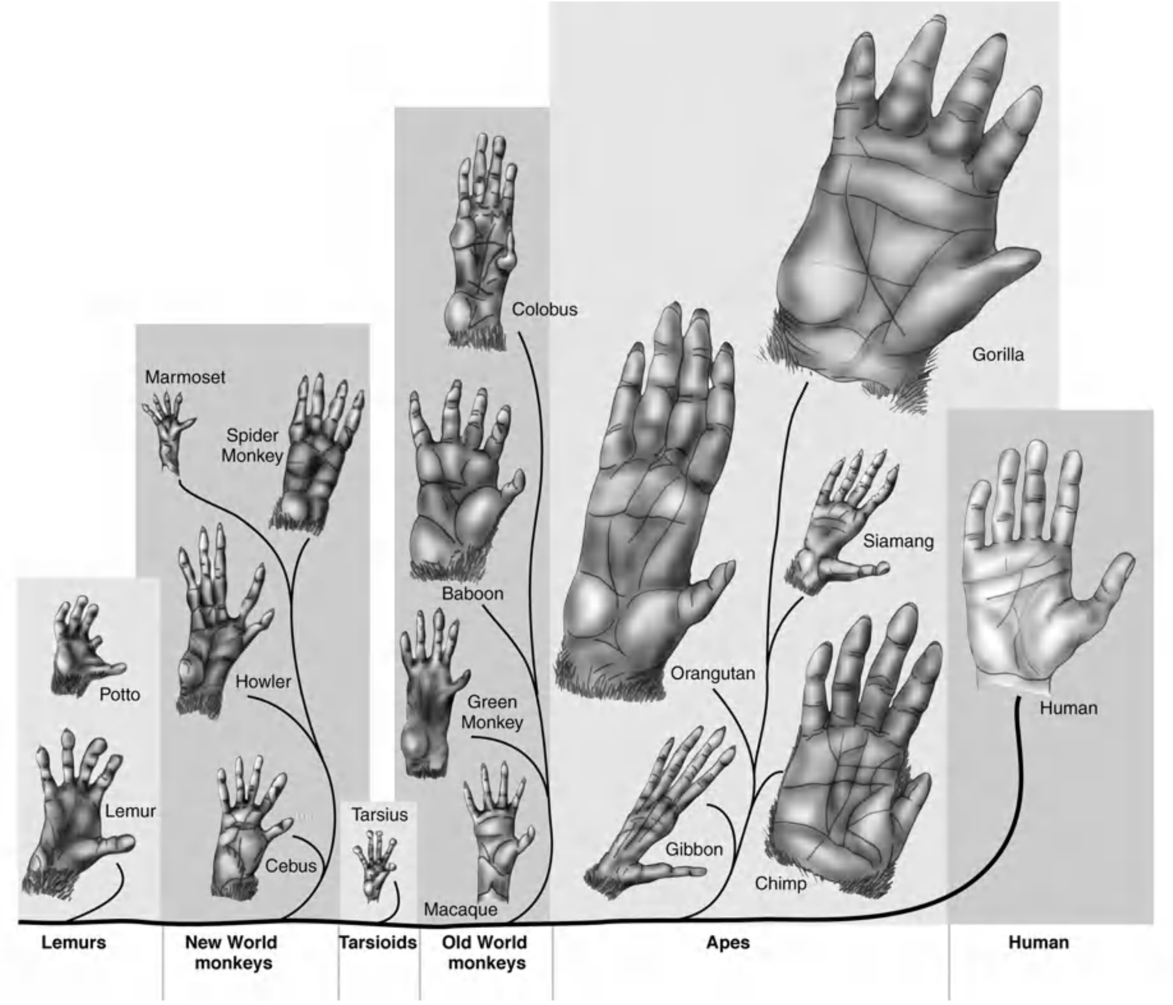


Figure 9.30. Modifications of the hands of primates for grasping. Note the opposable thumb in most species.

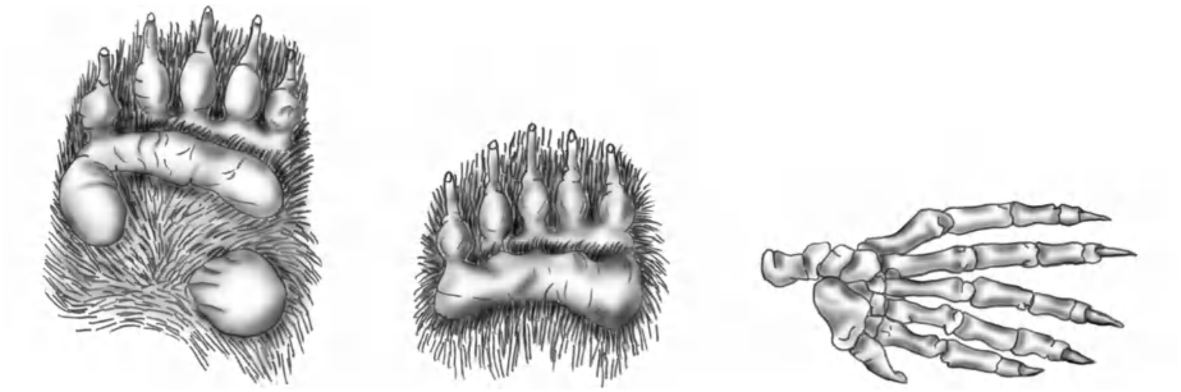


Figure 9.31. The giant panda’s peculiar thumb. The forepaw (*left*) shows the pseudothumb used to grasp bamboo stems. The skeleton of the forepaw (*far right*) shows that the pseudothumb is a modified wristbone, the radial sesamoid. The hindpaw (*middle*) is included for comparison.

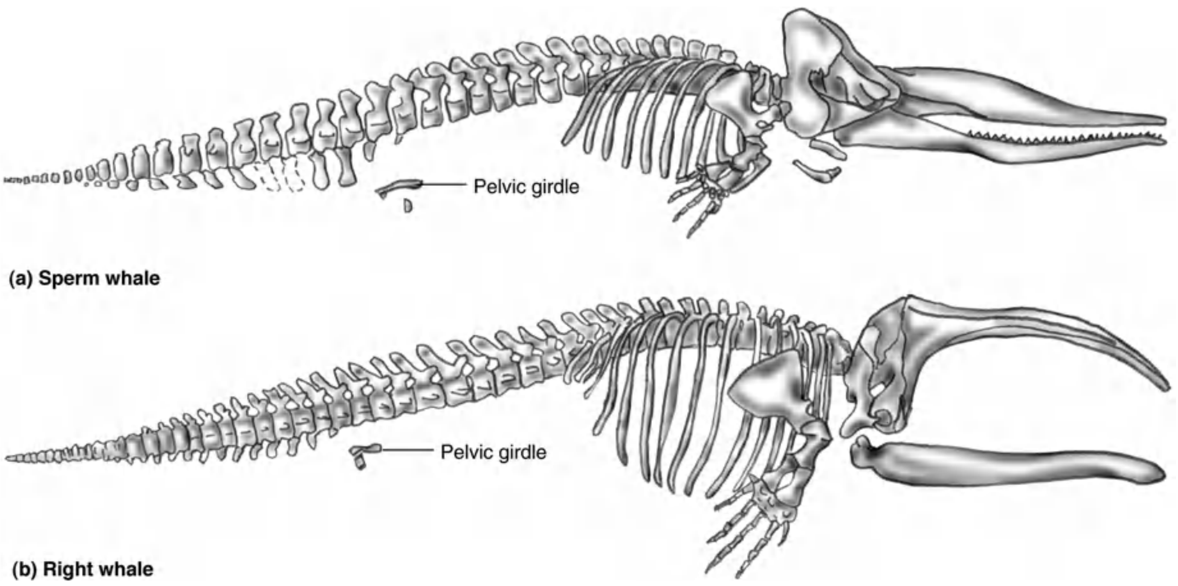


Figure 9.32. Skeletons of (*a*) sperm whale (*Physeter*) and (*b*) right whale (*Eubalaena*). Note vestiges of the pelvic girdle.

Two **innominate** (coxal, hip) **bones** make up the pelvic girdle and articulate with the sacrum dorsally (see Fig. 9.23). Each innominate bone consists of three fused elements: an anterior pubis, a posterior ischium, and a dorsal ilium. In most mammals, the two pubic bones unite to form a pubic symphysis. Because of the pubic symphysis and the uniting of the ilium with the vertebral column, the pelvic girdle forms a ring, the **pelvis**, around the caudal end of the digestive and urogenital systems. The pelvic girdle is vestigial or absent in all living cetaceans (Fig. 9.32) and sirenians. Cetaceans have lost all external manifestations of hindlimbs, but vestiges sometimes remain embedded within the body wall (see discussion of *Basilosaurus* on page **279**).

Two small **epipubic bones** articulate with the pubic bones and extend forward in the abdominal wall in marsupials and monotremes (see Fig. 9.34a). They have also been identified in two primitive Cretaceous eutherians (Novacek et al., 1997). Some researchers contend these bones support the abdominal pouch in which the young are transported, but this seems doubtful because the bones are developed in both sexes. These bones do show sexual dimorphism, as they are either longer or broader in females than in males of the same species. Nowak and Paradiso (1983) think it is more likely that epipubic bones are a heritage from reptilian ancestors and were associated with the attachment of abdominal muscles that supported large hindquarters. They may also have served to stiffen the median part of the ventral abdominal wall (Presley, 1997) and/or to have aided in locomotion by acting with the hypaxial muscles of the trunk to protract (move forward) the pelvic limbs (White, 1989).

The hindlimbs of mammals are comparable to those of reptiles. They consist of a femur, tibia and fibula, tarsals, metatarsals, and phalanges (see Fig. 9.23). In addition, a sesamoid bone (a bone that develops in a tendon), the patella, protects the knee joint. Semiaquatic mammals, like muskrats, beaver, and nutria, have webbing between their toes. In many primates, the big toe, or **hallux**, is opposable (Fig. 9.33). In opossums (*Didelphis*), the big toe is opposable and assists in climbing (Fig. 9.34).

Mammal limbs are variously modified for different forms of locomotion. Some, like insectivores, monkeys, apes, humans, and bears, walk by placing the entire surface of their foot on the ground with each step (Fig. 9.35a). Such mammals usually possess pentadactyl hands and feet. This ancestral method of locomotion is known as **plantigrade** locomotion.

Some mammals bear their weight on the ends of their metacarpals and metatarsals (see Fig. 9.35b). Their wrists and ankles are elevated, and the thumb has been reduced or lost. They can usually walk and run faster than plantigrade species. They also walk more silently and are more agile. This method of locomotion, called **digitigrade** movement, is common in mammals like rabbits, rodents, and many carnivores.

Ungulates illustrate the extreme in modification of the distal appendages. The number of digits has been reduced so that ungulates possess either four, three, two, or even one, and the animals walk on the tips of their remaining fingers and toes. This method of locomotion is known as **unguligrade** (see Fig. 9.35c). The weight of the body is borne on hooves, which represent modified claws that have become hardened and thickened. The metacarpals corresponding to the missing digits have been either reduced in size or lost, and those that remain are elongated and often united, a modification that greatly strengthens the lower leg and foot. The limbs are capable of only forward and backward movement; no twisting or rotation is possible. Muscles activating the lower portions of the limbs are located close to the body in order to lessen the weight of the limb each time it is raised; the appendicular muscles attach to the limb bones by long, lightweight tendons. Thus, the limbs and feet of hooved mammals, which are long, light, and capable of only fore and aft movements, are highly specialized for running and/or for maneuvering on rocky terrain.

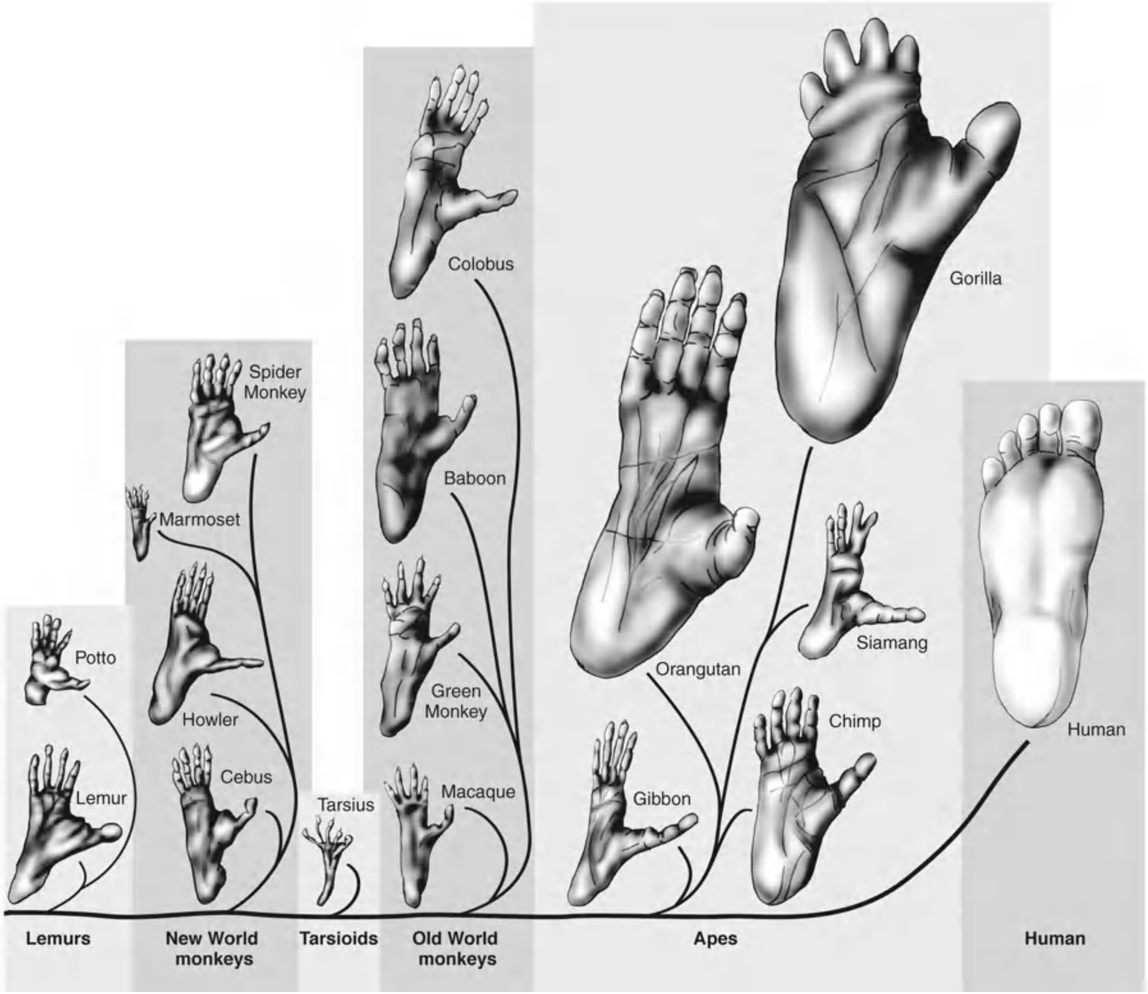


Figure 9.33. Modifications of the feet of primates. Note the opposable big toe in most species.

Two groups of ungulates have evolved. One group, the **artiodactyls**, have generally retained digits 3 and 4 as functional digits and their weight is equally distributed between them (Fig. 9.36a). Digits 2 and 5 are reduced, and digit 1 is lost. Because the weight of the body is borne on two parallel axes, they are said to have a **paraxonic foot** and a **cloven hoof**. This group includes pigs, peccaries, javelinas, and hippopotamuses (which have four digits) and camels, llamas, chevrotains or mouse deer, deer, elk, caribou, giraffes, okapis, pronghorns, antelopes, bison, buffalo, cattle, gazelles, goats, and sheep (which have two digits). In the second group, the **perissodactyls** (Fig. 9.36b), digit 3 has been retained as the primary functional digit in most forms, and it bears all of the body weight; digits 2 and 4 are reduced, and digits 1 and 5 are usually lost. These animals are said to have a **mesaxonic foot**. Thus, perissodactyls have an odd number of digits. They include horses, zebras, asses, tapirs, and rhinoceroses.

In whales, dolphins, and porpoises, the hindlimbs are absent and forelimbs have been modified into paddles. Fur seals and sea lions have large, naked front flippers and reversible hind flippers that can be brought under the body for locomotion on land (Fig. 9.37a, b, f). Hind flippers also are reversible in walruses. In hair (earless) seals (Fig. 9.37c, d, e), front flippers are haired and are smaller than the hind flippers, which are not reversible.

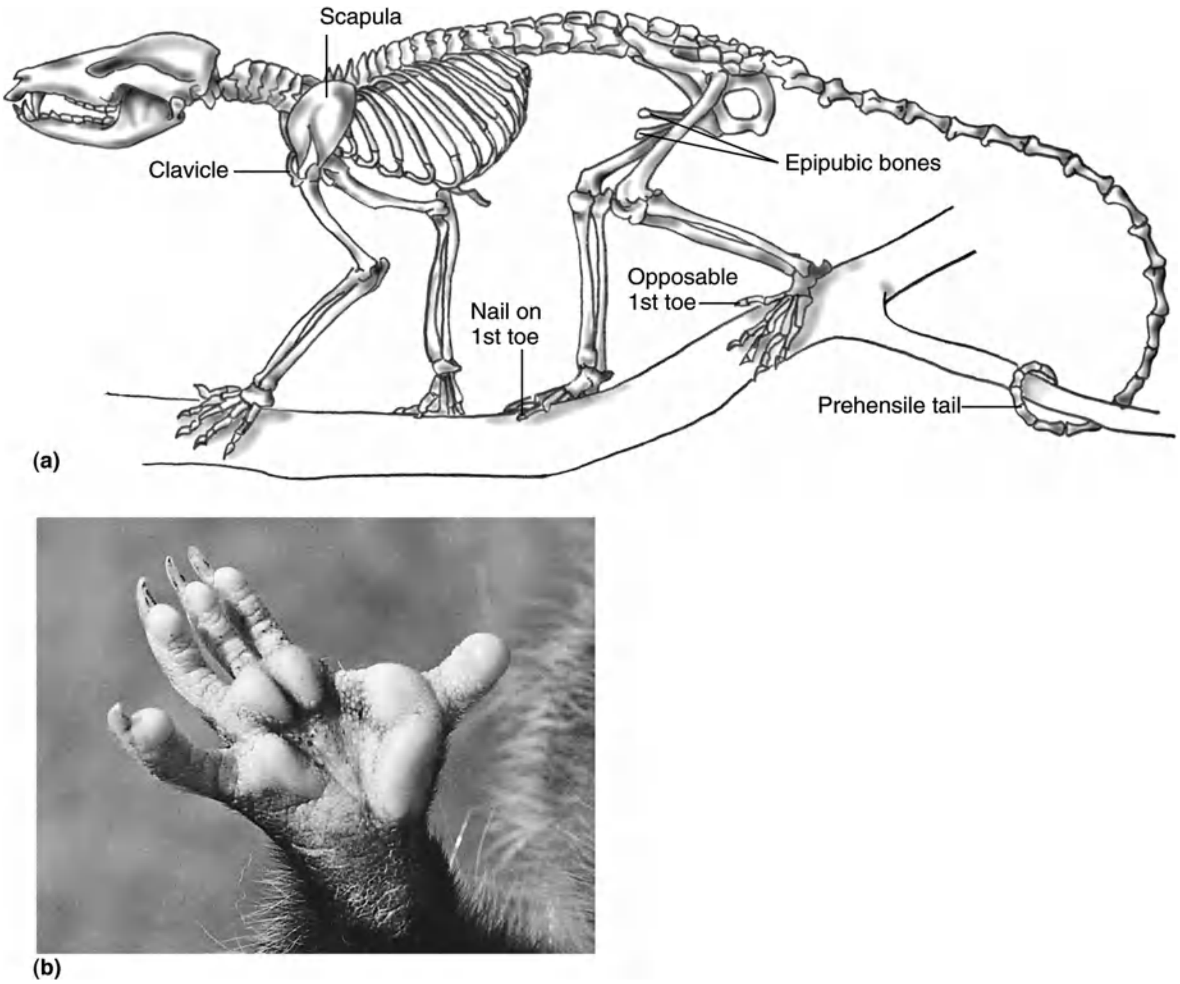


Figure 9.34. (*a*) Skeleton of the opossum (*Didelphis*) showing the opposable big toe, the epipubic bones, and the prehensile tail. (*b*) Right hind foot of a juvenile opossum with opposable clawless “thumb.” It was this handlike foot that prompted the discoverer of the opossum, Vicente Yanez Pinzon, in 1500 to describe the animal as “part monkey.”

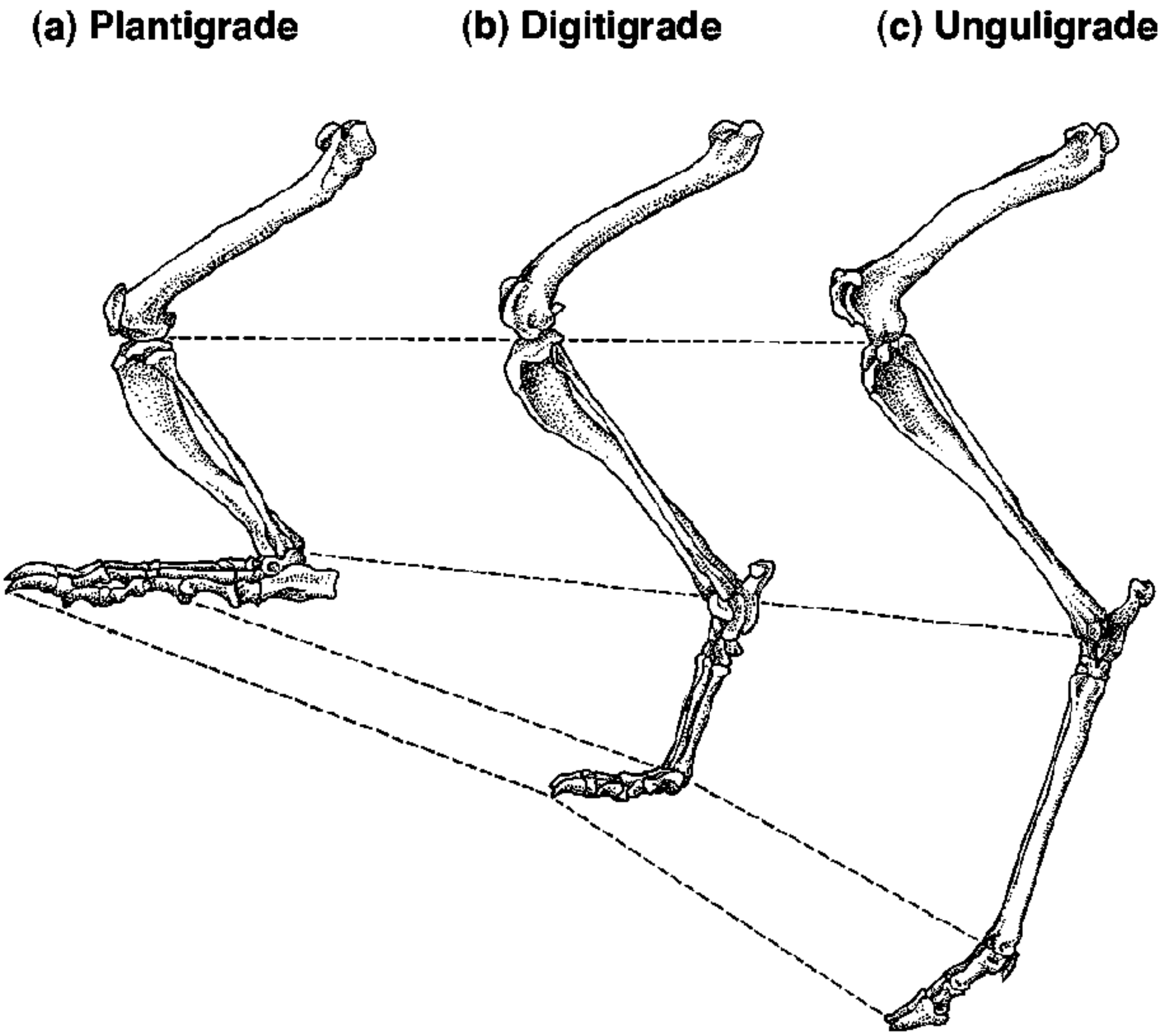


Figure 9.35. Modifications of mammal limbs for different forms of locomotion: (*a*) plantigrade, (*b*) digitigrade, (*c*) unguligrade. Note how changes in foot posture produce relatively longer limbs.

Muscular System

Epaxial muscles exist in bundles along the vertebral column but have become covered and partially obscured by the greatly expanded extrinsic appendicular muscles (Fig. 9.39). The function of epaxial muscles is the same in mammals as in other vertebrates. They allow side-to-side movement of the vertebral column and provide for the support and arching of the back. Appendicular muscles of mammals are basically similar to those of reptiles. Due to their expansion and differentiation, however, they obscure much of the epaxial musculature. Hypaxial muscles of the abdominal wall are well developed in most mammals and support the abdomen, assist in bending the vertebral column, and serve as the musculature of the tail. Specialized runners, like ungulates, have short muscles with long tendons in the lower parts of their legs that are slender in proportion to the forces they have to transmit. An extreme example is the plantaris muscle of the camel, in which the tendon runs almost the entire distance between the femur and the muscle's insertion on the phalanges (Alexander et al., 1982).

Branchiomeric muscles (muscles associated with the sides of the branchial arches) of the first pharyngeal arch continue to operate the jaws. Muscles of the second arch are attached to the hyoid skeleton. Muscles of arches III–VII continue to be associated with the pharynx and larynx.

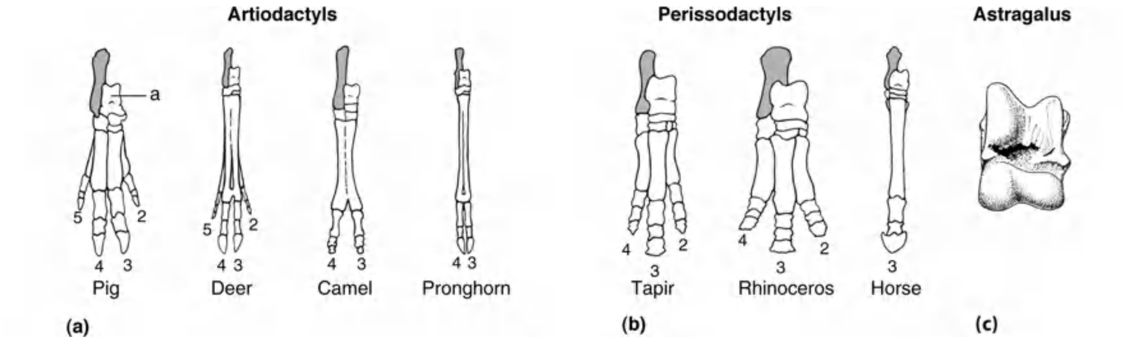
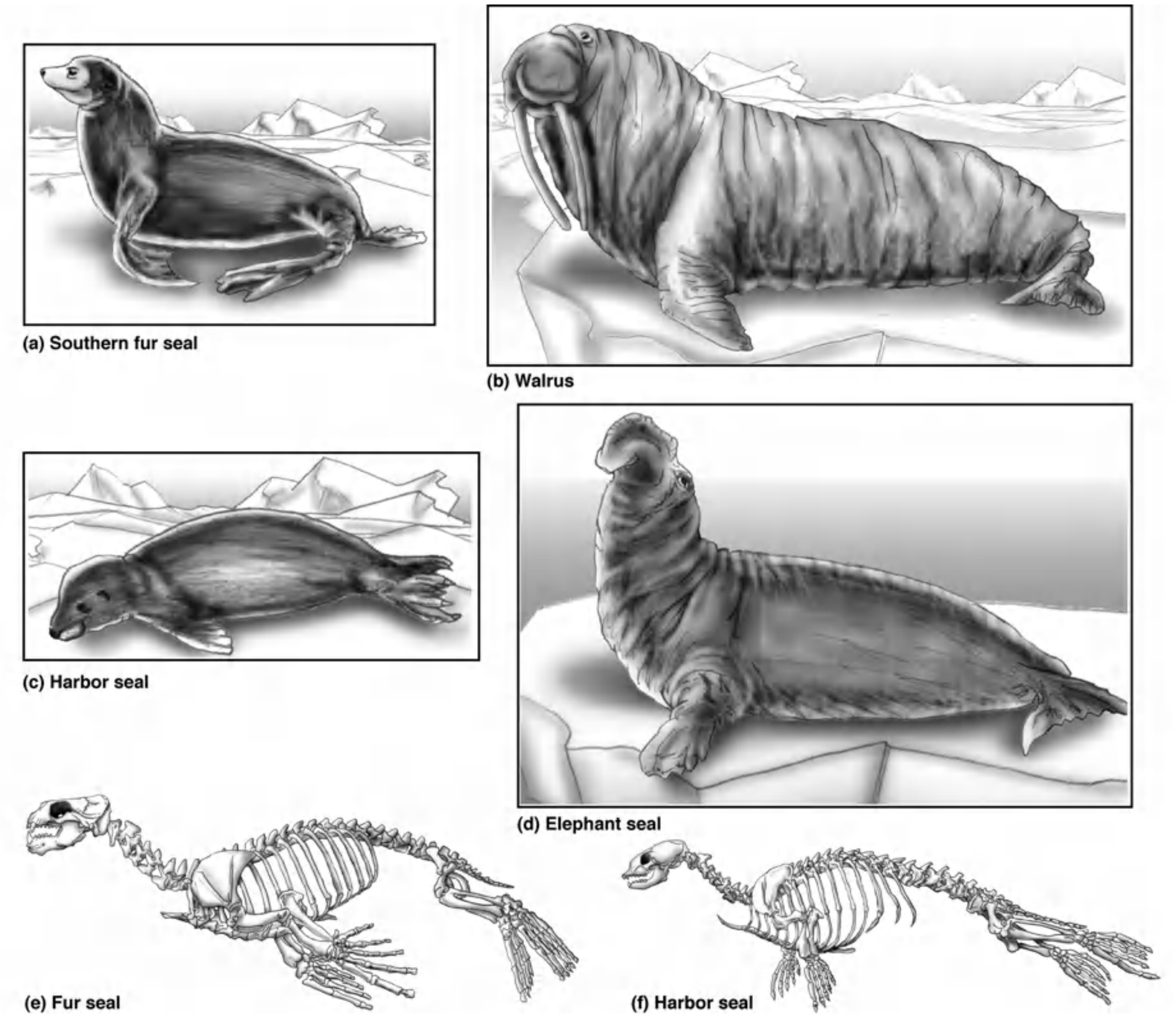


Figure 9.36. (*a*) Foot structure in artiodactyls. Weight is equally distributed between digits 3 and 4. (*b*) Foot structure in perissodactyls. Digit 3 is the only functional digit on each limb. In all examples, the heel bone (calcaneum) is shaded and articulates with the astragalus (*c*).



(a) Southern fur seal

(b) Walrus

(c) Harbor seal

(d) Elephant seal

(e) Fur seal

(f) Harbor seal

Figure 9.37. (*a*) Southern fur seals (*Arctocephalus*) and (*b*) walruses (*Odobenus*) possess hindlimbs that can be brought under the body for locomotion on land. (*c*) Harbor seals (*Phoca*) and (*d*) elephant seals (*Mirounga*) are unable to bring hindlimbs forward. Note the difference in the size of the forelimbs in the skeletons of (*e*) fur seal and (*f*) harbor seal.

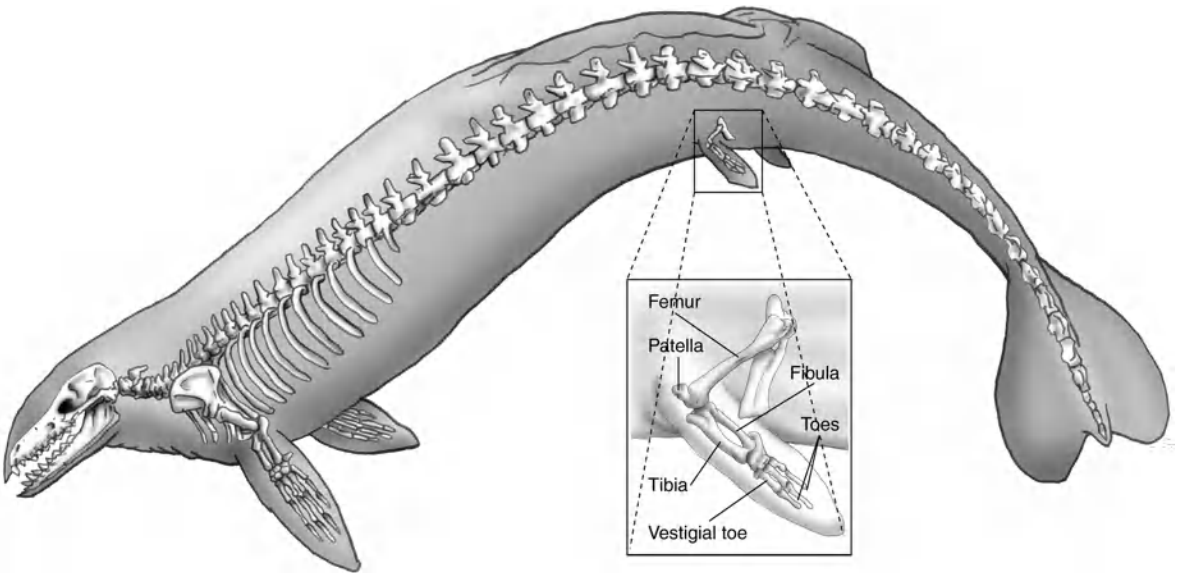


Figure 9.38. It is believed that whales diverged from primitive mammalian stock and that adaptation to a marine life is secondary. Specimens of *Basilosaurus isis* include the first functional pelvic limb and foot bones known in the order Cetacea. Distal portions of the hindlimbs show a paraxonic arrangement (the functional axis of the leg passes between the third and fourth digits), which is strikingly similar to that of an extinct group of ungulates, the mesonychid condylarths, as well as modern artiodactyls. In addition, the skull and dental structure of mesonychid condylarths are similar to those of primitive whales. These paleontological data are supported by protein sequence and cytochrome b sequence molecular data.

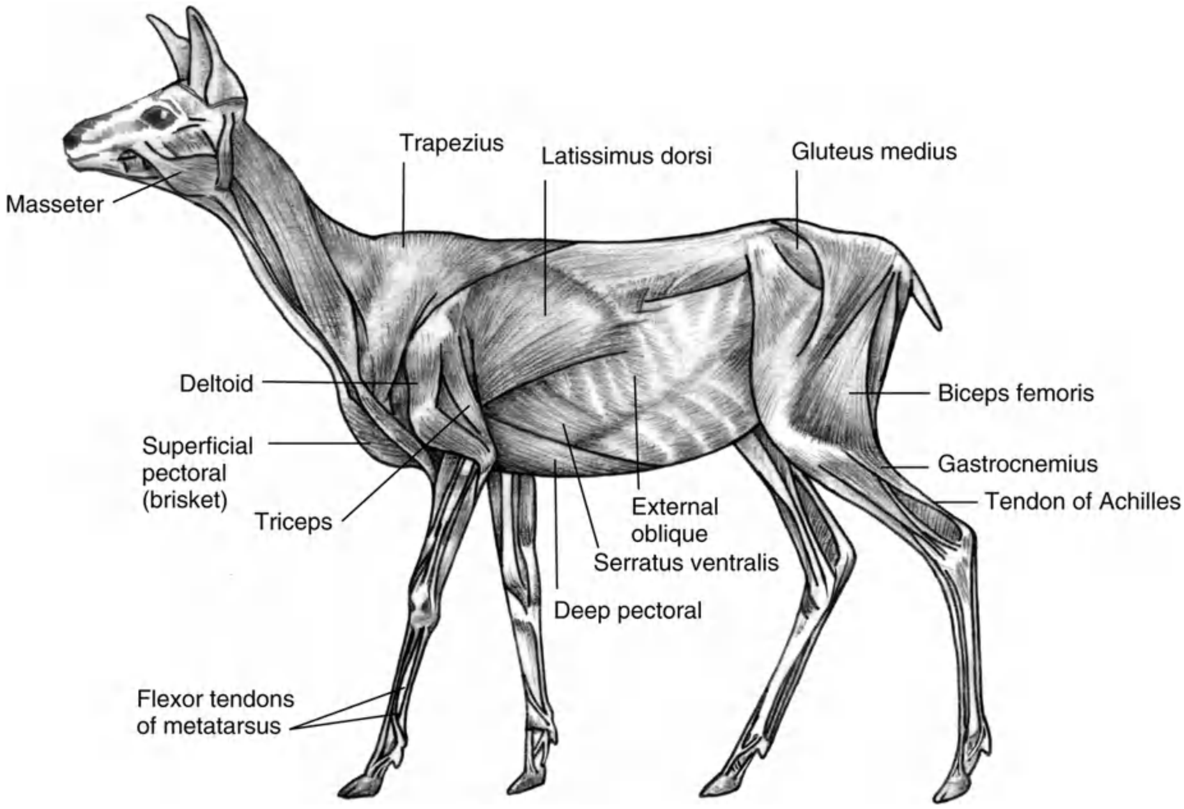


Figure 9.39. Superficial musculature of a white-tailed deer (*Odocoileus virginianus*). Epaxial muscles along the vertebral column are obscured by the greatly expanded, extrinsic appendicular muscles.

The branchiomeric muscles in some mammals are extremely well developed. For example, approximately 25 percent of the naked mole rat's muscle mass is concentrated in the jaw region (Sherman et al., 1992). This subterranean burrower uses its incisors and powerful jaws to excavate burrows in the semideserts of Kenya, Somalia, and Ethiopia. In contrast, a human jaw contains less than 1 percent of the body's muscle mass.

Integumentary muscles are best developed in mammals. The arrector pili muscles, which cause the elevation of hairs for insulation or as a response to danger, have already been discussed in this chapter (see pages **260–61**). In some mammals, a derivative of the hypaxial musculature, the **panniculus carnosus** (cutaneous maximus), covers much of the trunk. Nipples and teats are surrounded by the compressor mammae muscle, a specialized part of the panniculus carnosus. Armadillos use the panniculus carnosus to roll into a ball when endangered. A portion of this muscle in marsupials forms a sphincter surrounding the entrance to the pouch. Many mammals, including horses and cows, make a portion of this muscle contract and "twitch" the skin in order to shake off flies. It is either poorly developed or absent in primates.

The Origins of Whales

It is believed that whales diverged from primitive mammalian stock and that adaptation to a marine life is secondary. Two main hypotheses exist for the relationship of the mammalian order Cetacea (whales, dolphins, and porpoises). The first hypothesis, mainly supported by DNA sequence data, is that one of the groups of artiodactyls (e.g., hippopotamuses) is the closest extant relative of whales. The second hypothesis, mainly supported by paleontological data, identified mesonychians as the sister group to whales. The oldest whale (*Pakicetus*) dates from 50 Mya. Recent evidence from 40-million-year-old Eocene fossils discovered in Egypt seems to confirm a long-suspected connection between cetaceans and early artiodactyl relatives. Specimens of *Basilosaurus isis* include the first functional pelvic limb and foot bones known in the order Cetacea (see Fig. 9.38). Distal portions of the hindlimbs show a paraxonic arrangement (the functional axis of the leg passes between the third and fourth digits), which is strikingly similar to that of an extinct group of ungulates, the mesonychid condylarths, as well as to that of modern artiodactyls. The skull and dental structure of mesonychid condylarths are similar to those of primitive whales (archaeocetes). These paleontological data are supported by new protein sequence and cytochrome b sequence molecular data. However, new fossils have weakened the links between the whales and the mesonychians and show that whales are probably cousins of the ungulates, if not actual members of that group.

An ancient four-legged whale walked the land on hooved toes and swam in the sea like an otter. The newly discovered species, *Peregocetus pacificus*, turned up in 2011 in a cache of fossilized bones in Playa Media Luna, a dry coastal area of Peru. Jawbones and teeth pegged the animal as an ancient whale, but don't match any other whale in the fossil record. At 42.6 million years old, the fossilized whale skeleton is the oldest found in the Americas. About 4 m (13 ft.) long, the animal was roughly the size of a small beluga whale. Big, possibly webbed, feet and long toes would have allowed *P. pacificus* to dog-paddle or swim freestyle. The whale's vertebrae suggest the tail functioned like a paddle, as seen in modern beavers and otters.

Goodman et al., 1985; Gingerich et al., 1990; Irwin et al., 1991; Novacek, 1992; Normile, 1998; Thewissen et al., 1998; Lambert et al., 2019

Mimetic muscles, or muscles of facial expression, have evolved from the platysma muscle and have spread onto the faces of mammals. They are best developed in primates, with humans possessing approximately 30 of these muscles, the largest number in any mammal. By contracting one or more of these muscles, actions and expressions can be conveyed: for example, wrinkling the skin of the forehead, raising the eyebrows, closing the eyes, depressing the corner of the mouth, elevating the upper lip to expose the canine teeth, and dilating the nostrils.

Cardiovascular System

The two atria and two ventricles of the heart are separated by interatrial and interventricular septa, respectively (Fig. 9.40). Atria exhibit unique, earlike lobes—the **auricles**. The sinus venosus is incorporated into the wall of the right atrium.

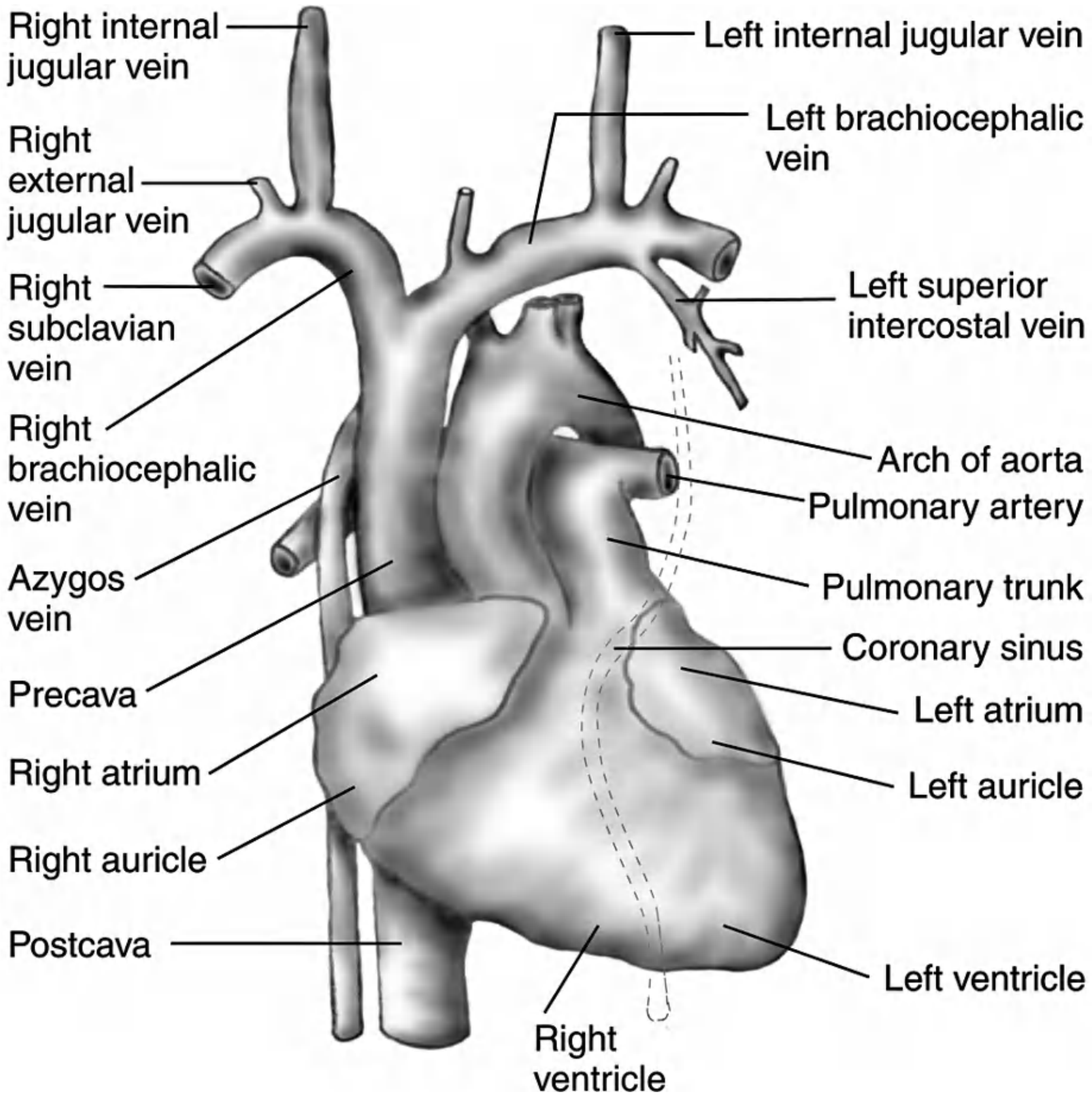


Figure 9.40. The mammalian heart, ventral view. The four-chambered heart consists of two atria and two ventricles.

Normal heart rates can vary from fewer than 25 per minute in the Asiatic elephant (*Elephas maximus*) to more than 1,000 per minute in some shrews. Blood pressure is highest in the aorta and decreases as it flows through the smaller arteries, arterioles, capillaries, venules, and veins. All blood being pumped from the left ventricle goes through the former left fourth aortic arch (arch of the aorta) prior to going to the head, to the front limbs, or into the descending aorta (see Fig. 9.40). This route is opposite to the condition in birds (i.e., right aortic arch in birds rather than left). The right brachiocephalic artery, when present, is a remnant of the right fourth arch, as is the proximal part of the right subclavian. During embryonic development in mammals, the six homologous aortic arches are represented but are never all present at the same time; some regress before others form.

In mammals that dive to great depths, modifications of the circulatory system are necessary to withstand the increased pressure and to provide oxygen to vital organs while the animal is underwater. Some species may remain underwater as long as two hours. Vast networks of arteries (*retia mirabilia*) are located in protected positions along the vertebral column under the transverse processes, within the bony neural canal and within the thoracic cavity. All of the *retia* are interconnected, supplied by branches of the aorta, and drained by efferent arteries. When a whale dives, the abdominal wall is compressed against the vertebral column by external pressure. This increased pressure forces abdominal viscera into the thorax, and air is forced out of the lungs into the trachea. The increased pressure causes the constriction of all arteries except those of the brain, which are protected by the skull. Blood forced out of the organs collects in large quantities in the *retia*, and these pools form protected reservoirs of oxygenated blood that are available for use by the brain.

The Aerobic Pronghorn

Cheetahs are fast: over short stretches, they can sprint at 95 km (60 mi.) per hour. But for high-speed, long-distance running, nothing beats the pronghorn, or American, antelope. The most reliable estimates show that pronghorns comfortably can cover 11 km (6.8 mi.) in 10 minutes —an average speed of 65 km (40 mi.) per hour.

The pronghorn's secret is a series of physiological and structural adaptations that allow it to consume oxygen with more than three times the expected efficiency. For this reason, the pronghorn can process much more oxygen than other mammals its size.

Pronghorns have spectacularly large lungs, which are three times as large as those of comparably sized goats. The heart is unusually large and the blood of the pronghorn is rich in hemoglobin, which means that more oxygen can be delivered to the muscles in less time. The pronghorn's skeletal muscle cells also are densely packed with mitochondria, the intracellular structures involved in aerobic metabolism.

Together, these adaptations provide the pronghorn with speed and endurance, both of which may be essential for escaping from predators in the exposed habitat of the North American prairie.

Lindstedt et al., 1991; Rennie, 1992

Retia serving other functions are found in ungulates, xenarthrans, carnivores, and birds and are not uncommon in lower vertebrates, especially on the pathways of arteries leading to the brains of fishes and in the linings of swim bladders (red glands) (see Chapter 4). *Retia* frequently regulate pressure in arteries distal to themselves. In the desert-dwelling oryx (*Oryx* sp.) and Grant's gazelle (*Gazella granti*), a *rete* system serves to cool arterial blood supplying the brain (Fig. 9.41).

Seals and whales have flippers and flukes that lack blubber and are poorly insulated. These appendages are composed of bone and cartilage and are not well supplied with blood vessels. Nonetheless, these relatively thin structures with their large surfaces can lose substantial amounts of heat and aid in heat dissipation. Excessive heat loss from blood in the flippers is prevented by the arrangement of the arterial and venous vessels, which allows for countercurrent heat exchange. In the *retes*, which are located just inside the contour of the body adjacent to the flippers, each artery is completely surrounded by veins, and as warm arterial blood flows into the flipper, it is cooled by cold venous blood that surrounds it on all sides. The arterial blood, therefore, reaches the flipper precooled and loses little heat to the water. Heat has been transferred to the venous blood, which thus is prewarmed as it enters the body. If the heat exchange is efficient, the venous blood nearly reaches arterial temperatures and thus causes virtually no cooling to the core of the whale's body.

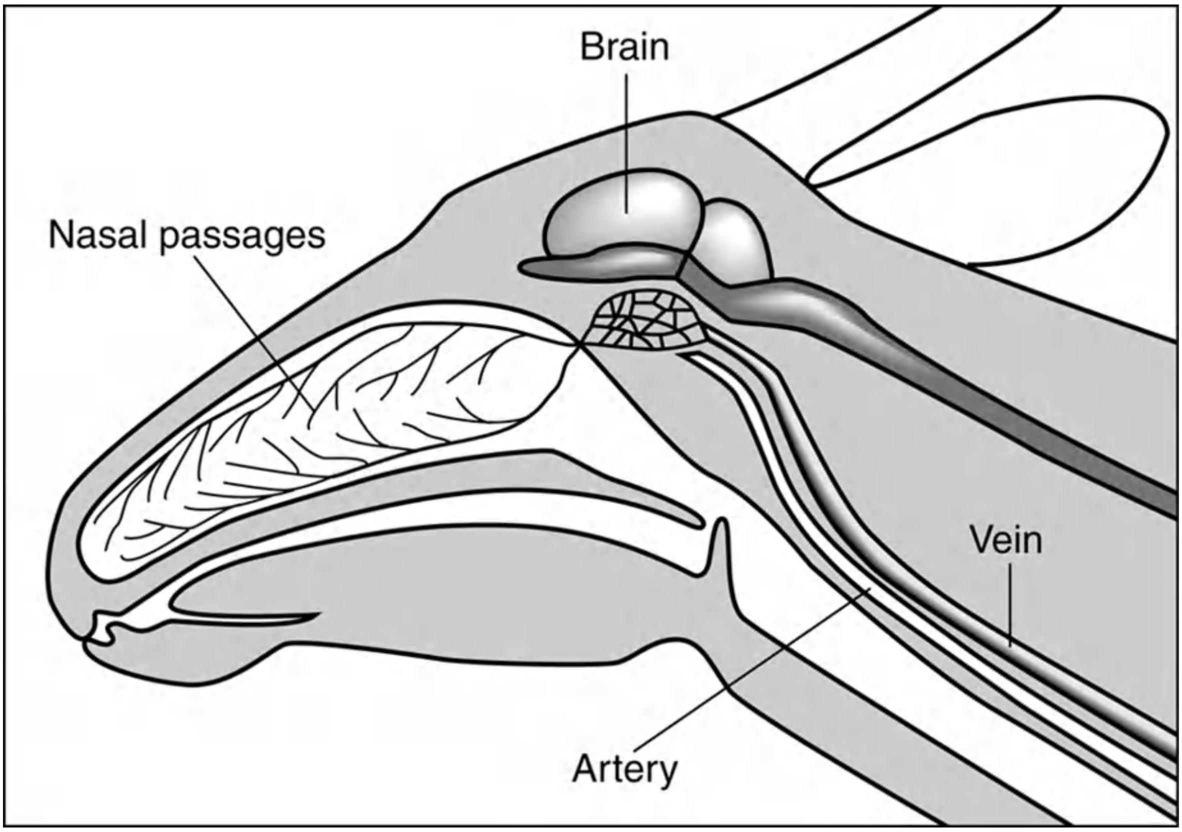


Figure 9.41. In the oryx (*Oryx* sp.), countercurrent cooling of arterial blood occurs in the cavernous sinus, on its way from the heart to the brain. Within the sinus, the carotid artery ramifies into hundreds of smaller vessels. Also within the sinus, venous blood from the oryx's nasal passages, cooled by respiratory evaporation, lowers the arterial blood temperature. Since oryx inhabit desert areas, having a brain cooler than the body temperature may be vital for its survival.

The oral cavity of baleen whales, which is relatively large in order to accommodate the filtering surface composed of baleen, is potentially a major site for heat loss during feeding in colder waters. In the gray whale (*Eschrichtius robustus*), heat loss is substantially reduced by the presence of numerous individual countercurrent heat exchangers found throughout the massive tongue, which may comprise 5 percent of the body's surface area (Heyning and Mead, 1997). Cool venous blood returning from the surface of the tongue flows first ventrally, then posteriorly toward the back of the tongue. Heat exchangers converge at the base of the tongue to form a bilateral pair of large vascular *retia*. Although the tongue is much more vascularized and has much less insulation than any other body surface, temperature measurements indicate that more heat may be lost through the blubber layer over the body than through the tongue. The lingual *retia* of the gray whale form one of the largest countercurrent heat exchangers described in any endotherm.

The blood of mammals contains erythrocytes (Fig. 9.42), leukocytes, and thrombocytes. With only one exception (camels), mature circulating erythrocytes of mammals are non-nucleated, biconcave disks. During the process of erythropoiesis (erythrocyte formation) in red bone marrow, the cells contain a nucleus, ribosomes, and mitochondria, but these gradually disappear before the erythrocytes are released into the circulating blood.

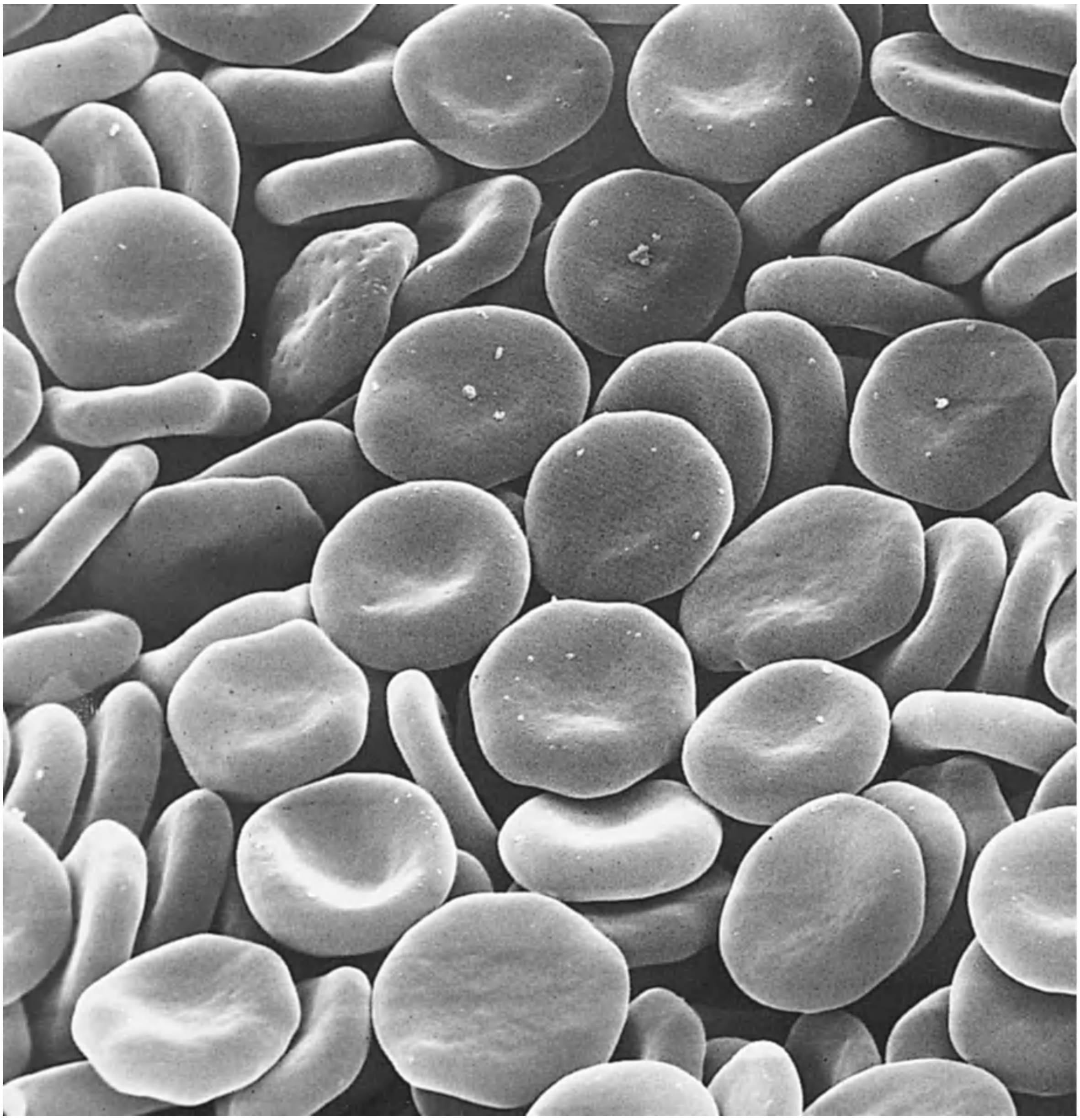


Figure 9.42. As shown by scanning electron microscopy, mammalian erythrocytes (red blood cells) are biconcave disks.

Camels possess non-nucleated *biconvex* erythrocytes that are reinforced by a hoop made of a bundle of microtubules (Weibel, 1984). This is thought to be an adaptation to allow the cells to shrink without being deformed when the animal is subjected to periods of considerable water loss.

Heart Size

In mammals, heart size increases with body size, but relative to their body size, small and large mammals have approximately the same heart size. The mass of the mammalian heart, irrespective of the size of the mammal, averages 0.59 percent of the body mass. Heart sizes of birds average 0.82 percent of body size. A reptile's heart size is approximately 0.51 percent of its body weight, whereas that of an amphibian is 0.46 percent. Although the proportions of heart mass to body mass in reptiles and amphibians are only slightly lower than in mammals, metabolic rates of reptiles and amphibians are only approximately one-tenth of mammalian rates. Hearts of fishes average only about 0.2 percent of their body weight.

Schmidt-Nielsen, 1997

Mammals regulate their body temperature by continuously monitoring the outside temperatures on the surface of their skin and at the hypothalamus. Heat-absorbing and heat-transporting capabilities of the blood are vital in maintaining homeostasis. When overheating occurs, some mammals sweat. The liquid drops of perspiration that appear on the surface of the skin cause a cooling effect as evaporation occurs. Thermal panting is characteristic of canids (Schmidt-Nielsen et al., 1970). The major portion of inhaled air enters through the nose and exits via the mouth. As exhaled air passes over the moist tongue and mucous membranes, it causes the evaporation of saliva, which in turn cools blood circulating in the capillaries of the tongue and adjacent tissues.

Thermal imaging has revealed a heat-radiating stripe on each wing of free-tailed bats (*Tadarida brasiliensis*) (Milius, 2010). The narrow, ladder-like array of blood vessels seems to act as thermal windows, like the blood vessels in a toucan's beak (see Fig. 8.13). Animals flush these zones with blood to cool down and shunt blood away to avoid chills. Radiator stripes have only been found in the family that includes this species.

Respiratory System

The paired external nares lead into paired nasal passageways (canals) that are partially occluded by several scroll-like bones, called **nasal conchae** or turbinal bones (Figs. 9.43 and 9.44), covered by ciliated mucous epithelium. Conchae slow down air flow in order to allow it to be filtered, warmed, and moistened. The nasal passageways are located dorsal to the hard and soft palates, which effectively separate the respiratory passages from the oral cavity. The olfactory epithelium is located in the posterodorsal portions of each nasal passageway. The nasal passageways open via internal nares into the nasopharynx above the soft palate.

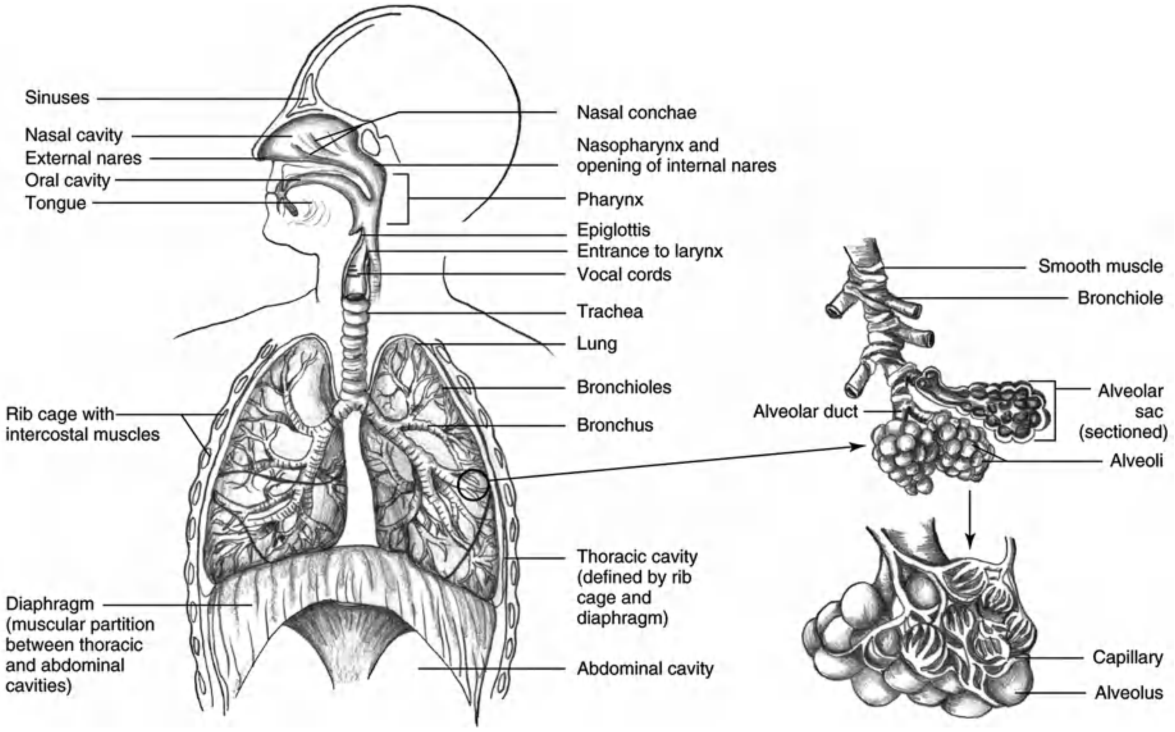


Figure 9.43. The human respiratory system. Note the muscular diaphragm.

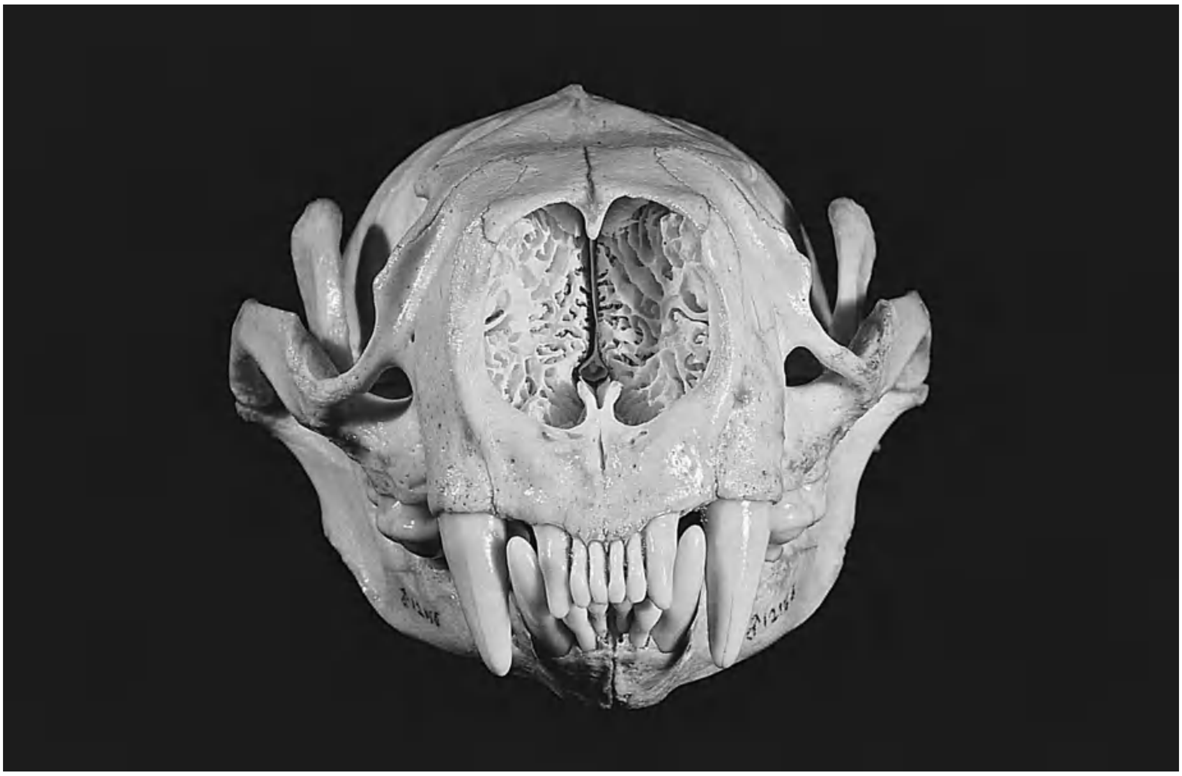


Figure 9.44. Front view of the skull of a sea otter (*Enhydra lutris*) showing the highly developed, scroll-like structure of the nasal conchae. Nasal conchae slow down the passage of air so that it can be filtered, warmed, and moistened prior to traveling through the respiratory system.

The soft palate separates the dorsal **nasopharynx**, which contains the openings of the auditory (Eustachian) tubes, from the **oropharynx**. Ventral to the oropharynx is the **laryngopharynx**, which leads to the glottis and esophagus. A cartilaginous flap, the **epiglottis**, covers the glottis when food is being swallowed. The food and air pathways cross in the laryngopharynx. Air must pass through the pharynx and enter the slitlike glottis at the top of the larynx, whereas food must enter the esophagus on its route to the stomach. The larynx, or voice box, which is located near the anterior (superior) end of the trachea, contains vocal cords, which in most mammals may vibrate during exhalation. Cartilaginous rings surround the trachea to prevent it from collapsing.

The trachea branches into two bronchi, each of which divide into secondary and tertiary branches. Tertiary branches give rise to the smallest air passageways, the **bronchioles** (see Fig. 9.43). Bronchioles lead into delicate, thin-walled **alveoli**, or respiratory pockets, which vastly increase the surface area of the lung available for gas exchange. Alveoli are surrounded by dense capillary beds. It is here that the exchange of gases between the inspired air and the blood occurs. Large surface areas are essential for the high rates of oxygen uptake required by the high metabolism of homeotherms. An efficient respiratory system enhances the maintenance of a relatively constant high body temperature.

The lungs of most mammals are divided into lobes, with each lung occupying a separate pleural cavity. In some mammals, including monotremes, only the right lung is lobed. In others, like whales, sirenians, elephants, and perissodactyls, both lungs lack lobes.

Carbon dioxide normally diffuses across the alveolar-capillary membrane in the lung and is expelled through the process of exhalation. Some bats, however, may lose carbon dioxide through their large, highly vascularized, hairless wing membranes. In the big brown bat (*Eptesicus fuscus*), 0.4 percent of the total carbon dioxide production is lost from the wing skin at 18°C (64°F). The amount increases with temperature, and at an air temperature of 27.5°C (81.5°F) as much as 11.5 percent of the total carbon dioxide is lost this way (Herreid et al., 1968). Uptake of oxygen through the wing membranes, however, is not sufficiently great to be of any physiological significance.

Most mammals do not carry on gas exchange through their skin because they have high metabolic rates and because diffusion through the skin is poor. The Julia Creek dunnart (*Sminthopsis douglasi*) is a small marsupial mouse with one of the smallest newborns of any mammal (Mortola et al., 1999). Following a gestation period of approximately 13 days, the newborn is about 4 mm (5/32 in.) long and weighs about 17 mg. During the first few days following birth, the predominant form of oxygen and carbon dioxide exchange is through the skin. In young mammals with body weight below 100 mg (0.0035 oz.), gas exchange through the skin exceeds that through the lungs. In mammals 20 to 21 days of age with an average weight of 290 mg (0.01 oz.), skin exchange is about one-third that of the lungs. Gas exchange through the skin apparently allows these very small animals to be born before the respiratory apparatus is fully functional.

A muscular, dome-shaped **diaphragm**, an extension of the body wall musculature, separates the pleural cavities from the abdominal cavity. At rest, the diaphragm is dome-shaped (see Figs. 9.43 and 9.45). When the diaphragm contracts, it flattens and enlarges the thoracic cavity. In conjunction with the elevation of the ribs by external intercostal muscles, these actions also lower the internal pressure in the pleural cavities below atmospheric pressure and allow air to flow into the lungs.

Relaxation of the diaphragm, a passive process, and contraction of the internal intercostal muscles decrease the volume and increase the pressure in the thoracic cavity above atmospheric pressure, thus forcing air out of the lungs.

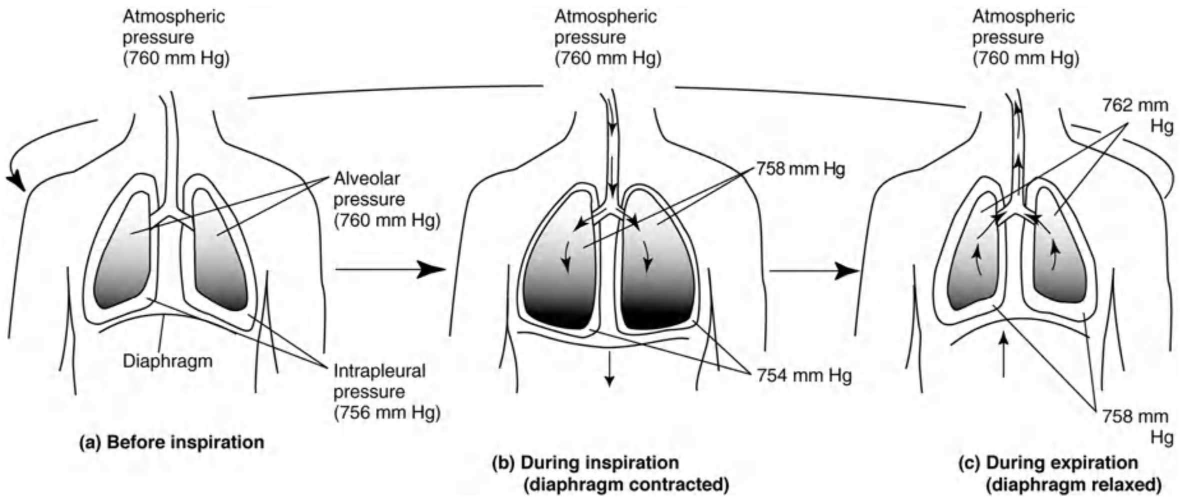


Figure 9.45. Pulmonary ventilation: pressure changes. (*a*) Prior to inspiration, the diaphragm is dome-shaped and the alveolar and atmospheric pressures are the same. (*b*) At the beginning of inspiration, the diaphragm contracts, the external intercostal muscles elevate the ribs causing the chest to expand, and alveolar pressure decreases. (*c*) As the diaphragm relaxes, internal intercostal muscles lower the ribs, and alveolar pressure rises, forcing air out until the alveolar pressure equals the atmospheric pressure.

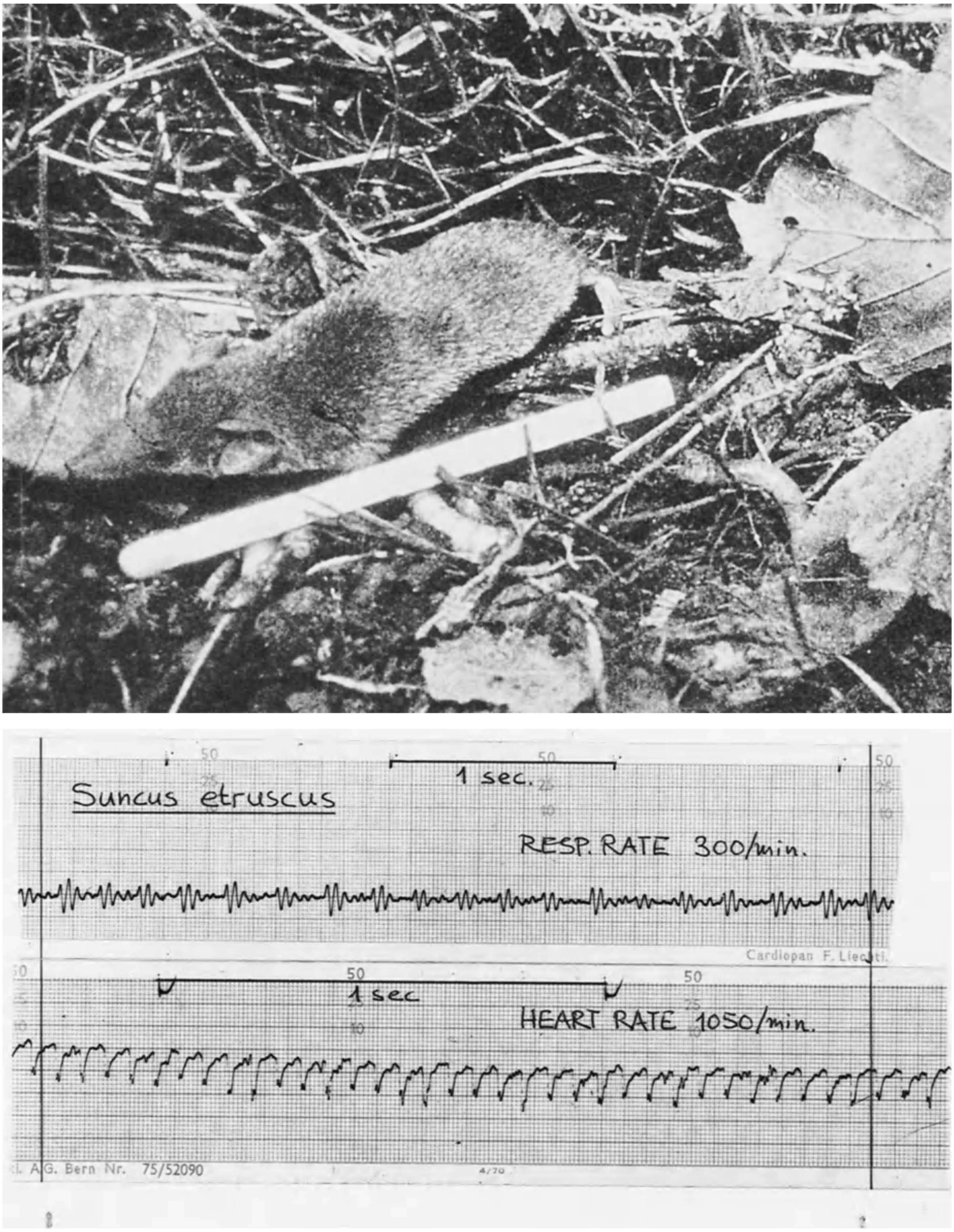


Figure 9.46. One of the smallest mammals, the Etruscan shrew (*Suncus etruscus*), weighing 2.5 g (0.09 oz.), is shown beside a match (*top*). Recordings of the respiratory and heart rates of the Etruscan shrew at rest (*bottom*).

When resting, humans generally renew about 10 percent of the air in the lungs in a single breath. Some mammals, like the manatee, can renew about 90 percent of the air in their lungs in a single breath while resting

(Reynolds and Odell, 1991); this explains why they can remain underwater up to 20 minutes. Weddell seals in Antarctica may plunge hundreds of meters below the ocean’s surface to hunt for fish and squid. Although most dives last 5 minutes or less, the longest recorded dive lasted 48 minutes (Harding, 1993). The deepest recorded dive was 600 m (1,968 ft.). Northern elephant seals have been known to descend 1,530 m (5,018 ft.) and remain submerged for 77 minutes (Harding, 1993). Sperm whales (*Physeter macrocephalus*) often dive to depths of at least 1,000 m (3,280 ft.) and remain submerged up to 90 minutes (Riedman, 1990). An acoustic recording of a sperm whale at a depth of 2,250 m (7,380 ft.) was reported by Norris and Harvey (1972).

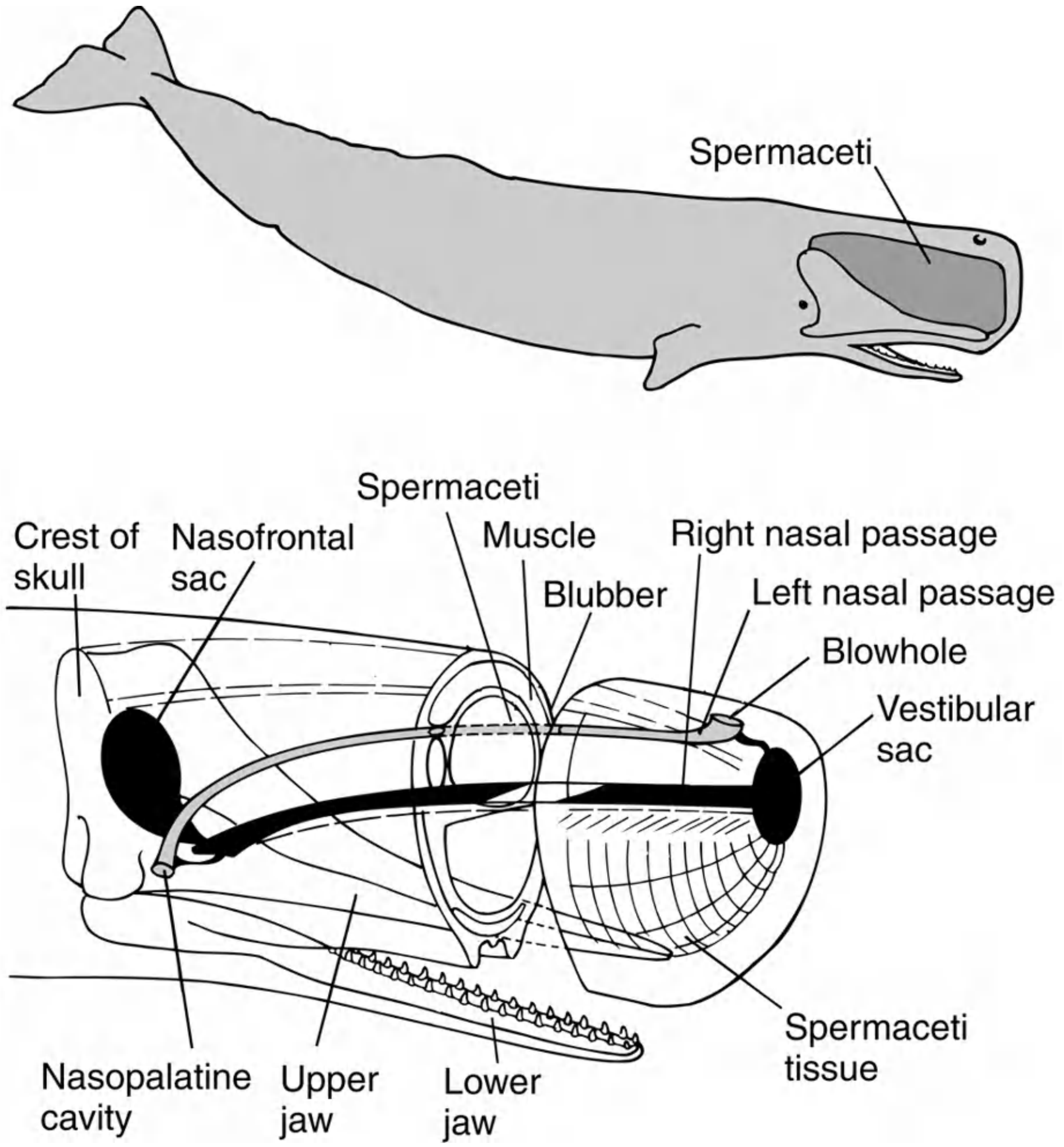


Figure 9.47. Sperm whales (*Physeter catodon*) regulate their buoyancy by warming or cooling the oil in the spermaceti tissue in their large heads. The two nasal passages are asymmetrical, with the left passage running from the nasopalatine cavity to the blowhole, and the right running through the spermaceti organ. Cool water channeled through the spermaceti organ causes the surrounding oil to crystallize and become denser, thus enabling the whale to descend. Warming of the organ changes the crystallized oil into a liquid and increases the whale's buoyancy.

Cat Vocalizations

There are 37 species of cats on Earth. Most howl or yowl, meow or purr, but only four—the tiger, leopard, jaguar, and African lion—can roar. The reason: these species have a unique vocal apparatus. Bones supporting the larynx are linked by an elastic ligament rather than more solid bone, and a length of tough cartilage runs up the hyoid bones to the skull. This feature prevents purring, but stretching of this ligament enlarges the air passage, facilitating a full-throated, resonant noise that may be heard up to 8 km (5 mi.) away. The purring of the smaller cats—house cats, bobcats, ocelots, lynxes, and others—occurs when the cat vibrates its larynx, which in turn, allows the delicate hyoid bones to resonate. Muscles create the continuous purring vibration—one twitch per second—during both inhalation and exhalation. Purring is independent of age, sex, weight, and size and is controlled by the brain. One big cat that purrs but cannot roar is the cheetah.

Sissom et al., 1991; Stewart, 1995

The blue whale, bottlenose dolphin, Weddell seal, and elephant seal all cut diving energy costs 10 to 50 percent by simply gliding downward (Williams et al., 2000). Their buoyancy decreases because water pressure squeezes their bodies into a smaller volume and flattens air sacs in their lungs. As the animals sink, they save energy for the swim back up.

When a marine mammal dives, muscles in its nose relax and the nasal openings close. Almost immediately the heart rate drops more than 50 percent, and blood flow is reduced to all but the most vital organs, like the heart and brain. For example, in bottlenose dolphins (*Tursiops truncatus*), the heart rate drops from 110 beats per minute while at the surface to about 50 while submerged. Orcas, or killer whales (*Orcinus orca*) have a rate of about 60 beats per minute at the surface and 30 per minute while submerged (Rice, 1967). At the same time, extra red blood cells pour into the bloodstream from the spleen and become available to transport increased oxygen.

For humans, breathing is an involuntary reaction. Whales, however, are voluntary breathers, which means they have to keep their brains active in order to breathe—they cannot be completely unconscious. Whales are thought to rest and not sleep. Many scientists believe that whales and dolphins can shut down half of their brains at a time. In this condition, the brain is alert enough to trigger the body to control surfacing and breathing. This is thought to happen when they rest in a semiconscious state near the water’s surface—an activity called *logging*.

Deep-diving mammals do not use their lungs as their major oxygen storehouse. Because they have higher concentrations of red blood cells and hemoglobin than other animals, they can store large amounts of oxygen in myoglobin (a form of hemoglobin) in their muscles—as much as 13 times the amount held in the lungs. To cope with extreme pressure, most deep-diving mammals have cartilage-reinforced air passageways that allow the lungs to collapse and then reinflate (Fig. 9.48). The lungs contract slowly as pressure increases during the descent, and they gradually open back up during the ascent (Williams et al., 2000).

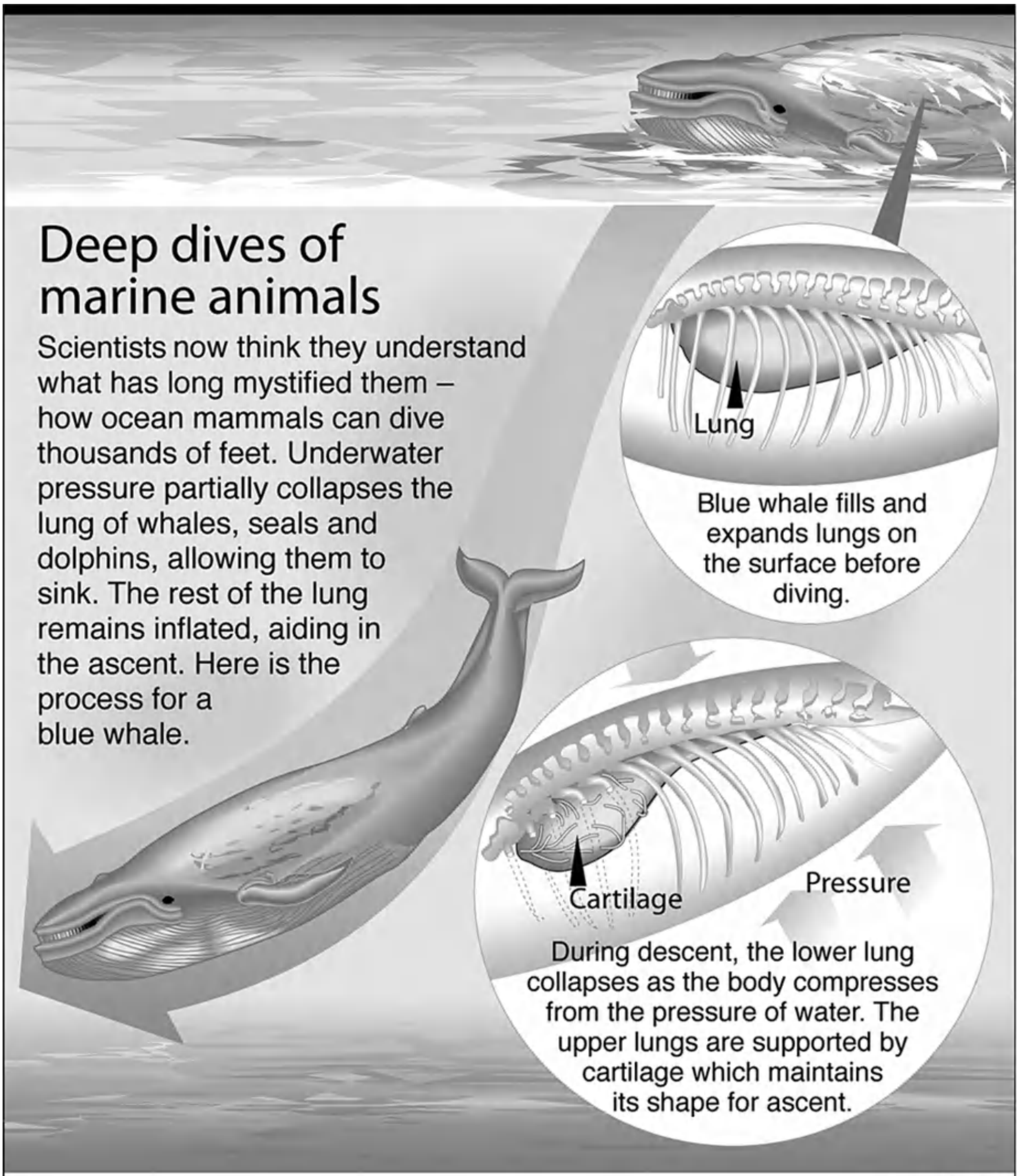
Lungs to the Limit

The mammalian respiratory system reaches its ultimate potential in the smallest known mammals like the Etruscan shrew (*Suncus etruscus*), which weighs about 2 g (0.07 oz.) (see Fig. 9.46), and Kitti's hog-nosed bat (otherwise known as the bumble-bee bat) of Thailand (*Craseonycteris thonglongyai*), which weighs approximately 1.7 g (0.06 oz.). The shrew has the highest metabolic rate of any known mammal. Its heart rate is more than 1,000 beats per minute and its respiration rate is more than 300 breaths per minute. The heart fills about half of the left chest cavity, leaving little room for the left lung. The lungs, which consist of a maze of tiny alveoli and blood capillaries, have a gas exchange surface whose density is eight times as large as that of a human and three times as large as that of a mouse. The air-blood barrier within the lung consists of a very fine barrier of extremely thin endothelium.

Weibel, 1984

Deep dives of marine animals

Scientists now think they understand what has long mystified them – how ocean mammals can dive thousands of feet. Underwater pressure partially collapses the lung of whales, seals and dolphins, allowing them to sink. The rest of the lung remains inflated, aiding in the ascent. Here is the process for a blue whale.



Blue whale fills and expands lungs on the surface before diving.

During descent, the lower lung collapses as the body compresses from the pressure of water. The upper lungs are supported by cartilage which maintains its shape for ascent.

Depth of dives

Seals are able to dive the deepest — some up to nearly a mile. Here are the depths of the dives for the mammals in the study.

Figure 9.48. Underwater pressure partially collapses the lungs of some marine mammals, allowing them to dive to great depths.

Digestive System

The major components of the digestive system of mammals are the oral cavity, pharynx, esophagus, stomach, small intestine, large intestine, rectum, and anus. The oral cavity (mouth) is bounded by the lips, cheeks, hard palate, and tongue. The lips of many mammals are highly vascularized and function in determining the texture and temperature of foods. Teeth begin the mechanical breakdown of food; saliva secreted by the salivary glands initiates the chemical breakdown. The tongue, which is roughened by the presence of papillae on its dorsal surface, manipulates the food in the mouth and plays a major role in swallowing by forcing the food back into the pharynx.

Figure 9.49. The eastern chipmunk (*Tamias striatus*) has internal cheek pouches that can be filled with seeds to be carried to a storage cache. Although chipmunks are inactive during severe winter weather, they are active during warmer winter periods. They attempt to store at least one-half bushel of food to carry them through the winter months.

Some mammals, like eastern chipmunks (*Tamias striatus*), have large, membranous, internal cheek pouches on the medial surfaces of the cheeks (Fig. 9.49), whereas others, like pocket gophers (*Geomys* sp.), have external cheek pouches. Cheek pouches are used to transport seeds and other foods to the nest site or storage chambers.

Most mammals have teeth composed of dentin and enamel. Enamel is the hardest substance in the body, but once damaged or destroyed, it is not replaced. Dentin, which is almost as hard as enamel, surrounds the pulp cavity that contains blood vessels and a nerve.

A few mammals, like armadillos, sloths, and anteaters, have reduced dentition, or they have lost their teeth entirely (Fig. 9.50e). When present, teeth are confined to the jaws and are much less numerous than in other vertebrate groups. Only in mammals is there a specific number of teeth in a given species.

The Spermaceti Organ

One problem that whales have is maintaining neutral buoyancy while they are diving and when they remain at a particular depth. Neutral buoyancy control by sperm whales at various depths and temperatures is maintained by means of the **spermaceti organ** and its oil. The spermaceti organ, which is richly supplied by blood vessels, is a massive heat exchange device that controls the temperature and density of the oil. Spermaceti oil (unlike water, which freezes suddenly at 0°C, or 32°F) becomes increasingly crystalline over a range of several degrees. To swim downward, substantial effort is needed to overcome the initial buoyancy of the lungs. This causes the whale’s body temperature to rise significantly. When the time comes for surfacing, blood courses through the spermaceti organ, transferring the surplus heat to the oil and liquefying it. The resulting increase in its buoyancy greatly facilitates the whale’s return to the surface. Thus, efficient use is made of the surplus heat generated in diving.

As the whale descends, its lungs continue to collapse until at about 200 m (650 ft.) they no longer contribute significantly to the whale’s buoyancy. During the descent, cold water circulating through the spermaceti organ continuously cools the oil and reduces its buoyancy (see Fig. 9.47). By the time the whale arrives at its hunting depth, it has achieved neutral buoyancy and can, in effect, turn off its engines and conserve energy.

One of the two nasal passages that link the blowhole to the mouth passes through the spermaceti organ. The left passage retains its respiratory function. The right nasal passage, however, has become highly modified and passes controlled amounts of cold seawater through the spermaceti organ, countering the warming effect of the blood. A sperm whale remains submerged for about 50 minutes in a typical dive, although dives of 90 minutes have been observed. Each dive is followed by about 10 minutes of heavy breathing at the surface.

Cooke, 1991

Some mammals experience a forward progression of their teeth so that new teeth form at the rear of the jaw and gradually move forward to replace worn teeth. This type of tooth replacement is known to occur in one species of manatee, in one species of kangaroo, and in elephants (see Fig. 9.50b). Elephants have the use of 24 molar (cheek) teeth during their lifetime. Each adult molar is enormous, measuring 20 cm (8 in.) or more in length and weighing 3.5 to 4.0 kg (7.75–8.75 lb.). Only one, or parts of two, on each side of each jaw are in use, or in existence, at any one time. While the first group of four teeth are being worn down, four new teeth are growing behind them. These gradually move forward, replacing the old teeth, which are eventually shed. The process is then repeated, with each successive tooth being larger than the last. When six teeth have passed through each half of each jaw, no other teeth can be grown, and the animal finds itself unable to chew its food. Thus, in its lifetime, an elephant has 24 cheek teeth (molars) in all, the first 12 being milk teeth.

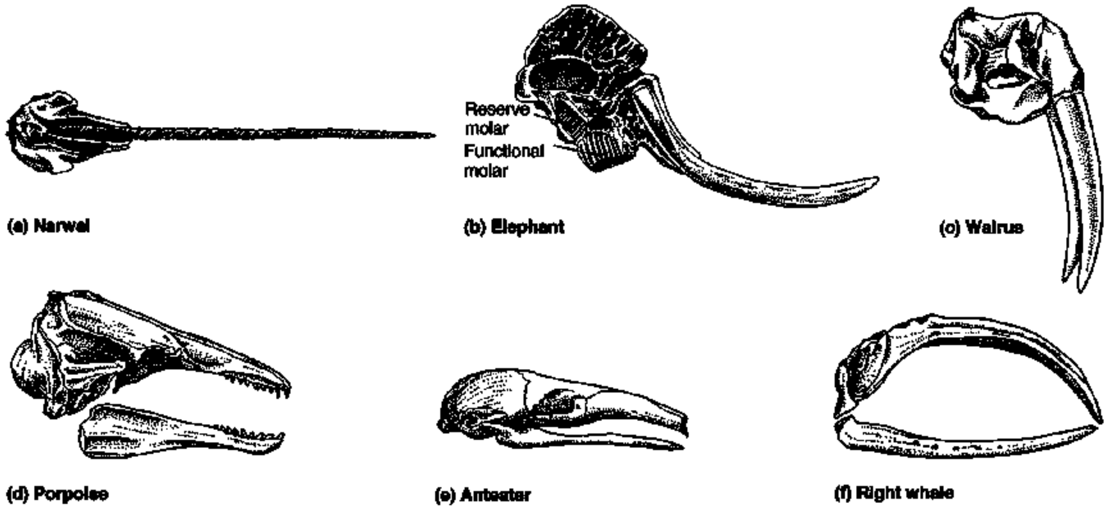


Figure 9.50. Specialized mammalian teeth. (*a*) The single tusk of the narwhal is a modified upper left incisor. (*b*) The paired tusks of the elephant are modified upper incisors. (*c*) The tusks in the walrus are modified canines. (*d*) Peglike teeth of a porpoise. Teeth are absent in adult anteaters (*e*) and baleen whales (*f*).

Baleen whales are toothless and are specialized for feeding on plankton. They may employ filter-feeding (suspension-feeding) or suction-feeding or both. A filtering apparatus consisting of 200 to 400 horny plates, called **baleen**, attached to the upper jaws hangs down on both sides (see Fig. 9.15). Depending on the species, each lightweight plate may be from 0.25 to 3 m (9 in. to 9.5 ft.) long. In a form of filter-feeding known as ram-feeding, the whales take water into their mouths as they swim forward. Water that is taken into the oral cavity flows over and between the plates, which serve as massive strainers to remove minute food particles. Any plankton caught in the hairlike edges of the plates is directed into the esophagus. Plankton-eating whales include blue whales, the largest living animals, which may attain weights of more than 90,000 kg (200,000 lb.).

Whereas most vertebrates have a succession of teeth throughout their lives (**polyphyodont condition**), most mammals develop only two sets of teeth (**diphyodont condition**). The first set is known as the **milk** (**deciduous**) **teeth.** Milk teeth usually erupt following birth but may erupt before birth in some species. These teeth are rooted in individual bony sockets (thecodont dentition) and will gradually be replaced by the **permanent**, or **adult**, **dentition**. Thereafter, a damaged or injured tooth will not be replaced in most mammals. Incisors, canines, and premolars are preceded by milk teeth; molars are not.

Some mammals have homodont dentition in which teeth are similar in size and appearance (see Fig. 9.50). Most mammals, however, have teeth that are modified for different purposes. This **heterodont dentition** often includes incisor, canine, premolar, and molar teeth (Fig. 9.51).

Incisors, the most anterior teeth in the oral cavity, are chisel-like and specialized for cutting and gnawing. In rodents and lagomorphs (rabbits and hares), these teeth continue to grow throughout life (see Fig. 9.51b). Enamel is present only on the anterior surface of these enlarged incisors and wears down more slowly than the dentin on the posterior surface; thus, these teeth continually have sharp, chisel-like edges. Incisors may be totally absent, as in sloths, or absent just from the upper jaw, as in deer.

The tusks of elephants (see Fig. 9.50b) are enlarged upper incisors that continue to grow throughout the life of the animal. In a young elephant, two deciduous tusks grow to a length of approximately 5 cm (2 in.) and remain for about a year before being replaced by the permanent tusks growing behind them (Haynes, 1991).

The four lower incisors of flying lemurs (order Dermoptera, family Cynocephalidae) are unique among mammals in that each is pectinate, or compressed, into a fine-toothed comb. Each lower incisor may have as many as 20 prongs radiating from one root. Comb teeth may serve as food strainers or as scrapers, or they may be used to groom the fur (Aimi and Inagaki, 1988).

Canines are located immediately behind the incisors. In carnivorous mammals, these teeth are used for piercing and tearing flesh. Canine teeth are always absent in rodents and lagomorphs; the resultant gap between the incisors and cheek teeth is called a **diastema**. Walrus tusks are modified canine teeth (see Fig. 9.50c).

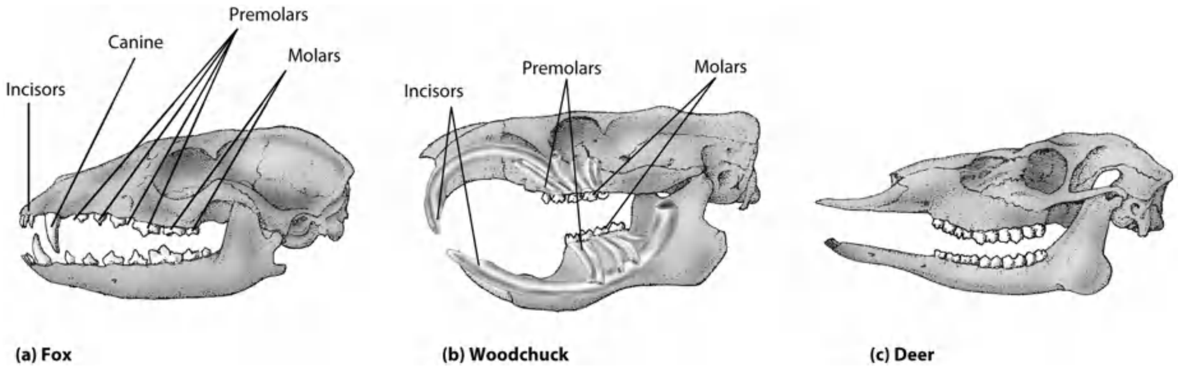


Figure 9.51. Teeth adapted for processing three principal kinds of food: (*a*) fox—meat, (*b*) woodchuck—grassy vegetation, (*c*) deer—mast (berries, acorns, nuts, etc.).

Premolars and molars are known as cheek teeth and are modified for crushing and grinding (see Fig. 9.51). Cheek teeth in herbivorous mammals possess large, flat grinding surfaces, an evolutionary adaptation for feeding on vegetation. In carnivores, the number of cheek teeth may be reduced, cusps may be present, and at least one pair in each jaw may have very sharp cusps for cracking bones and shearing tendons. These are known as **carnassial teeth** (see Fig. 9.51a). Grinding is deemphasized in carnivores, and food is swallowed with little chewing. The cheek teeth of omnivorous mammals are intermediate in form. In some primates, cutting edges form on the upper canines and lower premolars—the **sectorial teeth**. These teeth are used in defense or in fights between individuals.

Because each species of mammal has specific numbers and kinds of teeth, dental formulas are useful for taxonomic purposes. Primitive placental mammals had 3 incisors, 1 canine, 4 premolars, and 3 molars in each half of the upper and lower jaw for a total of 44 teeth; therefore, the dental formula was 3/3, 1/1, 4/4, 3/3. Representative examples of dental formulas for other adult mammals include dogs (*Canis familiaris*), 3/3, 1/1, 4/4, 2/3; rabbits (*Sylvilagus* sp.), 2/1, 0/0, 3/2, 3/3; beavers (*Castor canadensis*), 1/1, 0/0, 1/1, 3/3; horses (*Equus caballus*), 3/3, 0/1, 3/3, 3/3; white-tailed deer (*Odocoileus virginianus*) 0/3, 0/1, 3/3, 3/3; and humans (*Homo sapiens*) 2/2, 1/1, 2/2, 3/3.

Most mammals have a muscular tongue that can be protruded out of the mouth. Its surface usually bears papillae, whose function is to increase friction and assist in the manipulation of food by the tongue. Taste buds are located on or among the papillae. Some insectivorous mammals, as well as pollen- and nectar-eating bats, have a tongue as long as their entire body. Whales have a tongue, but in most species it cannot be extended.

The giant anteater, *Myrmecophaga tridactyla*, has an elongate, tubular snout, a tiny, toothless mouth, and a long, slender, sticky tongue that can project to a distance greater than the cranial length. A unique hyoid arrangement enables *Myrmecophaga* to project the tongue with great speed and precise positional control so that it can probe deep into the nests of ants and termites. Most mammals open their mouth by contracting the digastric muscle to move the lower jaw. The giant anteater has no digastric muscle, and the lower jaw depresses only slightly during feeding. Instead, it opens its mouth by the medial rotation and depression of the two halves of its elongate lower jaw (the mandibular rami) about their long axes (Naples, 1999). This allows an anteater to open and close its mouth rapidly. The protraction and retraction of the elongated tongue permits feeding in ant and termite nests, where the spaces are too narrow for the mouth to open wide.

Narwhal

Sometimes called the unicorn of the sea, the male narwhal's (*Monodon monoceros*) single tusk is actually a tooth, and it grows directly through the whale's upper lip instead of pushing the lip aside (see Fig. 9.50a). It is an extremely large version of a left canine tooth that always grows in a spiral to the left—the only tooth known to do so. Otherwise, narwhals are practically toothless, with only vestigial stubs that stop growing during development and rarely emerge into the mouth. Electron microscopy studies have shown that a single tusk possesses some 10 million nerves running from its surface to its core. Abundant pores in the outer layer (cementum) allow the salinity of surrounding water to trigger special cells called odontoblasts that connect to nerves in the tusk's inner pulp. This sensitive tooth appears capable of detecting changes in water temperature, pressure, and particle gradients linked with salinity and prey. Unlike in human teeth, no enamel protects the outside of a narwhal tusk.

Nweeia et al., 2014

Oral glands, which secrete mucus and digestive enzymes, are abundant in mammals and serve to begin the chemical digestion of certain foods. Most mammals have three major pairs of salivary glands: the **parotid**, **mandibular** (also known as submandibular or submaxillary), and **sublingual** (Fig. 9.52). These glands secrete saliva to moisten food and begin the initial digestion of starch. Saliva consists of mucin, water, and the digestive enzyme amylase.

The esophagus shows no special modifications. An esophageal (cardiac) sphincter, whose function is to prevent the backflow of contents from the stomach, is located at the point where the esophagus enters the stomach.

The stomach is a muscular organ that varies from a single saclike compartment to the four-chambered stomach of ruminants, where digestion is aided by microorganisms (Fig. 9.53). Dwarf and pygmy sperm whales (*Kogia* sp.), river dolphins, and beaked whales (Ziphiidae) also have multichambered stomachs. In a typical stomach, a series of longitudinal ridges—the **rugae—**line the inner surface and permit the stomach to distend. Three types of cells are present in the stomach. **Mucous cells** secrete mucus; **chief cells** secrete the principal gastric enzyme precursor, pepsinogen, which is subsequently converted to pepsin; and **parietal cells** secrete hydrochloric acid. The hydrochloric acid provides the acidity necessary for pepsin to be effective. The mucus serves as a protective lining for the stomach wall cells. Together, the secretions of these cells form **gastric juice**. The stomach terminates at the pyloric sphincter, where it joins the small intestine.

Some mammals, like ruminants (cattle, goats, sheep, bison, camels, deer, giraffes, and others), are foregut fermenters and have a stomach consisting of several chambers (Fig. 9.55a). After being chewed briefly, food is swallowed and passes into the first and largest chamber, the **rumen**, where it is acted on by microorganisms. The rumen serves as a large fermentation vat where food is mixed with large numbers of bacteria and protozoans and undergoes extensive fermentation. Microorganisms break down cellulose, making it available for further digestion. The food then may be regurgitated, formed into a cud, and rechewed. When swallowed, this rechewed food passes first into the **reticulum**, a small accessory chamber with a honeycombed texture, then into the **omasum**, where it is acted on by the salivary enzyme amylase. Finally, it enters the glandular **abomasum**, where gastric glands secrete gastric juice.

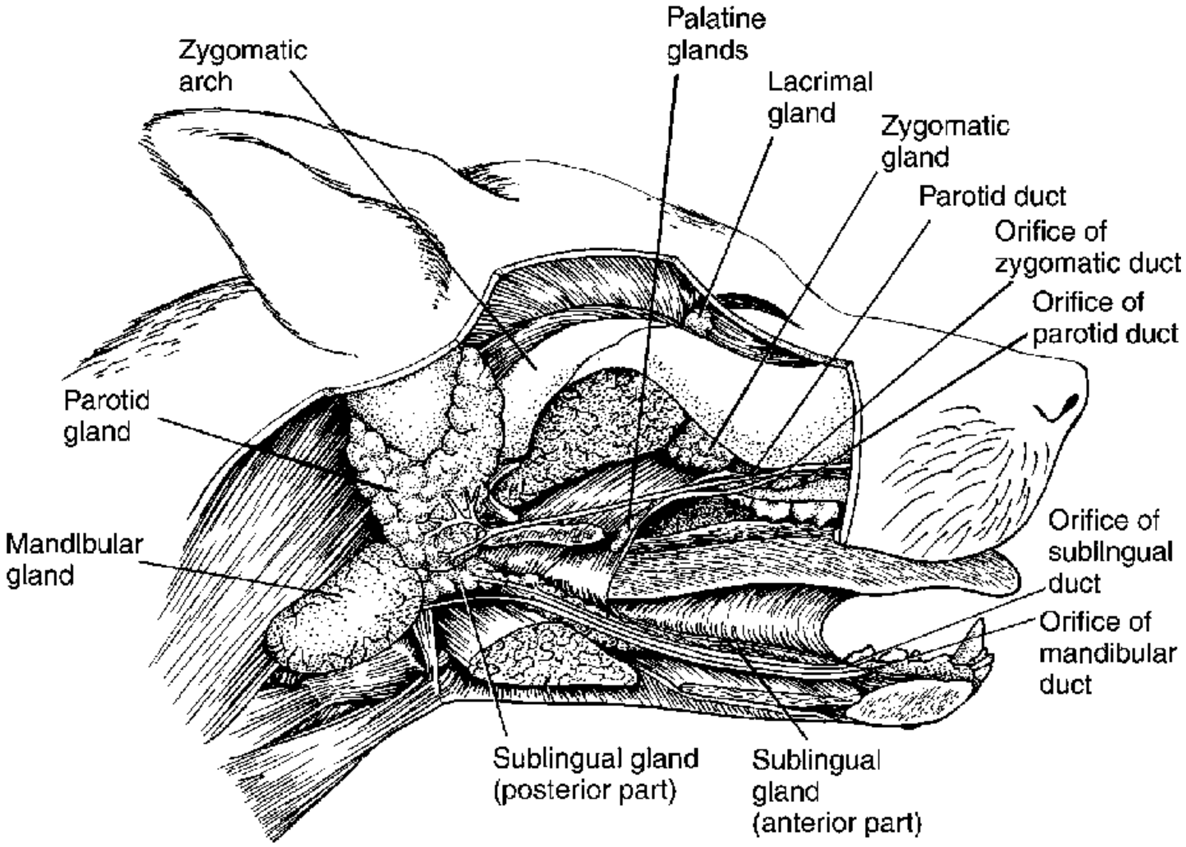


Figure 9.52. Salivary glands of a dog. All mammals possess three main salivary glands—parotid, mandibular, and sublingual. In addition, some mammals may possess smaller glands, like palatine glands above the palate. A zygomatic gland is present only in dogs and cats. Each gland has a duct opening into the oral cavity.

Horses and some other mammals are hindgut fermenters (Fig. 9.55b). There is no four-chambered stomach. Fermentation takes place in the large caecum near the junction of the small and large intestines.

The small intestine in most mammals is long and convoluted (see Fig. 9.53). The absorptive surface, which is the chief site of digestion and absorption, is increased by finger-like projections known as **villi** and **microvilli**. The small intestine generally is longer in herbivorous mammals than in carnivorous forms in order to provide more opportunity for digesting the cellulose cell walls of plant cells. The small intestine consists of three portions: the **duodenum** (anterior), the **jejunum** (middle), and the **ileum** (posterior). Pancreatic juice and bile are secreted into the duodenum. Pancreatic juice is alkaline and contains enzymes (amylase, lipase, maltase, and sucrase) that continue the digestive processes. Bile, which is also alkaline, emulsifies fats.

The large intestine consists of the colon, caecum, and rectum. Its major functions are the reabsorption of water and electrolytes, which result in the compaction of wastes that must be eliminated from the body. The **colon** may be divided into **ascending**, **transverse**, and **descending** portions. The ileum opens into the ascending colon through the **ileocecal valve**. A blind sac, the **caecum** (see Fig. 9.53), is located at the juncture of the small intestine and colon. In mammals that feed on cellulose, the caecum often contains cellulose-digesting bacteria and ciliate protozoans (Oxford, 1958), which also synthesize vitamin B, amino acids, and proteins. In some mammals, including rabbits, rodents, monkeys, apes, and humans, the distal end of the caecum is mostly vestigial and terminates in a **vermiform appendix**. In humans and possibly some other mammals, the appendix may have a limited lymphatic function. The descending colon terminates in the rectum, which serves as a temporary storage chamber for feces. Feces consist of indigestible materials, water, electrolytes, and some bacteria. Feces are eliminated from the rectum via the anal canal, which opens to the exterior via the anus. Anal control is through internal and external anal sphincter muscles.

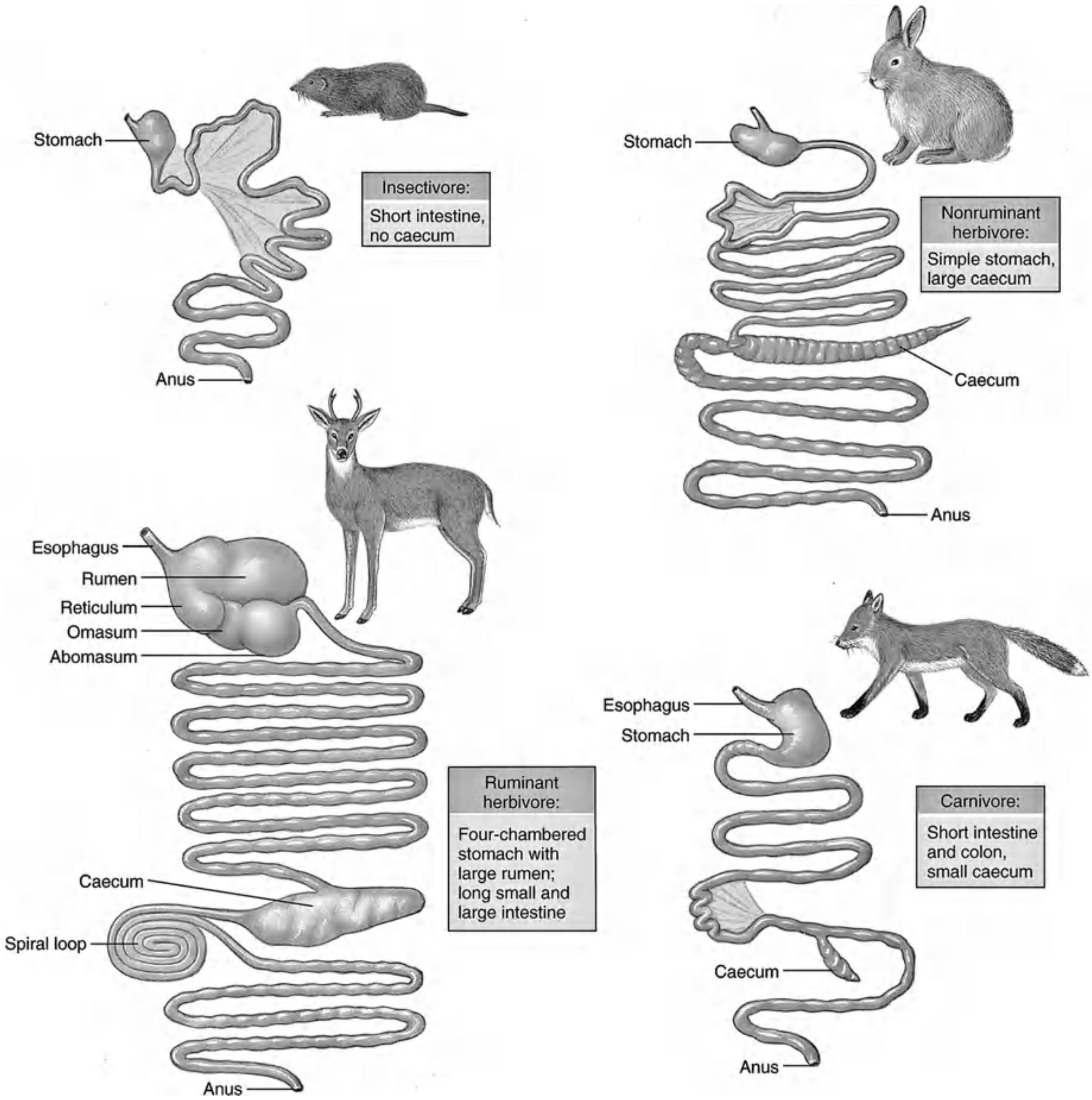


Figure 9.53. Digestive systems of mammals illustrating different modifications for different diets. The digestive tract of an herbivore is considerably longer than the digestive tract of a similar-size carnivore; this provides additional time for microorganisms to break down the cellulose cell walls of plant cells.

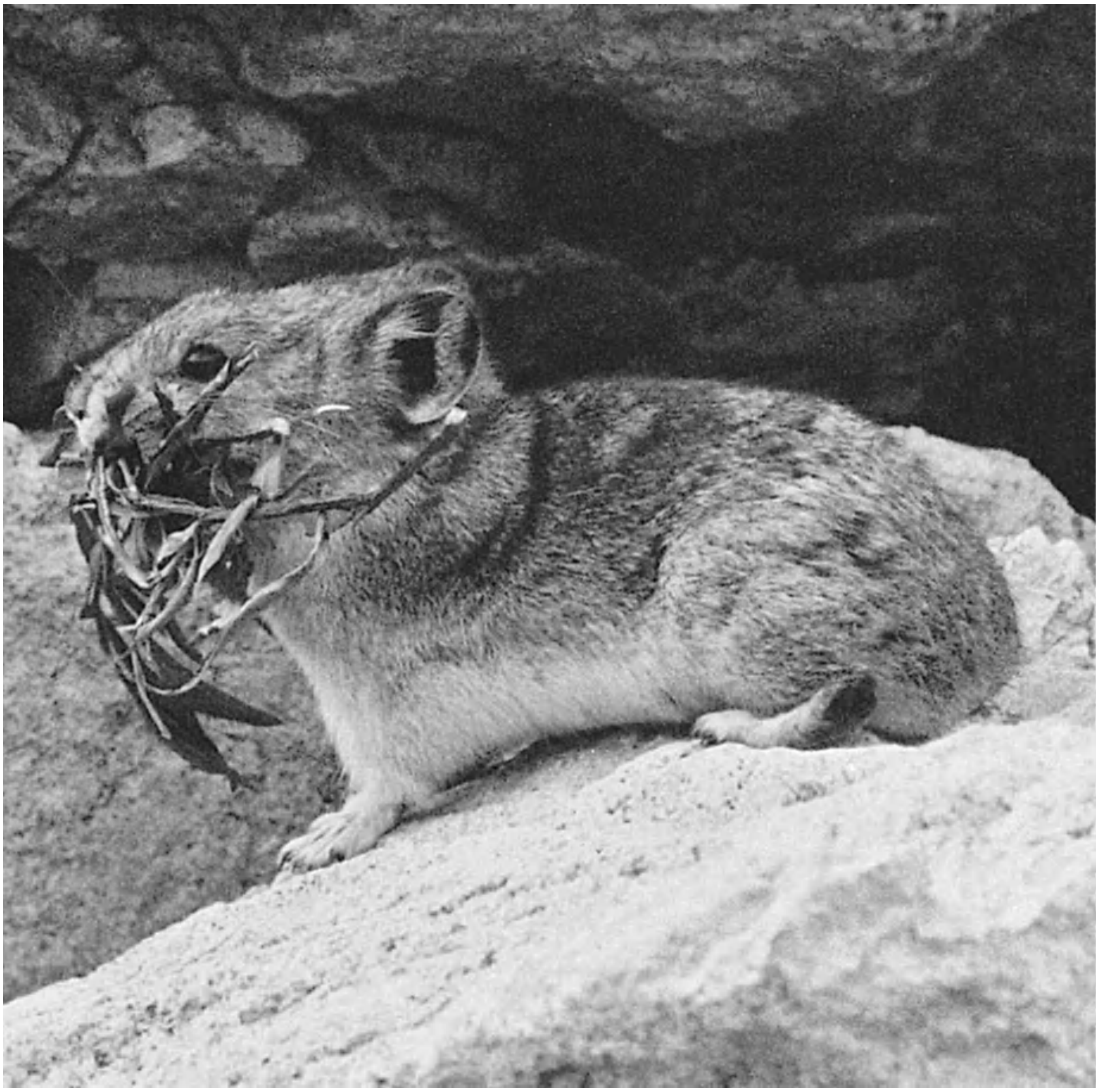


Figure 9.54. The North American pika (*Ochotona* sp.), also known as little chief, whistling hare, cony, rock rabbit, mouse hare, and haymaker, averages approximately 15 cm (6 in.) in total length. It looks like a miniature rabbit, but its ears are not as long, its hind legs are nearly as short as its front legs, and it lacks a tail. Its voice varies from a sharp, shrill whistle to a bleat like that of a lamb. It dwells among tumbled rock piles near the summits of mountain ridges.

The diet of lagomorphs is restricted to vegetation. Two types of fecal pellets are expelled—brown pellets and greenish pellets. The reingestion of partially digested vegetation from the greenish pellets is common; this practice is known as **coprophagy** (Fig. 9.56). It allows the animals to spend relatively little time exposed to predators while in the field actually feeding. They consume green vegetation rapidly and then make optimum use of it in the safety of their brushpile or burrow. It is somewhat analogous to cud-chewing in ruminant animals. These pellets have a high protein content and contain large amounts of B vitamins produced by intestinal bacterial (Hansen and Flinders, 1969).

Manatees have a large digestive system, which is necessary to process giant quantities of low-protein, low-calorie food. An adult manatee must consume 10 percent of its 360 to 540 kg (800–1,200 lb.) body weight daily. Captive manatees may eat more than 70 heads of lettuce and 10 to 15 bunches of kale a day.

Artificial bat roosts in Costa Rica attract fruit-eating bats, whose droppings help spread seeds beyond the forest edge. Bat roosts were constructed near a nature reserve ravaged by agriculture and logging. Bats of 10 different species readily flocked to the roosts, significantly increasing the number and types of seeds in the neighborhood. Most of the seeds were of "pioneer" species like nightshade, which grows well in open areas. This represents the first documented effort to harness bats' ability to help restore lost habitat.

Nervous System

The proportion of brain to body size is usually greater in mammals than in other vertebrates. Pound for pound, the record for brain size is probably held by fruit-eating South American squirrel monkeys (genus *Saimiri*), whose brains account for an average of 5 percent of their body weight (Nilsson, 1999–2000). For humans, the figure is approximately 2 percent. The big whales have the smallest brains of all the mammals: that of the blue whale (*Balaenoptera musculus*) represents about 0.005 percent of its body mass.

The four major regions of the adult brain include the **brain stem** (medulla oblongata, pons, midbrain), **diencephalon** (epithalamus, thalamus, hypothalamus), **cerebrum**, and **cerebellum** (Fig. 9.57). Four spaces known as **ventricles** are present in the mammalian brain. They are filled with **cerebrospinal fluid**, which is secreted by choroid plexuses in the roof of each ventricle. Cerebrospinal fluid serves as a transport medium within and around the brain and spinal cord. The entire brain is enclosed and protected by three meninges (dura mater, arachnoid, and pia mater).

The **medulla oblongata** is continuous with the spinal cord and acts as a major relay center for all ascending and descending tracts. In addition, it contains several specialized areas, including the respiratory center and cardiac center. The respiratory center controls the rhythmic movements of the diaphragm and intercostal muscles. It is sensitive to increased carbon dioxide or increased acidity in cerebrospinal fluid caused by an increased concentration of carbon dioxide in the blood (Schmidt-Nielsen, 1997). The pons assists the respiratory center in controlling the rate and depth of breathing; it also serves as a relay center to higher portions of the brain and between the cerebellum and other parts of the nervous system. The mesencephalon in mammals serves in a limited way for visual and auditory reflexes.

Pika Haypiles

Pikas (*Ochotona* sp.) (see Fig. 9.54) are small, rodent-like, lagomorph mammals of the mountains of the western United States and Asia. They work prodigiously during the summer gathering enormous amounts of grasses and wildflowers into mounds, known as haypiles, which serve as their winter food. Each pika gathers the equivalent of about 29 kg (63 lb.) of plants. This is roughly comparable to a 58 kg (127 lb.) person collecting 9,000 kg (20,000 lb.) of vegetation by making 5,000 shopping trips. As much as 75 percent of some haypiles consists of *Acomastylis rossii*, a plant whose phenolic compounds presumably inhibit bacterial growth and act as a preservative during the long, cold, mountain winter.

Dearing, 1993

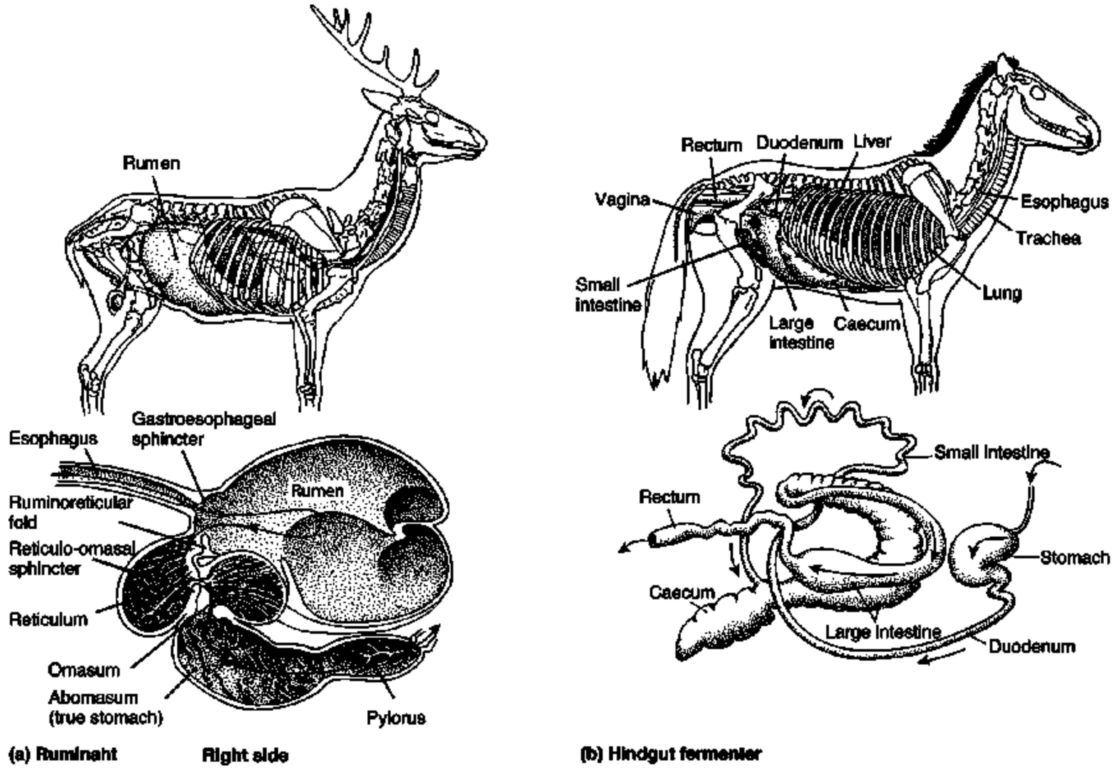


Figure 9.55. Alimentary canal of foregut and hindgut fermenters. (*a*) Ruminants (deer, cows, and others) ferment food in their foregut. These grazing animals swallow partially chewed plant material, which moves into two stomach-like chambers (rumen and reticulum). Then they regurgitate the material, chew it, and swallow it again. The double chewing (commonly referred to as "chewing a cud") breaks apart the plant tissues and better exposes the cellulose fibers. The cellulose is broken down by digestive enzymes that are produced by symbiotic bacteria living in the gut. The double chewing gives the enzymes more time and more surface area on which to act. The rumen, reticulum, and omasum are derivatives of the esophagus. The fourth compartment, the abomasum, is the true stomach. (*b*) Hindgut fermenters, like the horse, possess a large caecum near the juncture of the small and large intestines. The caecum is the major site of fermentation. There is no four-chambered stomach in hindgut fermenters.

The thick walls of the diencephalon make up the **thalamus**, which serves as a relay center to the cerebrum. The thalamus contains clusters of nuclei that are associated with motor fibers leading posteriorly in the brain and with sensory pathways leading anteriorly. Perception of pain and pleasure takes place in the thalamus. The thinner, ventral walls and floor of the diencephalon, the **hypothalamus**, contain clusters of nuclei that control autonomic functions of the body like water balance, temperature regulation, appetite and digestion, blood pressure, sleep and waking, and sexual behavior. It also serves as an endocrine gland, producing antidiuretic hormone, oxytocin, releasing factors, and release-inhibiting factors. The releasing factors and release-inhibiting factors control the release of hormones from the adenohypophysis (anterior pituitary gland). These hormones, in turn, affect other endocrine glands (see Endocrine System).

On the ventral surface of the diencephalon is the **optic chiasma**, the point where the optic nerves converge and cross. In humans, about 50 percent of the nerve fibers cross over; in other mammals, the proportion may be higher (Carter, 1967). Just posterior to the optic chiasma is the **hypophysis** (pituitary gland), which also functions as an endocrine gland. Posterior to the hypophysis are a pair of **mammillary bodies**, which function in olfaction and are a part of the limbic system, a portion of the brain involved in the expression of emotions (which are important to survival) and in short-term memory. Two structures are found on the dorsal portion of the diencephalon in most mammals. The **habenula** contributes to the coordination of olfactory reflexes, whereas the **pineal body** (**gland**), also known as the epiphysis, functions as an endocrine gland. It secretes the hormone melatonin, which appears to regulate certain cyclical functions of the body. The effects of melatonin are discussed in greater detail later (see Endocrine System). A pineal body is absent in xenarthrans (anteaters, sloths, and armadillos) and, perhaps, dugongs (Wurtman et al., 1968).

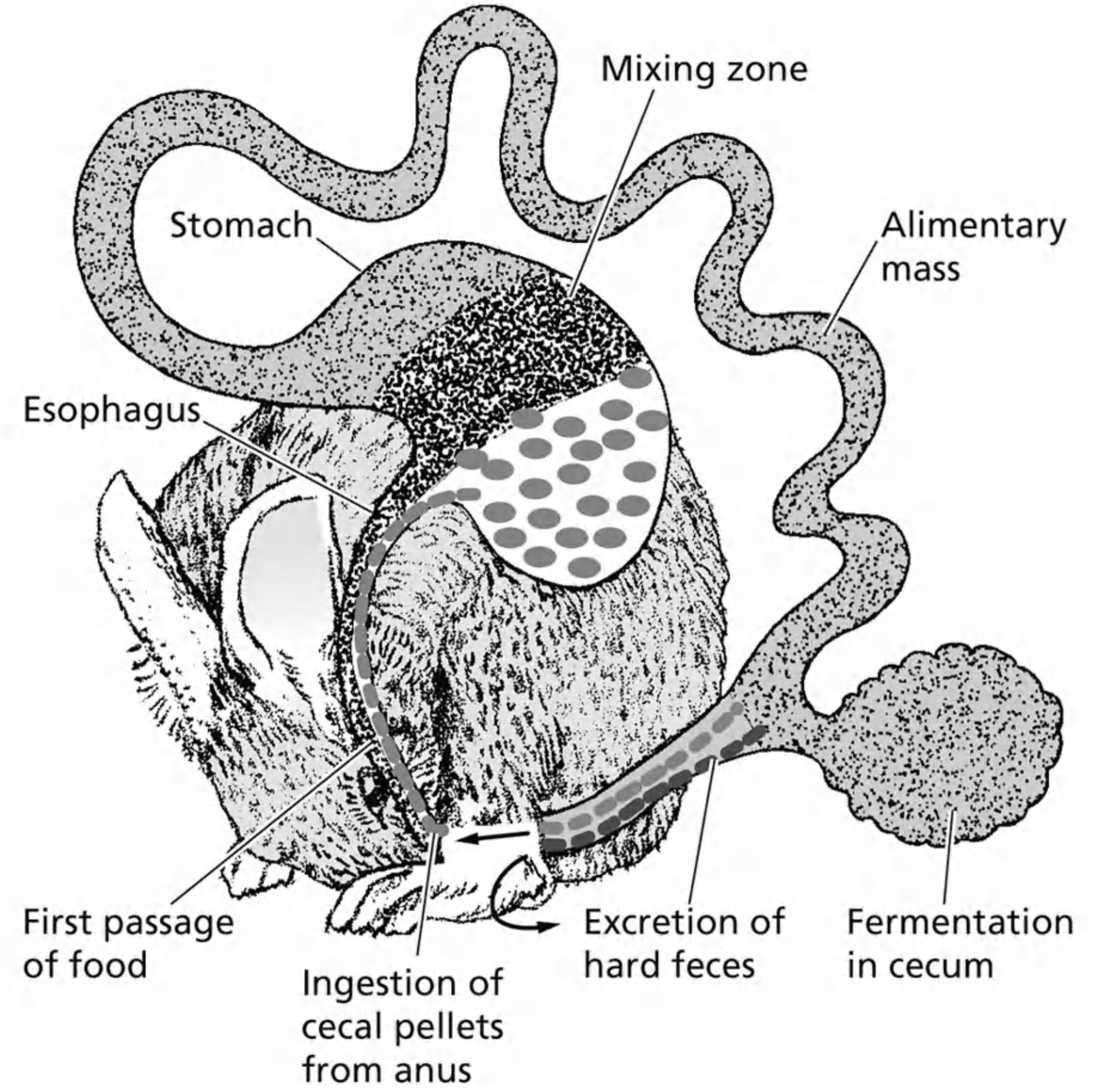
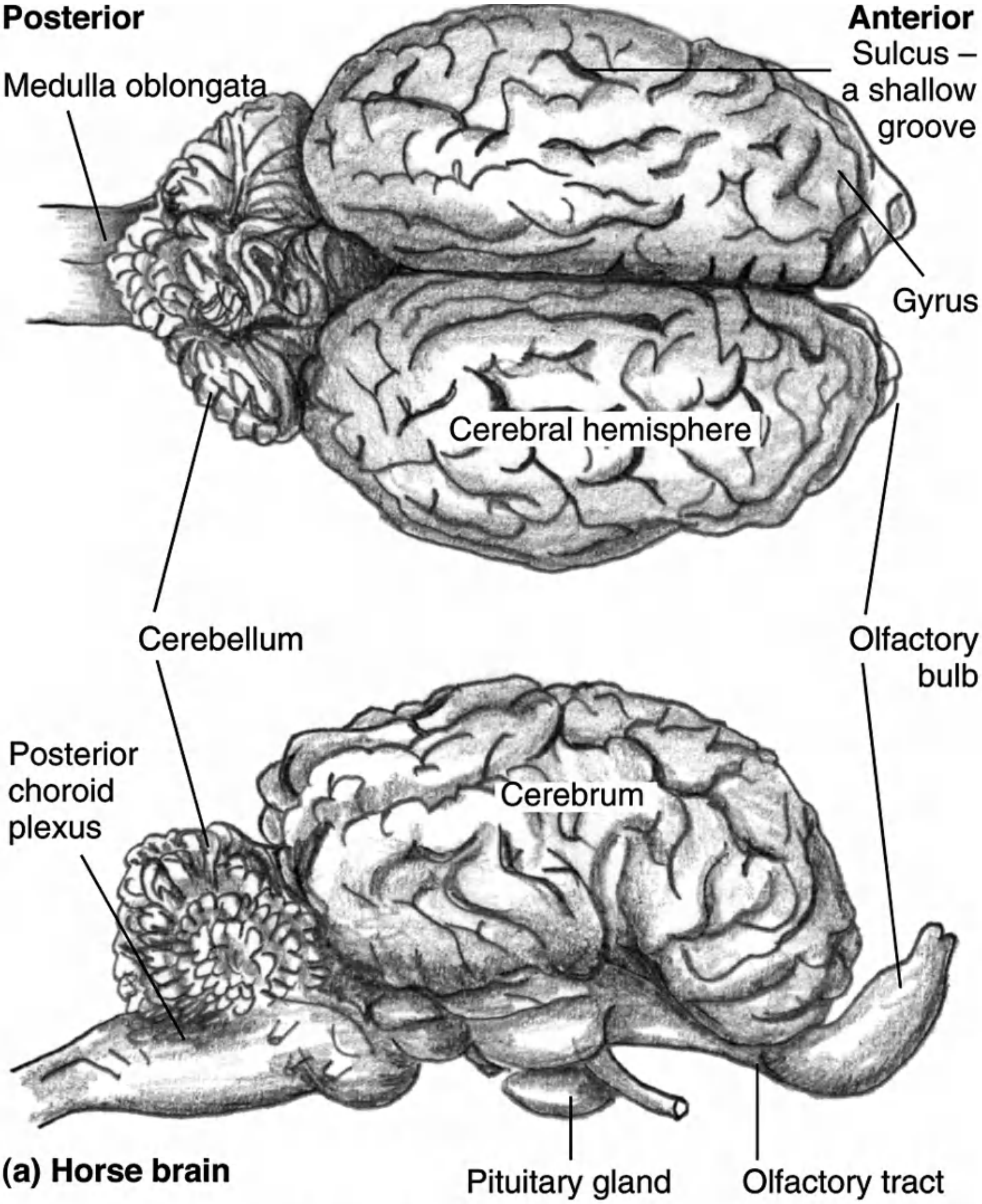


Figure 9.56. Coprophagy occurs in shrews, rodents, and lagomorphs. The digestive tract of lagomorphs is highly modified for coping with large quantities of vegetation. The alimentary canal has a large caecum, which contains bacterial flora to aid in the digestion of cellulose.

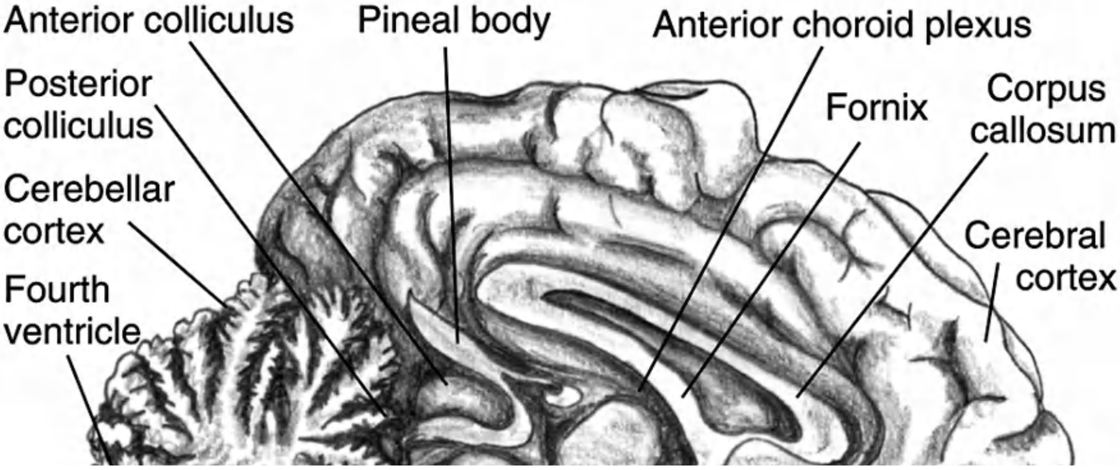
The cerebrum consists of a pair of greatly expanded cerebral hemispheres that have grown upward, over, and backward so that the diencephalon and mesencephalon are hidden from dorsal view (see Fig. 9.57). In many mammals, the surface of the cerebrum (cerebral cortex) is folded into a series of **gyri** (ridges) and **sulci** (grooves). The **longitudinal fissure** separates the cerebrum into right and left halves, or **hemispheres**. The two cerebral hemispheres are connected internally and are coordinated by a broad transverse sheet of nerve fibers, the **corpus callosum**. The cerebrum contains centers for interpreting sensory impulses arriving from various sense organs as well as centers for initiating voluntary muscular movements. It stores past experiences as memory, controls certain emotions, and is a center where data may be correlated, analyzed, and employed in making choices. It is the "thinking" part of the brain. **Olfactory lobes**, responsible for the sense of smell, are located on the anteroventral surface of the cerebrum.

Muscular coordination is regulated by the cerebellum, the second largest region of the brain, which covers the mesencephalon and much of the medulla oblongata.

The roof of the telencephalon, known as the **pallium** (**hippocampus**), is an area critical to processing spatial information and essential in converting short-term memory to long-term memory. Damage to the hippocampus does not destroy memory prior to the injury, but causes loss of recent memory by making it impossible to form long-term memory traces. Jacobs et al. (1990) found that the hippocampus takes up a significantly greater portion of the total brain in the polygamous male meadow vole (*Microtus pennsylvanicus*) than in the monogamous male woodland vole (*Microtus pinetorum*). Females of both species have a hippocampal size closely matching that of the male woodland vole. Breeding male meadow voles range over large areas in search of sexually receptive mates, whereas male woodland voles and females of both species stick close to home. Polygamous males also performed better in laboratory mazes that tested their abilities to discern information about space and their orientation. These voles apparently evolved superior spatial skills—and larger hippocampi to regulate those skills and to remember what they discovered—in order to navigate efficiently throughout their surroundings during the breeding season.



(a) Horse brain



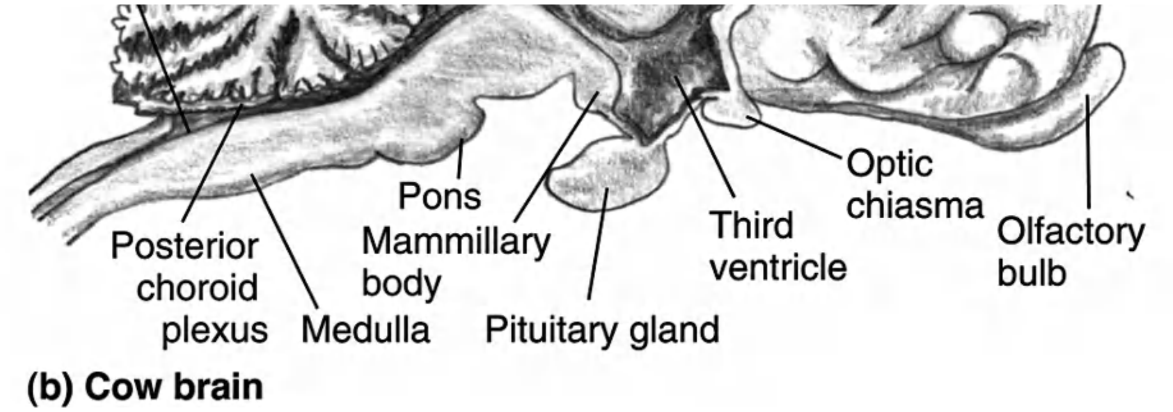


Figure 9.57. Mammal brains: (*a*) dorsal and lateral views of a horse brain; (*b*) sagittal section of a cow brain.

DNA from Coprolites

Researchers studying coprolites (dung) from Gypsum Cave near Las Vegas, Nevada, have been able to unlock DNA trapped in the ancient feces. The mitochondrial DNA (mtDNA), which presumably came from intestinal cells shed into the feces, probably came from an extinct ground sloth (*Nothrotheriops shastensis*) about 20,000 years ago. In addition, researchers were able to extract a wide variety of plant DNA from the coprolite—clues to the vegetarian sloth's diet. Plant DNA sequences were identified from eight plant families and included grasses, yucca, grapes, and mint. The plant assemblage that formed part of the sloth's diet exists today at elevations about 800 m (2,625 ft.) higher than the cave. Such studies may help provide answers as to why these and other large animals vanished from North America about 10,000 years ago.

DNA analysis performed on preserved coprolites from the Balearic Islands cave goat (*Myotragus balearicus*) provided data refuting evidence for direct human influence on its extinction. Together with pollen analyses performed on the same coprolites, researchers determined that *Myotragus* was heavily dependent on *Buxus balearica* (Balearic boxwood) during part of the year and that the extinction of the mountain goat approximately 5,000 years ago was related to climate change—the drastic decline and regional extinction of *Buxus balearica* that occurred on the Balearic Islands (an archipelago of Spain in the western Mediterranean Sea including Mallorca and Menorca) by increased aridity occurring throughout the Mediterranean.

Poinar et al., 1998; Welker, 2012

The remainder of the central nervous system, the spinal cord, is protected by vertebrae, fat, and the three meninges. The length of the spinal cord varies among mammals. It may extend as a single structure nearly to the end of the vertebral column, or it may be shorter, as in humans, where it extends to about the third lumbar vertebra as a single structure before splaying out and forming the **cauda equina** (horse's tail) portion. Cervical and lumbar enlargements of the spinal cord are present, with bats having an unusually large cervical enlargement associated with their highly developed flight muscles.

Sense Organs

EARS

The membranous labyrinth and the sense of hearing are highly developed in mammals. The human ear, for example, is sensitive to regular compression waves in air in a range of approximately 16 to 20 kHz (Kare and Rogers, 1976). A dog, however, can perceive higher frequencies that are completely inaudible to humans, up to 30 or 40 kHz, and bats can perceive frequencies as high as 100 kHz (Schmidt-Nielsen, 1997).

The **pinna** (part of the outer ear) serves to funnel sound waves into the **external auditory meatus** (ear canal), where they are conveyed to the eardrum (**tympanum**) (Fig. 9.58). Some species, like galagos and deer, have pinnae that can be directed independently toward the source of the sound. All mammals have a middle ear that contains three bones: the **malleus** (hammer), **incus** (anvil), and **stapes** (stirrup). These three auditory ossicles transmit vibrations from the eardrum to the oval window in the cochlea of the inner ear. A **Eustachian** (auditory) **tube** connects the middle ear cavity with the nasopharynx and serves as a means to equalize pressure in the middle ear. The middle ear cavity is enclosed by a bony **auditory bulla**. The **cochlea**, containing the **organ of Corti** (spiral organ), is the portion of the inner ear concerned with hearing. Hair cells in the organ of Corti convert mechanical energy into nerve impulses, which in turn are transmitted to the brain by the auditory nerve (VIII).

The remainder of the inner ear is devoted to balance and equilibrium and consists of the **vestibule** and three **semicircular canals** (see Fig. 9.58). Within the vestibule are two regions—the **utricle** and the **saccule**—which contain patches of sensory epithelia known, respectively, as **maculae** and **cristae**. They function in determining static equilibrium (position of the head in relation to the ground surface or gravity). The semicircular canals each lie in different planes and terminate in enlarged **ampullae**. The fluid contained within the semicircular canals (as well as within the vestibule and cochlea) is known as endolymph. Movements of fluid within the semicircular canals is responsible for dynamic equilibrium (movement of the body through space).

Some mammals obtain information from the faint reflections, or echoes, of sound they themselves produce, thus enabling them to avoid obstacles and to locate food. This **echolocation**, or animal sonar, is particularly well developed in bats (Chiroptera) (Fig. 9.59) and also exists in shrews (Insectivora), whales (Cetacea), seals (Pinnipedia), and manatees (Sirenia). The potential to echolocate also may be present in many other kinds of mammals. High-frequency sound (short wavelengths) is particularly useful for mammals that are active in the dark and in deep or murky waters. In those mammals that use echolocation, the auditory bullae have no connection with other bones of the skull; rather, they “float.” These loosely connected auditory bullae allow the ear to act somewhat independently of skull vibrations. The pulses used by most bats during echolocation are produced by the larynx and range in frequency from 30 to 120 kHz, which is above the range of human hearing. When resting, a bat may emit 5 to 10 ultrasonic “cries” per second. When flying and approaching an object, these may increase to more than 100 per second. More than 85 percent of living bat species use echolocation to navigate. The rest belong to a single family—the Old World fruit bats, sometimes called flying foxes, which apparently lost the ability and instead rely strictly on sight and smell to find the fruit and flowers they feed on (Simmons, 2008).

Cat Brains, from Past to Present

Dr. Robert Williams of the University of Tennessee Medical School compared the brains of the modern house cat with those of a Spanish wildcat that appears to be almost identical to the species that was domesticated by the ancient Egyptians more than 3,500 years ago. The modern house cat was found to have significantly fewer (50 percent fewer) brain cells than the wild creature from which it evolved.

Williams et al., 1993

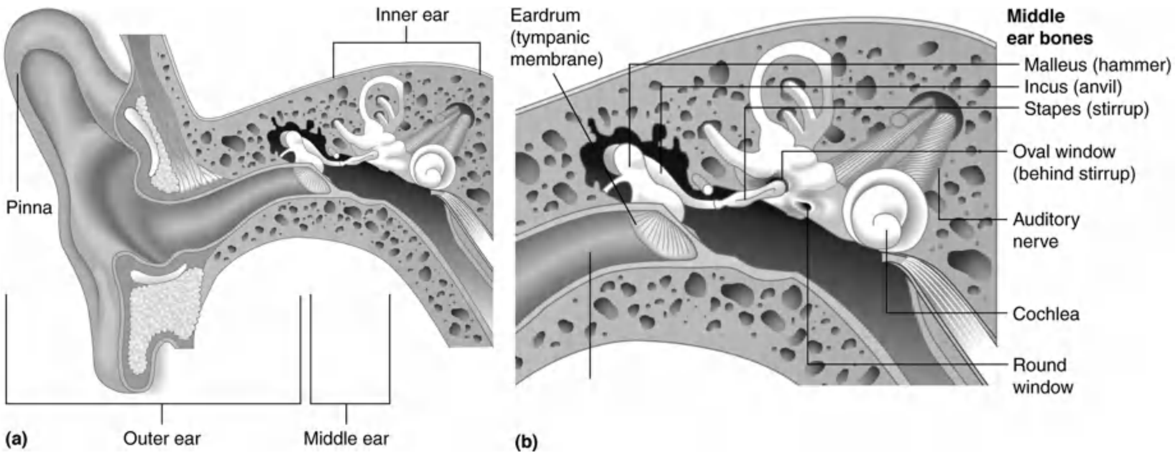


Figure 9.58. Hearing in humans. (*a*) Sound waves are funneled into the external auditory canal by the pinna. (*b*) Pressure waves strike the eardrum (tympanic membrane), causing it to vibrate at the same frequency as the waves. This, in turn, causes the ear ossicles (malleus, incus, and stapes) to vibrate in the middle ear. The stapes articulates with the oval window, which bows in and out, causing fluid pressure waves in the perilymph of the scala vestibuli and scala tympani. These waves cause the round window to bulge under pressure. The sensory receptors for hearing are located in the coiled cochlear duct portion of the inner ear. The organ of Corti, which contains sensory hair cells, sits atop the basilar membrane within the cochlea. Vibrations of the basilar membrane move patches of hair cells against an overhanging flap (the tectorial membrane). Signals from these hair cells initiate action potentials that are carried to the brain by the auditory nerve. The inner ear consists of an outer area known as the bony labyrinth and an inner area, the membranous labyrinth. The semicircular canals are responsible for dynamic equilibrium (movement of the body through space).

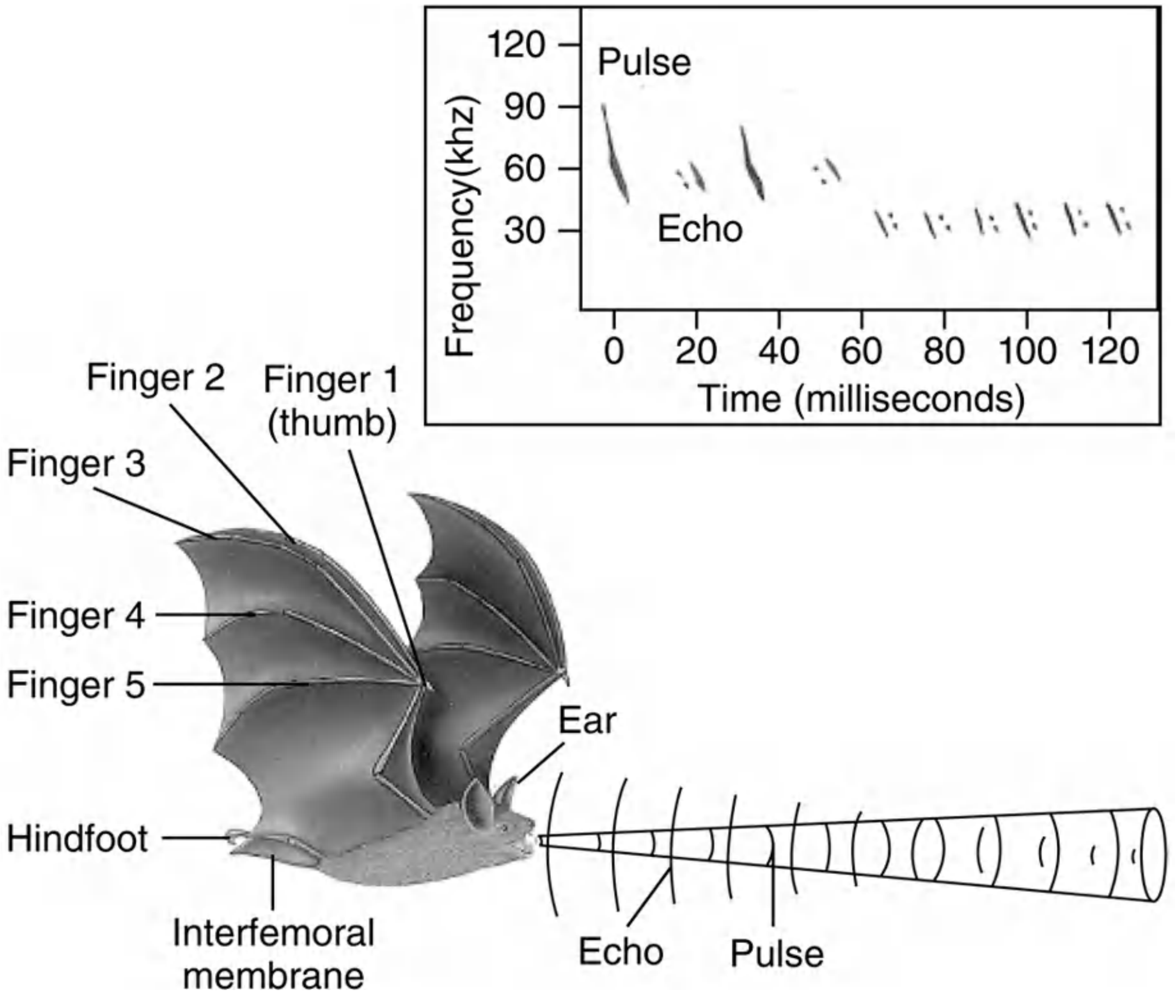


Figure 9.59. Echolocation by the little brown bat (*Myotis lucifugus*). Frequency-modulated pulses are directed in a narrow beam from the bat's mouth. When the pulses meet an object, their echoes are picked up by the bat's sensitive hearing apparatus. As the bat nears its prey, it emits shorter, lower-frequency signals at a faster rate.

In bats that use echolocation, the cerebellum is large, and the ears are highly specialized with large pinnae and large cochlea. Within each pinna is a **tragus**, a fleshy projection rising from the inner base of the ear. It has not been shown to function in hearing, and despite much speculation and research, its significance remains unknown.

Human-generated noise in the oceans has increased over the last century, which has raised concern about its impact on marine mammals (reviewed by Malakoff, 2010). Some cetaceans may be particularly sensitive to changes in their acoustic habitat because they rely on vocalizations and a well-tuned auditory system for communication, detection of prey and predators, and orientation. The impacts of chemical pollution on the development of hearing is largely unexplored. Odontocetes (toothed whales, dolphins and porpoises) have been shown to accumulate extremely high levels of polychlorinated biphenyls (PCBs) in their blubber (Kannan et al., 1993; Muir et al., 1996; Ross et al., 2000; Hansen et al., 2004) and have been shown to pass this burden on to their offspring (Wells et al., 2005).

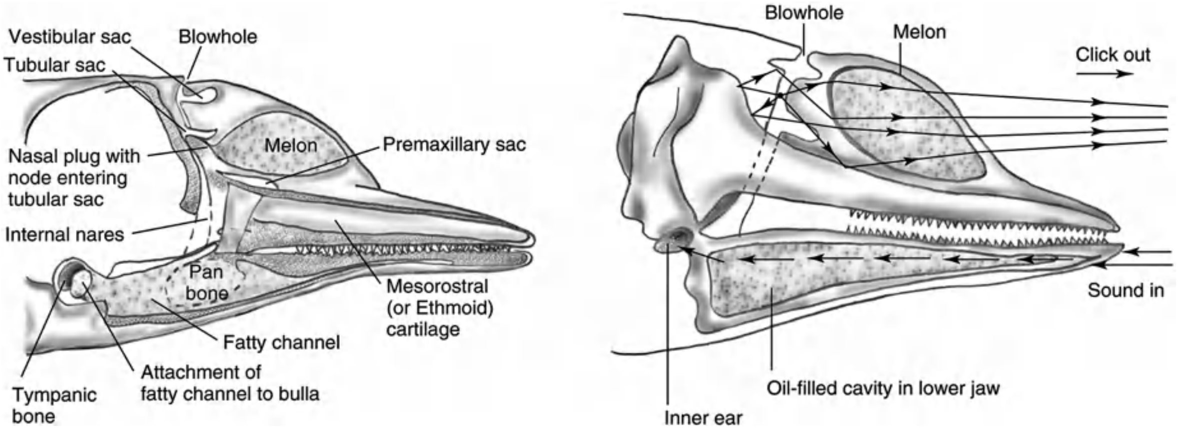


Figure 9.60. Sound propagation and reception in a dolphin (family Delphinidae). The melon acts as an acoustic lens, focusing the clicks, while the oil-filled cavity of the lower jaw acts as a wave guide to conduct the sound received to the ear. The oil-filled channel passes posteriorly to contact the tympanic bone, which is connected to the malleus.

Toothed whales and dolphins (suborder Odontoceti) are often considered hearing specialists with highly derived auditory characteristics. Most are able to detect a wide frequency range from 150 to 180 kHz. They use both audible and ultrasonic sounds in order to communicate, avoid obstacles, and locate food. They differ in the shape of the lower jaw suggesting that hearing pathways may vary between species, potentially influencing hearing directionality and noise impacts. Sounds produced by toothed whales originate in the nasal region by pneumatic actuation of phonic lip pairs within the blowhole just below the blowhole in the area of the nasal plugs (Fig. 9.60). The sound then is reflected from the bony surface of the skull, which acts as a parabolic reflector, producing a focused beam. The forehead (melon) probably acts as an acoustic lens, concentrating the sound energy in a narrow beam. Madsen et al. (2013) showed that nasal sound in *Tursiops truncatus* and *Pseudorca crassidens* was unilateral: the animals click with their right pair of phonic lips and whistle with their left pair.

Previous experiments and anatomical studies found that sounds entered a toothed whale’s head through a structure known as the acoustic window, an area of the lower jaw that is very thin on the outside, with a large pad of fat on the inside. Sounds were thought to vibrate the thin layer of bone and then travel through the fat to the ear. The sound waves then went through the throat, and passed through a hole in the back of the jaw to the fat by the ear. Sound reception in delphinids includes fusion of the middle and inner ears into the tympanoperiotic complex, the separation of the bullar complex from the skull, air-filled sinuses surrounding the bulla, and mandibles that are hollow but contain fats that channel sound to the middle and inner ears. In studies of Cuvier’s beaked whale, however, sound seemed to be traveling under the jaw, not through the acoustic window (Cranford et al., 2008). The sound waves then went through the throat, and passed through a hole in the back of the jaw to the fat by the ear. CT images of pygmy killer whales revealed mandibles that were hollow, lacked a bony lamina medial to the pan bone, and contained mandibular fat bodies that extended caudally and abutted the tympanoperiotic complex (Montie et al., 2011). This is the first study to focus on the hearing of this rarely observed pelagic species. The lowest hearing thresholds occurred between 20 and 60 kHz, with the best hearing sensitivity at 40 kHz. The larynx of toothed whales lacks vocal cords.

Figure 9.61. Sea lions, as well as seals, dolphins, and porpoises, die by the thousands each year after becoming entangled in plastic debris, especially broken and discarded fishing nets.

Sensing Barometric Pressure

Some bats, including eastern pipistrelles (*Perimyotis* [*Pipistrellus*] *subflavus*), apparently can sense changes in barometric (air) pressure and use these changes to govern their foraging strategies during the spring and fall when they are roosting deep inside caves. Low air pressure means light, rising air and warm, cloudy weather—conditions suitable for insect activity. High pressure during spring and fall indicates a cold, clear night and few insects.

Most pipistrelles leave their roosts on hunting forays only when barometric pressure falls below 73.69 cm (29.1 in.) of mercury. They can detect pressure changes smaller than one-tenth of an inch by using a middle ear receptor known as the Vitali organ. This is the same organ that migrating birds use to detect air pressure changes to avoid bad weather. The Vitali organ connects to the hypothalamus of the brain, which controls metabolism. Air pressure changes also may be used to control the bat's metabolic activities, which are known to slow down greatly during roosting, with some bats even entering into a hibernation-like torpor on high-pressure days. This ability to maintain a low metabolism while roosting serves as an adaptation for conserving vital energy.

Paige, 1996

Sound reception in delphinids has been reviewed by Mead (1972), Evans and Maderson (1973), and Popper (1980). Some, like bottlenose dolphins (*Tursiops truncatus*), produce a narrowband pure-tone "whistle," whereas other species use pulsed sounds. Those species using whistles are typically highly social and often form large herds, whereas those without whistles tend to be solitary or are found most commonly in small groups (Herman and Tavolga, 1980). Janik (2000) found that individual bottlenose dolphins respond to each other using learned, matching whistles over distances of up to half a kilometer, while Deecke et al. (2002) discovered that harbor seals can differentiate between the calls of local killer whales who feed primarily on fish and the mammal-eating killer whales. It is theorized that sound enters the fat-filled lower jaw and is conducted to the auditory bullae (ear bones), apparently bypassing the tiny external auditory meatus (ear canal) (Reynolds and Odell, 1991).

Audiograms of a Risso's dolphin (*Grampus griseus*) revealed jaw hearing thresholds were lowest (most sensitive) at two locations along the anterior, midline region of the lower jaw (the lower jaw tip and anterior part of the throat). Low responses were also detected along a more posterior region of the lower mandible, considered the area of best hearing in bottlenose dolphins (Mooney et al., 2015). Left- and right-side differences were also noted suggesting possible left-right asymmetries in sound reception or differences in ear sensitivities. Dolphin echolocation sound fields, when reflected from objects, contain embedded shape information that can be recovered and imaged by a CymaScope instrument (Kassewitz et al., 2016). The recovered images of objects can be displayed both as 2-D images and 3-D printed objects.

Studies conducted off the west coast of Greenland (Koblitz et al., 2016) revealed that narwhals (*Monodon monoceros*) possess the most powerful directional sonar of any animal on Earth. These toothed whales live in Arctic waters that often are covered by ice during winter. Because they repeatedly must swim to the surface for air, the animals need to quickly and precisely locate holes in the ice. Researchers placed hydrophones under ice packs, then tracked the whales' movements from helicopters. They discovered that narwhals generate as many as 1,000 echolocation clicks per second; some bats, by comparison, can produce roughly 200 clicks per seconds. Narwhals also can direct their clicks with unequaled accuracy.

Vocalizations of mysticete whales are very different from those of odontocetes and are more difficult to classify. Generally, they are at lower frequency, of narrower bandwidth, and of longer duration than odontocete sounds (Norris, 1969). Social functions proposed for the sounds of mysticete whales include long-range contact, assembly calls, sexual advertisement, greeting, spacing, threat, and individual identification (Herman and Tavolga, 1980).

Manatee sounds, described as chirps, whistles, or squeaks, have peak energies in the 3 to 5 kHz range and are probably produced in the larynx. It has been suggested that the most sensitive location on the manatee's head for sound reception is an area near the cheek bones, which are large and in direct contact with the ear bones.

Protecting Dolphins, Porpoises, Seals, and Sea Lions from Fishing Nets

One of the most serious dangers to dolphins, porpoises, and marine life around the world is the threat from various forms of gill-net fishing (see Fig. 9.61). Acoustic alarms have proven effective in reducing the number of deaths of harbor porpoises (*Phocoena phocoena*) in sinking gill nets. Active alarms were placed 92 m (302 ft.) apart and emitted a broadband signal with a frequency of 10 kHz and a loudness level of 132 dB. The signal lasted for approximately 300 milliseconds and was repeated every 4 seconds.

Kraus et al., 1997

Figure 9.62. Infrasound is used by elephants to communicate with other members of the herd and to coordinate their movements. These low-frequency calls can travel several miles through the air.

Wilson and Hare (2004) reported the first known example of **ultrasonic** *alarm calls* by an animal. Richardson's ground squirrels (*Spermophilus richardsonii*) produce short screeches at a frequency of about 50 kHz. Experiments showed that the calls caused nearby squirrels to assume alert postures and be on the lookout for predators. Both male and female giant pandas are capable of hearing surprisingly high ultrasound frequencies (Owen et al. 2016).

Infrasound is utilized by some mammals. Elephants, for example, make calls at frequencies of 14 to 35 Hz that can be heard by other elephants at distances up to 6 km (4 mi.) (Poole et al., 1988). These low-frequency calls are probably used to communicate between individuals in a herd of these highly social animals (Fig. 9.62). The calls, which can travel several kilometers through the air, are also thought to help different elephant families coordinate their movements from afar and occasionally meet with each other. Elephants' large ears are designed to capture these calls. Scientists have also found that low-frequency sounds from other elephants cause seismic ground vibrations that the pachyderms can feel in their feet (O'Connell-Rodwell, 2007). Anatomical studies suggest that manatees also are capable of hearing infrasound. Infrasound by estrous females may attract males. “Confrontational roars” of tigers contain infrasonic energy and can be heard by other tigers, but such sounds are absent from the “territorial roars” that tigers use to maintain their vast domains.

Blue whales have the deepest voices: most of their vocalizations are pitched far too low for people to hear. Blue whales of both sexes make short calls, but only the males are known to sing, suggesting the songs may enable them to attract mates or advertise their presence to other males. Their songs repeat a series of eerie tones, blips, and creaks and may carry on for hours or even days. Researchers have found that the whales sing several variations of songs, each correlated with a particular region of the sea. Under certain conditions, their songs can travel thousands of kilometers, communicating to other whales across vast ocean distances.

EYES

The eyes of mammals are similar to those of most amniotes (Fig. 9.64). Rods (black-and-white vision) are sensitive to low levels of illumination, whereas cones are sensitive to colors in bright light. As in birds, the lens is elastic, and its shape is altered for near and far viewing by action of the ciliary muscle on the suspensory ligament. The eyes of a cat and many other mammals have about 100 million receptor cells in the retina of each eye. Oil droplets, either colorless or colored, are found in the cone photoreceptors of some mammals (Robinson, 1994). Colored droplets absorb particular wavelengths of light. Colorless droplets are found in marsupials and monotremes (Bowmaker, 1986). Many nocturnal species, like lemurs, galagos, cats, and ungulates, possess a **tapetum lucidum**, a reflective structure in the choroid layer that improves night vision by reflecting light back onto the retina.

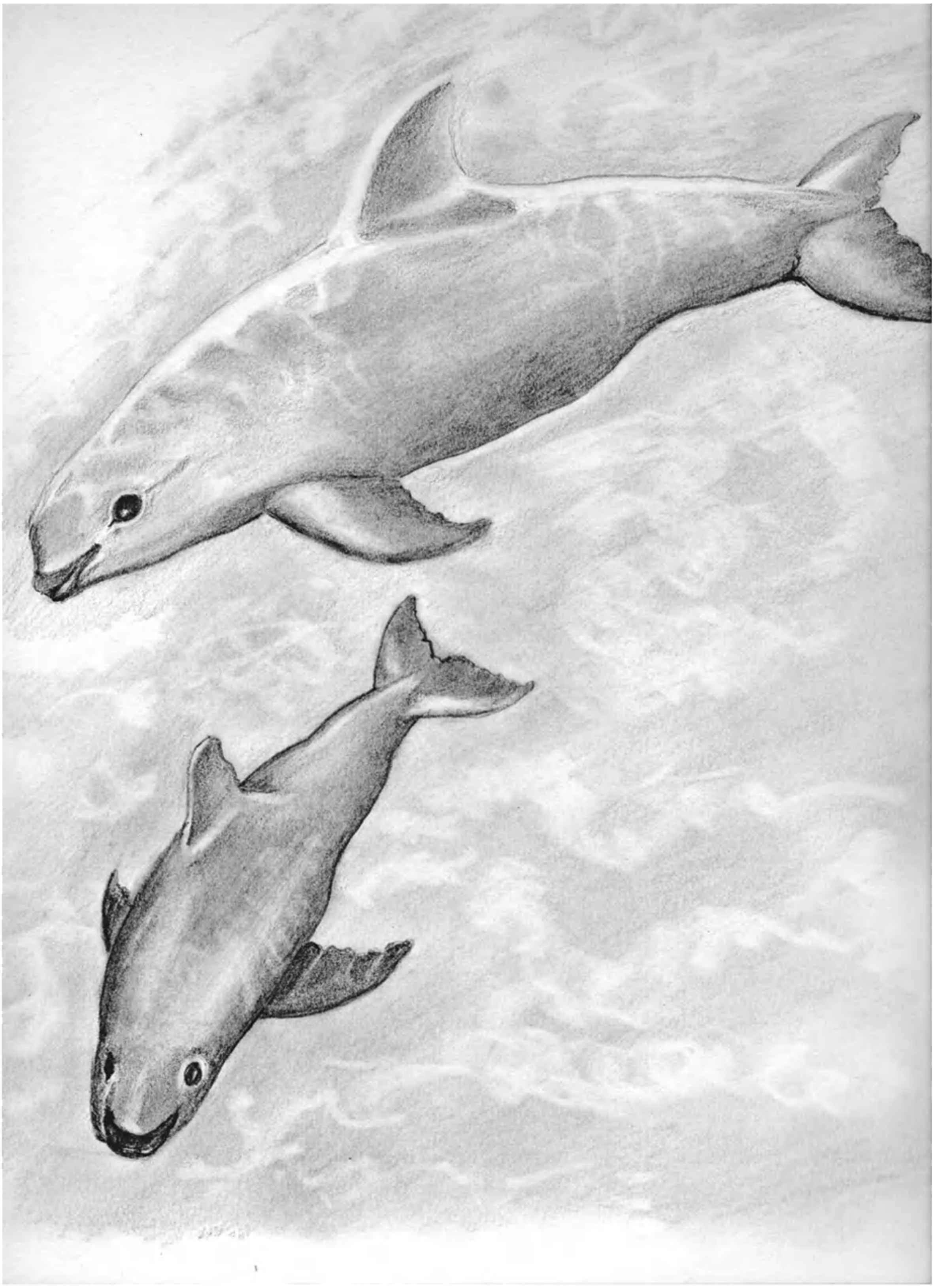


Figure 9.63. The vaquita (*Phocoena sinus*), the smallest and rarest cetacean.

Many mammals, including whales and seals, are color-blind (Peichl et al., 2001). As they evolved, they seem to have lost the ability to see colors (Stewart, 1995). Because early mammals were active at night, they apparently came to rely more on scent and hearing than vision. **Dichromatic** (two-color) vision is present in dogs (*Canis familiaris*) and probably a number of other mammals (Neitz et al., 1989). Humans and many other primates are diurnal and have three types of cone cells (S, M, and L cones), each containing a different photopigment. Thus, primates have trichromatic vision and can detect blue, green, and red colors. Roorda and Williams (1999) recorded the first images of the arrangement of S, M, and L cones in the living human eye.

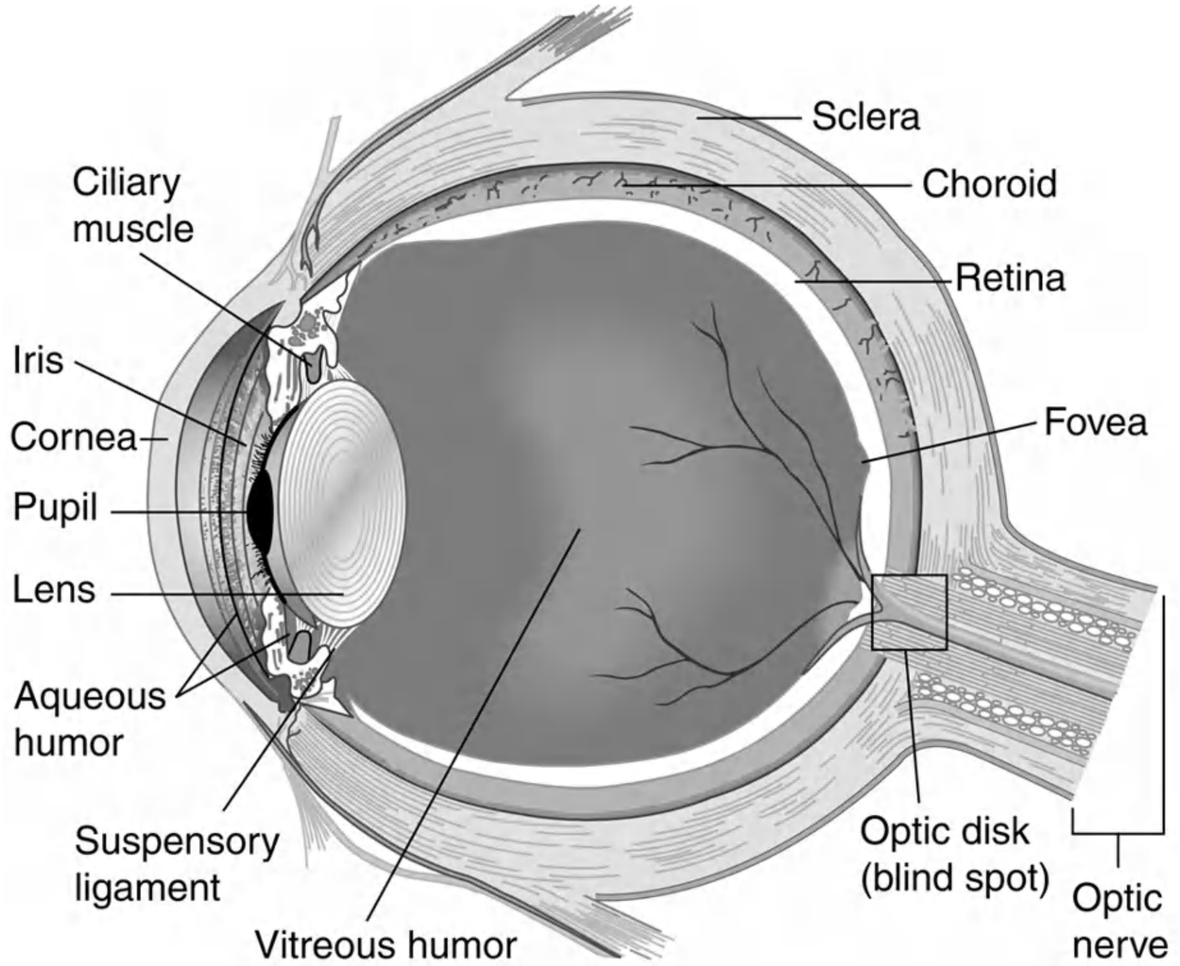


Figure 9.64. The mammalian eye. The retina contains the photosensitive rods and cones. Rods permit vision under dimly lit situations, whereas cones provide sharpness of vision under brightly lit situations while also providing color vision in some mammals.

Dogs are somewhat similar to color-blind humans, having their greatest color discrimination in the blue region of the spectrum. Colors in the blue-green spectrum may appear gray to dogs. They also do not see differences between colors in the red-green spectrum region, but they can tell red from blue and green from blue. The red-green color blindness explains why dogs often cannot find a red ball in the grass but can easily spot a yellow one.

The pupils of vertebrate eyes may be circular or slit-shaped. Researchers examined the eyes of 20 vertebrates with an infrared camera and found slit pupils only in animals with multifocal lenses (Malmstrom and Kroger, 2005). Vertebrates with slit-shaped pupils include the marine toad, crocodiles, lesser bush baby, slow loris, domestic cat, red fox, elk, red deer, and reindeer. These animals focus light of different wavelengths through different concentric zones, producing a sharper image than a lens with a single focal point at the center, like those of humans. In a multifocal lens, a circular pupil would contract to obscure entire concentric regions needed to focus some wavelengths, whereas with a slit-shaped pupil, light always passes through a portion of each concentric ring.

Some mammals, like moles and mole rats, have vestigial eyes. Mole rats (*Spalax*) carry eye reduction to its extreme among mammals. Spending most of their lives in total darkness in underground runways, mole rats have eyes that are reduced to less than 1 mm (0.04 in.) in diameter, 100 times as small as above-ground rodents of the same body size (Diamond, 1996). Each eye is covered permanently with thick skin and fur; lies embedded in a large gland; and lacks a pupil, functional lens, and eyeball muscles.

Tosini and Menaker (1996) have shown that the retinas of hamsters produce the hormone melatonin in quantities that ebb and flow daily. This retinal biological clock appears to control such daily cycles as the regeneration of light receptors and increased sensitivity to light, rhythms that are maintained on a roughly 24-hour cycle. Williams (cited in Holden, 1996a) has found the first clues to what may be a second circadian clock in the mammalian eye—not in the retina, but in the iris of a rat. How these clocks are coordinated with the biological clock in the brain (pineal gland) and whether such clocks exist in other mammals are still undetermined.

Can the Vaquita Be Saved?

The vaquita (*Phocoena sinus*) (see Fig. 9.63), the world’s rarest marine mammal and the most endangered of the 128 species of marine mammals alive in the world today, is on the edge of extinction. It is listed as critically endangered (defined as facing an extremely high risk of extinction in the wild). With a maximum length of 1.5 m (5 ft.) and a weight up to 54 kg (120 lb.), this little porpoise was not even discovered until 1958. Found only in the northern Gulf of California, vaquita are often caught and drowned in gill nets used in illegal fishing operations in marine protected areas within Mexico’s Gulf of California. They are most often found close to shore in the Gulf’s shallow waters, although they quickly swim way if a boat approaches.

Nearly one out of every five vaquita get entangled and drown in gill nets intended for other marine species (bycatch) like large blue shrimp (a delicacy that American restaurant-goers crave) and the totoaba, a critically endangered large sea bass also found in the upper Gulf of California. During the shrimping season, about 700 km (435 mi.) of gill nets are set within the vaquita area every day. The totoaba is a large fish that grows to over 1.8 m (6 ft.) long and weighs up to 135 kg (300 lb.). Totoaba were overfished by the mid-1970s and were listed as endangered by Mexico in 1975 and by the United States in 1979. International trade in totoaba is banned under the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), but high demand from China for its swim bladder, highly prized as a traditional health food, has led to a boom in illegal totoaba fishing in the past few years.

Thousands of swim bladders are dried and smuggled out of Mexico, often through the United States. Each pound of totoaba swim bladder is worth approximately $4,000—equivalent to half a year's income from legal fishing activities. It is this illegal trade that is currently driving the precipitous decline in vaquita numbers.

In July 2016, President Barack Obama and President Enrique Peña Nieto of Mexico announced bilateral collaboration measures to protect the vaquita. As a follow-up to this meeting, Mexico's National Institute of Fisheries and the World Wildlife Fund Mexico established an international committee of experts, *Comité Internacional para la Recuperación de la Vaquita* (CIRVA), to further develop and urgently implement vaquita-safe fishing technologies.

In 1997, the vaquita population was estimated to be approximately 567 individuals. By 2008, the estimated population was down to 150. CIRVA estimated about 200 vaquitas remaining in 2012 but fewer than 100 surviving individuals in 2014. In May 2016, only approximately 60 vaquitas remained—a decline of more than 92 percent since 1997.

Mexico enacted an emergency ban on gill nets in 2015. But as of November 2016, passive acoustic monitoring estimated the entire vaquita population at no more than 30 individuals. Urgent and immediate measures are needed immediately to save the last of the vaquitas.

As a final, desperate measure, CIRVA and the Mexican government brought a team of experts to San Felipe, in the state of Baja California, for a two-week effort to locate some of the vaquita and corral them in nets. They had hoped to transfer 10 to 12 of these rare survivors to a safe sea pen off San Felipe and, eventually, release them in a part of the gulf that is free of illegal fishing activity. However, the effort was ended following the death of a breeding age female that had been captured.

As of March 2018, it was estimated that only 12 vaquita porpoises remained (Mongabay.com., March 8, 2018). As of March 2019, the entire population consisted of an estimated 10 individuals. If vaquitas vanish, they would be the first known cetacean in North America to do so, and the first in the world since the Chinese river dolphin was declared extinct in 2006.

Rojas-Bracho and Reeves, 2013; Jaramillo-Legorreta et al., 2017; Thomas, 2017; Marine Mammal Center, 2017; https://news.mongabay.com/2019/03/possible-vaquita-death-as-scientists-say-only-10-are-left

NOSE

Olfactory mechanisms are highly developed in most mammals. Nasal passages are large and are elongated by the presence of both a hard palate and a soft palate, so that the internal nares open into the nasopharynx and are lined with ciliated mucous epithelium. The olfactory epithelium occupies the dorsal wall of the nasal cavity. Olfactory cells serve as chemoreceptors and respond to chemicals dissolved in the film of mucus covering the olfactory epithelium. When stimulated, chemoreceptors cause nerve impulses to be transmitted along olfactory nerves and through the cribriform plate to the olfactory bulb near the anterior end of the brain. The impulses then travel along olfactory tracts to portions of the cerebrum where specific odors are interpreted.

Figure 9.65. The nose of the star-nosed mole (*Condylura cristata*). The 22 fleshy processes that surround the nostrils are covered with tens of thousands of touch receptors (Eimer's organs), which are used to explore the environment by touch.

Figure 9.66. The northern water shrew (*Sorex palustris*) has a fringe of hairs along the lateral edge of each of its rear feet to assist in swimming.

Vomeronasal (Jacobson's) organs are well developed in monotremes, marsupials, and some insectivores. Cats, some rodents, and elephants (Shoshani, 1997) also retain these structures, but in most mammals they are vestigial. The vomeronasal organs of both sexes of laboratory mice were found to contain neurons specific for the pheromones of either sex

(Holy et al., 2000). The neurons responded to natural stimuli. Compared with many other mammals, humans have a poor sense of smell. Even so, the human nose can distinguish up to 10,000 different odors (Dajer, 1992).

The eastern mole (*Scalopus aquaticus*) tracks down prey by recognizing the slightly different odor cues entering each nostril (Catania, 2013). The findings suggest that even though mole nostrils are separated by only a fraction of a centimeter, each gets its own scent information (bi-nostril smelling).

The trunk of an elephant is a conjoined upper lip and nose, with the nostrils running like two parallel hoses from the trunk's base down to its tip. Most breathing is done through the nostrils. Elephants, which have a keen sense of smell, possess seven turbinal bones within their nasal cavity (Shoshani, 1997).

Scent and sound are particularly important to nocturnal animals. Most primitive primates (galagos, lorises, lemurs, and tarsiers) feed and mate in the dark and rely extensively on their senses of smell and hearing (Finkbeiner, 1993). One such primate, the aye-aye, is found only on the island of Madagascar and is considered the world's most endangered primate because it is the only extant member of its family. Adults spend more than 80 percent of their time alone, but recent studies have shown that females have definite home ranges and never stray into another female's range. The invisible boundaries are formed by scent marks left by streaking urine along branches. Chemicals that elicit a response from other members of the same species are known as pheromones and are discussed in greater detail in Chapter 13.

TASTE

Taste buds are abundant in mammals (see Table 8.2) and are found mainly on the tongue, posterior palate, and pharynx. Those on the tongue are located on the sides of papillae. Each taste bud consists of a cluster of gustatory cells that are the primary chemoreceptive cells. Each gustatory cell possesses a sensory hairlike process that projects through the epithelium via a taste pore. These chemoreceptors are stimulated by substances dissolved in the saliva. The sense of taste recognizes only five basic qualities: salty, sweet, sour, bitter, and umami.

ELECTRORECEPTORS

The duck-billed platypus seeks food in muddy streams. When it dives, it usually has its eyes, ears, and nose shut. It has long been known that the bill contains densely packed receptor organs, and it has been assumed that these are extremely sensitive mechanoreceptors. This is undoubtedly true, but the presence of electrosensitivity has been demonstrated in the platypus. It can home in on weak electrical fields, whether emitted by prey animals or by an artificial source (Scheich et al., 1986).

Endocrine System

In most cases, the endocrine organs of mammals are homologous to those of the other vertebrates. Some, however, have unique functions in mammals. For example, the hormone prolactin, which is secreted by the anterior lobe of the pituitary (adenohypophysis), stimulates milk production by mammary glands. Oxytocin, produced by the hypothalamus and secreted by the posterior lobe of the pituitary (neurohypophysis), causes uterine contractions and also contractions of muscles in the mammary glands. In some species, oxytocin and antidiuretic hormone play a role in pair bonding and stimulation of a mother's interest in her newborn (Insel and Carter, 1995).

The thyroid gland secretes thyroxin, triiodothyronine, and calcitonin. Thyroxin and triiodothyronine regulate overall metabolism, whereas calcitonin reduces calcium levels in the blood and prevents bone resorption. Parathyroid hormone increases the levels of calcium and phosphate in the blood by increasing the rate of calcium and phosphate absorption from the gastrointestinal tract. It also stimulates the breakdown of bone tissue in order to release additional calcium and phosphate into the blood.

The adrenal medulla produces epinephrine and norepinephrine, vasoconstrictors of the circulatory system and stimulators of increased production of adrenocortical hormones in times of extreme and/or prolonged stress. Epinephrine and norepinephrine also accelerate the heart rate, increase blood pressure, and increase the amount of blood sugar in times of sudden metabolic need. Additionally, epinephrine increases blood flow in the heart muscle, skeletal muscle, and lungs, and it decreases blood flow in the smooth muscle of the digestive tract and skin. Epinephrine is the primary hormone involved in the "fight-or-flight" response to fear, pain, and aggression.

Studies of the “stress hypothesis” (having higher levels of adrenocortical hormones when under stress) have been done on many species with varying conclusions. Healthy, free-ranging Chinese water deer (*Hydropotes inermis*), shot as part of a management program, had lower cortisol levels than diseased deer or free-ranging deer that were either netted and manually restrained or anesthetized by dart (Hastings et al., 1992). Adrenal glands of deer with various, mostly chronic, disease conditions weighed significantly more than those of healthy deer. Koala (*Phascolarctos cinereus*) adrenal glands increased in size in response to the stress of disease (Booth et al., 1991). The increase in size associated with disease varied with the type of disease.

The little brown bat (*Myotis lucifugus*), which has exceptionally high levels of the glucocorticoids cortisol and corticosterone (Gustafson and Belt, 1981; Widmaier et al., 1993), has a pronounced diurnal rhythm in glucocorticoid levels with peak levels just prior to the onset of the active (feeding) phase of the animal’s diurnal cycle, a pattern observed in most mammals (Gibson and Krieger, 1981; Widmaier et al., 1994). In addition, *M. lucifugus* has seasonal cycles of steroid hormone levels that are correlated with hibernation periods (Gustafson and Belt, 1981). Certain megachiropteran bats (*Pteropus pumilus* and *P. hypomelanus*) have been shown to respond to stress with increases in glucocorticoids and glucose (Widmaier et al., 1994). Stress probably activates the sympathetic branch of the autonomic nervous system in bats, as it does in other mammals, and is a significant contributing factor in the development of hyperglycemia.

The effects of stress on the adrenal gland and on population size were dramatically illustrated in the 1950s and early 1960s in Maryland. In 1916, four or five Sika deer (*Cervus nippon*) were released on the 115 hectare (284 acres) James Island near Cambridge, Maryland. By 1955, the population had increased to 300 healthy animals. In 1958, about half of them died, although the food supply was adequate. The population continued to decrease to 80 animals during succeeding years. Animals examined during the years of the decline showed medullary enlargement and histological changes in the adrenal glands that indicated that the stress caused by the overpopulation may have contributed to the decline (Christian 1959, 1963). Other factors and mechanisms undoubtedly were also involved in this complex process.

The Star-Nosed Mole

The nose of the star-nosed mole (*Condylura cristata*) consists of 22 fleshy processes that surround the nostrils (see Fig. 9.65). Besides being used for the sense of smell, the mole's unique nose, which is covered with tens of thousands of complex touch sensors known as **Eimer's organs**, is used to explore the environment by touch. It contains more than five times as many nerve fibers as innervate the mechanoreceptors in the entire human hand and may be one of the most sensitive and highly developed touch organs among mammals. The nose appendages differ in size and shape and also seem to be used differently when food is encountered. The longest appendages usually make the initial contact with the prey, whereas others are used for detailed tactile exploration once the prey has been located.

When filmed in slow motion underwater, the star-nosed mole has been found to use its unusual nose not only to touch the objects it encountered but also to blow air bubbles at them that it sucked back in rapidly. Moles were able to follow scent trails very accurately, thus demonstrating the ability to use smell to find food underwater. The northern water shrew (*Sorex palustris*), the world's smallest mammalian diver, has also been shown to use its sense of smell by sniffing air while submerged (see Fig. 9.66).

Researchers at Vanderbilt University have found that a star-nosed mole can eat 10 mouthful-size chunks of earthworm, one at a time, in 2.3 seconds, or 0.23 seconds a chunk. It is the fastest eating ever measured in any mammal.

Gould et al., 1993; Catania and Kaas, 1996; Catania, 2006, 2008

Density-dependent stress has been studied in tree shrews (*Tupaia glis* and *T. belangeri*) (Autrum and von Holst, 1968; von Holst, 1969). Stress causes a delay in the development of the young and changes in the behavior and physiology of the adult. Females under stress produce less milk or none at all. The sternal gland, located on the chest, ceases secretion, and females thus cannot mark their young with its secretion. Without this protection, the young get eaten by their cage mates or even by their mother. Under strong stress, females do not reproduce, and the testes of males recede into the body cavity.

Marked adrenocortical and adrenomedullary response to the stress of capture has been reported in the duck-billed platypus (*Ornithorhynchus anatinus*) (McDonald et al., 1992). Seasonal data revealed a distinct influence of time of year on the adrenocortical response to capture. That of males was greatest just prior to mating, whereas that of females was greatest during pregnancy and early lactation.

The pineal gland is a dorsal evagination of the midbrain. Due to its 24-hour cycle, the pineal gland and the hormone melatonin may play a role in the synchronization of other 24-hour circadian cycles like sleeping, eating, and adrenocortical function. Diurnal rhythms of the melatonin level in the retina have been reported (reviewed by Zachmann et al., 1992). Melatonin may also play a role in regulating the estrous cycles in mammals. Many species inhabiting Arctic or Antarctic regions have been reported to have extremely large pineal glands (reviewed by

Miché et al., 1991). Reproductive synchronization is essential in these areas where annual variations in daylength and climatic conditions are drastic. However, studies in Norway from 2004 until 2010, led by University of Tromsø biologist Karl-Arne Stokkan, have shown that reindeer lack a biological clock (a first for mammals) and have no daily fluctuation in melatonin. Reindeer live high in the Arctic, where they experience months of winter darkness and summer light. During these seasons, the activity of the animals is independent of the time of day. Researchers found melatonin levels rose in darkness and dropped sharply in light, regardless of what the circadian clock genes did, suggesting that the animals respond to light cues alone, rather than their circadian clock. Turning off the clock may help reindeer keep to their non-stop schedule of grazing for a few hours, napping for a few hours, and then grazing some more, even in winter, when the sun never rises. Melatonin may also play an important role in temperature regulation of hibernating mammals and has been shown to be involved in the reproductive process (reviewed by Rismiller and Heldmaier, 1987).

Mammals track seasons by measuring the length of days—which grow longer in spring—through an internal clock in the brain, and this length is what controls breeding. The clock, called the suprachiasmatic nucleus (SCN), monitors light through a pathway from the retina and conveys information about daylength to the pineal gland, at the base of the brain. In response to these signals, the pineal gland modulates its secretion of melatonin, dubbed the sleep hormone because it is released only in dim light or the dark. As nights shorten in spring, the brain's release of melatonin goes down. Some investigators suspect that this decline contributes to the increase in sexual activity, as well as in overall energy, in spring.

The pineal gland also is known to inhibit gonad function and development in rats, humans, and some other mammals. Sperm production is suppressed significantly by melatonin in adult male deer mice (*Peromyscus maniculatus*) housed under long photoperiod, but had no additional suppressive effects on mice housed under a short-day regimen (Blank and Freeman, 1991). Berria et al. (1990) reported that melatonin plays a role in regulating the seasonal testicular cycle of the spotted skunk (*Spilogale putorius*). Melatonin induced fall molt, the growth of white pelage, and testicular regression in male short-tailed weasels (*Mustela erminea*) (Rust and Meyer, 1969). The endogenous circannual reproductive seasonality rhythm in male red deer (*Cervus* *elaphus*) was affected significantly by melatonin implants; treatment with melatonin implants in November or December advanced reproductive development, whereas treatment from June to August delayed development (Webster et al., 1991).

The cane mouse (*Zygodontomys brevicauda*) is a year-round breeder in Venezuela and is not reproductively responsive to either variation in photoperiod or to continuous exposure to melatonin (Bronson and Heideman, 1992). Thus far, the cane mouse is the only mammal known in which the reproductive system shows no photoresponsiveness. Because Venezuela receives nearly 12 hours of daylight year-round, photoperiod cannot serve as an environmental cue.

Urogenital System

Mammalian embryos pass through both the pronephric and mesonephric stages of kidney development. The mesonephros serves as the functional embryonic kidney; in mammals, it reaches its peak of development earlier than in birds—approximately one-fourth of the way through the gestation period. The number of functional tubules varies among species. Before the last mesonephric tubules have formed near the caudal end of the nephrogenic mesoderm, the earliest ones formed at the anterior end have already been resorbed.

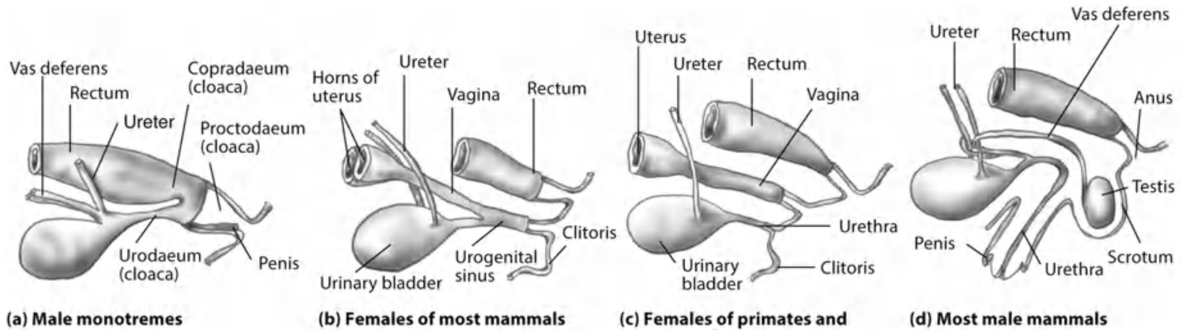
Although basically an embryonic kidney, the mesonephros functions for a short time following birth in monotremes and marsupials. When the metanephros begins to function, the mesonephros degenerates. Mesonephric ducts remain as sperm ducts in male mammals, but they become nonfunctional in females and remain only as short, blind Gartner’s ducts embedded in the mesentery of the oviducts.

The metanephros continues to develop from the caudal end of the nephrogenic mesoderm but is displaced anteriorly and laterally. Although some embryonic kidneys are lobulated, most adult kidneys are smooth and more or less bean-shaped. The renal artery, renal vein, nerves, and ureter enter and/or leave at the median notch, or **hilum**. **Nephrons** are the functional units of the kidney (see Fig. 1.22). Blood enters each kidney via renal arteries, whose branches (arterioles) each end in a network of specialized capillaries known as a **glomerulus**. Each glomerulus is partially enclosed by one end of a nephron, known as the **renal** (**Bowman’s**) **capsule**. The functional unit formed by a glomerulus and renal capsule is a **renal corpuscle**.

The process of **filtration** occurs as blood passes through the glomerulus. Waste products like urea, uric acid, and creatinine, as well as water, glucose, and many other substances, are filtered from the blood and enter the **proximal convoluted tubule**. After passing through this structure, the filtrate flows through the **loop of Henle** and **distal convoluted tubule** before entering a **collecting tubule**, which drains into the **renal pelvis** of the kidney. The renal pelvis is the expanded opening into the ureter. Each kidney is drained by a ureter. During its passage through the nephron, many substances like water and glucose are reabsorbed by a process known as **tubular reabsorption**, while in some cases, substances that were not filtered out in the glomerulus, like ammonia or hydrogen ions, are moved from capillaries into the filtrate by a process known as **tubular secretion**.

Ureters empty into the cloaca in monotremes (Fig. 9.67). In placental mammals, however, ureters empty into the urinary bladder, which is an evagination of the ventral wall of the cloaca. The bladder is drained by the urethra. Urine excreted by mammals contains mostly metabolic byproducts (nitrogenous wastes) that collect within the body and must be voided in order to avoid possible toxic effects. Urea is the primary waste product and is excreted in a relatively concentrated urine in order to conserve water. Urine excreted by desert mammals is very concentrated.

Reproduction in most mammals involves numerous adaptations for internal fertilization and viviparity. Unlike birds, both ovaries in most female mammals are functional in the production of ova, or eggs, although only one may function during each breeding cycle. Only the left ovary is functional in the duck-billed platypus, and, while two uteri are present, eggs develop only in the left uterus (Pasitschniak-Arts and Marinelli, 1998). Monotremes possess an ovary with fluid-filled cavities (lacunate), whereas other mammals possess a compact ovary with no chambers or lacunae. Growth of the ovary in mammals is controlled by hormones from the pituitary and pineal glands, and the ovary itself produces estrogen and progesterone. The size and shape of the ovary varies with age, reproductive stage, and species.



(a) Male monotremes **(b) Females of most mammals** **(c) Females of primates and some rodents** **(d) Most male mammals**

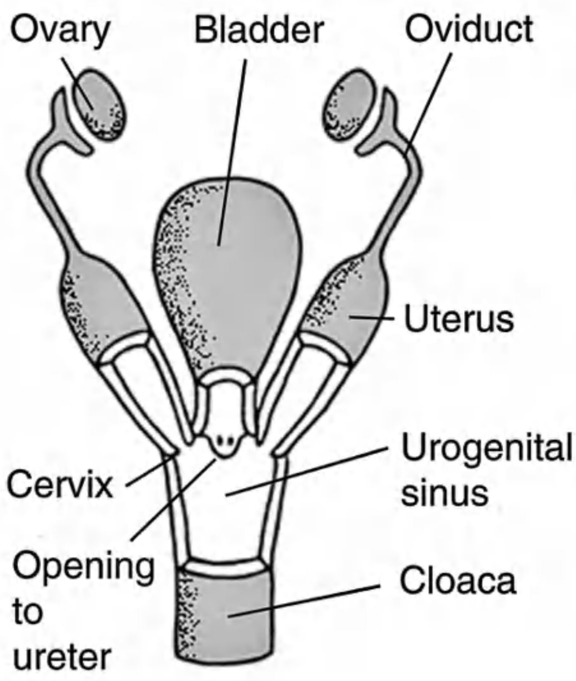
Figure 9.67. Representative divisions of the cloaca and their relations with urogenital tracts and the urinary bladder in male and female mammals: (*a*) ureters empty into the cloaca in monotremes; (*b*) females of most other mammals; (*c*) females of primates and some rodents; (*d*) most male mammals.

In female mammals, a Müllerian duct arises parallel and next to the embryonic mesonephric duct before the mesonephric duct regresses. The Müllerian duct, rather than the Wolffian duct, forms the oviducts, uterus, and vagina.

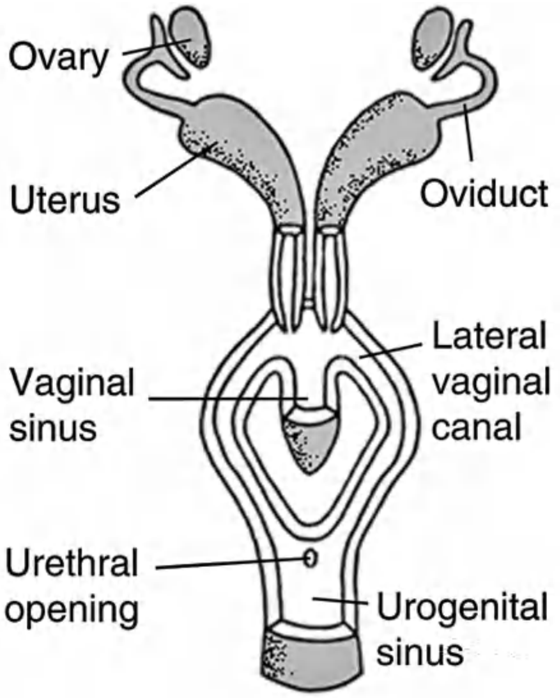
Female mammals possess **oviducts** (also known as uterine tubes or fallopian tubes), a **uterus**, and a **vagina** (see Fig. 9.68). The convoluted and ciliated oviducts are relatively short and small in diameter. In monotremes, there is no fusion of the Müllerian ducts, and the genital tract is double all the way to the urogenital sinus. The posterior ends of the tracts are modified to form shell glands in these oviparous mammals (Fig. 9.68a).

In marsupials, the two Müllerian ducts meet to form a median vagina just beyond the paired uteri (see Fig. 9.68b). The median vagina may or may not be paired internally. Beyond the median vagina, the two ducts continue as paired (lateral) vaginae. The median vagina is separated from the urogenital sinus by a septum. At birth, the fetus usually is forced through the septum directly into the urogenital sinus, although in some marsupials both the median and lateral routes may be used as birth canals. The new passageway may remain open throughout life and is known as a pseudovagina. It closes in opossums.

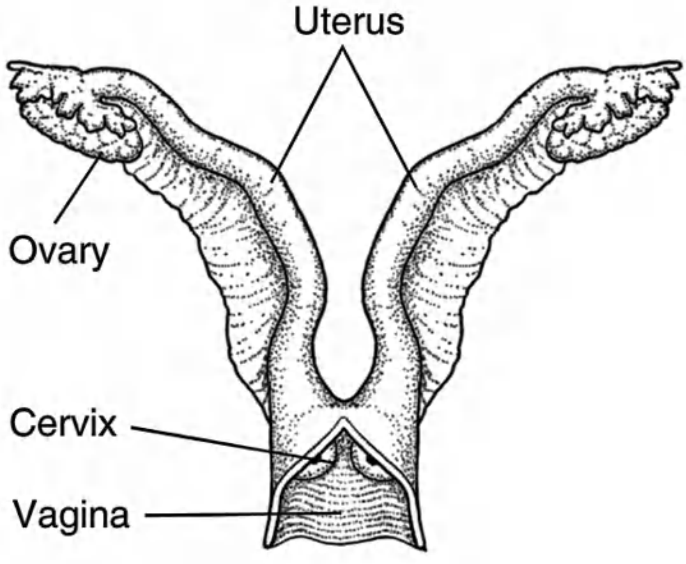
In placental mammals, there are varying degrees of fusion that result in two uterine horns, a single uterine body, and a single vagina. If the uteri are completely separate (each with a separate **cervix** opening from the vagina), but are joined to a single vagina, the uterus is said to be **duplex** (see Fig. 9.68c). This arrangement occurs in rodents and rabbits. In a **bipartite** uterus, there is a single cervix and the lower portions of the two uteri are fused, but in the major part of their length, the uteri are still separate (see Fig. 9.68d). Implantation of embryos usually occurs in the unfused portions of the uteri. This type of uterus occurs in most carnivores and in some ruminants. If the lower two-thirds of the two uteri are fused into a single structure but the upper third of each uterus remains separate, it is a **bicornuate** uterus (see Fig. 9.68e). Implantation usually occurs in the lower portion. This condition exists in many ungulates. In a **simplex** uterus, the uteri are fused into a single structure, there are no uterine horns, and the oviducts empty directly into the body of the uterus (see Fig. 9.68f). A simplex uterus is found in some bats, armadillos, and primates.



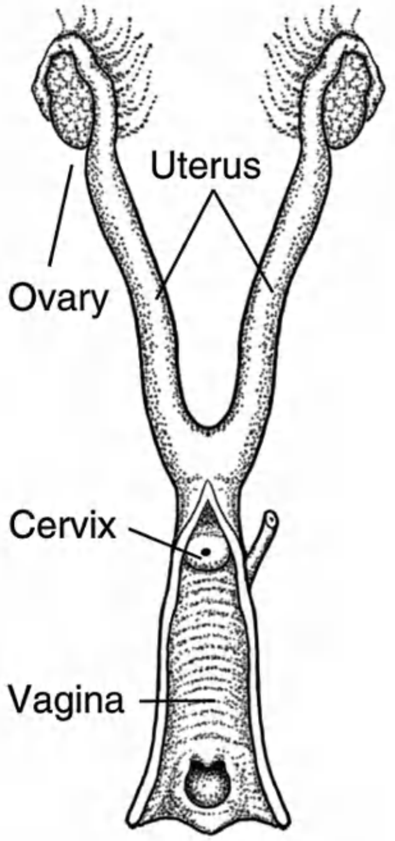
(a) Monotreme



(b) Marsupial



(c) Duplex



(d) Bipartite

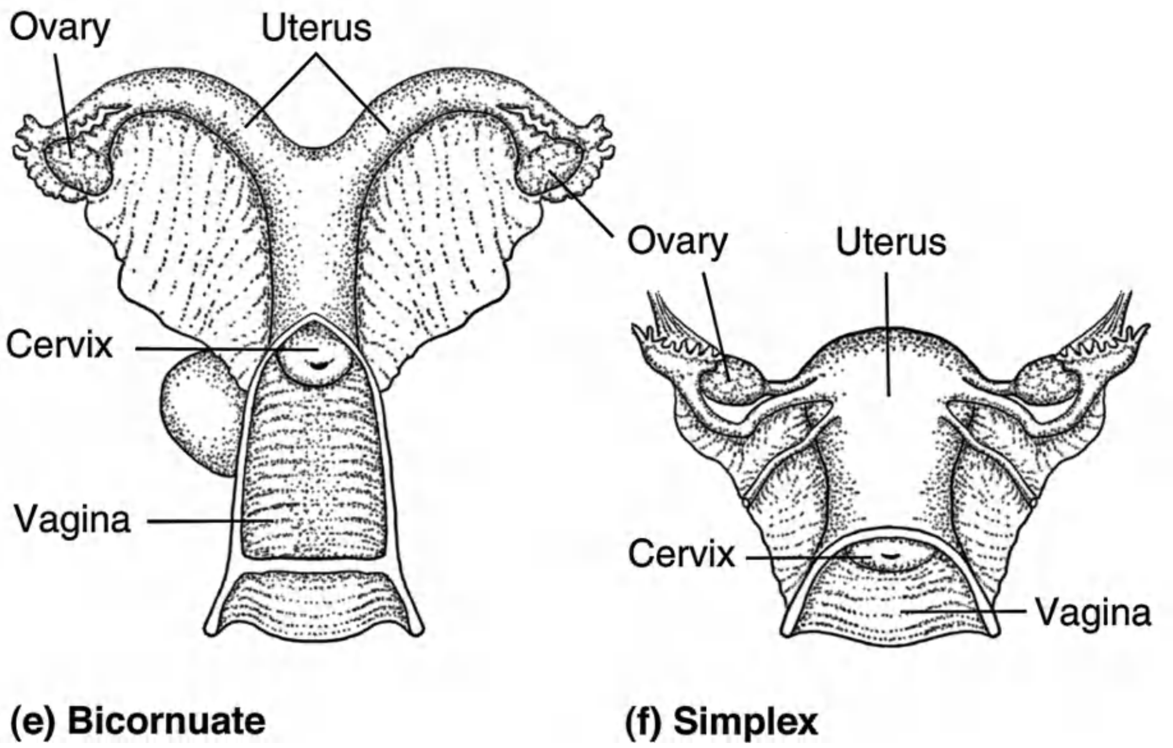


Figure 9.68. Types of female reproductive tracts: (*a*) monotremes, (*b*) marsupials, (*c*–*f*) placental mammals: (*c*) duplex, (*d*) bipartite, (*e*) bicornuate, (*f*) simplex.

The inner layer of the uterus, or endometrium, becomes highly vascularized prior to implantation of the blastocyst. It contributes to the formation of the placenta and serves as a favorable environment for the developing young. The thickest layer of the wall (myometrium) of the body of the uterus consists of smooth muscle, which at the end of the gestation period contracts and assists in expelling the fetus.

In all mammals except monotremes, the embryonic cloaca becomes subdivided into a dorsal rectum and a ventral urogenital sinus. The rectum opens to the exterior via the **anus**. In the developing male, the urogenital sinus extends into the penis as a continuation of the urethra running from the bladder. In the developing female of some mammals (some rodents, most primates), the urogenital sinus expands to form a shallow **vestibule** into which the reproductive system (vagina) and excretory system (urethra) open separately.

In mammals, the body of the uterus narrows to form a cervix, which projects into the vagina. Formed by the fusion of the terminal portion of the Müllerian ducts, the vagina usually opens into the urogenital sinus. In many rodents and primates, however, the vagina opens directly to the exterior of the body.

A **clitoris**, composed of columns of spongy erectile tissue, is present in females. Upon sexual stimulation, a series of reflex actions causes the spongy tissue to fill with blood and the clitoris to become erect. In otters, several rodents, rabbits, and a number of other mammals, a bone, the **os clitoris**, develops in the clitoris. An os clitoris is homologous to the baculum and develops in females of those species in which males have a baculum.

In males, the caudal pole of each embryonic testis is connected by a ligament, the **gubernaculum**, to the labioscrotal pouch. As development proceeds, these pouches increase in size and become the **scrotal sacs** (Fig. 9.69). Partly as a result of shortening of the gubernaculum and partly because growth of the gubernaculum does not keep pace with elongation of the trunk, the testes of many species are displaced caudad toward the scrotal sacs.

The testes remain retroperitoneal (behind the peritoneal membrane lining the peritoneal or abdominal cavity) and descend permanently into the scrotal sacs in most mammals. In some, like bats, rabbits, and rodents, the testes move back and forth seasonally between the abdominal cavity and the scrotal sacs. The passage between the two chambers is the **inguinal canal**. In species that retract their testes, the canal remains broadly open. In others, as in humans, the canal is only wide enough to accommodate the spermatic cord consisting of the vas deferens, arteries, veins, lymphatics, and nerves. These structures descend into the scrotal sacs along with the testes.

Depending on the species, the temperature in scrotal sacs is 1°C to 6°C (1.8°F to 10.8°F) cooler than in the abdominal cavity, thus allowing spermatogenesis to take place and viable sperm to be produced. Each testis consists of interstitial cells and tightly packed seminiferous tubules. Interstitial cells secrete the male sex hormone testosterone, which causes undifferentiated cells in the seminiferous tubules to undergo cell division (meiosis) to form spermatozoa (**spermatogenesis**).

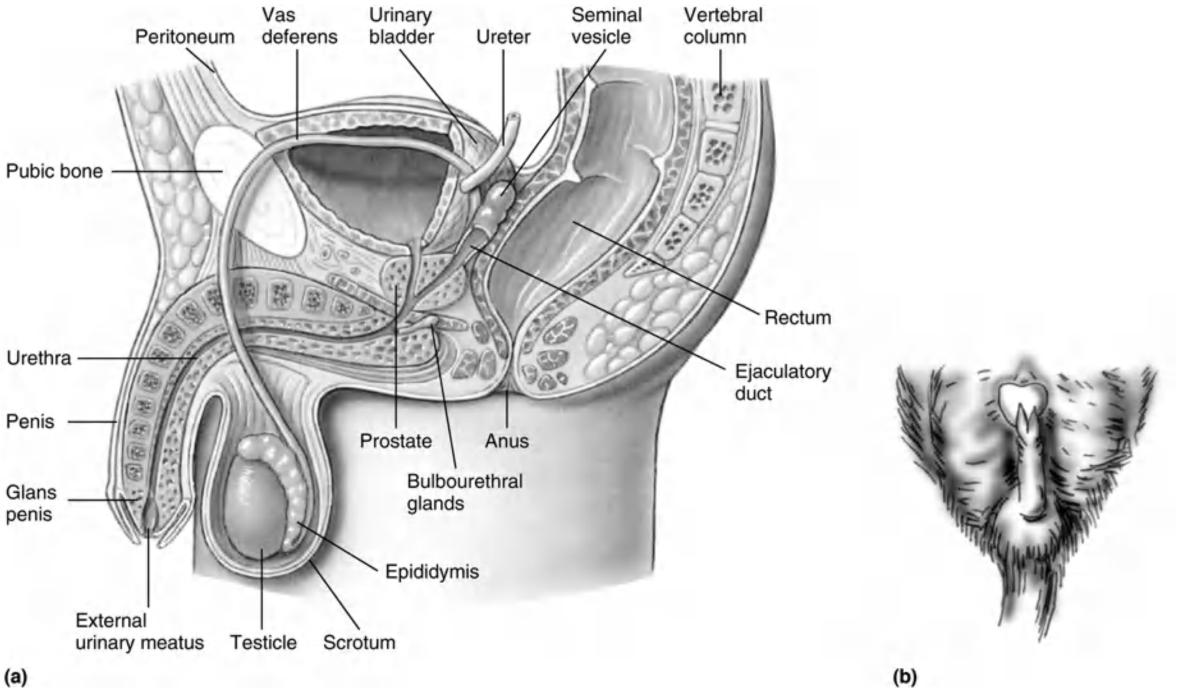


Figure 9.69. (*a*) Human male reproductive system. (*b*) Ventral view of the male external genitalia of the opossum (*Didelphis virginiana*). The penis is caudal to the scrotum, and its gland is bifurcate. The ureter opens between, not at the tips, of the bifid prong. A groove to direct sperm into the female's vagina extends along the medial side of each part of the glans penis for more than half its length.

In some mammals, the testes remain permanently in the abdomen, and scrotal sacs do not develop. Such is the case with monotremes, some insectivores, the xenarthrans (edentates), sirenia, cetaceans, elephants, hyraxes, rhinoceroses, and most seals. As mentioned above, in some mammals, like chipmunks, squirrels, many mice, some bats, and some primates, the testes descend temporarily into the scrotum during the breeding season. Why some mammals have evolved a scrotum and others have not is still not understood.

Spermatic ducts (vasa deferentia) empty into the urethra (see Fig. 9.69a). Due to descent of the testes, spermatic ducts must loop over the ureters en route to the urethra. One or more accessory sex glands (a single prostate, paired seminal vesicles, and paired bulbourethral or Cowper's glands) are located near the junction of the spermatic ducts and the urethra.

Most male mammals have an unpaired erectile penis. Erectile tissue in the penis consists of the single medial **corpus spongiosum** and two lateral masses, the **corpora cavernosa**, which surround the urethra. In monotremes, the penis is reptile-like and nonprotrusible. In more derived mammals, the penis becomes external. The tip of the penis (called the

glans penis), which is glandular and richly supplied with sensory nerve endings, is covered with loose skin, known as the **prepuce** or **foreskin**.

As an adaptation to the dual vaginae of the female, the penis of male marsupials is forked at the tip (see Fig. 9.69b). One tip enters each lateral vagina during copulation. The ureter opens between the prongs, and not at the tips, of the penis. A groove on the medial side of each glans penis directs semen into each vagina. The penis of the platypus (*Ornithorhynchus*) is also bifid as an adaptation to the paired Müllerian ducts.

Spermatogenesis via Transplantation

Mouse donor spermatogonial stem cells from a fertile testis transplanted to an infertile recipient mouse testis were successful in establishing spermatogenesis in the seminiferous tubules of the host, and normal spermatozoa were produced. Testis cells from rats also have been transplanted to testes of immunodeficient mice, with rat spermatogenesis occurring in all recipient mice. The inducing of rat spermatogenesis in mouse testes opens the possibility that spermatogonial stem cells of other species could be transplanted. The mouse could potentially become an *in vivo* host for spermatogenesis of many mammalian species.

Brinster and Avarbock, 1994; Brinster and Zimmermann, 1994; Clouthier et al., 1996

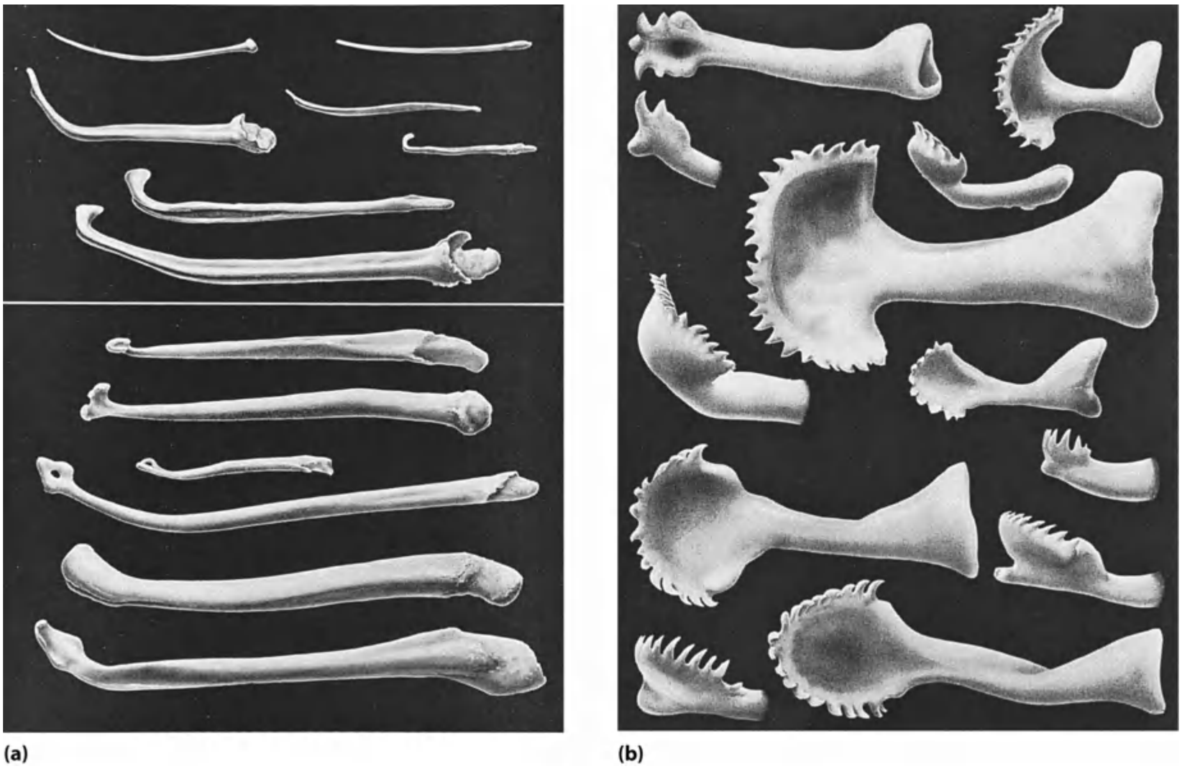


Figure 9.70. Representative bacula of families (*a*) Mustelidae and Mephitidae and (*b*) Sciuridae.

A heterotopic bone, the **os penis** or **baculum**, is found in the penis of some mammals, including marsupials, insectivores, bats, rodents, carnivores, bovines, and lower primates (Fig. 9.70). The structure and size of the baculum have been used as taxonomic characters and as an indicator of age. The baculum appears to be the ossification of a corpus cavernosum (Gunderson, 1976).

Thus, the trend in reproductive systems in vertebrates has been toward a reduction in number of zygotes that must be produced. This has been accomplished principally through (1) internal as opposed to external fertilization; (2) viviparity as opposed to oviparity; and (3) parental care of the young.

REPRODUCTION

Most mammals are viviparous with the young (embryo and fetus) being retained within the female's uterus. The embryo/fetus is nourished by means of a placenta, to which it is attached by an umbilical cord. Gestation ranges from approximately 12.5 days in the opossum

(*Didelphis virginiana*) up to 24 months in elephants. The only exceptions are the oviparous monotremes, which incubate their eggs after depositing them in a nest (duck-billed platypus) or in a temporary pouch on their abdomen (echidna).

Many mammals breed at specific times of the year and are known as seasonal breeders. Others, like elephants, rhinoceroses, giraffes, and humans, have no specific breeding season. Seasonal breeding and reproductive rhythm are the result of not just a single external stimulus, but rather a combination of nutritional, visual, auditory, tactile, environmental, and social factors. Most smaller mammals, which have shorter gestation periods, begin breeding as photoperiods increase. The quantity and quality of food may affect such things as the length of the breeding season and litter size, whereas pheromones can affect the reproductive behavior and actions of individuals by stimulating their central nervous system. Temperature has only an indirect effect on mammalian reproduction.

Naked mole rats (*Heterocephalus glaber*) are unique among mammals in that a single dominant individual (queen) can control the reproduction of all males and females in the colony (Faulkes and Abbott, 1991). The queen selects her breeding partners and initiates mating behavior. She suppresses reproduction in nonbreeding females and may control the reproductive endocrinology of breeding males because testosterone secretion in males becomes synchronized with the ovarian cycle of the queen.

Climatic disruptions thousands of kilometers away can affect the breeding of some species like Weddell seals (*Leptonychotes weddellii*) in Antarctica. The climatic phenomenon known as the El Niño/Southern Oscillation (ENSO) occurs when a tropical pool of warm water shifts eastward from the western Pacific and alters weather in much of the tropical and temperate latitudes. It apparently causes a drop in the birth rate of Weddell seals living some 6,000 km (3,700 mi.) away (Monastersky, 1992). The lowered birth rate represents the most southern biological effect ever recorded for an ENSO. The decline may result from changes in the fish population caused possibly by shifts in ocean currents and water temperatures.

Seasonal breeding in deer mice is regulated by photoperiod and by food availability (Nelson et al., 1992). Short photoperiods and restricted food intake cause a reduction in gonad size and sperm production. Many small mammals, like shrews, mice, and voles, may have several litters of young during the warmer months of the year. A female of a given species in northern North America may produce two or three litters annually, whereas a conspecific female in a southern state may be able to breed throughout the year, thereby producing more litters and young. Females are usually receptive to males immediately following the birth of a litter. There are records of a single meadow vole (*Microtus pennsylvanicus*) having 17 litters in a 12-month period (Bailey, 1924) and a golden mouse (*Ochrotomys nuttalli*) having 17 litters within 18 months (Linzey and Packard, 1977). However, larger mammals tend to have fewer litters per year. The number of young may vary from one in many species to approximately 18 in the American opossum. Bats, although small, breed only once a year in temperate regions and normally have either one or two young, usually in the spring. Many tropical species of bats breed more than once annually. Female canids, felids, and other related groups normally come into breeding condition twice each year, whereas larger mammals (deer, elk, buffalo, sheep) produce young only once a year. Some of the largest mammals, like elephants, may breed only every two years due to the extreme length of their gestation period.

Some mammals that breed only once a year, like bears, seals, weasels, badgers, and many deer, mate immediately after giving birth to their young in the spring. Although fertilization occurs, development ceases after a short time and the embryo (blastocyst) floats freely in the uterus for several months. Not until implantation occurs does the embryo resume development. Thus, the total gestation period for mammals with such **delayed implantation** may be as long as 350 to 360 days and allows the young to be born at the time of year most favorable for their survival (Table 9.1). A somewhat similar embryonic diapause occurs in many kangaroos (*Macropus*) (Fig. 9.71). As long as a joey is in the pouch, development of the next generation's blastocyst is suppressed. Thus, female kangaroos may have an embryo in diapause, a joey in the pouch, and a young kangaroo that is out of the pouch but still nursing daily. The mammary glands are capable of providing two kinds of milk simultaneously: high-protein, low-fat milk (from one teat) to the joey in the pouch, and low-protein, high-fat milk (from the other teat) to the older offspring.

Table 9.1. Periods during Which Blastocysts Remain Dormant in Some Mammals with Delayed Implantation

Species	Dormancy of Blastocyst (in months)
Order Chiroptera	
Equatorial fruit bat (*Eidolon helvum*)	3+
Jamaican fruit bat (*Artibeus jamaicensis*)	2½
Order Edentata [Cingulata]	
Nine-banded armadillo (*Dasypus novemcinctus*)	3½–4½
Order Carnivora	
Black bear (*Ursus americanus*)	5–6
Grizzly bear (*Ursus arctos*)	6+
Polar bear (*Ursus maritimus*)	8
Marten (*Martes americana*)	8
Fisher (*Martes pennanti*)	10–11
Badger (*Taxidea taxus*)	6
River otter (*Lutra canadensis*)	9–11
Mink (*Mustela* [*Neovison*] *vison*)	½–1½
Long-tailed weasel (*Mustela frenata*)	7
Alaskan fur seal (*Callorhinus ursinus*)	3½–4
Harbor seal (*Phoca vitulina*)	2–3

Gray seal (*Halichoerus grypus*)	5–6
Walrus (*Odobenus rosmarus*)	3–4
Order Artiodactyla	
Roe deer (*Capreolus capreolus*)	4–5

Source: Table from Vaughan, 1972. Copyright © Saunders College Publishing, Philadelphia. Used by permission.

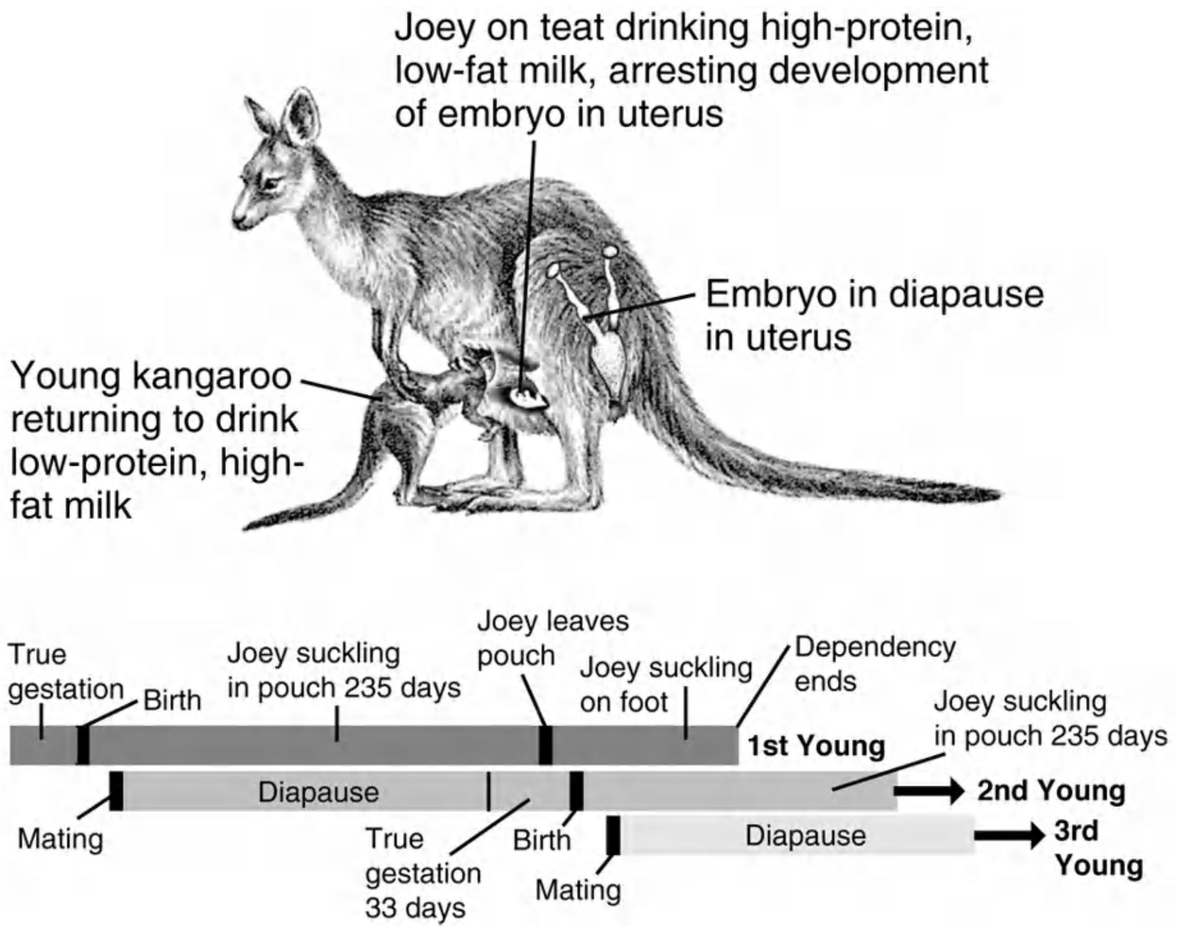


Figure 9.71. Kangaroos have a complicated reproductive pattern in which the mother may have three young in different stages of development at any one time. As long as a joey is in the pouch, development of the next generation's blastocyst is suppressed.

The length of time required to reach sexual maturity is more variable than that of any other vertebrate group. Female meadow voles are reproductively mature at 20 days of age. At the other extreme some elephants do not mature until 15 years of age.

Mammals may use most of the sensory processes—smell, vision, hearing, and touch—when seeking a mate. Scent glands that produce pheromones are better developed in mammals than in any other group of vertebrates. Odor is especially advantageous because many mammals are nocturnal, and most individuals are fairly widely separated from each other. A variety of sounds, including howling, bellowing, barking, roaring, and squeaking, may be used to attract members of the opposite sex. Some, like drills and mandrills, develop brightly colored buttock pads. Humans adorn their bodies with alluring clothes, jewelry, and perfumes in an attempt to make themselves more attractive to members of the opposite sex. Male members of the family Cervidae (deer, elk, caribou, moose, and others) annually grow sets of antlers on their heads (see Figs. 9.17 and 9.72). Antlers are used for defense, but this sexual characteristic may also be an important visual factor in sex recognition and determining male “quality” for the female. Courting may involve grooming, nuzzling, and other forms of bodily contact. Some females, including humans, are presented with “gifts” by courting males. Male cottontop tamarins of South America court females by carrying young cottontops around as a display of paternal devotion.

Mammals may be monogamous, polygamous, or promiscuous. Earlier estimates that 2 to 4 percent of mammalian species were monogamous now seem high: recent studies show that many of these “monogamous” species engage in extra-pair copulations (EPCs) (Stone, 1991). The existence of EPCs does not mean there is no primary bonding relationship between a male and a female. We know that more than 90 percent of mammalian species are polygynous, with monogamy restricted to the few species in which paternal care is necessary or in which females are widely dispersed (Amos et al., 1994).

Figure 9.72. Male members of the family Cervidae, like the moose (*Alces alces*) shown here, annually grow sets of antlers on their heads. Antlers are used for defense, but this sexual characteristic may also be an important visual factor in sex recognition by the female.

Data obtained by DNA analyses reveals that female chimpanzees (*Pan troglodytes verus*) from the Ivory Coast may seek to mate outside their own social group (Gagneux et al., 1997). High-ranking female chimpanzees were shown to have significantly higher infant survival, faster-maturing daughters, and more rapid production of young (Pusey et al., 1997; Wrangham, 1997). High rank probably influences reproductive success by helping females establish and maintain access to good foraging areas.

Female elk (*Cervus canadensis*) will mate with several males a day throughout the breeding season. In contrast, the California mouse (*Peromyscus californicus*) mates for life and is monogamous (Ribble and Salvioni, 1990). Prairie voles (*Microtus ochrogaster*) are also exceptionally monogamous (Insel and Carter, 1995). Many gray seals (*Halichoerus grypus*) mate with previous partners, even though the species has been described as polygynous.

During the four- to six-week-long mating season, male red deer (*Cervus elaphus*) roar repeatedly. Besides serving to warn other males, the calls apparently induce females to ovulate sooner (McComb, 1987). This is reproductively advantageous to the male in that it gives him a better chance to mate before possibly being replaced by a stronger male, and he can father more offspring than a noncalling male. The female's advantage of early mating lies in giving birth earlier in the spring so her calf has a better chance of surviving. In addition, the female has more time to recover so that she can give birth the next season.

All mammals use internal fertilization. Storage of viable sperm in the female urogenital tract for variable periods of time prior to fertilization of ova, called **delayed fertilization**, is known in every vertebrate group except the jawless fishes (Howarth, 1974). In some species of hibernating bats, sperm are stored for as long as six months prior to ovulation (Wimsatt, 1966, 1969). Copulation in temperate bats usually occurs in September, but fertilization does not occur until emergence from hibernation in April or May. Delayed fertilization means that females do not have to expend energy on mating immediately after emerging from hibernation when their energy stores are low. It also probably allows for embryonic development to begin earlier in the spring. Spermatozoa within the female reproductive tract obtain nourishment from the uterine and oviductal epithelium. The presence of zinc in the tails of spermatozoa, in the cauda epididymides, and in the seminal fluid may suppress sperm metabolism and reduce their need for sustenance during the period of storage (see review by Crichton et al., 1982). The prostate gland has been found to be the major source of zinc in both *Myotis lucifugus* and *M. velifer*.

Sperm competition leads to selection for increased sperm numbers and motility (Parker, 1982; Smith, 1984). When ejaculates from different males compete within the reproductive tract of a single female, males with a numerical sperm advantage statistically would be most successful at fertilizing that female's egg(s) (Parker, 1982). Among those primates and rodents in which females are promiscuous, sperm are longer in total length than in monogamous species. Sperm length is positively correlated with maximum sperm velocity (Gomendio and Roldan, 1991).

If longer sperm can swim faster, they can reach ova sooner, thus hypothetically out-competing rival sperm.

Some sperm produced by a male are better swimmers than others and can reach and fertilize eggs far more easily than others. However, males of all species produce a high percentage of "abnormal" sperm—two heads, two tails, and the like. In some species, like mice, bats, marsupials, and monkeys, a vaginal plug is left behind by the male after copulation. These plugs are thought to prevent leakage and to make more difficult the deposition of sperm by another male. Plugs themselves are composed of abnormal, misshapen sperm meshed together like a spider's web (Baker and Bellis, 1988, 1989a). Thus, although abnormal cells cannot fertilize an egg, they are important in forming a barrier that keeps out sperm from other males. Sperm not capable of fertilization might also be able to deactivate and/or kill foreign sperm with enzymes.

Males can vary their sperm counts quickly when mating situations change. Studies with rats (*Rattus norvegicus*) show that males that have no familiarity with their new mate ("unguarded") ejaculate an average of 51.6 million sperm as opposed to only 29.7 million for males that have been housed in the same divided cage with their mate ("guarded") (Bellis et al., 1990). In humans, sperm counts for ejaculations during intercourse decreased the more time couples spent together and increased after long periods away from their mates. (When faced with females who are out of sight and possibly mating with unknown partners, human males subconsciously perceive sperm competition and release more gametes, but when a female partner is close at hand, males reserve their sperm supplies [Baker and Bellis, 1989b].) No conscious or unconscious physiological mechanism has been suggested to account for this ability of males to alter their sperm counts in response to specific social situations.

Human females have the ability to influence sperm competition by controlling or manipulating the sequence and frequency with which they mate with different males, the time interval between in-pair and extra-pair copulations, and the ejection of sperm following copulation (Baker and Bellis, 1993). The occurrence and timing of female orgasm in relation to copulation and male ejaculation also influences the number of sperm retained.

Ralt et al. (1991) provide evidence of a chemotactic factor in the human female reproductive tract that attracts spermatozoa to the egg.

Although the specific chemotactic factors are unknown, they are thought to be contained in the follicular fluid that bathes the oocyte; this fluid is released at the time of ovulation. Until this discovery, it had been thought that sperm swam “upstream against the current” until they reached the fallopian tubes and a chance collision with an egg. More recently, researchers have found that rabbit sperm find their way toward an unfertilized egg by heading toward higher temperatures within the animal’s fallopian tubes (Bahat et al., 2003). The egg rests at a spot slightly warmer than the site where sperm begin the final leg of their journey, and sperm can sense that temperature difference. They also found evidence of thermotaxis with human sperm.

Relatives in some species who act altruistically toward each other improve the odds that their family gene pool will survive, even though every individual may not breed. This “kinship theory” is supported by studies of birds, wolves, and lions (Flam, 1991). In African lions (Packer et al., 1991; Packer and Pusey, 1997), brothers who banded together in large prides and participated in group defense as nonreproductive “helpers” often forfeited their own chances for fathering cubs so that their brothers could succeed. Thus, brothers who stick together in large prides stand a better chance of passing on some of their own genes than do others who go their separate ways, even though some brothers do not always breed themselves. Because brothers share about half their genes, the altruistic siblings hypothetically gain an evolutionary advantage from their reproductive sacrifice. Paternity analyses reported by Packer et al. (1991) revealed that resident males fathered all cubs conceived during their tenure in the pride.

GROWTH AND DEVELOPMENT

Prenatal Development (Oviparous)

The only oviparous mammals are the duck-billed platypus (*Ornithorhynchus anatinus*), which occurs in Australia and Tasmania, the short-beaked echidna (*Tachyglossus aculeatus*), and the long-beaked echidna (*Zaglossus bruijni*), the latter two of which are found in parts of New Guinea, Australia, and Tasmania (see Fig. 9.6). The nest of the platypus is located in a tunnel excavated by the female in the bank of a stream or pond with burrows extending as far as 18 m (60 ft.)

horizontally and opening above water level. Normally, two spherical eggs about the size of the eggs of a house sparrow are laid two weeks after breeding. Eggs are incubated for approximately 10 days by the female. Female echidnas develop a temporary breeding pouch on their abdomens during the breeding season. The one to three eggs are transferred directly from the cloaca to the pouch. The young remain in the pouch for approximately eight weeks following hatching.

Prenatal Development (Viviparous)

All other mammals are viviparous. Developing young are attached to a placenta by means of an umbilical cord (Fig. 9.73). Gas exchange, nutrient supply, and the removal of wastes all occur through the placenta.

The appearance and reproductive behavior of a female rodent can be affected by the sex of her immediate neighbors in utero (Clark and Galef, 1998). In house mice (*Mus musculus*) and gerbils (*Gerbillus* spp.), male fetuses secrete testosterone during the last week of gestation. The testosterone enters the amniotic fluid and is absorbed by the fetuses on either side of the male. Exposure to the hormone exerts masculinizing effects on both males and females, causing, among other things, both sexes to mature later. Twenty-seven of 28 female gerbils that matured late had been either next to a male or between two males; by contrast, 21 of 22 early maturing females had developed without an immediate male neighbor. Additional preliminary studies on gerbils show that eggs produced by the right ovary are more likely to develop into males than are eggs from a left ovary (Clark and Galef, 1998).

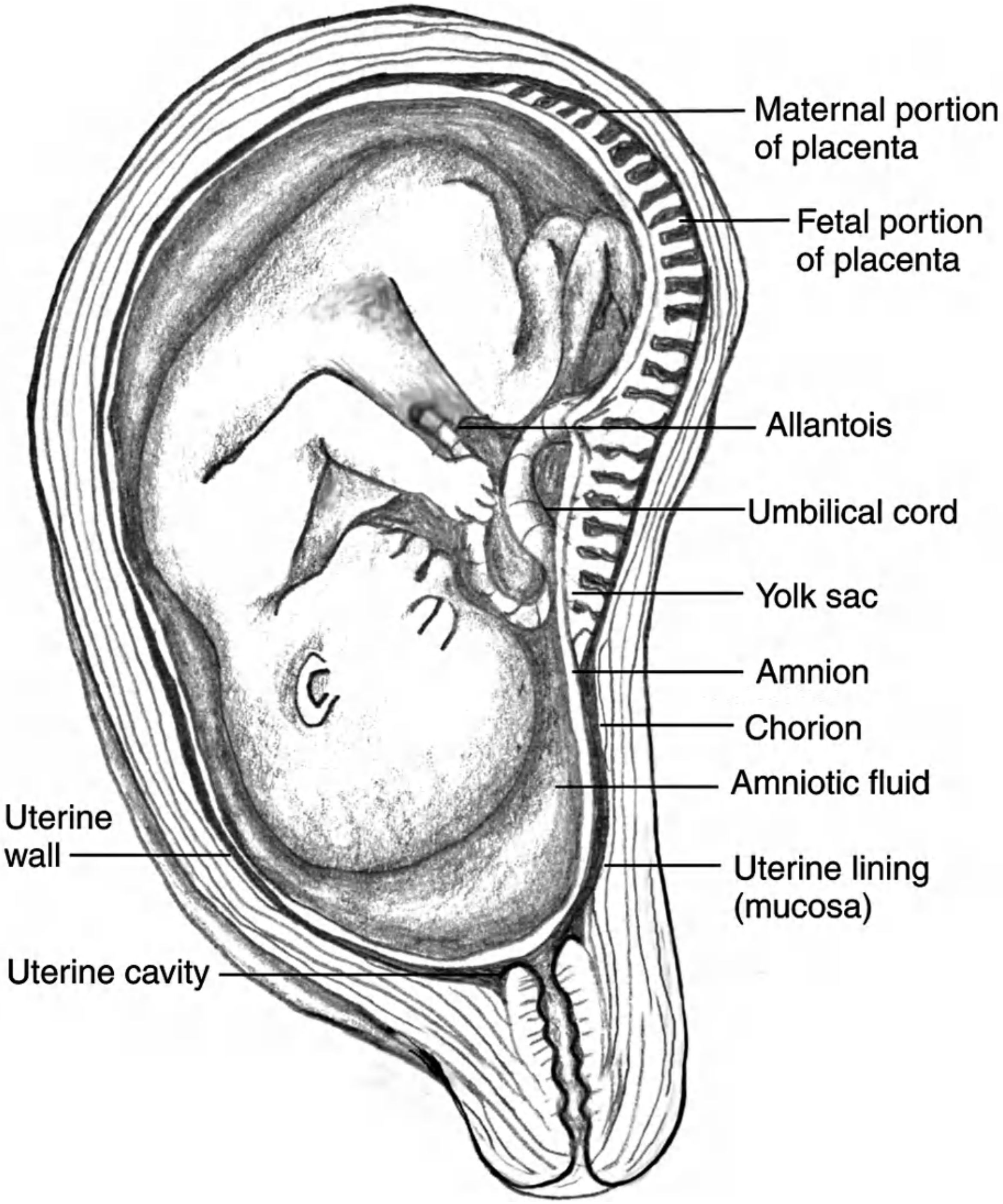
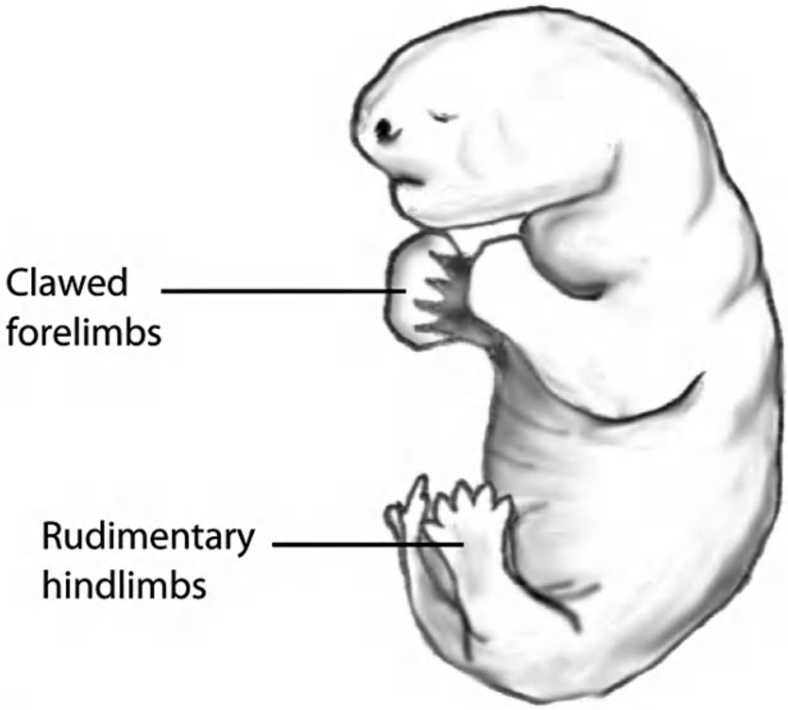


Figure 9.73. The young of viviparous mammals develop within the uterus. They are attached to a placenta by means of an umbilical cord. Gas exchange, nutrient supply, and waste removal all occur through the placenta.

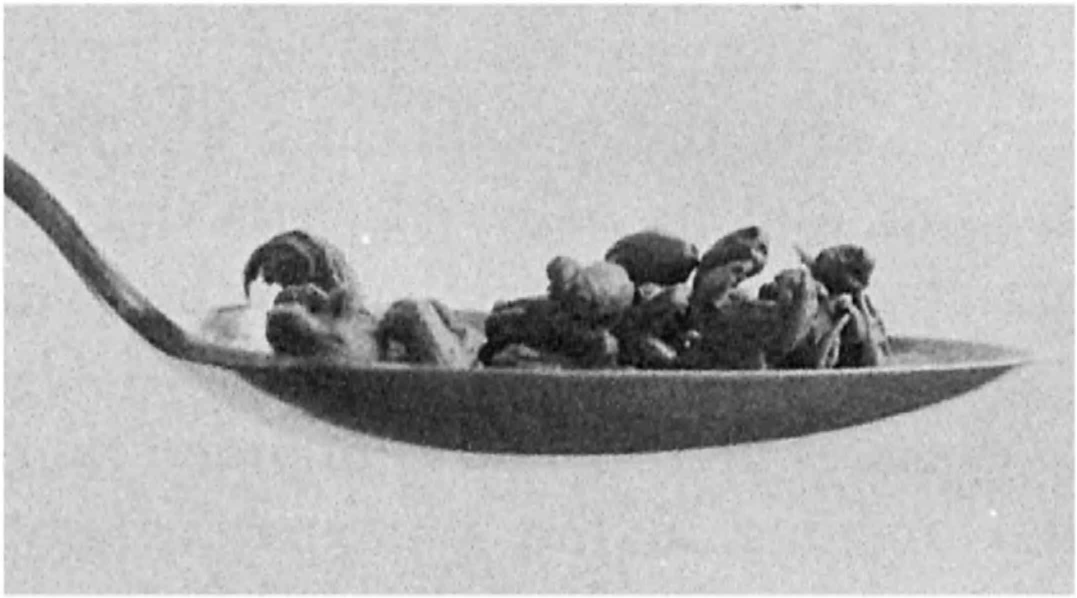
Duration of Embryonic/Fetal Development

Among mammals, the shortest gestation period of 12.5 days occurs in the American opossum (*Didelphis virginiana*), a marsupial, whereas the longest gestation period of 22 to 24 months belongs to the elephants. The duck-billed platypus, a monotreme, incubates her eggs for approximately 14 days.

Young marsupials are born in a very undeveloped condition, so much so that newborn opossums have been referred to as “living embryos” (Fig. 9.74). They immediately crawl into the marsupium, attach to a nipple, and undergo the rest of their development within the pouch. All marsupials have greatly delayed tooth development because they spend a considerable part of their early life attached to a nipple. As a result, modern marsupials largely bypass having deciduous (baby) teeth in favor of adult teeth, which erupt after the period of intense suckling. The only deciduous teeth to be replaced are one pair of premolars in each half of the upper and lower jaws.



(a)



(b)

Figure 9.74. (*a*) Detail of a newborn opossum (*Didelphis virginiana*). (*b*) Eighteen newborn opossums in a teaspoon. Actual size. (*c*) Long-nosed bandicoot (*Perameles nasuta*), a marsupial. Litter of three young at about four days after birth.

High-resolution X-ray computer tomography of a fossil baby *Alphadon*, a 70-million-year-old mouse-size mammal, has revealed a pattern of tooth replacement exactly like that of modern marsupials. Discovery of this same tooth pattern in an ancient mammal from the time of the dinosaurs suggests that the marsupial reproductive system already had evolved as far back as the Cretaceous period (Cifelli et al., 1996).

Female armadillos normally have an eight- to nine-month gestation period, after which identical quadruplets are born. However, females apparently can delay delivering young for up to 24 months in some cases (Storrs et al., 1988). Either the fertilized embryos must remain free-floating in the uterus most of this time, or the female can store viable sperm for extended periods.

Hatching and Birth

Most mammals are enclosed only in the amniotic sac, which ruptures either before or during parturition (see Fig. 9.73). Females usually aid newborns in freeing themselves from the ruptured membranes. In monotremes, pressure exerted by the front paws as well as an egg tooth on the top of the bill enable them to break out of their shells.

Parental Care

Parental care is universal among mammals. Altricial species require proportionately longer to develop and become independent than do precocial species. The duration of parental care ranges from several weeks in small rodents to many years in some higher primates.

For their first month of life, Malaysian tree shrews (*Tupaia tana*) reside in a nursery nest in a tree cavity apart from the mother (Emmons and Biun, 1991). The mother visits the nest only once every other day to nurse them. The mean time spent inside the nest cavity is 2.74 minutes per visit. The total time that the mother spends with her young during their first month of life is less than 50 minutes. The short and infrequent visits of *Tupaia* mothers is thought to be an adaptation to prevent the production of heavy scent trails, since the nests of these animals are close to, or in, the ground and prone to predation.

Communal nursing has been reported in many mammals ranging from bats (Wilkinson, 1992) and prairie dogs (Hoogland et al., 1989) to Hawaiian monk seals (Boness, 1990) and fallow deer (Birgersson et al., 1991). For example, communal nursing in evening bats (*Nycticeius humeralis*) rarely occurred prior to two weeks before weaning, but after that time, more than 18 percent of nursing bouts involved nondescendant offspring (Wilkinson, 1992). It occurred most frequently when pups began hunting on their own and when lactating females attained their lowest average pre-fed body weight. Wilkinson (1992) hypothesized that if a female with extra milk reduced her weight by dumping milk prior to her next foraging trip, she could obtain an immediate energetic benefit and maintain maximum milk production. Milk production, which is under the control of the hormone prolactin, continues to remain high as long as milk is removed from the mammary glands.

Growth

Oviparous

Female platypuses normally produce two blind, naked young annually in a nesting chamber within a burrow (see Fig. 9.6a). Nipples and teats are absent in monotremes, and breasts do not form. Milk is released from ducts onto the flattened milk patch, or areola, on the surface of the skin, where vigorous suckling permits its ingestion by the young. The eyes of the young open at about 6 weeks of age, at which time the fur is about 6 to 8 mm in length. The young emerge from the burrow when they are about 4 months of age (Orr, 1982; Nowak, 1991).

Female echidnas normally produce a single egg, which is transferred from the cloaca into a temporary pouch on the female's abdomen. The young echidna is nourished by thick, yellowish milk produced by the mammary glands that open into the pouch, and it remains in the pouch for six to eight weeks (Nowak, 1991).

Viviparous

The young of some viviparous species are well developed and alert at birth and are capable of taking care of themselves to some extent (**precocial**). Fishes, anurans, lizards, snakes, crocodilians, and some mammals like hares, cetaceans, and ungulates are precocial (Fig. 9.75). Parents often provide protection for these young, and in the case of mammals, the young are nourished by nursing from the mother. Young pronghorns (*Antilocapra americana*) are particularly precocious. Within four days following their birth (although still somewhat unsteady on their feet), pronghorn young can outrun a human, and at 1 week of age they can outdistance the average dog (Einarsen, 1948). Wildebeests are able to run with the herd within hours of their birth.

Other newborn mammals, however, require extensive parental care for their survival. Their eyes and ears are sealed at birth, they have little or no hair on their bodies and are usually unable to thermoregulate, and the distal portions of their limbs may not be fully formed. These **altricial** species include shrews, rabbits, mice, squirrels, dogs, and cats.

Differential growth rates between spring-born and fall-born litters have been recorded for a number of species of small mammals (Meyer and Meyer, 1944; Dunaway, 1959; Davis and Golley, 1963; Linzey and Linzey, 1967; Martinet and Spitz, 1971). Variation in body growth seems to be primarily dependent on photoperiod and food quality. Spring-born cotton rats (*Sigmodon hispidus*) were consistently heavier than fall-born rats throughout a 220-day study period (Dunaway, 1959). Spring-born golden mice (*Ochrotomys nuttalli*) were heavier at birth than fall-born mice, but were shorter in tail length and total length (Linzey and Linzey, 1967). The greater weight of spring-born individuals may be correlated with the smaller litter size at this time, since it might be expected that females would produce either large numbers of lighter young or smaller litters with heavier individuals.

(a)

(b)

(c)

Figure 9.75. Birth of a white-tailed deer (*Odocoileus virginianus*). The fawn is born with its eyes and ears open and has a full coat of hair. It is able to stand, nurse, and walk shortly after birth.

As juvenile mammals grow, they undergo one or more pelage changes. These pelage changes occur in a specific pattern in each species and result in a **juvenal** pelage that may be considerably different in coloration from the adult pelage. For example, young deer mice (*Peromyscus* spp.) are grayish and do not attain their typical tan adult pelage for several months.

Attainment of Sexual Maturity

The time required to reach sexual maturity in mammals ranges from several weeks in some rodents to as long as 10 to 15 years in such species as elephants, gorillas, and humans. The shortest known time required to reach sexual maturity occurs in female meadow voles (*Microtus pennsylvanicus*), which are ready to breed when 3 weeks of age (Hamilton, 1943). The quantity and quality of the food and water supply may affect the age of attaining sexual maturity in some mammals.

Sexual maturation of juvenile female California mice (*Peromyscus californicus*) is delayed if they remain in physical contact with their mother (Gubernick and Nordby, 1992). In contrast, puberty was unaffected by exposure to the father or a strange adult male. Females exposed to their mother, but prevented physical contact by a double wire-mesh barrier, showed an intermediate delay in sexual maturation. Actual physical contact with the mother, and not solely a urinary chemosignal, is necessary to delay sexual maturation in this species. The delay in sexual maturation of juvenile females may be a means of avoiding competition with their mothers until the young females disperse. It may also serve as an incest avoidance mechanism to prevent fathers from mating with their daughters.

Table 9.2. Longevity of Some Species of Mammals

Species	Maximum Age (years)
Tachyglossidae	
Short-beaked echidna (*Tachyglossus aculeatus*)	49.5
Ornithorhynchidae	
Duck-billed platypus (*Ornithorhynchus anatinus*)	22.6
Didelphidae	
American opossum (*Didelphis virginiana*)	6.6
Macropodidae	
Red kangaroo (*Macropus rufus*)	25
Megalonychidae	
Two-toed sloth (*Choloepus didactylus*)	36.8

Species	Maximum Age (years)
Soricidae	
Big short-tailed shrew (*Blarina brevicauda*)	2.2
Vespertilionidae	
Big brown bat (*Eptesicus fuscus*)	19
Little brown bat (*Myotis lucifugus*)	34
Brandt’s bat (*Myotis brandtii*)	41
Hominidae	
Chimpanzee (*Pan troglodytes*)	59.4
Orangutan (*Pongo pygmaeus*)	59
Gorilla (*Gorilla gorilla*)	60.1
Canidae	
Gray wolf (*Canis lupus*)	20.6
Coyote (*Canis latrans*)	21.8
Dog (*Canis familiaris*)	24
Red fox (*Vulpes vulpes*)	21.3
Felidae	
Lion (*Panthera leo*)	27
Cougar (*Puma concolor*)	23.8

Species	Maximum Age (years)
Bobcat (*Lynx rufus*)	32.3
House cat (*Felis catus*)	30
Mustelidae	
Northern river otter (*Lontra canadensis*)	27
American badger (*Taxidea taxus*)	25
Mephitidae	
Striped skunk (*Mephitis mephitis*)	13.9
Procyonidae	
Raccoon (*Procyon lotor*)	21
Ursidae	
American black bear (*Ursus americanus*)	34
Brown bear (*Ursus arctos*)	40
Polar bear (*Ursus maritimus*)	43.8
Balaenidae	
Bowhead whale (*Balaena mysticetus*)	211
Southern right whale (*Eubalaena australis*)	70
Eschrichtiidae	
Gray whale (*Eschrichtius robustus*)	77

Species	Maximum Age (years)
Physeteridae	
Sperm whale (*Physeter macrocephalus*)	77
Delphinidae	
Bottlenose dolphin (*Tursiops truncatus*)	51.6
Orca, or killer whale (*Orcinus orca*)	90
Elephantidae	
Asiatic elephant (*Elephas maximus*)	65.5
African bush elephant (*Loxodonta africanus*)	65
Equidae	
Horse (*Equus caballus*)	57
Suidae	
Wild boar (*Sus scrofa*)	27
Hippopotamidae	
Nile hippopotamus (*Hippopotamus amphibius*)	61.2
Camelidae	
Llama (*Lama glama*)	28.9
Bactrian camel (*Camelus bactrianus*)	35.4
Cervidae	

Species	Maximum Age (years)
Red deer (*Cervus elaphus*)	31.5
Antilocapridae	
Pronghorn (*Antilocapra americana*)	15.5
Bovidae	
Domestic cow (*Bos taurus*)	20
American bison (*Bison bison*)	33.5
Domestic goat (*Capra hircus*)	20.8
Sciuridae	
Eastern Fox squirrel (*Sciurus niger*)	16
Eastern Gray squirrel (*Sciurus carolinensis*)	23.6
Eastern chipmunk (*Tamias striatus*)	9.5
Woodchuck (*Marmota monax*)	14
Castoridae	
American beaver (*Castor canadensis*)	23.4
Cricetidae	
Deer mouse (*Peromyscus maniculatus*)	8.3
Golden mouse (*Ochrotomys nuttalli*)	8.5
Muridae	

Species	Maximum Age (years)
House mouse (*Mus musculus*)	4
Black rat (*Rattus rattus*)	4.2
Leporidae	
European rabbit (*Oryctolagus cuniculus*)	9
Eastern cottontail (*Sylvilagus floridanus*)	9.8

Source: Human Ageing Genomic Resources (HAGR), 2017.

Longevity

The life span of an elephant may be 60 or 70 years (Table 9.2). More and more humans are living past the century mark as medical science continues to find cures for disorders and diseases. In general, mammalian longevities are inversely correlated with body size and metabolic rate. Bats, however, are an exception. On average, bats live three times longer than other mammals with similar basal metabolic rates (Austad and Fischer, 1991). Banded Brandt's bats (*Myotis brandtii*) have lived 41 years, and little brown bats (*Myotis lucifugus*) have been recorded as living for more than 34 years. Brunet-Rossinni (2004) produced data showing that reduced free-radical production was at least a partial explanation for the extreme longevity of bats. Among small mammals, a golden mouse (*Ochrotomys nuttalli*) lived for 8 years and 5 months in captivity (Linzey and Packard, 1977). This represents the longest life span of any North American cricetine rodent.

Review Questions and Topics

1. List at least five major functions of mammalian skin.
2. List five major functions of hair. Give an example of a specific mammal illustrating each function.
3. Differentiate between horns and antlers. Give one example for each.

4. Differentiate between sudoriferous and sebaceous glands. Discuss the functions of each.
5. How does the middle ear of mammals differ from that of all other vertebrates?
6. Compare and contrast the vertebral columns of vertebrates (kinds of vertebrae, types of articulating surfaces, etc.).
7. Distinguish between plantigrade, digitigrade, and unguligrade locomotion. Give examples of mammals that use each type.
8. Differentiate between artiodactyls and perissodactyls. Give examples of each.
9. Describe the anatomy and function of the respiratory system of a terrestrial mammal.
10. Trace a bolus of food in a carnivore from the oral cavity until it is absorbed from the small intestine. List all of the structures and organs involved and their functions.
11. Differentiate between ultrasonic communication and infrasound. Give an example of a mammal that uses each method.
12. Describe a nephron. Trace the filtrate from the glomerulus to the urinary bladder.
13. Differentiate between duplex, bipartite, bicornuate, and simplex uteri. Give an example of each.
14. Differentiate between an altricial species and a precocial species. Give several mammalian examples of each.
15. Define delayed fertilization.
16. Define delayed implantation. What are some of its adaptive advantages? Give several examples of mammals in which delayed implantation occurs.
17. Distinguish between monogamy and polygamy.
18. Which mammalian-like characteristics were possessed by early synapsids?
19. Most mammals are viviparous; a few are oviparous. List several advantages and disadvantages of each of these methods of reproduction.

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Vertebrate Internet Sites

1. Primate Information Network

   www.primate.wisc.edu

   Aimed at both specialists and the general public, this clearinghouse at the Wisconsin National Primate Research Center in Madison logs 45,000 hits a month from visitors eager to learn about chimps, gorillas, monkeys, lemurs, and their kin. Dedicated to conducting humane research with nonhuman primates to advance knowledge in primate biology and address human and animal health concerns. Fact sheets cover the world's 235 species of primates. Links delve more deeply into the biology, taxonomy, and conservation of primate species (many of which are reeling from habitat destruction and wanton hunting). Other offerings include a bibliography, a discussion forum, searchable indices of researchers and organizations worldwide, and a jobs list.

2. National Museum of Natural History: Tour the Hall of Mammals

   www.naturalhistory.si.edu/exhibits/kenneth-e-behring-family-hall-mammals

   Website explores how all mammals, past and present, are related to each other by virtue of common descent. Bibliography and websites.

3. Bat Conservation International

   www.batcon.org

   Information on the ecology and conservation of bats.

4. WhaleNet

   http://whale.wheelock.edu

   Originally sponsored by Wheelock College in Boston, WhaleNet contains much information on marine mammals, updates on strandings and entanglements, information about the satellite tracking program, and many links.

5. Animal Diversity Web: Class Mammalia

   http://animaldiversity.ummz.umich.edu/site/accounts/information/Mammalia.html

   Diversity, geographic range, habitat, systematic and taxonomic history, physical descriptions, development, reproduction, longevity, behavior, communication and perception, food habits, predation, ecosystem roles, conservation, and references.

6. Gorilla/Species/WWF

   www.worldwildlife.org/species/gorilla

   Ecology, threats, disease, ecotourism, preserving habitat, and more.

10 | Vertebrate Zoogeography

We must protect the forests for our children, grandchildren and children yet to be born. We must protect the forests for those who can't speak for themselves such as the birds, animals, fish and trees.

Native American Words of Wisdom, 2019

INTRODUCTION

The study of the geographic distribution of animals and the mutual influence of the environment and animals on each other is known as **zoogeography**. Because animals and plants of a community are interdependent ecologically, zoogeographic studies usually must further include a consideration of plants. Zoogeography also attempts to explain how species have come to be distributed as they are, which requires a knowledge of historical changes in climates, geography, and the distributions of species. Thus, zoogeography is related intimately to both ecology and geology. Four major branches of zoogeographic research are recognized: faunal, comparative, historical, and ecological.

Faunal zoogeography includes the preparation of faunal lists of animal populations for specific areas and forms the basis on which all other zoogeographic research relies. **Comparative zoogeography** attempts to classify the distribution of animals according to their external features. When fauna from different areas are compared, their distribution may not be consistent with the present geologic and geographic divisions of the Earth. For example, amphibians, reptiles, and birds of North Africa are much more closely related to forms in southern Europe than to those in Africa south of the Sahara. The fauna of southern Asia is more closely related to that of trans-Saharan Africa than it is to the fauna of Asia north of the Himalayas. Many groups of North American birds and mammals differ more widely from their corresponding groups in Central and South America than from those in Europe and northern Asia. Homologies among such comparable faunas are based on genetic relationships and common evolutionary origins.

A few species of vertebrates have natural ranges that are virtually cosmopolitan in distribution: mallards (*Anas platyrhynchos*), ospreys (*Pandion haliaetus*), common terns (*Sterna hirundo*), bank swallows (*Riparia riparia*), sperm whales (*Physeter catodon*), and blue whales (*Balaenoptera musculus*). The ranges of others, like starlings (*Sturnus vulgaris*), rock doves (*Columba livia*), house sparrows (*Passer domesticus*), house mice (*Mus musculus*), and Norway rats (*Rattus norvegicus*), which now occur in all but the coldest parts of all of the continents, are the result of human-induced dispersal.

The geographic range of most species, however, is limited in varying degrees to a particular geographic region. In addition, species are restricted to specific communities or groups of communities, with some being very restricted, a situation called being **narrowly endemic**. For example, the giant panda (*Ailuropoda melanoleuca*) inhabits only the few remaining bamboo forests of China, tuataras (*Sphenodon*) are found only on islands along the coast of New Zealand, the koala (*Phascolarctos cinereus*) is restricted to small areas of eastern Australia, and the entire family Todidae (small birds related to kingfishers) is restricted to Caribbean islands.

The distribution of a vertebrate species can be expressed in terms of its current geographic range, its geologic range, and its ecological distribution. The **geographic range** designates the specific land or water area where the vertebrate currently occurs. Taxa that occur in widely separated localities are said to have a **disjunct** distribution. The family Camelidae, for example, has representatives in Asia (camels) and in South America (llamas and their relatives). The **geologic range** refers to a taxon’s past and present distribution in time. A description of the **ecological distribution** provides information on the major biotic communities of which the species is a member.

Closely related species of animals will generally have adjacent ranges; it is assumed that the area in which they evolved from their common ancestor was the common origin of their current distribution. Two major factors affect the subsequent distribution of a new species: the means of dispersal available to an animal and the existing physical and biotic barriers to such dispersal. External barriers affect the different groups of vertebrates in diverse ways. Aquatic animals are limited in their dispersal by land, and terrestrial animals are often limited by water. Many land animals are unable to cross mountain ranges, whereas flying species are the least affected by barriers of any kind. Barriers are always relative, and a barrier for one species may well be a main dispersal route for another. Water might be a barrier for a terrestrial species, but normally not for a fish. Topographic barriers, like mountains, may form more effective barriers in the tropics than in temperate regions because tropical species are not as well adapted for the cooler temperatures present at higher elevations (Janzen, 1967). Climate, the lack of suitable food, the presence of more successful competitors, or the presence of enemies may present barriers to the dispersal of any group.

Barriers may be of three types: physical, climatic, or biological. Land, water, elevation, soil types, and topography are examples of **physical barriers**. Certain types of physical barriers may serve as “psychological” barriers to some species. For example, some small mammals will not cross roads (even dirt roads), some neotropical birds will not cross open spaces, and some birds will not cross relatively narrow bodies of water. **Climatic barriers** include temperature, humidity, rainfall, and sunlight, whereas such things as lack of food and the presence of either predators or effective competitors represent **biological barriers**.

The means of dispersal for a species remain relatively unchanged through long periods of time; however, the position of barriers to dispersal becomes altered with geologic changes in the Earth’s surface. For example, many river courses have changed over time, new mountain ranges have arisen (while others have eroded), and formerly well-watered areas may now be desert.

Land connections (bridges) either currently exist or once existed between such areas as North America and Eurasia, North America and South America, and North Africa and southern Europe. The discovery of a 66-million-year-old marsupial tooth in the Netherlands provides fresh proof that a land bridge connected the North American and European continents during the age of dinosaurs (Martin et al., 2005). The upper molar belonged to *Maastrichtidelphys meurismeti*, a species formerly known only from Canada, Montana, Wyoming, and South Dakota. Some evidence exists for the presence of a land bridge across the Mozambique Channel between Africa and Madagascar (Anonymous, 1997d). Such a connection would help answer the question of how the ancestors of such unique mammals as lemurs, tenrecs, and fossas got to Madagascar. The appearance and disappearance of connections like these mean that formerly continuous ranges of related animals may be separated, or alternatively, regions may be united whose faunas were only distantly allied. The older the division between groups of vertebrates, the more times such changes of barriers probably will have occurred during their history.

The marsupials of Australia are thought to have migrated there some 70 Mya by way of land bridges from South America to Antarctica and across that continent to Australia (Fig. 10.1a, b). The fossilized remains of a marsupial belonging to the extinct family Polydolopidae were found in Late Eocene deposits on Seymour Island, off the northern Antarctic Peninsula (Woodburne and Zinsmeister, 1982, 1984). This discovery, the first land mammal in Antarctica, supports the hypothesis of an early dispersal of marsupials across the southern continents. Because the Australian continent was isolated from all others, and because no placental mammals were present, marsupials underwent extensive adaptive radiation without competition. Because they were filling niches similar to those filled in the rest of the world by placentals and were subject to similar selection pressures, they evolved striking convergent similarities to the placentals (Fig. 10.1c).

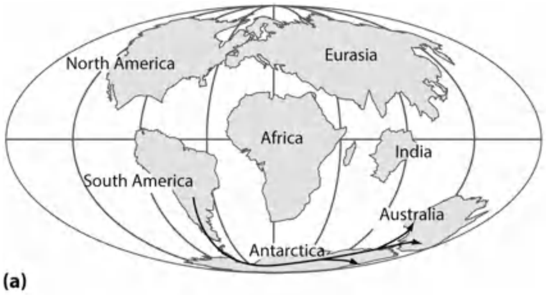
Historical zoogeography attempts to work out the development in geologic time of present-day distributions by studying the historical similarities of animal distribution. Studies of spatial and temporal distributions of organisms attempt to provide explanations for these distributions based on past events.

In contrast to historical zoogeography, **ecological zoogeography** investigates the analogies between animal communities in similar habitats. It looks at how animals adapt to the conditions of their native regions. It deals with present conditions, which are more easily subjected to analyses and testing.

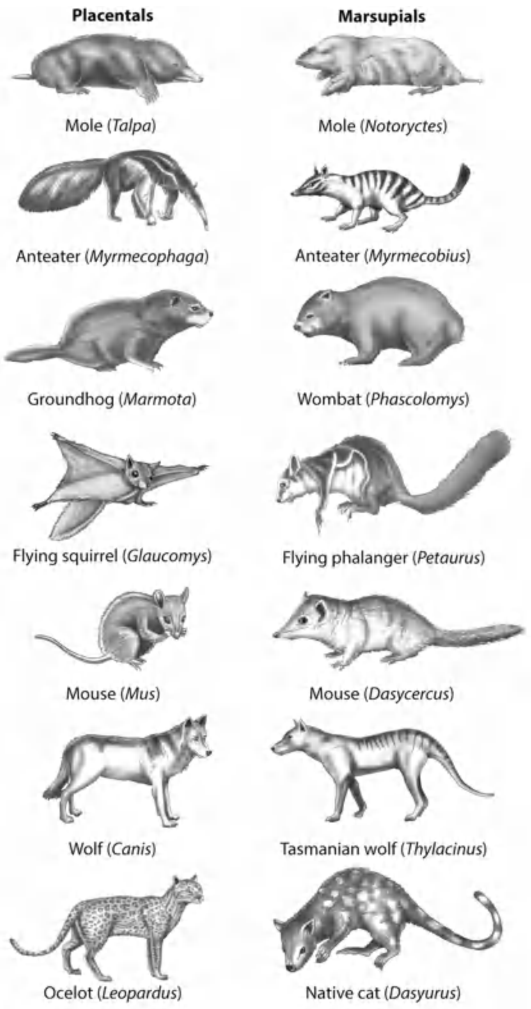
DISTRIBUTION

Distribution in time depends on continued reproduction, whereas distribution in space depends on the active or passive transport of animals to areas with suitable environments. Vertebrates have the ability to move from one place to another on their own. Some, like salamanders and frogs, usually move only short distances; others, like geese, ducks, plovers (Fig. 10.2), warblers, hummingbirds, bats, and whales, may move thousands of miles twice a year in order to reach suitable living or breeding conditions.

Some species may be transported passively by storms or by rafting on floating islands of vegetation (Fig. 10.3). Most accounts of rafting have recorded instances of single vertebrates (summarized by King, 1962; Hardy, 1982). However, Boyd (1962) reported multiple individuals of toads (*Bufo* [*Anaxyrus*] *woodhousii fowleri*) in Mississippi. Censky et al. (1998) documented the overwater dispersal of a group of large vertebrates (green iguanas, *Iguana iguana*) swimming ashore to an island, in the Lesser Antilles in the Caribbean, that previously had no iguanas. Oceanic dispersal via rafting has also been proposed as the method by which New World monkeys reached South America from Africa (Prothero, 2015; Bond et al., 2015), a possible explanation as to how lemurs reached Madagascar (Kappeler, 2000), and a possible method by which iguanas and boine snakes reached the Pacific islands of Fiji and Tonga (Noonan and Sites, 2010). Longrich et al. (2015) suggest multiple oceanic dispersal events for the early distribution of worm lizards (Amphisbaenia). The distribution of vertebrates has been, and currently is, influenced by geography, geology, climate, ecology, and human activity.

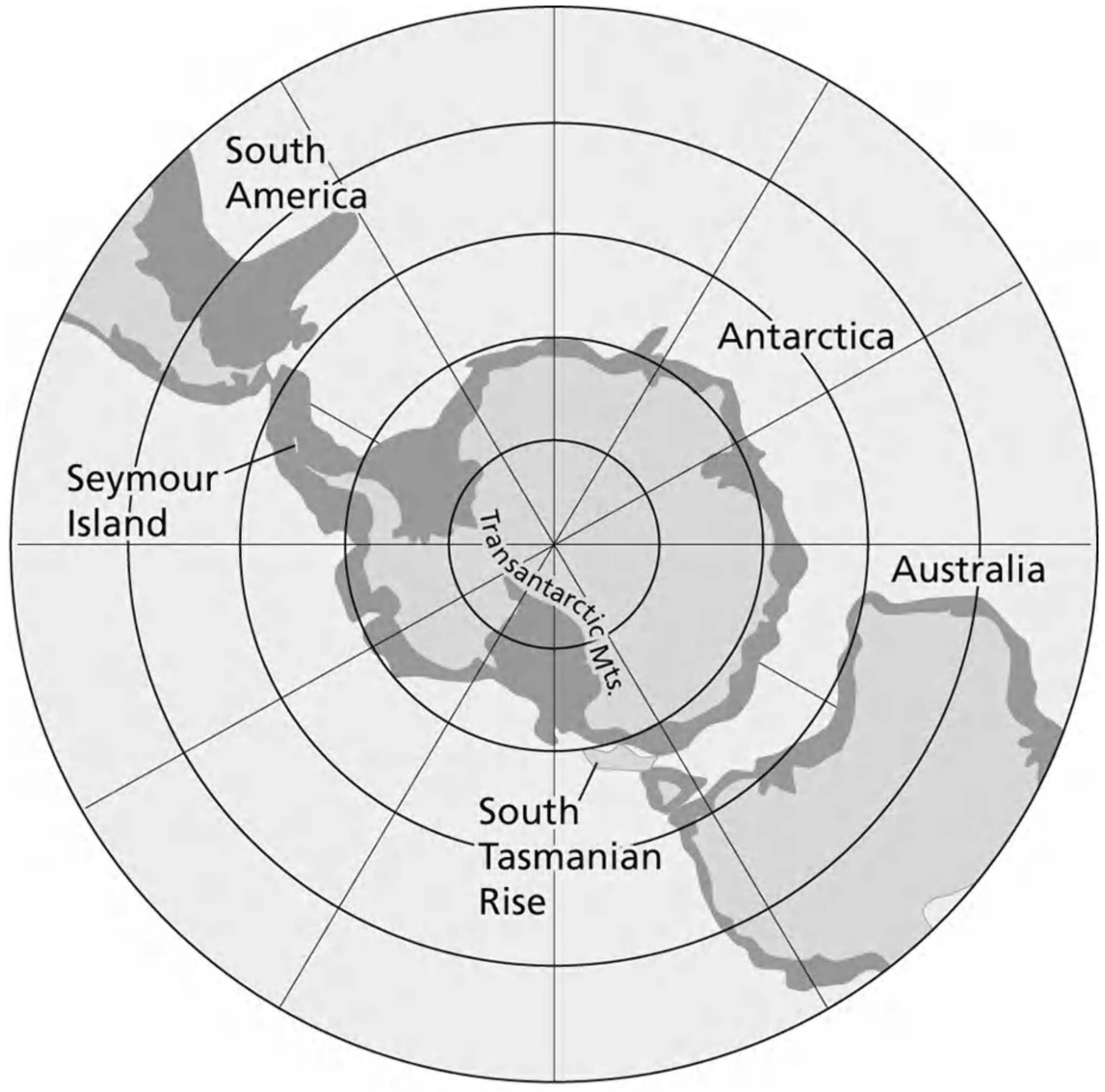


(a)



Mole (*Talpa*)
Mole (*Notoryctes*)
Anteater (*Myrmecophaga*)
Anteater (*Myrmecobius*)
Groundhog (*Marmota*)
Wombat (*Phascolomys*)
Flying squirrel (*Glaucomys*)
Flying phalanger (*Petaurus*)
Mouse (*Mus*)
Mouse (*Dasycercus*)
Wolf (*Canis*)
Tasmanian wolf (*Thylacinus*)
Ocelot (*Leopardus*)
Native cat (*Dasyurus*)

(c)



(b)

Figure 10.1. (*a*) Marsupials are thought to have emigrated from South America across Antarctica (arrow) by way of land bridges some 70 Mya. (*b*) Dark shading indicates continental shelves less than 2,000 m (6,500 ft.) deep. After they reached Australia, the continent became isolated from all other continents. Because they encountered no competition from placental mammals, marsupials underwent extensive adaptive radiation. (*c*) Australian marsupial mammals evolved in parallel with placental mammals on other continents.

Geographic Distribution

Although a few species are almost cosmopolitan in distribution, the ranges of most species are restricted to a particular geographic region. A. R. Wallace (1876) and other early biogeographers recognized that many taxa have more or less congruent distributions. In an attempt to divide the land masses into a classification reflecting the affinities of the terrestrial flora and fauna, Wallace recognized six major **biogeographic regions**, each of which possessed a characteristic fauna (Fig. 10.4). These regions were named the Palearctic, Nearctic, Oriental, Neotropical, Ethiopian, and Australian. This system is still widely accepted today. Wallace's system of classification was similar to the classification proposed for birds in 1856 by Sclater.

Faunal regions do not always correspond to continental boundaries. They sometimes meet along a major barrier to dispersal, like the Sahara Desert or the Himalayan Mountains.

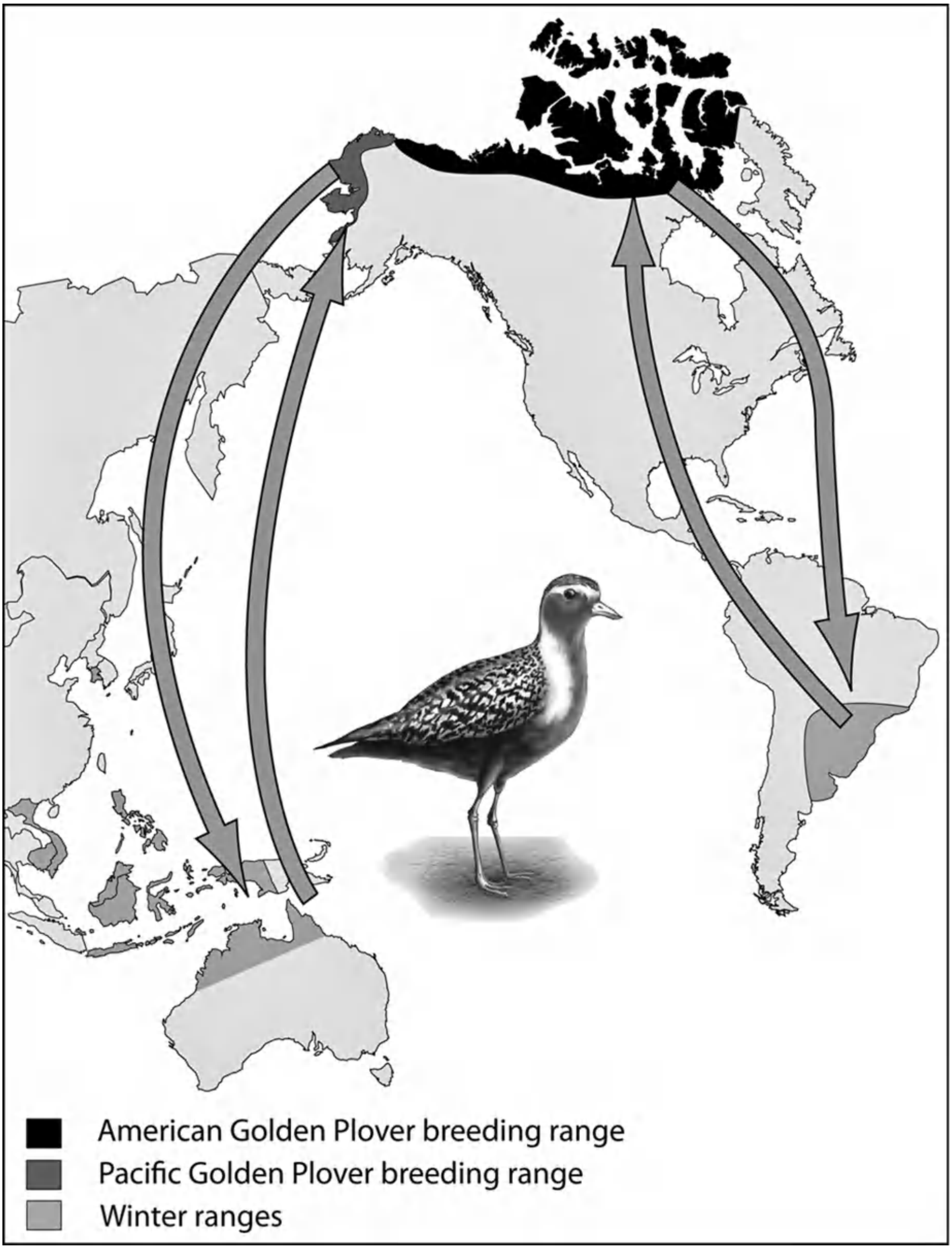


Figure 10.2. Distribution and migration of the American golden plover (*Pluvialis dominica*). Adult American golden plovers migrate across northeastern Canada and then by a nonstop flight reach South America. In the spring, they return by way of the Mississippi Valley. Their entire route forms a great ellipse. The Pacific golden plover (*Pluvialis fulva*) breeds in Alaska and makes a nonstop flight across the Pacific Ocean to southeastern Asia, Australia, and various Pacific islands. It returns in the spring along the same route.

Palearctic Region and Nearctic Region (Holarctic)

This region encompasses most of the Northern Hemisphere in both the Old World and the New World. Although the two continents have been connected many times and have many species in common, they are usually separated by vertebrate zoologists (but not by many others, e.g., botanists) into two subregions. The Palearctic Region comprises all of Eurasia (Europe and Asia) not included in the Oriental Region and northern Africa, whereas the Nearctic Region consists of North America down to the southern edge of the Mexican plateau (central Mexico). Because a number of kinds of plants and animals occur in both the Nearctic and Palearctic, the term *Holarctic* is frequently used. This term implies circumpolar distribution. Species that occur in both subregions include snowy owls (*Nyctea scandiaca*), northern harriers (*Circus cyaneus*), lemmings (*Lemmus* sp.), Arctic foxes (*Alopex lagopus*), polar bears (*Ursus maritimus*), and caribou (*Rangifer tarandus*).

Figure 10.3. Rafting is thought to be a means of dispersal for some vertebrate species. Entire trees, portions of trees, or clumps of vegetation may serve as rafts. Numerous islands of vegetation can be seen floating down the Guayas River toward the Gulf of Guayaquil in Ecuador after heavy rains in the Andes. These islands may harbor many forms of life. The native dugout canoe (*center*) gives some idea of the size of these floating masses.

Oriental Region

The portion of Asia south of the Himalayan Mountains comprises the Oriental Region. This includes the Indian subcontinent, Southeast Asia, most of Indonesia, and the Philippines. Unique species include reticulated and Indian pythons (*Python reticulatus* and *P. molurus*), king cobras (*Ophiophagus hannah*), big-headed turtles (*Platysternon megacephalum*), pea-fowl (*Pavo*), tarsiers (*Tarsier*), gibbons (*Hylobates*), orangutans (*Pongo pygmaeus*), Indian elephants (*Elephas maximus*), Javan and Indian rhinoceroses (*Rhinoceros sondaicus* and *R. unicornis*), and water buffalo (*Bubalus*).

Neotropical Region

This region has two distinct zoogeographic subregions: mainland South America and Central America. The Central American subregion has been alternately submerged and exposed and has served as a major corridor between the Neotropical and Nearctic regions. The Neotropical Region contains such unique vertebrates as the South American lungfish (Lepidosirenidae), aquatic caecilians (Typhlonectidae), poison dart frogs (*Dendrobates* and *Phyllobates*), anacondas (*Eunectes murinus*), rheas (*Rhea*), toucans (*Ramphastidae*), llamas and alpacas (*Lama*), giant anteaters (*Myrmecophaga*, *Tamandua*, and *Cyclopes*), howler monkeys (*Alouatta*), capybaras (*Hydrochaeris*), and sloths (*Bradypus* and *Choloepus*).

Ethiopian Region

This is the region of Africa south of the Sahara Desert. Ostriches (*Struthio camelus*), guinea fowl (Numididae), zebras (*Equus*), African elephants (*Loxodonta africana* and *L. cyclotis*), gorillas (*Gorilla gorilla*), aardvarks (*Orycteropus afer*), giraffes (*Giraffa camelopardalis*), and hippopotamuses (*Hippopotamus amphibius*) are characteristic species. Fish zoogeographers consider the entire African continent to make up the African Region. This has been a rather stable tropical region with intermittent connections to other continents. It contains many ancient fishes, including the lungfishes (Protopteridae), the bichirs (Polypteridae), and the Osteoglossiformes (Moyle and Cech, 2004; Nelson, 2016).

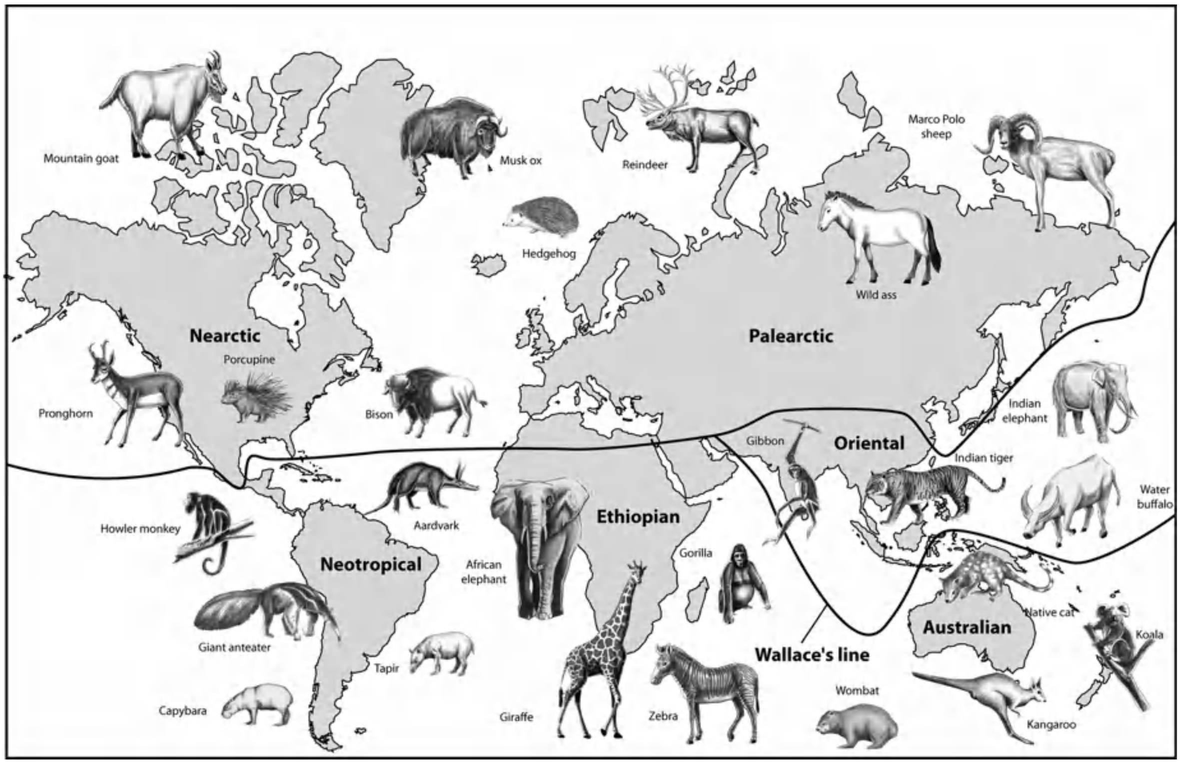


Figure 10.4. Present and past climates and dispersal pathways have largely been responsible for determining the six biogeographic regions of the world. Different native types of mammals inhabit those regions that were separated from each other during the Mesozoic era, a time when early mammals were diversifying. Although Australia and Southeast Asia lie in close proximity to one another, their faunas are quite different because these regions have always been separated. This separation has been recognized by a boundary known as Wallace’s Line, which crosses through the island of Sulawesi.

Australian Region

The most distinct of the faunal regions is that of Australia, New Zealand, New Guinea, Tasmania, and surrounding islands. This region is separated from the Oriental Region by Wallace’s Line, an invisible line running through the ocean (see Fig. 10.4). The native mammalian fauna of the Australian Region consists of marsupials of diverse morphologies and ecological preferences. In addition, emus (*Dromiceius*), cassowaries (*Casuarius*), lyrebirds (*Menura*), and the egg-laying monotremes (duck-billed platypus [*Ornithorhynchus anatinus*], short-nosed echidna [*Tachyglossus aculeatus*], and long-nosed echidna [*Zaglossus bruijni*]) inhabit the region. No native placental species occur naturally, although many have been introduced. Only two fully freshwater species, both of ancient ancestry, occur here: the Australian lungfish (*Neoceratodus forsteri*) and the southern saratoga (*Scleropages leichardti*), an osteoglossid. The remainder of the native fish fauna is made up of diadromous or marine families (Moyle and Cech, 2004; Nelson, 2016).

Geologic Distribution

It is estimated that the Earth formed some 4.6 Bya (Futuyma, 1986). Prior to 2008, the oldest rocks discovered on Earth were dated at 3.85 billion years (Woese, 1981; Hayes, 1996; Witze, 2017a), with the earliest fossilized living organisms being marine microbes that were found in rock dated radioactively at 3.3 to 3.5 Bya from Western Australia. These microfossils are the remains of giant colonies of presumably photosynthetic bacteria.

A search for geochemical evidence of past biotic activity (preserved within minerals that are resistant to metamorphism) used ion-microprobe measurements of the carbon-isotope composition of carbonaceous inclusions in rock dating to 3.8 to 3.85 Bya (Mojzsis et al., 1996). These studies of rocks on Akilia, a tiny, barren island off the southwest coast of Greenland, yielded isotopically light carbonaceous inclusions, suggesting that life was present on Earth at least 3.8 Bya. These findings have been widely discussed and intensely scrutinized over the years (Eiler, 2007).

By measuring tiny variations in the chemical composition of the Nuvvuagittuq greenstone from Hudson Bay, O’Neil et al. (2008) were able to date various rock samples to between 3.8 and 4.28 Bya. Previously, the oldest piece of bedrock was the Acosta Gneiss in Canada’s Northwest Territories, which is 4.03 billion years old. Zircon grains found in Western Australia have been dated to 4.36 billion years, but these are individual materials, not intact sections of bedrock.

Since its inception, Earth has been undergoing continuous geological changes. Some of these processes, like volcanic eruptions and earthquakes, are evident and easily observed. In addition, the Earth’s crust consists of rigid, slablike plates about 100 km (62 mi.) thick that float on the underlying mantle. These plates are constantly in motion due to a process, known as seafloor spreading, in which material from the mantle arises along oceanic ridges and pushes the plates apart (Fig. 10.5). Where they converge, one plate may plunge beneath another, as occurred in Chile in February 2010, when the Nazca plate plunged beneath the South American plate, a process known as **subduction**. A powerful 7.2-magnitude earthquake struck Ecuador’s central coast on

April 17, 2016; two earthquakes measuring magnitudes 8.2 and 7.5 struck Mexico on September 9 and 19, 2017; and a magnitude 7.1 quake struck off Peru's coast on January 15, 2018. The magnitude 7.3 quake that struck Venezuela's northeastern coast on August 21, 2018, was the largest to strike Venezuela since 1900. Plates also may move laterally past one another along a fault (**strike-slip fault**), as happened in Haiti in January 2010, causing one of the most destructive earthquakes in human history. California's San Andreas fault is another example of a strike-slip fault. Two giant April 2012 earthquakes struck in the eastern Indian Ocean (magnitude 8.6 and 8.2). The first was the largest ever recorded in the middle of a tectonic plate, rather than at a plate's edges where most quakes happen. It was also the largest earthquake recorded along a strike-slip fault, and it was the most complex strike-slip rupture ever seen, breaking along at least four separate faults. The ultimate driver of Himalayan earthquakes is the slow-motion collision of the Indian subcontinent with mainland Asia, which is also pushing the mountains skyward. Some 15 km (9 mi.) below the surface, a nearly horizontal thrust fault marks the plane where the future Indian plate is plunging beneath southern Tibet at a rate of about 18 mm (0.75 in.) per year. This, together with the 2004 killer Sumatra quake (magnitude 9.1), two nearby great quakes in 2005 and 2007, two quakes in 2012, and a devastating magnitude 7.8 quake extending deep below the Himalayas in Nepal in April 2015, indicates that one great slab of Earth's crust, the Indo-Australian plate, is slowly fracturing into two (Shen, 2012). The two slabs are moving in different directions, so that millions of years from now, the Indo-Australian plate will split into an Indian plate and an Australian plate.

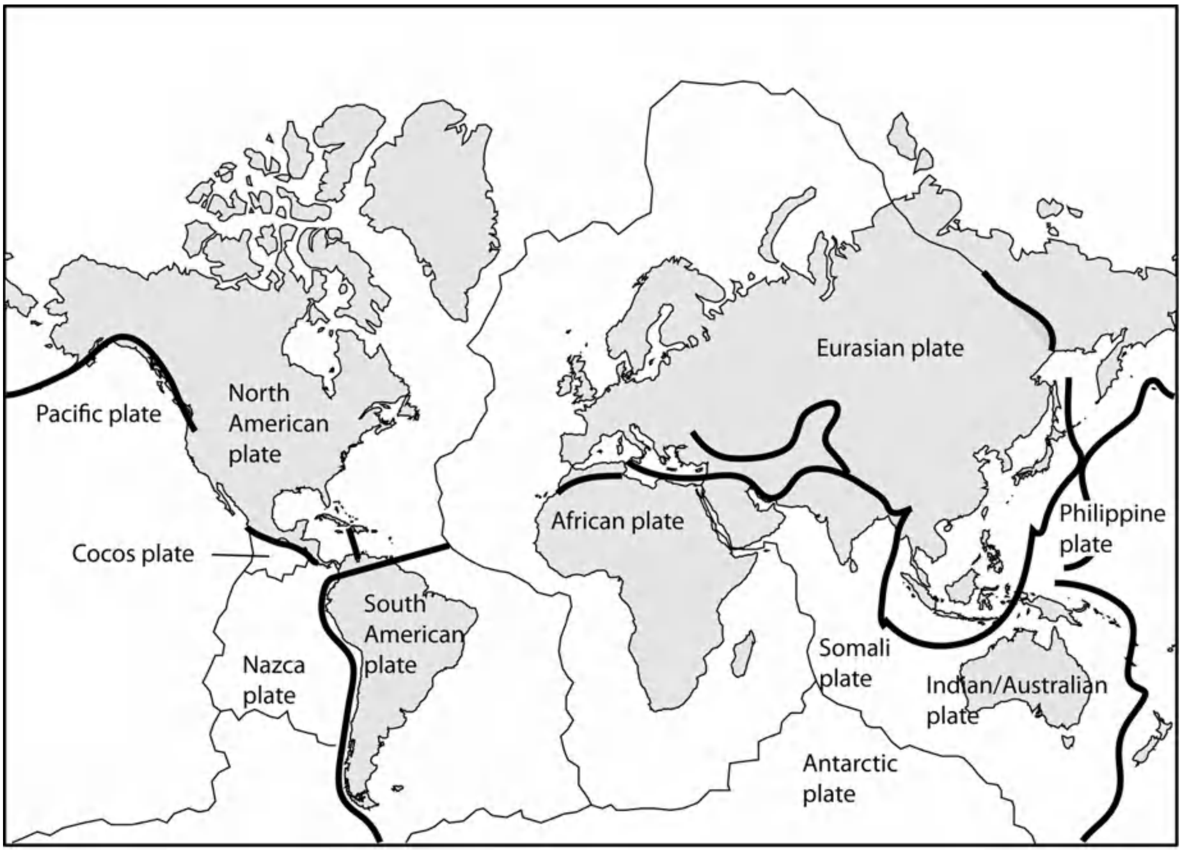


Figure 10.5. Major plates of the Earth’s crust. As the plates push against continental margins, they are often thrust beneath them. This thrusting causes the crumpling and upheavals that have created most of the Earth’s major mountain ranges. On a regional scale, many major plates are fractured or composed of numerous smaller plates. As these smaller plates shift, they create Earth tremors and earthquakes. The boundary between two plates is known as a fault. One well-known fault is the San Andreas Fault in California.

Because most plates move only a few centimeters a year, their movement is not easily observable and must be measured with sophisticated devices like lasers. The arrangement of these plates and their movements is known as **plate tectonics**. Although F. B. Taylor and Alfred Wegener first scientifically formulated the theory of continental drift in 1910 and 1912, the basic elements of the concept were suggested by Abraham Ortelius in 1596 (Romm, 1994). The movement of these plates and the continents has significantly affected climates, sea levels, and the geographic distribution of vertebrates throughout time (van den Ende et al., 2017).

Most paleogeologists agree that from Cambrian through Silurian times (420–600 Mya) six ancient continents probably existed. These primitive blocks of land were known as **Laurentia** (most of modern North America, Greenland, Scotland, and part of northwestern Asia); **Baltica** (central Europe and Scandinavia); **Kazakhstania** (central southern Asia); **Siberia** (northeastern Asia); **China** (China, Mongolia, and Indochina); and **Gondwana** (southeastern United States, South America, Africa, Saudi Arabia, Turkey, southern Europe, Iran, Tibet, India, Australia, and Antarctica) (Murphy and Nance, 1992).

Due to the continuing movement of these plates, the land masses collided to form supercontinents and then split apart to allow new oceans to form. Between 380 and 420 Mya, the continental land mass known as Laurentia collided with Baltica, forming a supercontinent known as **Laurasia**. Between 270 and 360 Mya, Laurasia collided with Gondwana, thereby forming the world continent **Pangaea** (Murphy and Nance, 1992). Siberia and China remained as subcontinents until the Late Triassic, when they also became part of Pangaea.

Pangaea, the result of multiple collisions that took place over many millions of years, consisted of a single large land mass extending northward along one face of the Earth from near the South Pole to the Arctic Circle (Fig. 10.6). A world ocean stretched from pole to pole and was twice as wide at the equator as the Pacific Ocean is at present (Futuyma, 1986). Pangaea was not static; it slowly drifted northward from Carboniferous through Triassic times, causing climatic changes in various areas.

During the Permian and Triassic, the eastern part of what is now North America was in contact with Europe and Africa, and South America was joined to Africa. During much of this period, the higher latitudes were relatively warm and moist, while the low and middle latitudes were probably much drier. Triassic deposits from Antarctica and Greenland, for example, have yielded specimens of large amphibians. Regional differences in rainfall and temperature, as well as the formation of the Appalachian Mountains, led to the development of specific floras and faunas.

During the Late Triassic, Pangaea began splitting apart into separate continents. This marked the beginning of the independent development of regional biotas. *Biota* is defined as the combined plants (flora) and animals (fauna) of a region. Animals depend on the plants growing in a particular region; thus, a biota is a group of complex interrelationships. Asia and Africa began separating from each other. This was followed in the Early Jurassic by the beginning of a westward movement of North America away from Africa and South America, although North America still was connected to Europe in the north. This separation, which began in the Jurassic, has continued. By the Late Jurassic, a narrow seaway had formed between North America and Eurasia, connecting the Arctic Ocean to the Tethys Sea, a broad seaway that separated Eurasia from Gondwana. During the Jurassic and Cretaceous, sea levels began to rise, resulting in the flooding of low-lying areas and the formation of shallow inland seas across much of western North America, Canada, and central Eurasia. The Sierra Nevada, Andes, Himalayas, and Rocky Mountains were formed during this period. Since then, the paths of drifting continents are fairly well understood from evidence in the seafloor. Because no part of the ocean floor is older than 200 million years, the earlier paths must be deduced from other evidence. This process of drifting and colliding has resulted in the current location of our continents and is continuing at the present time.

Is the Atlantic Ocean beginning to close?

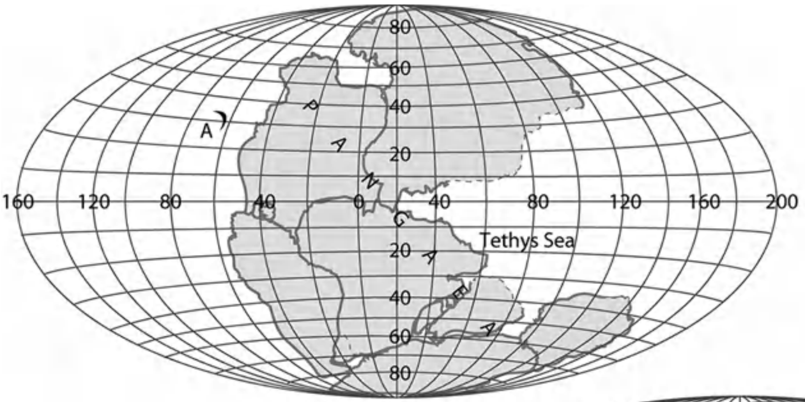
Dr. João Duarte, from Monash University's school of geosciences, has found evidence the ocean floor off the coast of Portugal and Spain is beginning to fracture, signaling the Atlantic is in the early stages of closing. The fracture is thought to be an embryonic subduction zone, where one of the Earth's tectonic plates moves beneath another. Duarte et al. suggest that it will take 20 million years for the fracture to become fully active, and about 220 million years for the reunion of Europe and North America to be complete.

Duarte et al., 2013

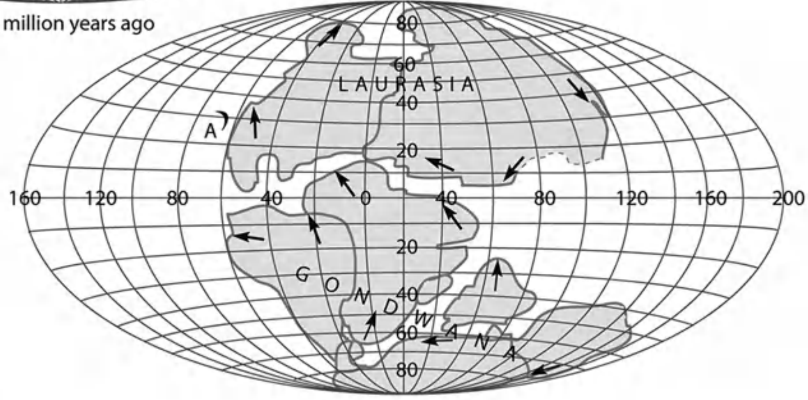
Gondwana, which began breaking up by mid-Cretaceous, split into Africa, South America (which remained in contact with Africa in the north), and a land mass consisting of Australia, Antarctica, and India. By the Late Cretaceous, India had broken free and was moving northward, eventually to collide with Asia, resulting in the formation of the Himalayan Mountains; South America had separated completely from Africa but was still narrowly joined in the south to the Antarctica-Australia land mass; and North America had moved so far to the west that it was separated fully from western Europe, but it had made contact with northeastern Asia to form the Bering land bridge in the region of Alaska and Siberia. (Bridge is somewhat of a misnomer, for the land mass ranged up to 1,600 km [994 mi.] in width.) A massive regression of **epicontinental seas** (seas covering portions of continents) in the Late Cretaceous exposed a great deal of land.

The Atlantic Ocean, which was much narrower during the Early Tertiary than at present, continues to expand due to the westward movement of the Americas away from the mid-oceanic ridge. During the Late Pliocene, the Panamerican isthmus (Central America) arose, connecting North and South America. The isthmus provided a corridor for the migration of animals between North and South America, forever changing the fauna of both continents (Fig. 10.7). It also blocked a current that once flowed west from Africa to Asia, thus dividing the marine biota of the eastern Pacific from that of the Caribbean.

The formation of the Panama land bridge has been associated with one of the biggest biological exchanges in Earth history as numerous species migrated from one continent to the other. However, the timing of formation of the land bridge is still much debated. Montes et al. (2015) propose that the Central American Seaway, which separated South and North America, closed about 15 to 13 Mya, more than 10 million years earlier than previously thought, with important implications for ocean circulation, climate, and biotic exchange.



200 million years ago



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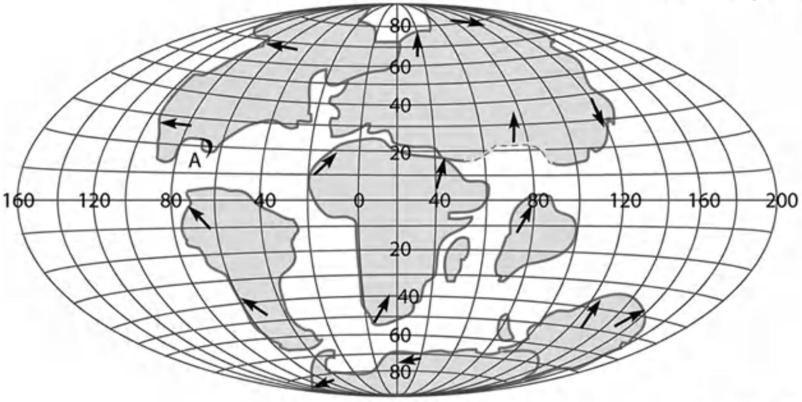
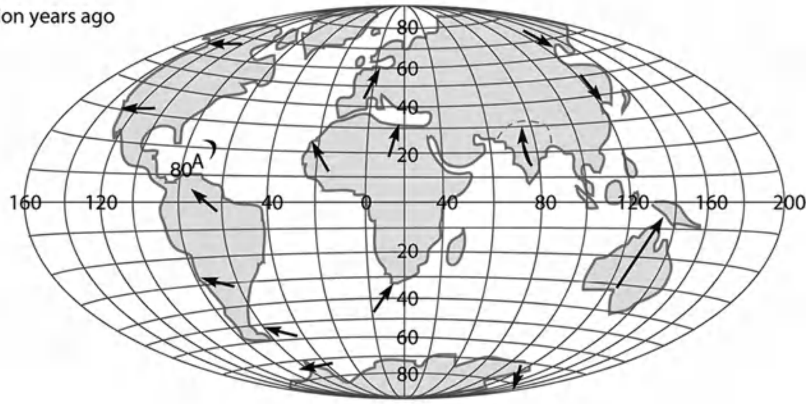


65 million years ago



Today

Figure 10.6. The current position of the continents is not where they have always been. The continents have drifted over the past 200 million years from an original single land mass (Pangaea) to their present positions. Pangaea separated into two supercontinents known as Laurasia and Gondwana, which later broke up into smaller continents. The arrows indicate vector

movements of the continents. The black crescent labeled “A” is a modern geographical reference point representing the Antilles arc in the West Indies.

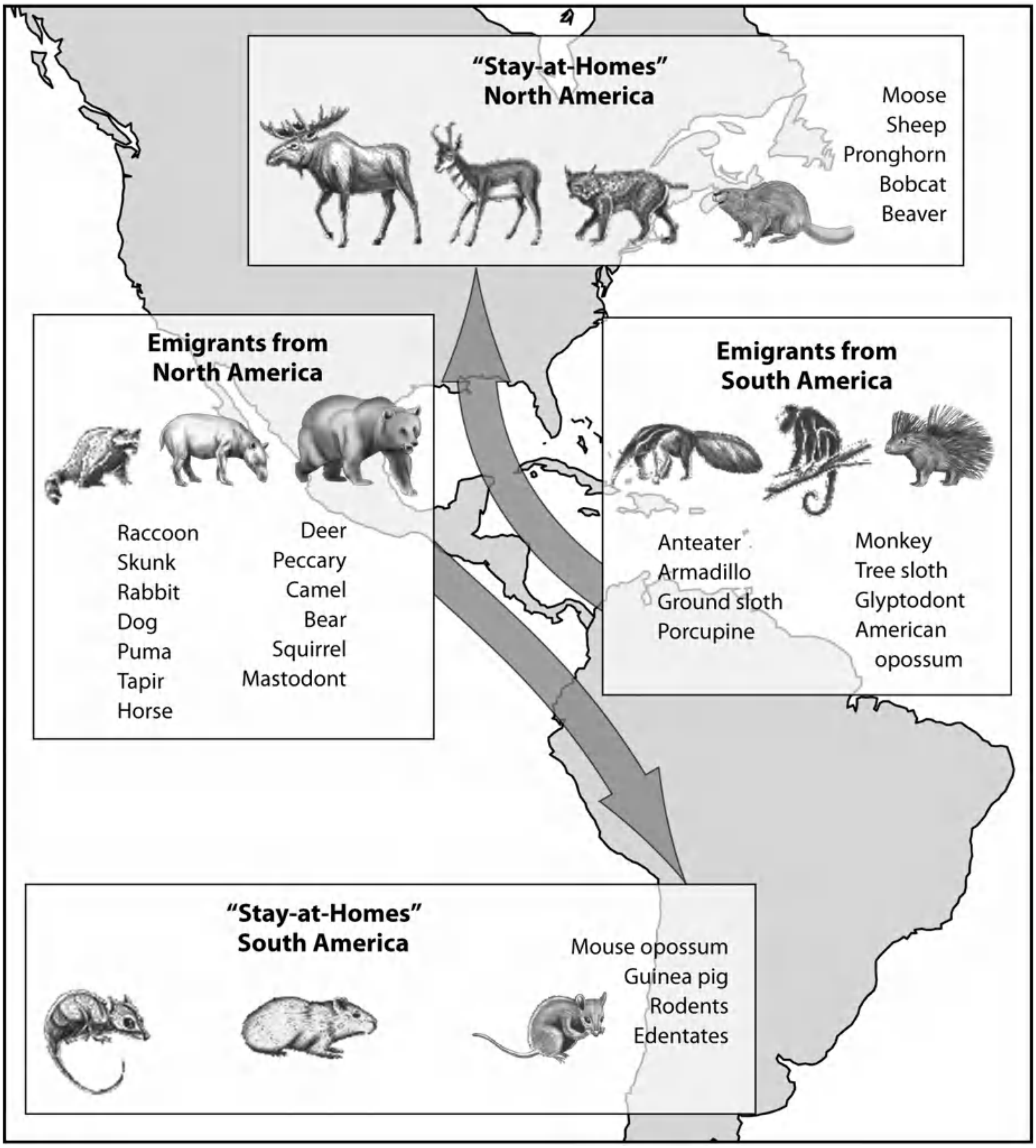


Figure 10.7. The Great American Interchange. The Plio-Pleistocene land bridge allowed the exchange of fauna between North America and South America. This bridge ended millions of years of isolation on the southern continent and changed forever the fauna of both continents.

Steven Stanley, a paleobiologist at Johns Hopkins University, has hypothesized that when the isthmus interrupted the flow of water between the Atlantic and Pacific oceans, it triggered an Ice Age that had a crucial impact on the evolution of hominids in Africa (Svitil, 1996). The dry trade winds that blow west off the Sahara Desert cause water to evaporate from the Atlantic, making it saltier as the water evaporates. Prior to the emergence of the isthmus of Panama, saltier Atlantic waters could mix with Pacific waters. After the emergence, such mixing could not occur, so that at present the salinity is low on the Pacific side but very high on the Atlantic side. The salty Atlantic water moves northward to the vicinity of Iceland, where it sinks to the ocean floor and moves southward to Antarctica. Formerly, the Atlantic water was not salty enough to sink, and it continued northward to the Arctic. This flow kept the Arctic relatively warm. After the isthmus formed and the saltier Atlantic water began to sink near Iceland, the Arctic region began to cool. Pack ice, which reflected the sun’s rays, formed and cooled the region even further. As the cold spread south, glaciers formed and the Ice Age began. The Ice Age—a long period of waxing and waning of ice sheets—caused Africa to become colder, windier, and drier. This caused rain forests to shrink and desert and grassland regions to expand (see Fig. 10.26). If *Australopithecus* was semi-arboreal, these changing conditions would have made it necessary to develop mechanisms for survival on the ground. Approximately 3 Mya, *Homo* appeared as a branch of *Australopithecus*. The climatic changes proposed by Stanley are supported by marine sediment cores drilled off the African coast.

Because the Pacific Ocean is flanked by subduction zones around the Ring of Fire (a major area in the basin of the Pacific Ocean where many earthquakes and volcanic eruptions occur), the Pacific Plate is shrinking over time. Some geologists predict that it will vanish entirely in the future, leaving North America and Asia to merge into the next supercontinent, Amasia (Witze, 2017b). Others have devised different possible paths to Amasia, such as the closing of the Arctic Ocean rather than the Pacific. Speculation is that such an event will occur about 250 million years from now.

When tectonic plates slide, sink, and shift the Earth’s continents to form large landmasses, or supercontinents, ocean basins open and close in tandem. As these basins change shape, they can strike forms that amplify and intensify their tides. Green et al. (2018) have proposed that simulations projected hundreds of millions of years into the future suggest the Earth is now in the nascent stage of a tidal energy maximum, where strong tides will persist for roughly 20 million years. The oceans will go through several tidal cycles as the next supercontinent forms over the next 250 million years.

Continental drift may account for the distribution of certain vertebrates like the ratite birds, which include the kiwis (*Apteryx australis*), African ostriches (Struthionidae), South American rheas (Rheidae) and tinamous (Tinamidae), and emus (Dromiceiidae) and cassowaries (Casuariidae) of the Australian region (Fig. 10.8). Some ornithologists argued against this, claiming that these birds had converged from different ancestors, and so had evolved independently, *in situ*. Evidence from morphology and from DNA hybridization has indicated that the ratites are likely monophyletic (Cracraft, 1974; Sibley and Ahlquist, 1990), and continental drift is now favored as the most plausible explanation for their current zoogeographic distribution.

Climatic Changes

The Earth has undergone a series of climatic shifts throughout its evolution. Periods of rain have alternated with periods of drought, and periods of cooler temperatures have alternated with periods of warmer temperatures. Changes in global temperature have caused sea levels to rise and fall and glaciations to occur. Falling ocean levels have permitted land (filter) bridges to appear in various parts of the world (Fig. 10.9). Land bridges, which permit an exchange of some species from one continent or area to another (hence the term *filter*), have served as major passageways for the dispersal of many vertebrates (see discussion in Chapter 16).

Glaciations have occurred several times during the history of the Earth, including the Late Precambrian, Carboniferous, Permian, and Pleistocene. A cooling trend began in the Early Tertiary. By Oligocene time, northern latitudes were considerably cooler and drier than they had been, and grasslands and deciduous forests had become widespread. In the Pleistocene, beginning about 1.7 Mya, the climate changed drastically. The mild climate of the polar and subpolar regions became much colder, polar ice caps formed, and glaciers spread and withdrew repeatedly over the northern portions of the northern continents and parts of western South America. Numerous minor glacial episodes and at least four major ones are known to have occurred. The most recent, called the **Wisconsin glaciation**, withdrew only a little more than 10,000 years ago (Fig. 10.10). During the glacial episodes, sea level dropped throughout the world by as much as 100 m (328 ft.) as water became locked up in ice caps, and the climate in tropical and subtropical areas became drier. During interglacial episodes, climates became warmer and wetter and sea level rose (Futuyma, 1986).

(a) Ostrich

(b) Rhea

(c) Emu

(d) Cassowary

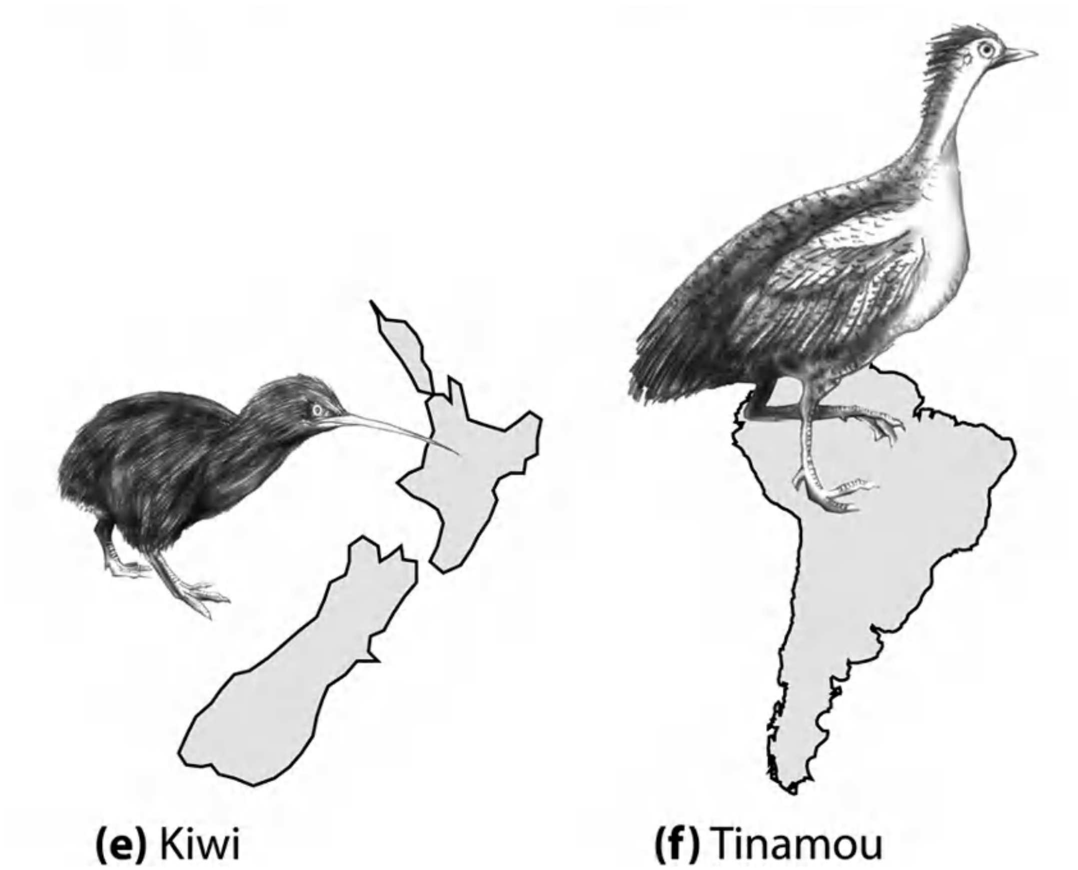


Figure 10.8. The living families of ratite birds: (*a*) Struthionidae (ostrich), Africa; (*b*) Rheidae (rhea), South America; (*c*) Dromiceiidae (emu), Australia; (*d*) Casuariidae (cassowary), Australia and New Guinea; (*e*) Apterygidae (kiwi), New Zealand; (*f*) Tinamidae (tinamou), tropical America. Despite their disjunct distribution, these birds (which, except for the tinamou, are flightless) are a monophyletic group. Continental drift is now favored as the most plausible explanation for their current zoogeographic distribution.

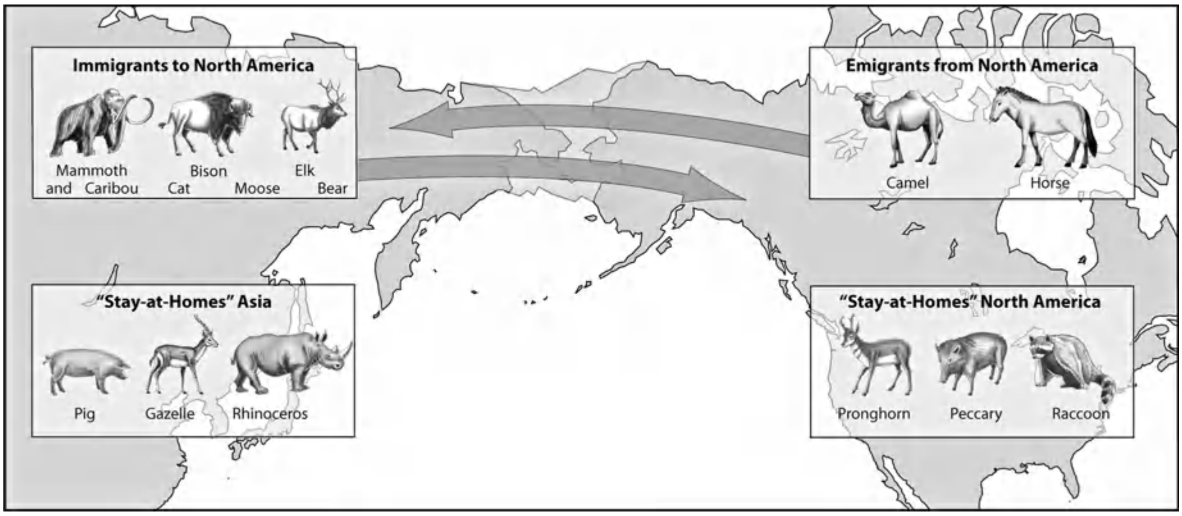


Figure 10.9. The Pleistocene filter bridge across the Bering Strait permitted the exchange of species between Asia and North America.

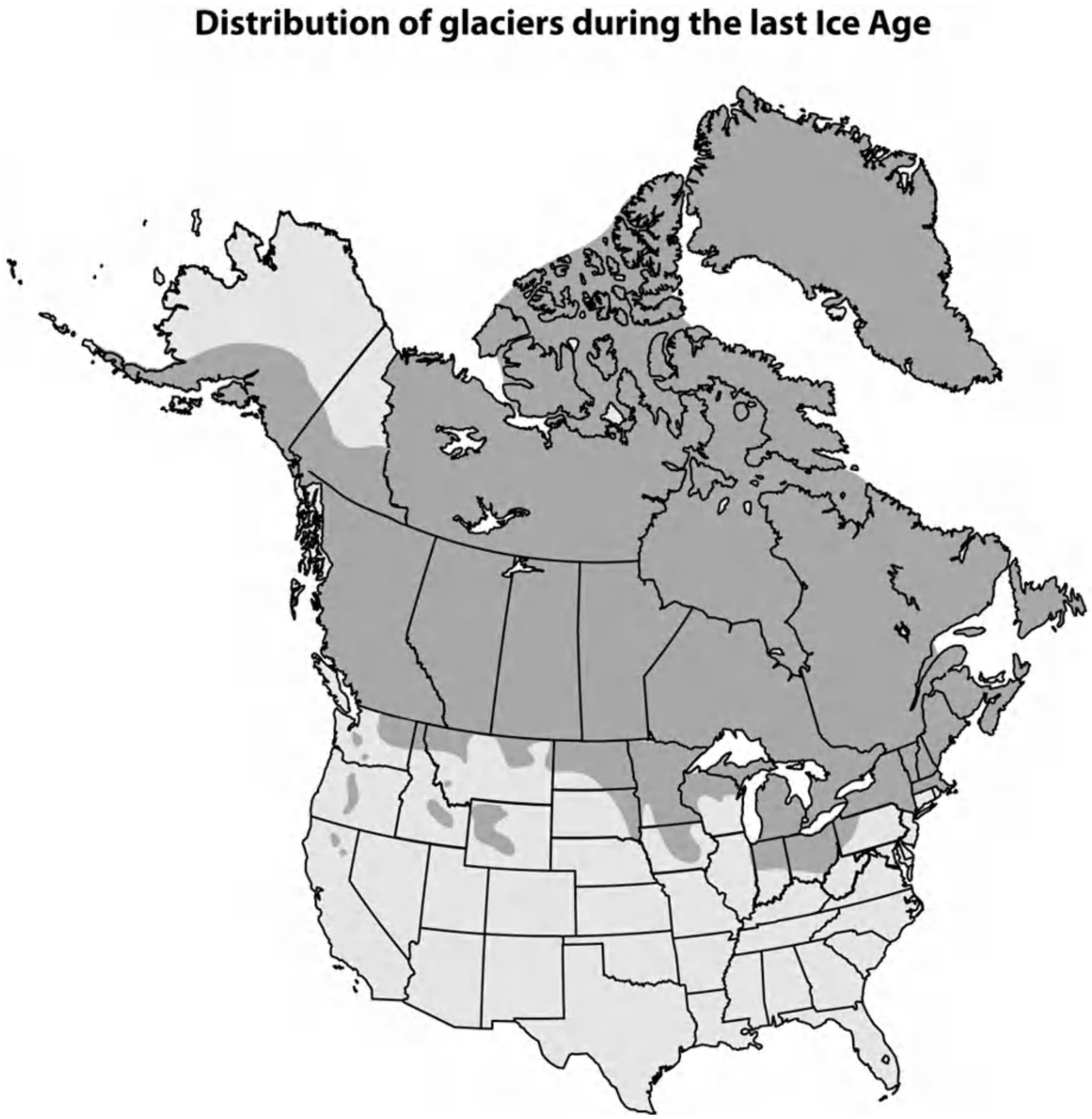


Figure 10.10. During the last Ice Age, some 15,000 to 20,000 years ago, extensive ice sheets formed over eastern Canada and moved south and west into northern portions of the United States. Other glaciers formed over Scandinavia and moved southward over northwestern Europe and over the arctic regions of Eurasia and North America. The ice sheets covering Greenland and Antarctica also grew larger. Glaciers locked up so much water in the form of ice that sea levels worldwide were lowered by approximately 100 m (328 ft.). We are now in a period of global warming. Temperatures are increasing, remaining glaciers are receding, and large pieces of ice are breaking free from Antarctica. If this warming trend continues, it will undoubtedly affect the worldwide distribution of plants and animals.

Many vertebrates ranged far north of their present distribution during the warm interglacial periods. For example, elephants, hippopotamuses, and lions once occurred in England (Futuyma, 1986). Fossils of large, 2.4 m (8 ft.) long, champosaurs, which are extinct crocodile-like reptiles, have been found at a site just 960 km (596 mi.) from the North Pole (Tarduno et al., 1998). Temperatures at the fossil site now routinely drop to –30°C (–22°F) in the winter, but when the champosaur lived there 86 to 92 Mya, temperatures rarely reached freezing and summertime readings of 26°C (79°F) were common. During glacial episodes, the climate throughout much of the world became cooler and drier, and parts of the Earth were covered by sheets of ice 2 to 3.5 km (1–2 mi.) thick (Kerr, 1994; Peltier, 1994). During these periods, the distributions of animal and plant species became more restricted and shifted toward the tropics.

During glacial maxima, biomes were shifted from 10° to as much as 20° latitude south from their present locations, but they still occupied the same relative positions north to south as they do today. North-south mountain ranges in North and South America permitted Arctic and Boreal taxa to extend their ranges far southward in cool situations (Brown and Gibson, 1983), whereas Europe’s east-west mountain ranges served as barriers to many species, and prevented their southward dispersal.

Many species could not adapt and became extinct. Those that could adapt shifted their ranges southward ahead of the advancing ice sheets, with many northern species finding suitable living conditions in the Appalachian and Rocky Mountain ranges (Fig. 10.11). After glaciers receded, many of these populations reinvaded their original northern ranges. Some, however, remained at the higher elevations in the mountains far south of their ancestral ranges and were restricted to “refuges” or “refugia”—isolated local pockets of favorable habitat. Today, these species are known as **disjunct** forms and are usually uncommon in the southern parts of their ranges. Four-toed salamanders (*Hemidactylium scutatum*), wood frogs (*Rana sylvatica*), northern water shrews (*Sorex palustris*), and northern flying squirrels (*Glaucomys sabrinus*) (Fig. 10.12) are examples of species with disjunct distributions.

Figure 10.11. Spruce-fir forest on Clingmans Dome in Great Smoky Mountains National Park at an elevation of 1,830 m (6,000 ft.). Many disjunct species that are common in more northern areas find suitable habitat at high-elevation sites as far south as Tennessee and North Carolina.

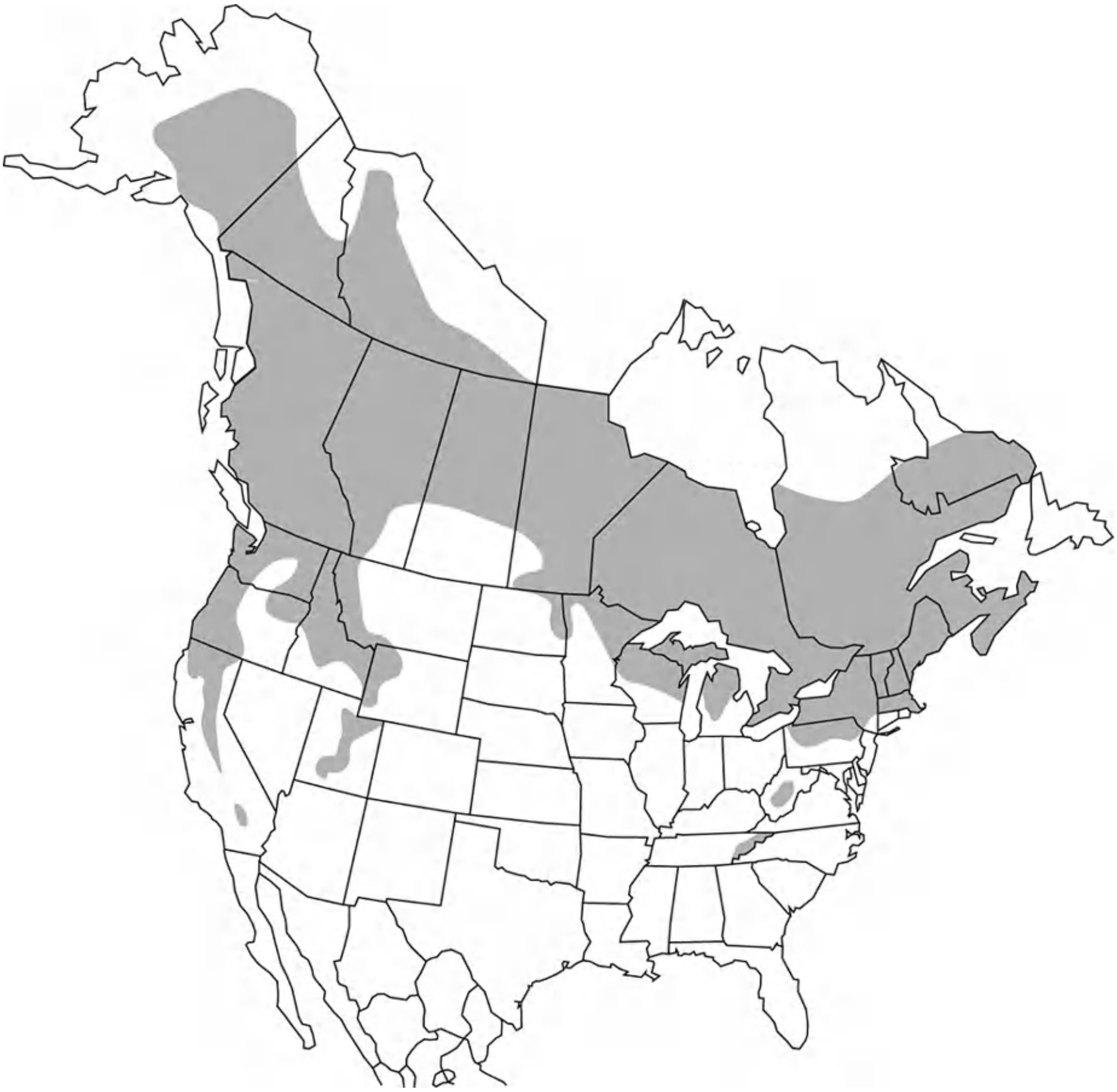


Figure 10.12. Present distribution of the northern flying squirrel (*Glaucomys sabrinus*). The southern extension of the range of this species along the Appalachian Mountains in the east and the Rocky Mountains in the west consists of disjunct populations.

For many years, biologists thought that tropical climates remained virtually unchanged while the great ice sheets of North America and Europe waxed and waned through the Pleistocene. Rain forests were once thought to have continuously clothed South America’s equatorial lowlands since its Cretaceous separation from Africa about 80 Mya. Current evidence, however, suggests that the Amazon may have been quite a bit drier and that the rain forest may, at times, have been segmented and was therefore much smaller (Schneider, 1996). Snow lines, even at equatorial latitudes, were substantially lower during Ice Ages. During nearly 2 million years of the Quaternary period, as glacial climates became more zonal and more extreme, savannas expanded, forcing rain forests into refugia. Savanna versus rain forest dominance oscillated as semiarid glacial epochs alternated with humid interglacials at least three times during the last 100,000 years. As forested areas were reduced to isolated patches, they became refuges for populations of tropical plants and animals. Following the next wetter episode, forest patches expanded and coalesced to cover large areas of tropical forest. Formerly isolated animal populations, which had reached various degrees of genetic divergence in their refugia, followed the spread of the forest. Some had become full species, whereas others had reached the level of subspecies. Thus, geologists and biologists now have documented a dynamic evolutionary history to explain the rich neotropical fauna and flora (Vanzolini, 1973).

Ecological Distribution

Basic environmental factors affecting a species' existence include water, salinity, humidity, temperature, light, oxygen, pressure, and food. Each of these factors has upper and lower limiting values for each species of vertebrate. If the tolerance ranges (within which the species exists) are extensive, the species can live in a variety of habitats. If the limits within which the species can exist are narrow, it will be limited to one or a few types of environments.

Three major ecological environments are recognized. These are marine, freshwater, and terrestrial environments.

Marine Environment

The marine environment is the largest. It consists of the oceans, seas, and bays, and it covers 70 percent of the Earth's surface. Oceans form a single vast, interconnected water mass only partially separated into divisions by the continents. The unbroken connection of the oceans and the continuous diffusion of seawater by means of currents, tides, and storms result in a *general* equality in the composition and amount of the substances dissolved in seawater. Although temperature varies, this widespread uniformity of conditions is accompanied by an extremely wide distribution of many marine species of animals.

Ocean depth varies from intertidal zones, which are covered by water only part of the time, to depths of 10.8 km (6.25 mi.). Water temperature varies from 32°C (90°F) in the tropics to –2.2°C (28°F) in the Arctic. Even though this worldwide range is great, water temperature in any given area rarely fluctuates more than 5°C (9°F). Dissolved salts are relatively constant in concentration (approximately 35 parts per 1,000), whereas dissolved gases like oxygen, carbon dioxide, and nitrogen vary with temperature and depth.

Based on the penetration of sunlight, the sea can be divided into two vertical zones: **photic** and **aphotic** (Fig. 10.13). The depth of the photic zone increases from coastal waters, where light rarely penetrates more than 30 m (98.5 ft.) because of organisms and inanimate particles suspended in the water, to the open ocean, where it may extend to a depth of 100 m (328 ft.) or more (Brown and Gibson, 1983). Light penetration is also affected by surface motion. Most producer organisms inhabit the upper 150 m (492 ft.) of water, but traces of light can be detected at a depth of 1,000 m (3,281 ft.) in the open ocean in the subtropical zone by means of photographic plates (Allee and Schmidt, 1951). The wavelengths of ordinary light are differentially absorbed by water, but below 1,000 m (3,281 ft.) there is permanent darkness. Pressure increases at the rate of 1 atmosphere (14.7 pounds per square inch) for every 10 m (33 ft.) depth (Riedman, 1990), so that organisms living in deeper parts of the ocean are exposed to great pressures. At a depth of 600 m (1,969 ft.), for example, the underwater pressure is equivalent to that of about 60 atmospheres, or 60 times the pressure at the surface.

The marine environment is divided into **pelagic** (open waters) and **benthic** (ocean floor) regions (see Fig. 10.13). Two groups of pelagic organisms are recognized: plankton and nekton. **Plankton** are the mostly passive floating plants, called **phytoplankton**, and animals, called **zooplankton**, which move by means of wind, waves, and currents. Plankton serve as food for a variety of vertebrates of all sizes, including the blue whale (*Balaenoptera musculus*), the largest living animal. All free-swimming marine organisms are classed as **nekton**. Nekton include fishes, turtles, and marine mammals like sea otters, porpoises, manatees, and whales.

The pelagic region includes the **neritic zone** (above the continental shelf) and the **oceanic zone**, which extends outward from the continental shelf. The neritic zone has a much greater density of organisms because nutrients are more abundant and sunlight penetrates the shallower waters. Both producers and consumers are abundant.

The oceanic zone is further divided into the epipelagic, mesopelagic, bathypelagic, abyssopelagic, and hadopelagic zones (see Fig. 10.13). The **epipelagic zone** receives abundant sunlight. Phytoplankton and zooplankton are abundant and serve as the bases of food webs. The semidark **mesopelagic zone**, 200 to 1,000 m (656–3,281 ft.), is known as the twilight zone. Fishes are the primary vertebrate inhabitants there; cetaceans visit, but cannot live there.

The **bathypelagic zone**, 1,000 to 4,000 m (3,281–13,123 ft.), is inhabited by a lesser number of fishes—some of the latter have developed bioluminescent organs. This is an area of cold quiet water, permanent darkness, and increased pressure. The **abyssopelagic zone**, 3,000 to 6,000 m (9,843–19,685 ft.), comprises a region with an almost constant physical environment. It is continually dark, cold (4°C or 39°F), and virtually unchanging in chemical composition. Rattails (Macrouridae), brotulas (Ophidiidae), lumpfishes (Cyclopteridae), and batfishes (Ogcocephalidae) are representative of the benthic fish fauna inhabiting the abyssopelagic zone. Many are eel-like, are blind, and have well-developed cephalic lateral-line canals and senses of smell and touch. The area beyond 6,000 m (19,685 ft.) is known as the **hadopelagic zone**.

Two species of fish vie for the title of deepest living fish. The actual deepest living fish known (Ophidiidae, *Abyssobrotula galatheae*) is a blind, elongate fish that feeds on benthic invertebrates and lives at depths ranging from 3,100 to 8,370 m (almost 5 miles deep) in the Puerto Rico Trench (Nielsen et al., 2016) (Fig. 10.14). However, the Marianna snailfish (*Pseudoliparis swirei*), described in 2017, was taken at 7,966 m (26,135 ft.) in the Marianna Trench in the Pacific Ocean (Gerringer, et al., 2017). Video used by the researchers spotted some Marianna snailfish as deep as 8,098 m (26,569 ft.), and a Japanese research team spotted one at 8,178 m (26,830 ft.) (Mandelbaum, 2017; Welch, 2017). The fish have no scales, no big teeth, and are not bioluminescent.

The benthic division includes organisms that live on the floor of the continental shelf, on the continental slope, and on the abyssal plain. This includes the **intertidal** (littoral) **zones** that alternately are covered by water and exposed to air twice a day. The majority of benthic forms are invertebrates, and many serve as food for species of marine vertebrates. A few vertebrates, like flounders and sole, spend much of their time on the ocean floor.

Estuaries, salt marshes, rocky shores, and coral reefs are unique shallow-water marine communities. Estuaries (Fig. 10.15) contain brackish water, a mixture of fresh water and salt water, because they are located where rivers flow into the oceans. Estuaries trap the nutrients brought in from the sea by the tides and prevent the escape of nutrients carried by the rivers. These areas, which are particularly rich in larval shrimps, mollusks, and fishes, are often referred to as the "nurseries of the sea" because more than half of all marine fishes develop in the protective environment of estuaries (Moyle and Cech, 2004).

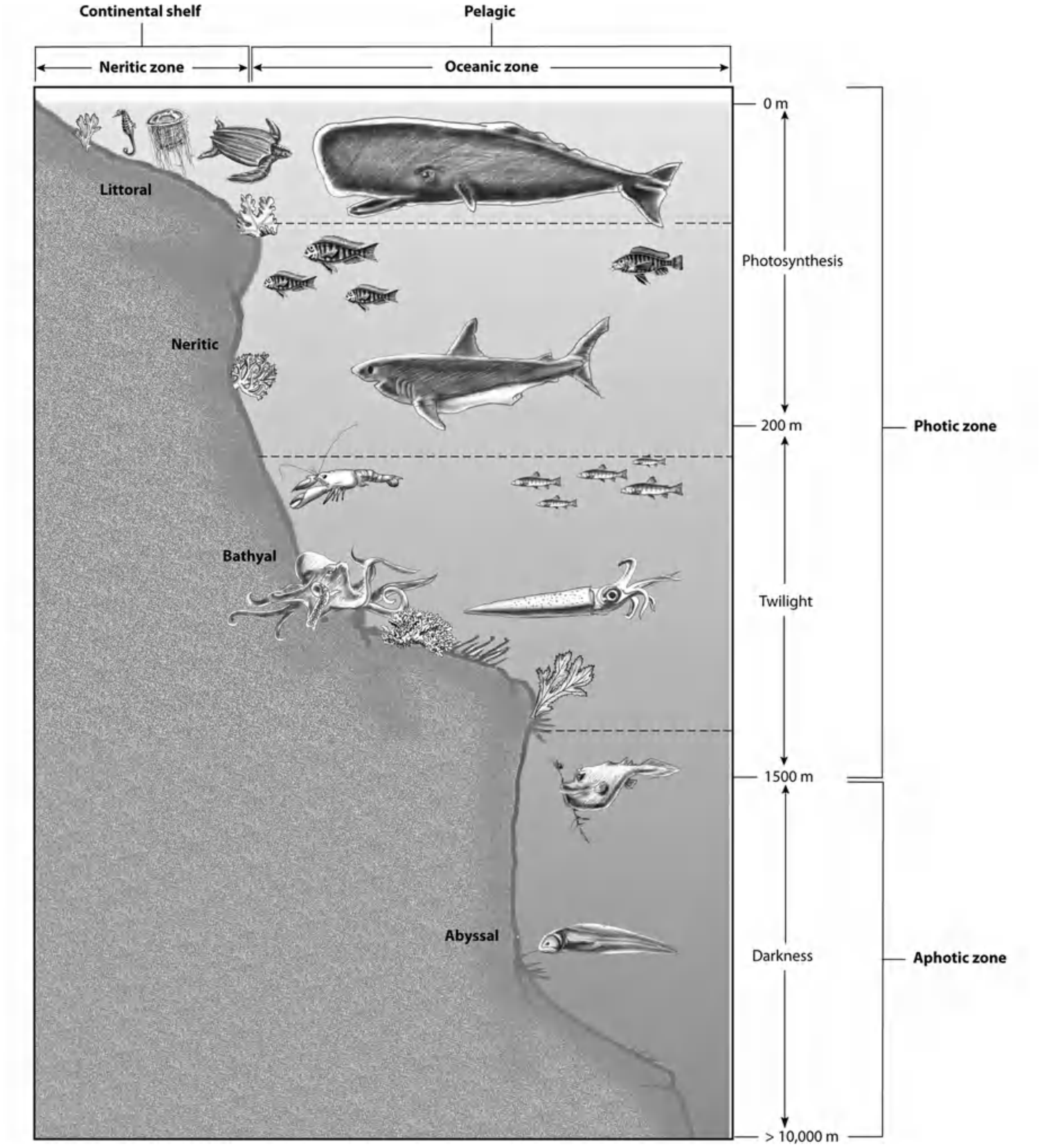


Figure 10.13. Based on the penetration of light, the oceans can be divided into two vertical zones: the photic zone is the area of light penetration, whereas the aphotic zone is the region of perpetual darkness. Each zone supports a distinct community of organisms.

Salt marshes, which are an important habitat for many vertebrates, are often adjacent to estuaries and contribute nutrients to them (Fig. 10.16). Rocky shores and sandy beaches serve as habitats for many forms of invertebrates that provide food for a wide variety of shorebirds. Coral reefs, which form in warm, shallow seas, provide a haven for many invertebrates as well as many fishes.

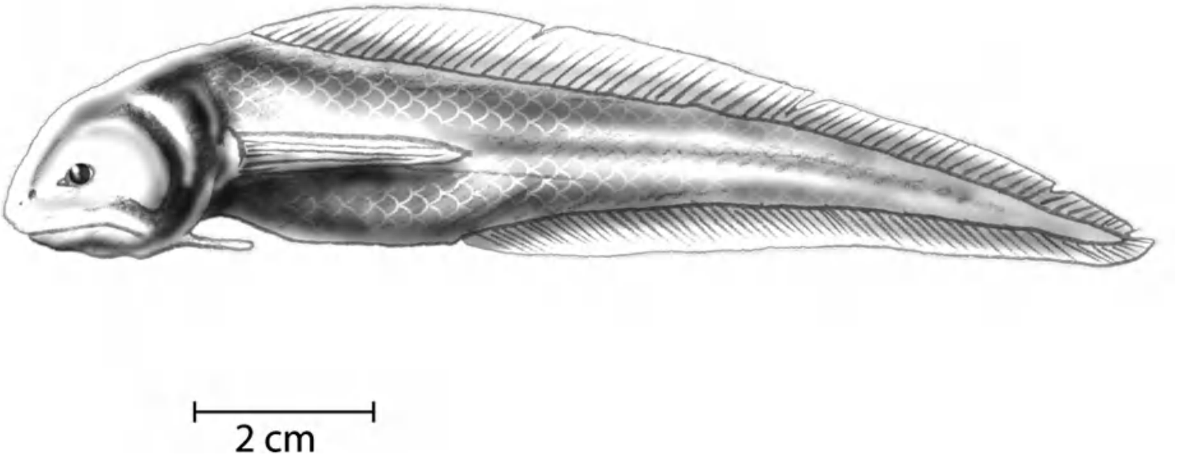


Figure 10.14. The deepest-living fish known, *Abyssobrotula galatheae*, is a blind, elongate fish that feeds on benthic invertebrates and lives at depths ranging from 3,100 to 8,370 m (10,170–27,460 ft.).

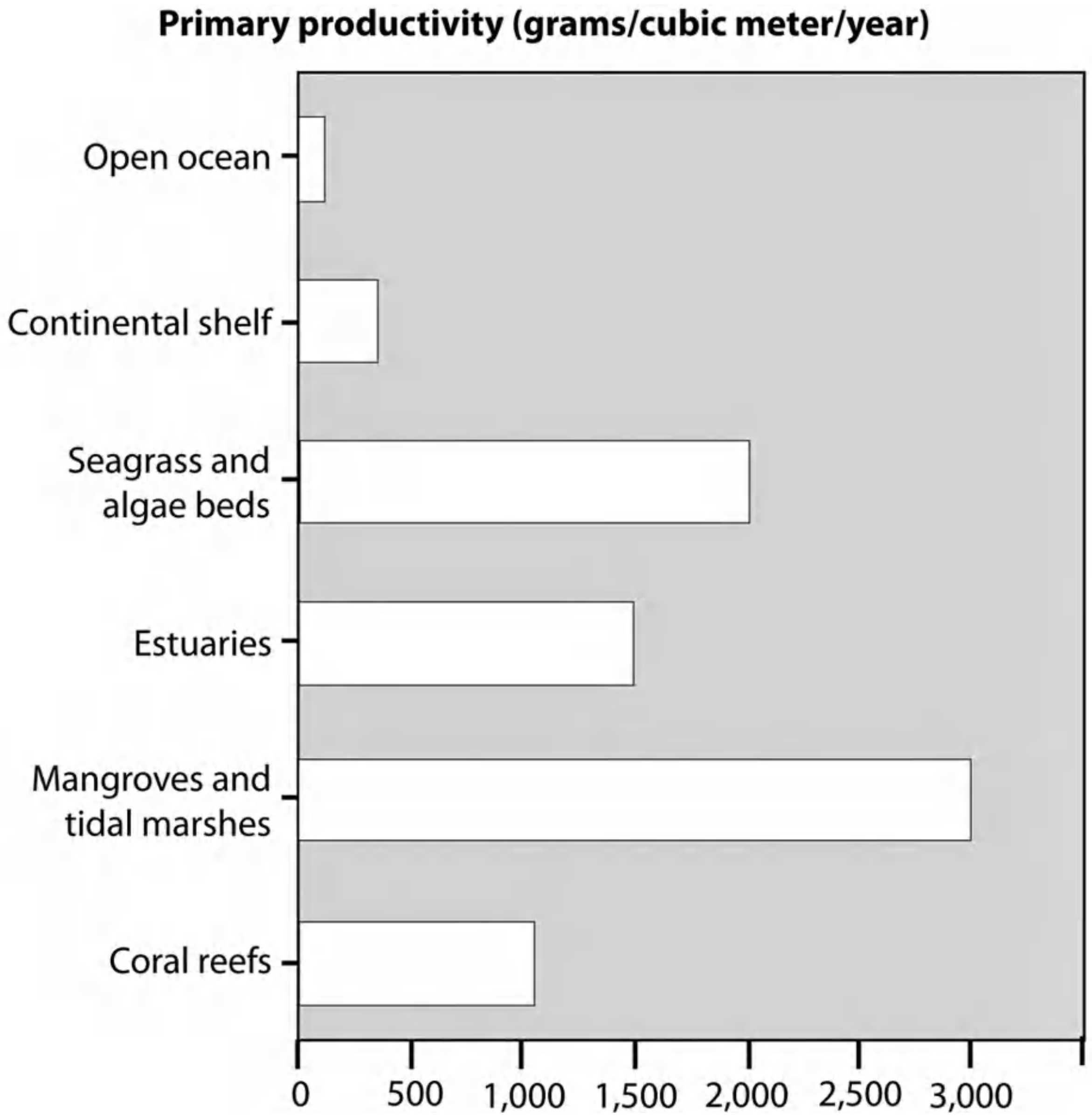


Figure 10.15. The biological productivity of mangroves, tidal marshes, seagrass and algae beds, estuaries, and coral reefs far surpasses that of all other marine environments. These areas not only provide protection for many marine vertebrates but are also rich in nutrients.

Freshwater Environment

This is the smallest of the three major environmental types (Fig. 10.17 a, b). It includes rain puddles, swamps, ponds, hot springs, lakes, streams, and rivers. Freshwater habitats may consist of flowing water, called a **lotic system**, or still water, called a **lentic system**, and range in temperature from below freezing to boiling. They may be clear or turbid, and the amount of dissolved oxygen may vary widely. Even the hardest fresh waters have salinities of less than 0.5 parts per 1,000. Maximum depth may range to 1,700 m (5,577 ft.) or more.

The degree of acidity or alkalinity, or pH, of the water reflects the carbon dioxide content as well as the presence of organic acids and pollution. The higher the pH of stream water, the richer natural waters generally are in carbonates, bicarbonates, and associated salts. Such streams support more abundant aquatic life and larger fish populations than streams with acid waters, which are generally low in nutrients.

Figure 10.16. New England salt marsh. An estuary is a partially enclosed coastal region where seawater mixes with nutrient-rich fresh water from rivers, streams, and runoff from the land. Estuaries and coastal marshes are vital feeding grounds and nurseries for many invertebrate and vertebrate species. The major producer in coastal salt marshes is cordgrass or marsh grass (*Spartina*). Broad, shallow estuaries include Chesapeake Bay, Mobile Bay, and San Francisco Bay. Estuaries in Alaska, British Columbia, and Norway are narrow and deep; in Norway, they are known as fjords. From Maryland to Texas, many coastal marshes lie behind narrow strips of sand known as barrier islands.

The variable temperature of a stream is ecologically important because temperature affects the stream community, influencing the presence or absence of cool-water and warm-water organisms. Streams shaded by trees, shrubs, and high banks will be cooler than those with large areas exposed to sunlight. Small, shallow streams tend to follow (but lag behind) air temperatures, warming and cooling with the seasons but rarely falling below freezing in winter. The constant churning and swirling of stream water over riffles and falls gives greater contact with the atmosphere; thus, the oxygen content of the water is high, often near the saturation point for existing temperatures (Fig. 10.18).

In slow-flowing streams where current is at a minimum, streamlined forms of fish give way to species like small-mouth bass (*Micropterus dolomieu*), shiners (*Notropis*, *Cyprinella*), and darters (*Etheostoma*, *Percina*, *Ammocrypta*). They trade strong lateral muscles needed in fast current for compressed bodies that enable them to move through beds of aquatic vegetation. Bottom-feeding fish, like catfish, feed on life in the silty bottom.

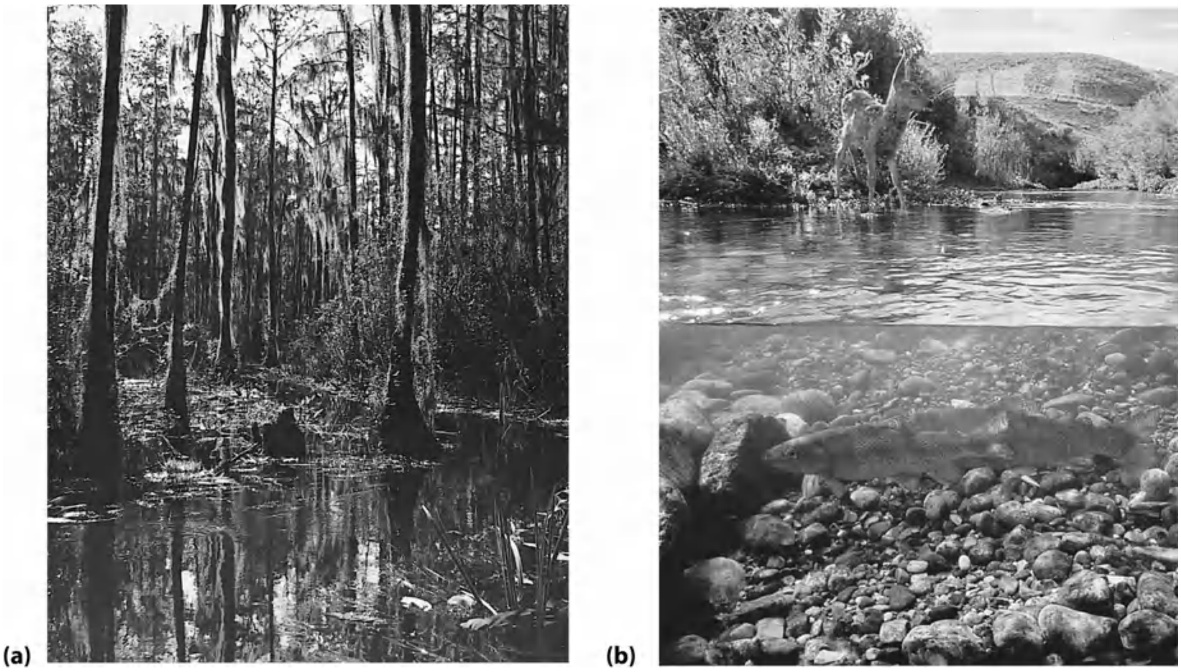


Figure 10.17. (*a*) Woodland swamp. (*b*) Two worlds of land and water meet in a Montana stream as a fawn encounters trout—a striking example of the barriers that separate two animals so near in space yet so isolated in their ways of life.

Figure 10.18. The oxygen content of stream water flowing over riffles and falls is often near the saturation point. Many species of salamanders find suitable habitat in and near waterfalls.

Lake Formation

Lakes are formed by several processes. Those formed in basins created by movements of the Earth’s crust are known as **tectonic lakes**. Reelfoot Lake in Tennessee, which was formed as a result of an earthquake in 1811, is an example of a tectonic lake. As the Earth’s crust shifts, fissures may form or a narrow strip of land may sink, a process known as faulting. Such fissures or sinks may fill with water and form long, narrow lakes known as **rift lakes**. The deepest lakes known—Lake Baikal in Russia, 1,741 m (5,710 ft.), and Lake Tanganyika in Africa, 1,435 m (4,707 ft.)—are of this type.

Volcanic lakes form when a volcano becomes extinct and its hollow interior fills with water. Also known as crater lakes, they are usually circular in outline and also may be deep. Crater Lake in Oregon, for example, is 608 m (1,994 ft.) deep.

Glacial action has formed many of the world’s lakes, including North America’s Great Lakes. As glaciers move over the land, they gouge out previously existing valleys. When the glacier melts, its waters often collect in these valleys to form deep **glacial lakes** with steep sides. Minnesota has about 11,000 lakes formed by the action of glaciers. Many of the smaller lakes (e.g., pot-hole lakes) in northeastern North America were formed in this manner, including the Finger Lakes of central New York.

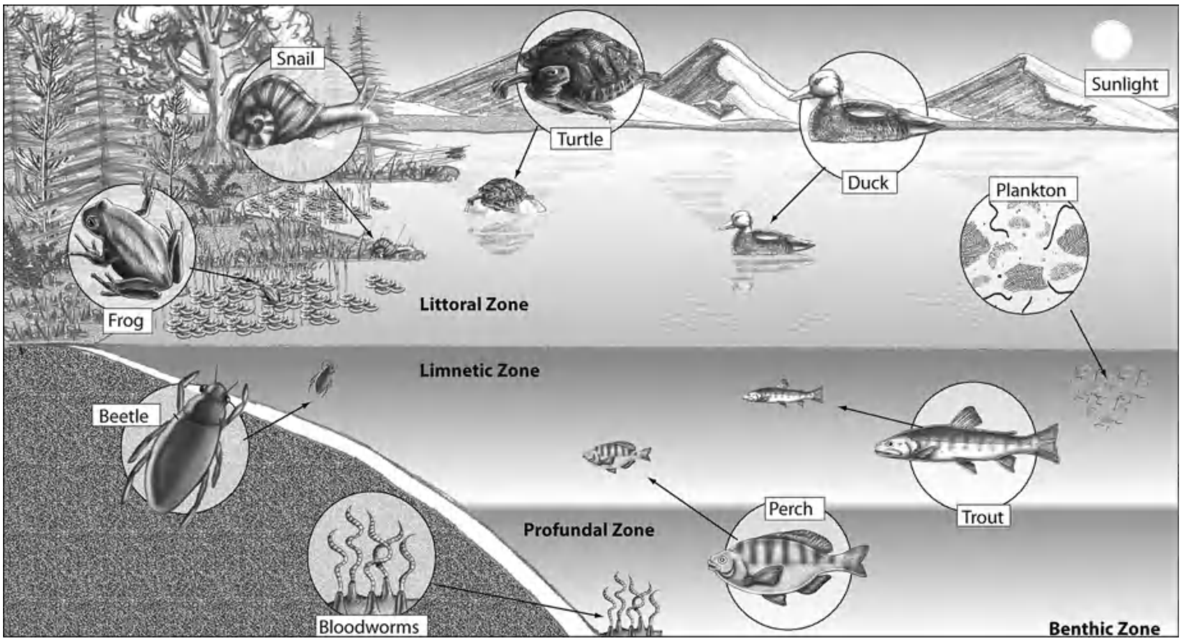


Figure 10.19. Four major zones of life in a lake. The littoral zone includes the shore and the shallow, nutrient-rich waters near the shore where sunlight penetrates to the lake bottom. It contains free-floating producers, rooted aquatic plants, and other aquatic life like snails, frogs, and turtles. The limnetic zone is the open water that receives enough sunlight for photosynthesis to take place. It contains floating phytoplankton, plant-eating zooplankton, and fish. The profundal zone is the deep, open water beyond the limit of light penetration. It is too dark for photosynthesis to take place and is inhabited by fish adapted to its cooler, darker water. The benthic zone at the bottom of the lake is inhabited by large numbers of decomposers and detritus-feeding clams and wormlike insect larvae. These detritivores feed on dead plant debris, animal remains, and animal wastes that descend from above.

Lakes contain four life zones (Fig. 10.19). The **littoral zone** is closest to shore and supports rooted plant growth. The **limnetic zone**, which is the main body of a lake, is the water too deep to support rooted plants but that receives sufficient light to support photosynthesis. Both of these zones contain phytoplankton, zooplankton, and nekton. In deep lakes, the region of open water below the depth of light penetration is known as the **profundal zone**. It is inhabited primarily by invertebrates and by fish adapted to cooler, darker water. The **benthic zone** at the bottom of a lake is inhabited primarily by decomposers that feed on animal wastes as well as dead plants and animals.

Although the freshwater environment is the smallest of the three types, it is vital to most classes of vertebrates. Some fishes and some salamanders live their entire lives in bodies of fresh water. Some fishes, like eels, are **catadromous**—they spend most of their adult lives in freshwater lakes and streams, but return to the ocean to spawn; others, like salmon, are **anadromous**—they spend most of their adult lives in the ocean, but return to the rivers where they were born in order to spawn. Many salamanders and anurans live in or near streams, ponds, marshes, and swamps their entire lives. These areas assist in keeping the skin of these vertebrates moist, and they also provide sites for egg deposition, hibernation, and a means of escape from predators.

Alligators, many snakes, and many turtles are aquatic or semiaquatic. Many turtles hibernate in the mud on the bottoms of ponds and lakes. Ducks, geese, swans, shorebirds, and many others depend on freshwater habitats for protection, nesting, and food resources. Muskrats, beaver, mink, otters, water shrews, and many other mammals are semiaquatic.

Terrestrial Environment

This is the most variable of the three major environments. Elevations in the terrestrial environment range from below sea level to more than 8,500 m (27,887 ft.) in the Himalayas. Air temperature varies from –60°C to 60°C (–76°F to 140°F) and decreases approximately 1.2°C (2.16°F) for every 305 m (1,000 ft.) increase in elevation above sea level. Precipitation varies from only a fraction of a centimeter over several years to more than 1,250 cm (492 in.) per year in some tropical areas (Fig. 10.20).

Various systems have been devised to classify terrestrial environments. Among these are the biome, life zone, and biotic province systems.

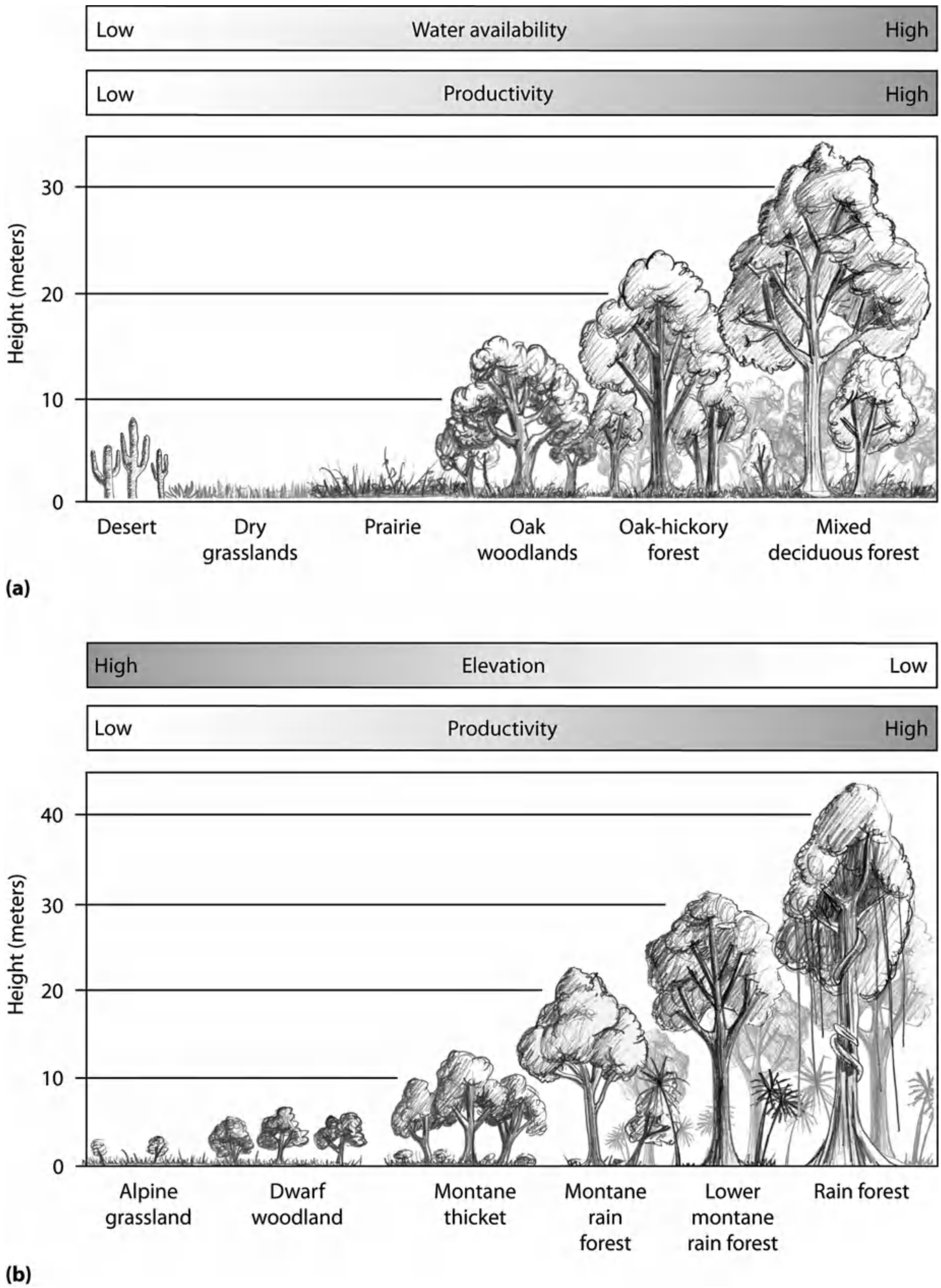


Figure 10.20. Plant species diversity and distribution, as well as plant forms, are influenced by water availability, elevation, and other factors like temperature and soil drainage characteristics. (*a*) Moisture gradient for temperate North America. (*b*) Elevation gradient for tropical South America.

BIOMES

The biome system of classification is based on natural climax communities and was originally proposed by Clements and Shelford in 1939 (Fig. 10.21). Because these communities are influenced primarily by temperature, rainfall, and soil conditions, they correspond closely to the distribution of climatic zones and soil types. For these reasons, they vary with latitude as well as with altitude, with the number of animals decreasing steadily with increasing latitude and altitude (Fig. 10.22). The size of species that range from the lowlands to the tops of mountains also often decreases with altitude (Allee and Schmidt, 1951).

The transition area between two adjacent communities or between two biomes is known as an **ecotone**. Species diversity of such areas is usually high because they contain resources from both biomes. Where forest grades into grassland, for example, the ecotone will have some characteristic forest species, some grassland species, and some additional species that require resources from both kinds of vegetation.

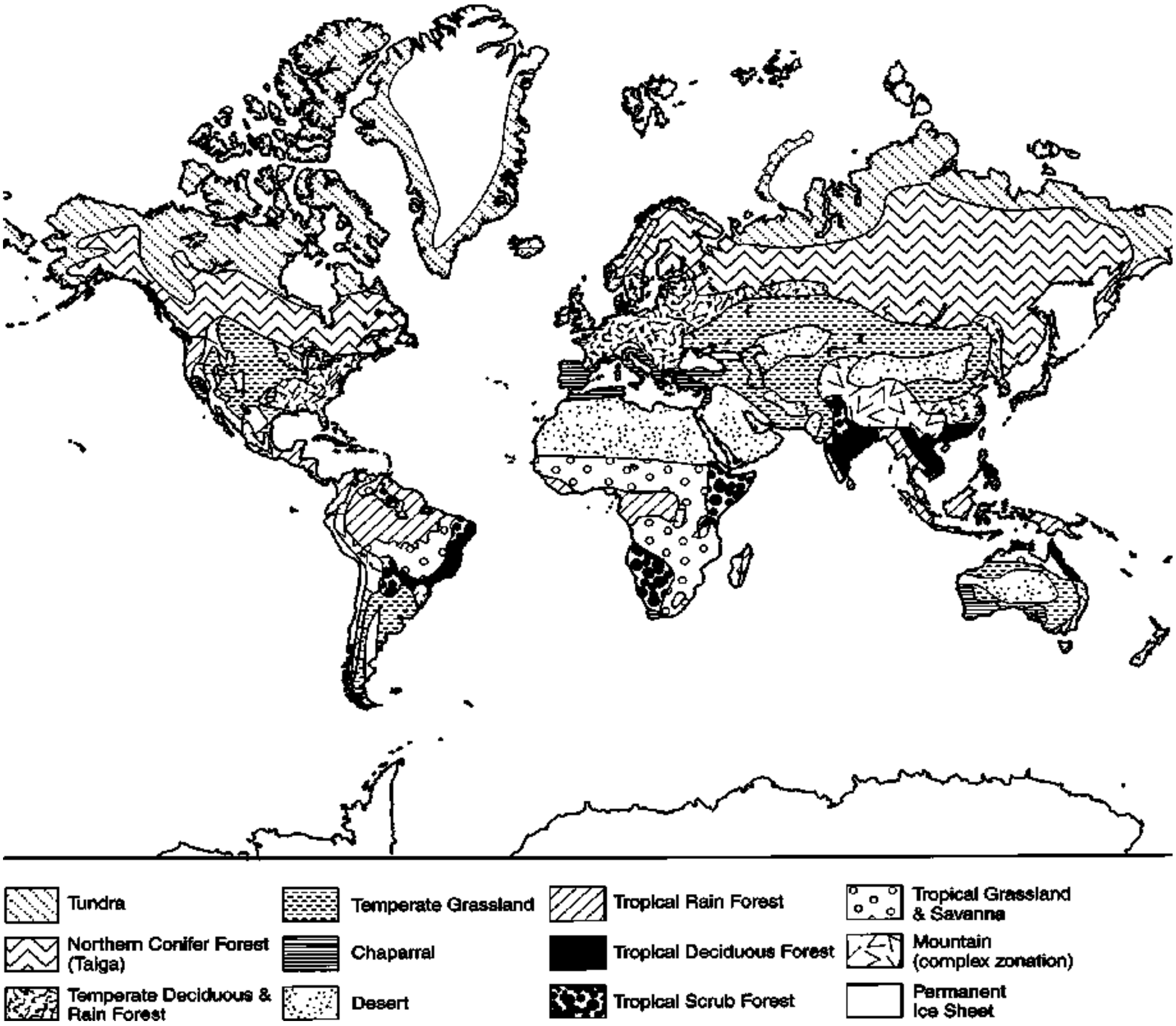


Figure 10.21. The biomes of the world.

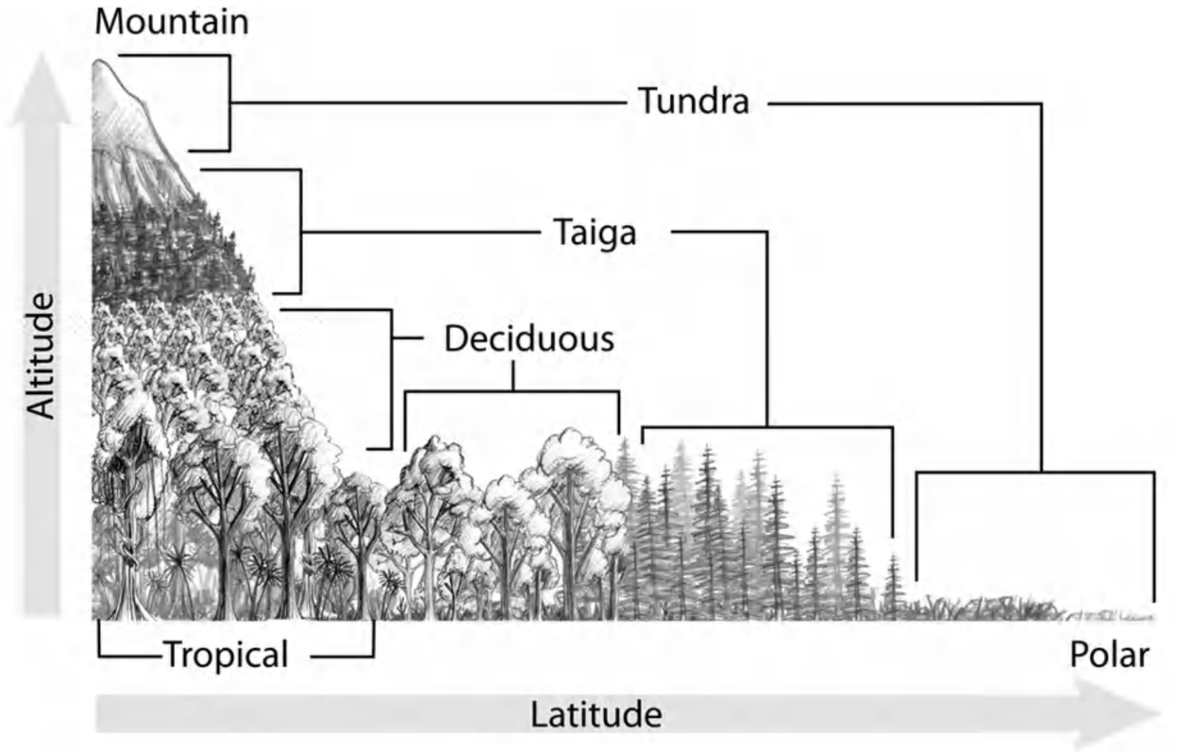


Figure 10.22. Biomes change not only with latitude (*bottom*), but also with altitude (*left*). Numbers of vertebrate species decrease steadily with increasing latitude and altitude.

TUNDRA

This is a treeless biome that encircles the Earth just south of the ice-covered polar seas in the Northern Hemisphere (Fig. 10.23). For the most part, the tundra exists within the Arctic Circle, but it extends southward in Canada and along the western Alaskan shore. It also occurs at high elevations much farther south in the western United States; it is the area above the tree line. It extends as far as 1,900 km (1,180 mi.) south of the Arctic Circle along the shores of Hudson Bay. This cold biome, which receives approximately 20 cm (8 in.) of precipitation a year, has extreme seasonal fluctuations in photoperiod ranging from a 24-hour period of sunlight at the summer solstice (June 21–22) to one 24-hour period of nighttime at the winter solstice (December 21–22). Only during a short summer growing season does the temperature rise above the freezing point of water, and even the warmest summer months have a mean temperature of no more than 10°C (50°F). Table 10.1 shows typical air and soil temperatures for winter and summer. Even during the summer, only the top few inches or so of soil thaw; the remainder is permanently frozen and is known as **permafrost**. This makes tree growth impossible. The frozen subsoil prevents the escape of water by seepage, so that the melting ice and snow of winter produce innumerable lakes and ponds.

Sedges, shortgrasses, lichens, and mosses—all plants that do not require a deep root system—cover the ground and must complete their flowering and fruiting cycles quickly. Lemmings (*Lemmus*, *Dicrostonyx*), ptarmigan (*Lagopus*), musk ox (*Ovibos moschatus*) (Fig. 10.24 a), polar bears (*Ursus maritimus*), and caribou (*Rangifer tarandus*) (Fig. 10.24 b) are permanent residents. Many shorebirds and waterfowl are summer residents.

Figure 10.23. Aerial view of the arctic tundra near Point Barrow, Alaska. Numerous small lakes are characteristic of this region.

Table 10.1. Typical Temperature Gradients (in Degrees Celsius) in Winter and Summer in Tundra

Height	Winter (February)	Summer (July)

Height	Winter (February)	Summer (July)
8 m (air)	–25°	**8°**
1 m (air)	–31°	**9°**
Snow surface (about 0.3 m)	–35°	—
Soil surface	–22°	**11°**
–0.25 m (soil)	–19°	**1°**
–1 m (soil)	–16°	–3°
–4 m (soil)	–10°	–8°

Source: Data from Brewer, 1988.

Note: Temperatures above freezing are in bold type.

TAIGA

This is a coniferous forest biome that extends in a broad belt across northern Eurasia and North America. It also occurs at high elevations in more southern areas like Clingman's Dome in the Great Smoky Mountains National Park in Tennessee, Mount Mitchell along the Blue Ridge Parkway in North Carolina, and numerous areas in the western states. Spruce (*Picea*), fir (*Abies*), hemlock (*Tsuga*), and pine (*Pinus*) are the dominant tree species in this region of long, cold winters and short, cool summers. These evergreen trees shed one-fourth to one-third of their leaves (needles) annually and reproduce by forming cones. Little light reaches the ground, which is covered with ground-level vegetation like lichens, mosses, and ferns. Soils are thin and nutrient-poor. Many lakes and swamps are present. Rainfall ranges between 40 and 100 cm per year, much of it in the form of heavy snow. The growing season is about 130 days. Snowy owls (*Nyctea scandiaca*), crossbills (*Loxia*), evening grosbeaks (*Hesperiphona vespertina*), lynx (*Lynx canadensis*), wolves (*Canis lupus*), moose (*Alces alces*), and bears (*Ursus*) are typical resident species.

A Cold-Water Frog

The tailed frog (*Ascaphus truei*) (see Fig. 5.30) is a streamside resident of clear, cold, well-oxygenated mountain streams in forests from near sea level to over 2,000 m (6,560 ft.) in northwestern North America. These largely nocturnal frogs have evolved numerous adaptations for life in rapidly flowing streams, including strongly webbed hind feet, a copulatory organ for internal fertilization (amplexus occurs underwater), and the lack of vocal sacs and tympana (these frogs do not call). Apparently visual cues are used by males and females to find one another. Courtship occurs in September and October. In addition to the rarity of internal fertilization among frogs, another unusual feature of the tailed frog is that the female stores sperm in her oviducts for nearly nine months; fertilization occurs at the time of ovulation and egg deposition from June to August. The large ova have extremely low rates of oxygen consumption due to the low temperatures at which they develop. After hatching, the length of the larval period varies from one to five years, depending on altitude and geographic location. The tadpoles live in fast-flowing water and have reduced tail fins, but have well-developed suctorial oral discs that firmly attach the tadpole to the substrate.

Noble and Putnam, 1931; Brown, 1977; Wallace and Diller, 1998

(a)

(b)

Figure 10.24. (*a*) Musk-ox and (*b*) caribou—permanent residents of the tundra.

TEMPERATE DECIDUOUS FORESTS

South of the taiga in eastern North America, eastern Asia, and much of Europe is a biome dominated by deciduous trees like beech (*Fagus*), oak (*Quercus*), and maple (*Acer*). These areas have well-defined seasons, and most trees lose their leaves during the colder winter months. The growing season ranges between 140 and 300 days, with annual precipitation being relatively evenly distributed throughout the year and ranging between 75 and 150 cm (29–59 in.). Enough light penetrates the canopy so that shrubs, herbaceous plants, mosses, and ferns make up the understory. Typical vertebrate species include lungless salamanders (Plethodontidae), skinks (*Eumeces*), garter snakes (*Thamnophis*), turkeys (*Meleagris gallopavo*), pileated woodpeckers (*Hylatomus pileatus*), black-capped chickadees (*Parus atricapillus*), squirrels (*Sciurus*), bobcats (*Lynx rufus*), foxes (*Vulpes* and *Urocyon*), and white-tailed deer (*Odocoileus virginianus*).

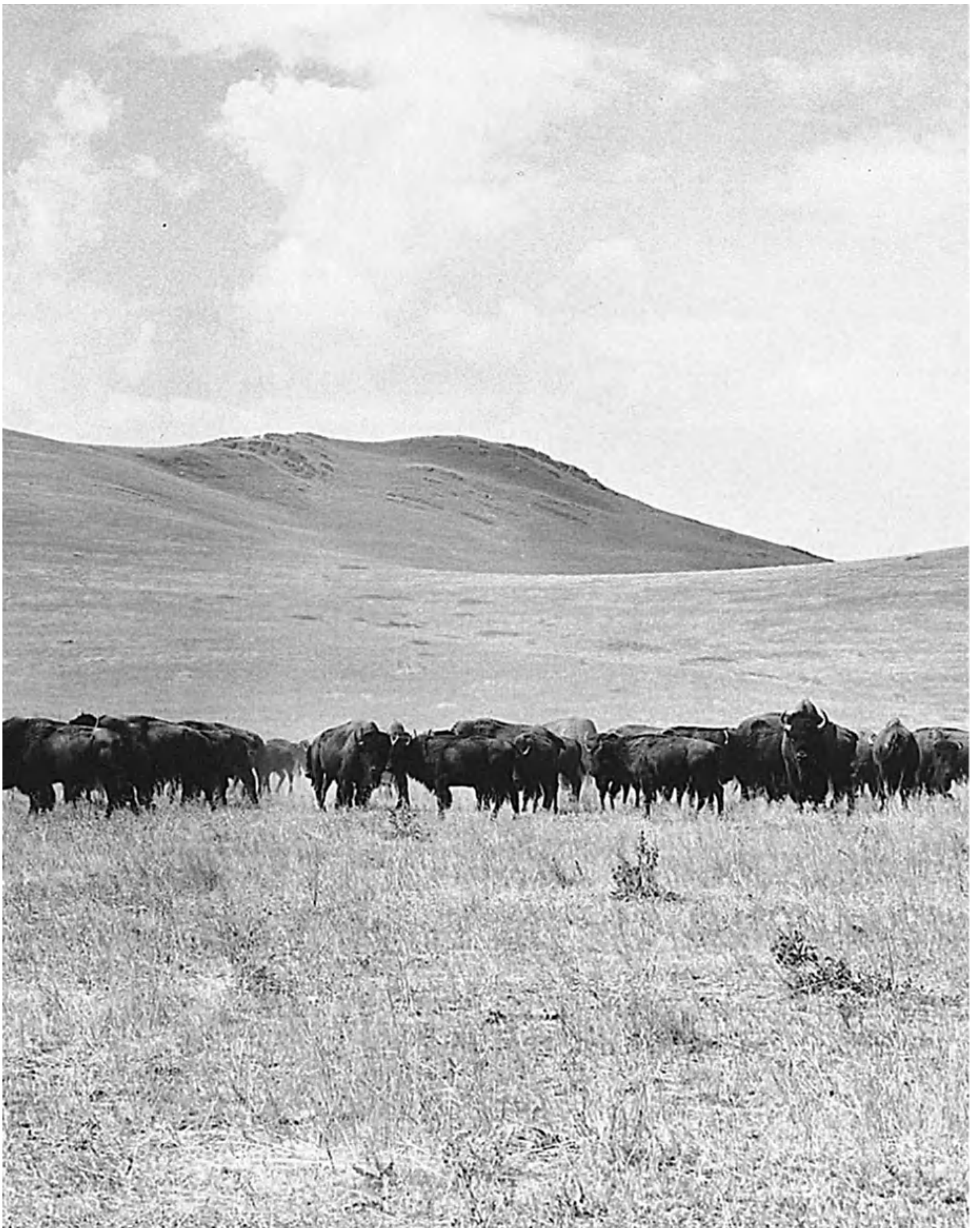


Figure 10.25. Rolling shortgrass prairie to the east of the Rocky Mountains. Grasses are the climax species in areas that receive more than 20 cm (8 in.) of rainfall annually but not enough precipitation to support tree growth.

GRASSLANDS

Grasses are the climax species in areas that receive more than 20 cm (8 in.) of rainfall annually but not enough precipitation to support tree growth. Extensive root systems absorb water efficiently and allow rapid recovery from droughts and fires. The buildup of organic matter forms rich soil.

The central portion of North America has vast grasslands known as **prairies** (Fig. 10.25). The easternmost grasslands are tallgrass prairies and receive greater annual rainfall than the more western shortgrass prairies. Plains spadefoot toads (*Scaphiopus bombifrons*), Great Plains narrow-mouthed toads (*Gastrophryne olivacea*), prairie skinks (*Plestiodon* [formerly *Eumeces*] *septentrionalis*), Great Plains skinks (*Plestiodon* [formerly *Eumeces*] *obsoletus*), prairie racerunners (*Cnemidophorus sexlineatus*), prairie lizards (*Sceloporus undulatus*), prairie rattlesnakes (*Crotalus viridis*), Plains garter snakes (*Thamnophis radix*), Graham's water snakes (*Natrix grahami*), burrowing owls (*Speotyto cunicularia*), short-eared owls (*Asio flammeus*), dickcissels (*Spiza americana*), horned larks (*Eremophila alpestris*), prairie dogs (*Cynomys*), black-footed ferrets (*Mustela nigripes*), badgers (*Taxidea taxus*), coyotes (*Canis latrans*), and large grazing animals like bison (*Bison bison*) and pronghorn antelope (*Antilocapra americana*) are typical inhabitants. The ecological roles and conservation challenges of social, burrowing, herbivorous mammals in the world's grasslands is discussed by Davidson et al. (2012).

Tropical grasslands are known as **savannas** (Fig. 10.26). Trees are distributed sparsely because of a severe summer dry season. The African savanna supports the greatest variety and number of large herbivores of all the biomes. These include elephants (*Loxodonta africana*), giraffes (*Giraffa camelopardalis*), many kinds of gazelles and antelopes, zebras (*Equus* spp.), wildebeests (*Connochaetes* spp.), African buffalo (*Syncerus caffer*), and rhinoceroses (*Diceros* and *Ceratotherium*). Typical predators include lions (*Panthera leo*), cheetahs (*Acinonyx jubatus*), and leopards (*Panthera pardus*), and scavengers like hyenas (*Hyaena brunnea*).

Figure 10.26. African savanna—a region of warm grasslands with isolated stands of shrubs and trees. More large ungulates like giraffes, Cape buffalo, zebras, impalas (*shown here*), gnus, and gazelles live here than anywhere else. Predators like lions and cheetahs and scavengers play important roles in the food web. Herds undertake annual migrations that coincide with rainy and dry seasons. When the rains come, herds return to the plains for the lush new grasses that are the preferred forage. Births are timed to coincide with the re-emergence of the grass, a fact well known to the predators.

In some regions of the world, most of the rain falls in the cool winter, and the summers are hot and dry. This results in dense, shrubby, fire-resistant scrubland known as **chaparral**. These areas occur in parts of southern Africa, in Western Australia, in central Chile, around the Mediterranean Sea, and in California. The shrubs have small, thick evergreen leaves and thick underground stems.

DESERTS

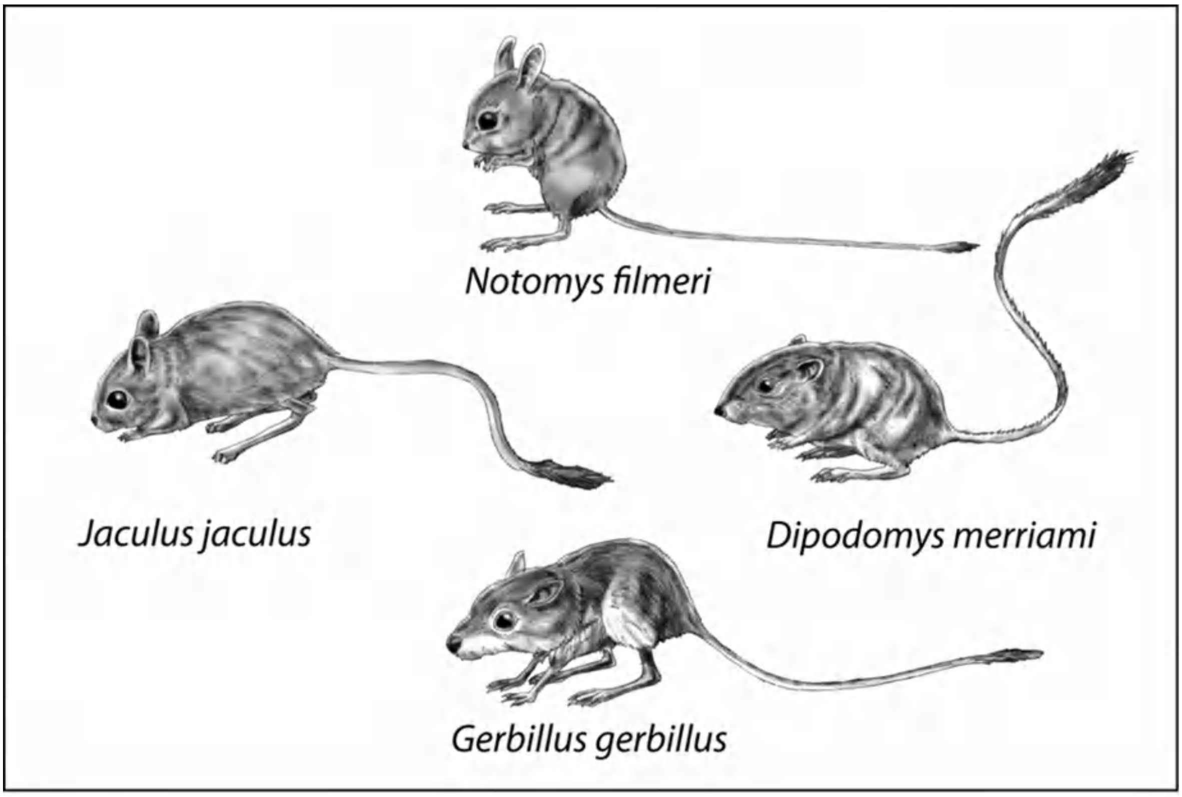
Large areas of desert occur in Africa, Asia, and Australia, with smaller areas in North and South America (Fig. 10.27a). These habitats experience hot days and cold nights and receive less than 25 cm (10 in.) of rainfall annually. When it does rain, much of it runs off or evaporates. Vegetation is sparse with cacti, Joshua trees (*Yucca*), sagebrush (*Artemis*), creosote (*Larrea*), and mesquite trees (*Prosopis*) among the typical plants in North American deserts. Following a rain, many desert plants burst into bloom and complete their lifecycle in a short time. Horned lizards (*Phrynosoma* spp.), earless lizards (*Holbrookia* spp.), Gila monsters (*Heloderma suspectum*), western diamondback rattlesnakes (*Crotalus atrox*), Mojave rattlesnakes (*Crotalus scutulatus*), cactus wrens (*Campylorhynchus brunneicapillus*), Chihuahuan ravens (*Corvus cryptoleucus*), roadrunners (*Geococcyx californianus*), and kangaroo rats (*Dipodomys* spp.) are among the species that have adapted to the desert environment. Many are burrowers or live in burrows of other species. Adaptations include the reduction of cutaneous glands, concentrated urine, and dry feces. Many species can survive for months without drinking. They obtain limited water from their plant and animal food resources together with water produced by the processes of metabolism. Estivation (a period of inactivity during the summer) occurs in some species.

Some geographically separated, seed-eating desert rodents have undergone convergent evolution and developed similar morphological, physiological, ecological, and behavioral adaptations to their xeric habitats (see Fig. 10.27b). These bipedal saltatorial forms have independently evolved (convergent evolution) on four continents (North America, Asia, Africa, and Australia).

TROPICAL FORESTS

Two major types of tropical forests occur. Tropical deciduous forests consist of broad-leaved trees that lose their leaves because of a dry season. Tropical rain forests, which occur in areas of abundant rainfall (more than 250 cm, or 98 in., per year) and continual warmth (20°C to 25°C, or 68°F to 77°F), are the richest of all of the biomes (Fig. 10.28). The canopy consists of several layers, with epiphytes common and lianas, or woody vines, encircling the trees. In open areas or clearings below the canopy, vegetation is dense and forms a thick jungle. Most animals spend a substantial amount of time in the trees. Treefrogs, iguanas (*Iguana*), anacondas (*Eunectes*), caimans (*Caiman*), parakeets, parrots, toucans, monkeys, and jaguars (*Panthera onca*) are representative of the vertebrate life.


(a)



(b)

Figure 10.27. (*a*) Warm desert near Tucson, Arizona. Vegetation includes column-like saguaro cacti, prickly pear cacti, creosote bushes, and tall, multistemmed ocotillo. Deserts experience hot days and cold nights and receive less than 25 cm (10 in.) of rainfall annually. (*b*) Morphological convergence of seed-eating desert rodents on four continents. Illustrated forms

include Jaculus (Dipodidae) from Asia, Notomys (Muridae) from Australia, Dipodomys (Heteromyidae) from North America, and Gerbillus (Muridae) from Africa. Each of these groups has independently evolved bipedal, hopping rodents that are similar in morphology.

Morphological convergence is strikingly evident in some African and South American rain forest mammals that occupy similar ecological niches (Fig. 10.29). Many of the species are in different families and even different orders.

Deforestation—mainly the conversion of tropical forests to agricultural land—shows signs of decreasing in several countries but continues at a high rate in others. Total forest area declined by 3 percent, from 4.128 million hectares (10,200,700 acres) in 1990 to 3.999 million hectares (9,881,929 acres) in 2015. The annual rate of net forest loss halved from 7.3 million hectares (18,039,030 acres) in the 1990s to 3.3 million hectares (8,154,478 acres) between 2010 and 2015 (Keenan et al., 2015). Natural forest area declined from 3.961 million hectares (9,787,844 acres) to 3.721 million hectares (9,194,791 acres) between 1990 and 2015, while planted forest (including rubber plantations) increased from 168 million hectares (415,137,041 acres) to 278 million hectares (686,952,960 acres). From 2010 to 2015, tropical forest area declined at a rate of 5.5 million hectares (13,590,796 acres)—only 58 percent of the rate in the 1990s—while temperate forest area expanded at a rate of 2.2 million hectares (5,436,318 acres). Boreal and subtropical forest areas showed little net change. Forest areas expanded in Europe, North America, the Caribbean, East Asia, and Western-Central Asia, but declined in Central America, South America, South and Southeast Asia, and all three regions in Africa.

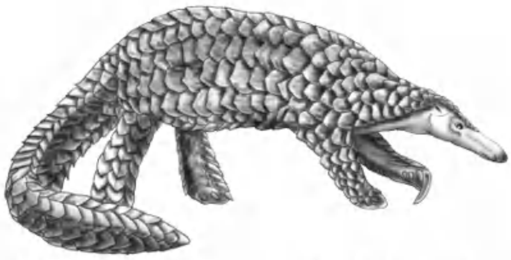
Figure 10.28. Tropical rain forests are the richest of all of the biomes. They receive abundant rainfall of more than 250 cm (98 in.) per year and are continually warm, usually 20°C–25°C (68°F–77°F). Epiphytes and woody vines are characteristic of the rain forest biome.

See additional discussion in Chapter 19 concerning current rates of loss and conservation efforts.

LIFE ZONES

In an attempt to combine the regional distributions of North American plants and animals into one ecological classification scheme, C. Hart Merriam (1890, 1898) proposed the concept of **life zones** (Fig. 10.30). Dr. Merriam was the founder and chief of the US Bureau of Biological Survey, which later became the US Fish and Wildlife Service. Merriam developed his life zone concept around the following two principles: (1) animals and plants are restricted in northward distribution by the total quantity of heat during the season of growth and reproduction; and (2) animals and plants are restricted in southward distribution by the mean temperature of a brief period covering the hottest part of the year. Life zones are broad belts that run longitudinally across the continent with southern horizontal extensions along the mountain chains or around individual mountains. These zones were biotic in concept, but their boundaries (isotherms) were determined by a given mean temperature. Each zone has a theoretical temperature range of approximately 4°C (7°F).

Africa



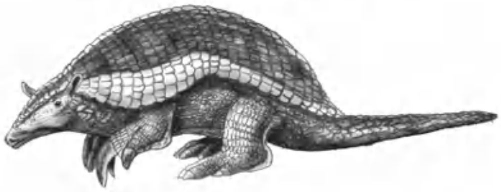
Terrestrial pangolin (*Manis*)
Pholidota, Manidae

Pigmy hippopotamus (*Choeropsis*)
Artiodactyla, Hippopotamidae

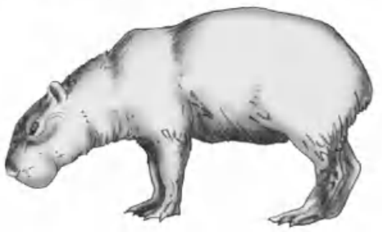
Chevrotain (*Hyemoschus*)
Artiodactyla, Tragulidae

Yellow-backed duiker (*Cephalophus*)
Artiodactyla, Bovidae

South America



Giant armadillo (*Priodontes*)
Edentata, Dasypodidae



Capybara (*Hydrochoerus*)
Rodentia, Hydrochoeridae

Paca (*Cuniculus*)
Rodentia, Cuniculidae

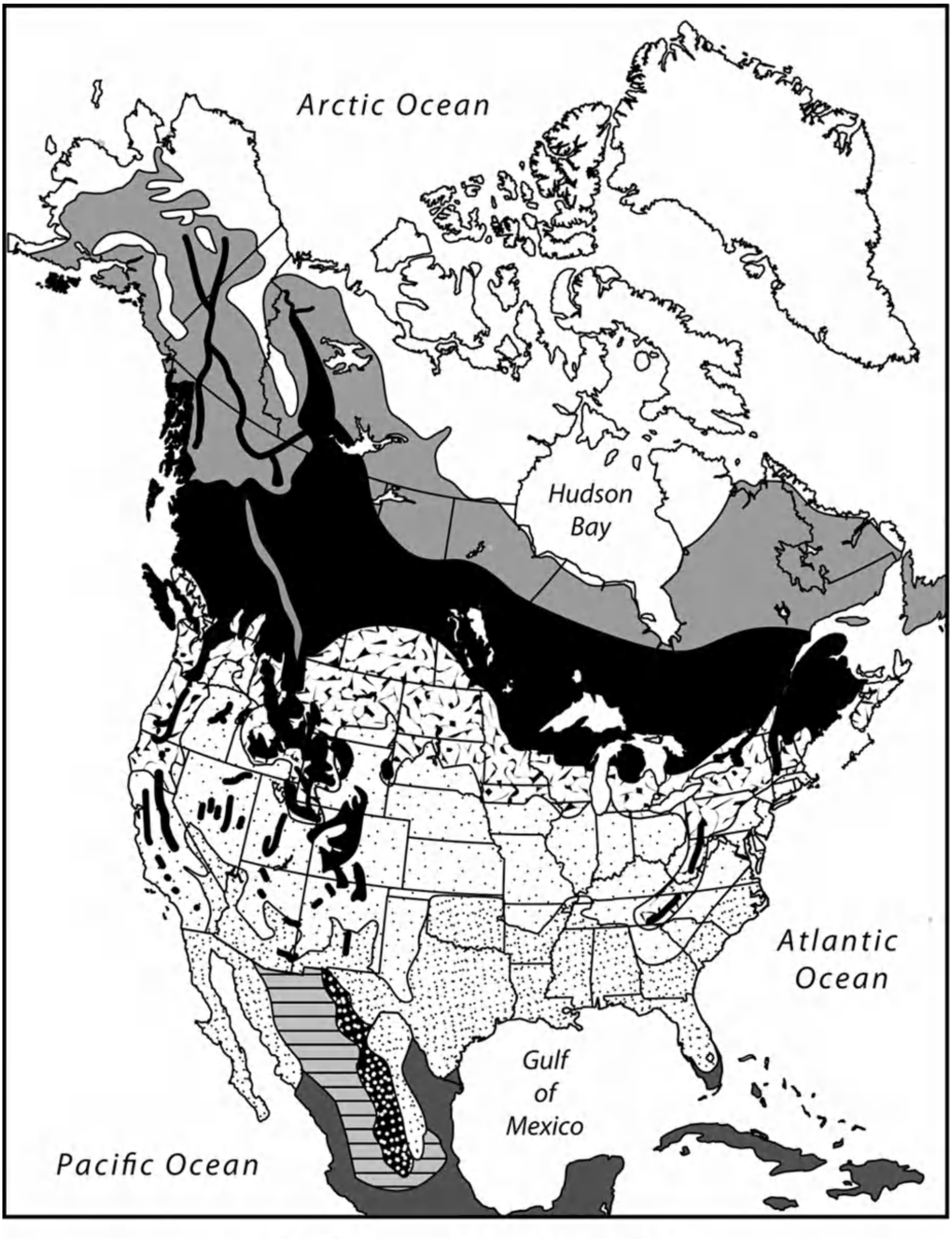
Brocket deer (*Mazama*)
Artiodactyla, Cervidae

Royal antelope (*Neotragus*)
Artiodactyla, Bovidae

Agouti (*Dasyprocta*)
Rodentia, Dasyproctidae

Figure 10.29. Morphological convergence among African and South American rain forest mammals that occupy similar ecological niches. Many of the species are classified in different families and even different orders.

Merriam initially divided the North American continent into three primary transcontinental regions: Boreal, Austral, and Tropical. The Boreal region extends from the northern polar area to southern Canada, with southward extensions along the Appalachians, the Rocky Mountains, and the Cascade-Sierra Nevada Range. The Austral region comprises most of the United States and a large portion of Mexico, and the Tropical region includes southern Florida, extreme southern Texas, some of the lowlands of Mexico, and most of Central America. Each of these regions is further subdivided into life zones.



Life Zones of North America

- □ 1. Arctic-Alpine
- ▒ 2. Hudsonian
- ■ 3. Canadian
- ▨ 4. Transition
- ⁘ 6. Lower Austral (Lower Sonoran in West)
- ☰ 7. Mexican pine
- ▓ 8. Tropical

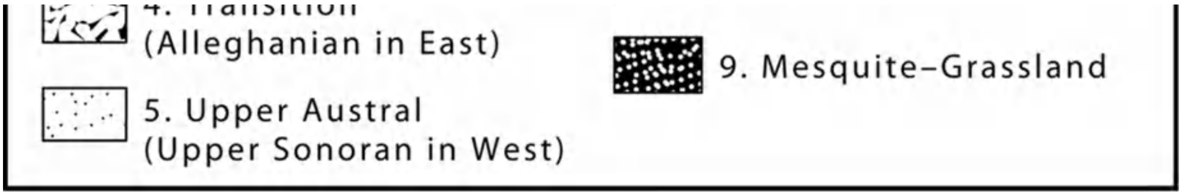


Figure 10.30. Life zones of North America.

BOREAL REGION

Arctic-Alpine Zone. This zone encompasses the area north of the limit of tree growth, including the tundra (Fig. 10.31), and mean temperature ranges from 6°C to 10°C (43°F–50°F). Lichens, grasses, Arctic willow, and Arctic poppy are typical plants, while Arctic foxes (*Alopex lagopus*), Arctic hares (*Lepus arcticus*), and lemmings (*Lemmus*, *Dicrostonyx*) are permanent residents. Snowy owls (*Nyctea scandiaca*) are also generally considered permanent residents. However, about every four years, large flocks of owls migrate southward in the fall to the northern United States and adjacent Canadian provinces. These migrations coincide with the low point in the population cycles of lemmings, their major prey (see Chapter 11 for further discussion of cycles).

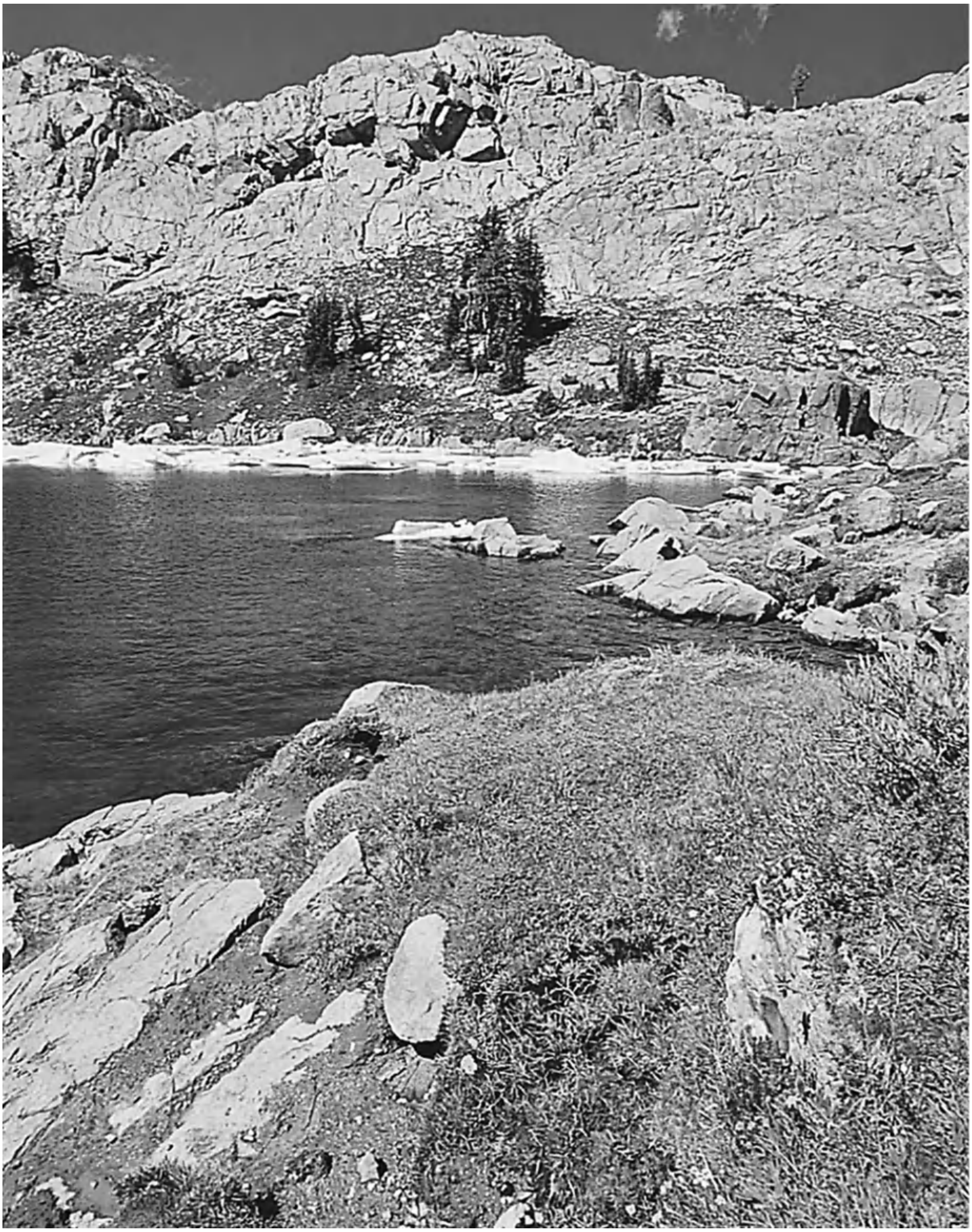


Figure 10.31. Arctic-Alpine Life Zone in the Sierra Nevada of California at approximately 3,300 m (10,800 ft.). Alpine willow (*Salix anglorum*) inhabits this area but rarely attains a height of more than 15 cm (6 in.).

Hudsonian Zone. This is the region of northern coniferous forests with southern extensions along the higher mountain ranges (Fig. 10.32). Mean temperatures range from 10°C to 14°C (50°F–57°F). Spruce and fir are the dominant trees, with typical vertebrates including great gray owls (*Strix nebulosa*), pine grosbeaks (*Pinicola enucleator*), olive-sided flycatchers (*Nuttallornis borealis*), moose (*Alces alces*), wolverines (*Gulo gulo*), and timber wolves (*Canis lupus*).

Canadian Zone. This zone includes the southern part of the boreal forest and the coniferous forests that cover the higher mountain ranges extending southward (Fig. 10.33). Mean temperatures range from 14°C to 18°C (57°F–64°F). Characteristic vertebrates include Canada jays (*Perisoreus canadensis*), spruce grouse (*Canachites canadensis*), varying hares (*Lepus americanus*), and lynx (*Lynx canadensis*).

AUSTRAL REGION

Transition Zone. This zone extends across the northern United States and runs south on the major mountain ranges (Fig. 10.34). As its name implies, this is a zone where the coniferous forest and deciduous forest intermingle. Mean temperatures range from 18°C to 22°C (64°F–72°F). In the east, this zone is known as the Alleghenian Zone. Typical Transition Zone plants include hemlock (*Tsuga*), walnut (*Juglans*), beech (*Fagus*), birch (*Betula*), oak (*Quercus*), ponderosa pine (*Pinus ponderosa*), and sagebrush (*Artemisia tridentata*). The American chestnut (*Castanea dentata*) was one of the most important eastern hardwoods until the early 1900s, when a fungus reached the United States from eastern Asia. The fungus proved to be lethal, and most chestnuts succumbed. Vertebrates in this zone include sage grouse (*Centrocercus urophasianus*), sharp-tailed grouse (*Tympanuchus phasianellus*), Columbian ground squirrels (*Spermophilus columbianus*), northern flying squirrels (*Glaucomys sabrinus*), and black bears (*Ursus americanus*).

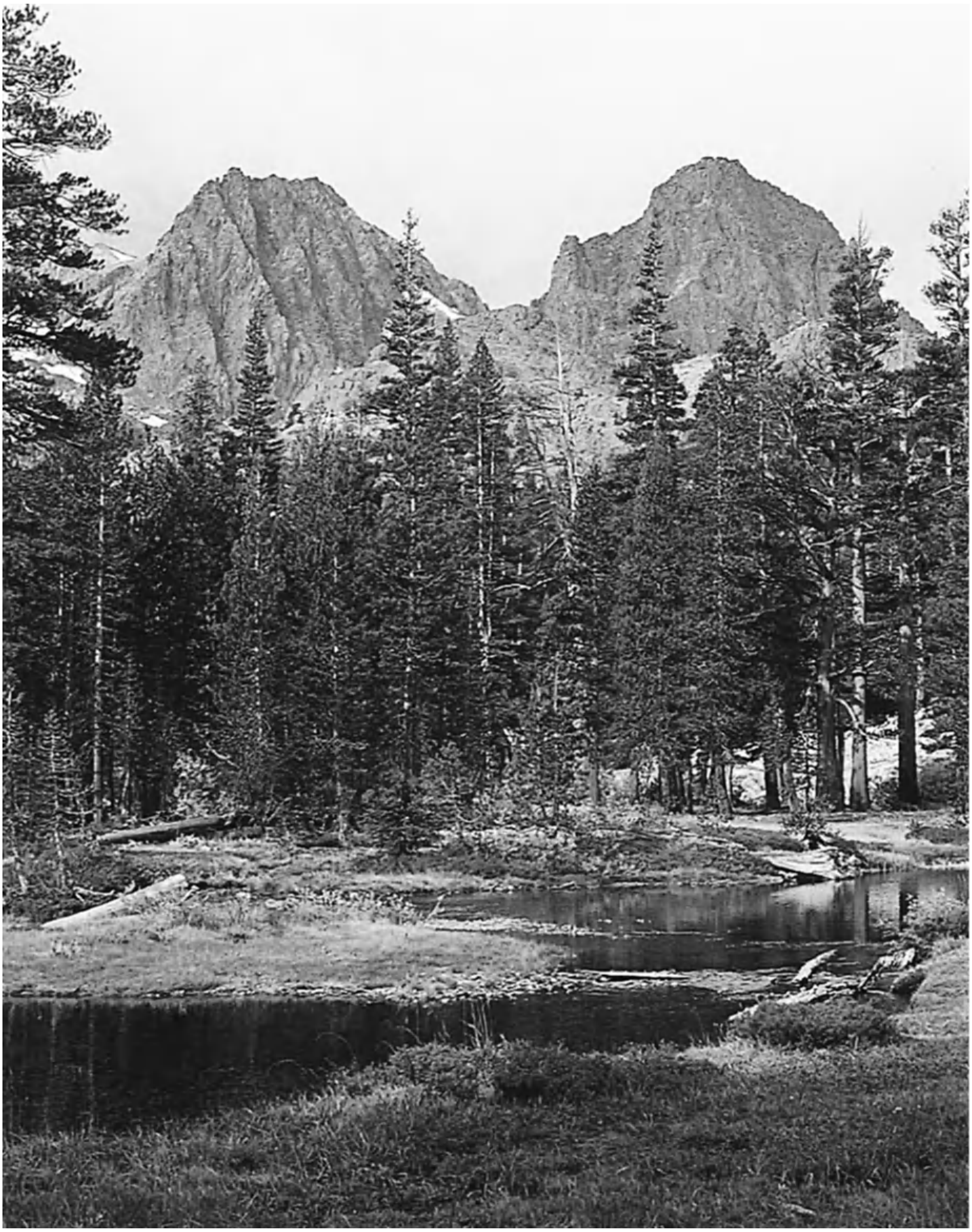


Figure 10.32. Hudsonian Life Zone in the Sierra Nevada of California. Lodgepole pine (*Pinus contorta*) and mountain hemlock (*Tsuga mertensiana*) form the major vegetation near lake level, with prostrate forms of the whitebark pine (*Pinus albicaulis*) covering the peaks in the distance.

Upper Austral Zone. This broad, irregular transcontinental belt is subdivided into the Carolinian area (east of the Great Plains) and the Upper Sonoran in the semiarid west (Fig. 10.35a, b). Mean temperatures range from 22°C to 26°C (72°F–79°F). The Carolinian area is humid in summer and is characterized by such species as oaks (*Quercus*), hickory (*Carya*), sweet gum (*Liquidambar*), sycamore (*Platanus*), eastern wood frogs (*Rana sylvatica*), Carolina wrens (*Thryothorus ludovicianus*), cardinals (*Richmondena cardinalis*), eastern wood rats (*Neotoma*), and fox squirrels (*Sciurus niger*). Typical species of the Upper Sonoran include pinyon pine (*Pinus cembroides*), buckeye (*Aesculus glabra*), sagebrush (*Artemisia tridentata*), junipers (*Juniperus* spp.), scrub jays (*Aphelocoma coerulescens*), Bewick's wren (*Thryomanes bewickii*), ring-tailed cats (*Bassariscus astutus*), and northern grasshopper mice (*Onychomys*).

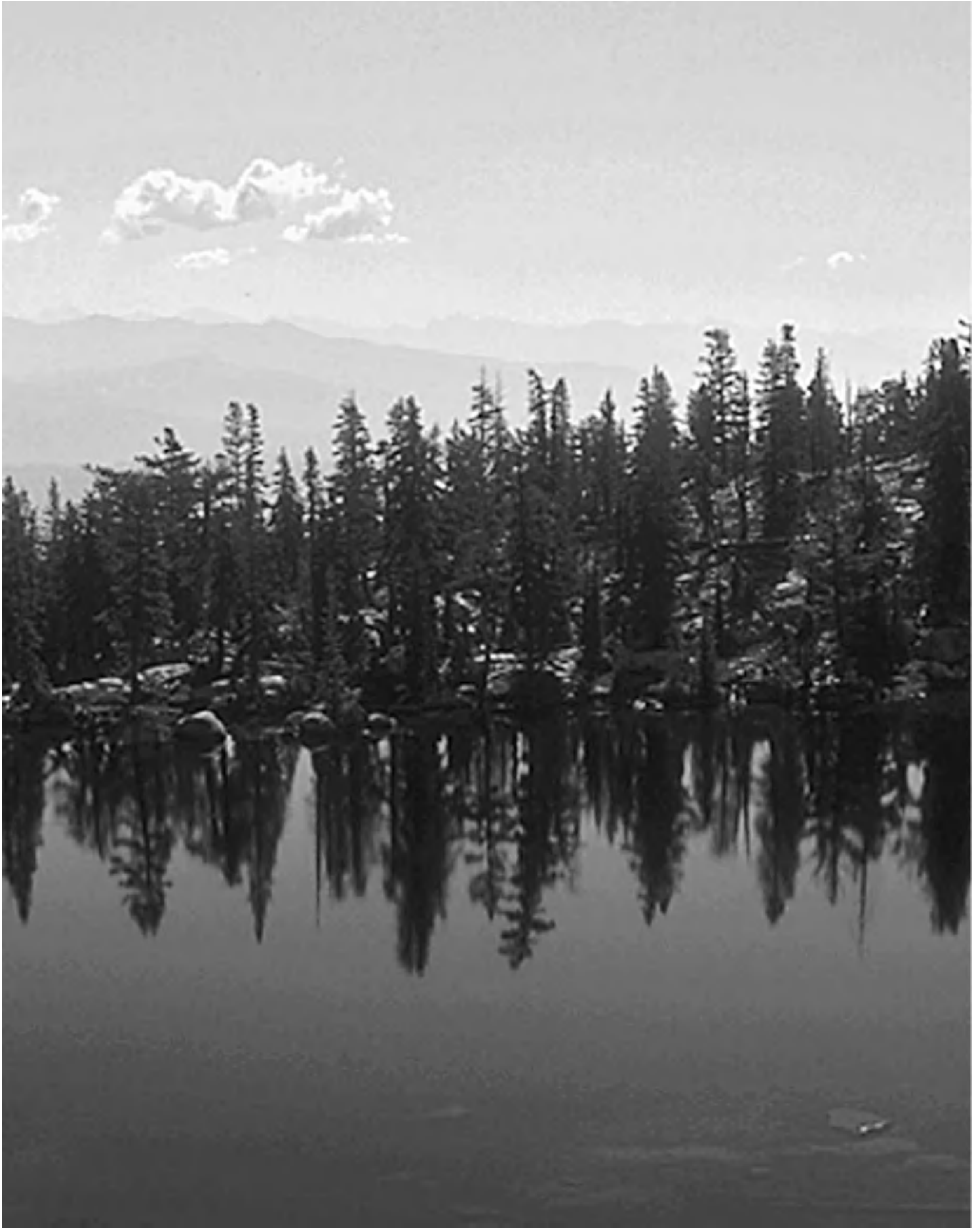


Figure 10.33. A Canadian Life Zone forest consisting of red fir (*Abies magnifica*) in the Sierra Nevada of California. This zone includes the southern part of the boreal forests and the coniferous forests on large mountain ranges extending much farther south.

Lower Austral Zone. This region encompasses the southern United States from the Carolinas and the Gulf states to California (Fig. 10.36a, b). Mean temperatures range from 26°C (79°F) to approximately 30°C (86°F). The more humid eastern area (Austroriparian) is characterized by such plants as bald cypress (*Taxodium distichum*), magnolia (*Magnolia* spp.), and long-leaf pine (*Pinus palustris*), and by such vertebrates as pig frogs (*Rana grylio*), river frogs (*Rana heckscheri*), alligator snapping turtles (*Macroclemys temminckii*), green anoles (*Anolis carolinensis*), brown pelicans (*Pelicanus occidentalis*), boat-tailed grackles (*Cassidix mexicanus*), chuck-will's widow (*Caprimulgus carolinensis*), rice rats (*Oryzomys palustris*), and cotton rats (*Sigmodon hispidus*). Indicator species of the arid western area (Lower Sonoran) include many types of cacti, ocotillo, mesquite, creosote bush, patch-nosed snakes (*Salvadora*), Gambel's quail (*Lophortyx gambelii*), cactus wrens (*Campylorhynchus brunneicapillus*), kit foxes (*Vulpes macrotis*), kangaroo rats (*Dipodomys*), and some species of pocket mice (*Perognathus*).

Figure 10.34. Ponderosa pine (*Pinus ponderosa*) is the dominant conifer in the Transition Life Zone over much of western North America.

TROPICAL REGION

This region is often divided into the Arid Tropical and Humid Tropical life zones. This, however, represents an oversimplification of a complex biotic region that more accurately is subdivided into seven major tropical zones: arid tropical scrub, thorn forest, tropical deciduous forest, savanna, tropical evergreen forest, rain forest, and cloud forest.

BIOTIC PROVINCES

A third method of classifying North American plant and animal communities and their distribution is by **biotic provinces.** A biotic province "covers a considerable and continuous geographic area and is characterized by the occurrence of one or more important ecologic associations that differ, at least in proportional area covered, from the associations of adjacent provinces" (Dice, 1943). The classification of biotic provinces is based largely on vegetation, because plants often indicate the characters of climate and soil on which animals also are dependent. Animals also directly or indirectly depend on plants for food and often for shelter and breeding places.

Each province is characterized by vegetation type, ecological climax, fauna, climate, physiography, and soil. Each includes both the climax communities and all the successional stages within its geographic area, including the freshwater communities. One or more climax associations may be present. Each biotic province is subdivided further into ecologically unique subunits known as **biotic districts** (subdivisions covering a definite and continuous part of the geographic area of a biotic province) and **life belts** (vertical subdivisions). Life belts, like a grassland belt, a forest belt, or an alpine belt, are based primarily on altitude. They frequently are not continuous, but may occur under proper conditions of altitude and slope exposure on widely separated mountains within one biotic province. Boundaries of the provinces, districts, and life belts often coincide with physiographic barriers rather than with vegetation types, and they are often difficult to locate precisely because the different areas merge gradually into one another. The area covered by a particular biotic province varies from time to time because of the production of new habitats through ecologic succession, and also because of slow, but more or less permanent modifications of climate (Dice, 1943).

(a)

(b)

Figure 10.35. (*a*) Carolinian Life Zone in Ohio. Dominant trees are white and red oaks (*Quercus* sp.) with an understory of hickory (*Carya* sp.). (*b*) Upper Sonoran Life Zone in western Nevada. Sagebrush (*Artemisia tridentata*) and Utah juniper (*Juniperus osteosperma*) are common in this region.

(a)

(b)

Figure 10.36. (*a*) Austroriparian Life Zone in South Carolina. View of a bald cypress (*Taxodium distichum*) swamp forest. (*b*) Lower Sonoran Life Zone of a desert in western North America. Creosote bush (*Larrea divaricata*) is the dominant perennial plant. It produces chemicals that prevent the growth of other plants.

Changes Caused by Human Activity

Humans have had a major impact on the distribution of vertebrates through domestication of some species, extinction of others, alteration of habitat, and both intentional and unintentional transport and introduction of great numbers of animals to regions where they were originally absent.

Dogs, cats, cattle, goats, horses, pigs, rabbits, and others have been domesticated from their wild ancestors. Domesticated vertebrates have served as invaluable human companions as well as important agricultural resources. Some of these species were taken on early sailing ships to provide food. When released on foreign shores and islands, they frequently survived, multiplied, and became feral (wild). European rabbits (*Oryctolagus cuniculus*) were released in Australia with devastating effects on both the flora and fauna (Fig. 10.37) (see discussion in Chapter 11). Horses and cattle were introduced into various parts of North and South America in this manner. Cattle were brought to Australia, and pigs and goats established feral populations on many islands, including the Galápagos Islands and New Zealand.

Thirteen young European wild boars were brought to Murphy, North Carolina, in April 1912 and released on a game preserve. In about 1920, an estimated 60 to 100 boars escaped from the preserve. As they dispersed, they hybridized with free-ranging domestic pigs and have since spread throughout several southeastern states. They are the most unwelcome mammal ever to invade Great Smoky Mountains National Park. Hogs feed on mast, roots, and herbs, as well as on invertebrates and small vertebrates like salamanders, voles, and shrews (Figs. 10.38a, b, c). Each wild hog is a little bulldozer, rooting up vegetation in its search for food (Linzey, 2016a).

The Norway rat (*Rattus norvegicus*), black rat (*Rattus rattus*), and house mouse (*Mus musculus*) are native to Europe. By stowing away aboard early sailing ships, they were transported around the world. They are highly adaptable and flourish in most areas today.

Figure 10.37. European rabbits (*Oryctolagus cuniculus*) around a water hole in Australia. In 1859, a farmer in southern Australia imported a dozen pairs of wild European rabbits with the intention of introducing them as game animals. Within six years, the 24 rabbits had mushroomed to 22 million, and by 1907 they had reached every corner of the continent. By the 1930s, their population had reached an estimated 750 million.

The starling (*Sturnus vulgaris*), native to western Europe, was intentionally released into New York in 1896 (Fig. 10.39). These birds are largely commensal with humans, using our structures for nesting sites and agricultural habitats for food sources. They are aggressive, bullying birds that often drive native hole-nesting birds like flickers, purple martins, and bluebirds away from suitable nesting sites.

The English (house) sparrow (*Passer domesticus*) was introduced into New York in 1852. It reached the Pacific Coast in the early 1900s and is presently one of the most successful North American birds, ranging from coast to coast and from Guatemala to central Canada. Like the starling, it is usually abundant only around areas of human habitation. This species is undergoing extremely rapid evolution at the racial level. Local populations already have evolved distinctive combinations of traits. For example, birds in the northeastern United States are large and dark-colored, whereas those inhabiting the southwestern deserts are small and pale. These differences appear to represent adaptations to local climates and other factors.

Mongooses (*Herpestes* spp.) have been widely introduced to kill rats and snakes (see Fig. 10.40a). Nowak (1999) noted that populations of mongooses, *H. auropunctatus* (native to the region from Iraq to the Malay Peninsula), had become established on most Caribbean islands, the northeastern coast of South America, and the Hawaiian and Fiji Islands. He noted that several individuals also had been taken on the mainland of North America. In addition to killing rats, mongooses destroy harmless reptiles, birds, and mammals. A great deal of circumstantial evidence points to the mongoose being responsible for the extinction of many native West Indian birds and reptiles, but definitive proof is lacking. They have also become pests by preying on poultry. The importation or possession of mongooses now is forbidden by law in some countries. In many areas, rats now live in trees, where they are safe from mongooses.

The nutria (*Myocastor coypu*), a South American rodent, was brought to North America as a potential fur-bearer (see Fig. 10.40b). Most of the animals in the United States are thought to have originated from 20 animals brought to Louisiana in 1938 (Nowak, 1999). These mammals have established themselves in marshes in more than 20 states, with the most extensive populations being in the south-central part of the country. They are direct competitors of the native muskrat, as well as with waterfowl.

Brook trout once populated at least 885 km (550 mi.) of the 1,207 km (750 mi.) of fishable streams in Great Smoky Mountains National Park. Before the park was established in 1940, factors like logging and the resulting silting that clogged park streams, inadequately regulated fishing, and the introduction of the brown trout from Europe and the western rainbow trout brought about a reduction in numbers and distribution of the brilliantly colored native brook trout. Rainbow trout, introduced into nearly every watershed in the early 1900s, established themselves as the dominant game species and encroached upon many brook trout populations. When brook trout distribution data from the year 2000 was compared to data collected in 1936–37, it was possible to assess change over a 60-year period. In 17 watersheds surveyed between 1992 and 2000, brook trout populations lost 0.5 to 3.5 km (0.3–2.1 mi.)

of range per stream to rainbow trout during the 60-year period. A brook trout restoration project was begun in 1998. By September 2018, fisheries biologists had been able to restore 13 stream segments totaling 49 km (30.5 mi.) to pure brook trout populations (Matt Kulp, GSMNP Supervisory Fish Biologist, personal communication, September 25, 2018).

(a)

(b)

(c)

Figure 10.38. (*a*) Adult wild hog. (*b*) The lower jaw of a hog showing the enlarged canine teeth. These teeth are most prominent in males. (*c*) Damage caused by hogs.

Many of the small native fishes in the southwestern United States, like pupfishes, have suffered great reductions in their geographic ranges and complete extinction of local populations as a result of introductions of large predatory game fish, especially largemouth black bass (*Micropterus salmoides*), into their habitats. The native fishes are not adapted to large, specialized predators because they have evolved in isolated lakes, streams, and springs for thousands of years during postglacial periods.

The construction of dams and reservoirs has a drastic effect on riverine fauna. Some species can adapt to live in the warmer, more stable hydrological regime; others cannot. Most reservoir fishes stay close to shore, in the mouth of tributaries, and in shallows. Deeper waters are often poorly utilized.

Lake trout (*Salvelinus namaycush*) were distributed widely over northern North America, but they were absent from bodies of water occupied by sea lampreys. Until the construction of the Welland Canal in

1829, the upper Great Lakes were protected by Niagara Falls, which formed a natural barrier impenetrable by sea lampreys. Following the opening of the canal, however, sea lampreys had access to the Great Lakes, and populations of trout were decimated. The first sea lamprey was reported in Lake Erie in 1921 (Dymond, 1922). They were discovered in Lake Michigan in 1936, Lake Huron in 1937, and Lake Superior in 1939. By the late 1940s, the sea lamprey was established in all of the Great Lakes and was causing severe damage to the native fishes, particularly lake trout, which experienced major declines. See additional discussion under Lampreys in the Great Lakes in Chapter 3.

Numerous tropical and semitropical vertebrates, from fishes to mammals, have been released or have escaped in Florida and have become established. The walking catfish (*Clarias batrachus*), marine toad (*Bufo marinus*), brown anole (*Anolis sagrei*), Burmese python (*Python molurus bivittatus*), and several species of neotropical monkeys are just a few examples.

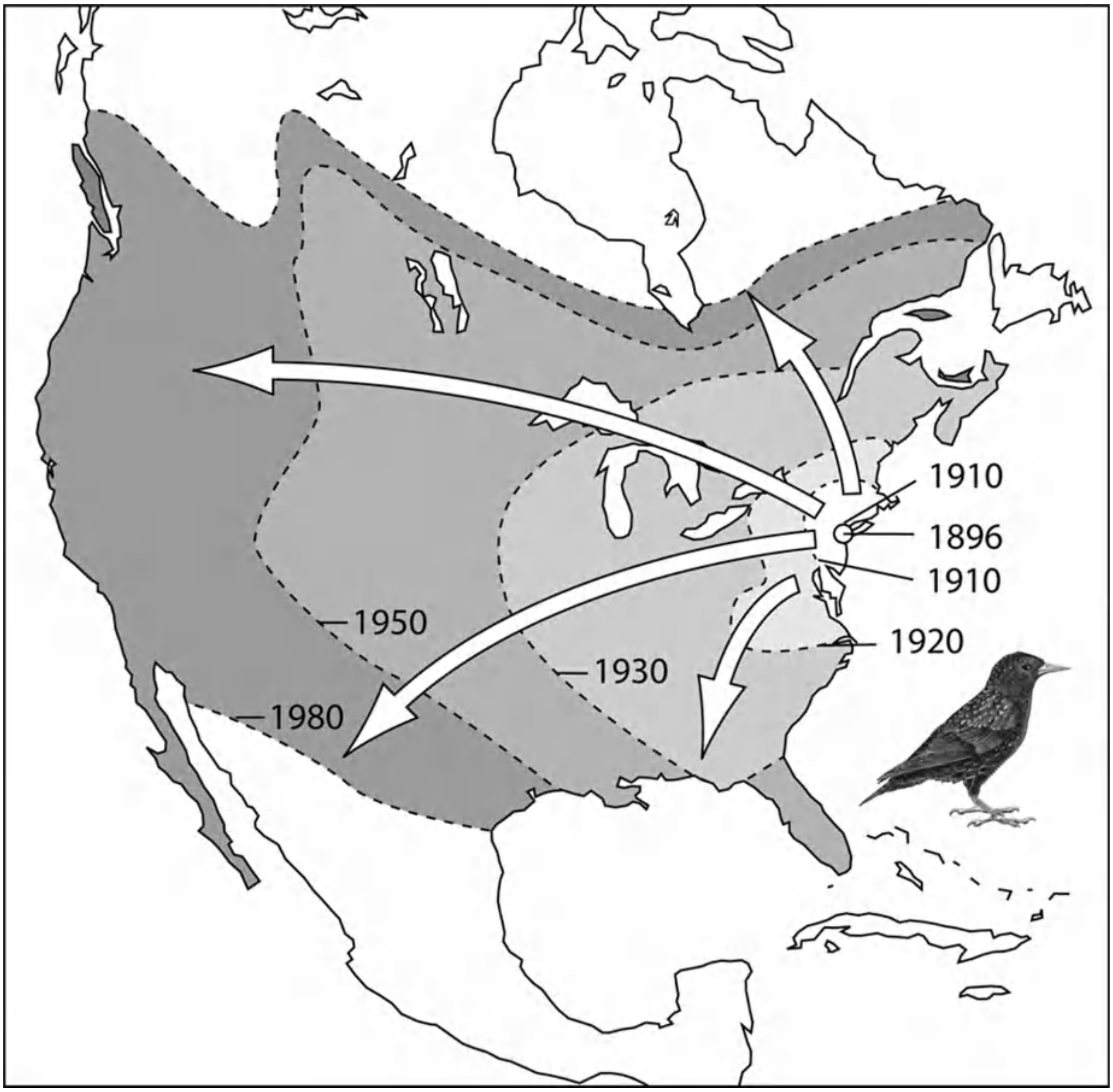


Figure 10.39. The European starling (*Sturnus vulgaris*) (*inset*), which was intentionally introduced into New York in 1896, has rapidly expanded its range in North America. These birds are extremely aggressive and often drive native hole-nesting birds, like bluebirds (*Sialia sialis*), away from suitable nesting sites.

Although most vertebrate introductions have been detrimental to the habitat and/or to other species, some have proved successful. Many of the trouts, including rainbow, brown, and brook trout, have been transported all over the world. The ring-necked pheasant (*Phasianus colchicus*) of Asia and eastern Europe has established itself in some regions of North America. The eastern gray partridge (*Perdix perdix*) became an important game bird in the wheat country of western Canada.

Human activities have been responsible for increasing the rates of extirpation and extinction of species throughout the world. These topics will be discussed in Chapter 16.

Cutting of forested areas for lumber, for farmland, and for villages, towns, and cities has destroyed the habitat of many forest-dwelling species. It has, however, allowed a few species to become more widely distributed. The prairie deer mouse (*Peromyscus maniculatus bairdii*) originally inhabited the prairie grasslands of central North America, but as eastern forests were cleared, it gradually extended its range eastward and colonized agricultural cropland and old fields (Baker, 1968). White-tailed deer in North America are more abundant now than they have ever been. Part of the reason for their abundance has been the elimination of predators like cougars (*Puma concolor*) and wolves (*Canis lupus* and *C. rufus*). Another factor, however, has been the cutting of the forests, which opened vast new areas of fields and second-growth timber, which are ideal deer habitat. This same activity has allowed the coyote (*Canis latrans*) to spread eastward to the Atlantic Ocean and to occur in all 48 contiguous states (Fig. 10.41).

(a)

(b)

Figure 10.40. (*a*) The Egyptian mongoose (*Herpestes ichneumon*) was introduced into Portugal and Spain to kill rats and snakes. (*b*) The nutria (*Myocastor coypu*) is a South American rodent that was brought to North America as a potential commercial fur-bearer.

The Millennium Ecosystem Assessment (MEA) was a four-year (2001–05) study designed to bring the world's best science to bear on the present choices that humans face in managing the global environment. This was the first comprehensive global assessment of the world's major ecosystems, and it examined the state of the world's grasslands, forests, farmlands, oceans, and fresh waterways. The MEA focused on the linkages between ecosystems and human well-being and, in particular, on "ecosystem services." An ecosystem was defined as a dynamic complex of plant, animal, and micro-organism communities and the nonliving environment interacting as a functional unit. The MEA dealt with a full range of ecosystems—from those relatively undisturbed, like natural forests, to landscapes with mixed patterns of human use, to ecosystems intensively managed and modified by humans, like agricultural land and urban areas. Ecosystem services are the benefits people obtain from ecosystems. These include *provisioning services* like food, water, timber, and fiber; *regulating services* that affect climate, floods, disease, wastes, and water quality; *cultural services* that provide recreational, aesthetic, and spiritual benefits; and *supporting services* like soil formation, photosynthesis, and nutrient cycling. The human species, while buffered against environmental changes by culture and technology, is fundamentally dependent on the flow of ecosystem services. The Full Report and Synthesis Reports can be found in the Supplemental Reading and Vertebrate Internet Sites sections.

Figure 10.41. The coyote (*Canis latrans*) has extended its range eastward to the Atlantic Ocean and now occurs in all 48 contiguous states. It has benefited from timber cutting, which has opened vast new areas that were formerly forested.

Review Questions and Topics

1. Discuss the three types of barriers to vertebrate distribution. Give several specific examples of each.
2. Distinguish between biogeographic realms and biomes. In which biome do you live?
3. List the six major biogeographic regions as proposed by Wallace. Give several species of vertebrates that inhabit each region.
4. Define plate tectonics. How has this process affected climate and the distribution of vertebrates?
5. Land bridges have played a major role in the distribution of vertebrates. Name two land bridges and discuss the significance of each.

6. Contrast the effect of mountain ranges in Europe and North America on the distribution of vertebrates during glacial episodes.
7. List several survival adaptations developed by desert species.
8. Differentiate between plankton and nekton.
9. Explain the importance of estuaries to marine communities.
10. What is the difference between the littoral and profundal zones of a lake ecosystem?
11. Which life zone do you live in?
12. Define ecotones and describe their significance.
13. Differentiate between tundra and taiga.
14. Why do you think that amphibians and reptiles are unable to inhabit the Arctic tundra?

Supplemental Reading

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Vertebrate Internet Sites

1. The World's Biomes

   www.ucmp.berkeley.edu/exhibits/biomes/index.php

   Information and links to the six major types of biomes.

2. Rocky Intertidal Habitats

   www.montereybay.noaa.gov/sitechar/rocky.html

   Sections on biological diversity, distribution patterns, temporal changes, links with other habitats, and resource management issues and needs.

3. Plate Tectonics

   www.ucmp.berkeley.edu/geology/tectonics.html

   Information on the history and mechanisms driving plate tectonics. Animations.

4. Alfred Wegener's Theory of Continental Drift

   www.ucmp.berkeley.edu/history/wegener.html

   Discusses the theory that was not fully accepted until the late 1950s.

5. Volcano World

   http://volcano.oregonstate.edu

   Up-to-date information about volcano activity worldwide. Photographs, virtual field trips, and much more.

6. Rainforest Action Network (RAN)

   www.ran.org

   Founded in 1985, RAN works to protect rain forests and the human rights of those living in and around those forests by transforming the global marketplace through education, grassroots organizing, and nonviolent direct action.

7. Tropical Rainforests: Rainforest FAQs

   https://rainforests.mongabay.com/faqs.html

   Many rain forest facts and discussions, photographs, statistics, and much more.

8. Bering Land Bridge National Preserve

   www.nps.gov/bela/index.htm

   National Park Service information on the region, climate, continental glaciation, and native peoples.

9. Millennium Ecosystem Assessment

   www.millenniumassessment.org

   Access the entire Report as well as all of the Synthesis Reports.

11 | Population Dynamics

Birds … are sensitive indicators of the environment, a sort of "ecological litmus paper." … The observation and recording of bird populations over time lead inevitably to environmental awareness and can signal impending changes.

Roger Tory Peterson, 2008

INTRODUCTION

Animal populations, which are dynamic and constantly changing, depend on successful reproduction to maintain their existence. Other important factors in maintaining viable populations include an adequate food supply, sufficient home sites, and the effects of dispersal, immigration, emigration, climate, predation, disease, and parasites. The impact of some of these factors is **density-dependent**—that is, the effect varies according to the population density; for others, the impact is **density-independent**—that is, unrelated to population size.

POPULATION DENSITY

Population density is an important variable that can influence the level of competition for scarce resources. Every habitat has a theoretical maximum number of individuals of a given species that it can support for an extended period of time. This level is known as the **carrying capacity**

(Fig. 11.1a) and is determined by environmental resistance factors acting on the reproductive (biotic) potential of a population. It is primarily determined by the availability of food and shelter.

Vertebrates exhibit three basic types of population growth. Once many species reach the environmental carrying capacity of their range, they maintain relatively stable populations (see Fig. 11.1b). This is especially true of species inhabiting some tropical regions where temperature and rainfall show little variability. Some species that normally maintain relatively stable populations experience sharp population increases at irregular intervals. Such **irruptions**, which cause the population to exceed its carrying capacity, may be the result of such transient factors as a reduction in predators, an increase in food, a favorable change in the weather, or any combination of these. Still other species experience sharp increases in their population sizes at regular intervals, followed by crashes. Species exhibiting regular cyclic population increases usually do so either every 3 to 4 years or approximately every 10 years.

REPRODUCTIVE (BIOTIC) POTENTIAL

The maximum number of young that a population can produce under ideal conditions during a particular time period is referred to as the **reproductive (biotic) potential** of that population. In a healthy, natural population, the birth rate will equal, if not exceed, the death rate, but due to environmentally limiting factors, the reproductive potential is rarely, if ever, reached. Dispersal, immigration, and emigration may affect the reproductive potential to a limited degree.

Most populations will level off after the population reaches a certain size (the carrying capacity). The point at which population growth levels off varies with the species, the habitat, and the climate. A natural population will continue to show fluctuations (seasonal, annual), but they will generally not be far removed from the average carrying capacity (see Fig. 11.1c).

Each individual can affect the reproductive potential of its species in one or more of the following ways:

1. By producing more offspring at a time.

2. By having a longer reproductive life, so that it reproduces more often during its life span.
3. By reproducing earlier in life. The shorter the generation time of a species (that is, the younger its members when they first reproduce), the higher its reproductive potential (Fig. 11.2).

Reproductive rates vary widely among the vertebrates. Some fishes like sturgeon and cod may produce several million eggs annually, whereas many mammals normally give birth to only a single young. Factors like climate and predation of eggs and/or young have undoubtedly been factors in the evolution of egg production. Numerous hypotheses have been proposed to explain clutch size in birds. These were summarized by Lack (1954), who presented arguments for and against each hypothesis. Among the principal hypotheses are the following:

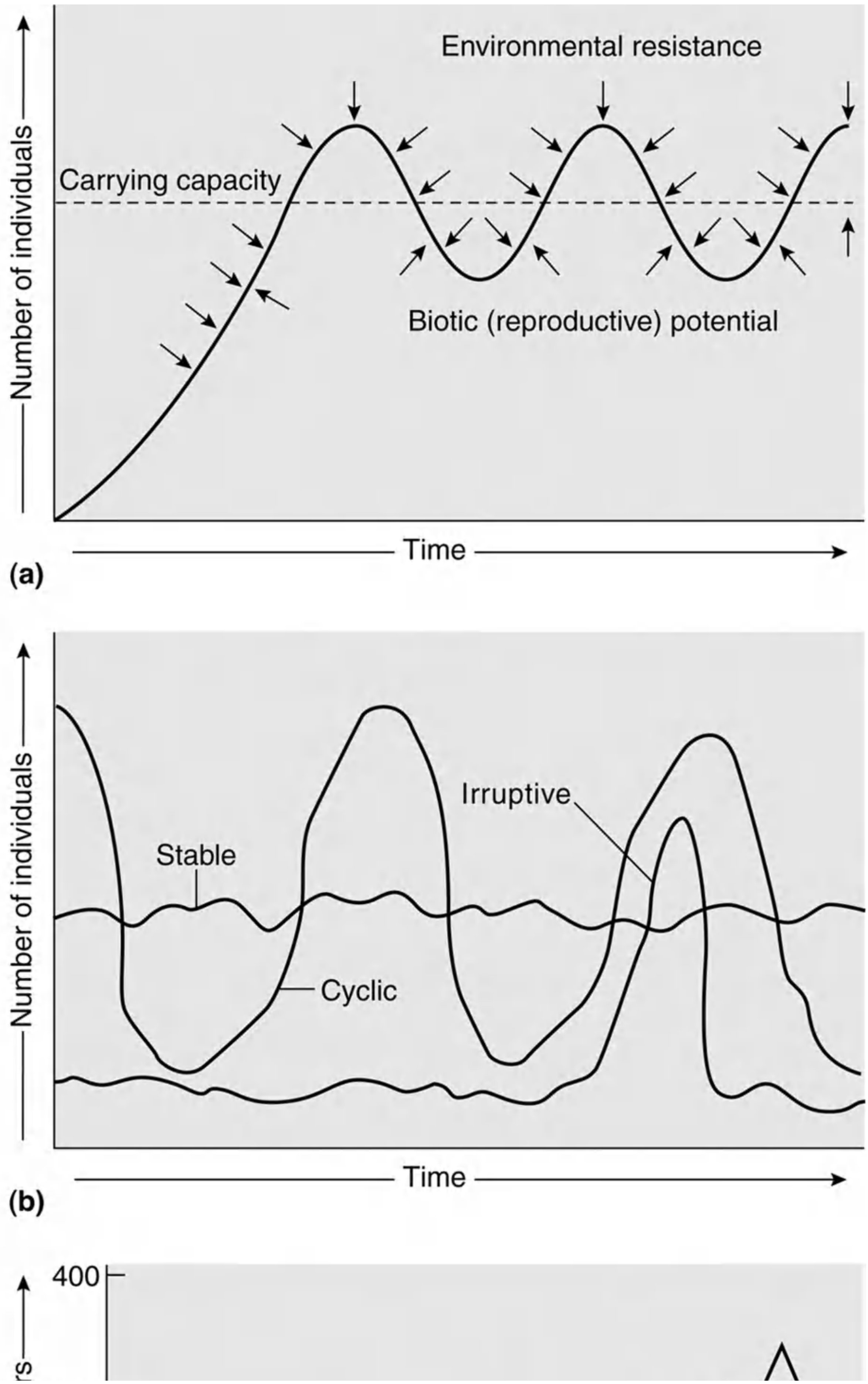

Environmental resistance
Carrying capacity
Biotic (reproductive) potential
Number of individuals
Time
(a)
Irruptive
Stable
Cyclic
Number of individuals
Time
(b)
400
rs

Figure 11.1 (*a*) The theoretical number of individuals of a given species that can be supported for an extended period of time in a habitat is known as the carrying capacity. It is determined by environmental resistance factors (primarily food and shelter) acting on the reproductive (biotic) potential of the population. (*b*) Some populations remain relatively stable after reaching the carrying capacity of their range, some experience regular cyclic population increases, and others experience sharp population increases (irruptions) at irregular intervals. (*c*) A stable population is illustrated by the number of breeding pairs of gray herons (*Ardea cinerea*) in northwestern England. After recovering from the severe winter of 1947, this population showed little fluctuation over a 15-year period.

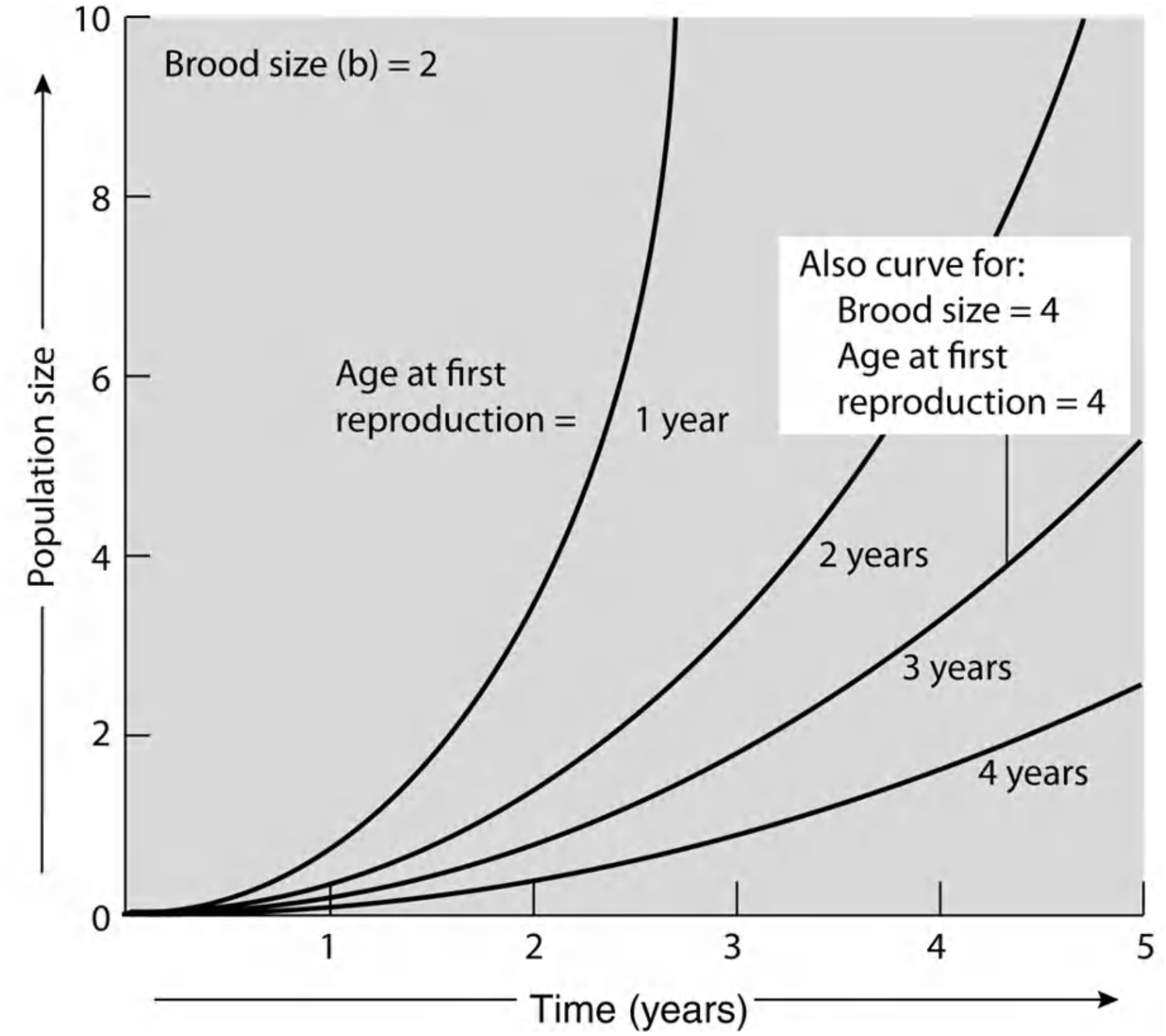


Figure 11.2. Population growth is dramatically affected by the age at which females first reproduce. In each of these examples, females produce two offspring per year, but the age at which females first reproduce differs for each curve (first reproduction at 1, 2, 3, or 4 years of age). Changing the age of first reproduction from 4 to 3 years has the same effect as doubling the brood size from two to four.

1. Females produce as many eggs as they are physiologically capable of producing.
2. Females produce as many eggs as they can successfully incubate.
3. Females produce approximately the number of eggs and young that the parent(s) can satisfactorily feed and care for.

Whereas each of these hypotheses holds true for many species, many exceptions exist. For example, many birds will lay additional eggs in their nests if one or more of the original eggs is removed. This fact has been of extreme importance in the attempt to increase the population of endangered whooping cranes (*Grus americana*). Females normally produce two eggs. When biologists removed one egg for artificial incubation in order to increase the size of captive flocks, the female usually produced and incubated a third egg.

Although many birds apparently produce as many eggs as they can satisfactorily incubate, there are other species that seemingly could incubate more than the number of eggs they produce in the average clutch. Critics of the third hypothesis point out that precocial birds do not need to expend time and energy feeding their offspring.

In studies where clutch size was adjusted experimentally during incubation, larger clutches were associated with significantly lower percentage hatching success in 11 of 19 studies, longer incubation periods in 8 of 10 studies, greater loss of adult body condition in 2 of 5 studies, and higher adult energy expenditures in 8 of 9 studies (Thomson et al., 1998). Since incubation does involve metabolic costs and since the demands of incubation increase sufficiently with clutch size to affect breeding performance, Thomson et al. (1998) proposed that optimal clutch size in birds may in part be shaped by the number of eggs that the parents can afford to incubate.

Among mammals, small prey species like mice, voles, rabbits, and ground squirrels usually produce several litters annually, each of which consists of several young. Many of these species make up the primary consumer level in a food web or food pyramid; they are subsequently consumed by secondary and tertiary consumers (Fig. 11.3). Bailey (1924) recorded a meadow vole that produced 17 litters within 12 months. Larger species, like most ungulates, breed only once a year and produce a single offspring. Although smaller species generally produce greater numbers of young annually than larger species, longevity is also a factor. Many small mammals have a life expectancy of approximately one year. However, most bats, although small, are long-lived—up to 41 years for a Brandt’s bat (*Myotis brandtii*) that was banded in Siberia (Khritankov and Ovodov, 2001) and at least 34 years in *Myotis lucifugus* (Keen and Hitchcock, 1980; Tuttle, pers. comm., 1992). Twenty-three other individuals of *M. brandtii*, all males, survived 25 or more years in the same area. Seven species have been recorded living more than 30 years. Of these, six were observed in the wild: long-eared bat (*Plecotus auritus*), 30 years; little brown bat, Brandt’s bat, Blyth’s bat (*Myotis blythii*), 33 years; mouse-eared bat (*Myotis myotis*), 37 years; and the greater horseshoe bat (*Rhinolophus ferrumequinum*), 30.5 years. One species was kept in captivity, the Indian flying fox (*Pteropus giganteus*), and it lived 40 years (Human Ageing Genomic Resources, 2017).

Hibernating species live on average six years longer than nonhibernating species. With the exception of lasiurine bats, most North American species produce a single young annually. Many predators, like mustelids, canids, and felids, produce only one or two litters annually.

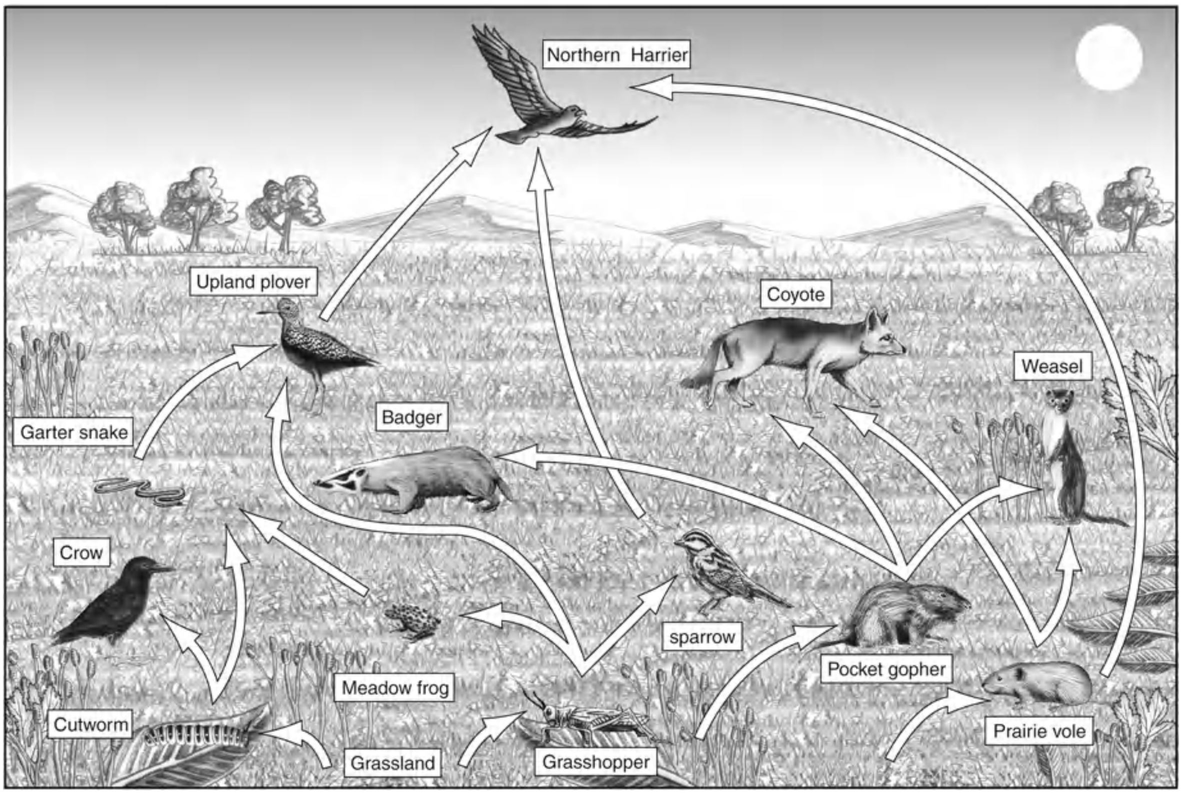


Figure 11.3. A food web for a prairie grassland in the midwestern United States. Arrows flow from the grassland (producer) to various levels of consumers.

The ratio of adults to juveniles varies during the year. Juveniles form a larger proportion of the population during and immediately after the breeding season in temperate regions. By fall and early winter, many juveniles have either matured and become part of the adult population or have been lost. Most temperate populations, therefore, reach their largest size in late fall and early winter. Loss of individuals during the harsher conditions of winter usually leads to low population levels in late winter, just prior to the breeding season of many species. In years when the climate is favorable and food is plentiful, many species may breed well into the fall, resulting in larger populations the next year.

ENVIRONMENTAL RESISTANCE

Although populations have the biotic potential to increase, a variety of factors act to limit the number of young actually produced or that survive. These factors represent the **environmental resistance**. Climate (including rainfall, flooding, drought, and temperature) is a primary controlling factor. Other controls are exerted by intraspecific aggression, inadequate supply of den sites, predation, disease, and parasites. Resistance factors can be grouped into two categories: density-dependent and density-independent.

Density-Dependent Factors

Density-dependent factors are those factors whose effects vary directly with the density of the population. For example, as population density increases, suitable home sites and food may become scarcer per individual. As the rate of individual contacts increases, intraspecific aggression may increase, females may stop breeding, the rate at which nestling young may be killed and/or cannibalized by their parents may increase, and the rate at which juveniles are forced to disperse may be greater than what occurred at lower densities. Parasites can increase in response to population size of the host, and diseases can spread much more rapidly. For example, when waterfowl congregate in dense flocks, the incidence of infection and the chances of an epizootic are increased (Fig. 11.4).

Approximately 600 Mediterranean monk seals (*Monachus monachus*) remain in the wild, mostly in groups of about 20. From May to August 1997, a catastrophic epizootic struck the largest social group (Osterhaus, 1997; Harwood, 1998). Of 270 seals living in a pair of caves on West Africa’s Mauritanian coast, only about 70 survived the disease. Osterhaus (1997) reported that most of the seals examined harbored a dolphin morbillivirus, a virus similar to the one that causes distemper in dogs. Hernandez et al. (1998), however, carried out histopathological examination of lung and other tissues from 14 fresh carcasses and found no indication of typical morbillivirus lesions. There was no evidence of primary viral damage or secondary opportunistic infections in lung tissue, which are hallmarks of morbillivirus infections in other aquatic mammal species. The terminally ill seals exhibited clinical signs of lethargy, motor incoordination, and paralysis in the water—symptoms consistent with drowning caused by paralysis due to poisoning. Hernandez et al. (1998), who identified three species of toxic dinoflagellates in eight water samples collected from near the colony during the mortality event, suggested that poisoning by paralytic algal toxins may have been the cause of death.

Figure 11.4. A concentration of snow and blue geese. When waterfowl congregate in dense flocks, the incidence of infection and the chances of an epizootic like fowl cholera are increased.

Optimal densities may vary seasonally in temperate areas. For example, the lower flow of many streams during summer determines the annual carrying capacity for species like trout (*Salmo*). The winter food supply may determine the annual carrying capacity for many species, even though more animals can be supported during the summer months. In ungulates, food limitation as a cause of density-dependent population regulation has been shown for roe deer (*Capreolus*), wild reindeer (*Rangifer*), kangaroos (*Macropus*), wildebeests (*Connochaetes*), and white-eared kobs (*Kobus*) (reviewed by Skogland, 1990).

One effect of high population density in herbivores is overgrazing. Skogland (1990) reported increased tooth wear and lowered body size and fat reserves in wild reindeer (*Rangifer tarandus*). The author stated:

> During late winter foraging, lichen mats in the Loiseleuria-Arctostaphylion plant alliance become the only available vegetation type due to snow cover (Skogland, 1978). As the unrooted lichens are grazed off, the animals substitute easily digestible lichens in their diet by the dead parts of grasses, dwarf shrubs, and also mosses, with insufficient nutrient content (Skogland, 1984a). Increased use of crustaceous lichens with encrusted small rock particles as well as soil particles and detritus in the ingested diet accelerated molar wear. This lowers chewing efficiency and increases the passage time of larger plant particles into the digestive system whose ability to process energy is slowed down (Skogland, 1988).

Although the adult female survival rate was not affected, a significant negative correlation existed between population density and juvenile winter survival rate. Calves normally were not able to compete successfully with conspecifics of higher rank. Neonatal survival was directly related to maternal condition during the last part of gestation and the calving season (Skogland, 1984b).

Male common toads (*Bufo bufo*) tend to call at low densities, but are more likely to remain silent at high densities (Hoglund and Robertson, 1988). Male wood frog (*Lithobates* [*Rana*] *sylvatica*) density has a significant effect on the behavior of searching male wood frogs at breeding ponds (Woolbright et al., 1990). When the male population density is low, males are more likely to be stationary. As male density increases, more males actively search for females.

High density reduces growth rates in amphibians, thus lengthening exposure to predators and possible unfavorable environmental conditions (Petranka and Sih, 1986; Wilbur, 1987, 1988). Van Buskirk and Smith (1991) recorded significantly reduced survival and growth rates and an increase in the skewness of the size distributions of individuals with increasing density in blue-spotted salamanders (*Ambystoma laterale*) in Michigan. Individuals in high-density populations showed an increased skewness in body size, with only a few salamanders becoming large and most remaining small. This tendency did not occur in populations with lower densities.

Some species seem to have an inherent self-regulating population control mechanism. This is especially true in territorial species in which individuals space themselves so that they have an adequate supply of food and shelter. In other species, when the population increases to a certain size, food and home sites become scarcer, intraspecific aggression increases, and breeding decreases or ceases. Many, but not all, members of the population may emigrate from the area. The best known example is the lemming (*Lemmus*) of Norway. As many members leave the area, more home sites and food become available for those left behind. Intraspecific aggression falls, individuals become better nourished, breeding resumes, and the population begins growing again.

Some species exceed the carrying capacity of their range. Because of all the environmental factors acting to control population increase, this is rare for a natural population. It is most common in those populations that are managed by humans, like herds of deer and elk that are confined to military reservations, parks, and refuges. In addition, herds of elephants whose ancient migration routes and feeding areas are being encroached on by an expanding human population are, through no fault of their own, exceeding the carrying capacity of their dwindling range. In their attempts to locate food, they frequently trample crops and break down fences.

In some areas, predator control measures are undertaken in efforts to increase the numbers of another species, usually a game species. Predators often cull sick, lame, injured, and old individuals from a population. When the predator control measure is implemented, the protected species often increases and may exceed the carrying capacity of its range.

To prevent overpopulation, the levels of many game species are controlled by federal and state agencies. These agencies set limits on the number of individuals of each sex of a given species that can be killed during certain seasons of the year. Formerly, many people were subsistence hunters and utilized most parts of an animal that they killed. Today, some hunters still fall into this category, but most hunters are looking for trophy animals (e.g., the biggest rack of antlers). They attempt to kill the largest, healthiest male specimens in order to mount their heads. Only in recent years have regulatory agencies promoted efforts to cull females from the population in order to balance the sex ratio and manage reproductive rates. In deer and many other species, one male will breed with multiple females; thus, populations can be more efficiently managed by culling some females rather than by focusing exclusively on males.

A coyote-proof enclosure was erected encompassing 391 hectares (966 acres) of pasture on the Welder Wildlife Foundation Refuge in Texas in 1972 (Teer et al., 1991). The immediate response was an increase in the size of the deer (*Odocoileus virginianus texanus*) herd (Fig. 11.5). Fawn survival was 30 percent higher inside the enclosure than outside, where coyotes (*Canis latrans*) were uncontrolled. After several years, the high number of deer caused forage to become scarce, and deer began to die. Studies showed that mortality was caused primarily by lack of adequate food. Parasite loads also had increased. The deer herd reached a low point in 1980, after which it began to increase as food supplies returned to normal. Beginning in 1982, coyotes were once again present within the enclosure, and predation prevented the herd from increasing as it had during the years of predator control.

A classic example of a species exceeding the carrying capacity of its range involved the Kaibab mule deer (*Odocoileus hemionus*) in northern Arizona. In 1906, President Theodore Roosevelt set aside approximately 750,000 acres as the Grand Canyon National Game Preserve. Overgrazing by herds of sheep, cattle, and horses had taken place on the plateau since the 1880s. During that time, many predators had been killed by ranchers and bounty hunters. By the time that the game preserve was established, most domestic stock had been moved elsewhere. At that time, an estimated 4,000 deer inhabited the area. Not only was hunting prohibited, but a predator control program was led by the United States Forest Service. Within the next 10 years, 600 mountain lions were killed. The small wolf population living on the area was almost exterminated by 1926, and it was completely eliminated by 1939. By 1939, more than 7,000 coyotes had been killed (Table 11.1). The winter food supply was the limiting factor that determined the annual carrying capacity, which was estimated to be about 30,000 animals. By 1920, however, an estimated 100,000 deer were present on the refuge. During the next two winters, 60 percent of the population died of starvation. An estimated 75 percent of the fawn crop was lost during the winter of 1924–25.

The numbers continued to decrease due to the depleted range. By 1939, the population had declined to 10,000 animals. However, publicly funded coyote control (trapping, shooting, and poisoning) continued in the area from 1940 until May 1963, resulting in phenomenally high deer densities in the early 1950s (McCulloch, 1986). Presumably due to the high density and inadequate food supply, deer were in poor physical condition and reproduction was low. Due to the high density, a reduction in numbers was required to protect the winter range from overuse. Doe hunts during this period were reinstated to help control the deer population. Beginning in the fall of 1950, corral traps were built and over the next decade about 300 deer were trapped and translocated. Even with the translocations and the increase in the number of hunting permits issued, more and more damage was detected on the winter range browse, but the herd continued to grow. In the winter of 1954, the plateau experienced another deer die-off and, combined with the hunts, reduced the deer herd by about two-thirds. After that, range conditions improved and the body weights of deer started to increase again as the herd recovered. McCulloch (1986) noted that absolute comparisons of herd size estimates could not be made for the different eras like 1906–40 versus 1950–61 versus 1972–79 because the deer inventory methods varied and were not compatible. Private sport hunting and fur trapping continued after 1963. Mountain lions were designated as game animals in 1971, and can now normally be taken only during designated hunting seasons by sport hunters. As of 1977, an estimated 40 adult mountain lions inhabited the Kaibab (McCulloch, 1986). During the period 1972–79, the deer population experienced a decline of 9 percent per year (Barlow and McCulloch, 1984). The authors stated: “Reasons for the decrease in deer abundance from 1972 to 1979 are not yet known. Climatic factors and increased natural predation are both suspected. We know, however, that the decline has not continued. Pellet counts indicate that the number of deer in Kaibab has increased dramatically since 1979, and now may have exceeded the 1972 population size.” Thus, high levels of reproduction and deer in good physical condition have been achieved without predator control programs. The effects of fire, such as the Warm Fire during the summer of 2006, are largely positive in providing aspen, forb, and grass response. Today, the Arizona Game Commission manages the area, controlling the numbers of deer as well as predators, and issues hunting permits to keep the deer in balance with the range. Helicopter surveys are done every four years to arrive at a population estimate. Does are collared with GPS collars that record their exact location several times each day. A new winter range monitoring protocol, begun in 2009, collects data from 21 permanent plots scattered across Kaibab winter range. Hunter check stations provide data on age structure, antler characteristics, body condition, signs of disease, genetics, and more from harvested deer. As of October 2018, the Arizona Game Commission estimate of the Kaibab deer population was 14,000

(Tom McCall, Biologist, Arizona Game Commission, personal communication, October 14, 2018).

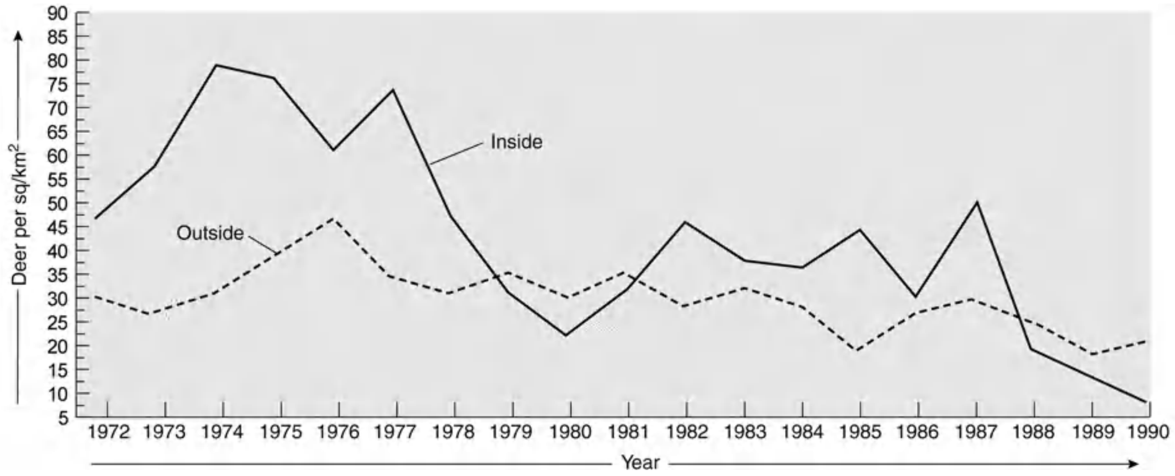
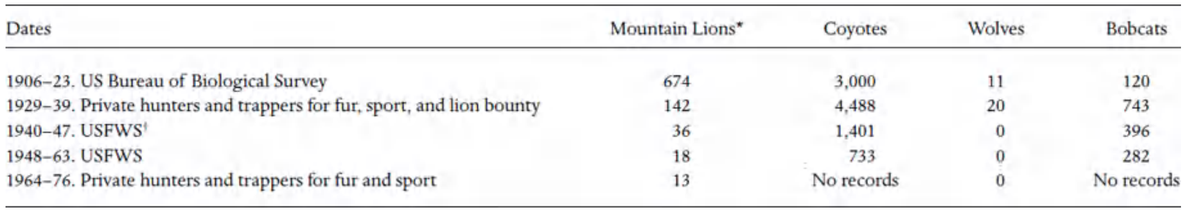


Figure 11.5. White-tailed deer (*Odocoileus virginianus texanus*) population estimates inside and outside the coyote-proof pasture from 1972 until 1990 at the Welder Wildlife Foundation Refuge in Texas.

Table 11.1. Number of Predators Removed from Kaibab Deer Habitat



Dates	Mountain Lions*	Coyotes	Wolves	Bobcats
1906–23. US Bureau of Biological Survey	674	3,000	11	120
1929–39. Private hunters and trappers for fur, sport, and lion bounty	142	4,488	20	743
1940–47. USFWS†	36	1,401	0	396
1948–63. USFWS	18	733	0	282
1964–76. Private hunters and trappers for fur and sport	13	No records	0	No records

Source: From McCulloch, 1986. Copyright © The Southwestern Naturalist. Used by permission.

* Mountain lion bounty ended 1970.

† US Fish and Wildlife Service

In many areas of the world, increasing wildlife populations are creating problems. The spread of communicable diseases, like rabies, has been slowed by reducing the populations of striped skunks, raccoons, and foxes (Bickle et al., 1991). Various control methods involving shooting, trapping, and poisoning have been used. More recently, fertility-inhibiting implants and immunocontraceptive vaccines are being used for birth control purposes (Moore et al., 1997). Norplant implants containing levonorgestrel, a synthetic progestin, have proved to be effective fertility inhibitors in several species, including Norway rats (*Rattus norvegicus*), rabbits (*Oryctolagus cuniculus*), striped skunks (*Mephitis*), and humans (*Homo sapiens*) (Phillips et al., 1987; Bracke et al., 1990; Bickle et al., 1991).

Immunocontraception is a nonhormonal form of contraception based on the same principles as disease prevention through vaccination. An immunocontraceptive causes the production of antibodies against some essential element of the reproductive process, thus preventing pregnancy. The most effective immunocontraceptive currently in use is a vaccine made from pig ovaries known as porcine zona pellucida (PZP). The vaccine is made of minced pig ovaries that are distilled until only the membrane of the eggs (zona pellucida) is left. This is then mixed with a substance that helps stimulate the immune system. When the mixture is injected, it causes an animal’s body to form antibodies that bind to the outside of the egg when the female ovulates, blocking the sperm receptor sites there and preventing fertilization (Daley, 1997). In laboratory tests, the vaccinations have proven to be 90 percent effective and reversible. Fertility returns within a year.

PZP prevents pregnancy in a large number of species, including many different kinds of deer, many zoo animals, dogs, coyotes, burros, free-ranging horses, elephants, water buffalo, and others. A single administration of PZP was effective for more than three years in gray seals (*Halichoerus grypus*) (Brown et al., 1996). It has been used successfully as a contraceptive to control wild horse populations on Assateague Island in Maryland and white-tailed deer on Long Island (Kemp, 1988; Daley, 1997). Annual injections are being used to control bison on Santa Catalina Island off the California coast.

In 2009, the Environmental Protection Agency registered a new gonadotropin-releasing hormone immunocontraceptive vaccine known as GonaCon for use with female white-tailed deer 1 year of age or older. This single-shot, multi-year vaccine stimulates the production of antibodies that bind to gonadotropin-releasing hormone (GnRH), a hormone in an animal's body that signals the production of sex hormones (e.g., estrogen, progesterone, and testosterone). By binding to GnRH, the antibodies reduce GnRH's ability to stimulate the release of these sex hormones. All sexual activity is decreased, and animals remain in a nonreproductive state as long as a sufficient level of antibody activity is present. Deer may need to be injected only once to become infertile for up to five years. Whereas PZP causes multiple estrous cycles in female deer, GonaCon prevents female deer from entering estrus.

Old World rabbits (*Oryctolagus cuniculus*) were introduced successfully to Australia by British settlers in 1859 and to New Zealand a few years later (Grzimek, 1990). The rabbits reproduced until they numbered in the hundreds of millions, causing an ecological disaster in the southern half of Australia (see Fig. 10.37). Unchecked, the burgeoning rabbit population creates deserts by devouring plants, shrubs, and seedlings. The widespread destruction of vegetation seriously harmed the sheep-raising industry. A number of native Australian marsupial species have been endangered or totally eliminated through competition with, or by having their habitats destroyed by, the Old World rabbit. Competition with rabbits for burrows has caused the extinction of one species of bilbie, or rabbit-eared bandicoot (*Macrotis leucura*), and has caused a second species (*Macrotis lagotis*) to retreat to northern Australia, where it is listed as endangered. Other marsupials adversely affected by rabbits include mulgaras (*Dasycercus cristicauda*), hairy-nosed wombats (*Lasiorhinus latifrons*), long-nosed potoroos (*Potorous tridactylus*), and banded hare-wallabies (*Lagostrophus fasciatus*). Livestock, including introduced sheep and cattle, struggle to compete with the rabbits for pasture.

In the early 1950s, Australian government scientists released myxomatosis, a rabbit-killing virus (Kaiser, 1995; Drollette, 1996; Seife, 1996; Adler, 1996a). Although quite successful at first, myxomatosis gradually became less effective, particularly in Australia's dry rangelands. In 1991, researchers began testing a calicivirus known as rabbit hemorrhagic disease (RHD) virus. It kills quickly and fairly painlessly by causing blood clots in the lungs, heart, and kidneys. In March 1995, following laboratory testing, it was injected into rabbits quarantined on Wardang Island in Spencer Gulf, South Australia. By late September, however, the virus had evaded containment (possibly by flying insects) and spread to the mainland, killing rabbits hundreds of kilometers inland. It appears to kill 80 to 95 percent of the adult rabbits it encounters. In September 1996, the Australian government announced a nationwide campaign to reduce the annual $472 million damage that rabbits cause to agriculture. The lethal rabbit virus was released at 280 sites. The expectation was that, after the calicivirus killed most of the rabbits, it would remain in the reduced population and act as a long-term regulator of the rabbit population.

The virus appears to be working exactly as animal control and health officials had hoped (Drollette, 1997). The wild rabbit population has dropped by 95 percent in some regions, and native fauna and flora have begun staging a comeback.

Opponents feared that the virus could jump the species barrier (Anonymous, 1996c). For this reason, the New Zealand Department of Agriculture decided not to introduce the virus pending further study (Duston, 1997). Rabbits had been introduced into New Zealand around the 1830s and have long created problems for farmers. They cost an average of $36 million in lost production, and approximately $20 million in pest control, each year. However, in August 1997, officials confirmed that several dead rabbits near Cromwell in New Zealand tested positive for the rabbit calicivirus (Pennisi, 1997d). It is suspected that the virus, RHD, may have been released intentionally. The virus quickly spread across hundreds of miles, making containment and eradication impossible. The virus, which only affects rabbits and not other animals, was initially effective, but after more than 20 years, the rabbits have become immune to it. In March 2018, the New Zealand government released a new Korean strain, known as RHDV1-K5 (BBC News, February 28, 2018). This strain had been released in Australia in 2017. As with the earlier strain, it causes fever, spasms, blood clots, and respiratory failure. According to the New Zealand Ministry for Primary Industries, this strain supposedly works faster, killing rabbits within two to four days of infection.

Elephant Birth Control Programs

The elephant population in South Africa is estimated at about 20,000 animals. From the 1960s to the 1990s, sharpshooters in Kruger National Park—which holds South Africa's largest elephant population—flew in helicopters over herds and wiped out entire families in order to control the ever-expanding elephant population. Before contraception and other nonlethal means of slowing population growth, culling was thought necessary to protect the plants and habitats elephants and other species depend on. Relocation of some animals has also been tried on occasion.

Female African elephants usually are in heat just two days of every 17 weeks. In an attempt to control the expanding elephant population in South Africa's Kruger National Park, testing began on two forms of contraception in 1996. The first method involved injecting specially designed estrogen implants into 31 nonpregnant females. The implant is designed to slowly release hormones into the bloodstream in much the same manner as the contraceptive pills used by women. In six months, no cow became pregnant. However, the contraceptive caused the females to be permanently in heat, which in turn caused the bulls to be in a perpetual state of sexual excitement. These unintended side effects resulted in a breakdown of the close-knit elephant societies and social responsibilities, including the loss of several baby elephants because their mothers were permanently distracted by as many as eight sexually excited males at one time. Although unwanted pregnancies were prevented, the social cost was too high, and this population control program was discontinued in April 1997.

The second method is based on creating an immunological response with porcine zona pellucida (PZP). PZP contains pig proteins that cause the elephant's immune system to create antibodies. The antibodies bind to the surfaces of the elephant's eggs, blocking sperm from fertilizing, and so make the elephant temporarily sterile without affecting its reproductive hormones. Aerial vaccinations have proven highly effective. Animals are darted from a helicopter, the dart will fall out, and there is no further impact on the herd. The animals are then marked with a pink dye to indicate they have been vaccinated. Annual boosters are required to maintain contraception. The results have been encouraging as the number of calves being born has more than halved. Some of the country's most eminent elephant experts, however, are opposed to the contraception program.

Daley, 1997; Plaut, 2012; Lange, 2015

New Zealand has set a goal of eradicating all non-native predators including stoats, rats, possums, and feral cats by 2050. Prime Minister John Key says the animals kill 25 million native birds each year, and getting rid of them will be "the most ambitious conservation project attempted anywhere in the world" (Davison, 2016).

Density-Independent Factors

Climatic factors like rainfall, flooding, drought, and temperature often play a major role in limiting population growth. Fires and volcanic eruptions also affect populations without regard to their density.

Most species in temperate areas are seasonal breeders, with temperature being a major factor affecting reproduction. They produce their young during the time of year that is most favorable for their survival. Most fishes, amphibians, and reptiles breed in late winter or spring. Birds breed and raise their young during the warmer months of the year. Most mammals produce their young during the same optimum period. Most bats breed in the fall, but because of delayed fertilization (see Chapter 9), the ova are not fertilized until late winter or early spring, and young are born shortly thereafter.

Temperature controls the food supply for many species. A late spring freeze that kills flying insects or forces them to become dormant can have disastrous effects on insectivorous birds like swallows and purple martins (*Progne subis*), as well as on bats. A freeze that kills the buds of oak, hickory, and other mast-bearing trees can create hardship for many animals in late summer, fall, and winter. For example, turkeys, squirrels, deer, bears, and others depend on acorns, hickory nuts, and other mast for their late summer food supply. Mass emigrations of some forms like gray squirrels have been reported during years of poor food supply (Seton, 1920; Flyger, 1969; Gurnell, 1987). During such mass movements, more individuals are susceptible to predation, and many more than normal are struck and killed by vehicles; natural mortality probably also increases. Some species, like black bears, often leave the protective confines of parks and refuges in search of food. Many are shot as nuisance bears when they wander into civilization; others become victims of hunters or motor vehicles.

Members of a species living in an optimal habitat generally produce more young than members of the same species living in a poor habitat. A study of mule deer (*Odocoileus hemionus*) in California revealed that does in good shrubland habitat produced an average of 1.65 fawns annually, whereas does in poor chaparral habitat averaged 0.77 fawns each (Taber, 1956) (Fig. 11.6). At this rate over a four-year period, shrubland does will produce an average of 6.48 fawns, whereas does in chaparral habitat will produce only an average of 3.08 fawns.

The breeding season following a poor food year also usually results in fewer young being born. Litter and clutch sizes will be smaller in many species. Depending on the severity of the food shortage, female white-tailed deer may resorb a developing fetus or give birth to no more than one young. Herd sizes obviously will decrease as the average production per female decreases.

Rainfall, or the lack thereof, can drastically affect the breeding of certain groups, especially amphibians and waterfowl. If breeding ponds and pools dry up before the larvae and tadpoles can successfully metamorphose, annual recruitment may approach zero. Many nesting waterfowl are much more susceptible to predators during periods of drought. Extensive periods of rainfall and flooding also can be disastrous for many species.

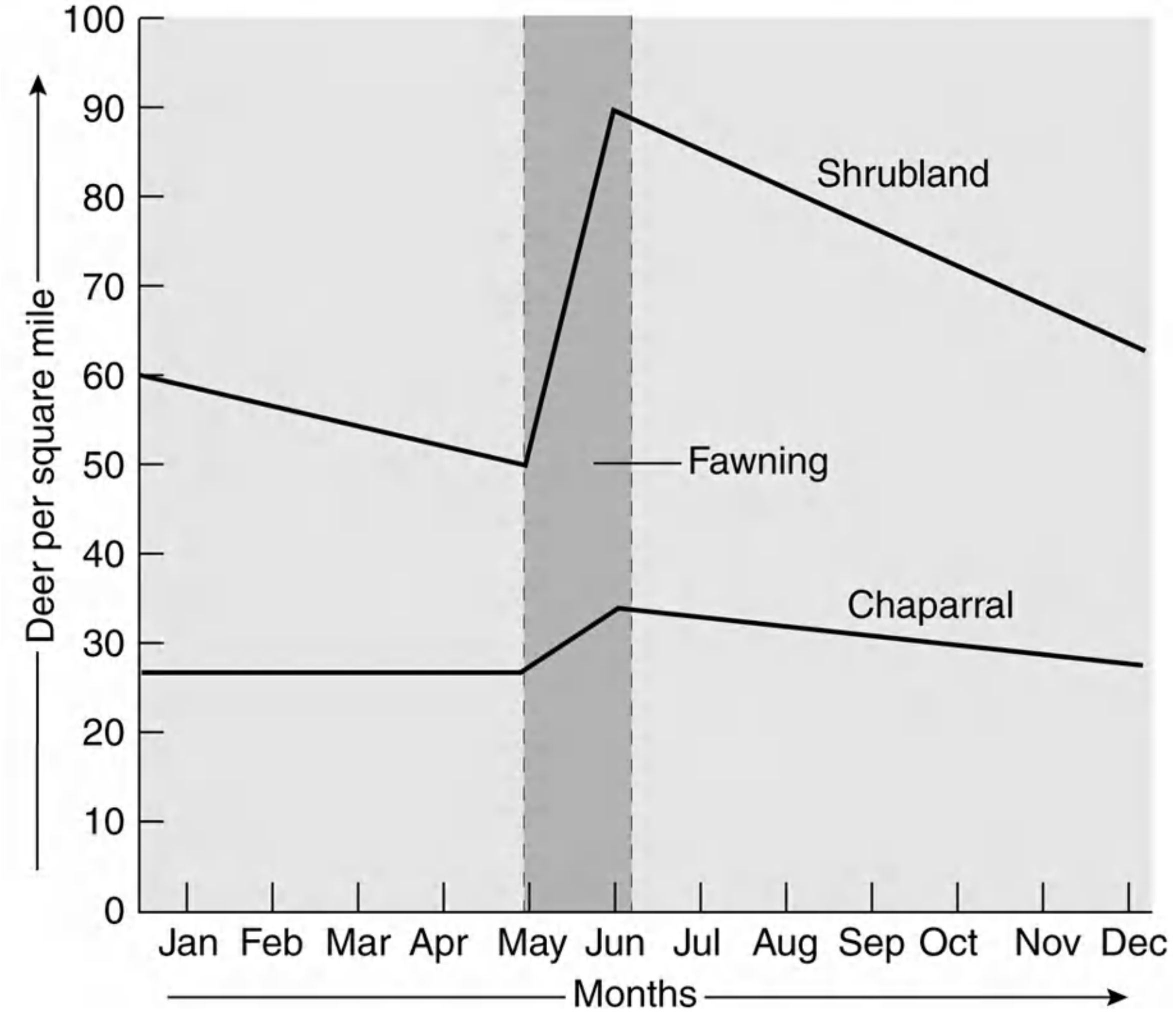


Figure 11.6. Comparison of mule deer (*Odocoileus hemionus*) population density through the year on poor range (chaparral) and good range (shrubland) in California. Females living in shrubland produced an average of 1.65 fawns annually, whereas does in chaparral habitat averaged 0.77 fawns annually. Over a four-year period, shrubland does will produce an average of 6.48 fawns, whereas in chaparral habitat does will produce an average of only 3.08 fawns.

CYCLES

Populations of some species like lemmings and voles show rhythmic fluctuations (Fig. 11.8). Their populations increase for several years and then fall dramatically. This cycle is repeated with some regularity. Three- or four-year cycles are characteristic of certain species inhabiting tundra and northern boreal forests, like lemmings (*Lemmus* and *Dicrostonyx*), voles (*Microtus*), ptarmigan (*Lagopus*), and spruce grouse (*Falcipennis canadensis*), as well as some of the birds and mammals that prey on these species. Some species inhabiting the northern coniferous forests, like lynx (*Lynx canadensis*), hares (*Lepus americanus*), and ruffed grouse (*Bonasa umbellus*), have a longer 10-year cycle.

Due to the intricacies of most food webs, anything affecting one species also will affect one or more additional species. When a prey species is abundant, its numbers will be reflected in increasing numbers of the predatory species (Fig. 11.10). Better-nourished females will be able to produce and successfully care for a larger number of offspring than if they were malnourished and/or emaciated (Madsen and Shine, 1992). In addition, many predators will turn their efforts to a secondary prey if their primary prey becomes scarce. Erlinge et al. (1991) suggested that predation has a significant influence on the pattern of change in a population. In ecosystems dominated by predators specializing on a single species, a cyclic pattern is promoted, whereas in ecosystems dominated by switching "generalist" predators, cyclicity is limited.

Numerous studies of snowshoe (varying) hares (*Lepus americanus*) and a variety of predators have shown significant predator responses to hare cycles (Brand et al., 1976; Brand and Keith, 1979; Powell, 1980; Todd et al., 1981; Thompson and Colgan, 1987) (see Chapter 14). For example, snowshoe hares are the primary prey of many fisher (*Martes americana*) populations. Bulmer (1974, 1975) examined fur sale records in Canada and concluded that population fluctuations of fishers were linked to hare cycles. However, a study of fishers in Minnesota during eight winters when the snowshoe hare population declined revealed that fishers consumed less hare as the hare population declined (33 percent of the diet during 1977–79, but only 3 percent in 1984). Consumption of small mammals (deer mice, *Peromyscus*; voles, *Microtus*, *Clethrionomys*; lemmings, *Synaptomys*; shrews, *Blarina*, *Sorex*; and moles, *Condylura*), however, increased from 4 to 5 percent during 1977–79, to 19 percent of the weight of the stomach contents in 1984. Fat deposits and reproduction (proportion of pregnant females, mean number of corpora lutea, and proportion of juveniles in the fisher harvest) by the fishers did not decrease during the period of the study (Kuehn, 1989).

Figure 11.7. During the winter months, manatees (*Trichechus manatus*) congregate in the Crystal River in Florida, a sanctuary of warm water with an abundance of water hyacinth.

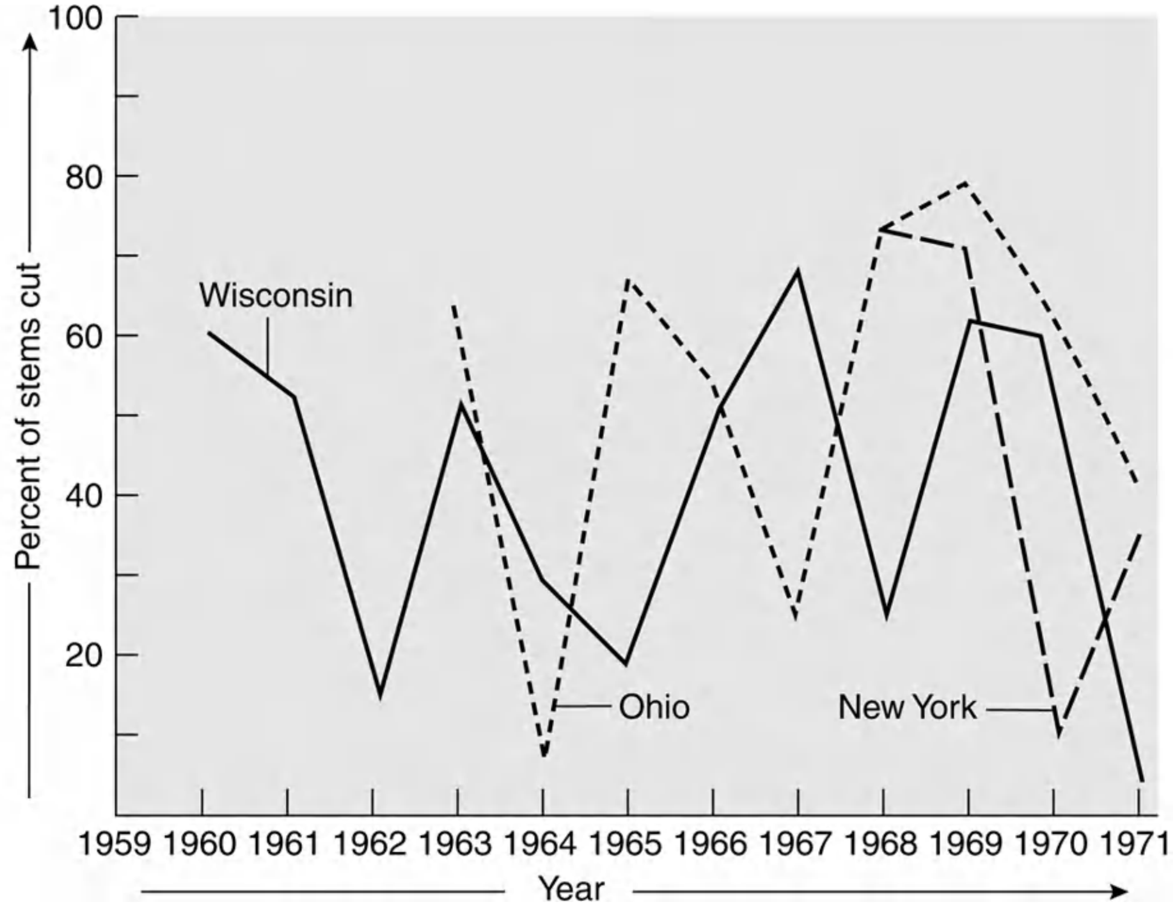


Figure 11.8. Comparison of cyclic population fluctuations of the meadow vole (*Microtus pennsylvanicus*) in Wisconsin, Ohio, and New York based on percentage of stems cut in vole habitats.

MacLulich (1937) presented the original data on cyclic fluctuations of snowshoe hare and Canadian lynx (*Lynx canadensis*) populations obtained from records of pelts received by the Hudson's Bay Company and covering the period from 1845 to 1935 (Fig. 11.11). These data show that these cycles have been going on for as long as records have been kept in North America. It now serves as a classic study of how the cyclic fluctuations of one species (prey) apparently affect another species (predator). More recent studies have shown, however, that lynx are not the primary cause of periodic drops in hare populations, although they may be a contributing factor in the decline. Furthermore, Stenseth et al. (1999) found that the dynamics of lynx populations could be grouped according to three geographical regions of Canada that differed in climate and proposed that external factors like weather influence lynx population density.

In reference to snowshoe hares, Lack (1954) stated: "It is suggested that the basic cause of the cycles is the dominant rodent [snowshoe hare] interacting with its vegetable food to produce a predator-prey oscillation. When the primary consumers decline in numbers, their bird and mammal predators become short of food, prey upon and cause the decrease of the gallinaceous birds of the same region, and themselves die of starvation and/or emigrate." Keith (1974) and Keith and Windberg (1978) proposed an essentially identical theory to explain the 10-year snowshoe hare and grouse cycles. A similar theory was also proposed to explain the three- to four-year vole-predator-small game cycle in Sweden (Hornfeldt, 1978).

Figure 11.9. The brown tree snake has eliminated Guam’s native lizards and many species of Guam’s native forest birds.

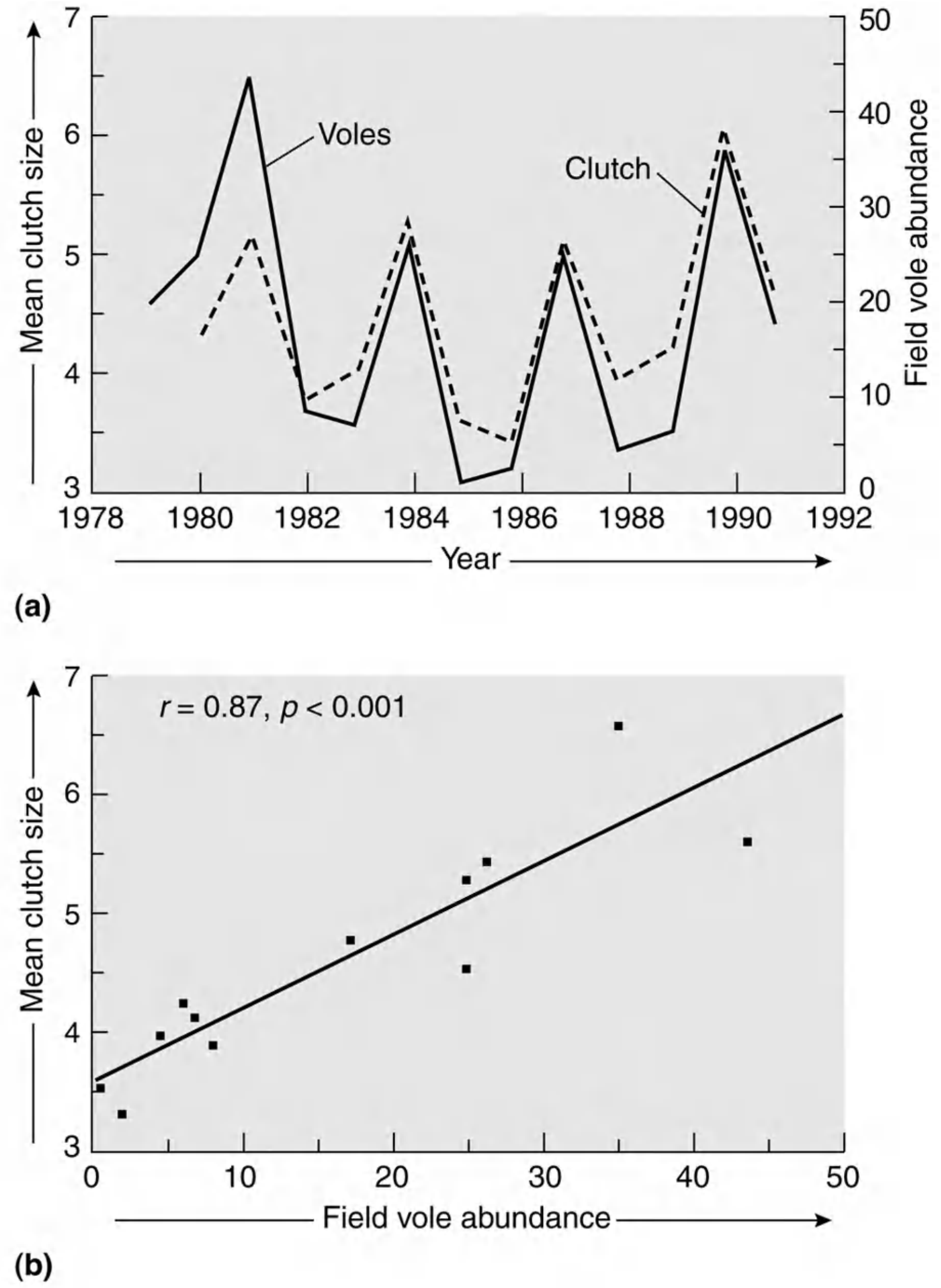


Figure 11.10. (*a*) Average annual clutch sizes of barn owls (*Tyto alba*) show a cyclic pattern clearly in synchrony with the field vole (*Microtus agrestis*) cycle near Esk, Scotland. (*b*) Average barn owl clutch sizes in the Esk study area were closely correlated with spring field vole abundance.

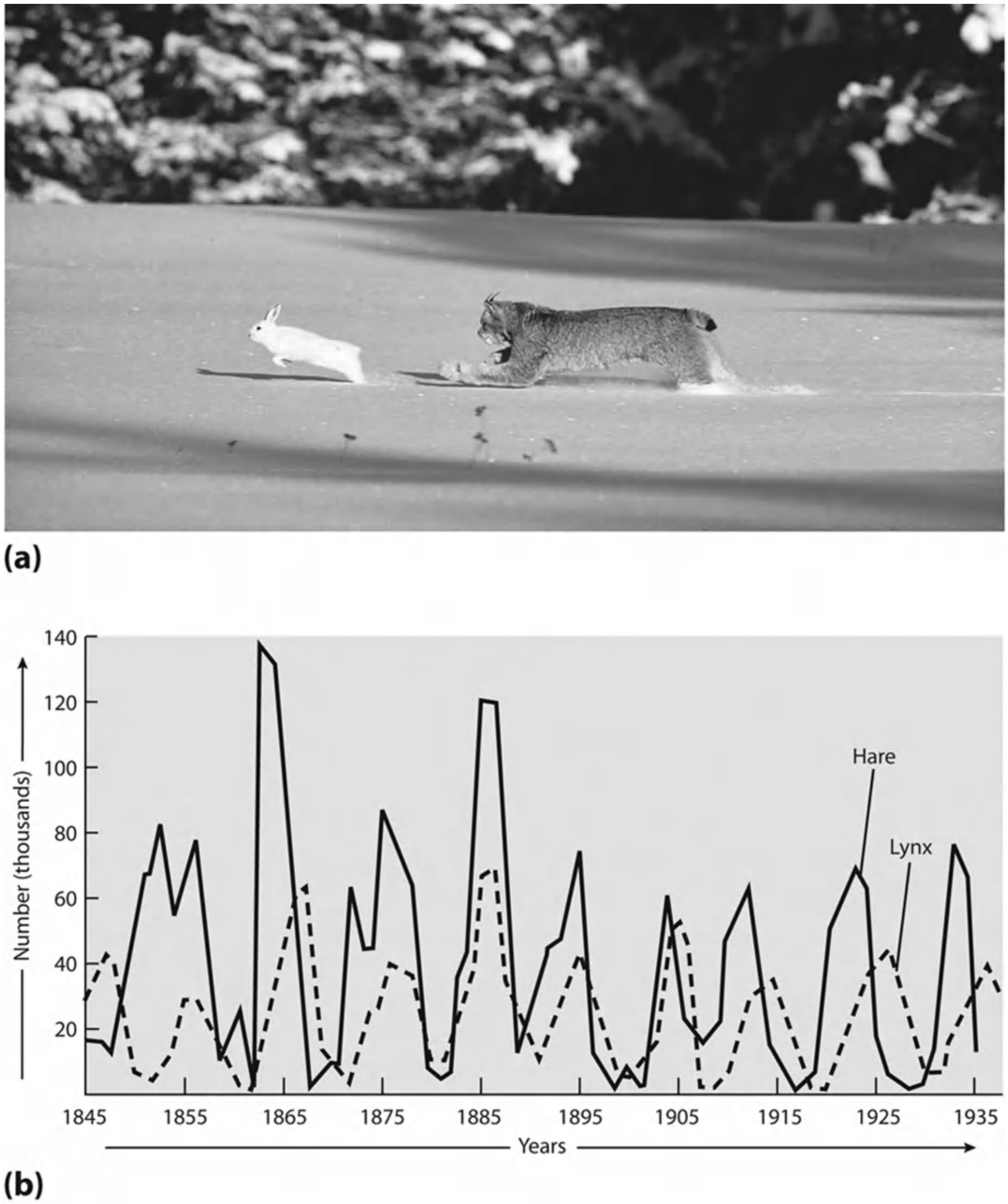


Figure 11.11. (*a*) The snowshoe hare (*Lepus americanus*) and its major predator, the Canadian lynx (*Lynx canadensis*). (*b*) Population cycles for the snowshoe hare and Canadian lynx. The 9- to 10-year cycles are based on records of the Hudson's Bay Company. Increases and decreases in the hare population are followed by corresponding increases and decreases in the lynx population.

Hares normally feed on the bark and twigs of birch, poplar, alder, and black spruce (Fig. 11.12). As hare populations increase, food becomes scarcer, and the hares are forced to feed on the young shoots of these plants, which contain large amounts of toxins (see Chapter 14). The plant toxins act as antifeedants, resulting in a loss of weight and a decline in health in the hares, which causes them to be more susceptible to predation (Jogia et al., 1989; Reichardt et al., 1990a, 1990b). Thus, it appears that the chemical defenses of certain plants serve as a density-dependent means of regulating hare populations, at least indirectly. While hare populations are low, the vegetation recovers, stimulating a resurgence of hare populations and initiating another cycle. It may well be a combination of limited food resources, climatic conditions, and predation—rather than any single phenomenon alone—which explains cycles in hare populations.

Red Tide and Manatees

The deaths of 158 West Indian manatees (*Trichechus manatus*) along Florida's Gulf Coast between Naples and Fort Myers during a three-month period in the spring of 1996 was caused by red tide algae. Red tide is caused by a tiny, plantlike natural alga (*Karenia brevis*) bloom that sporadically occurs along the coast and produces brevetoxins, powerful neurotoxins that cause gastrointestinal and neurological problems when eaten. Animals accidentally ingest the algae while feeding and become almost comatose. Unseasonably cold weather farther north brought a large concentration of manatees to Florida's Gulf Coast (they cannot tolerate temperatures below 20°C (68°F) for extended periods of time), and a strong northwest wind blew a potent strain of the red tide algae deep into manatee feeding areas (see Fig. 11.7). Manatees swam in contaminated water, drank it, and ate sea grass infected with it. When the toxin level got high enough, it attacked the manatees' nervous systems. One of the first nerve centers to be incapacitated was the one that regulates the diaphragm—the major muscle used by mammals for breathing. Many manatees suffocated. Levels of brevetoxin 50 to 100 times normal were found in tissues from the lungs, stomachs, kidneys, and livers of the manatees (Holden, 1996b). The result was the greatest number of manatee deaths from a single event since record keeping began in 1974.

A total of 415 manatees died from red tide, other natural causes, cold weather stress, boats on Florida's waterways, and other undetermined factors in 1996—more than twice as many as the previous record of 206 deaths in 1990. The total Florida manatee population in 1996 was estimated at 2,639.

When aerial surveys began in 1991, there were an estimated 1,267 manatees in Florida. The estimated population in the southeastern United States and Puerto Rico in 2017 was approximately 6,500 with more than 6,300 in Florida's waters.

An algal bloom in 2005 spent 13 months plaguing the gulf from the Alabama border to the Florida Keys. It was the longest in Florida's records and was considered to be the worst to hit Florida since 1971. It started as a small patch of discolored water about 32 km (20 mi.) west of St. Petersburg in January 2005, but it became one of the worst outbreaks of red tide in Florida history. It created a "dead zone" of approximately 3,219 km^2 (2,000 $mi.^2$)—an area in the Gulf of Mexico devoid of oxygen and sea life. It stayed that way until Hurricane Katrina passed through the gulf in August 2005 and whipped up the ocean enough to restore some oxygen. The bloom finally disappeared by February 2006. It killed everything from bait fish and crabs to rays and dolphins. The final death toll included thousands of fishes and birds that fed on infected animals. Red tide killed 93 manatees and more than a hundred sea turtles.

Nobody knows what causes the scattered patches of microscopic red tide algae that float in the Gulf of Mexico all year to suddenly multiply by the millions and turn the water the color of rust. The blooms start 16 to 64 km (10–40 mi.) offshore, and then winds and currents move them toward shore. Are Florida's red tides human-caused or entirely natural? Many researchers believe the algae feeds on the nutrient-rich agricultural runoff from land, causing it to stick around longer and rage more intensely. Others suggest waste from leaking sewage lines and septic tanks could be to blame. Kate Hubbard, a research scientist at the Florida Fish and Wildlife Research Institute in St. Petersburg (the agency in charge of monitoring the bloom), believes that dust from the Sahara Desert may act as a potential nutrient source. Every year, from spring through the fall, winds in Africa pick up tiny dust particles from the desert and carry them thousands of miles across the Atlantic Ocean where they land in and around the Caribbean Sea and the Gulf of Mexico. One of the minerals found in the dust is iron. As the dust falls into the gulf, it attracts a plantlike bacterium known as *Trichodesmium*. The bacteria use that iron to convert any nitrogen in the water into a form that can be consumed by other marine organisms. One of these organisms that absorbs the converted nitrogen is red tide algae. A 2014 study by the National Oceanic and Atmospheric Administration found that, out of 12 possible sources, *Trichodesmium* provided the most nitrogen for red tide blooms.

Another devastating eruption began in October 2017 and was still continuing as of August 2019 with no end in sight. Turtles have been hard hit; hundreds were killed in 2018. Many are the critically endangered Kemp's Ridley sea turtles. For each year from 2013 to 2017, biologists counted more than 6,000 manatees swimming in Florida's waterways. A big cold snap early in 2018 proved deadly for manatees. A total of 804 manatees died in Florida waters during 2018, close to the record of 830 in 2013. Boats killed 119 manatees in 2018, breaking the record of 106 set in 2016 and tied in 2017. As of October 1, 2018, 103 manatee deaths were attributed to the red tide bloom. The 2017 total was 538 with 106 killed by boaters. In 2016, boaters also killed 106. The highest manatee mortality for a single year was 830, a record set in 2013 amid a cold snap and a wave of red tide poisonings, as well as a mysterious ailment in manatees found in the Indian River lagoon.

In addition to red tide, Florida's inland waterways are clogged with a bloom of green cyanobacteria. Runoff from cattle farms and residential developments that lie north of Florida's largest body of fresh water, Lake Okeechobee, carries in nutrients, turning the waters of the lake into a thick greenish mass. Development and sugar farms south of the lake prevent the natural trickling and filtering of overflow through the Everglades. Instead, to prevent flooding of nearby towns, heavy rains force engineers to release polluted water into the estuaries that lead out to the sea.

In 2017, the US Fish and Wildlife Service decided that manatees, Florida's official marine mammal, were no longer on the brink of extinction and should no longer be listed as endangered. They were reclassified as threatened. However, their low tolerance for cold water and their susceptibility to red tide toxins may prove difficult obstacles to overcome.

Anonymous, 1997b; US Fish and Wildlife Service, 2017f; Pittman, 2018a, 2018b; Tavel, 2018

Figure 11.12. Snowshoe hare (*Lepus americanus*) browsing intensively on an early successional shrub. As the density of hare populations increases, trees like alder, poplar, black spruce, and birch become overbrowsed. The new shoots that emerge contain high concentrations of toxins, which result in a loss of weight and decline in health of the hares, causing them to be more susceptible to predation. As the hare populations decline, the vegetation recovers.

Some researchers feel that some cycles can be explained by another type of nutrient recovery, namely, seed production (Pitelka, 1964). Many northern plants have seed cycles of approximately three and a half years. These plants require this time to build up sufficient nutrient material to produce seeds. Such a cycle corresponds closely to the population cycles of many small mammals.

In northern Scandinavia, microtine rodent populations are cyclic. Interestingly, the production of willow ptarmigan (*Lagopus lagopus*) chicks is usually low in microtine rodent crash years. Although some plants in this region produce compounds (estrogens) that have negative effects on bird and mammal reproduction, it could not be found that intense herbivory from the microtine rodents induced production of plant estrogens in the spring food plants of the ptarmigan (Hanssen et al., 1991).

Gliwicz (1990) proposed that an important intrinsic factor regulating population diversity is a regular dispersal of first-born young of the year from their natal habitats. Population cycles in microtine rodents are an ecological consequence of this dispersal behavior, which normally results in annual cycles. Multiannual cycles occur only under certain sets of extrinsic factors. Low abundance of predators or sufficient snow cover to reduce predation is required for cycles to occur.

Cyclicity only occurs in communities with few predators (Hansson and Henttonen, 1988). High predation pressure normally prevents small rodents from population cycling by keeping their densities low, especially during winter and early spring (Hansson, 1979; Erlinge et al., 1983; Erlinge, 1987).

Although many possible explanations, including extraterrestrial events like sunspot cycles, have been proposed to explain cycles (reviewed by Keith, 1963; Roseberry and Klimstra, 1984), their most immediate and probable cause is the interaction of the population and its environment. In addition, some species may possess an inherent self-regulation (biological clock) that triggers the cyclic events. Cyclic trends in local populations are poorly documented, primarily because intensive, long-term data for such populations are generally lacking.

Red grouse populations in England exhibit cyclic fluctuations in abundance with periodic crashes. By experimentally reducing burdens of a nematode parasite in the grouse, Hudson et al. (1998) were able to prevent population crashes, thus demonstrating that the impact of a nematode parasite on the host was the cause of the cyclic fluctuations in this species.

Invasion of the Brown Tree Snakes

The US territory of Guam is being overrun by brown tree snakes (*Boiga irregularis*), a nocturnal, tree-climbing, bird-eating, egg-gobbling reptile that can reach 3 m (almost 10 ft.) in length (see Fig. 11.9). They are a rear-fanged semiconstrictor that is mildly venomous. Due to the placement of the fangs and their grooved, rather than hollow architecture, the venom is difficult to convey into a bite on a human, and thus is delivered in small doses. The venom appears to be weakly neurotoxic and possibly cytotoxic with localized effects that are minimal for adult humans.

Brown tree snakes, which were accidentally introduced, most likely by the US military in the late 1940s or early 1950s, and are native to Australia, Papua New Guinea, and the Solomon Islands, encountered no natural predators in Guam and an abundant food supply. The population of these snakes has soared to an estimated 2 million or more—about 10,000 per 1.6 km^2 (approximately 400 acres). Localized estimates sometimes reaching 20 or more snakes per acre (0.4 hectare) of jungle are among the highest snake densities ever recorded. The snakes are active at night and inhabit trees, shrubs, and forests. They hang like vines from trees, fences, and power poles. Power outages caused by electricity arcing across snakes spanning power lines have become a frequent problem. These snakes have caused the extirpation of most of the native forest vertebrate species. They have eliminated Guam's native lizards and 9 of 18 species of Guam's native forest birds; six of the remaining species are endangered and the other three are rare. The ravaging of the island's birdlife has had a serious effect on the surrounding tree population since birds are primary seed dispersers. With more than two-thirds of the island's trees relying on animals to distribute and germinate their seeds, the impact of the reduction is expected to be a devastating drop of between 61 and 92 percent in seedling recruitment. The snakes have also caused widespread loss of domestic birds and pets.

Current research on the breeding patterns of the brown tree snake is being conducted in hopes of further understanding how environmental stressors such as lack of shelter, climate change, overcrowding, and loss of prey are affecting the population density. A study by Moore et al. (2005) suggested that a lack of food resources was placing individuals under chronic stress, resulting in suppression of the reproductive system.

The US Department of Agriculture (USDA) began airdropping biodegradable bait cartridges, each consisting of a dead mouse and 80 mg (0.003 oz.) acetaminophen tablets—the generic equivalent of Tylenol (which is deadly to the reptiles)—into the forests surrounding Naval Base Guam. The mice are attached to two pieces of cardboard and a streamer. The rodents get caught in tree branches, where the snakes can easily find and eat them. Considerable reduction efforts were achieved leading to more widespread application. In addition, the USDA's Wildlife Services program uses snake trapping in high-risk areas, trained snake-detector dogs in cargo, nighttime spotlight searches, and public education as tools to achieve their goal of preventing these snakes from being transported to vulnerable locations. The USDA spends $5 million annually to keep the snakes from getting into Guam's outbound cargo. In 2016, more than 10,000 snakes were removed from areas surrounding Guam's airports and seaports.

Extensive efforts are being taken to prevent this snake from invading Hawaii, which is home to 40 percent of the nation's endangered birds (many of which are already threatened by introduced wildlife). Snake-sniffing beagles and their handlers closely inspect every commercial and military flight from Guam. In 2017, the USDA expanded its arsenal of snake traps near Honolulu airport.

Currently, the brown tree snake population on Guam is declining with an equilibrium population size predicted to be approximately 30 to 50 snakes per hectare (12–20 per acre). The decline may be identified as a result of depleted food resources, adult mortality, and/or suppressed reproduction.

Douglas, 1997; Allen, 1998; Fritts and Rodda, 1998; Moore et al., 2005; Mortensen et al., 2008; Lendon, 2010; Rogers et al., 2017; Zannes, 2017; Guam Wildlife Services, 2018

IRRUPTIONS

Enormous numbers of animals sometimes occur in a given area for brief periods of time because of certain environmental and climatic conditions. Abnormally high numbers of a given species are known as irruptive growth (Malthusian growth) and are of limited duration (see Figs. 11.1b and 11.13). Conditions leading to irruptions may involve a combination of mild winters, an abundant food supply, and the removal of predators (as with Kaibab deer). Using long-term trapping records (22 years) of desert small mammals in the Simpson Desert in central Australia, Greenville et al. (2012) demonstrated that extreme climatic events drive mammal irruptions. They used 100-year trends to show that irruptive events are driven by extreme rainfalls and that increases in the magnitude and frequency of extreme rainfall events are likely to drive changes in the populations of these species through direct and indirect changes in predation pressure and wildfires.

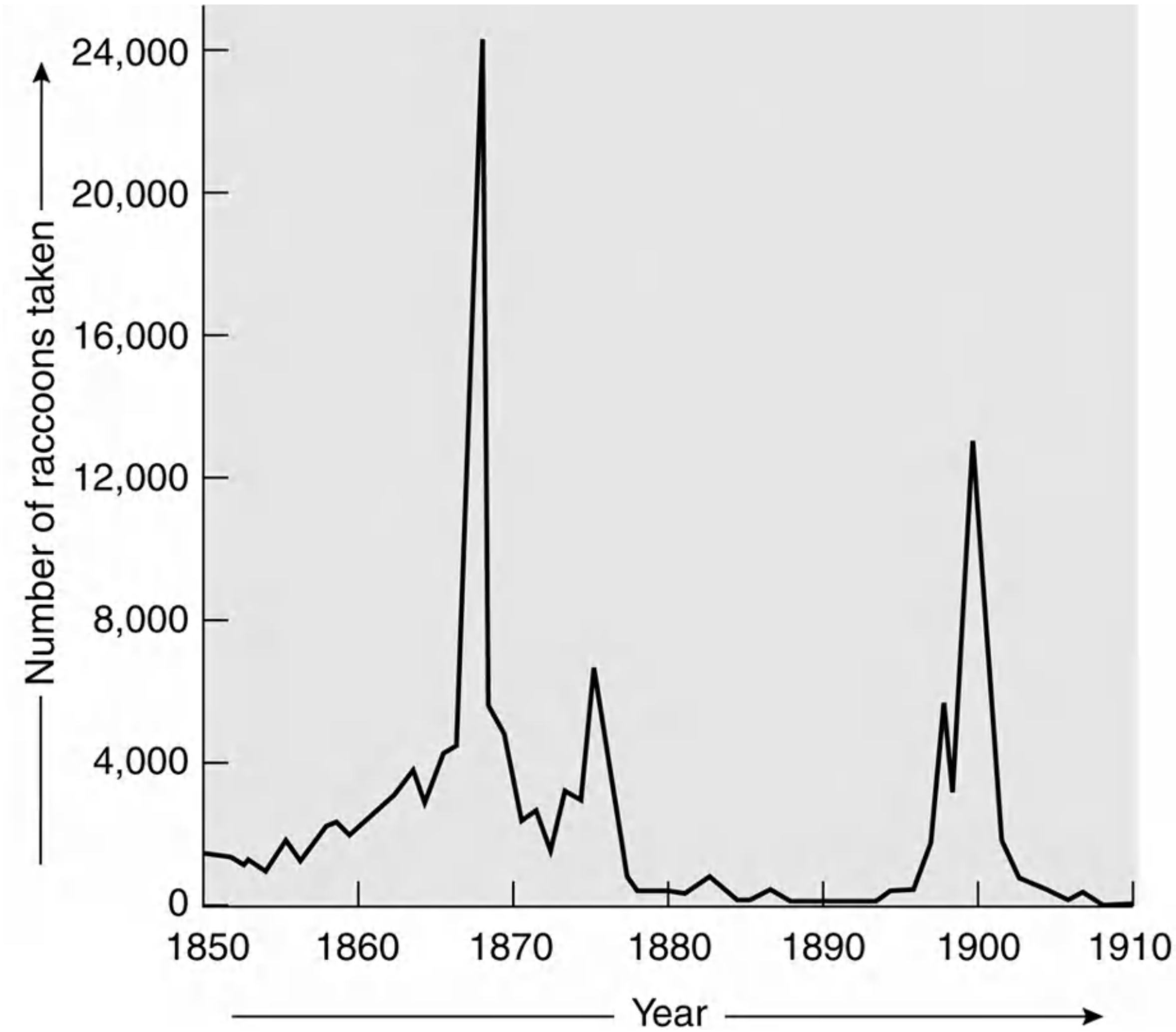


Figure 11.13. A 60-year record of raccoon pelts taken in the same general area and purchased by the Hudson's Bay Company illustrates the irruptive changes in the population. These irruptive changes were caused by occasional improvements in the weather followed by returns to more normal conditions.

Species known as r-strategist species are characterized by rapid development, early reproduction, small body size, and shorter lifespans, whereas K-strategist species exhibit slow development, delayed reproduction, large body size, and longer lifespans (Vandermeer and Goldberg, 2013). Variable population sizes occur in r-strategist species, and these species are more likely to exhibit irruptive growth than K-strategist species, whose populations are usually constant and remain at or close to the carrying capacity of their environment. Higher productivity (number of offspring produced) results from r-selection, while K-selection leads to high efficiency (refers to the quality and the probability of survival of individual offspring).

The greatest irruption ever recorded in North America involved the montane vole (*Microtus montanus*) (Fig. 11.14). This spectacular irruption occurred in 1906–08 in Nevada and California (Piper, 1909). In some areas, estimated population density exceeded 25,000 voles per hectare (2.5 acres). Approximately 10,000 hectares (24,711 acres) of alfalfa—stems, leaves, and roots—were destroyed in Humboldt County, Nevada. In 1957–58, a smaller, but more extensive, outbreak of montane voles occurred in California, Oregon, Washington, Idaho, Nevada, Utah, southwestern Montana, and western Wyoming (Spencer, 1959; White, 1965). Although most densities per hectare were in the hundreds, maximum population density in some areas was estimated to be between 5,000 and 7,500 individuals per hectare (2.5 acres). Predator populations (owls, hawks, gulls) increased (by immigration) and helped to lower vole densities. A high incidence of tularemia, caused by the bacterium *Pasteurella tularensis*, was found among these animals during the subsequent decline and may have been a (density-dependent) factor in the population decline. Another factor in the decline of high populations may be the exhaustion of the adrenal gland (see the Endocrine System section in Chapter 9) brought on by stress caused by the high level of intraspecific interaction (Christian, 1950, 1959, 1963; Autrum and von Holst, 1968; von Holst, 1969). Stress stimulates the adrenal medulla to secrete epinephrine (adrenaline) and norepinephrine (noradrenaline). These adrenal secretions assist in preparing an animal's body for stressful situations by altering blood flow, adjusting heart and breathing rates, decreasing action of the digestive system, and so forth. Under conditions of continuous stress, this chemical control system may cease functioning.

Figure 11.14. The most extensive irruptions ever recorded in North America have involved the montane vole (*Microtus montanus*).

Review Questions and Topics

1. What defines the carrying capacity for a particular environment? How are carrying capacities for game species regulated by state wildlife agencies?
2. List several factors that affect carrying capacity.
3. How does carrying capacity relate to humans? List several ways in which humans have increased the carrying capacities for certain regions.
4. Differentiate between density-dependent and density-independent factors. Give examples of limiting factors that come into play when a population of mammals reaches very high density.
5. List some modern techniques that are being used to control exploding vertebrate populations.
6. The release of the rabbit hemorrhagic disease virus in Australia has been very controversial. If the virus should jump the species barrier, what steps would you undertake to keep it under control?

7. List several theories that have been proposed to explain cyclic fluctuations in mammals.
8. How do irruptions differ from cyclic fluctuations?

Supplemental Reading

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Vertebrate Internet Sites

1. The Great Backyard Bird Count

   www.birdsource.org/gbbc

   A joint project of the Cornell Lab of Ornithology and the National Audubon Society. An annual four-day event that engages bird watchers of all ages in counting birds to create a real-time snapshot of where the birds are across the continent. Anyone can participate, from beginning bird watchers to experts. Information on how to participate, photos, online bird guide, tips for identifying birds, how to choose and use binoculars, bird feeding tips, and more.

2. Mammals: Arctic Biodiversity

   www.arcticbiodiversity.is/index.php/the-report/chapters/mammals

   The Arctic Biodiversity Assessment by the Arctic Council is a report submitted to the Arctic Biodiversity Congress in Rovaniemi, Finland in October 2018. It is a set of status and trend reports, key findings, and policy recommendations. Chapters include Species Diversity, Mammals, Birds, Amphibians and Reptiles, Fishes, and more.

3. The Lynx-Snowshoe Hare Cycle

   www.enr.gov.nt.ca/en/services/lynx/lynx-snowshoe-hare-cycle

   Department of Environmental and Natural Resources, Northwest Territories. Discusses density, food habits, population declines, and effects of cycles on the lynx and snowshoe hare.

12 | Movements

Migratory birds bind up the corners of this increasingly fragmented globe—uniting the poles and the tropics, forests and deserts, wilderness and cities. A planet that sustains them will sustain us; their fate is our fate.

Scott Weidensaul, 1999

INTRODUCTION

Vertebrates are mobile animals that move about to secure food, to locate suitable homes and nesting sites, to avoid unfavorable periods of the year, and to find mates. Some species move very little during their lifetimes, whereas others, like golden plovers (*Pluvialis dominica*) and elephant seals (*Mirounga angustirostris*), may cover more than 20,000 km (12,427 mi.) annually. Some movements are seasonal, or annual, whereas other movements occur only once in a lifetime. Orientation consists of two different phenomena: the control of an animal's position and stability in space and the control of an animal's path through space (Wiltschko and Wiltschko, 1994). Movements undertaken by vertebrates can be categorized on the basis of where and when they occur—home range movements, dispersal, invasions, migration, homing, and emigration. Alternatively, movements can be classified by the mechanisms by which the movement is achieved—vision, hearing, olfaction, navigation, or compass orientation. Our understanding of the way in which animals know how, when, and where to orient and navigate around their environment has grown considerably over the last few decades.

HOME RANGE

Home range is highly variable and is often difficult to define. It is the area around the home of an individual that is covered by the animal in its normal activities of gathering food, mating, and caring for its young. Home ranges may be linear, two-dimensional, or three-dimensional.

Home range generally is correlated with the size of the animal. Small forms usually have relatively small home ranges, whereas larger species normally have larger home ranges. Among mammals of the same size, carnivorous species like cougars (*Puma concolor*) generally have larger home ranges than herbivorous forms like white-tailed deer (*Odocoileus virginianus*). A carnivore must expend considerably more energy and cover a much greater area in order to secure sufficient food. However, some small aerial species, including bats, hummingbirds, and warblers, cover great distances during their daily activities.

Other factors affecting home range size include habitat, population density, sex, age, body size, and season of the year. In polygynous and some monogamous species, males generally have larger home ranges than females; in polyandrous birds, however, the female’s home range is larger (Blair, 1940d; Adams, 1959; Linzey, 1968). Very young and very old individuals of many species usually have the smallest home ranges. Animals living in marginal habitats generally need larger ranges than members of the same species living in better habitats. For example, Layne (1954) found that red squirrels (*Tamiasciurus hudsonicus*) living on the maintained portion of the Cornell University campus in central New York had an average home range of 2 to 2.5 hectares (5–6.2 acres), while red squirrels living in the more diverse and natural habitats of the nearby gorges had average home ranges of 0.12 to 0.16 hectares (0.3–0.4 acres).

Population density may also play a significant role in determining the home range, with the average size of the home range generally decreasing as population density increases. Linzey (1968) recorded an average home range of 0.26 hectares (0.6 acres) for male golden mice (*Ochrotomys nuttalli*) and 0.24 hectares (0.6 acres) for females over a three-year period in the Great Smoky Mountains National Park. During a portion of this study, the population decreased drastically in size. During this period, the male home range more than doubled to 0.63 hectares (1.6 acres), but the female home range, possibly because of nesting responsibilities and caring for young, remained approximately constant at 0.21 hectares (0.5 acres). The density of large trees, and possibly population density, were factors that affected koala (*Phascolarctos cinereus*) home ranges in Australia—males, 1 hectare (2.5 acres); females, 1.18 hectares (2.9 acres) (Mitchell, 1991b). Some animals that live in northern regions, like white-tailed deer, have a larger home range during the warmer months of the year but live in small restricted areas, termed *yards*, during the winter months.

Few long-term home range studies exist. One such study of three-toed box turtles (*Terrapene carolina triunguis*) covered a period of 25 years. It revealed permanent home ranges varying from 2.2 to 10.6 hectares (5.4–26.1 acres) in size for turtles known to have inhabited the study area for all 25 years (Schwartz and Schwartz, 1991).

Home range figures are subject to a great deal of variation; therefore, these figures must be used with a great deal of caution. Many methods can be used to calculate the home range of a species; thus, results are somewhat subjective. Figure 12.1 illustrates three basic methods of calculating home range using the same capture sites. The minimum area method, calculated by computing the area within the actual capture sites, results in the smallest measured range. The boundary strip methods utilize a boundary strip that extends half the distance to each of the nearest traps around it. This method recognizes that even though an animal entered a particular trap, it probably also utilized some of the adjacent areas. The inclusive boundary strip method connects the outer points of the boundary strips, includes the greatest amount of area, and results in the largest home range estimate. The exclusive boundary strip method allows the investigator to utilize his or her judgment about unsuitable areas of habitat when drawing the perimeters of the home range. This home range value will be between the minimum area estimate and the inclusive boundary strip estimate. Though it is possible to gain an approximate idea of the size of the home range of a species, such statistics should not be accepted as absolute. Table 12.1 lists typical home ranges for selected vertebrates.

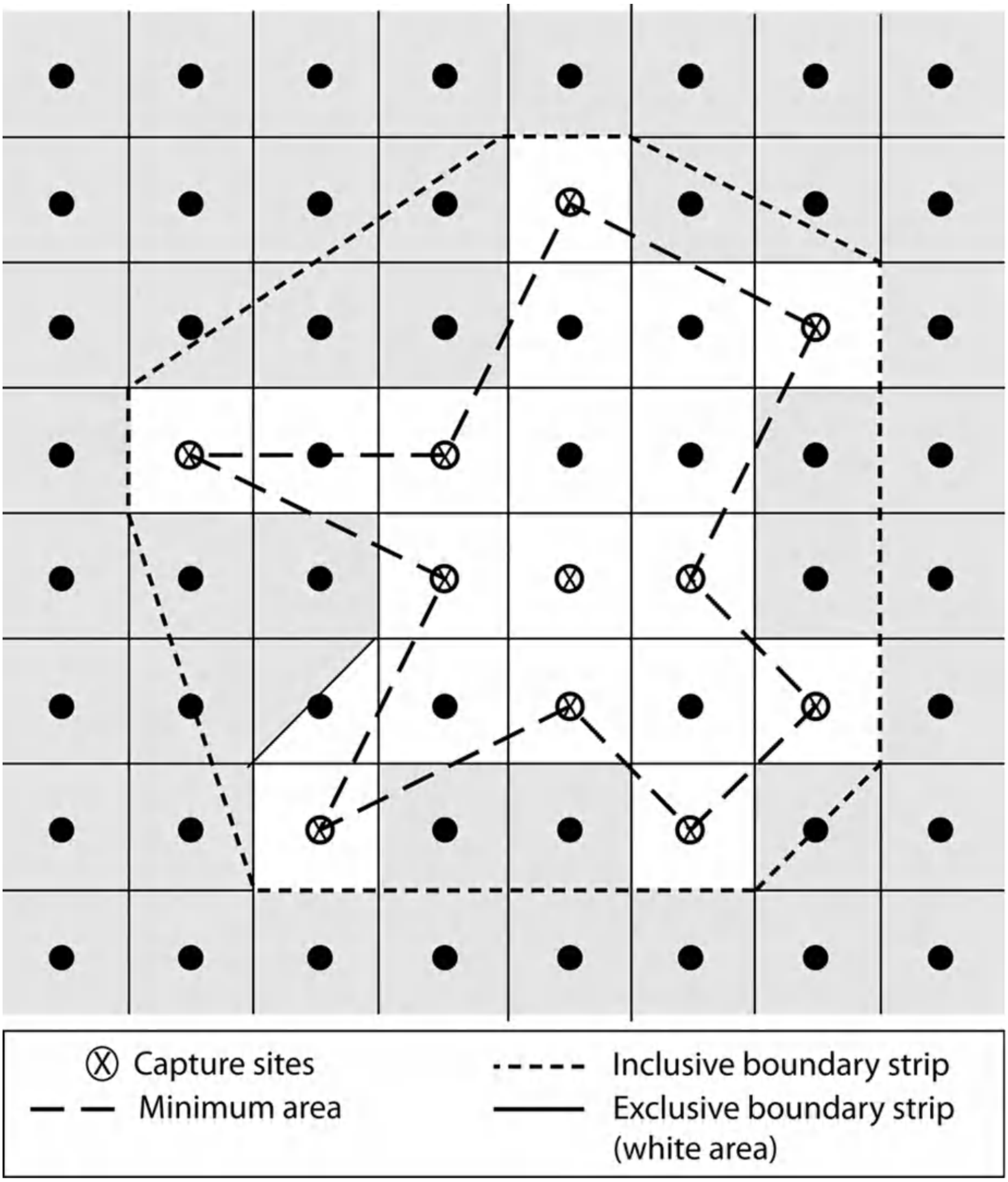


Figure 12.1. Three standard methods of calculating home range.

Under normal conditions, many animals have permanent ranges and spend their entire lifetimes within these areas. Most frogs, salamanders, lizards, turtles, snakes, moles, shrews, woodchucks, chipmunks, deer mice, and many others establish permanent home ranges. For example, after dispersing from their parental (natal) area, many lizards will remain in the same area throughout their lives. The home range generally will center around a favorable basking site or perch (Fig. 12.2). Migratory species like sea turtles, many birds, elk, and caribou have seasonal home ranges. Their summer home ranges usually include the locations where they reproduce and care for their young, and their winter range is in a different area in order to allow them to survive adverse seasonal or climatic conditions.

Most home ranges are usually amorphous or amoeboid in shape. Some may be bounded by natural landmarks like a river, whereas others are bounded by human-made structures like roads or railroad tracks. Home ranges and even "core areas" (areas of high-intensity use) of several members of the same species often overlap. For example, giant pandas have ranges between 3.9 and 6.2 km^2 (1.5 and 2.4 mi.^{2}) that may overlap extensively (Catton, 1990). Most pandas, especially females, tend to concentrate their activity within core areas of 0.3 to 0.4 km^2 (0.1–0.15 mi.^{2}).

Overlapping areas usually are not used at the same time; this helps to avoid conflict. However, in western North Carolina, neighboring black bears often use areas of overlap for the same activities (e.g., feeding, denning) at the same time (Horner and Powell, 1990). In Alabama, adult home ranges of long-nosed (nine-banded) armadillos (*Dasypus novemcinctus*) overlapped extensively, and there was no indication of territorial or aggressive interactions (Breece and Dusi, 1985). Adults often were seen feeding within 3 m (9.8 ft.) of each other, and on one occasion, three adults were seen leaving one den.

Home ranges often are marked by means of glandular secretions (pheromones), urine, or excrement. Ungulates, like deer, use secretions from tarsal and metatarsal glands on their lower legs and orbital glands on their head to mark their home ranges. Tenrecs (*Echinops telfairi*) put saliva on the object to be marked and transfer their body odor by alternately scratching themselves with a foot and then rubbing the foot in the saliva. Galagos (*Galago* sp.) urinate on the palms of their hands and rub the urine into the soles of their feet. When climbing about, they leave obvious scent marks that also are visible as dark spots. Some mammals in which the anal glands are well developed, like martens (*Martes*) and hyenas, use pheromones from anal glands to mark their home range. Gray squirrels (*Sciurus carolinensis*), fox squirrels (*S. niger*), and red squirrels (*Tamiasciurus hudsonicus*) use cheek-rubbing to deposit scent from glands in the oral-labial region (Benson, 1980; Koprowski, 1993). Rabbits use their pheromone-containing chin glands, urine, and feces for marking. Small mounds of fecal pellets indicate that an area is occupied.

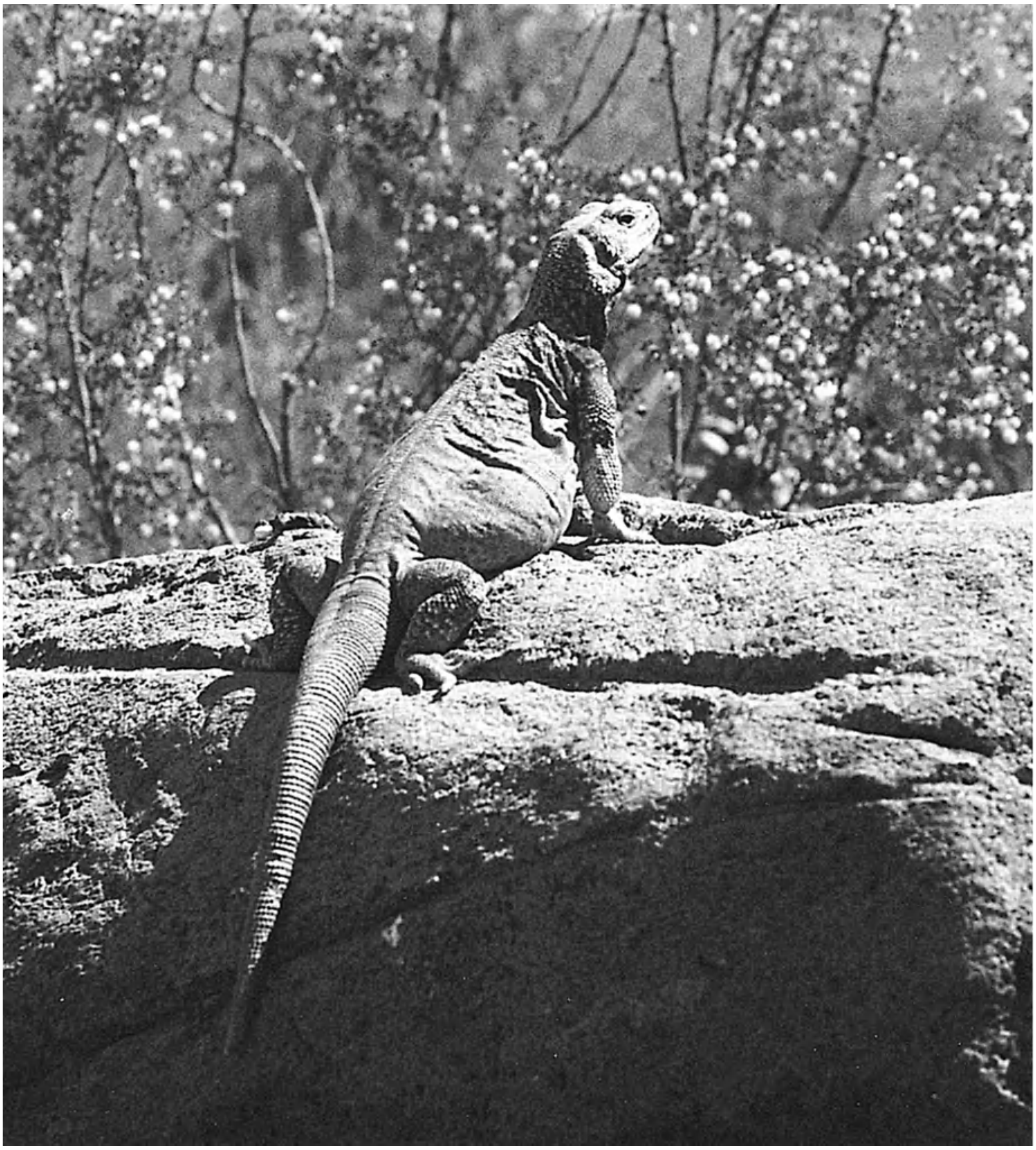
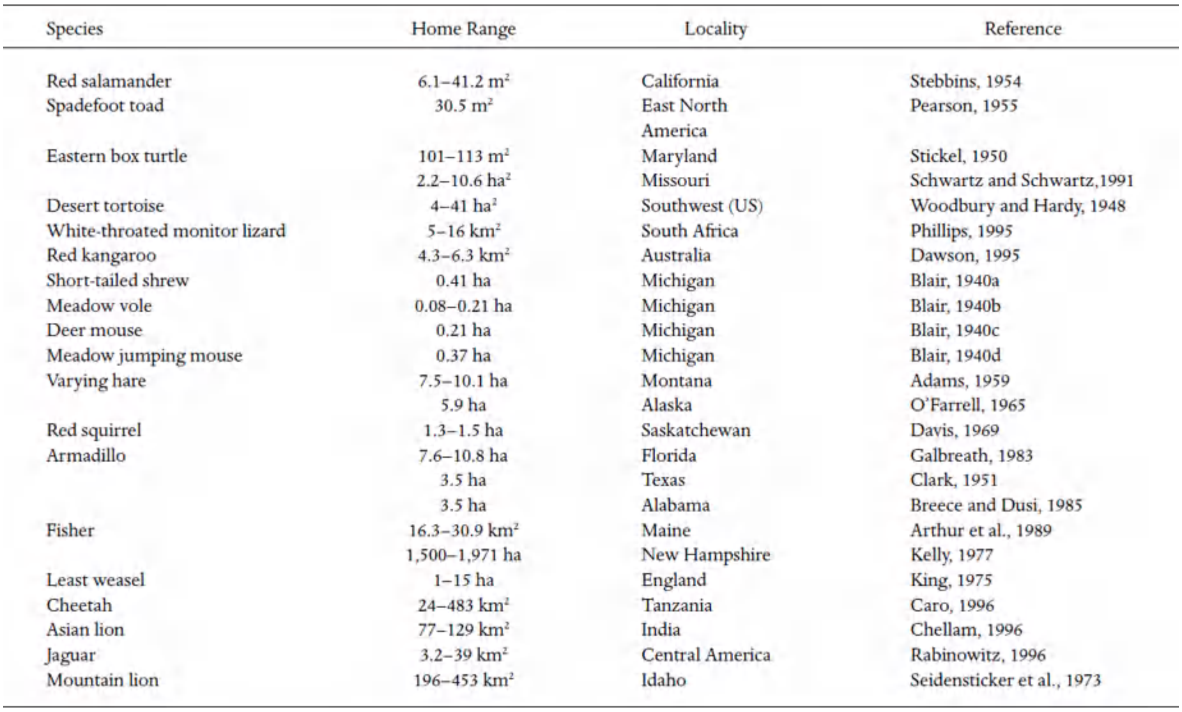


Figure 12.2. A chuckwalla (*Sauromalus obesus*) basking in the warm Arizona desert sun.

Table 12.1. Home Ranges of Selected Vertebrates



Species	Home Range	Locality	Reference
Red salamander	6.1–41.2 m^2	California	Stebbins, 1954
Spadefoot toad	30.5 m^2	East North America	Pearson, 1955
Eastern box turtle	101–113 m^2	Maryland	Stickel, 1950
	2.2–10.6 ha^2	Missouri	Schwartz and Schwartz,1991
Desert tortoise	4–41 ha^2	Southwest (US)	Woodbury and Hardy, 1948
White-throated monitor lizard	5–16 km^2	South Africa	Phillips, 1995
Red kangaroo	4.3–6.3 km^2	Australia	Dawson, 1995
Short-tailed shrew	0.41 ha	Michigan	Blair, 1940a
Meadow vole	0.08–0.21 ha	Michigan	Blair, 1940b
Deer mouse	0.21 ha	Michigan	Blair, 1940c
Meadow jumping mouse	0.37 ha	Michigan	Blair, 1940d
Varying hare	7.5–10.1 ha	Montana	Adams, 1959
	5.9 ha	Alaska	O'Farrell, 1965
Red squirrel	1.3–1.5 ha	Saskatchewan	Davis, 1969
Armadillo	7.6–10.8 ha	Florida	Galbreath, 1983
	3.5 ha	Texas	Clark, 1951
	3.5 ha	Alabama	Breece and Dusi, 1985
Fisher	16.3–30.9 km^2	Maine	Arthur et al., 1989
	1,500–1,971 ha	New Hampshire	Kelly, 1977
Least weasel	1–15 ha	England	King, 1975
Cheetah	24–483 km^2	Tanzania	Caro, 1996
Asian lion	77–129 km^2	India	Chellam, 1996
Jaguar	3.2–39 km^2	Central America	Rabinowitz, 1996
Mountain lion	196–453 km^2	Idaho	Seidensticker et al., 1973

The "**home**" is within the home range and serves as a refuge from enemies and competitors. It may be in the form of an underground burrow, a cave, a tree cavity, a rotting log, an arboreal nest, or a brush pile. It may be the nest of a bird, the temporary "form" (nest) of a rabbit, or the more permanent burrow of a gopher tortoise (*Gopherus*) or woodchuck (*Marmota*). It may serve a single animal (cougar), a pair of adults and their offspring (beaver, *Castor canadensis*), or a colony of animals (flying squirrels, *Glaucomys*; golden mice, *Ochrotomys*). Some species, like harvest mice (*Reithrodontomys*), have been shown to have a metabolic rate ranging from 7 percent to as much as 24 percent lower when in their nest than when they are active (Kaye, 1960).

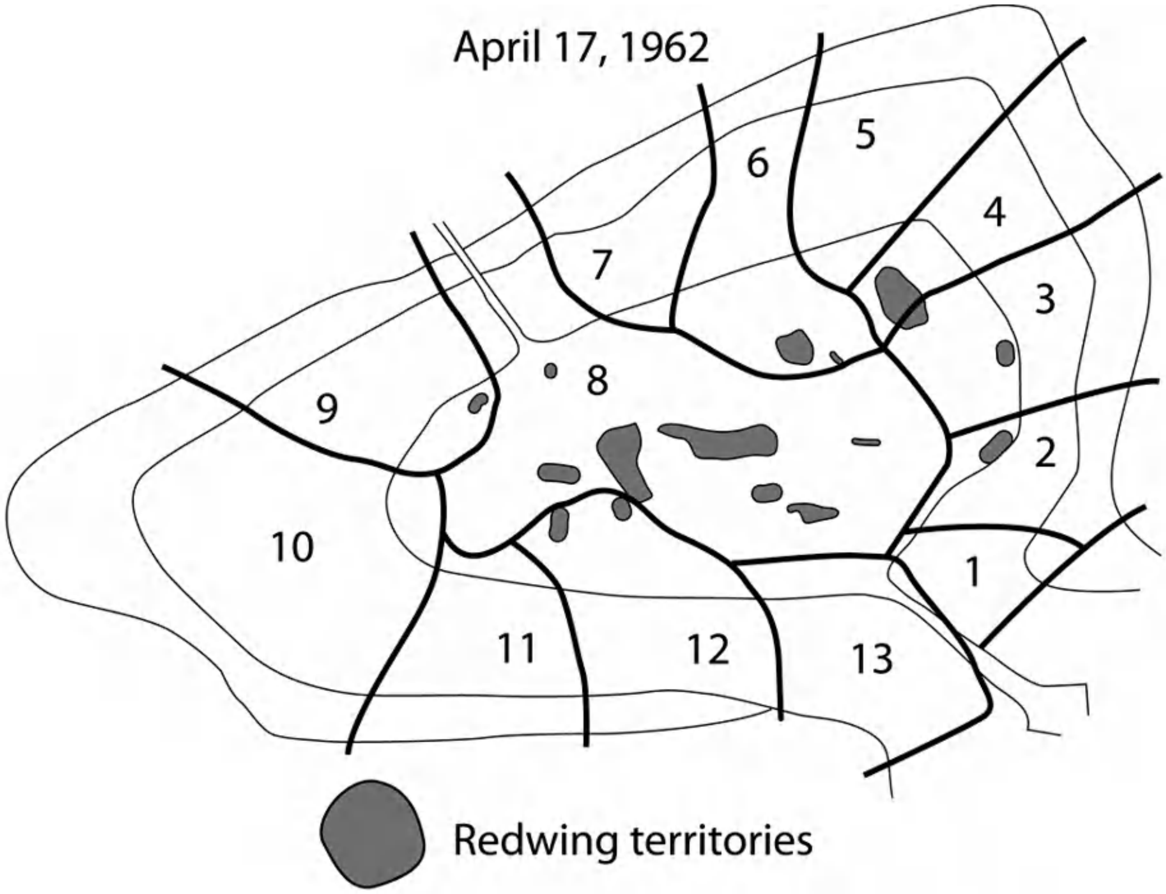
Radio transmitters attached to subterranean naked mole rats (*Heterocephalus glaber*) revealed that the network of tunnels constructed by a colony currently comprising 87 animals was more than 3 km (1.9 mi.) long and occupied an area greater than 100,000 m^2 (1,076,391 $ft.^2$)—about the size of 20 football fields (Sherman et al., 1992) (Fig. 12.3). Much of the tunneling to dig their vast network of tunnels is a cooperative effort to find food. One animal gnaws at soil, while others, in turn, transport it to a surface opening, where it is ejected by a larger colony mate. (See Chapter 13.)

Figure 12.3. Naked mole rats (*Heterocephalus glaber*) live in a cooperative eusocial society. These subterranean mammals dig vast networks of tunnels—in some instances, more than 3 km (1.9 mi.) long—to locate food.

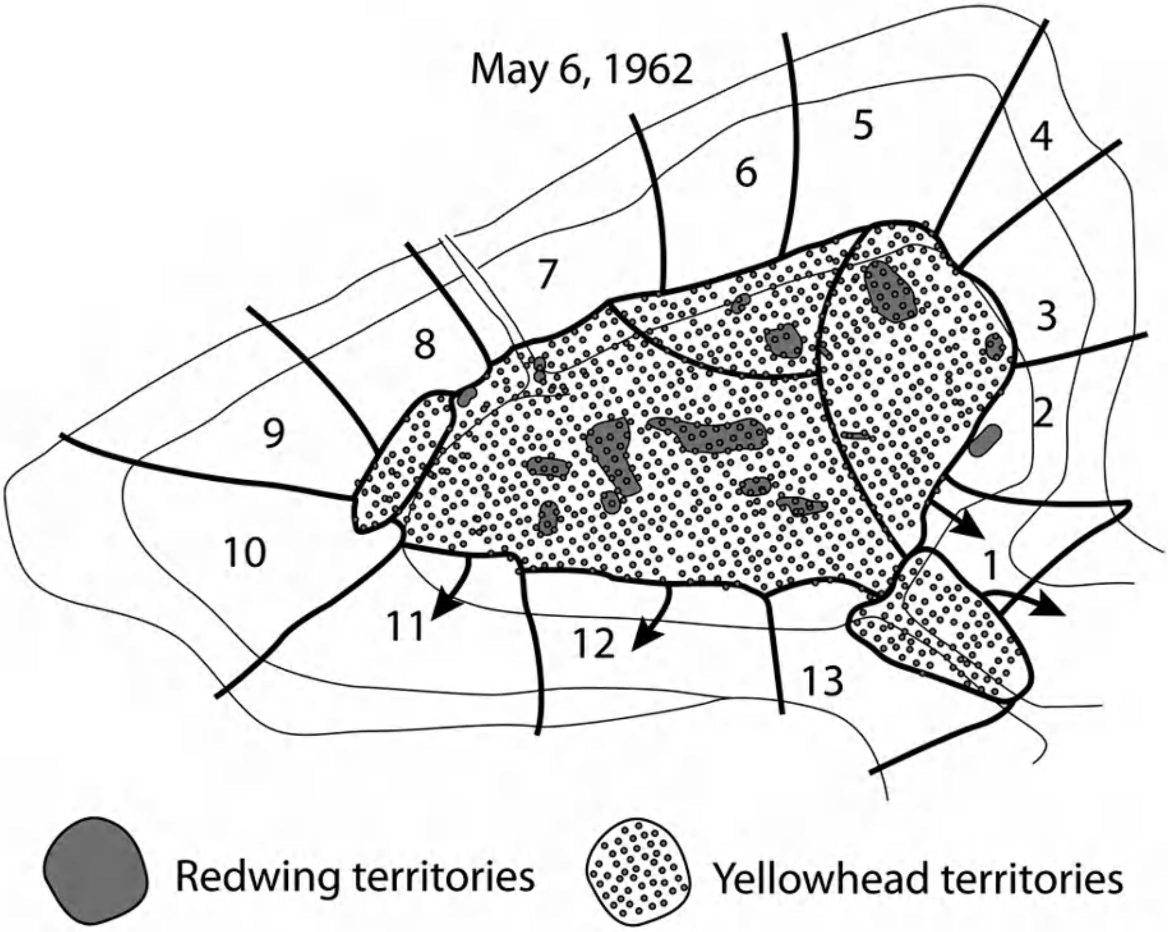
Some vertebrates actively defend a portion of their home range. The defended area is known as the **territory** and contains the home or nest site. In general, an individual or a group of animals is considered to be territorial when it has exclusive use of an area or resource with respect to other members of its species and defends it in some way (either actively through aggression or passively through advertisement). Habitat quality, particularly the availability of food, can influence territorial behavior and territory size. Thus, optimal size may vary from year to year and from locality to locality.

The territory may be fixed in space, or it may be mobile, as in bison (*Bison bison*), barren ground caribou (*Rangifer tarandus*), and swamp rabbits (*Sylvilagus aquaticus*)—where a male may defend an area around an estrous female. Some male cichlid fishes occupy the same territory for as long as 18 months (Hert, 1992). Drifting territoriality has been reported in a red fox (*Vulpes vulpes*) population in England (Doncaster and Macdonald, 1991). Troops of howler monkeys (*Alouatta* spp.) have little or no area of exclusive use, but they do defend the place where they happen to be at a given time. During the breeding season, male northern fur seals (*Callorhinus ursinus*) come onto land, choose and defend a breeding area against other bulls, and then collect a harem within this area.

Territoriality is one of the most important behavioral traits affecting the spatial organization of animal populations and population dynamics. As a result of territorial behavior, some individuals are forced into suboptimal habitat, which reduces the relative fitness of these individuals (Fig. 12.4). Territorial behavior may prevent overpopulation and overexploitation of the available habitat by ensuring a certain amount of living space or hiding places for an individual or a group of animals (Alcock, 1975). Territories may be defended by a single individual (Fig. 12.5), by a pair of adults, or by larger groups like a flock of birds, a pack of wolves, or a troop of baboons or gorillas. Although defense is usually by the male, both males and females may share in defending the territory. In some cases, like the American alligator, the female is the sole defender.



April 17, 1962



May 6, 1962

Figure 12.4. Interspecific territoriality between red-winged blackbirds (*Agelaius phoeniceus*) and yellow-headed blackbirds (*Xanthocephalus xanthocephalus*). Redwings that have established territories in the center of the marsh are evicted by the later-arriving yellowheads. Arrows indicate areas with intensive interspecific aggression.

The defended territory is usually much smaller than the home range, although in a few species the territory and the home range may be equivalent. As the size of the territory increases, the cost of defending the territory increases. Many fishes, lizards, crocodilians, birds, and mammals, as well as some salamanders, will actively defend an area immediately around their nests and/or homes, particularly during the breeding season and, if they provide parental care, during the time they are caring for their young. Many colonial birds nest just out of range of pecking distance of their neighbors (Fig. 12.6). Both male and female red-backed salamanders (*Plethodon cinereus*) mark their substrates and fecal pellets with pheromones (Jaeger and Gergits, 1979; Jaeger et al., 1986; Horne and Jaeger, 1988) and defend these feeding territories (Jaeger et al., 1982; Horne, 1988; Mathis, 1989, 1990a). Territoriality may affect the mating success of males because territorial quality has been found to be positively correlated with body size in *Plethodon cinereus* (Mathis, 1990b, 1991a, 1991b).

Figure 12.5. The striking wing pattern of the willet (*Catoptrophorus semipalmatus*) is important in advertising its territory and in defense.

Some anurans defend their territories, which may include feeding sites, calling sites, shelter, and oviposition sites. During the breeding season, for example, male bullfrogs (*Lithobates* [*Rana*] *catesbeiana*) defend an area surrounding their calling site from other males. A resident frog floats high in the water with its head raised to display its yellow throat, and it calls frequently. Initial defensive behavior consists of a vocal challenge followed by an advance toward the intruder. This is followed by another vocal challenge and an advance of a few feet, and so on until the intruder leaves. If the intruder does not leave, the two frogs push and wrestle each other and grasp each other's pectoral regions, each attempting to throw the other on its back. As soon as one frog is forced onto its back, contact is broken and the winner begins calling again. After remaining submerged for several seconds, the loser usually swims away some distance underwater before surfacing (see Fig. 13.1b).

Little owls (*Athene noctua*) of Germany are a nonmigrating, all-year territorial species (Finck, 1990); however, distinct seasonal changes in territory size and in intraspecific aggressiveness of males have been observed. Territories were largest during the courtship season (March and April) and averaged 28.1 hectares (69.4 acres). They reached their smallest size, an average of 1.6 hectares (4 acres) during July and August, when the fledglings were still being fed in the parents' territory. As the young began to disperse in September, territories again began to increase in size.

Figure 12.6. Gannet (*Morus bassanus*) nesting colony. Note the precise spacing of nests so that each bird is just beyond the pecking distance of its neighbors.

Little, if any, evidence of territoriality has been reported among turtles and snakes. A study of male snapping turtles in Ontario revealed they do not occupy a fixed, exclusive, defended area (Galbraith et al., 1987). They do, however, occupy relatively stable home ranges that overlap, and whose spacing may in part be determined by aggressive interactions. Even in burrow-dwelling species like desert tortoises (*Gopherus agassizii*) that rarely share summer holes, there is no evidence for the existence of defended territories.

In most species, territorial boundaries are marked in the same manner as the boundaries of the home range. For example, some salamanders, like the red-backed salamander (*Plethodon cinereus*), produce fecal pellets that serve as pheromonal territorial markers (Jaeger and Gergis, 1979; Jaeger et al., 1986; Horne and Jaeger, 1988). Birds commonly use song and characteristic display behavior, whereas mammals use scents, urine, and excrement to mark the boundaries of their territories.

DISPERSAL/INVASION

Dispersal refers to the movement an animal makes from its point of origin (birthplace) to the place where it reproduces. This type of movement generally occurs just prior to sexual maturity and takes place in all vertebrate groups. Dispersal is significant for a number of reasons. It tends to promote outbreeding in the population, it permits range extension, it may contribute to the reinvasion of formerly occupied areas, and it tends to reduce intraspecific competition. Many of the gradual invasions made by vertebrate species into newly developed or previously occupied territories are the result of dispersal of the young and their selection of breeding territories for the first time.

In many species of vertebrates, dispersal is density-dependent. There is a tendency to move only if the population in a given area is high or if aggression is shown by the parents. This is the case with many amphibians, reptiles, and birds and is also true of mammals like beavers (*Castor canadensis*), bears (*Ursus*), and many species of mice. Other species, like spruce grouse, deer mice, voles, and chipmunks, tend to have an innate predisposition to travel away from their place of birth regardless of the density of the population. After reaching a certain age, members of these species tend to wander away in search of unoccupied areas (Fig. 12.7).

Five juvenile emperor penguins (*Aptenodytes forsteri*) were fitted with satellite transmitters and tracked for several weeks after leaving their place of birth at Cape Washington in Antarctica (Fig. 12.8) (Kooyman et al., 1996). The juveniles traveled beyond the Ross Sea, with one individual being recorded 2,845 km (1,768 mi.) from Cape Washington when last located. The fact that juveniles engage in such extensive travels suggests that adequate protection against human disturbance is not being provided during all phases of the lifecycle of this species. Of most concern is the impact of commercial fishing around the Antarctic continent.

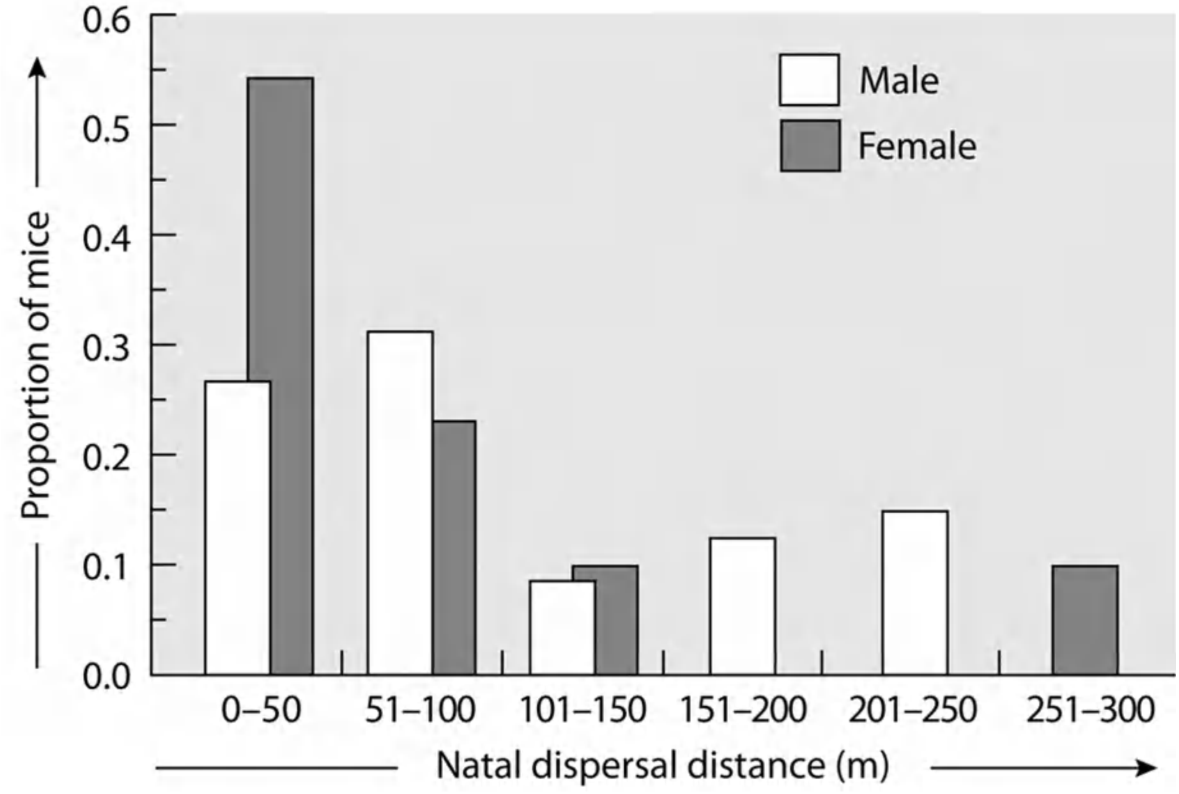


Figure 12.7. Natal dispersal distances for 22 male and 9 female juvenile white-footed mice (*Peromyscus leucopus*). This species has an innate predisposition to disperse regardless of the density of the population.

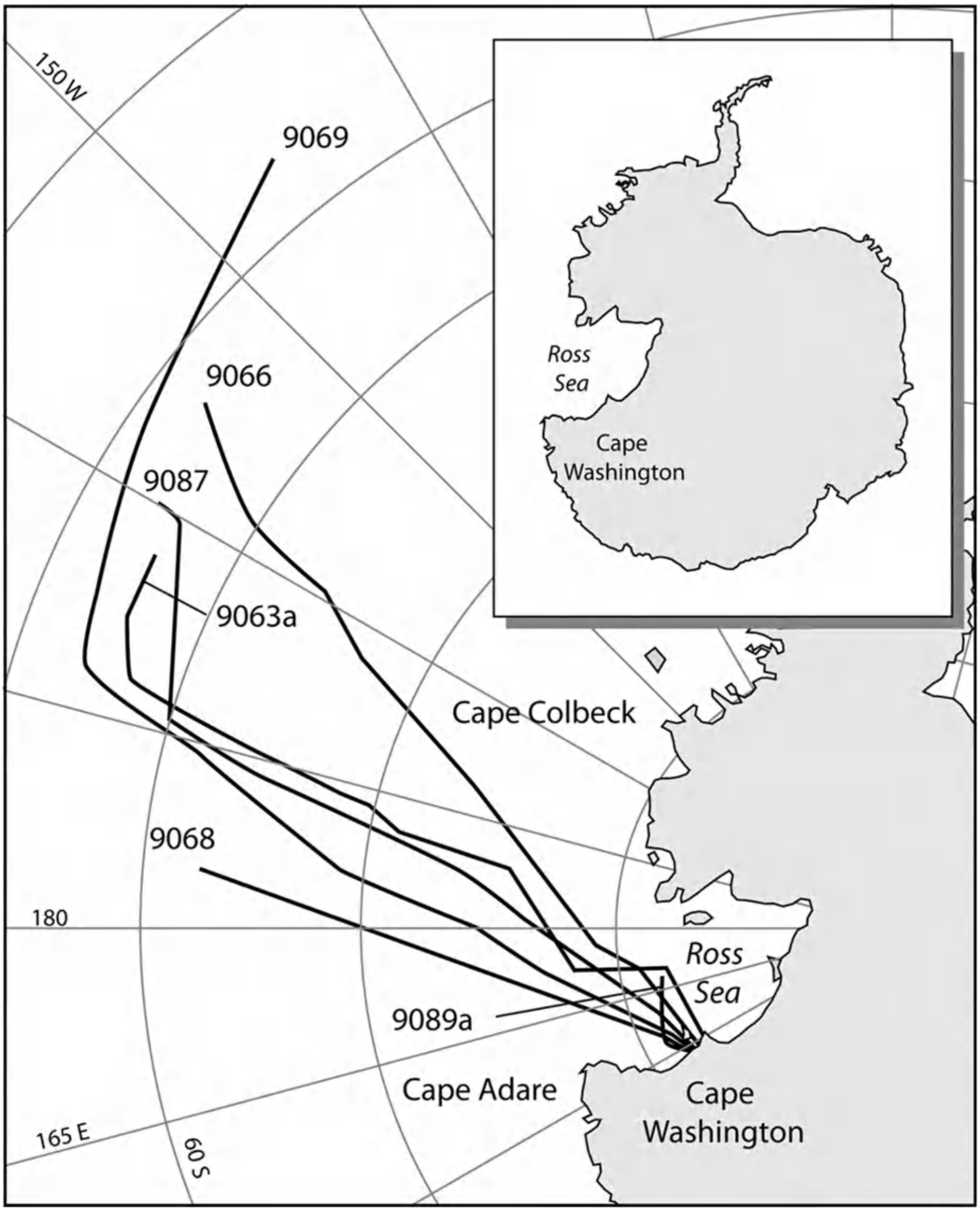


Figure 12.8. Routes of emperor penguin juveniles (*Aptenodytes forsteri*) obtained from satellite transmitters. From December 15 to 19, 1994, and during the same period in 1995, the birds were captured and released near the ice edge of Cape Washington. Within a few hours of release, the birds entered the water. Positions were monitored from January 4, 1995, to March 6, 1996. During this time, all birds had reached positions far enough north to be in the Westwind Drift. Although researchers had expected signals to continue during June, the lack of signal suggests that the birds remained in water north of the pack ice.

Among mammals that live in groups, males usually disperse about the time they reach breeding age. Sometimes it is voluntary, but other times they are pushed out of the group by dominant, older males who prevent adolescents from mating with the group's available females. In other groups, both males and females leave their birthplace. In a few species, like the African hunting dog (*Lycaon pictus*) and chimpanzees (*Pan troglodytes*), only the females leave the security of their home group and disperse. The dynamics of groups favoring female dispersal may be driven, in part, by the relative ages of dominant fathers and maturing daughters. In these groups, females that reach maturity while older-generation males are still breeding run a high risk of mating with their fathers or other close relatives. In these cases, it is genetically advantageous for them to leave in order to avoid inbreeding among closely related individuals.

The **invasion** of the Great Lakes by the sea lamprey (*Petromyzon marinus*) was made possible by the completion, in 1829, of the Welland Canal, which bypassed Niagara Falls. Niagara Falls had served as a natural barrier to aquatic dispersal prior to this time. The lampreys reached Lake Huron in the 1930s and Lake Superior by the mid-1950s. This invasion of lampreys drastically reduced populations of lake trout, lake whitefish, and burbot in most of the Great Lakes. Control measures, including the release of sterile males and the use of a lampricide specific for ammocoete larvae, have allowed the prey species to partially recover and reach an equilibrium with the lampreys. (See discussion of Lampreys in the Great Lakes in Chapter 3, page **63**).

The rapid spread of the English sparrow (*Passer domesticus*) (Johnston and Selander, 1964) and starling (*Sturnus vulgaris*) (see Fig. 10.39) serves as an excellent example of dispersal/invasion, as does the northward and eastward expansion of the coyote (*Canis latrans*) (see Fig. 10.41). The gradual northward expansions of the ranges of the gray fox (*Urocyon cinereoargenteus*), opossum (*Didelphis virginiana*), and armadillo (*Dasypus novemcinctus*) are less dramatic examples. All of these movements have resulted in the expansion of the range of the individual species.

The cattle egret (*Bubulcus ibis*) (Fig. 12.9) is a native of Africa. It crossed the South Atlantic under its own power and was first recorded in Dutch Guiana (now Suriname) in 1877 (Line, 1995). By the late nineteenth century, it had become established on the northeastern coast of South America and, since that time, has dispersed rapidly to become one of the most abundant herons in the Americas. The distance from the bulge of West Africa to the northeastern coast of South America is approximately 2,870 km (1,783 mi.). Taking into consideration the prevailing trade winds, it is estimated that the trip would have required about 40 hours. Even today, cattle egrets are routinely sighted at sea between Africa and South America.

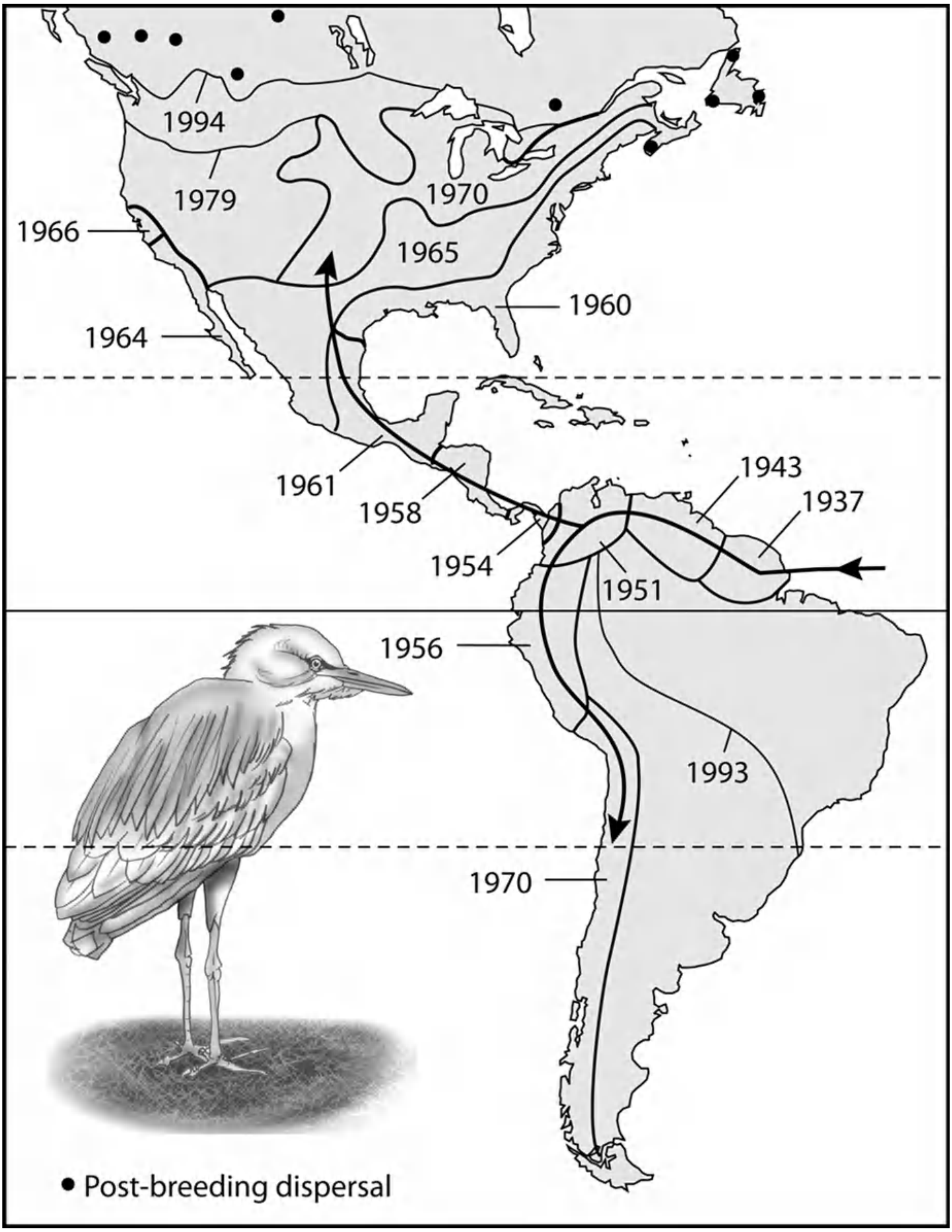


Figure 12.9. The cattle egret (*Bubulcus ibis*) is a native of Africa. It feeds on the insects disturbed by grazing ungulates. This species apparently crossed the South Atlantic Ocean from Africa under its own power and became established in northeastern South America by the late nineteenth century. It dispersed rapidly and is now one of the most widespread and abundant herons in the New World.

Gray wolves are moving into Maine and neighboring states. The source of these wolves is likely southern Quebec.

An Arctic fox (*Vulpes lagopus*) walked more than 4,345 km (2,700 mi.) to go from northern Norway to Canada's far north in four months. The Norwegian Polar Institute reported the young female fox left her birth place on Norway's Svalbard archipelago on March 1, 2018, and reached Canada's Ellesmere Island by way of Greenland on July 1, 2018. The fox, wearing a tracking collar, averaged nearly 48 km (30 mi.) a day, although some days it walked almost 160 km (100 mi.). The ground the small fox cumulatively covered was among the most ever recorded for an Arctic fox seeking a place to settle down and breed (Fuglei and Tarroux, 2019).

Young cougars are dispersing from the Black Hills of South Dakota. In June 2004, an individual marked in South Dakota was struck by a train in Oklahoma, a straight-line distance of 1,073 km (667 mi.) and, at that time, the longest documented movement of a cougar in North America. Another individual from the same population was tracked 483 km (300 mi.) into Manitoba. In 2005–06, a female mountain lion made a surprisingly long trek of 1,336 km (830 mi.) across Utah, Wyoming, and Colorado in nine months. A young adult male struck and killed by an SUV in Milford, Connecticut, on June 11, 2012, provided absolutely irrefutable proof that a wild mountain lion, at least occasionally, can make its way to New England. With the aid of modern DNA analysis technology and the availability of a camera in every cell phone, the story of this animal was pieced together in a way that would not have been possible just a few years ago. Over a period of a year and a half, the young male traveled 2,897 km (1,800 mi.) from the Black Hills of South Dakota to Connecticut.

MIGRATION

The periodic movement of a population or a part of a population of animals away from a region and their subsequent return to that *same* region is termed **migration**. Migration is a transfer of the home range to a distant region. The largest mammal migration ever known—60 million animals—involved the American bison on the Great Plains (Fig. 12.10). Many animals travel either at regular times during the year or at a particular time during their lives. Some travel to avoid cold or hot weather, some to find a steady food supply, and others to move to breeding sites or to special places to produce their young. The length of the trip varies from species to species, with many traveling in large groups, whereas others travel alone. Migratory movements—which may be daily, seasonal, or irregular in occurrence—may cover short distances or many thousands of kilometers. They may occur annually, as is the case in many birds and mammals, or they may require a lifetime to complete, as is true of some salmon and freshwater eels. Daily movements commonly occur among fishes that move upward and downward in the water column. Such movements are generally in response to similar movements of zooplankton, although some upward and downward movements are associated with predator avoidance. Hammerhead sharks (*Sphyrna* spp.) in the Gulf of California engage in nightly round trips to feeding sites using magnetic undersea peaks as navigational centers (Klimley, 1995). Crows (*Corvus brachyrhynchos*) and starlings move from roosts to feeding areas and back each day.

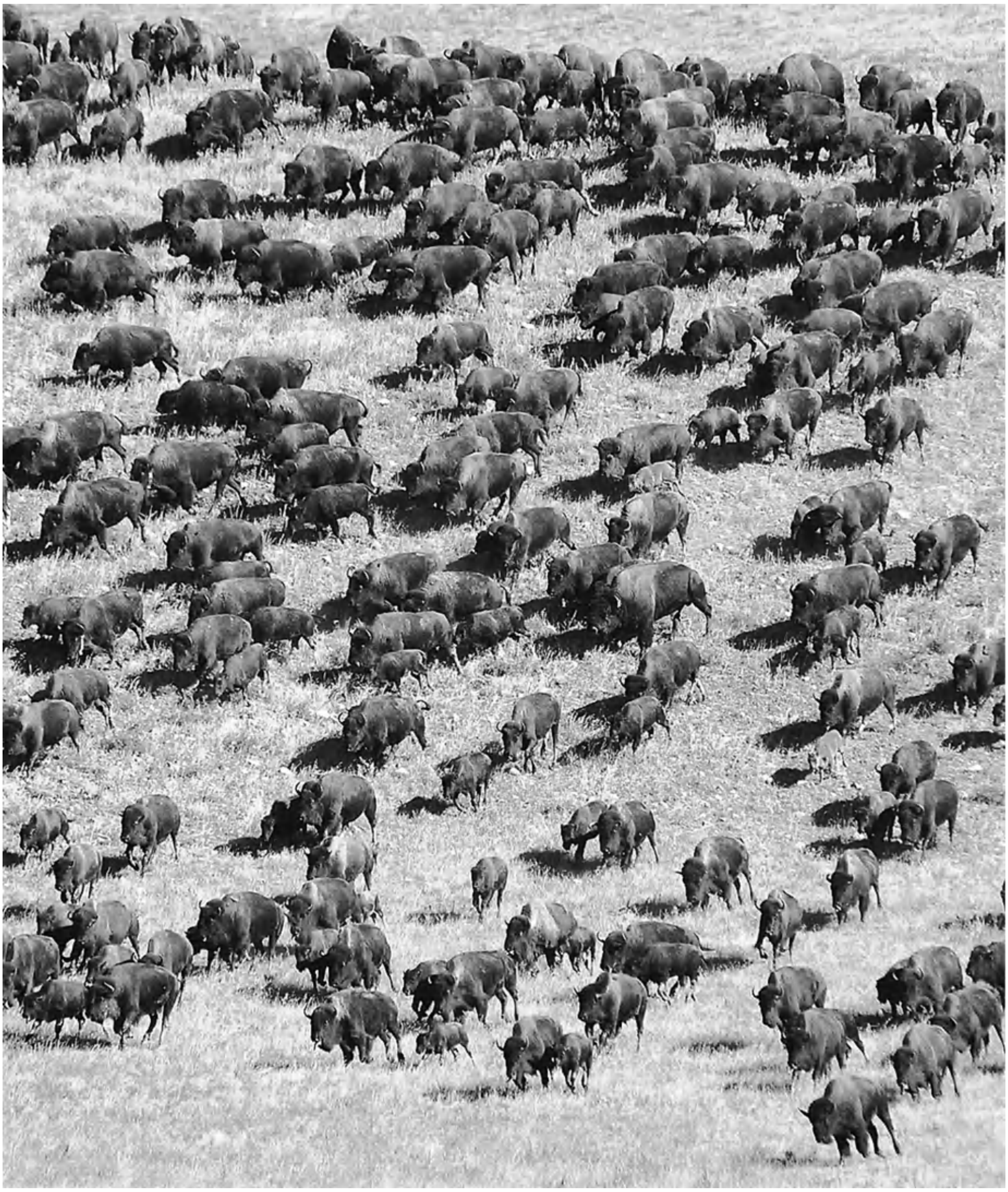


Figure 12.10. The largest mammal migration ever known involved the American bison on the Great Plains.

Some vertebrates inhabit areas that have suitable living conditions during only part of the year. During the colder winter months, these species must either hibernate or migrate. Thus, migration permits a species to leave an area with unfavorable conditions during a period of the year, for one with more favorable conditions, even though this move is only temporary.

Microgeographic (Short-Distance) Migration

Some species migrate only short distances. This local, or **microgeographic**, migration is typical of some ambystomatid salamanders that migrate from their subterranean hibernacula to their breeding pond (Fig. 12.11). They remain active and above ground for several weeks before returning to their underground existence. Many anurans move to breeding ponds in the spring. Norway rats (*Rattus norvegicus*), house mice (*Mus musculus*), and some snakes may move from fields into barns during the winter and then return to the fields in the spring. Mule deer (*Odocoileus hemionus*) in the western mountains move from their summer ranges on north-facing slopes to wintering grounds on south-facing slopes (Taber and Dasmann, 1958).

Figure 12.11. Some ambystomid salamanders, like (*clockwise from top*) the marbled salamander (*Ambystoma opacum*), tiger salamander (*A. tigrinum*), Jefferson's salamander (*A. jeffersonianum*), and spotted salamander (*A. maculatum*).

Figure 12.12. Elk (*Cervus canadensis*) spend the summer months in high mountain meadows and descend into lower valleys during the winter months. This altitudinal migration may lower insect harassment, reduce the risk of predation, and enable the elk to take advantage of a more nutritious food supply.

Altitudinal Migration

Some species that live in mountainous regions move between higher and lower elevations in a kind of **altitudinal migration**. For example, many elk (*Cervus canadensis*) in the western United States spend the summer months in high mountain meadows and descend into lower valleys during the winter months (Fig. 12.12). These movements may be to reduce insect harassment (e.g., black flies, mosquitos), to seek more abundant or nutritious forage, and/or to lower the risk of predation. Carolina dark-eyed juncos (*Junco hyemalis carolinensis*) and the Carolina chickadee (*Parus carolinensis*) in the southern Appalachians of North Carolina, Tennessee, and Virginia migrate several thousand meters in elevation, whereas closely related subspecies and species like the boreal slate-colored junco (*Junco hyemalis hyemalis*) and the black-capped chickadee (*Parus atricapillus*) migrate hundreds, sometimes thousands, of kilometers twice a year between their breeding and wintering areas. Altitudinal migrators face considerably fewer hazards and expend much less energy than long-distance migrators; thus, the survival value of this behavior is great.

Macrogeographic (Long-Distance) Migration

The best-known migrators are the **macrogeographic**, or long-distance, migrators like ducks, geese, swans, cranes, vireos, warblers, flycatchers, swallows, and thrushes. These species feed primarily on aquatic vegetation and/or flying insects, neither of which is available during the winter months in northern regions. Of the 650 North American migratory bird species, 332 (51 percent) spend from six to nine months of the year in the tropics of the Americas, where they live under environmental conditions very different from those of their breeding grounds. Many of these migratory birds, especially waterfowl and shorebirds, use four major flyways in North America. From east to west, these are the Atlantic Flyway, the Mississippi Flyway, the Central Flyway, and the Pacific Flyway (Fig. 12.13).

These four migration flyways were originally proposed by US Fish and Wildlife Service biologist Frederick Lincoln (1935), and many federal and state wildlife refuges have been established along the four routes. Although the concept of flyways is useful, especially for waterfowl and shorebird movements during fall migrations, it is an overly simple depiction of migration patterns of most other birds, particularly passerines. Studies by Bellrose (1968) and Richardson (1974, 1976) suggest that most species migrate over broad geographic fronts, particularly in spring, and do not follow narrow migratory corridors.

Not all birds migrate north and south; some fly east and west. For example, Pacific populations of harlequin ducks (*Histrionicus histrionicus*) overwinter in the western coastal waters from northern California to Alaska (Turbak, 1997). In the spring, they fly eastward to nest along mountain streams in Alaska, Washington, Oregon, Montana, Idaho, Wyoming, Alberta, British Columbia, the Yukon, and the Northwest Territories. A few even cross the Continental Divide to nest.

Harlequin society is matriarchal, with adult females returning salmon-like to their natal streams to reproduce. The Pacific population of harlequins is the only duck population in the world that divides its time between sea and mountains. A small eastern population breeds in maritime Canada and winters on the New England coast.

Why Do Migratory Birds Fly in a *V* Formation?

There are two well-supported and complementary explanations for why birds often fly in formation (see Figs. 12.14 and 12.15). (Both *V* and *J* structures are typical and readily recognizable flight formations for migratory birds; studies have shown that a *J* formation is, in fact, more common than a true *V*-shaped structure.) One theory to account for the phenomenon is that followers benefit from a supportive upwash of air created by the lead birds. The other is that regimented flight formation facilitates proper spacing, directional orientation, and group communication.

The relative importance of each benefit undoubtedly shifts along with changes in various factors, like the season of the year or the purpose of an individual flight. During local feeding flights, for example, energy conservation is probably much less important than careful orientation and collision avoidance. During long-distance migration, on the other hand, each member of the flock gains a great deal by optimizing its position to conserve energy.

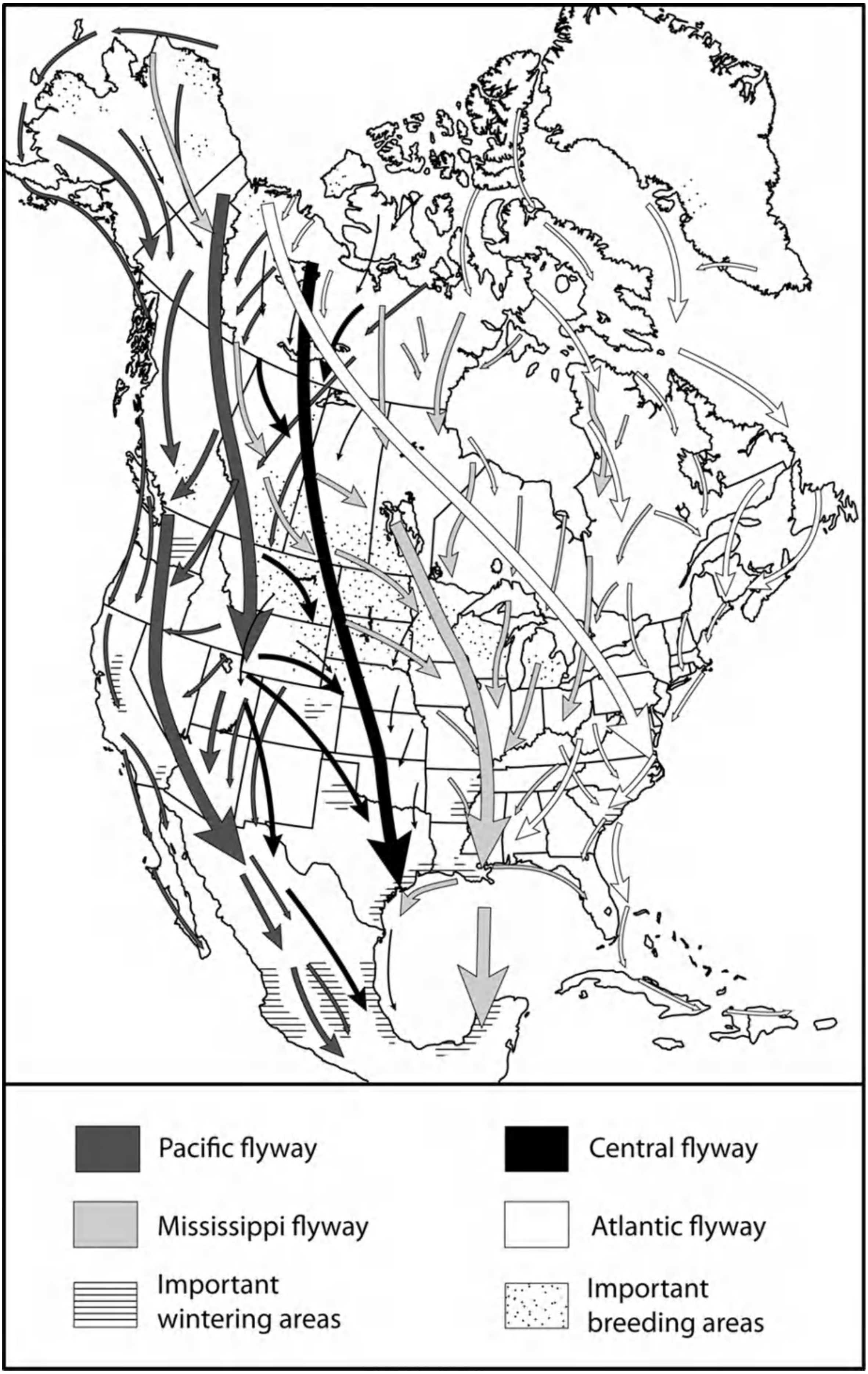

Pacific flyway
Central flyway
Mississippi flyway
Atlantic flyway
Important wintering areas
Important breeding areas

Figure 12.13. The four major flyways used by migratory birds in North America: the Atlantic, Mississippi, Central, and Pacific flyways.

The migratory journeys of some species are astounding because of their length and/or duration. Adult Pacific salmon (*Oncorhynchus*) of the North Pacific breed in freshwater streams or lakes, and the young migrate to the sea within the first two years of their lives. After two to four years at sea (during which time the salmon mature), they then travel back to the river system in which they were born. They swim upstream to the headwaters of rivers like the Columbia and Yukon, where they will spawn and die. Some of these fish will have covered several thousand kilometers during their migratory travels.

Figure 12.14. Some migratory birds fly in *V*- or *J*-shaped formations. Birds may use less energy by "drafting" behind the leaders. Such regimented flight may also assist in orientation and group communication.

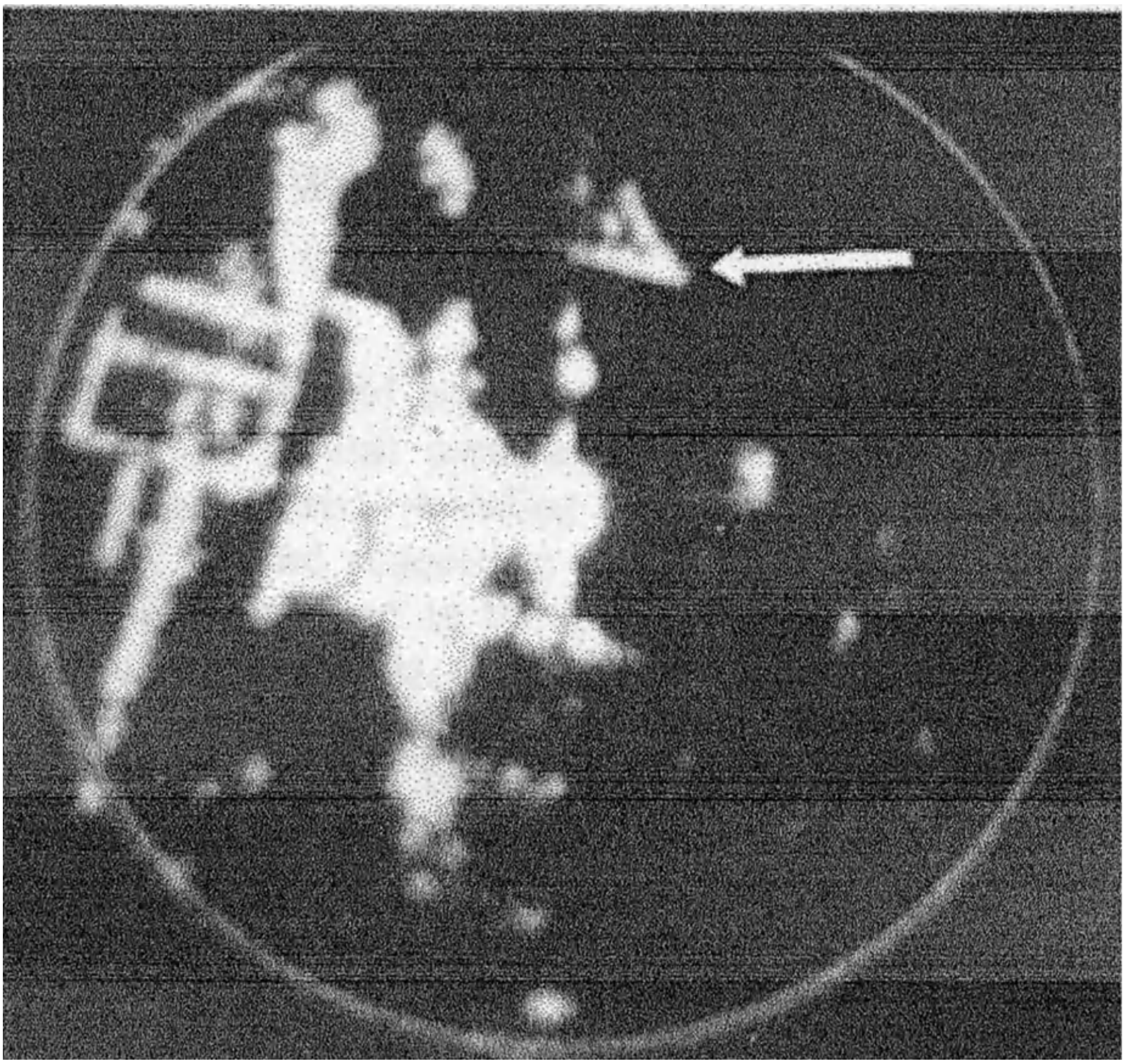


Figure 12.15. A single frame of the 8 mm film used to record radar data in March 1973 southwest of the Iroquois National Wildlife Refuge in western New York. Arrow points to a group of Canada geese flying in a *V*. Diameter of the area shown in radar display is 1.85 km (1.1 mi.). Other radar echoes are from objects on the ground (primarily trees and farm fences).

Eels

The North American (*Anguilla rostrata*) and European (*A. anguilla*) freshwater eels spawn in the Sargasso Sea, an area of relatively still water in the mid-Atlantic covered by seaweed that floats over its surface. Adult eels spawn in the winter and early spring. After spawning, the adults die. The eggs hatch into larvae, which are transported by ocean currents, mostly in a northwesterly direction to coastal regions of North America and Europe. Reaching coastal waters can take anywhere from a few months (in the case of the mid-Atlantic) to two or more years for Canada and Europe. During the trip, the larvae develop into transparent “glass” eels, which are just a few inches long. As the glass eels begin moving up the estuaries, they become pigmented with gray or brown and are known as “elvers.” Females tend to continue their migrations up freshwater rivers in the spring, while males may remain in brackish coastal waters for almost all of their lives. When the eels mature, which generally takes 8 years or less in warm climates, but 25 years or more in colder areas, they turn a bronze-black sheen and are known as silver eels. Their skin thickens, they store body fat, and they make the long swim back to the Sargasso Sea, a journey that begins in the fall.

Fish

Basking sharks (*Cetorhinus maximus*) have long been thought to exist in discrete populations along the continental shelf of Europe and the east coast of North America—two regions separated for thousands of kilometers by the Atlantic Ocean. However, in 2008, a basking shark tagged near the Isle of Man, United Kingdom, traveled 9,589 km (5,958 mi.) to a region east of the Newfoundland shelf. The shark’s nights were generally spent at depths of 200 to 300 m (656–984 ft.) and her days at 400 to 800 m (1,312–2,625 ft.), once reaching 1,264 m (4,147 ft.).

A female great white shark (tagged as P12) completed a transoceanic journey spanning the entire Indian Ocean, swimming coast-to-coast from South Africa to Australia and back—a journey of more than 20,000 km (32,200 mi.) in just under nine months (Bonfil et al., 2005). The shark was tagged off the coast of South Africa in November 2003 and traveled at a minimum speed of 4.7 km (2.9 mi.) per hour during its migration to western Australia in 99 days, the fastest sustained long-distance speed known among sharks. P12 returned from Australia to its original tagging site on August 20, 2004, evidencing site fidelity and outstanding navigational ability. This was the fastest transoceanic return migration ever recorded among marine fauna.

A tagged blue marlin (*Makaira nigricans*) was recorded as migrating 15,000 km (9,254 mi.) from the Atlantic Ocean to the Indian Ocean.

Sea Turtles

By using a satellite transmitter, Benson et al. (2007) tracked an adult female leatherback turtle (*Dermochelys coriacea*) that swam from Indonesia to Oregon and back to Hawaii in a journey of at least 7,920 km (4,921 mi.) searching for food. She began her journey on a nesting beach in Jamursba-Medi in Papua Province in Indonesia and was tracked for 647 days until the transmitter's battery ran out just off Hawaii. This represents the longest known journey of any sea turtle.

One population of the Atlantic green turtle (*Chelonia mydas*) (Fig. 12.16) nests on Ascension Island in the South Atlantic Ocean (Bowen et al., 1989). After depositing their eggs, females return to the warm shallow waters off the coast of Brazil, a distance of more than 1,600 km (994 mi.). After feeding on marine vegetation for several years, they return to the same beach to lay another clutch of eggs. In 2014, researchers at Swansea University used satellite tracking to record the world's longest green sea turtle migration—from the Chagos Islands in the Indian Ocean to the coast of Somalia in east Africa—a distance of 3,979 km (2,467 mi.) (Hays et al., 2014).

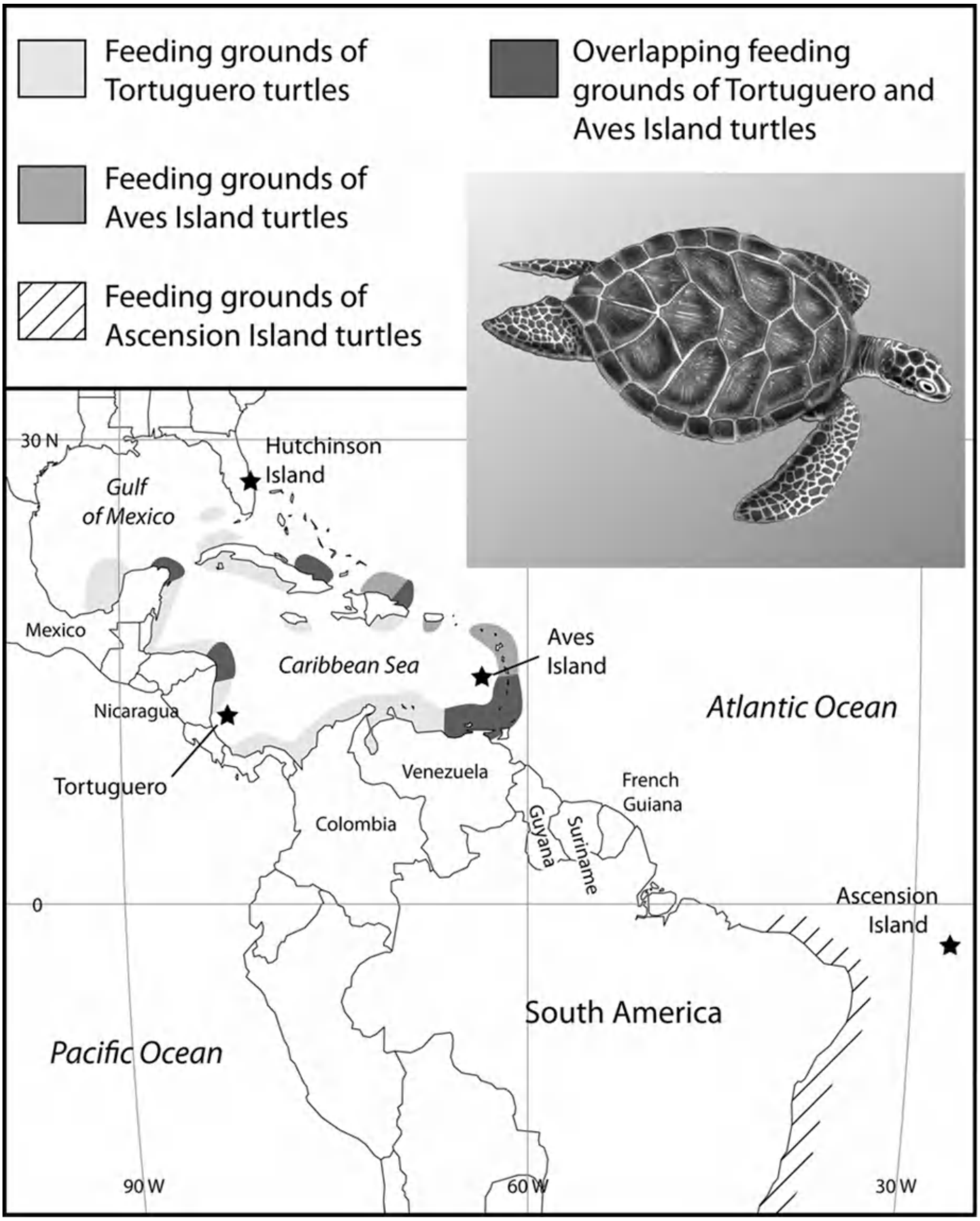


Figure 12.16. The Atlantic green turtle (*Chelonia mydas*) (*inset*) nests on Ascension Island in the South Atlantic Ocean but lives most of its life in the warm, shallow waters off the coast of Brazil. The foraging grounds in the Caribbean and West Central Atlantic Ocean are used by green turtles that nest at three of the four surveyed rookeries (the foraging grounds of the Florida colony are unknown).

Recent studies analyzing mitochondrial DNA (mtDNA) from eggs and hatchlings at four green turtle breeding sites in the Atlantic and Caribbean—Florida, Costa Rica, Venezuela, and Ascension Island—

have revealed slight differences in their genetic sequences; this may complicate efforts to preserve this endangered species, because each subgroup could be unique and irreplaceable (Bowen et al., 1989; Meylan et al., 1990). This finding lends credence to the natal homing theory, proposed in the 1960s, which holds that, while turtles hatched in different regions may share common feeding grounds away from home, the animals part company at breeding time, each swimming hundreds or thousands of kilometers to breed and nest at their own (natal) birthplace.

After nesting, female leatherback turtles (*Dermochelys coriacea*) from the largest extant nesting colony in the eastern Pacific at Playa Grande, Costa Rica, head southward, crossing the equatorial currents with rapid, directed movements. They travel within a migration corridor from Costa Rica, past the equator, and into the South Pacific Gyre, a vast, low-energy, low productivity region, into which the turtles disperse broadly (Morreale et al., 1996; Shillinger et al., 2008) (Fig. 12.17). They feed in offshore upwelling areas where their food, almost exclusively jellyfish, may be concentrated. Travel distances up to 2,700 km (1,678 mi.) have been recorded. Turtles in the western Pacific population nest in Indonesia and travel to many different feeding sites in the South China Sea, Indonesian seas, southeastern Australia, and the US West Coast, mainly in highly productive coastal areas.

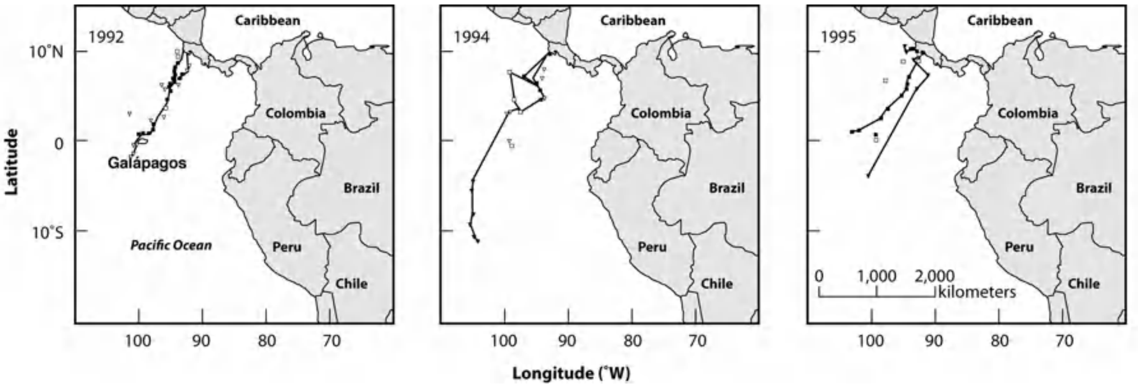


Figure 12.17. Migratory movements of eight leatherback turtles (*Dermochelys coriacea*) monitored by satellite transmitter after nesting near Playa Grande, Costa Rica. The Cocos Ridge runs beneath the first 1,500 km (930 mi.) of the migration corridor, extending out to the Galápagos Islands. Four turtles were tracked as they passed the Galápagos and continued beyond the ridge into deeper Pacific waters.

Sea Turtle Migration

Lohmann et al. (2012) showed that once young loggerhead turtles reach the open sea, they advance through a combination of strategic swimming interspersed with passive drifting on favorable ocean currents. By swimming only in places where they are in danger of being carried off course and drifting passively in other areas where ocean currents move in the same direction that the turtles want to go, young loggerheads can migrate long distances on limited energy stores. Young turtles rely on "smart swimming" to optimize their energy during migrations. These findings challenge a long-standing belief that young sea turtles drift passively and that their distribution is determined entirely by ocean currents. The findings were based on computer simulations combining ocean currents and "virtual turtles" swimming for various periods of time.

How do young loggerhead turtles know where they are and how to steer as they migrate around the North Atlantic basin? The Earth's magnetic field differs slightly in different geographic areas. The turtles' magnetic map enables them to instinctively use differences in these fields as navigational markers that serve as equivalents to road signs for turtles in the open sea. Each change in the magnetic field elicits a change in the turtles' swimming direction, which in turn steers the turtle along its migratory route at each location. The results indicate the turtles' brains are hard-wired to navigate their migratory routes. This ability appears to be inherited.

Lohmann et al., 2012; Putnam et al., 2012

Kemp's ridley (*Lepidochelys kempii*) is the smallest and most endangered of the world's seven sea turtle species. Unlike other sea turtles, Kemp's ridley sea turtles nest primarily during the day. In past years, most nesting occurred on a 26 km (16 mi.) stretch of beach at Rancho Nuevo on the Gulf Coast of Mexico, 160 km (99 mi.) south of Brownsville, Texas. Nests have also been documented in North Carolina, South Carolina, Georgia, Florida, and Alabama. The Kemp's ridley population underwent a devastating decline in the mid-1900s, primarily due to over-harvest of eggs and loss of juveniles and adults due to commercial fishing. Biologists did not know the location of the main Kemp's ridley nesting beach in Mexico until the early 1960s, and protection efforts at Rancho Nuevo were not initiated until the mid-1960s. Despite protection efforts by the Mexican government, the population continued to decline. Rancho Nuevo was declared a Natural Reserve by Mexico in 1977 and programs were begun to protect the nesting beach and reduce the poaching and natural mortality of eggs and turtles. In 1978, the United States joined Mexico in efforts to try to save the species from extinction and recover the population (National Park Service, 2018a). About 40,000 Kemp's ridley sea turtles were estimated at Rancho Nuevo in 1947. But by 1985, only 702 nests were recorded. On average, a single female lays up to about 100 eggs two and a half times during a single nesting season. Since 1978 about 50,000 hatchlings a year have been released on the beach. The effort at Rancho Nuevo has been extensive and successful as very few nests are now lost. Despite this protection, however, the number of Kemp's ridley sea turtles that nest each year is declining because of the continuing loss of turtles to incidental catch by shrimp trawls.

A Lengthy Turtle Trek

An estimated 10,000 juvenile loggerhead turtles (*Caretta caretta*) feed and develop off the coast of Baja California annually. The nearest known nesting sites, however, lie in Japan and Australia, some 10,000 km (6,200 mi.) away. Mitochondrial DNA (mtDNA) samples from Baja turtles, and from another group caught in the North Pacific, revealed that 95 percent (of both groups) carried the same distinctive genetic sequences as the baby turtles in Japan, while the remainder matched the DNA markers of the Australian turtles. The 10,000 km (6,200 mi.) trek to Baja—a distance spanning more than one-third of the globe—ranks among the longest documented marine vertebrate migrations.

Using satellite tracking, Hays and Scott (2013) investigated the upper ceiling on migration distances for five species of sea turtles compared to other walking, flying, and swimming migratory vertebrates.

Bowen et al., 1995; Hays and Scott, 2013

Between 1978 and 1988, scientists collected more than 22,000 eggs and released the young at Padre Island, Texas, in hopes that the turtles would imprint on the Texas site and return when they reached maturity in 10 to 15 years (Kaiser, 1996). Two turtles returned and nested in 1996. In addition, in May 1996, a Kemp's ridley sea turtle, originally tagged in the Chesapeake Bay near the mouth of the Potomac River in 1989, was found on the beach at Rancho Nuevo. This is the first known Kemp's ridley from the Atlantic Ocean to return to the turtles' ancestral nesting ground. In 1998, there were four confirmed nests on Padre Island. The record for nests at Padre Island National Seashore, set in 2017, was 219, with 353 found statewide. As of May 2018, the nesting count reached 110 on Padre Island and 200 statewide.

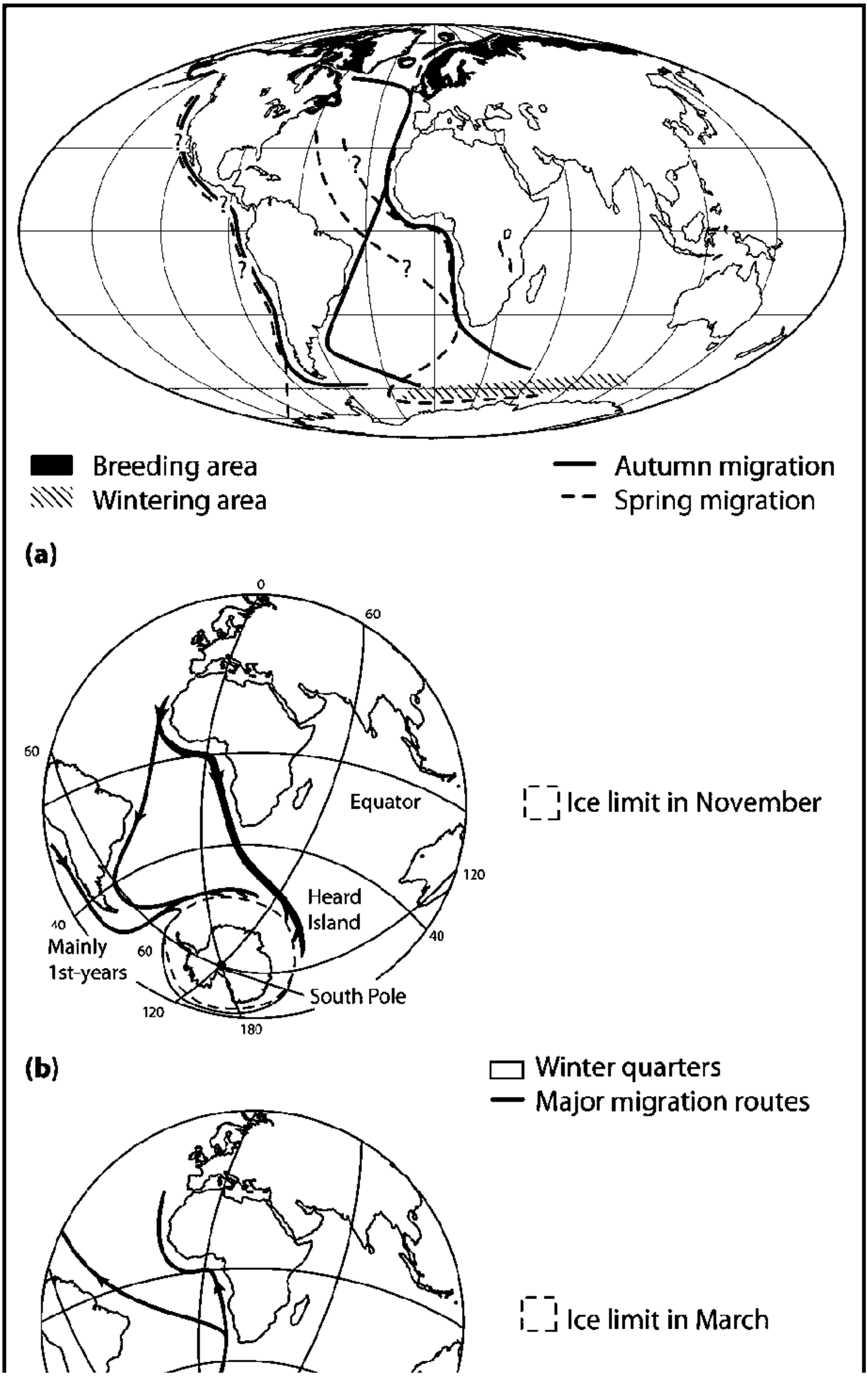
Studies of loggerhead sea turtles (*Caretta caretta*) show they recognize their home turf by using Earth's magnetic field (which varies across the globe) so that they always find their way back to the very stretch of coast where they hatched. Although long suspected, this hypothesis has been challenging to test. Brothers and Lohmann (2015) realized that if turtles homed in on beaches' unique magnetic signatures, the turtles should change their nesting locations as magnetic signatures drift slightly along coastlines. Over 19 years, the scientists found that the nests of sea turtles in Florida shifted along with gradual changes in magnetic fields: nesting density increased significantly in coastal areas where magnetic signatures of adjacent beach locations converged over time, whereas nesting density decreased in places where magnetic signatures diverged.

Birds

The golden plover (*Pluvialis dominica*) breeds in the Arctic and winters in southeastern South America. It is estimated that these birds cover a distance of 25,000 to 29,000 km (15,000–18,000 mi.) annually. The Alaskan population of the wheatear (*Oenanthe oenanthe*), which winters in southeastern Africa, can make annual journeys of about 30,000 km (18,600 mi.) (Kiepenheuer, 1984).

The annual round-trip journey from its Arctic breeding grounds near the North Pole to its winter quarters in Antarctica results in the 113 g (4 oz.) Arctic tern (*Sterna paradisaea*) traveling great distances. Previous investigations have used figures of 40,000 to 50,000 km (24,850–31,000 mi.) per year (Berthold, 1998) (Fig. 12.18). Using geolocators on Arctic terns from Greenland and Iceland, Egevang et al. (2010) found that these birds do travel huge distances—more than 80,000 km (49,710 mi.) annually for some individuals. They confirmed the location of the main wintering region and identified a previously unknown oceanic stopover area in the North Atlantic. At the end of the breeding season, 11 tagged birds traveled southwest to a stopover region of deep water in the eastern portion of the Newfoundland Basin and the western slope of the mid-North Atlantic Ridge where they remained for an average of 25 days.

The birds then continued their migration southeast toward the West African coast. South of the Cape Verde Islands, however, migration routes diverged: seven birds continued to fly south parallel to the African coast, whereas four others crossed the Atlantic to follow the east coast of Brazil. All birds spent the austral summer in the productive Atlantic sector of the Antarctic Ocean, which supports high densities of Antarctic krill (*Euphausia superba*). All birds began their return migration to breeding colonies in early to mid-April. Their return route was always over deep water at considerable distances from continental shelf margins. They flew counterclockwise around the South Atlantic and clockwise around the North Atlantic gyres. The northbound migration took less than half the time (40 versus 93 days), despite being three quarters the length—25,700 versus 34,600 km (15,969 versus 21,499 mi.)—of the southbound journey. The average annual distance traveled, from departing the breeding site in August to return in late May or early June was 70,900 km (44,055 mi.) (range 59,500–81,600 km, or 36,972–50,704 mi.). This is the longest round-trip animal migration ever recorded electronically. With an average lifespan of 30 years, this means the Arctic tern could cover approximately 2.4 million km (1,491,291 mi.) in its lifetime—the equivalent of going to the moon and back three times.



■ Breeding area
▨ Wintering area
— Autumn migration
-- Spring migration
?
(a)
0
60
60
Equator
Ice limit in November
120
Heard Island
40
40
Mainly 1st-years
60
South Pole
120
180
(b)
Winter quarters
Major migration routes
Ice limit in March

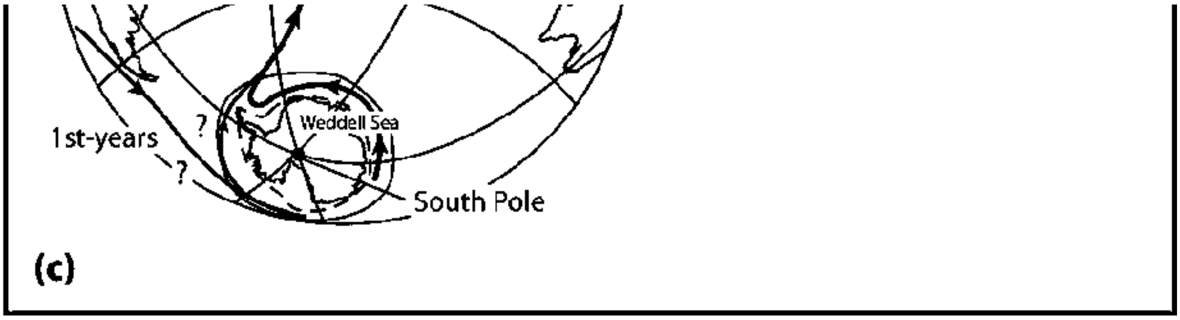


Figure 12.18. Distribution and migration routes of the Arctic tern (*Sterna paradisaea*). (*a*) Overall routes, with question marks indicating portions of migration pathways that have not been proved. (*b*) The migration routes to wintering areas along the edge of the pack ice in the Antarctic Ocean. Most terns arrive via Africa's western coast, but a significant number migrate along the coasts of South America. Most terns arrive in Antarctica during November and December. (*c*) The migration routes from the wintering areas in March. Adults and intermediate-age terns migrate mainly westward off the Antarctic coast before continuing north in the Atlantic. There are indications that first-years in particular migrate around the South Pole to summer on the Humboldt Current.

Sooty shearwaters (*Puffinus griseus*) fly some 64,000 km (39,600 mi.) traveling to and from their New Zealand breeding grounds each year (Shaffer et al., 2006). The birds fly roughly east from New Zealand to coastal South America, then northwest to the North Pacific, where they split off for Japan, Alaska, or California. The birds' round-trip routes describe big figure eights, some extending to feeding grounds as far north as Alaska. When the birds cross the food-poor waters at the equator, they speed up, averaging 910 km (560 mi.) a day. Their flight pattern puts them over food-rich waters in prime season for both the Northern and Southern Hemispheres. They finally arrive home to breed in the exact nesting burrows where they were first tagged.

Adélie penguins (*Pygoscelis adeliae*) migrate in a 13,000 km (8,000 mi.) circle around the Ross Sea off Antarctica, on "fast ice" that develops during the winter. Doing so means they stay in sunlight with the clockwise migration taking them back to land and their breeding colonies for the summer months.

Satellite tagging has revealed that the bar-tailed godwit (*Limosa lapponica*) makes the longest nonstop flight of any bird—an 11,700 km (7,300 mi.) trek from Alaska across the length of the Pacific Ocean to New Zealand and Australia (Wagner, 2009). It also makes the longest journey without pausing to feed of any animal. Several weeks before leaving Alaska, each godwit gorges on clams and worms, so much so that its dermis bulges with the highest fat content recorded in birds. At the same time, some of the bird's internal organs shrivel up. By the time a godwit takes off, it is little more than brains, fat, and flight muscle. A female was monitored from New Zealand to Alaska in spring 2007, and then back in the fall to New Zealand—a distance of 67,300 km (14,600 mi.).

One gray-headed albatross (*Thalassarche chrysostoma*) tracked by satellite after nesting on South Georgia Island flew twice around the world before coming back to breed, while another completed a round-the-world tour in just 46 days. These birds can accomplish such feats because they are highly efficient flyers, harnessing the combined forces of wind and gravity to propel themselves thousands of kilometers with hardly any exertion.

A pintail (*Anas acuta*) banded on September 2, 1940, in Athabasca County in northern Alberta, eluded hazards until January 1954, when it was shot near Naucuspana, Tabasco, Mexico. Considering the 4,830 km (3,000 mi.) between band site and death, and assuming the bird made the two-way migration each year for 13 years, the pintail would have logged nearly 50,000 km (31,000 mi.) during its lifetime (Anonymous, 2000b).

Using radar mounted on a Canadian Coast Guard ice-breaker vessel, Alerstam et al. (2001) provide clear evidence that migrating New World shorebirds, like plovers and sandpipers, fly along the Earth's great-circle routes and use their sun compass for orientation. Arctic shorebirds migrate from their breeding sites in the far northern latitudes, across the near-mythical Northwest Passage, to the eastern United States; then they fly down the east coast of North America to their winter quarters in South America. By tracking shorebirds migrating close to the magnetic North Pole, the researchers knew that the birds could not be using either magnetic or stellar cues for orientation, and inferred that they must be steering with their sun compass along the great-circle (orthodromic) routes.

Only three Southern Hemisphere birds—Wilson's petrel, the sooty shearwater, and the great shearwater—migrate north in large numbers to spend their winters in the Northern Hemisphere, in contrast to the hundreds that go south during North American winters. Wilson's petrel (*Oceanites oceanicus*), for example, breeds in the Antarctic and may be found as far north as Labrador, a distance of approximately 11,250 km (7,000 mi.).

Waterfowl and shorebirds that migrate long distances tend to fly at higher altitudes than do others. One species of shorebird, the red knot

(*Calidris canutus*), can reach altitudes of up to 3,700 m (12,000 ft.) while migrating over the Atlantic Ocean. Aided by favorable upper air currents, the birds can travel up to 970 km (600 mi.) per night during their long migration to wintering areas in South America. Ducks usually migrate at altitudes ranging from 300 to 1,220 m (200–4,000 ft.). However, a migrating mallard was struck by an airplane at 15,500 m (21,000 ft.)—the highest documented flight by North American waterfowl (McKnight, 2000).

Many neotropical migrants, like warblers, thrushes, bobolinks, tanagers, orioles, and hummingbirds, fly nonstop some 1,000 km (620 mi.) over the Gulf of Mexico from the Gulf Coast of North America to Central America, a journey requiring about 20 hours.

Blackpoll warblers (*Dendroica striata*) make a long-range transoceanic voyage stretching between 2,269 and 2,770 km (1,410 and 1,721 mi.). The birds, weighing just 12 g (0.4 oz.)—or slightly more than a US half-dollar—use a transatlantic route in the fall, but an overland route in the spring (Fig. 12.19). On their southward journey, some use the islands of Bermuda as a resting stop, whereas others fly nonstop from New England to South America. They reach landfall, most likely on the northeastern coast of South America, in just two or three days. From there, they head farther inland to northern Venezuela and Columbia. This is one of the longest nonstop overwater flights ever recorded for a songbird. Many migrants carry at least a 40 percent fat load, which serves as their source of energy for this strenuous journey (DeLuca et al., 2015).

The ruby-throated hummingbird (*Archilochus colubris*) breeds from the Gulf of St. Lawrence and Saskatchewan to the Gulf of Mexico. It normally weighs no more than 2.5 g (0.09 oz.), but increases its weight with at least 2 g (0.07 oz.) of fat before migrating over the sea (Alerstam, 1990). The rufous hummingbird (*Selasphorus rufus*) of western North America breeds from northern California, Oregon, Idaho, and Washington north-westward through British Columbia to the southeastern Alaskan coast, and it winters in Mexico. Thus, this 9 cm long bird may migrate a total of 3,000 km (1,850 mi.) each way between its summering and wintering grounds (Diamond, 1990b).

Songbirds have been found to cover more than 480 km (300 mi.) a day on their annual migrations, much faster than the 145 km (90 mi.) or so per day that had previously been estimated (Stutchbury et al., 2009).

The use of new tracking equipment, weighing only a little more than a paper clip, now allows for tracking of such small birds as purple martins and wood thrushes. Departure dates are much later than had been assumed. The species studied made better time going north in the spring than heading south in the fall.

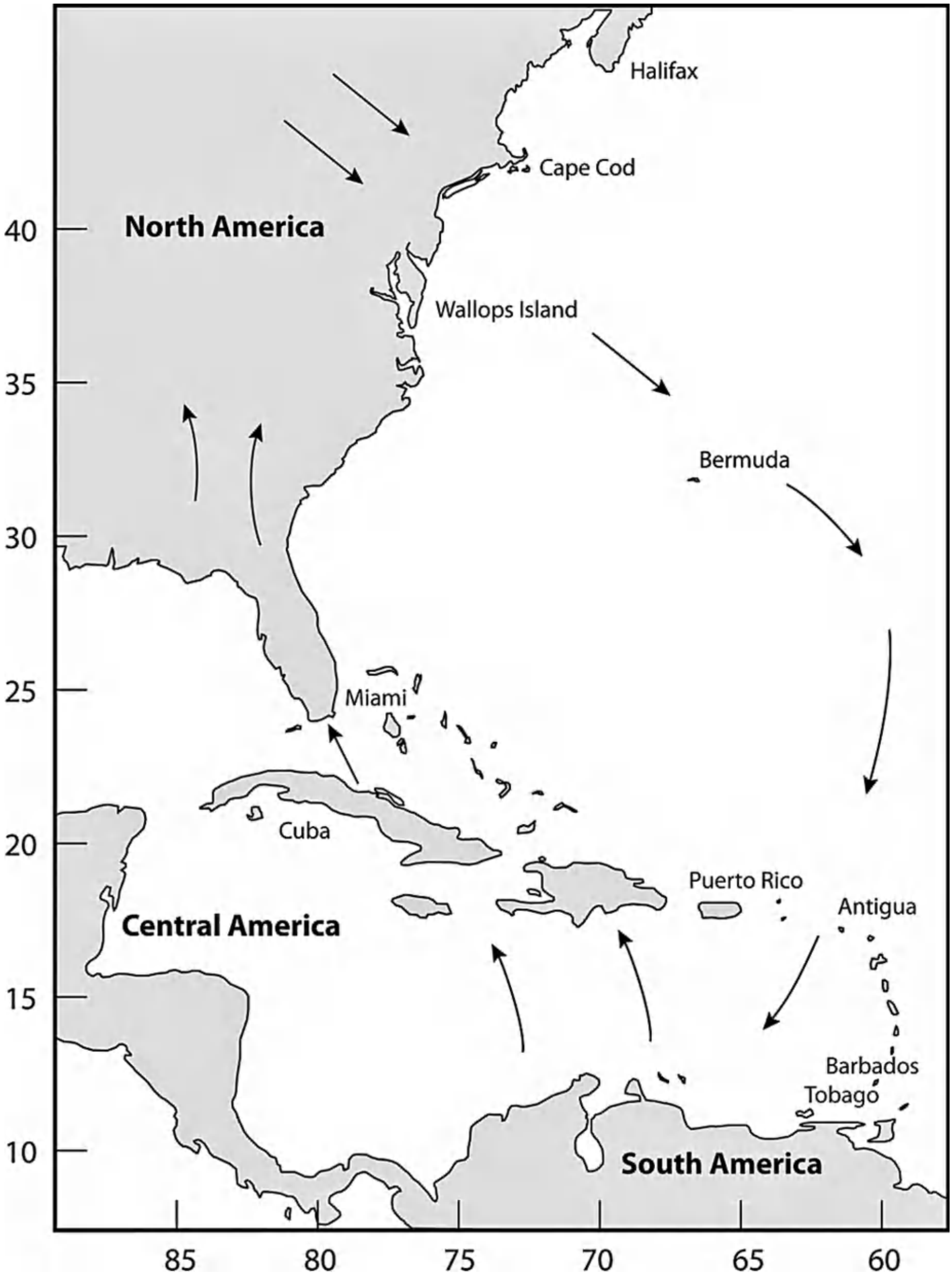


Figure 12.19. Migratory routes used by the blackpoll warbler (*Dendroica striata*). This species uses a transatlantic route in the fall, but an overland route in the spring.

In spite of these very long migratory distances, birds can perform accurate and direct migratory movements and are capable of regularly commuting between small breeding sites and wintering places, or of returning to remote tiny islands even after several years. Banding recoveries have revealed that some species migrate along narrow migration corridors and give evidence of remarkable breeding site, stopover area, and wintering site fidelity (Zink, 1973–85). Satellite tracking has allowed us to establish the directedness of migratory journeys in actual migrating individuals (Nowak and Berthold, 1991).

Researchers from the Center for Conservation Biology on Virginia's Eastern Shore (Delmarva Peninsula) began placing satellite transmitters on whimbrels (*Numenius phaeopus*) in 2008. The first whimbrel the team tagged stunned researchers by flying more than 5,150 km (3,200 mi.) in just six days to the Mackenzie River delta in the Northwest Territories and then, after a brief rest, continuing on to the North Slope of Alaska to breed (Weidensaul, 2012). They assumed these birds were coming back through the Delmarva every year, but they had no idea that the same bird would come back to the same creek, to exactly the same mudflat, year after year, showing an astounding level of site fidelity after roaming the world from the high Arctic, where they nest, to the mangrove swamps and mudflats of the Caribbean and northeastern South America, where they spend the winter. Another whimbrel, named "Hope" because she was captured on the tidal mudflats along Hope Creek on Virginia's Eastern Shore, was fitted with her 9.5 g (0.34 oz.), $3,500 solar-powered satellite transmitter in May 2009. For the next two and a half years, she was followed as she migrated back and forth on an annual round trip of more than 19,312 km (12,000 mi.). As her flight paths were monitored across half the Western Hemisphere, researchers came to realize how utterly dependent this bird was on just a handful of locations where she could rest and feed after epic flights. Hope basically used just four sites in the world encompassing just a few hundred acres (Mackenzie River for breeding; Southampton Island near Hudson Bay for rest and refueling; St. Croix for wintering; and Virginia's Eastern Shore, a critical staging area for migrating whimbrels) while crossing almost 19,312 km (12,000 mi.) a year. Habitat protection is vital.

Mammals

Among mammals, elephant seals and whales migrate the longest distances annually. Northern elephant seals (*Mirounga angustirostris*) make two migrations each year between the Channel Islands off the coast of Southern California and Mexico's Baja California northward to the Gulf of Alaska and the waters near the Aleutian Islands (Stewart and DeLong, 1995) (see Fig. 9.37d). The first migration starts at the end of the breeding season in early to mid-February. Females travel to the North Pacific near the Aleutian Islands and back, a round trip of about 6,440 km (4,002 mi.) lasting an average of 73 days. Males leave the California–Mexico area in late February to early March and swim to the Gulf of Alaska, approximately 2,730 km (1,696 mi.) north of the females. The male migration lasts about 120 days and covers approximately 12,000 km (7,456 mi.). The second female migration begins in May and lasts for approximately 234 days. During this time the females remain at sea and cover a total distance of at least 12,200 km (7,581 mi.) before returning to their home off the California coast to give birth and mate again. The second male migration begins in late August or early September, lasts for about 126 days, and covers between 9,650 and 11,250 km (5,996 and 6,990 mi.). Thus, the 19,000 to 22,000 km (11,806–13,670 mi.) annual journeys place elephant seals near the top of the list of long-distance mammalian travelers. No other vertebrate is known to undertake such a double migration.

Canada Geese—Resident or Migratory?

Canada geese migrating in formation have been a harbinger of changing seasons for decades. In the last 30 years, however, changes to Canada goose populations and the occurrence of nonmigratory resident geese have changed people's perceptions of these birds. "Resident" geese are defined by the US Fish and Wildlife Service (USFWS) as geese that hatch or nest in any Atlantic Flyway state, or in Canada at or below latitude 48° north and east of longitude 80° west, excluding Newfoundland. Geese are now resident throughout much of the Atlantic Flyway, and the problems they create are numerous and create impacts on property, human health and safety, natural resources, and agriculture. They present a potentially significant problem at airports. Geese that should be nesting in the subarctic expanses of northern Quebec are laying eggs in New York, New Jersey, Pennsylvania, Virginia, and adjacent states. Flocks that should be overwintering in the Carolinas are staying in the colder Northeast. Some geese are living their entire lives within a few miles of where they hatched. In Virginia, for example, the resident Canada goose population is estimated at 150,000 to 200,000 birds and is growing at a rate of 15 percent annually. To reduce the numbers of resident birds, state hunting seasons must be set for times when migratory birds are still in their northern breeding areas and have not yet begun to migrate.

Resident Canada geese become sexually mature and breed at 2 to 3 years of age and have a relatively high nesting success compared to migratory Canada geese. Resident Canada geese typically experience fecundity rates of 2.4 young per nesting female and 80 percent adult survival, which have resulted in an annual growth rate of 15 percent per year, although estimates have leveled off since 1997 after special hunting seasons were established throughout the Atlantic Flyway. Resident geese nest on islands and peninsulas, small ponds, lakes, and reservoirs, and along shorelines, as well as in parking lots, playgrounds, planters, and on rooftops. They molt (replace their feathers) and are flightless from mid-June through mid-July each year.

Part of the change in migratory habits is attributable to the establishment of wildlife refuges and preserves providing winter food and protection. Large concentrations of birds increase the risk of human confrontations as well as increasing the potential risk of density-dependent factors like the rapid spread of avian parasites and disease organisms.

Migratory populations of geese that nest in Canada and fly southward for the winter declined precipitously in the late 1980s and early 1990s as a result of bad weather on their Canadian breeding grounds and overhunting on their wintering grounds. Numbers were so low in 1995 that the USFWS instituted an unprecedented closure of all goose hunting seasons along the Atlantic coast—including Canada—in 1996. In a dramatic turnaround, an annual survey in 2001 indicated the number of breeding pairs had grown fivefold since 1995, and the number of breeding pairs has continued to increase.

The USFWS and the Atlantic Flyway states estimated the resident Canada goose population at 3.2 million in the United States (July 2017)—about 30 to 35 percent above the number states believe to be acceptable based on their needs to manage conflicts and problems caused by resident Canada geese. The population management goal is to reduce Atlantic Flyway resident Canada geese to 700,000 (spring estimate) by 2020. The plan calls for refining hunting regulations (seasons, bag limits, and zones) for special and regular hunting seasons to maximize the hunter harvest.

Cochran, 1996

How Hummingbirds Store the Energy to Migrate

Hummingbirds, which are among the smallest endothermic vertebrates, have a high metabolic rate. Flying hummingbirds must fuel their high rate of aerobic metabolism, and migratory hummingbirds have the additional problem of building up large fat deposits to meet the energy demand for their long migratory flights. They rely on different stores for the two activities. Fat stores for migration are built up by synthesizing fatty acids from sugar ingested in nectar. Burning the sugar during foraging spares fat stores and avoids the inefficiency of synthesizing fatty acid from glucose and then burning the fat. Migrating hummingbirds must burn fat because of its higher calorie yield per gram and because of the need to save weight in flight. To support such record-high metabolic rates, hummingbirds far surpass all other animals in their rates of intestinal glucose absorption, hepatic fatty acid biosynthetic capacity (more than 10 times that of mammals), and muscle levels of the enzymes hexokinase and carnitine palmitoyltransferase.

Suarez et al., 1990

Gray whales (*Eschrichtius robustus*) migrate some 9,600 km (5,900 mi.) from the Bering and Chukchi Seas to Baja California. From May to October, the whales inhabit the waters in the Bering Sea region. They begin swimming south in October, arriving off the California coast in mid-December, where they swim slowly and stay near the shore. The whale’s migration, which is viewed by millions of people each year, has been called one of the world’s outstanding wildlife spectacles. The northward migration begins in mid-February and comes in two waves: males and juveniles leave first, with mothers and calves following several weeks later. As temperatures rise, these age-old patterns are changing. The timing of the migration has begun to shift: the whales are leaving their calving grounds earlier and coming back later. Their feeding grounds are moving steadily north, and there is some evidence suggesting that some whales even spend the winter there. Increasingly warmer summer temperatures are melting the ice of the Bering Strait and Northwest Passage, opening a water highway between the Pacific and the Atlantic oceans. In 2010, a gray whale was photographed off the coast of Israel, and in 2013 another was spotted off the Atlantic coast of Namibia in southern Africa. Gray whales lived in the Atlantic for thousands of years, but had not been seen outside the Pacific Ocean since the eighteenth century, when whalers are thought to have harpooned the last Atlantic gray whale.

The population of gray whales was estimated to have dipped below 2,000 just before the turn of the century, primarily because of excessive whaling. The current population size, which is estimated to be about 20,000 animals, allowed this species to be removed from the endangered species list in June 1994.

Blue, fin, and humpback whales may travel more than 8,000 km (4,971 mi.) during their annual migratory journeys. Five feeding aggregations of humpback whales (*Megaptera novaeangliae*) exist in the North Atlantic Ocean from Maine to Iceland and Denmark. In the fall, whales from all feeding aggregations migrate to breed within the nearshore areas and banks of the West Indies near the Dominican Republic, Puerto Rico, and the Virgin Islands. More than 1,000 photographically verified resightings of individually known humpbacks demonstrate that individual whales return in the spring to their particular feeding region. Acoustic monitoring of humpback whale songs has provided useful information concerning their migratory routes (Clapham and Mattila, 1990). Stone et al. (1990) reported a humpback whale that migrated from the Antarctic Peninsula region to Colombia in South America, a minimum of 8,334 km (5,179 mi.). It was the first time that an Antarctic humpback whale had been known to cross north of the equator, and the first time an Atlantic humpback had been documented in South American Pacific Ocean waters. More recently, researchers at the Cascadia Research Collective in Olympia, Washington, tracked seven humpback whales from their summer feeding grounds in the Antarctic Ocean to their winter breeding grounds off the Pacific Coast of Central America (Bakalar, 2008). They found that humpbacks reproduce only in warm waters of 21°C–28°C (70°F–83°F), regardless of latitude. Coastal upwelling in the Southern Hemisphere results in cool waters as far north as the equator in the Pacific, driving the whales all the way to Panama and Costa Rica for the southern winter. A female North Pacific gray whale holds the record for the longest migration of any mammal at 22,511 km (13,957 mi.) (Mate, et al., 2015). She was affixed with a satellite-monitored tag on a feeding ground off Sakhalin Island, Russia, on November 24, 2011. She visited all three major eastern gray whale reproductive areas off Baja California, Mexico, before returning to Sakhalin Island on May 14, 2012. Since all Western North Pacific whales feed in the productive waters off the coast of northeastern Russia and then swim south into the Sea of Japan to breed, researchers question whether the female with the new record as well as several others were actually eastern gray whales that had ventured to new feeding grounds as their population expanded.

The Migratory Diet

Many species of migratory songbirds switch from an insect-rich diet to one based on fruit during their fall migration. In some, like hermit thrushes (*Hylocichla guttata*), red-eyed vireos (*Vireo olivaceus*), and yellow-rumped warblers (*Dendroica coronata*), fruit makes up 80 percent of their fall diet. A few, like American redstarts (*Setophaga ruticilla*), continue to feed exclusively on insects, even though insect-eaters put on less weight than fruit-eaters. The bigger the proportion of fruit in the diet, the greater the weight gain.

Parrish, 1997

A Migration Surprise

Until recently, it was thought that most of the humpback whales along Australia's eastern coast migrated each year from their feeding grounds in Antarctica to breed in tropical waters. When the migratory groups were surveyed by Peter Corkeron of James Cook University in Queensland and Miranda Brown of the University of Cape Town in South Africa, the male to female ratio turned out to be 2.4:1. Apparently, young females may spend all year in the Antarctic and migrate north only when they are sexually mature. The authors suggest that it may be energetically less taxing for a young whale to remain in cold waters year-round than to migrate to warmer waters. The results of this survey indicate that population estimates need to be increased, because only 60 percent of the population is being counted.

Brown et al., 1995

Previous research on humpback whales in both the Northern and Southern Hemispheres has reported site-specific male-biased sex ratios in breeding grounds and along migratory corridors. However, one recent Southern Hemisphere study (Franklin et al., 2017) reported a female-biased sex ratio in a feeding area (Hervey Bay, Queensland, Australia) within a coastal migratory corridor, indicating that females may preferentially occupy some habitats.

Northern fur seals (*Callorhinus ursinus*), Steller sea lions (*Eumetopias jubata*), and several other pinnipeds migrate several thousand kilometers annually. The northern elephant seal (*Mirounga angustirostris*) migrates twice each year from the Bering Sea to the Gulf of California. With the route being approximately 10,600 km (6,600 mi.) each time, the annual migration comprises an estimated 21,000 km (13,000 mi.).

Some bats hibernate in northern areas, but others are well-known migrators. The red bat (*Lasiurus borealis*), the hoary bat (*Lasiurus cinereus*), and the silver-haired bat (*Lasionycteris noctivagans*) regularly migrate 1,300 to 1,600 km (808 to 994 mi.). The two lasiurine bats (red and hoary) have been taken in Bermuda, a destination that required a nonstop flight of at least 950 km (590 mi.) (Orr, 1982). A Brazilian free-tailed bat (*Tadarida brasiliensis*) banded at Carlsbad, New Mexico, and recovered in Jalisco, Mexico, had a minimum recorded movement of at least 1,340 km (833 mi.) in 69 days (Villa-R. and Cockrum, 1962).

Among North American ungulates, the Porcupine caribou (*Rangifer tarandus*) (Fig. 12.20) has the longest land migration route of any land mammal, traveling as much as 300 to 650 km (185–400 mi.) annually between their winter range and calving grounds at the Beaufort Sea. They spend the summer on the tundra north of the timberline; however, beginning in July, they move south to the taiga and the edge of the tundra. Their migrations are under the shadow of possible oil exploration in the Arctic National Wildlife Refuge. Mule deer (*Odocoileus hemionus*) migrate approximately 240 km (150 mi.) through Wyoming crossing highways, fences, and rivers along the way.

Figure 12.20. Caribou make the longest migratory journey of any North American ungulate.

Vast herds of African gazelles, wildebeests, gnus, and many others travel many kilometers annually in search of food and water. According to a 2014 World Wildlife Fund study, the plains zebra (*Equus quagga*) undertakes the longest linear land-mammal migration in Africa. The journey between Namibia and Botswana is a round trip of over 500 km (300 mi.). The zebras face considerable disruption from man-made obstacles such as roads, fences, and farming causing habitat fragmentation. At the end of the rainy season, East African blue wildebeest (*Connochaetes taurinus*) head toward new pastures on a circular migration of between 800 and 1,600 km (500 and 1,000 mi.) around the Serengeti. Herds can stretch to 40 km (25 mi.) long as they cross the plains. Their migration is threatened by poaching and, as with the zebras, by habitat fragmentation when land is fenced off or cut up by roads.

Navigational Cues Used in Migration

Vertebrates can orient themselves in their environment via several methods. Some use their senses of taste and smell, whereas others, like bats, elk, and many birds, probably orient by using their sense of sight to recognize familiar landmarks. Other species use either celestial bodies (sun, stars, or moon) or the Earth's magnetic field as cues to enable them to successfully return to their home range.

Mechanisms possessed by species like salmon and birds that enable them to return to precise locations from distances of hundreds and even thousands of kilometers have been debated for centuries. Olfaction, celestial cues, sound, vision, and detection of the Earth's magnetic field appear to be involved in different species. Like other animals, birds are equipped with two types of biological or internal clocks, which play an important part in the spatiotemporal and physiological organization of migration as well as in other processes: circadian (endogenous diurnal rhythms) and circannual (endogenous annual rhythms or so-called internal calendars) (Gwinner, 1986, 1996; Berthold, 1996). Circadian rhythms are involved in such functions as the seasonal expression of migratory activity and fat deposition during migration, in mechanisms measuring daylength, and in synchronizing processes to the changing ecological requirements of the calendar year. Circannual rhythms seem to fix not only the dates of onset and termination of the first migratory period in naive first-time migrants, but also the course and the approximate distance to be covered.

The possibility that animals could sense the Earth's magnetic field has been under investigation for more than 100 years (Viguier, 1882; review by Gould, 1980; Able and Able, 1995). Studies during the 1970s suggested that birds possibly could sense low-intensity alternating-current electromagnetic fields and that they also could sense natural *fluctuations* in the Earth's magnetic field. Permanently magnetic iron oxide (probably magnetite, Fe_3O_4) has been found concentrated in the head and neck muscles of both migratory and nonmigratory birds, including western grebes (*Aechmophorus occidentalis*), pintails (*Anas acutus*), pigeons (*Columba livia*), white-crowned sparrows (*Zonotrichia leucophrys*), Savannah sparrows (*Passerculus sandwichensis*), northern bobwhites (*Colinus virginianus*), chimney swifts (*Chaetura pelagica*), cliff swallows (*Hirundo pyrrhonota*), tree swallows (*Tachycineta bicolor*), Carolina wrens (*Thryothorus ludovicianus*), European starlings (*Sturnus vulgaris*), red-winged blackbirds (*Agelaius phoeniceus*), brown-headed cowbirds (*Molothrus ater*), house sparrows (*Passer domesticus*), and European robins (*Erithacus rubecula*) (Edwards et al., 1992). This magnetic material is thought to be coupled to a magnetic-sensitive muscle receptor like a muscle spindle. These nerves respond to magnetic field changes. The iron-based crystals might realign like a tiny compass or somehow detect or magnify magnetic fields and send a signal to the brain that allows a bird to gauge the strength or direction of a magnetic field. The Earth's magnetic field varies in strength and its orientation to the Earth's surface as one travels between the North and South Poles.

Wandering Manatees

Manatees generally stay in the warm waters around Florida. Few venture much farther north than Georgia. However, a male Florida manatee (*Trichechus manatus*) was captured in Maryland's Chesapeake Bay in the fall of 1994, the first time since the 1800s that one of these large mammals was spotted this far north. It was fitted with a radio transmitter and airlifted back to Florida to save it from cold weather. During the summer of 1995, "Chessie" became the first known Florida manatee to swim to New England and back to Florida. He got as far as Point Judith, Rhode Island, a distance of approximately 3,220 km (2,000 mi.) north of Fort Lauderdale, on August 16 before turning around. Satellite readings from his radio transmitter in July 1996 indicated that he had crossed the North Carolina–South Carolina border and was again headed north at an estimated speed of approximately 40 km (25 mi.) a day. Prior to 2001, he was last seen in August 1996, swimming south past Portsmouth, Virginia. In August 2001, however, Chessie was again sighted in Chesapeake Bay, then along the Virginia coast in early September where he was inside a lock along the Intercoastal Waterway, waiting for the lock to fill so he could presumably continue his trip south.

In May 2002, several manatee sightings were reported in the James River near Norfolk and Newport News. In June 2002, the first known sighting of a manatee within the Richmond, Virginia, city limits occurred. In each instance, the manatee had different scars than those of Chessie. Chessie was not seen again for almost 11 years until a confirmed sighting occurred on July 5, 2011, in a Calvert County marina in Chesapeake Bay. Chessie was positively identified by distinctive markings and scars on his body.

Anonymous, 1996d, 2001, 2002a, 2011

Edmonds (1992) stated: "There are at least three independent magnetic field detectors in the bird's head, one associated with the pineal gland which helps control melatonin secretions, one in the eye which requires light to function, and a third of high sensitivity for which the transducer is unknown but a magnetite-based detector is suspected." A pigeon's optic nerves may respond to differences in the angles of magnetic fields, and magnetic crystals bound to cranial nerves may detect field strength. Pigeons flying under an overcast sky with magnets attached to their bodies become disoriented, whereas control birds affixed with brass bars of the same weight show no disorientation. Thus, the ability to perceive magnetic fields could provide birds with both a map and a compass sense. So far, no differences in the sensitivity to magnetism have been found between migratory and nonmigratory birds.

Some birds may use their eyes to sense direction using the Earth's magnetic field. A light-sensitive pigment called *cryptochrome* found in nerves in the brain and the retina of the eye becomes sensitive to the magnetic field when it absorbs blue light. The blue light at dusk may be the best time for birds to take a compass reading. Signals from the eye to the brain might be interpreted as a compass direction. Recently, Zapka et al. (2009) demonstrated that in European robins, a visual center in the brain and light-sensing cells in the eye—not magnetic-sensing cells in the beak—allow the songbirds to detect which direction is north and migrate correctly.

Researchers have identified three clusters of nerve endings on each side of the homing pigeon's beak, each cluster oriented along one of the bird's three perpendicular axes (beak-tail, wing-wing, and back-belly). Inside the nerve cells they discovered two kinds of magnetic iron oxide—square platelets of maghemite and bullet-shaped particles of magnetite. The investigators propose that an extremely delicate arrangement of those intracellular minerals constitutes the long-sought receptor for birds' magnetic sense (Fleissner et al., 2007).

Researchers have long thought birds navigate by the stars and use the Earth's magnetic field as a backup on cloudy nights. However, Weindler et al. (1996) showed that young garden warblers (*Sylvia borin*) from Germany need information from both the magnetic field and the stars to choose the right heading on their first migration. Their migratory route is southwest for several weeks, then southeast. This route avoids the Alps, the Mediterranean, and most of the Sahara Desert. Birds raised under an "artificial" sky with only celestial cues flew due south.

Polarized light can be used by some day-migrating species, like yellow-faced honeyeaters (*Lichenostomus chrysops*), when no other known cues are available (Munro and Wiltschko, 1995). Savannah sparrows (*Passerculus sandwichensis*) have been shown to use polarized light cues from the region of sky near the horizon to recalibrate the magnetic compass at both sunrise and sunset (Muheim et al., 2006). It is suggested that skylight polarization patterns are used to derive the geographic directional system that provides the primary calibration reference for all of the compasses of migratory songbirds.

Magnetic material also has been found in the brain of loggerhead turtles (*Caretta caretta*) and in the blubber, bone, muscle, and brain of several cetaceans, including the Atlantic bottlenose dolphin (*Tursiops truncatus*), goosebeak whale (*Ziphius cavirostris*), Dall's porpoise (*Phocoenoides dalli*), and humpback whale (*Megaptera novaeangliae*)

(Klinowska, 1986). Magnetic crystals also have been found in the dura mater of the common dolphin (*Delphinus delphis*) (Zoeger et al., 1981).

Olfaction plays a major role in some species. Salmon can identify their home streams by chemical cues that are present in the stream water (Hasler and Wisby, 1951; Hasler and Scholz, 1983; Brannon and Quinn, 1990) or by pheromones released into the water by resident juveniles (Nordeng, 1971, 1977). Juvenile salmonids are thought to imprint on particular odors specific to home-stream waters (Harden-Jones, 1968), which they use as cues when returning as adults. Both olfactory and gustatory receptors are extremely sensitive in fishes, and both may be employed by anadromous species (Keefe and Winn, 1991). In contrast, white bass (*Roccus chrysops*) migrate by means of sun-compass orientation (Hasler et al., 1958).

The newt *Taricha* also uses olfactory mechanisms, as apparently do many other amphibians, especially salamanders. Vocalizations by male frogs and toads are especially important in attracting females to breeding ponds. Amphibians also use visual cues and can orient by using solar, lunar, and stellar cues in conjunction with an internal clock mechanism (Ferguson and Landreth, 1966; Ferguson, 1967).

Leatherback (*Dermochelys coriacea*) (Fig. 12.21) and green (*Chelonia mydas*) sea turtle hatchlings emerging from underground nests on oceanic beaches are immediately confronted by two separate problems in orientation. First, hatchlings use their vision to seek out bright, open horizons to find the sea (Lohmann et al., 1990). Both species orient toward violet and blue-green wavelengths (360–500 nm) as opposed to yellow-orange and red light (600–700 nm). Some level of spectral quality assessment must exist for both species, with possibly heightened sensitivity in the short wavelengths being an adaptation for vision in seawater (Witherington and Bjorndal, 1991). Once they reach water, they must orient *into* the waves, swimming toward approaching waves and oceanic swells. Thus, these turtles employ two separate orientation systems, each based on different cues. The sea-finding orientation is not a prerequisite for wave orientation. Although both land and sea orientation systems can function independently, they may both be operational and interact under natural conditions (Lohmann et al., 1990).

Hatchling loggerhead turtles (*Caretta caretta*) use wave direction as their primary cue during the early phases of offshore migration (Salmon and Lohmann, 1989). In addition, particles of the magnetic mineral magnetite have been found in their brains. This allows these turtles to carry a remarkably sophisticated magnetic compass in their heads, enabling them to sense the magnetic field of the Earth and, further, to distinguish between different field intensities found along their migratory route and orient themselves to them (Lohmann, 1991, 1992; Lohmann and Lohmann 1992, 1993, 1994a, 1994b, 1996a, 1996b). The compass, which also enables them to sense how far north or south they have traveled, gives them the minimal sensory abilities necessary to approximate global position (latitude and longitude) using a bicoordinate magnetic map. Turtles use this magnetic sense along with two other directional cues—light reflecting off the ocean surface and wave motion—to orient themselves in the world. Some researchers also feel that olfaction is another major factor in turtle orientation (Seachrist, 1994).

Figure 12.21. A leatherback sea turtle (*Dermochelys coriacea*) instinctively makes its way to the sea upon hatching. It seeks out bright, open horizons and orients toward violet and blue-green wavelengths.

Young loggerhead turtles must navigate across the Atlantic Ocean and back to their natal beaches, a migratory journey lasting for years and covering an 12,875 km (8,000 mi.) path around the Atlantic Ocean. It is essential that they stay within the Atlantic gyre, an oceanwide current of warm water. The gyre forms a huge, circular ocean current, moving clockwise from the US East Coast, across the North Atlantic, and then south along the coasts of Spain and Africa, before turning west to complete the circle. After hatching, baby turtles swim into this current and flow with it, nudged along by warm waters rich in food. If they leave the gyre, the turtles die, killed by the surrounding frigid waters. They need to stay in the warm waters to survive. The turtles apparently use both the intensity and direction of the magnetic fields to navigate (Lohmann et al., 2001).

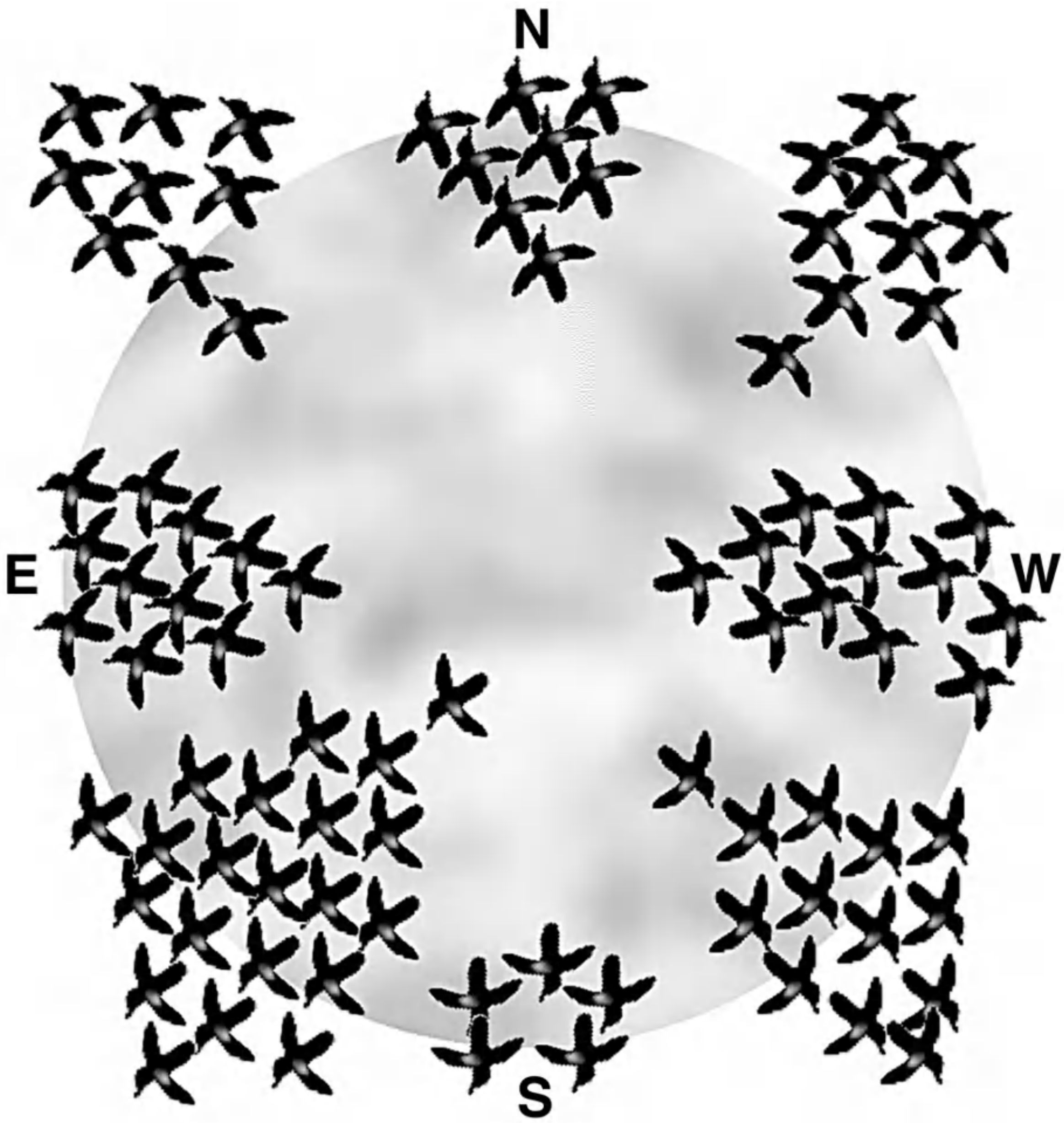
The annual return migration between summer feeding ranges and winter denning sites is a common behavior in many populations of northern temperate zone snakes. Plains garter snakes (*Thamnophis radix*) use solar cues as an orientation guide (Lawson and Secoy, 1991). The use of solar and other celestial cues also has been demonstrated in rattlesnakes (*Crotalus atrox*), water snakes (*Nerodia sipedon* and *Regina septemvittata*), alligators (*Alligator mississippiensis*), and some turtles (common box turtle, *Terrapene carolina*; spiny softshell turtle, *Apalone* [*Trionyx*] *spinifera*; and the painted turtle, *Chrysemys picta*) (Landreth, 1973; Newcomer et al., 1974; Murphy, 1981; DeRosa and Taylor, 1982).

Birds may use visual and memory cues of familiar landmarks. In some species, the young may learn migratory routes from older birds. In others, however, the young leave nesting areas after the adults. In still others, the birds are either solitary migrants, or they migrate at night when terrestrial landmarks would be of little use except for celestial cues. It is now known that migratory bird populations have an internal annual rhythm, preprogrammed for the migratory journey with regard to both distance and direction (Able and Able, 1995; Weindler et al. 1996). The migratory bird follows this inborn instinct, which serves as an automatic-pilot system. Thus, the primary directions in migratory birds like blackcaps (*Sylvia atricapilla*) are genetically determined (Berthold et al., 1990, 1992; Helbig, 1991; Helbig et al., 1994). Migrating birds also rely on interacting compass senses—magnetic, the position of celestial bodies (sun, moon, stars), and polarized light—as major aids in navigation (Wiltschko and Wiltschko, 1995).

Starlings and white-throated sparrows apparently use the star pattern in the sky (Kramer, 1957, 1959; Sauer, 1958) (Fig. 12.22). Golden-crowned (*Zonotrichia coronata*) and white-crowned sparrows (*Z. leucophrys*), as well as white-throated sparrows caged outdoors, show a strong orientation toward the north in the spring and toward the south in the fall, indicating orientation by either the moon or stars. In addition, perception of ultraviolet light and linearly polarized light also may serve as navigational aids.

Infrasound may be another important factor enabling birds to navigate and orient themselves (Wiltschko and Wiltschko, 1994). Homing pigeons have been shown to detect frequencies as low as 0.05 Hz, well below the lower limit of human hearing, which is approximately 10 Hz. See further discussion of infrasound as a means of communication in Chapter 13.

Much less is known about navigation during migration in mammals than in birds. Olfaction is probably a major factor in some mammals, like large herbivores, because the presence of many scent-producing glands suggests that olfaction is well developed in these species. Such glands may be present on the face (preorbital), rump, and lower limbs (tarsal, metatarsal, interdigital). Pheromones from these glands are left as scents on the ground and on vegetation along the animal’s trail. These serve as a guide to other members of the same species traveling along that route. The recognition of familiar landmarks through memory and vision is undoubtedly important in many mammalian species. Marine species may be influenced by ocean currents, olfactory stimuli, ocean floor topography, and the Earth’s magnetic field.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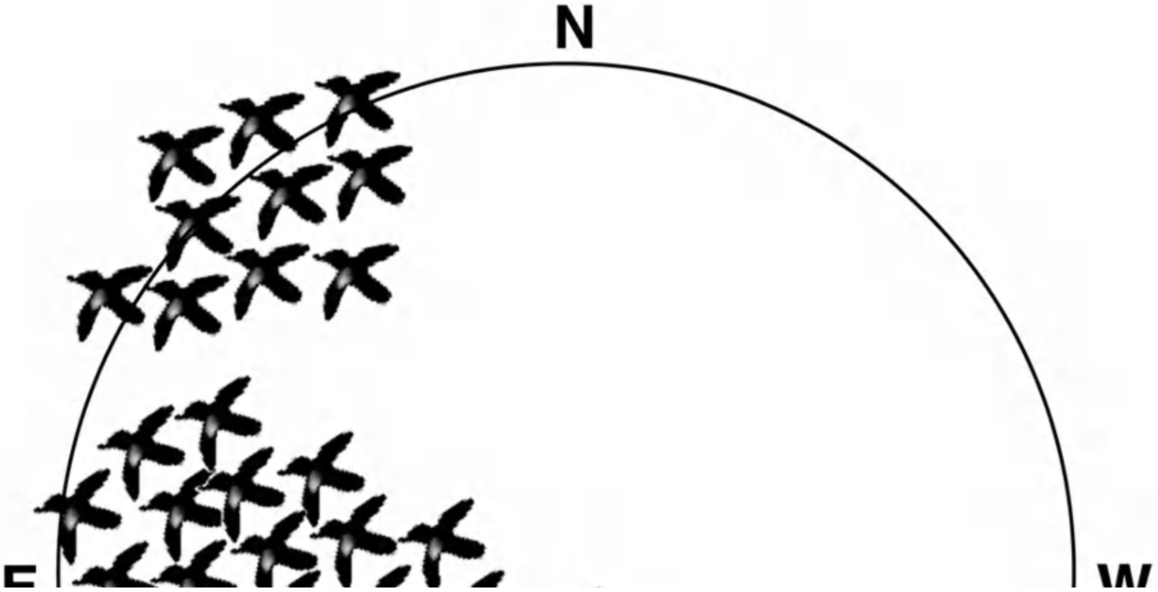
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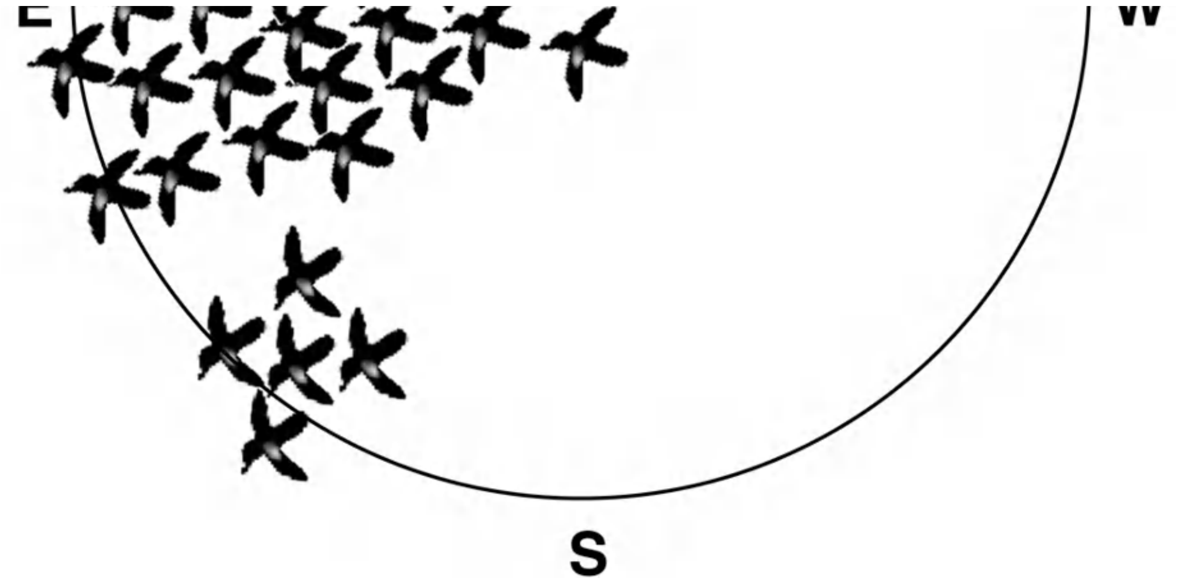

Figure 12.22. Influence of clouds on the orientation ability of captive starlings (*Sturnus vulgaris*). *Top*: dense clouds; here, the starling wanders at random. *Bottom*: clearing; in this situation, the starling immediately gets its bearings in the direction in which it is flying.

The study of migration continues to intrigue scientists. The mechanisms and processes employed by these long-distance migrators remain a fruitful field for investigation. Humanity's effects on the climate (climate change, global warming, acid rain, etc.) and on the world's ecosystems (habitat destruction, pesticide use, etc.) may cause drastic changes in the populations of migratory species during our lifetime. For example, populations of many songbirds in the Americas have been declining because of fragmentation of their breeding habitat in North America, reduction of wintering habitat caused by destruction of tropical habitat, and loss of resting and feeding areas due to urban development and/or pollution.

HOMING

Many vertebrates have an innate ability to return to their home after foraging, displacement, or migration. Birds return to their nests after foraging, to a specific place to rest at night, to winter ranges, and to breeding ranges during the appropriate season, sometimes after migratory journeys of thousands of kilometers. Homing pigeons return to their lofts year-round. This ability to return is known as **homing**. Displacement may occur through natural causes (flooding, drought, storm, fire), food-gathering activities (chasing prey into unfamiliar territory), or through human activities (trapping and relocating nuisance animals, restocking, racing pigeons, etc.). Homing success decreases as the distance the individual is displaced increases (Fig. 12.23). Homing ability within some species is also correlated with home range size. For example, Anderson et al. (1977) found that house mice (*Mus musculus*) with larger home ranges were able to home from greater distances than house mice with smaller home ranges. The ability to return home from any location requires information on the position of the present site in relation to the home site. Homing is a component of migration, but it can also be observed in nonmigrating animals.

Homing ability has been demonstrated in all of the vertebrate groups. A number of tidepool fishes can find their way back to their home pools by using olfactory and visual cues after being displaced several hundred meters away (Gibson, 1969, 1982; Dooley and Collura, 1988; Horn and Gibson, 1988). Some male rock-dwelling cichlids (*Pseudotropheus aurora*) may home over distances of up to 2,500 m (8,202 ft.) (Hert, 1992). Salmon can find their way back to their natal streams several years later after traveling thousands of kilometers in the open ocean (Braithwaite, 1998). By studying the chemical isotope bound up in the otoliths of weakfish (*Cynoscion regalis*), researchers have shown that these marine fish have a strong homing instinct, with up to 81 percent of the spawners being able to find their way back home (Thorrold et al., 2001).

Homing has been demonstrated in several species of salamanders. An average of 45 percent of mountain dusky salamanders (*Desmognathus ochrophaeus*) displaced 30 m (98 ft.) upstream and downstream from their capture sites in Ohio were able to return, some in less than 24 hours (Holomuzki, 1982). Eight percent of newts (*Taricha*) displaced 800 m (2,625 ft.) upstream or downstream returned to their homes within 12 months (Twitty, 1959; Twitty et al., 1967). Within two years, 15 percent had returned and by the end of three years, 29 percent had returned. A total of 2 percent (18 newts) displaced 4.8 km (2.98 mi.) away from their points of capture in a stream in a deep canyon on the other side of a 305 m (1,000 ft.) mountain ridge found their way back to their homes. Red-cheeked salamanders (*Plethodon jordani*) have returned from distances up to 150 m (492 ft.) (Madison, 1969). Forty-three of 83 Pacific tree frogs (*Hyla regilla*) (52 percent) returned from 275 m (902 ft.) to their breeding sites in one month (Jameson, 1957). Toads (*Bufo bufo*) have returned 3 km (1.9 mi.) to their home sites (Heusser, 1969). Leopard frogs (*Lithobates* [*Rana*] *pipiens*) displaced up to 1 km (0.62 mi.) from their capture site generally oriented correctly in their homeward direction and returned to their home range (Dole, 1968).

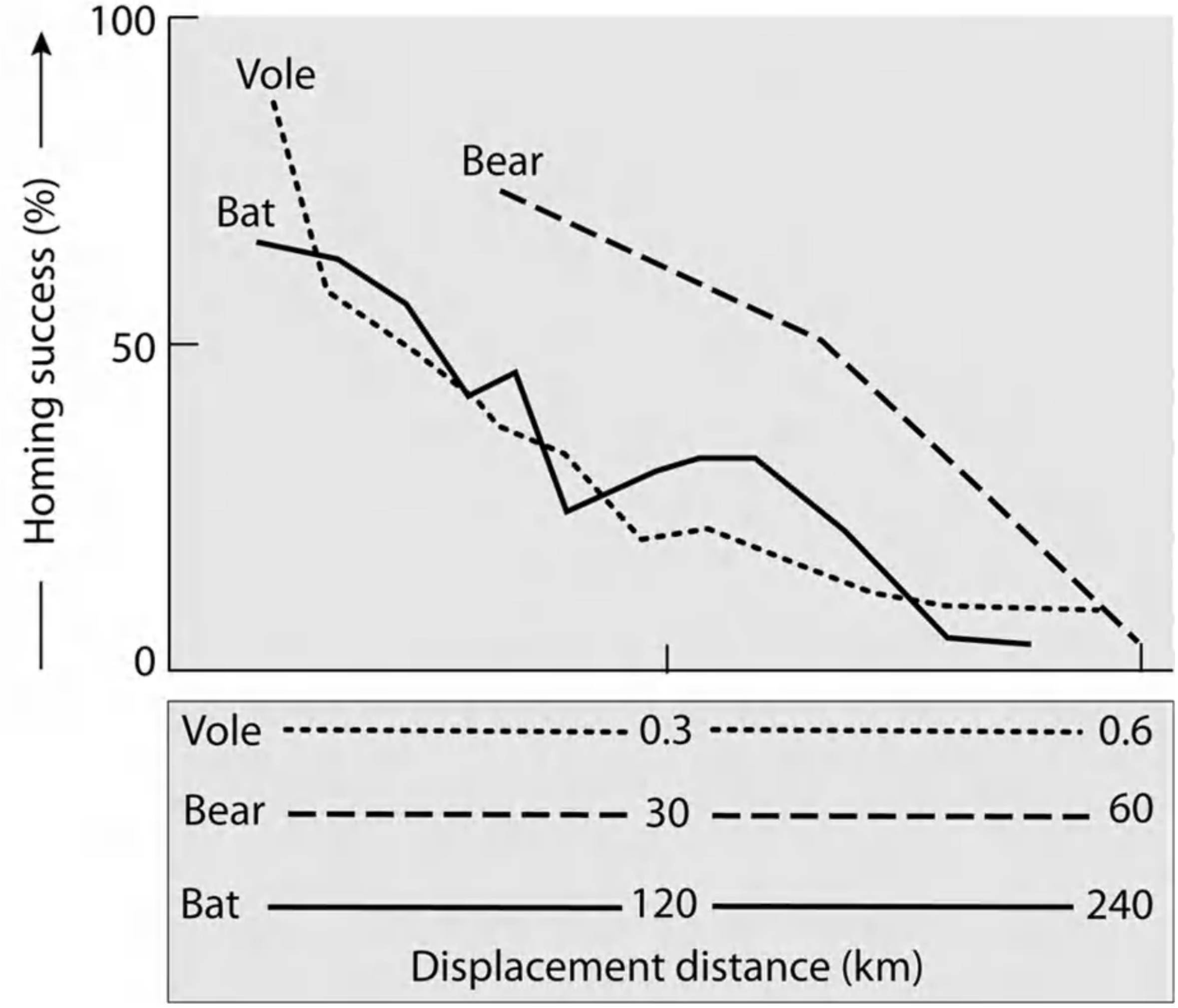

Figure 12.23. Homing success as a function of displacement distance in three species of mammals: Indiana bat (*Myotis sodalis*), n = 700; meadow vole (*Microtus pennsylvanicus*), n = 460; black bear (*Ursus americanus*), n = 112.

The late Steve Irwin and Craig Franklin, of the University of Queensland. captured three large crocodiles on the Cape York Peninsula in Australia's northeast tropics. After affixing satellite transponders to the crocodiles' backs, the researchers helicoptered them 56, 97, or 153 km (35, 60, or 95 mi.) away from their capture sites. After lingering in their new environments for as long as three months, the crocodiles traveled along the coast and returned to their original homes. One 4.6 m (15 ft.) crocodile who had been airlifted across the peninsula swam 402 km (250 mi.) around the coast in 20 days. He covered as many as 31 km (19 mi.) in a single day (Borrell, 2008).

Adélie penguins (*Pygoscelis adeliae*) leave their young for up to two weeks to forage for food at sea and then return. The Manx shearwater (*Puffinus puffinus*) is a European bird that has a north-south migration route. A breeding adult was transported by airplane 5,150 km (3,200 mi.)

westward to Boston, Massachusetts, and released; 12 days later, it was recaptured in its nesting burrow in Skokholm, an island off the southwest coast of Wales (Mazzeo, 1953). The bird had returned from outside the range of the species, along an east-west route, and at an average speed of more than 400 km (250 mi.) per day.

A total of 412 golden-crowned (*Zonotrichia coronata*) and white-crowned (*Z. leucophrys*) sparrows were transported from their San Jose, California, wintering grounds to Baton Rouge, Louisiana, a distance of 2,900 km (1,800 mi.), and released (Mewaldt, 1964). The following winter, 26 of these birds were recaptured in San Jose. Mewaldt then transported 660 birds (including 22 that had returned from Baton Rouge) to Laurel, Maryland, a distance of 3,860 km (2,400 mi.), and released them. The next winter, 15 (including 6 of the 22) had returned to San Jose.

Eleven nonmigratory dark-eyed juncos (*Junco hyemalis*) were transported distances ranging from 55 to 563 km (34–350 mi.) from their capture site at Mountain Lake, Virginia (Nolan et al., 1986). Four of six homed from 328 km (200 mi.) or less, and three of five did so from 563 km (350 mi.). Two of the latter individuals returned in 28 and 35 days, respectively. Estimated mean distances traveled per day ranged from 13 to 25.2 km (8–15 mi.).

Hitchcock and Reynolds (1942) showed that, among mammals, half of the little brown bats (*Myotis lucifugus*) returned to the home roost after being released more than 113 km (270 mi.) away. Schramm (1957) recovered 2 out of 34 little brown bats back at the home roost 17 and 22 days, respectively, after they had been released 435 km (270 mi.) away (Fig. 12.24).

In a study of the big brown bat (*Eptesicus fuscus*), 155 individuals were displaced 725 km (450 mi.) north of their point of capture in Ohio (Smith and Goodpaster, 1958). They were released on July 21. Three were found at the home roost on August 24, and four more were found on October 26. Some (2.5 percent) released 365 km (225 mi.) away returned within one to two years. On August 2, 18 bats were taken to western Tennessee, 547 km (340 mi.) southwest of Cincinnati, their point of capture. Fifteen days later, two of these, including a juvenile, had returned home.

Figure 12.24. Little brown bats (*Myotis lucifugus*) have returned to their home roost after being released 435 km (270 mi.) away.

Cope et al. (1961) released big brown bats at various distances from the home roost. Nearly all of those released 32 km (20 mi.) away returned the same night. Most bats released 64 km (40 mi.) away did not return until the second night, and most of those taken 161 km (100 mi.) away arrived on the third night. Of bats released 403 km (250 mi.) from home, some returned during the fourth night, and nearly all had returned by the end of the fifth night.

Eastern gray squirrels possess a strong homing tendency and may return from as far as 4.5 km (3 mi.) (Hungerford and Wilder, 1941).

How do homing animals return? In some cases, the animal can rely on information obtained en route during the outward journey. In others, the animal finds itself in territory that is somewhat familiar. Periodic exploratory movements out of its normal home range may have given the animal some familiarity with the surroundings, so that by using olfaction and/or vision, it may be able to return. One common mechanism is the use of landmarks surrounding the goal to which the animal is returning. This is also called *piloting* or *mnemotaxis*. Most species use visual landmarks. Landmarks used by fish may serve as beacons marking a goal, or the geometrical relationships between several landmarks can be used to calculate a trajectory to a destination. Some animals simply may begin wandering from their release site and, through random wandering, eventually return to their homes. Still others may engage in a directed search pattern following their release. Pigeons and sea gulls usually circle to get their correct orientation before heading homeward.

Vertebrates can orient themselves in their environment via several methods. Some use their senses of taste and smell, whereas others, like bats, elk, and many birds, probably orient by using their sense of sight to recognize familiar landmarks. Other species use either celestial bodies (sun, stars, or moon) or the Earth's magnetic field as cues to enable them to successfully return to their home range. The celestial compasses are based on visual information: compensation for the sun's apparent movement is done with the help of an internal clock (Schmidt-Koenig, 1960); the constant spatial relationship between stars is used for star compass orientation (Emlen, 1967).

Big brown bats are known to orient at night by echolocation, but this works over only a short range. Holland et al. (2006) demonstrated that these bats also rely on a magnetic compass to return to their home roost.

Kramer (1959) first demonstrated that homing pigeons primarily rely on the sun to orient or determine directions in space (compass), while some other mechanism was responsible for allowing pigeons to determine their position in space relative to home (navigational map). When displaced to some distant, unfamiliar release site, a homing pigeon will first determine its location relative to home by relying on its navigational map. For example, if the navigational map indicated that the pigeon was north of its home, it would rely on the sun as a compass to determine south and fly toward home. Thus, navigation is based on a two-step map and compass process (Fig. 12.25).

It is now known that homing pigeons may use visual, olfactory, and magnetic cues, as well as the sun, to get specific information concerning their position with respect to their home (Alerstam, 1990). Olfactory stimuli within approximately 100 km (60 mi.) of their home may be of considerable importance. Some may sample olfactory cues, changes in the Earth's magnetic field, and geographic landmarks en route to the release site. These mechanisms interact in a complex way, supplementing as well as replacing each other. With several means of orientation available to it, a pigeon can use the one that is most effective at any given time.

Young, inexperienced homing pigeons and adult, experienced pigeons differ in the weighting of different orientational mechanisms (Alerstam, 1990). The navigational system undergoes a change during the first few months of a pigeon's life. Initially, birds must rely on mechanisms like visual cues to determine their home direction. Later, as their flying experience increases, they develop a navigational map that employs several cue systems like odor, magnetic cues, and infrasound (Wiltschko and Wiltschko, 1994). During the development of the navigational system, the magnetic compass seems to control the sun compass, whereas later the sun compass dominates. The magnetic compass, however, continues to serve as a backup system for overcast days and in case the sun compass is impaired (Wiltschko and Wiltschko, 1994).

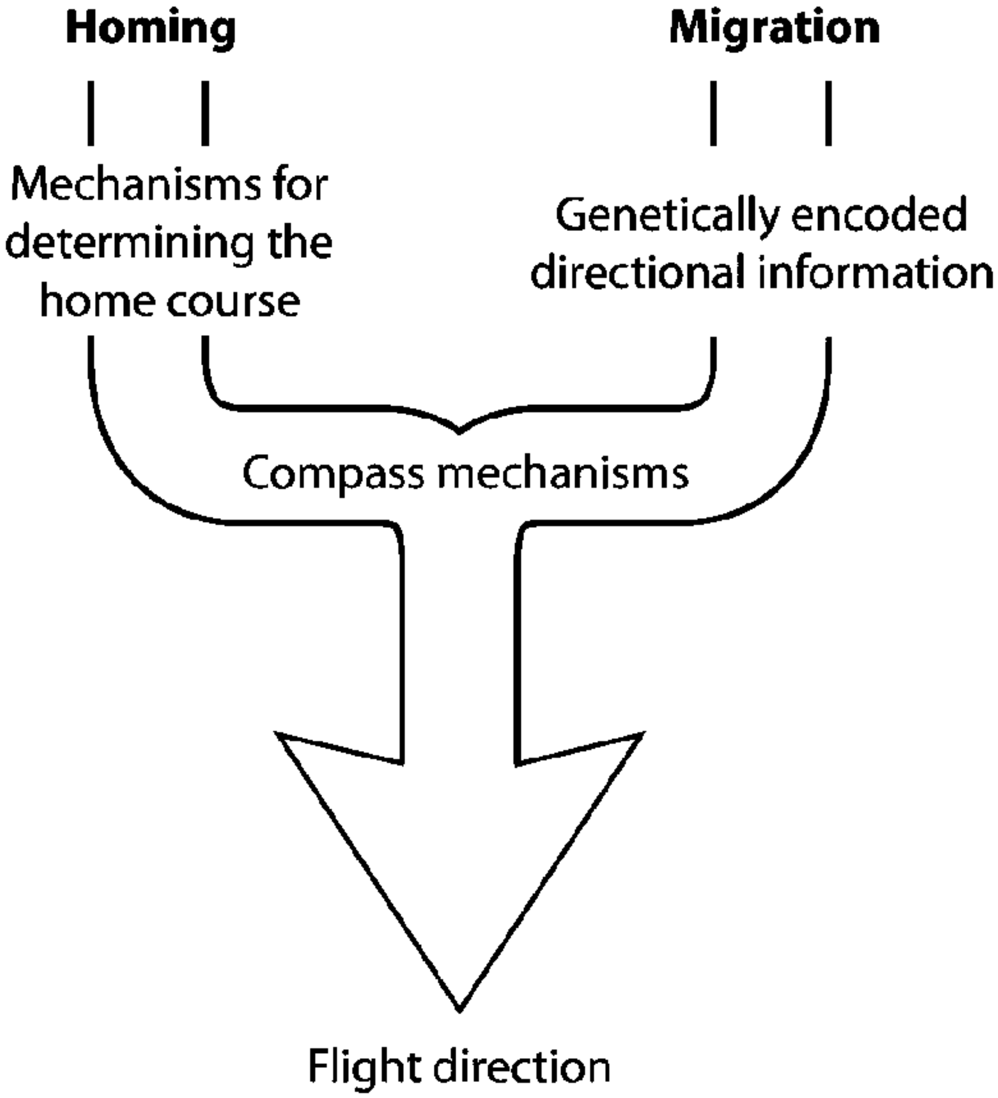

Figure 12.25. The current view of the avian orientation system. The nature of the first step, the determination of a direction as a compass course, varies according to the behavioral context of the orientation task. In migration, the course depends on the geographical relationship of the breeding ground and the wintering area. Birds possess innate information on this course, which is genetically transmitted from one generation to the next. The birds face the task of transforming this genetically encoded directional information into an actual migratory course. In homing, however, the correct course varies according to the bird's current position relative to its home. Here the bird must be able to interpret environmental information in order to determine the course, which is then located by compass mechanisms.

A magnetic compass was first described for European robins (*Erithacus rubecula*), a night-migrating passerine (Wiltschko, 1968). During the migration season, captive birds were restless. Their activity was concentrated in the part of their cage that pointed to the migratory direction of their free-flying conspecifics. When the magnetic field was experimentally altered around the test cage, the birds reacted to a shift in magnetic north with a corresponding deflection of their directional tendencies, thus indicating that they used magnetic information in direction finding.

Fishes are known to home by four methods: (1) orientation to gradients of temperature, salinity, and chemicals; (2) sun orientation; (3) orientation to polarized light; and (4) orientation to geomagnetic and geoelectric fields. Salmon hatch in freshwater streams but swim hundreds of kilometers out to sea, where they feed and grow for a year or more. When the fish mature, they return to breed in the stream where they hatched. Through their olfactory apparatus, they can recognize the odor of their home stream, which was imprinted in their brain before they left. By searching out this olfactory stimulus, each fish can return to the precise stream in which it was hatched (Hasler and Wisby, 1951). In addition, there is evidence that salmon may be able to detect pheromones given off by other members of their species and are able to discriminate one population from another (Groot et al., 1986).

Amphibians are known to home by using chemical, visual, and celestial cues, as well as the Earth's geomagnetic field. Some salamanders, like the eastern red-spotted newt (*Notophthalmus viridescens*), possess magnetic-compass orientation that is directly affected by the wavelength of light (Phillips and Borland, 1992). This wavelength dependence is due to a direct effect of light on the underlying magneto-reception mechanism. Celestial cues may be perceived by photoreceptors located outside the retinas of the eyes, in either the pineal body and/or frontal organ (Adler, 1971; Taylor and Auburn, 1978) or possibly in the upper part of the brain (Landreth and Ferguson, 1967a, 1967b; Taylor and Ferguson, 1970; Taylor, 1972; Adler, 1976; Demian and Taylor, 1977). Poison dart frogs, like *Dendrobates pumilio*, use both visual and chemical cues (Forester and Wisnieski, 1991).

The moon and stars are of primary importance to night-migrating birds and bats, whereas the sun is used by many diurnal migrators. Beginning in late summer, the night skies of the Northern Hemisphere are filled with birds of all sizes flying south to spend the winter (Fig. 12.26). Nocturnal migration allows diurnal birds to forage during the day. Birds that flap vigorously during their migration generate a great deal of heat, causing their resting body temperatures of about 38°C (100°F) to increase during strenuous flight to between 41°C and 43°C (106°F and 109°F) (Kerlinger, 1995). To avoid further overheating, many birds migrate during the night, when temperatures are lower. Some of the insect eaters (like kingbirds and swallows) that feed on the wing (i.e., while flying) migrate during the day.

Figure 12.26. Canada geese (*Branta canadensis*) silhouetted against the moon as they migrate south to spend the winter.

True goal-oriented homing requires an accurate internal clock in order to compensate for the ever-changing positions of the celestial bodies in the sky.

EMIGRATION

Some vertebrates engage in a general movement away from an occupied area. Such a one-way trip is known as an **emigration**. Emigrations are sometimes unidirectional, with all individuals moving in the same direction. In years when the mast crop is sparse, animals like gray squirrels and black bears may be observed emigrating to other areas in search of food (Flyger, 1969). Mast is divided into two groups. Soft mast consists of fruits like blackberries, blueberries, and cherries, whereas hard mast consists of acorns, hickory nuts, beech nuts, and formerly, chestnuts. In the southern Appalachians, the mast crop fails periodically. For example, in 1992 more than 900 black bears (*Ursus americanus*) were reported killed by hunters and vehicles in the four-state southern

Appalachian region (Anonymous, 1996b). Some biologists feel that 40 percent or more of the black bear population was lost.

Countless tales have been told about lemming emigrations. These stories, however, are a myth for most species. One species, *Lemmus sibiricus*, which ranges from the Bering Strait in Alaska to Baffin Island and south in Canada to British Columbia and Alberta, experiences regular fluctuations in population with peak numbers being reached every two to five years. As the excess population overutilizes its food supply, many animals begin a large-scale movement away from the area. At such times, many animals are seen swimming across rivers and lakes and often appear in human settlements. Many die because they cannot find suitable habitat. The Norwegian lemming (*Lemmus lemmus*) in parts of Fennoscandia, Norway, is best known for its spectacular emigrations. At roughly 30-year intervals, millions of Norwegian lemmings move at speeds of 5 km (3.1 mi.) per hour, covering distances up to 200 km (124 mi.) (Stenseth and Ims, 1994).

Orientation and navigation involve a multitude of integrated cues (innate, celestial, magnetic, visual, auditory, and olfactory), with the significance of some factors being adjusted with respect to that of others to bring the entire system into harmony. The different factors must be seen as integrated components of a complex system that is partially redundant and that tries to use all suitable factors provided by the environment.

Review Questions and Topics

1. Define home range. Discuss three methods of calculating home range. Which do you feel gives a more accurate representation?
2. Differentiate between territory and home range. Which is usually larger? Which is usually protected?
3. What are some adaptive advantages of territoriality?
4. Discuss several methods used by vertebrates to return to their home range (homing) if displaced.
5. List several adaptive advantages of dispersal.
6. Differentiate between migration and emigration.
7. Why must some species migrate?

8. List several adaptive advantages of altitudinal migration.
9. List the four major flyways used by waterfowl in North America. Why are they significant?
10. Discuss the two orientation systems used by hatchling leatherback sea turtles immediately after emerging from their underground nests.

Supplemental Reading

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Vertebrate Internet Sites

1. Migratory Bird Treaty Act

   www.fws.gov/birds/policies-and-regulations/laws-legislations/migratory-bird-treaty-act.php

   History, protection, laws, and listing of bird species protected by the Migratory Bird Treaty Act.

2. Greater Yellowstone Mammal Migrations

   www.cooperativeconservation.org/viewproject.asp?pid=551

   The Nature Conservancy and partners are committed to protecting critical seasonal ranges for Yellowstone's migrating mammals and preserving these historic overland movements. Results and accomplishments. Links to affiliated sites.

3. Movement of Atlantic Sharks

   www.nefsc.noaa.gov/nefsc/Narragansett/sharks/tagging.html

   From the National Marine Fisheries Service (NMFS) Cooperative Shark Tagging Program (CSTP). The CSTP was initiated in 1962. It is a collaborative effort between recreational anglers, the commercial fishing industry, and NMFS to study the life history of Atlantic sharks.

4. Sea Turtle Conservancy: Sea Turtle Tracking

   https://conserveturtles.org/sea-turtle-tracking

   View regularly updated maps showing the migratory movements of endangered sea turtles being tracked by satellite. Learn how satellite telemetry works.

13 | Intraspecific Behavior and Ecology

Some people say that we like wolves because they remind us of our dogs, but it is my assertion that we like our dogs because they actually remind us of our ancestral link with wolves, of the freedom that we still carry dormant, deep in our cells.

Teo Alfaro, 2019

INTRODUCTION

Very few animals are not, at one time or another, “social.” While the social nature of schools of fish, flocks of migrating geese, and herds of African big game animals is obvious, one might hesitate to use the word *social* to describe the intricate interaction between the members of a breeding pair or between parents and offspring. Likewise, the fighting between rival males in the spring might at first glance seem to deserve the epithet *antisocial* rather than *social*. The complex interactions of individuals with kin groups like Florida scrub jays (*Aphelocoma coerulescens*) are much different from the way individuals of nonkin groups, like a flock of gulls, interact. Yet all of these interactions have a great deal in common: all contribute to the success of the species and all depend on communication—albeit through many different methods—between individuals. In short, social behavior—the joint activities that make an animal community function—depends on various types of interactions among individuals, each playing its part in communication with others.

The common names for the sexes, young, and groups of animals are listed in Appendix C. Many have their origins quite far back in history; some descend from the hunting royalty of England, France, and Germany.

SOCIAL INTERACTIONS

Social animals do much more than merely stay together. They *do* things together; the activities of all members are jointly timed and oriented, and they do this, too, by influencing each other. A family of ducklings, for example, goes through a common diurnal rhythm. Part of the day they feed, keeping close together wherever they go. On other occasions, they bathe together and swim to the shore together, where they may spend half an hour or so preening, standing next to each other. Then they fall asleep, side by side.

Even while sleeping, ducks and many other birds continue to interact. Half-brain sleep—one cerebral hemisphere alert and the other asleep—has been documented in a wide range of birds and is thought to have evolved as a form of predator detection. Rattenborg et al. (1999) filmed rows of napping mallard ducks (*Anas platyrhynchos*). The end birds tended to keep open the eye on the side away from the other birds. Researchers found outer birds resorting to single-hemisphere sleep rather than total relaxation during 32 percent of napping time versus 12 percent for birds in internal spots, an increase of more than 150 percent. Furthermore, birds at the edge position oriented the open eye away from the group's center 86 percent of the time, whereas birds in the central position showed no preference for gaze direction. This study is believed to be the first evidence for an animal behaviorally controlling sleep and wakefulness simultaneously in different regions of the brain.

On many occasions, there is a division of labor among members of a group. Members of a flock of Canada geese take turns leading the *V*-shaped formation when migrating. Old, experienced chimpanzees (*Pan*) lead the group and keep a sharp lookout at all times. Perhaps the most extreme social hierarchy known among mammals occurs in naked mole rats.

There is also division of labor in more solitary animals, particularly between males and females. This applies both to different roles in mating and to different parental activities. Numerous examples of such division of labor in all vertebrate groups have been discussed in Chapters 4 through 9.

Social interactions may be beneficial in many ways. It has been estimated that 25 percent of all fishes school throughout their lives, and about half of all fishes spend at least part of their lives in schools (Moyle and Cech, 2004). Schooling can reduce the risk of predation, increase reproductive success, and, in some cases, increase the efficiency of finding food for fishes and many marine animals. For example, groups of dolphins and porpoises aid wounded members of their own species, raising them to the surface so they can breathe. They also circle a female giving birth in order to protect the mother and newborn against sharks.

Mobbing behavior, in which one to a few individuals approach and often chase and/or attack a potential predator, is common in birds. The primary purpose of mobbing is to force the predator to move on (Curio, 1978; Curio et al., 1978a, 1978b).

Clearly, no sexually reproducing species could exist without intricate cooperation between males and females for the purpose of mating. This period of interaction may last only long enough for fertilization to occur, or it may result in a lifetime bond. Many marine fishes simply discharge their gametes into the surrounding water. Most do this in response to an environmental stimulus that induces the synchronized release of gametes by both sexes. This simple mode of re-production ensures fertilization, genetic recombination in offspring, and, hence, variation in the population.

Mole Rat Societies

Naked mole rats (*Heterocephalus glaber*), which exhibit **eusociality**, or “true sociality,” usually live in colonies of 75 to 80 animals, although colonies of more than 250 animals have been recorded. Members of a colony, especially pups, engage in coprophagy—reingestion of feces—as a possible way of acquiring the gut bacteria needed to digest tough roots and tubers. Most colonies contain only a single reproductive female (see Fig. 12.3). Chores are performed by both males and females, but not by all individuals equally. For example, the primary role of the breeding female is to produce young, nourish the pups, and keep them clean. Subordinates (nonbreeders) help to clean and carry pups, even though they are not even their own. Their responses to pup vocalizations are induced by estradiol ingested through coprophagy of the queen’s feces—a previously unknown system of communication in naked mole rats, in which a hormone released by one individual controls the behavior of another individual. Hormones are powerful mediators of behavior, but their effects are normally limited to the body of the animal making them—not the bodies of totally separate animals. Subordinate response to pup voice was observed only during the queen's postpartum period and was preceded by an incremental rise in subordinate's fecal estradiol concentrations during the queen's gestation period. Nonbreeders also maintain and defend the colony's tunnel system. Labor is divided according to size with the larger nonbreeders defending their colony against mole rats from other colonies and also against predators.

Dominance hierarchies exist within colonies: the queen and breeding males dominate the nonbreeders; larger workers dominate smaller ones, regardless of sex.

Chemical, tactile, and acoustic forms of communication are used. At least 17 distinct categories of vocalizations have been recorded, with the vocal repertoire being the most extensive known among rodents.

Naked mole rats, which are ectothermic, are the only known mammals whose body temperature fluctuates with the ambient temperature. The temperature within their tunnels remains near 30°C (86°F) most of the year. If the animals get colder, they regulate their temperature by huddling with colony mates (social endothermy, like bees).

Inbreeding is a constant problem in such highly organized societies. Recently, a dispersal phenotype was discovered that may occasionally promote outbreeding. These dispersers are morphologically, physiologically, and behaviorally different from other colony members. These rare morphs are fatter than average, have higher than normal levels of luteinizing hormone, have a strong urge to disperse, and will mate only with noncolony members. Although rare, they are essential in producing the gene flow that maintains the heterogenicity required for reproductive compatibility between isolated populations.

Naked mole rats are the longest-lived rodent. They seem to flout the Gompertz law, a mathematical equation that describes aging. In 1825, British mathematician Benjamin Gompertz found that the risk of dying rises exponentially with age; in humans, for instance, it doubles roughly every eight years after the age of 30. The law applies to all mammals after adulthood. The first study to analyze the life histories of naked mole rats found that their risk of death does not go up as they grow older, as it does for every other known mammalian species. At advanced ages, their mortality rate remains lower than any other mammal that has been documented. Based on their size, mole rats would not be expected to live past 6 years of age. Instead, some live beyond 30 years, and even at that age breeding females stay fertile.

Sherman et al., 1992; O'Riain et al., 1996; Watarai et al., 2018; Ruby, et al., 2018

Species in which young receive parental care need close cooperation between parents and young. Mated pairs are usually more successful at raising offspring than a single animal working alone. Each member of a pair can share in food gathering, defending the territory, and protecting its mate and young from predators. Protection is even more effective when a group faces a potential predator. For example, gulls in a breeding colony attack predators in force. This concerted defense, quickly mounted as the birds alert each other by alarm calls, is much more successful than individual attacks. This response is elicited not just because the gulls nest close together, but also because they nest synchronously and will benefit almost equally. Likewise, many mammals, like musk ox and elephants, band together to protect their young from potential predators.

Social hierarchies occur in many groups of animals. In some, the female is dominant—a **matriarchal** hierarchy; in others, the male is dominant—a **patriarchal** hierarchy. The dominant individual is usually an older member of the group and controls activities until challenged and deposed by a younger rival. Classic studies of pecking orders in chickens have clearly demonstrated the nature of the dominant-subordinate behavior. Similar studies have been carried out on a variety of other vertebrates. Within a clan of spotted hyenas (*Crocuta crocuta*), for example, the highest-ranking female and her descendants are dominant over all other animals (Nowak, 1991). Although all resident males court females, only the highest-ranking male hyena was observed mating in a study by Frank (1986). Dominant individuals in nonkin groups, like flocks of sparrows, have been shown to gain access to better food sources and suffer lower risks of predation than do subordinate individuals. Thus, the value of social behavior accrues to a greater extent among dominant individuals than it does among subordinate individuals.

Studies of African elephants (*Loxodonta africana*) show that animals acquire and store information about social companions and that individuals possessing enhanced social knowledge derive biological fitness benefits (McComb et al., 2001). The possession of enhanced discriminatory abilities by the oldest female in a group can influence the social knowledge of the group as a whole. The key decision of recognizing friend or foe appears to rest heavily upon the memory and social knowledge of the matriarch. Female groups led by an older individual were shown to have higher per capita reproductive success. The removal of older, more experienced individuals can have serious consequences for the remaining animals in populations of advanced social mammals like elephants and whales.

Some species of birds, like the white-fronted bee-eaters (*Merops bullockoides*) of Africa, are cooperative breeders (Emlen and Wrege, 1992). They live in colonies averaging 200 individuals making up several clans. Young females remain in their parental group (clan) for one or two years until they begin to breed, at which time they leave their parents and join the clan of their mates. Males, however, do not leave their clans. Each clan establishes its own feeding territory, but all individuals of each clan roost and nest at the colony site.

Not all intraspecific interactions are peaceful. Competition in many birds, for example, begins in the nest as individuals compete for food and space. Intraspecific competition, whether for a mate, food, or territory, however, rarely results in injury to the participants. Most species have ritualized aggressive behaviors that are used in these situations. Many fishes engage in tail-beating, mouth-pulling, or mouth-pushing activities. Red-backed salamanders (*Plethodon cinereus*) raise their trunks off the substratum and look toward their opponent (Fig. 13.1a). A biting lunge directed toward the opponent's tail or nasolabial groove area may follow. Frogs attempt to topple intruders that come into their territory (Fig. 13.1b). Rattlesnakes wrap their bodies around each other and butt each other with their heads. Some lizards whip each other with their tails. Turkeys drive off their rivals by means of threatening calls and/or by jumping at them. Giraffes, deer, elk, and bighorn sheep butt each other with their heads (Figs. 13.2 and 13.3). Brown bears may charge, growl, and push one another with their forelegs. Oryx antelope possess sharp-pointed horns with which they stab potential predators like lions, but when faced with a conspecific adversary, they merely butt heads and do not attempt to stab each other.

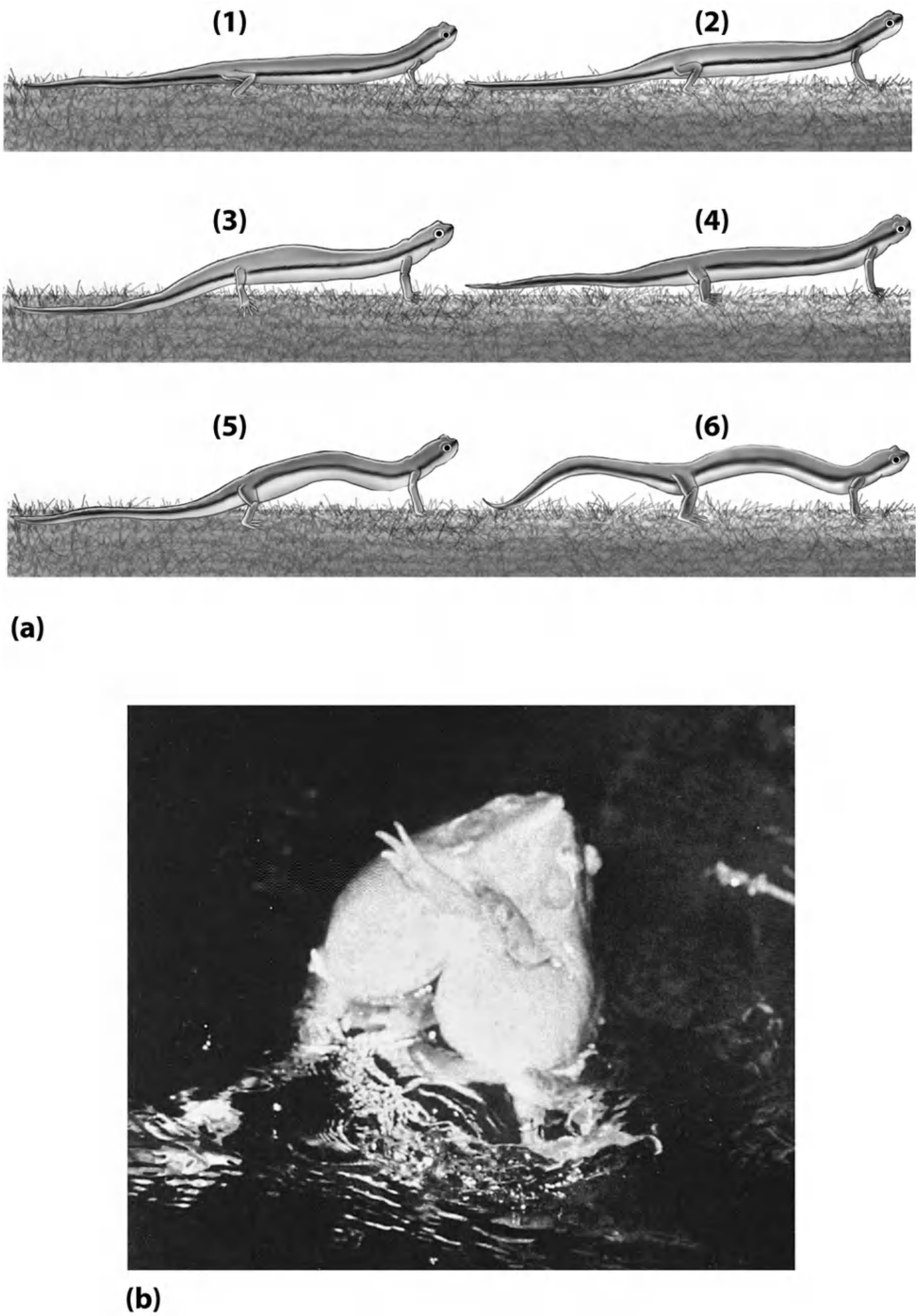


Figure 13.1. (*a*) Red-backed salamander (*Plethodon cinereus*) escalating the intensity (1–6) of its threat display toward an intruder. (*b*) Male bullfrogs (*Rana catesbeiana*) aggressively

defend territories used as egg deposition sites; fights are typically wrestling matches in which the larger male prevails.

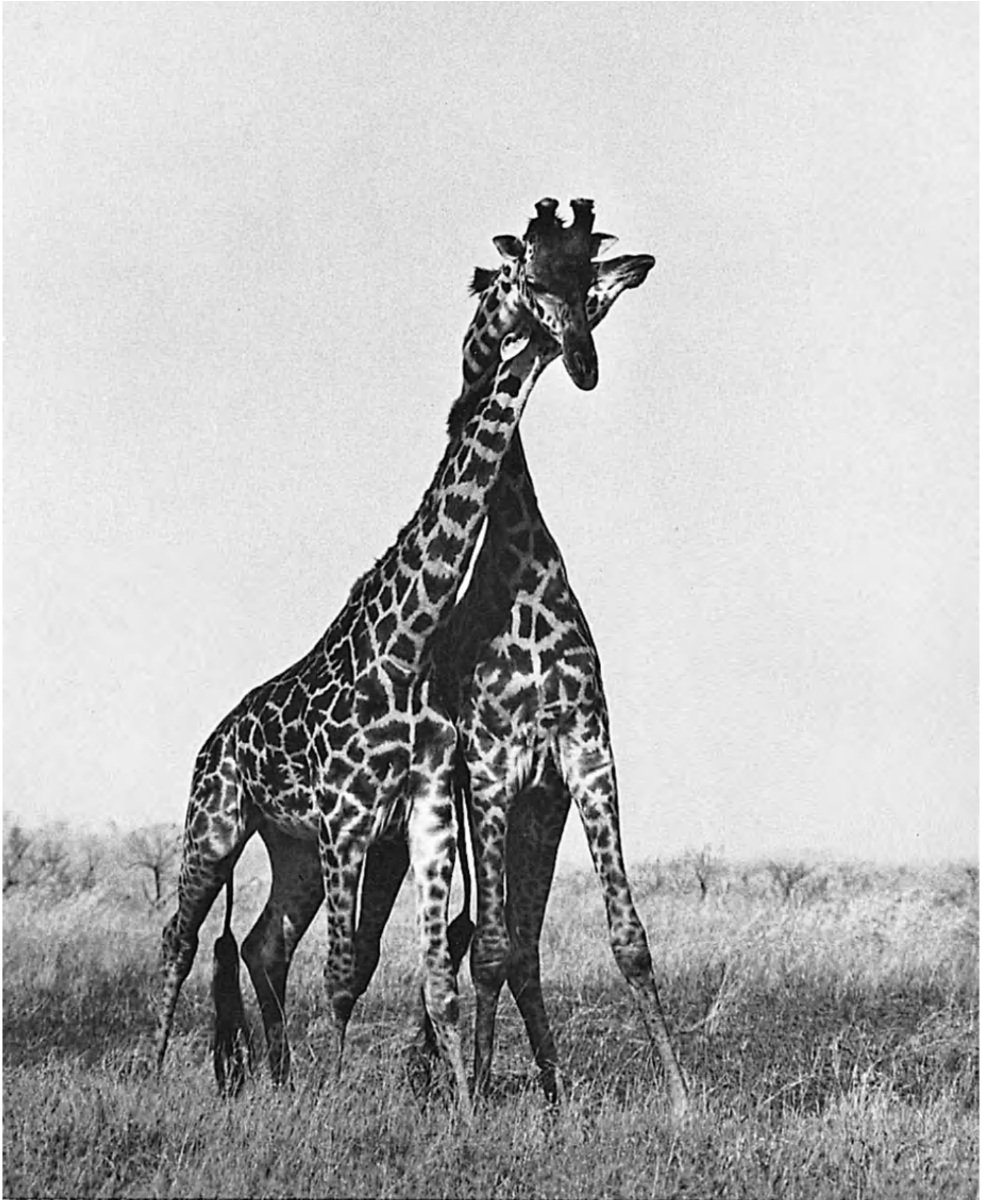


Figure 13.2. Male Masai giraffes (*Giraffa camelopardalis tippelskirchi*) sparring for social dominance. Such bouts are primarily symbolic and rarely result in injury.

In spotted hyenas (*Crocuta crocuta*), sibling rivalry is carried to a deadly extreme. Females generally give birth to twins in underground dens. Sibling fighting begins at the earliest possible moment, sometimes while the second pup is still in the amniotic sac. This instant antagonism lets the pups establish a ranking order that determines which one gets the most of a limited food supply: their mother's milk. The dominant animal generally grows larger and has a better chance of succeeding in the dangerous adult world. The loser often dies. Female twins fight the hardest and longest—probably because large size is favored if a female is to give birth to healthy pups of her own. Battles between male-female twins usually are not as intense (Frank et al., 1991).

Animals show submission in various ways. Some fishes collapse their fins and change coloration. Bullfrogs that maintain a low position in the water are not challenged or attacked. Iguanas flatten themselves to appear as small as possible. Many canids flatten their bodies and bring their ears to lie flat against their heads. The tails often will be tucked between their legs.

SENSORY RECEPTION AND COMMUNICATION

For effective organization to exist within a population that maintains a social structure like a family group, school, flock, or herd, some form of unambiguous communication must exist among the members of that population. This exchange of information influences the behavior of both the sender and the recipient. In general, those forms that live in social groups have the more highly developed sets of communication signals. However, even in solitary or unsocial animals, elaborate signals may be required to establish and maintain the species' dispersed spatial patterns (Bradbury and Vehrencamp, 1998).

Figure 13.3. Butting bouts among desert bighorn sheep (*Ovis canadensis*) appear to be contests of skill and stamina with little real antagonism involved. It has nothing to do with the premating collection and maintenance of a "harem," nor does it seem to result in the elimination of one ram from participation in mating activity with a certain ewe. It appears to have no objective whatever except the satisfaction of some deep-seated urge aroused by the mating instinct and demanding and receiving an outlet for its own sake. When males are 3.7 m (12 ft.) apart, with every muscle bulging for a final effort, and with amazing timing and accuracy, they lunge forward like football players tackling one another. The remarkable synchronization of movement pictured here is the rule, not the exception. Every effort seems to be made to ensure a perfect head-on and balanced contact. Note that both heads are tilted to the same side. Occasionally, one slips or miscalculates and a severe neck-twisting or nose-smashing results. The combined speed at impact has been estimated at 81 to 113 km (50–70 mi.) per hour and to be the equivalent of a 1,089 kg (2,400 lb.) blow. More than 40 blows between two rams have been counted in one afternoon.

Sensory reception and communication among vertebrates are accomplished in a variety of ways. They may use pheromones, sound, vision, tactile stimulation, electrical signals, signal patches, or a particular behavior like the slapping of the tail (beaver) on the surface of the water or foot-drumming (kangaroo rats).

Olfaction

Olfactory communication is widespread among vertebrates and may be the primary mode of communication for many species. Chemical signals exchanged between members of the same species are known as **pheromones** (Gr. *pherein*, to carry, + *hormon*, to excite). They *control* a wide variety of behaviors and physiological states and may be detected from considerable distances during both day and night. Normal, or nonpheromonal, chemoreception *influences* behavior. Both pheromonal and nonpheromonal chemoreception are important means of communication. Olfactory communication is effective beneath the surface of the ground and in dense vegetation, both areas where visual and auditory signals would be difficult to detect.

Pheromones may contain steroid or steroid-like organic compounds, which may be part of a mixture of compounds. Castoreum from the castor sacs of beaver (*Castor canadensis*), for example, consists of 6 alcohols, 14 phenols, 1 aldehyde, 15 amines, 6 ketones, 9 aromatic acids, and 5 esters (Müller-Schwarze and Houlihan, 1991). A total of 37 compounds has been identified from the temporal gland secretion of the Asian elephant (*Elephas maximus*) (Rasmussen et al., 1990). This gland, located in the mid-cheek region, is a modified apocrine sweat gland and has been implicated in chemical communication of African (*Loxodonta africana*) as well as Asian elephants. Secretions occur only during the physiological state of *musth*, the strange emotional state that periodically afflicts all male and some female elephants. *Musth* (a state of increased serum testosterone) occurs after elephants reach maturity and is accompanied by great activity of the temporal glands. The temples become puffy, and the glands exude a dark, strong-smelling, oily substance that stains much of the lower part of the face (Fig. 13.4). Elephants in *musth* either become highly excitable or dull and morose.

Intraspecific Parasitism

Although parasitism usually is considered an interspecies interaction, intraspecific brood parasitism occurs in a large number of bird species in which females lay eggs in the nests of conspecifics, who then provide parental care. Females without nests, as well as those with viable nests, engage in brood parasitism. In several species, parasitic eggs have been found to be less successful than nonparasitic eggs. Many parasitic females are young birds of poor competitive ability. Some lay eggs in the nests of other females before laying eggs in their own nests.

The addition of parasitic eggs to those already in a nest may result in more young than the host parents can rear successfully. This may lead to reduced incubation efficiency and overcrowding. Behaviors to protect against parasitism include nest guarding, aggression, ejection of eggs, and nest desertion.

Figure 13.4. Male African elephant (*Loxodonta africana*) showing the temporal gland and its secretion (*white arrow*). The glands exude a dark, strong-smelling, oily substance that stains much of the lower part of the face.

Biological activity of several compounds of a mixture may interact in synergistic, redundant, or addictive fashion. In some cases, individual components of a mixture are inactive, but when combined or dissolved in a fluid like urine, they become effective olfactory signals.

Pheromones may represent a primitive communication technique. They may attract members of the same species (including a mate), elicit courtship behavior, stimulate ovulation, serve as a warning when used to mark the boundaries of a territory, be used for defensive purposes, or, in some cases, indicate danger.

Among fishes, pheromones are important in species like catfishes, which lack keen eyesight. By means of pheromones, migrating salmon may be able to discriminate members of their own population from individuals of other populations, thus permitting increased precision in their homing.

Some salamanders can distinguish between odors produced by conspecifics and heterospecifics and distinguish between odors of familiar and nonfamiliar conspecifics (Mathis, 1990b). Pheromones, which may also convey information about gender, are used by many salamanders to mark their territories. The nasolabial grooves of plethodontid salamanders serve as specialized channels to transmit chemicals, like pheromones, to the vomeronasal organs (see Fig. 5.27).

During the breeding season, the glands of some turtles enlarge and are thought to secrete pheromones. Many lizards and snakes use pheromones for species and sex recognition as well as the recognition of eggs. Some, like male broad-headed skinks (*Eumeces laticeps*), have been shown to follow female conspecific odor trails (Cooper and Vitt, 1986). Chemical trailing of conspecifics occurs widely in snakes.

Skin lipids extracted from female red-sided garter snakes (*Thamnophis sirtalis parietalis*) are attractive to sexually active courting males (see Fig. 7.32). The lipids contain a female sex attractiveness pheromone consisting of a series of nonvolatile long-chain methyl ketones (Mason et al., 1989). When researchers added extracts of male lipids to female extracts, male courtship stopped, suggesting that males emit specific chemical cues that identify them as males. One chemical in the male lipid—squalene—caused a significant drop in courting and is an important part of the male sex recognition pheromone. Preliminary studies of related groups of snakes suggest that some of the same methyl ketones are found in females of several species.

Pheromones are well developed in mammals, especially those with the keenest senses of smell. Scent-marking is a well-recognized and important aspect of mammalian communication and has been observed in a variety of mammals (Fig. 13.5). Glandular secretions and urine are used as the principal means of chemical communication. Estrous female mole rats (*Spalax ehrenbergi*) are known to be attracted to substances in adult male urine. Menzies et al. (1992) reported the extraction of sexual pheromones from lipids and other fractions of the urine. Male meadow voles (*Microtus pennsylvanicus*) emit odors that are attractive to females at the beginning, but not at the end, of the breeding season (Ferkin et al., 1992). Some mammals can differentiate between individuals on the basis of odor. Female house mice (*Mus musculus*), for example, use smell to recognize related females (Manning et al., 1992). The similarity in smell results from related females sharing genes of the major histocompatibility complex (MHC), which is involved in fighting disease. In addition, if recently mated female mice are exposed to the urine or pheromones of strange males before implantation, pregnancy block occurs and pregnancy fails (Brennan et al., 1990).

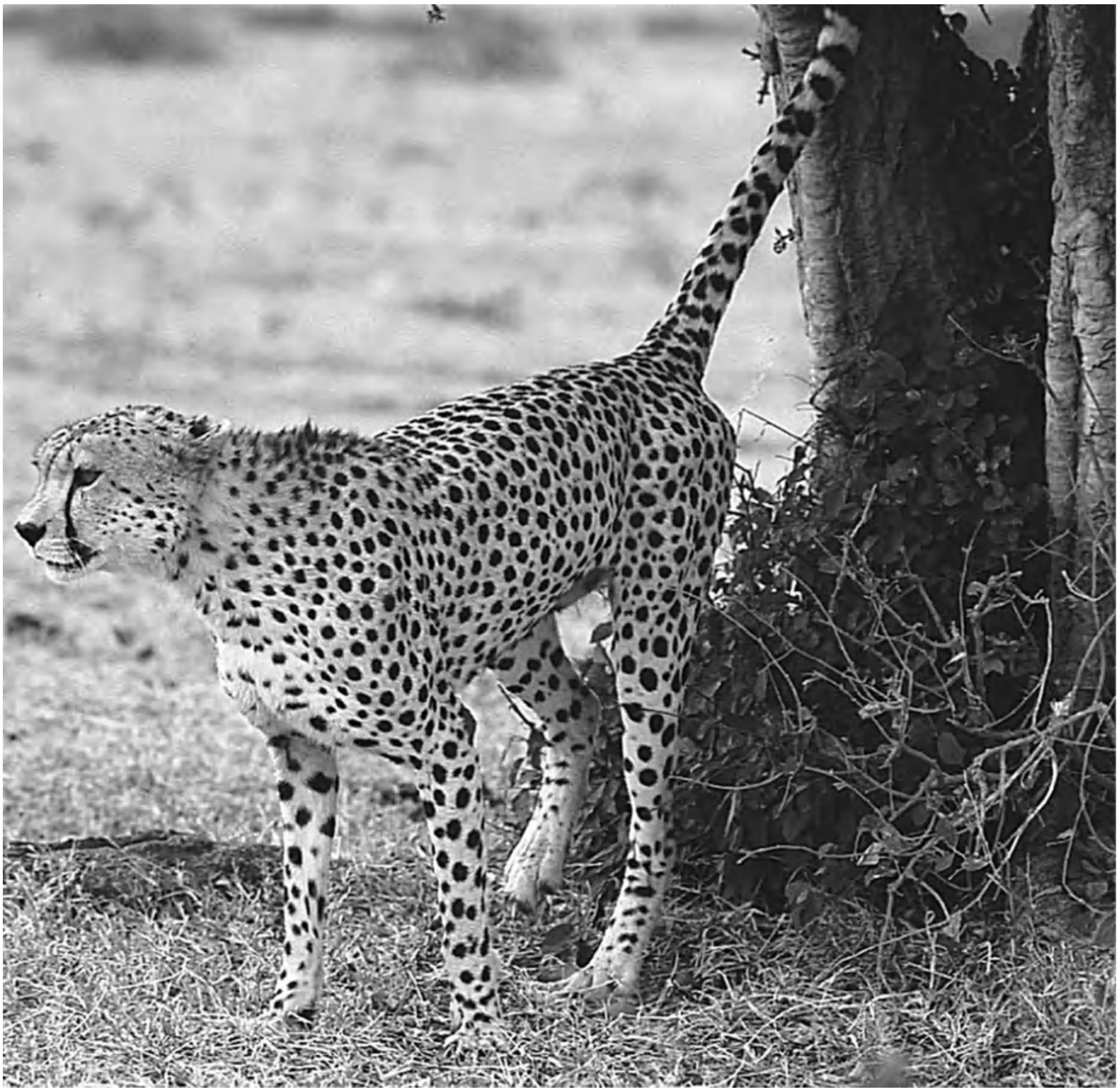


Figure 13.5. This male cheetah (*Acinonyx*) is spraying a pheromone onto a tree in order to mark his territory. Scent-marking is a well-recognized and important aspect of mammalian communication.

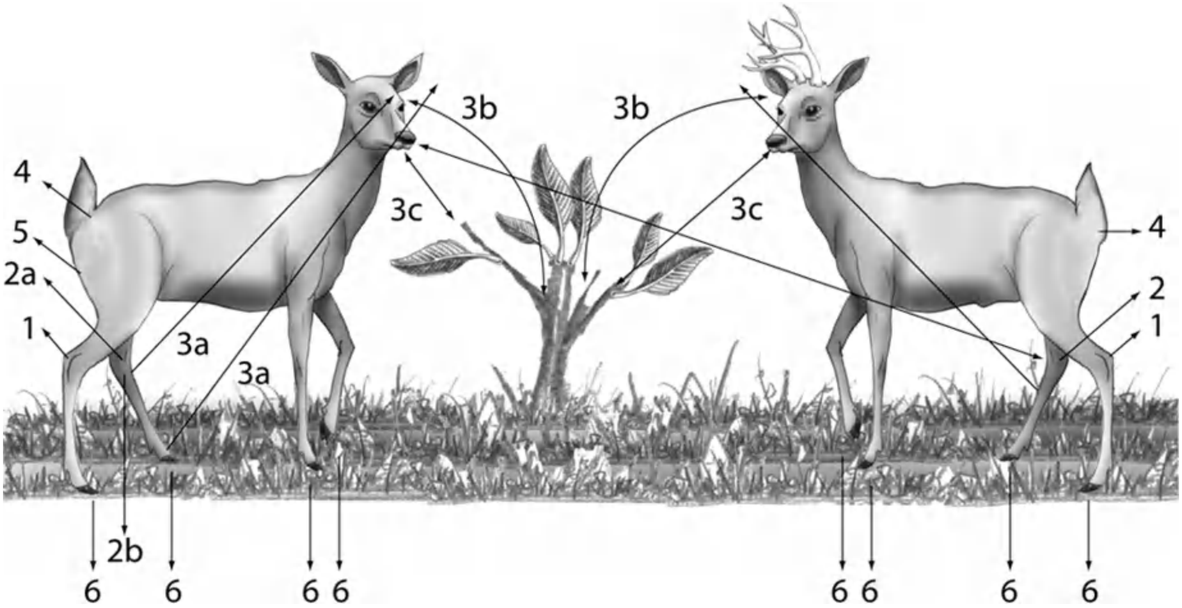


Figure 13.6. Pathways of social odors in black-tailed deer (*Odocoileus hemionus*). Scents of the tarsal organ (1), metatarsal gland (2a), tail (4), and urine (5) are transmitted through air. When the deer is reclining, the metatarsal gland touches the ground (2b). The deer rubs its hind leg over its forehead (3a). Marked twigs are sniffed and licked (3c). Interdigital glands leave scent on the ground (6).

In black-tailed deer (*Odocoileus hemionus*), secretions from four glands are considered important in social communication (Müller-Schwarze, 1971) (Fig. 13.6). The scent of the tarsal gland identifies the age and sex of an individual at close range. The scent from the metatarsal gland acts like an alarm pheromone over moderate distances. The scent of the forehead glands is left on branches when a deer rubs its head and serves to mark the home range. Scent from the interdigital glands, which also is used in marking the home range, is left on the ground.

Flehmen is a reaction of some mammals to direct physical contact with a scent mark and its incorporated pheromones. After sniffing the scent mark, the animal licks it and takes it into its mouth. The upper lip curls, the jaws open, and the head is raised and turned from side to side or is nodded up and down. The animal inhales deeply to move the scent into the vomeronasal organ. Flehmen occurs during the breeding season and is characteristic of many ungulates, especially members of the deer family (Cervidae). It is also known to occur in some cats (Felidae).

Glandular secretions may be deposited on the substrate or on objects in the environment, they may be applied to the animal's own body or to the bodies of other members of the social group, or they may be released into the air. Feces and/or urine often contain pheromonal secretions.

Koalas (*Phascolarctos cinereus*) and other marsupials use sternal glands, paracloacal glands, and urine for marking. Trees are marked by koalas as they climb, by rubbing their sternum on the tree. Mitchell (1991a) noted: “Although koalas produce scent and inspect their environment for scent, there was no direct evidence that they used scent to define space, recognize individuals or recognize physiological states.” Whole-body and pouch gland odors are important chemical signals between young Virginia opossums (*Didelphis virginiana*) and their mothers just prior to weaning (Holmes, 1992).

Some pheromones signal the presence of danger. Some wounded fishes release a substance from special cells in the epidermis, which induces other members of the school to flee for shelter. Similar effects have been recorded in amphibian tadpoles (Eibl-Eibesfeldt, 1949; Kulzer, 1954) and in mice (Heintz, 1954). Chemical signals also have been shown to facilitate schooling of young fish (Kühme, 1964).

Some pheromones are very similar in structure to sex steroid hormones that are used to attract the opposite sex. Humans secrete pheromones, but most humans continually remove the real musks by bathing and then apply scented animal musks (perfumes) as a substitute. The symbolic message is still communicated, and the opposite sex still responds.

The morphology and chemistry of scent glands and the role of pheromones in mammalian social communication have been discussed in Brown and Macdonald (1985) and Gorman and Trowbridge (1989). The influence of selective factors like substrate, persistence, intensity, and localizability on the signal structure in mammalian chemical communication systems has been reviewed by Alberts (1992).

Sound

The production and reception of sound is most highly developed in anurans, birds, bats, primates, and cetaceans. Many fishes, including grunters and croakers, produce sounds by contracting muscles attached to their swim bladders. Other fishes produce sounds by grinding their teeth or rubbing the base of a fin spine against the socket.

Sound production is limited in salamanders and caecilians, but auditory communication is highly developed in male anurans, particularly during the breeding season. Many males possess vocal sacs that serve as resonating chambers. The purpose of most anuran calls is to advertise for mating or to maintain territories or interindividual distances. Male gray tree frogs (*Hyla versicolor*) with long calls—known to be favored by females—sire higher-quality young than those with short calls (Welch et al., 1998). For two years, researchers compared how the offspring fared as tadpoles and after they metamorphosed into frogs, measuring their growth rates under regimes of scarce and plentiful food. Offspring of males with long calls always performed significantly better than or not significantly differently from offspring of males with short calls. Because female *H. versicolor* do not gain direct benefits from their choice of mate, the indirect genetic benefits suggest good-genes selection as a probable explanation for the evolution and maintenance of the female preference in this species. Among reptiles, vocal cords are present only in a few lizards, like geckos (Hickman et al., 1996).

Males of many species of birds have highly characteristic territorial songs announcing that the resident is a sexually mature male attempting to attract a suitable mate and defend an area against other males of the same species. Birds possess a unique modification of the lower trachea, the syrinx. Contraction of muscles attached to membranes within the syrinx produces the characteristic songs and calls of each species, which usually are heard most often during the breeding season. Individuality is common. Extensive studies on a variety of species show that songs differ among individuals in pitch, speed, and details of phrasing. In addition to their voices, some birds, like ruffed grouse (*Bonasa umbellus*), also communicate by vigorously moving their wings back and forth, creating a drumming sound.

During courtship displays, the male Anna’s hummingbird (*Calypte anna*) soars to some 30 m (98 ft.) and then dives, whizzing by a female so fast that his tail feathers chirp in the wind. As the bird pulls out of his plunge to avoid crashing, he experiences forces more than nine times the force of gravity. Initially, the birds flap their wings as they dive. Then for short periods, they fold their wings and drill down through the air, reaching speeds up to 98 km (61 mi.) per hour (Clark, 2009).

Young birds are predisposed to learn a specific kind of vocal information. Their learning pathways are highly selective and very sensitive to the “right” information (Adler, 1996b). For example, young male white-crowned sparrows (*Zonotrichia leucophrys*) and white-throated sparrows (*Z. albicollis*) possess a neural template that allows them to repeat the songs from males of their species. If the young bird does not receive this information during a critical song-learning period, it will not develop a typical full song five to six months later (Fig. 13.7). This song-learning period extends from the 10th to 50th day of its life. (Some other species do not show this critical learning period.) In addition, juvenile males must be able to hear themselves sing; otherwise, they will develop aberrant songs. While the songs of male white-crowned sparrows within a population are strikingly consistent from year to year, males of other distinct populations have easily recognizable dialects (Marler and Tamura, 1962) (Fig. 13.8a–c).

Sound production and reception are very efficient in mammals. Vocal cords for producing sound are well developed, and the middle ear contains three bones (malleus, incus, and stapes) for receiving sound. The pinnae of many mammals (e.g., deer) are mobile, and each can be controlled independently of the other to enhance hearing. Mammals may emit many sounds. They may squeak, bark, bugle, howl, bellow, roar, neigh, moo, oink, cry, laugh, and speak. They may engage in tooth-chattering, tail-rattling, and drumming on the ground with their hind feet.

Foot-drumming in kangaroo rats (*Dipodomys*) is individually distinct (Randall, 1989). Individual rates are higher in males than in females. Rates are also higher in young adults than in juveniles and older adults; thus, foot-drumming rates may be used to communicate age, sex, or vitality. Foot-drumming may also be important in territorial defense.

East African vervet monkeys (*Cercopithecus pygerythrus*) give different alarm calls in response to three major predators: leopards, eagles, and snakes (Seyfarth and Cheney, 1992) (Fig. 13.9). Each call elicits a distinct escape response from nearby vervets. Alarm calls about leopards cause vervets to run into trees. Eagle alarms cause them to look upward or run into the bushes, whereas snake alarms cause them to stand on their hind legs and look into the grass.

Prairie dogs (*Cynomys* spp.) have a “vocabulary” of 10 different calls ranging from a commonly used warning bark to a chuckle, a “fear” scream, and a fighting snarl (Waring, 1970; Smith et al., 1977). Each call results in a specific action by nearby individuals. Howler monkeys (*Alouatta* sp.) of Panama have a vocabulary of 15 to 20 calls (Sekulic, 1982). Their calls have been heard by people 3 km (1.9 mi.) away through the jungle and 5 km (3.1 mi.) away across lakes (Nowak, 1991). Koalas bellow, squeak, groan, and moan (Mitchell, 1991a). Twelve different social and communicative calls are given by white-tailed deer, including snorts, bawls, grunts, mews, bleats, and whines (Atkeson et al., 1988).

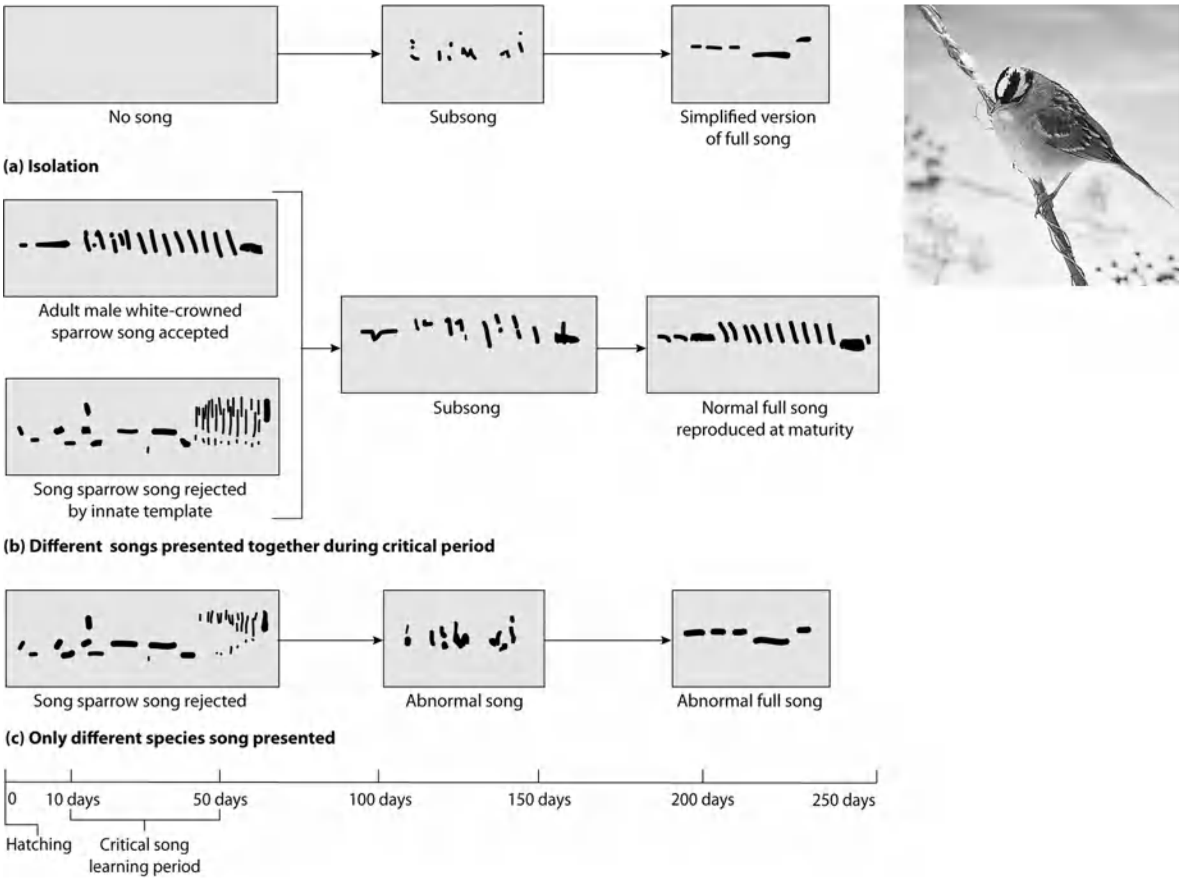
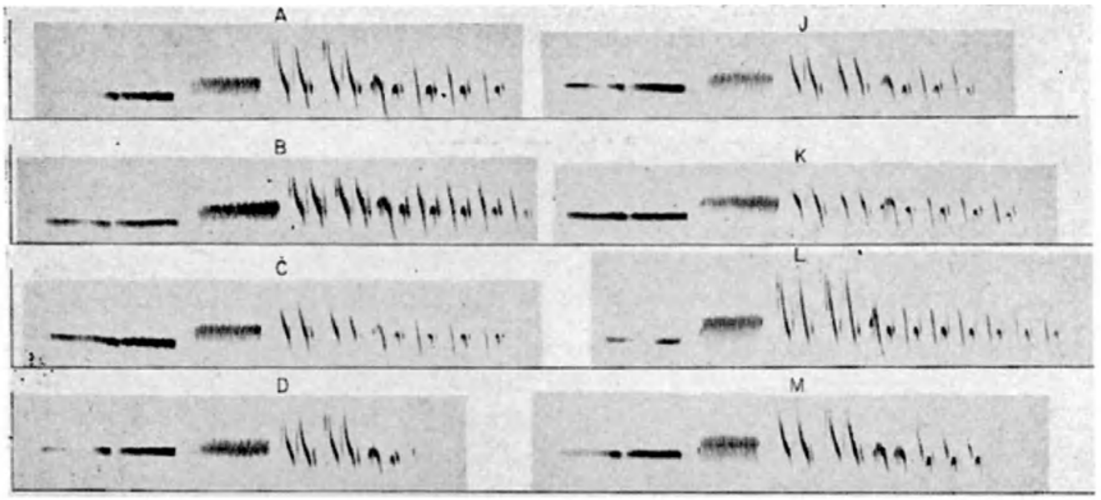


Figure 13.7. (*a*) Exposed to no song at all, male white-crowned sparrows (*Zonotrichia leucophrys*) produce a subsong, but develop only a rudimentary version of their species' normal song. (*b*) Exposed to tapes of both their own species' song and that of the related song sparrow, they produce a more complex subsong and a fully developed song characteristic of their own species. (*c*) Exposed only to the other species' song, they fail to learn.

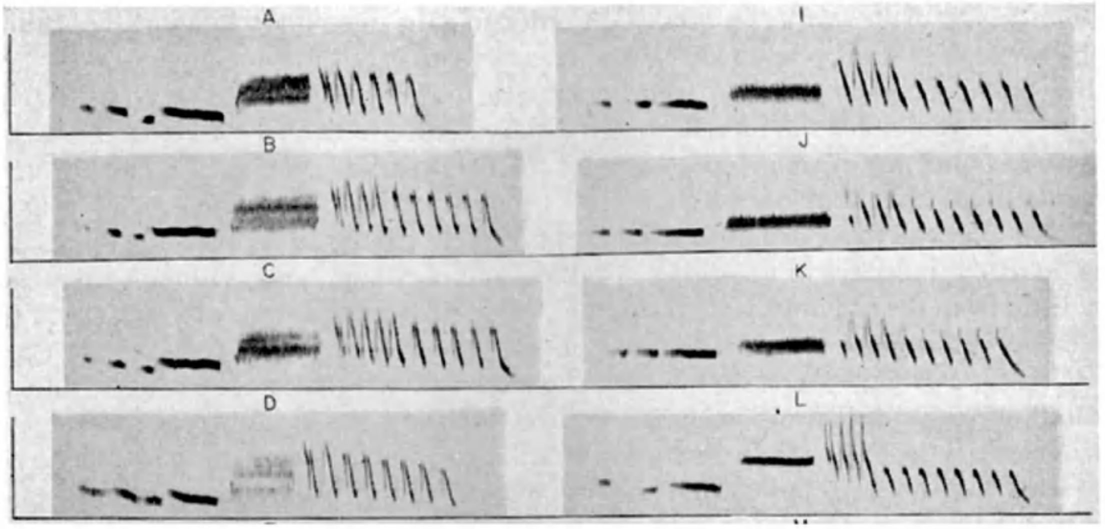
Sherman (1977) found that female Belding's ground squirrels (*Spermophilus beldingi*) (Fig. 13.10a) gave alarm calls when a predator was in the vicinity more often than expected by chance, whereas the converse was true for males (Fig. 13.10b). Females are generally sedentary (with respect to emigration) and mature and breed near their natal sites, whereas males always emigrate from their birthplace and do not aggregate with siblings after emigration. As such, females were warning close kin (often offspring) by giving such alarm calls, whereas no such benefit accrued to males for warning others about the presence of a potential predator. Further support for the kinship hypothesis includes evidence that "invading" (non-native) females gave alarm calls less frequently than native females.

The young of some bats and rodents, like house mice (*Mus musculus*), emit both audible and ultrasonic sounds. These calls elicit search behavior in the female for her young; they also reduce maternal aggression (Ehret, 1983). Richardson's ground squirrel (*Spermophilus richardsonii*) produces "silent" alarm calls at frequencies around 48,000 Hz. The upper limit of human hearing is about 20,000 Hz. The ground squirrel can direct its silent alarm, with laser-beam accuracy, to a nearby pup or other close relative, all without endangering itself by drawing the attention of a predator.

Many pinnipeds produce a variety of underwater and airborne sounds that appear to be related to breeding activities and social interaction (Riedman, 1990). Cetaceans produce a variety of pulsed calls and sounds. The eerie and plaintive songs of the humpback whale are repeated according to identifiable patterns. These sounds usually range between 40 Hz and 5 kHz in frequency and can be detected more than 30 km (18.6 mi.) away (Winn and Winn, 1978). They may last from 6 to 35 minutes before being repeated. One whale was recorded singing nonstop for at least 22 hours (Winn and Winn, 1978). Singing may take place during migration, as well as during courting. The singers are normally solitary males found in shallow coastal areas of 20 to 40 m (66–131 ft.) in depth (Evans, 1987). One function of the humpback's song is thought to serve "as a spacing mechanism for courting males advertising their sexual availability to females" (Tyack, 1981). Identification is an important function of the sounds made by many baleen and toothed whales. The sounds may give the location of the whale, its sex, status, emotional or activity state, and possibly even its individual identity (Evans, 1987).



(a)



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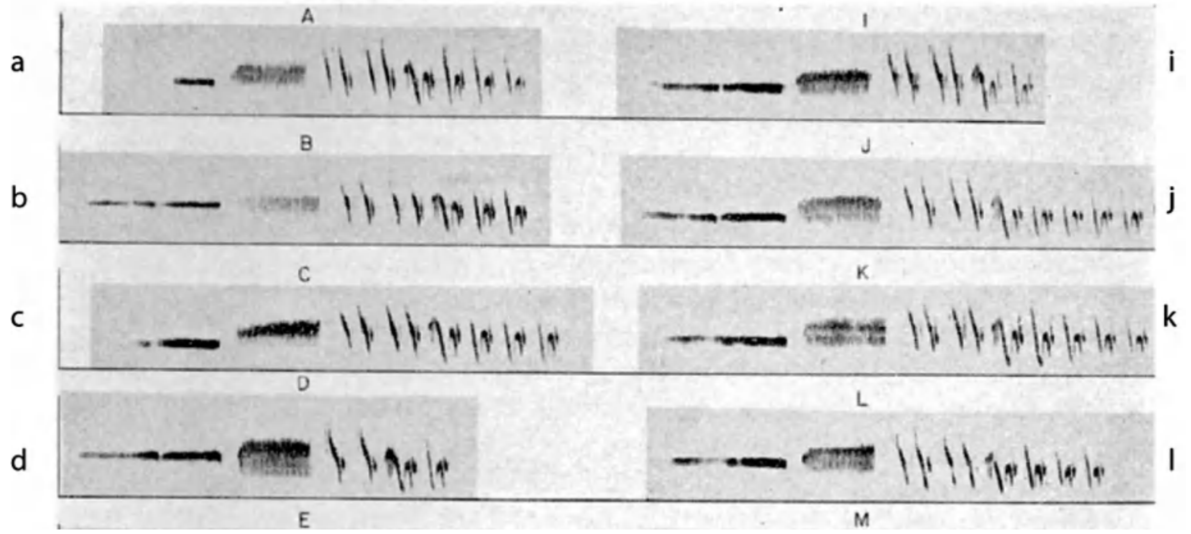


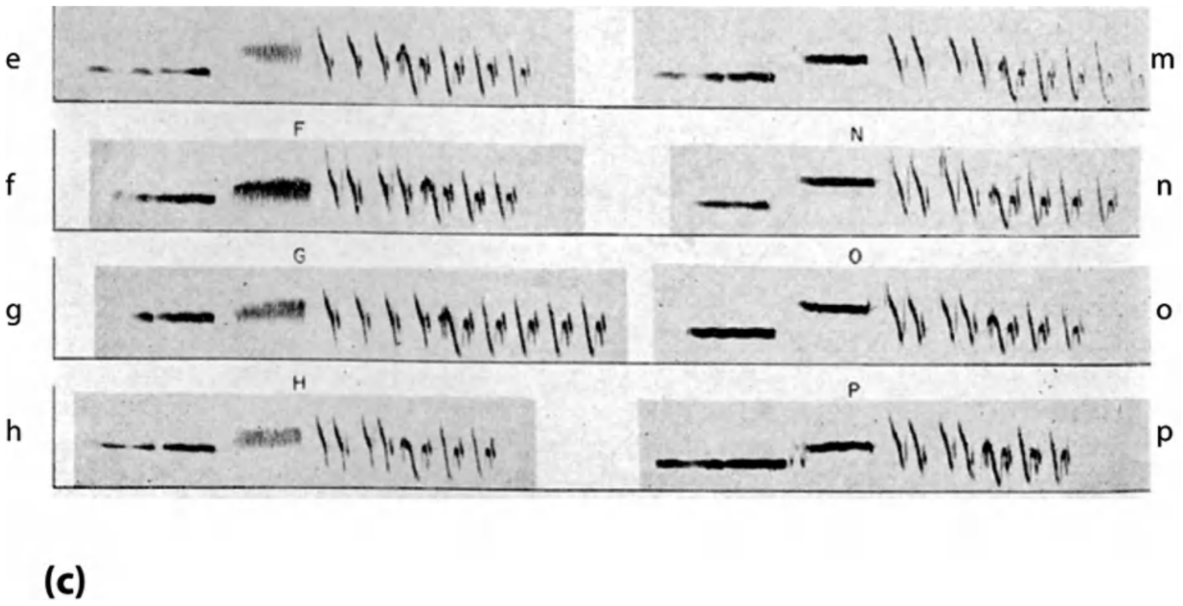
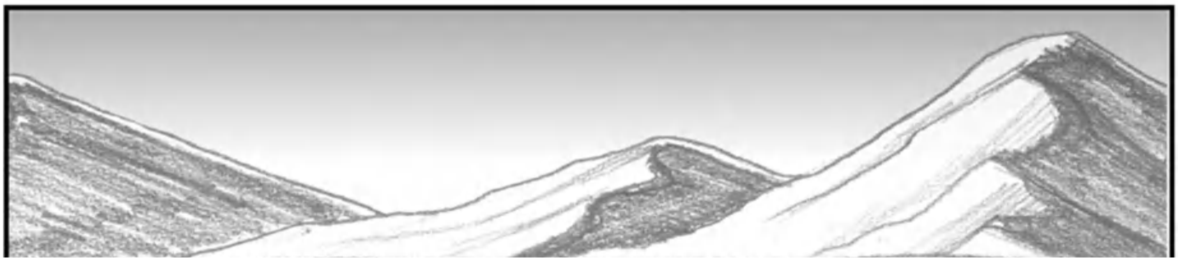


Figure 13.8. (*a*) Songs of eight male white-crowned sparrows (*Zonotrichia leucophrys*) recorded at Sunset Beach, Santa Cruz County, California, in April 1959. (*b*) Songs of eight white-crowned sparrows recorded at Sunset Beach in May 1960. Note the consistency of the song when compared with the songs of the same population of males in 1959. (*c*) A–H, songs of eight white-crowned sparrows recorded at Inspiration Point, Contra Costa County, California, in May 1960. I–P, songs of eight white-crowned sparrows recorded in Berkeley, Alameda County, in April 1959 and May 1960. Note the consistent difference in dialects in these birds from Contra Costa and Alameda counties from those in Santa Cruz County.



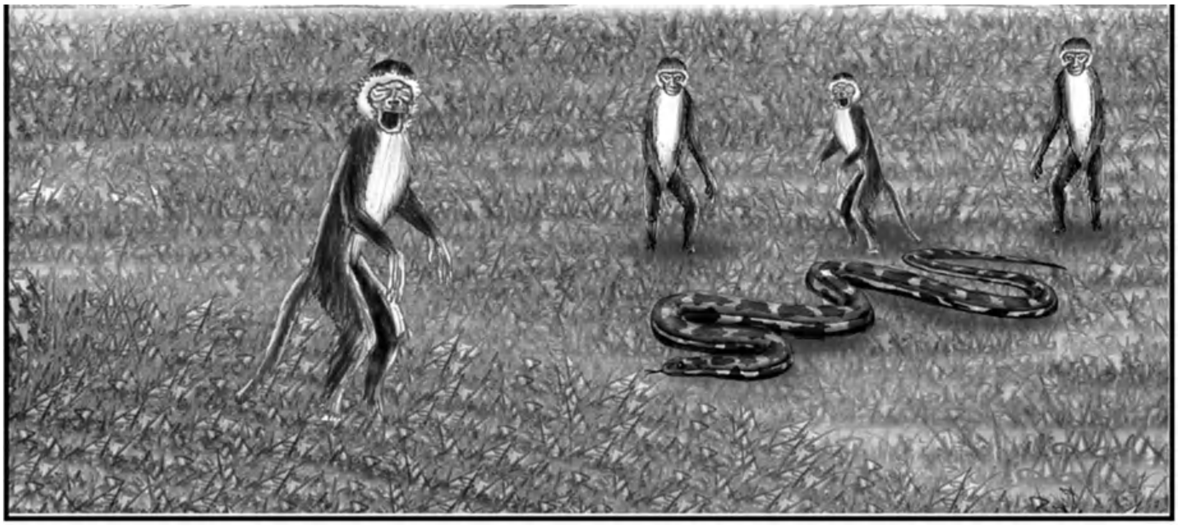


Figure 13.9. Different alarm calls are given by vervet monkeys (*Cercopithecus pygerythrus*) in response to the sighting of at least three major predators: leopards (*top*), martial eagles (middle), and snakes, like the African rock python (*bottom*). The monkeys change their escape route to match the specific alarm call.

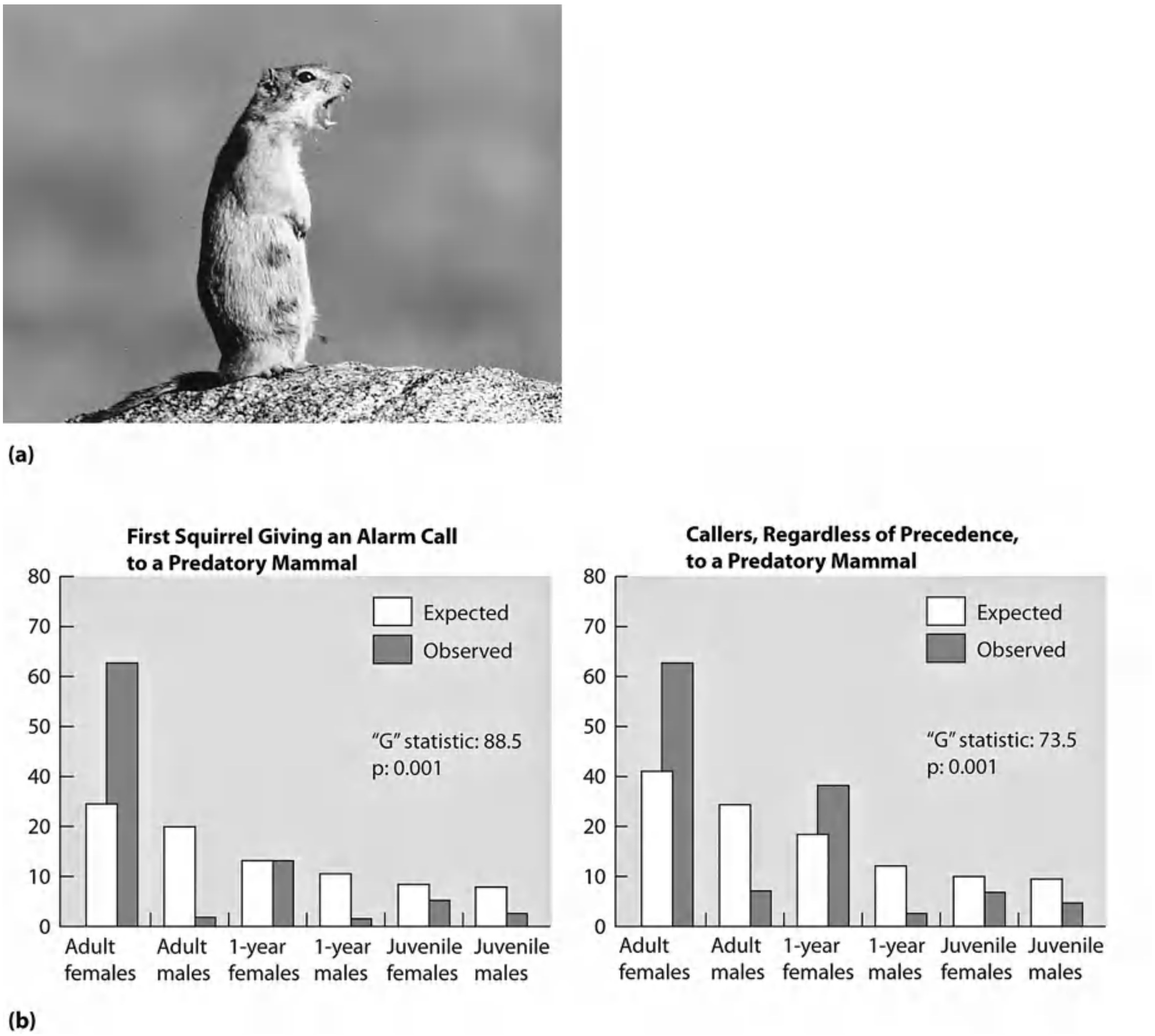


Figure 13.10. (*a*) A female Belding's ground squirrel (*Spermophilus beldingi*) emitting a predator alarm call. (*b*) Expected and observed frequencies of alarm-calling in Belding's ground squirrel. The overall significance of both comparisons is due to females calling more than expected and males calling less. Data based on 102 observations.

Bowhead whales sing unexpectedly loud, diverse songs 24 hours a day between November and April. Using underwater microphones off the east coast of Greenland, scientists identified 184 distinct songs from a population of about 300 bowheads (Stafford et al., 2018). Researchers reported: "If the humpback song is like classical music, bowheads are jazz. Their sound is more free-form." Examining four years of acoustic data, the scientists did not find any song types repeated between years, and each season had an entirely new set of songs. The researchers believe that only males sing.

The vocal repertoire of many toothed whale cetaceans consists of ultrasonic clicks. Most cetacean strandings, particularly those involving pilot whales, occur on gently sloping beaches. Some biologists believe that the gradual slope of the beaches may not reflect the whales' ultrasonic signals effectively. If the whales do not hear an echo, they may receive a false impression of deep open water ahead and continue swimming toward shore until it is too late.

A frog from Borneo, *Huia cavitympanum*, is the first non-mammalian vertebrate known to communicate with calls purely in the range above 20 kHz, which is about the upper limit of human hearing. These ultrasonic calls cause male frogs nearby to increase the frequency of their calls in response. Upon examining the frog's brain and ears, researchers found that its hearing was most sensitive above 20 kHz.

Bats (order Chiroptera) are the only mammals known to use ultrasonic echolocation as a principal means of locating prey. However, baleen whales (order Cetacea) and pinnipeds (order Pinnipedia) may use echolocation to a limited degree in intraspecific interactions. Some terrestrial species, like shrews, voles, tenrecs, oilbirds, and the cave swiftlet, appear to use echolocation in certain instances.

The vocal repertoire of high-frequency calls has recently been reported for two species of North American flying squirrels (Gilley et al., 2019). Using visual and auditory assessments, as well as quantitative measurements (i.e., spectral and temporal characteristics), 10 specific call types were identified for *Glaucomys sabrinus* and 27 specific call types for *Glaucomys volans*. The most common call types were chirps, tonal chirps, two-toned chirps, trills, barks, descending crows, and upsweeps. Acoustic detection is a monitoring technique that can be used for determining occupancy of these species in the wild as well as for conservation and management purposes.

Calls at frequencies below the level of human hearing—**infrasound**—may provide a significant means of communication in some social species like elephants (*Loxodonta africana*), hippopotamuses (*Hippopotamus amphibius*), and alligators (*Alligator mississippiensis*) (Payne et al., 1986; Langbauer et al., 1991a, 1991b; Montgomery, 1992). The long wavelengths of low-frequency sounds are not reflected or absorbed by vegetation or blocked by obstacles the way higher-frequency sounds are. The frequency of most elephant calls ranges from 14 to 24 Hz, with durations of 10 to 15 seconds. Fluttering (Fig. 13.11) in a particular area of the elephant's forehead can be observed during infrasonic calling. Infrasonic calls may be important in coordinating the behavior and activity of animals in thick vegetation or in communicating among separated groups of elephants. Fin whales were the first marine mammals known to produce infrasound; elephants were the first terrestrial mammals known to produce such sounds.

Cassowaries (*Casuarius* sp.) produce low-frequency booming sounds barely audible to humans—the deepest bird calls ever recorded. Researchers suspect that cassowaries use these calls to find mates in the dense forests they inhabit.

Hippopotamuses can produce infrasonic vocalizations both above and below the surface of the water (Montgomery, 1992). Above-water sounds are transmitted through the animal’s nostrils, whereas the underwater signal is delivered close-mouthed and is transmitted through the tissue of the head and neck.

Figure 13.11. Elephants in the breeding herd at Circus World, Haines City, Florida. The arrow indicates the region of the elephant's forehead where fluttering can be observed during the production of infrasonic calls.

Vision

Visual communication occurs in all vertebrate groups, with the eye being a highly specialized special sensory organ in most species. In most fishes, vision is an important sense for finding food and for communicating with other fishes. In many fishes, bright colors are arranged in a wide variety of elaborate patterns that are easily observed. Only in a few vertebrates have eyes degenerated due to a particular lifestyle (certain cave-dwelling and subterranean species). In some terrestrial vertebrates, vision is associated with special sensory patches of skin that can be displayed during courtship, territorial defense, or aggression, like the dewlap in anoles (*Anolis*) (see Fig. 7.31), the bright gular pouch in male frigate birds (*Fregata*), and the brightly colored buttock pads in drills and mandrills (*Mandrillus*). In birds, vision is associated with the evolution of special plumages (nuptial plumage) used for display during the breeding season.

In mammals, vision is important for recognizing the movements of facial and ear muscles (which can signal intensities of threat, submission, or greeting) and for recognizing special patches of hair that can be displayed at appropriate times, like the white rump patch and underside of the tail in white-tailed deer (see Fig. 9.14) and the white rump patch of pronghorn antelopes (*Antilocapra*) and elk (*Cervus*). Dugatkin (1997) listed six theories concerning tail flagging: (1) to warn conspecifics of potential dangers; (2) to close ranks and tighten group cohesion, perhaps to ensure group-related foraging and antipredator benefits in the future; (3) to announce to a predator that it has been sighted and should therefore abandon any attack; (4) to entice the predator to attack from a distance that is likely to result in an aborted attempt; (5) to cause other group members to respond, thereby confusing the predator and making the flagger itself less likely to be the victim of an attack; and (6) to serve as a sign for appeasing dominants, playing only a secondary role in antipredator behavior. Dugatkin (1997) points out that since data on the success rates of predators on flaggers and nonflaggers do not exist, it is difficult to evaluate which, if any, mechanisms of cooperation might account for signaling to a predator. Vision is also important in recognizing body posture, like the way a tail is carried in carnivores, and, in all vertebrate classes, interpreting the behavior and actions of other members (see Figs. 8.34 and 13.9).

Tactile Signals

Tactile signals are particularly important in the reproductive behaviors of some vertebrates. The tremble-thrusts of male sticklebacks were described in Chapter 4. The long nails on the front limbs of male painted turtles (*Chrysemys picta*) are used to stimulate the female during copulation.

Grooming, nuzzling, and licking are means of communication involving touch. These actions may be particularly important to altricial young before their eyes open. Touch receptors—**Meissner's corpuscles**—and pressure receptors—**Pacinian corpuscles**—are especially well developed in mammals. Mutual grooming in primates not only serves to eliminate ectoparasites, it is also extremely important in establishing and maintaining social bonds.

Electrical Signals

Some groups of fishes, especially the elephantfishes (Mormyriformes), knifefishes (Notopteridae), and electric eels (Gymnotiformes), use electrical discharges for intraspecific signaling. The discharges can be modified in a variety of ways and can be used for the recognition of individuals, courtship, and agonistic behavior. (See discussion of electric organs in Chapter 4.)

FEEDING BEHAVIOR

While some fishes, amphibians, and reptiles protect their eggs and young, they do not procure food for the young. Among most birds and mammals, however, one or both parents either secure food and bring it to young in the nest or teach the young how to secure their own food. Most adult birds and mammals secure their own food independently, but some, like eagles, buzzards, vultures, hyenas, wolves, and lions, will feed on the same food source with other members of their species.

Female mammals are equipped with mammary glands, which provide nourishment to their young. As the young grow, most parents are instrumental in showing their offspring how to secure proper food on their own. In some cases, this is the sole responsibility of the female. In others, both parents participate.

Feeding is a communal activity in those mammals that have developed highly social societies, like wolves (*Canis lupus*), which live and hunt cooperatively in packs. Rewards of the hunt are shared among all members of the pack. Lions (*Panthera leo*) are matriarchal, with lion prides consisting of several related adult females, their cubs, and a few males. The kill success rates of solitary females appear to be inversely correlated with prey size (Schaller, 1972; Scheel and Packer, 1991; Packer and Pusey, 1997). Although solitary hunters may have the highest kill success rates when hunting small prey like warthogs (*Phacochoerus aethiopicus*), female lions usually cooperate and hunt larger prey in groups. Hyenas (*Crocuta*, *Hyaena*) and hunting dogs of Africa (*Lycaon pictus*) are other social carnivores. Some primates, like chimpanzees (*Pan*), gorillas (*Gorilla*), orangutans (*Pongo pygmaeus*), and baboons (*Papio*), live in troops or family units and share the food source.

Tool-using as an aid in securing food has been recorded in several species. Alligators and crocodiles use twigs and sticks to attract nest-building birds (Chapter 8). Bottlenose dolphins off Australia's coast dive to the bottom of deep channels and use a sponge (held in their beaks) on the sandy ocean floor to flush out small fish that dwell there. Foragers then drop their sponges, gobble up available fish, and retrieve the sponges for another sweep. Dolphins hold the sponge with the bottom of their beaks and can sweep away much more sand than they could without the tool. This behavior has been identified as the first clear case of tool use by wild dolphins or whales. Researchers estimate that sponge-carrying dolphins devote at least 17 percent of their time to ferreting out bottom-dwelling fish using these beak-borne prods (Sargeant and Mann, 2009). Chimpanzees have been observed stacking boxes to stand on in order to grab otherwise unreachable bananas. Egyptian vultures will search 50-plus yards for the right rock to throw at an ostrich egg to crack it open. New Caledonian crows use twigs to probe for insects.

Predation usually is considered an interspecific action and is discussed in Chapter 14. However, cannibalism is a form of intraspecific predation and may play an important role in shaping the reproductive ecology of many species. It is surprisingly common in many species of fishes and is found in many other vertebrate groups. The main ecological factor favoring cannibalism is a low availability of alternative food (Elgar and Crespi, 1992). This, in turn, may be a consequence of the density of the population. Competition for reproductive dominance also may be an important factor in some species. The role of cannibalism in the reproductive ecology of the three-spine stickleback has been discussed by FitzGerald (1991, 1992).

To minimize cannibalism, many species of fish produce their young in areas away from adult feeding areas. Adult bullfrogs are known to ingest many different animals, including tadpoles and newly metamorphosed members of their own species. Male alligators will devour newly hatched alligators. Some female mammals under stress will partially or completely consume some or all members of their litter. Cannibalism is used by some males to eliminate unrelated young in order to increase the male's chances of mating with females who have previously bred (see Labov et al., 1985, for review). Infant rodents produce fewer ultrasonic vocalizations in the presence of odors from males than from females, but it is uncertain whether they can discriminate between infanticidal and noninfanticidal males on the basis of odor (Elwood, 1992).

The Bark of the Dog

The domestic dog is a member of the genus *Canis*, which forms part of the wolflike canids. The closest living relative of the dog is the extant gray wolf. The dog and the extant gray wolf are sister taxa, as modern wolves are not closely related to the wolves that were first domesticated. By comparing mitochondrial DNA (mtDNA) from wolves and dogs in different parts of the world today, researchers have found that about 100,000 years ago there was a genetic fork in the road of canine evolution—biologically separating wolf and dog. The archaeological record and genetic analysis shows the remains of the Bonn-Oberkassel dog buried beside human remains 19,200 years ago in Germany to be the first undisputed dog, although molecular dating of doglike fossils found elsewhere in Europe suggests an onset of domestication from 18,800 to 32,100 years ago. Both studies suggest a European origin of domestic dogs. The Bonn-Oberkassel date implies that the earliest dogs arose in the time of human hunter-gatherers and not agriculturalists. This data is older than that for cats, cows, and horses. Cattle were domesticated only about 8,000 to 9,000 years ago; horses, 6,000 to 7,000 years ago; cats, 5,000 to 6,000 years ago; and chickens, 4,000 years ago. Prior to the confirmation of the European findings, the earliest known evidence of the domestication of the dog was about 12,000 years ago when a tribe of hunter-gatherers in the Middle East, in the region now known as Israel, buried a person along with its favorite puppy.

Scientists do not agree as to why the dog was domesticated. Some argue that humans adopted wolf pups and that natural selection favored those less aggressive and better at begging for food. Others say dogs domesticated themselves by adapting to a new niche—human refuse dumps. Scavenging canids that were less likely to flee from people survived in this niche and succeeding generations became increasingly tame. Over time, dogs have become progressively less wolflike, evolving smaller teeth, a more delicate body, and puppy-like juvenile characteristics—traits more appealing to humans. On the basis of extensive DNA analyses from New World dog remains predating European influence, results show that early New Worlders did not domesticate their dogs anew. By constructing a family tree including modern dogs and wolves, researchers found that the ancient New World dogs were much closer to Old World dogs than to New World wolves. These results agree with previous studies that concluded that the earliest immigrants coming across the Bering land bridge brought their dogs with them.

Barking is the hallmark of the domestic dog (*Canis familiaris*). Coyotes and wolves, on the other hand, bark only rarely. In one study, only 2.5 percent of 3,256 vocalizations by captive wolves were barks. And when wild canids do bark, their barks tend to be brief and isolated, as opposed to the long, rhythmic barking of the domestic dog.

Repetitive barking in wolf pups is significantly more frequent than it is in adults. As the wild animal matures and develops normal adult behavior, it gradually loses its puppy-like characteristics.

Regulatory genes control an organism’s overall pattern and growth and the rate at which its individual parts grow. Any change in the timing of these regulatory genes is referred to as **heterochrony** (Gr. *hetero-*, different, + *chronos*, time). Heterochronic evolutionary mechanisms can speed up or slow down the rate at which an animal grows from a newborn into an adult. It may slow the rate so much that the animal may not attain its “normal” full adult form. Some biologists believe the dog “is an adolescent in a state of change”—reproductively capable but not yet endowed with the full physical and psychological maturity of a “real” adult. Heterochronic change is believed to have frozen *Canis familiaris* in mid-metamorphosis. It remains a “metamorphic” adolescent for life. Its bark is thought to be a juvenile characteristic serving no real function, but probably is motivated by indecision. Some dogs, however, learn to use barking as a means of communication, adapting this initially functionless behavior to serve specific functions like indicating when they want to be let in or out of the house, or when they want food or attention.

Coppinger and Feinstein, 1991; Vila et al., 1997; Morell, 1997d; Leonard et al., 2002; Savolainen et al., 2002; vonHoldt et al., 2010; Thalmann et al., 2013; Freedman et al., 2014; Janssens et al., 2018

TORPOR (DORMANCY)

Torpor occurs in amphibians, reptiles, birds, and mammals. It may last for only hours (e.g., as in some hummingbirds and many bats that undergo an almost daily cycle of torpor during which they reduce both their body temperature and metabolic rate in order to conserve energy), or it may last for as long as weeks or months (amphibians, reptiles, many mammals). Black-capped chickadees (*Parus atricapillus*) go into regulated hypothermia to lower their body temperature, in a controlled manner, to about 9°C to 11°C (12°F–15°F) below their normal daytime temperature of 42°C (108°F). This allows the birds to conserve almost 25 percent of their hourly metabolic expenditure when the outside temperature is at freezing. The lower the outside temperature, the more energy the birds conserve (Harrison, 2008).

Certain periods of the year may be environmentally unfavorable for certain species of vertebrates, and they become inactive. If this unfavorable period of the year occurs during the colder winter months, some mammals (including many bats) greatly reduce their body temperatures and metabolic rates in order to survive for a prolonged period without food intake (Schmidt-Nielsen, 1997). Such dormancy during the winter is known as **hibernation**. Some vertebrates become dormant for varying periods of time during the hotter summer months. This dormancy is known as **estivation**.

Although torpor is a physiological state, some vertebrates gain advantage during hibernation by clustering together with other members of their own species. In particular, many species of bats hibernate in clusters in caves, presumably as a means of reducing heat and water loss (see Fig. 13.17). Black bears give birth and nurse their young during dormancy. Flying squirrels (*Glaucomys* spp.), golden mice (*Ochrotomys* *nuttalli*), and others, although not hibernators, have been found in large aggregations during the winter months in some areas. Thus, torpor/dormancy is included in this chapter.

Winter Survival and Hibernation

Hibernation is a well-regulated physiological state of torpor characteristic of temperate-zone animals (Schmidt-Nielsen, 1997). A recently discovered hormone may play a major role in triggering and maintaining hibernation (Kondo et al., 2006). Known as hibernation-protein complex (HPc), the hormone is made of four proteins. Studies in Siberian chipmunks show that HPc fluctuates on a seasonal schedule. HPc is absent in brain fluids during the summer, but rises as hibernation begins and remains steady during hibernation.

In the case of ectothermic groups, like amphibians and reptiles, body temperature and metabolic activities decrease as the ambient temperature drops. Thus, they are forced to seek a safe refuge (hibernaculum) either on land or in water in order to survive the colder winter months. Selective pressures over time have resulted in most of these groups seeking protected areas where the temperature will remain above freezing and where relative humidity remains fairly constant. Examples of hibernacula include caves, rock crevices, underground burrows, muskrat houses, decaying logs and stumps, sawdust piles, and beneath mud and debris on the bottoms of bodies of water. Several species of anurans, including the wood frog (*Lithobates* [*Rana*] *sylvatica*) and the gray treefrog (*Hyla versicolor*), are freeze-tolerant and can survive temperatures below 0°C (32°F) (Layne, 1999, 2000).

Some closely related species select different types of hibernacula under natural conditions. For example, leopard frogs (*Lithobates* [*Rana*] *pipiens*) are aquatic hibernators, whereas wood frogs (*Lithobates* [*Rana*] *sylvatica*) are terrestrial hibernators (Licht, 1991).

Reptiles seek out the same types of protected areas as amphibians in order to survive the winter. Terrestrial turtles may use existing burrows, or they may simply burrow several inches into loose soil or leaf litter. Aquatic turtles may hibernate in beaver lodges, in muskrat houses, or in the mud on the bottoms of ponds and lakes. Lizards and snakes may overwinter in caves, hollow trees, sawdust piles, ant hills, houses, and barns.

Hibernating adult Great Basin rattlesnakes (*Crotalus viridis lutosus*) showed differences as great as 4°C (7°F) in body temperature when measured at the same time in a single den. The lowest body temperature experienced by any Great Basin rattlesnake was 4.2°C (39.6°) (Peterson and Cobb, 1991). Mcartney et al. (2011) used radiotelemetry (implanted temperature-sensing radio transmitters) to monitor temperatures of hibernating rattlesnakes (*Crotalus viridis*) in southern British Columbia and garter snakes (*Thamnophis sirtalis*) in northern Alberta. Body temperatures recorded during winter were as follows: rattlesnake #1, average 7°C, range 6.9°C to 7.3°C (44.4°F–45.1°F), and rattlesnake #2, average 5.2°C, range 4.3°C to 6.2°C (39.7°F–43.1°F); for a single garter snake, average 3.9°C, range 1.8°C to 6.5°C (35.2°F to 43.7°F).

Hibernation is rare among birds. However, the poorwill (*Phalaenoptilus nuttalli*) of western North America is known to hibernate in the wild (Fig. 13.12). During this time, its body temperature may drop to as low as 7°C (44.6°F). Laboratory studies have demonstrated that the trilling nighthawk (*Chordeiles acutipennis*) is also capable of hibernation (Marshall, Jr.,1955).

Nectar is the main source of energy for hummingbirds, but they also prey on small insects. The amount of food stored during the day determines whether a hummingbird undergoes a period of torpor at night as a means of conserving energy. During torpor, hummingbirds reduce both their metabolic rate and body temperature (Fig. 13.13). During this time, their metabolic rate may be reduced up to 10-fold (see review by Powers, 1991). Torpor has both advantages and disadvantages. Energy savings is a definite advantage, whereas vulnerability to predation is a major disadvantage in terms of species survival.

Mammals living in cold environments are adapted in several ways to withstand the rigorous winter period. Small mammals use runways beneath the snow as a means of avoiding both cold temperatures and predators. Shivering (muscular thermogenesis) produces some heat through muscle contraction. Some mammals (like bats) have brown adipose tissue that generates heat rather than adenosine triphosphate (ATP) when it is metabolized, a process known as **nonshivering thermogenesis**. Fur becomes thicker, and often white, in winter to provide insulation and camouflage (Fig. 13.14). Underfur plays a key role in trapping a layer of air next to the skin, which provides insulation. The limbs and other extremities, however, remain poorly insulated. Seals, sea lions, walruses, narwhals, and whales develop thick insulating layers of blubber around most parts of their bodies (Fig. 13.15). The flippers and flukes, however, lack blubber and are poorly insulated.

Figure 13.12. Common poorwill (*Phalaenoptilus nuttallii*) in a rock crevice in California.

Northern species of birds and mammals possess peripheral countercurrent heat exchange mechanisms in their extremities (nose, ears, legs, flippers, and tail) to minimize heat loss (Fig. 13.16) (Schmidt-Nielsen, 1997; Hildebrand and Goslow, 2001). These parts of the body are maintained at much cooler temperatures than the rest of the body, sometimes almost approaching the freezing point. The major artery and vein supplying an extremity lie side by side. As warm arterial blood flows into the extremity, heat diffuses into the cooler adjacent vein and is carried back to the core of the body. Thus, while the core body temperature remains relatively high, the temperature in the extremities may actually be below 0°C (32°F). Fats in the extremities have much lower freezing points than elsewhere in the body and serve to keep the limbs flexible and supple at low temperatures.

Minor fluctuations in body temperature may occur in northern mammals that remain active through the winter. In northern Minnesota and Michigan, adult beavers had a mean daily body temperature of 36.3°C (97.3°F) with a mean daily fluctuation of 1.4°C (2.52°F) from late October through early November (Smith et al., 1991). From fall to winter, the body temperature of adult beavers declined at an average rate of 0.01°C (0.018°F) per day and the average daily winter body temperature was 35.3°C (95.5°F). In early March, average daily adult body temperatures began increasing at a rate of 0.03°C (0.054°F) per day. Juvenile (kit) beavers did not undergo a significant body temperature decline during the winter. Lowering energy demands by reducing body temperature during the winter may be an adaptation by adult beavers that aids in their survival during times of resource scarcity.

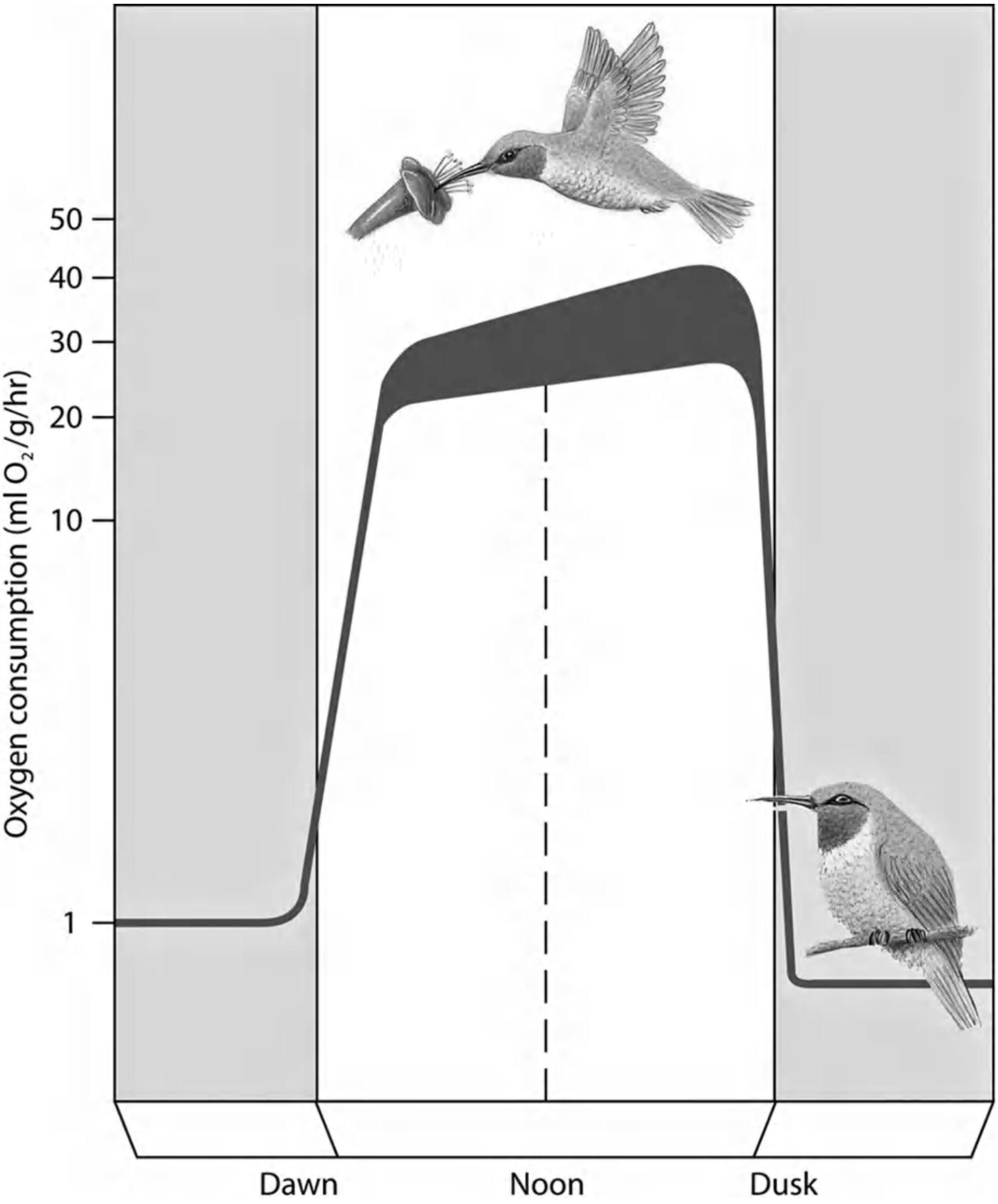


Figure 13.13. Torpor in hummingbirds. Body temperature and oxygen consumption are high when hummingbirds are active during the day, but may drop to 1/20 of these levels during periods of food shortage at night. Torpor vastly lowers demands on the bird's limited energy reserves.

Woodchucks (*Marmota*), grizzly bears (*Ursus arctos*), western ground squirrels (*Spermophilus*), jumping mice (*Zapus*, *Napaeozapus*), pygmy possums (Burramyidae), and some bats living in northern areas are among the true hibernators. During hibernation, they have a lower metabolic rate, a body temperature near the ambient temperature, much lower heart and breathing rates, lowered blood pressure, and inactive endocrine glands. In certain species, this state of inactivity may last for as long as six months in some regions.

A grizzly's den is usually a chamber excavated by the bear into a forested, steep, high-altitude, north-facing slope. North-facing slopes provide good snow cover, which better insulates the bear. The den is often lined with conifer branches or other vegetation and is just big enough to accommodate the sleeping bear. In the den, grizzlies live off stored body fat and do not eat, drink, or excrete any bodily waste for up to six months. Overall, their metabolic rate decreases by 50 to 60 percent with their body temperature dropping from a normal 37.8°C (100°F) to around 31.1°C (88°F), and respirations dropping from 10 breaths per minute to only 1 every 45 seconds. Normal metabolic wastes are produced, but instead of excreting them, bears recycle these waste products into proteins, allowing them to maintain lean body mass, even though overall body mass decreases by up to 30 percent. By spring, all of a bear's fat is typically gone.

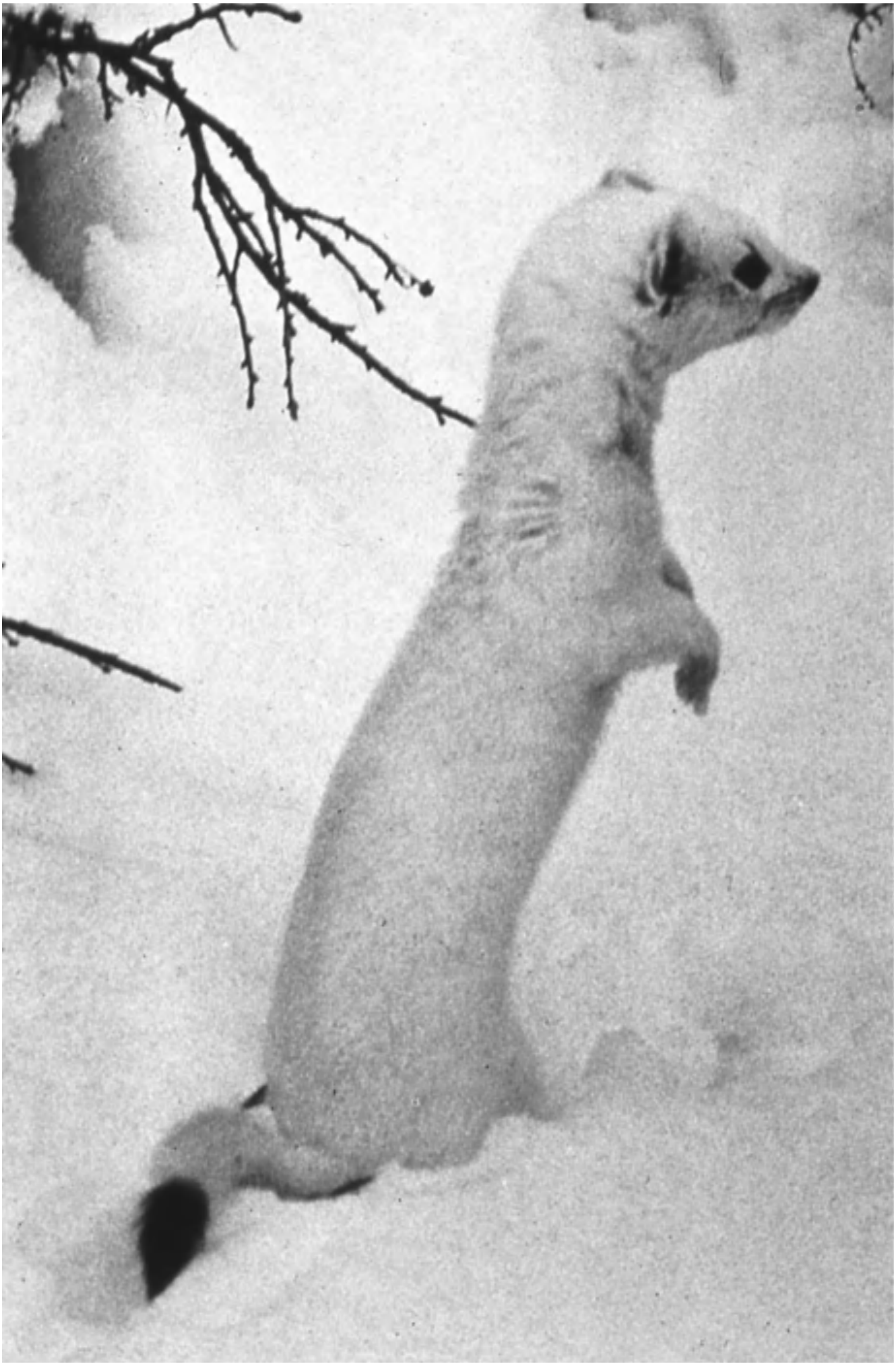


Figure 13.14. In northern portions of its range, the brown pelage of the long-tailed weasel (*Mustela frenata*) is replaced in the fall with a mostly white coat to provide better insulation and camouflage.

Hibernating bats and ground squirrels arouse periodically during winter; these arousals are thought to be energetically very costly and account for 75 to 85 percent of winter fat depletion. It is thought that arousals may be provoked by the depletion of certain metabolic substances, the accumulation of wastes to unacceptable levels, or evaporative water loss (EWL) (Thomas, 1990). Because more than 99 percent of EWL occurs cutaneously, bats can significantly reduce EWL by selecting hibernacula with high humidities and by clustering to reduce exposed surface areas (Thomas and Cloutier, 1992) (Fig. 13.17).

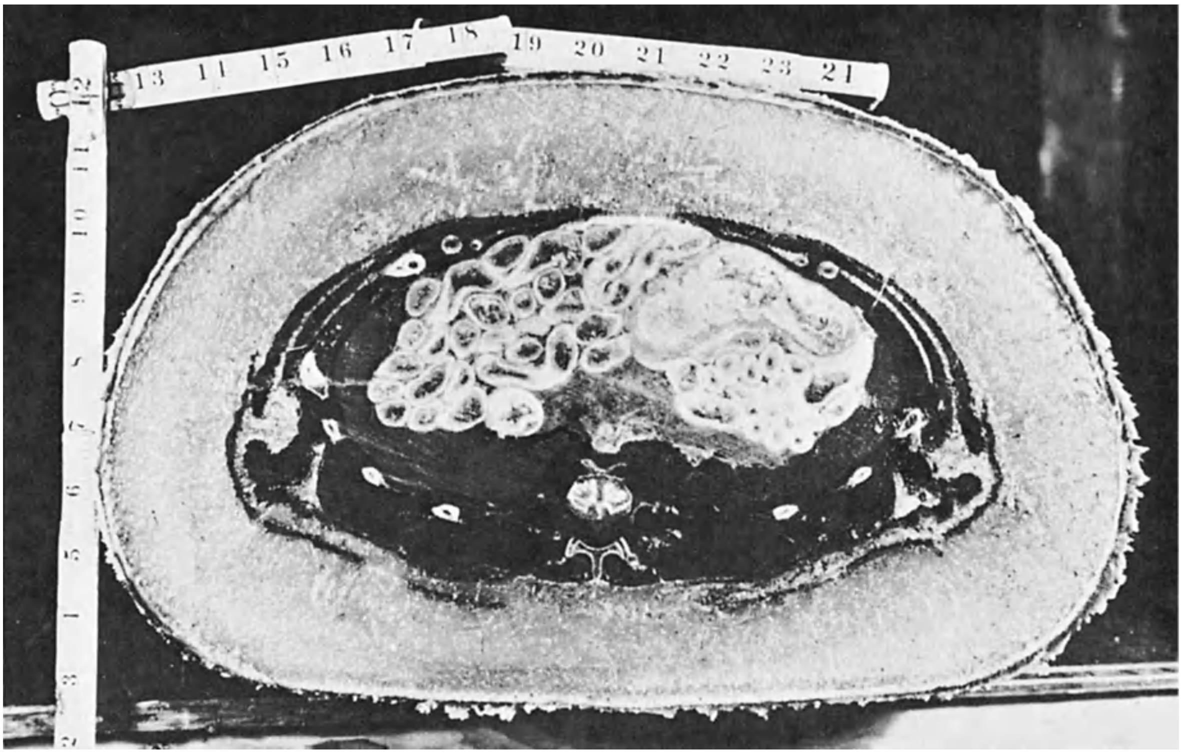


Figure 13.15. Seal blubber. This cross section of a frozen seal reveals the thick layer of blubber. Of the total area in the photo, 58 percent is blubber and the remaining 42 percent is muscle, bone, and visceral organs. The scale of the ruler is in inches.

Energy cost and number of arousals are key factors in determining the energy expenditures of hibernators during winter. For a 6.58 g (0.23 oz.) little brown bat (*Myotis lucifugus*), Thomas et al. (1990) calculated that warming from 5°C to 37°C (41°F–98.6°F) required the metabolism of 14.5 mg (0.0005 oz.) of fat. During the warming phase, heat is generated by brown adipose tissue, the liver, and muscles. During a hibernation period of 193 days in the Quebec–Ontario region of Canada, little brown bats will arouse about 15 times and require 1,618.5 mg (0.06 oz.) of fat to cover arousal costs. This fat reserve represents 29.3 percent of the bat's mass at the start of hibernation. These data correlate with an earlier study by Fenton (1970), who found that little brown bats in Ontario lost 25 percent of their mass during hibernation.

Golden-mantled ground squirrels (*Spermophilus saturatus*) hibernate for about 64 percent of each year but use only about 17 percent of their annual energy expenditure during that time (Kenagy et al., 1989) (Fig. 13.18). A ground squirrel's core body temperature drops from 36°C to 2°C (96.8°F–35.6°F), and its heart slows from 350 beats per minute to as few as 2 per minute.

Semidormant hibernators include such mammals as black bears (*Ursus americanus*), eastern chipmunks (*Tamias striatus*), skunks (*Mephitis mephitis*), raccoons (*Procyon lotor*), badgers (*Taxidea taxus*), and opossums (*Didelphis virginiana*). These species do not experience the drastic changes in their bodily systems that occur in true hibernators. During winter dormancy, their body temperatures are not much lower than their normal body temperatures. Although a black bear's heart rate may fall from a normal sleeping rate of 40 beats per minute to 8, its body temperature does not fall more than about 6°C (9°F) from a normal reading of about 38°C (100.4°F). Whereas small hibernators are slow to rouse, a torpid black bear can become fully alert in moments. They often may be seen moving about outside their dens during the warmer periods of winter.

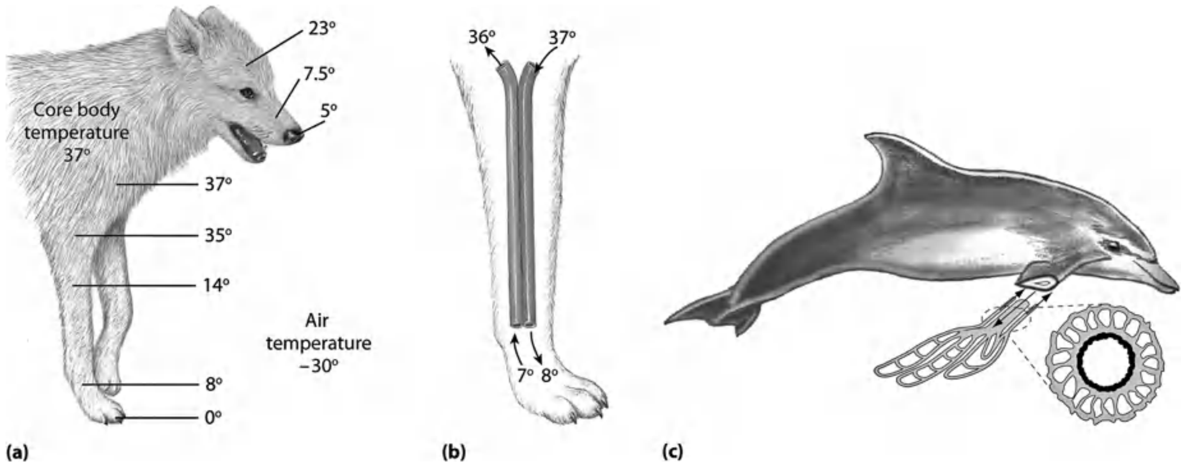


Figure 13.16. Countercurrent heat exchange in the leg of an arctic wolf and in a dolphin. (*a*) Illustration of how the extremities cool when the animal is exposed to low air temperatures. (*b*) A portion of the main artery and vein serving the front leg, showing how heat is exchanged between outflowing arterial and inflowing venous blood. Heat is thus shunted back into the body. (*c*) Each artery in the flippers and fluke of a dolphin is surrounded by several veins. This arrangement permits the venous blood to be warmed by heat transfer from the arterial blood before it re-enters the body.

Figure 13.17. A group of Townsend's big-eared bats (*Plecotus townsendii*) in Jewel Cave, South Dakota, where the thermometer indicates a temperature of 4°C (36°F). Clustering reduces exposed surface areas, thereby reducing evaporative water loss and heat loss.

Skeletal muscle biopsies of bears prior to denning, during denning, and following spring arousal revealed no significant differences in glycogen, triglyceride, and protein concentrations (Koebel et al., 1991). In addition, the activity of citrate synthase, a mitochondrial oxidative enzyme, was not significantly different during these three time periods. A slight degree of muscle atrophy may occur during the denning period, however.

Figure 13.18. Photograph of a hibernating golden-mantled ground squirrel (*Spermophilus saturatus*). The head is tucked under the body, and the tail is curled over the head.

Deer mice (*Peromyscus maniculatus*) undergo daily torpor in some areas. During torpor, they undergo significant intracellular and extracellular acidosis (Nestler, 1991, 1992). Carbohydrate levels are significantly lower, and fatty acid and ketone levels are significantly higher during torpor.

Southern flying squirrels (*Glaucomys volans*) do not hibernate and enter torpor only during extended periods of food shortage or low temperature. To reduce their exposure to cold temperatures and conserve energy, squirrels form small aggregations in nest-lined tree cavities. Research shows that huddling in groups of three and six reduced energy expenditure by 27 and 36 percent, respectively, at 9°C (48.2°F) (Stapp et al., 1991), whereas nest insulation decreased heat loss by 37 percent for single squirrels. Aggregating reduced winter daily energy expenditure by 26 to 33 percent.

Factors that trigger an animal to enter hibernation vary. Climatic factors like colder temperatures, cold rains, and snow are ultimately responsible. Change in daylength has been suggested as a possible triggering mechanism in some species, as well as a biological clock that recognizes seasonal rhythms. Recent research efforts have been aimed at isolating the hibernation induction trigger, a chemical compound that appears to be related chemically to opiates like morphine, which depress certain operational aspects of the nervous system.

Some individuals hibernate singly, whereas others hibernate in groups. Where favorable hibernacula are scarce, snakes of several species may hibernate in large aggregations, or **dens**. One such den in Manitoba was in an active ant hill and contained 257 snakes: 148 green snakes (*Opheodrys vernalis*), 101 red-bellied snakes (*Storeria occipitomaculata*), and 8 garter snakes (*Thamnophis radix*) (Criddle, 1937). An ant hill excavated in Michigan yielded 62 snakes of seven species and 15 amphibians belonging to three species (Carpenter, 1953).

Many mammals hibernate in a characteristic *C*-shape configuration in order to reduce heat loss and water loss (Orr, 1982) (see Fig. 13.18). Many bats hibernate individually, but some hibernate in clusters (see Fig. 13.17). It has been suggested that this may be the result of selective pressure to conserve heat. Each individual is kept partially warm by the bodies of surrounding bats.

For a period of weeks and even months prior to hibernation, all endotherms and some ectotherms store fat. Just before entering hibernation, many bats appear to fast. Black bears purge their digestive tracts and form an anal plug just prior to entering their hibernaculum. Even though they may become active for short periods during the winter, they will not ingest any food until spring. Those mammals that enter daily torpor have only hours to prepare for significant reductions in metabolism and body temperature.

A major difference between hibernation in endotherms and ectotherms is that endotherms actively terminate torpor by internal heat production. While they all actively raise their body temperature, the rewarming rate is inversely related to their body mass, with most small mammals rewarming faster than larger mammals (Geiser and Baudinette, 1990; Stone and Purvis, 1992). Even though marsupials lack brown adipose tissue, there is no significant difference in warm-up rates between marsupials and eutherian mammals.

Many ectotherms, primarily invertebrates, experience winter temperatures below the freezing point of their body fluids. Those overwintering above the frostline must survive either by extensive supercooling or by tolerating the formation of ice within body tissues. Similar adaptations have been identified in certain vertebrates (Costanzo and Lee, 2013).

Some fishes avoid freezing solid at temperatures below the freezing point in one of three ways: they produce a solute that lowers the freezing point of body fluids, much as salt lowers the freezing point of slush; they produce an antifreeze protein that binds to ice crystals and inhibits the crystals' growth; or they supercool themselves by lowering the freezing point of their serum and defy the normal freezing temperature (Moyle and Cech, 2004).

Some fish species, like the naked dragon fish (*Gymnodraco acuticeps*), live in polar oceans with water temperatures ranging between –2°C and 0°C (28.4°F and 32°F). These species manage to remain fluid and flexible in supercooled waters by carrying antifreeze molecules in their blood. A variety of proteins or protein-sugar compounds (antifreeze glycoproteins, or AFGPs) adsorb to the surfaces of forming ice crystals and inhibit crystal growth (Raymond et al., 1989; Rubinsky et al., 1992).

Chen et al. (1997a, 1997b) report that Arctic cod and Antarctic notothenioid fishes have very similar AFGPs, but that the genes for these antifreeze proteins evolved through completely different pathways. Through convergent evolution, both groups of fishes achieved the same result. Recent studies have shown that fish AFGPs also can protect mammalian cells and organs from damage caused by hypothermic exposure (Rubinsky et al., 1991; Lee et al., 1992). Human medicine may be significantly affected by the hypothermic preservation of transplant organs for longer periods without damage.

A few species of terrestrial vertebrates can withstand freezing of part of their body fluids (Claussen et al., 1990). Freeze tolerance has been demonstrated in five frogs (*Lithobates* [*Rana*] *sylvatica*, *Pseudacris triseriata*, *Hyla* [*Pseudacris*] *crucifer*, *H. versicolor*, *H. chrysoscelis*), one snake (*Thamnophis sirtalis*), and two turtles (*Chrysemys picta* and *Terrapene carolina*) (Costanzo et al., 1992b). *Lithobates* [*Rana*] *sylvatica*, *Hyla* [*Pseudacris*] *crucifer*, *Hyla versicolor*, and *Pseudacris triseriata* hibernate on the forest floor and can survive days or weeks of freezing with as much as 65 percent of their total body water as ice. The Siberian salamander (*Hynobius keyserlingi*)—the only land-hibernating amphibian found in the tundra—may survive exposure to –35°C (–31°F) (Storey and Storey, 1992).

Eastern box turtles are the largest vertebrates known to withstand freezing. The depth beneath the soil of hibernacula of box turtles in Ohio averaged 4 to 5 cm (1.6 to 2.0 in.) and never exceeded 14 cm (4.3 in.). Leaf litter averaged 8 cm (3.1 in.) in depth. Body temperatures of these turtles approximated, but were sometimes lower than, adjacent soil temperatures. Some box turtles experienced body temperatures of –0.3°C (31.5°F) or below (Claussen et al., 1991) (Fig. 13.19).

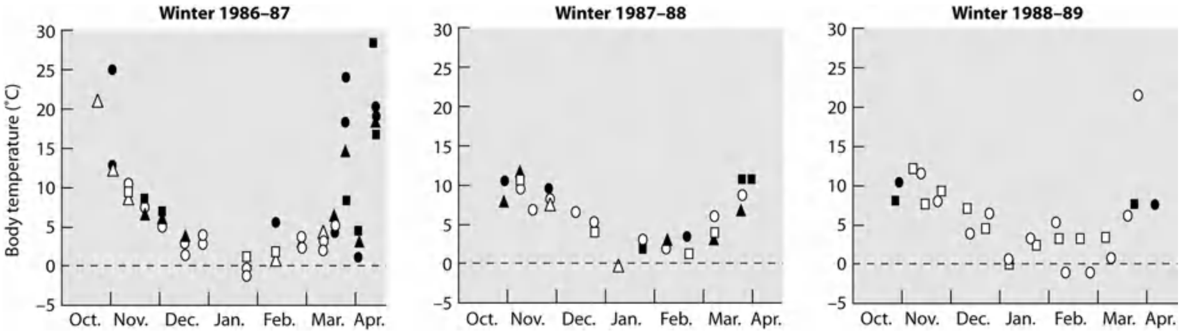


Figure 13.19. The body temperatures of eastern box turtles (*Terrapene carolina*) in Ohio during three consecutive winters. Five turtles were monitored in 1986–87, three in 1987–88, and two in 1988–89. Filled symbols depict animals on the surface.

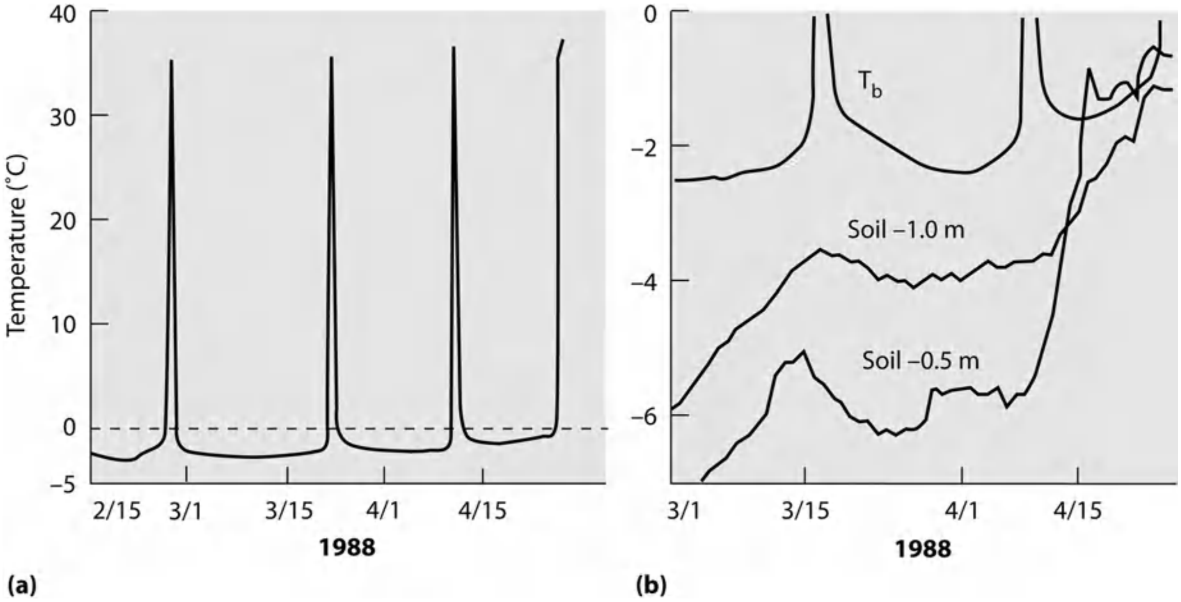


Figure 13.20. (*a*) Body temperature of a hibernating female arctic ground squirrel (*Spermophilus parryii*) as recorded by an abdominal temperature-sensitive radio transmitter. (*b*) With an expanded scale, abdominal temperature during the last three arousals from torpor and concurrent adjacent soil temperature.

Several anurans (*Lithobates* [*Rana*] *sylvatica*, *Pseudacris triseriata*, *Hyla* [*Pseudacris*] *crucifer*, and *H. versicolor*) have evolved a tolerance to slow freezing by generation of increased blood glucose levels as a cryoprotectant (Licht, 1991; Costanzo et al., 1992b). In addition, striated muscle function of *R. sylvatica* remains intact at below-freezing temperatures (Miller and Dehlinger, 1969), its cardiac function remains nearly unchanged under low temperatures (Lotshaw, 1977), and its organs undergo dehydration, presumably to prevent mechanical injury during freezing (Costanzo et al., 1992b). Rapid cooling is lethal, because this species inhibits the production and distribution of cryoprotectant and organ dehydration during freezing (Costanzo et al., 1991a, 1991b, 1992b).

The hibernating Arctic ground squirrel (*Spermophilus parryii*) is the only known endothermic animal that can survive without freezing at a body temperature below the freezing point of water (Figs. 13.20 and 13.21). Some individuals have survived after their body temperature dropped as low as –2.9°C (26.8°F) (Barnes, 1989). Because the freezing and melting points of plasma from animals held at temperatures below freezing were identical, the presence of antifreeze molecules was ruled out as a freezing survival mechanism. Because no solute was found, it is thought that the animals must have the ability to supercool themselves.

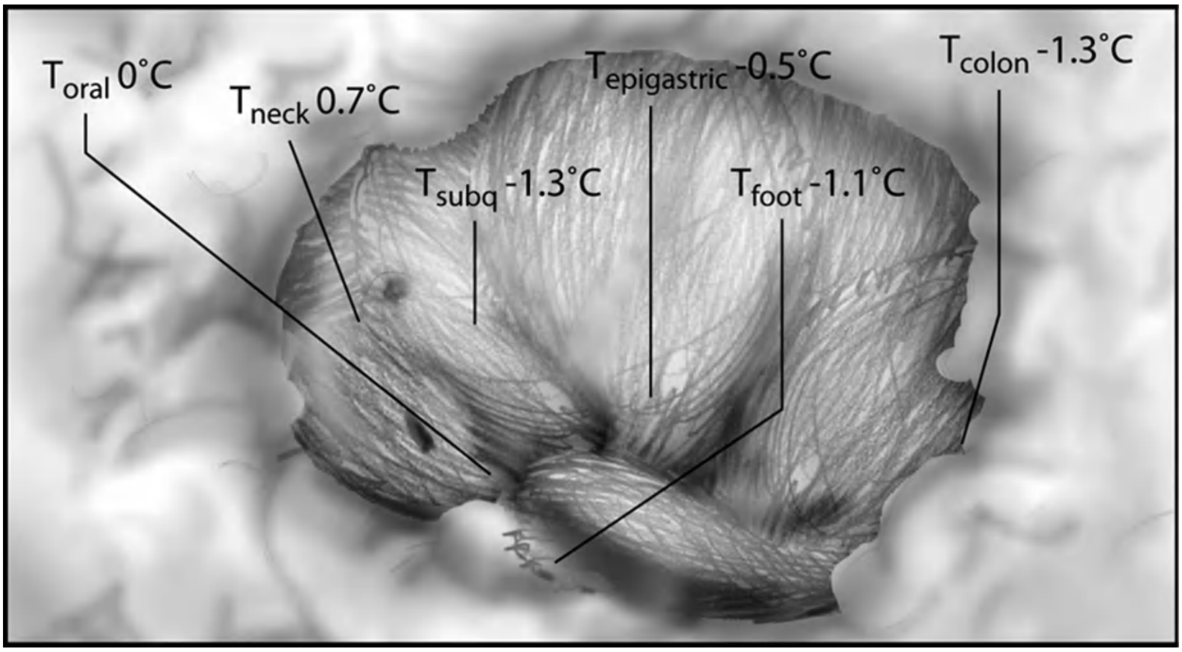


Figure 13.21. Regional body temperatures of a single hibernating arctic ground squirrel housed at an ambient temperature of –4.3°C (24°F). Additional data gathered of average temperatures (± standard error) and depth of temperature probe for 6 to 11 animals also at –4.3°C (21°F) were as follows: colon: 0.62°C ± 0.11°C (33°F ± 0.2°F), 6 cm (2.3 in.); foot: –0.65°C ± 0.15°C (30.8°F ± 0.3°F), 3 mm (0.1 in.); abdominal: –0.59°C ± 0.13°C (30.9°F ± 0.2°F), 2 cm (0.8 in.); thoracic: 0.49°C ± 0.12°C (32.9°F ± 0.2°F), 1 cm (0.4 in.); oral: –0.16°C ± 0.16°C (31.7°F ± 0.3°F).

Estivation

Dormancy during periods of great environmental stress, like extreme heat, drought, or lack of food, is known as **estivation** (Lat. *aestas*, summer). In many forms, it merely consists of long periods of little or no activity, with no decrease in the metabolic rate below the normal resting rate. In others, it is similar to hibernation in that most of the metabolic activities slow down, but because ambient temperature is not low, the metabolic rate is not as reduced as it is during the winter. Estivation is thought to be triggered by either a reduction in the food supply or by the reduced water content in the food.

South American (*Lepidosiren*) and African (*Protopterus*) lungfishes live in areas subject to flooding and extensive droughts. Both genera can estivate by digging vertical burrows into the mud that end in enlarged chambers. Burrows extend less than 1 m (3.28 ft.) beneath the surface. Heavy mucous secretions cover the lungfish’s body, encasing it in a cocoon. Atmospheric air is breathed through a small vent that extends upward through the hardened, sunbaked mud of the dried-up lake or river. Metabolism continues at a very low rate, using muscle proteins as an energy source. Most lungfishes spend less than six months in estivation, but some have been revived after four years of enforced estivation. When the rains return and begin filling the sites with water, lungfishes break free from their entombment and resume swimming. Until the next drought, they will inspire air into their lungs and eliminate most of the carbon dioxide through their vestigial gills (Moyle and Cech, 2004).

Some salamanders, frogs, and toads estivate, with some Australian desert frogs remaining in estivation for several years. Box turtles submerge most of their body in a stream and become torpid for periods of up to several days at a time. Several species of snakes have been found estivating. A number of mammals including jerboas (Dipodidae) and pocket mice (*Perognathus*) are known to estivate during the summer months. These mammals usually seek out an underground burrow where the ambient temperature is considerably cooler than it is on the surface.

Review Questions and Topics

1. Discuss the characteristics of eusociality in a naked mole rat colony.
2. What are pheromones? What is their significance?
3. Why do male frogs call from their breeding ponds?
4. Why does each species of male frog and toad have a distinctive, species-specific call?
5. Define infrasound. How is it used by some vertebrates?
6. List several reasons that cannibalism may occur.
7. Develop a hypothesis for this observation: male lions kill the offspring of females they acquire. They do so after they chase away the males that had been the mates of these females.
8. Distinguish between hibernation and estivation.
9. Differentiate between semidormant and true hibernation. Give several examples of each.
10. List several methods used by fish to prevent freezing solid at temperatures below the freezing point of water.
11. Many mammals hibernate either in a characteristic *C*-shape position or in clusters. What are some adaptive advantages of these behaviors?

Supplemental Reading

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Vertebrate Internet Sites

1. The Animal Files: Flehmen Response

www.theanimalfiles.com/glossary/flehmen_response.html

Definition, photo, and links.

2. Difference between Hibernation and Aestivation (Estivation)

https://biodifferences.com/difference-between-hibernation-and-aestivation-estivation.html

Discusses hibernation and estivation. Utilizes specific vertebrate examples.

3. Desert Animal Survival

www.desertusa.com/survive.html

Excellent site concerning vertebrate adaptations to desert survival, including estivation.

14 | Interspecific Interactions

Each species is a masterpiece, a creation with extreme care and genius.

Edward O. Wilson, 2013

INTRODUCTION

Because organisms depend on each other for food and other biotic factors, they inevitably interact with each other. Although the most intense relationships exist between members of the same species, individuals do not live apart from members of other species. Living in close association, different species may compete for a shared resource like food, space, or moisture. These interactions can be classified into several categories: **competition**, **symbiosis** (commensalism, mutualism, parasitism), **predation**, and **human interactions**. In competition, both species are affected adversely; in commensalism, one species benefits and the other is unaffected; in mutualism, species benefit each other; in parasitism and predation, one species benefits and the other is harmed. Human interactions may benefit both species, only one species, or possibly, neither species.

COMPETITION

The concept of interspecific competition is one of the cornerstones of evolutionary ecology. Charles Darwin based his idea of natural selection on competition, the struggle to survive.

Whenever different species occupy the same place at the same time, there will likely be competition for common resources, like food, water, or space, that are in limited supply. Such interspecific competition consumes both time and energy. Stress caused by such competition may decrease growth and birth rates and/or increase the death rate; if intense, competition can slow or even halt population growth and cause the population to decline. If ecological requirements of two species are similar but not identical, selection pressure will tend to cause the species to diverge from each other through morphological, physiological, and/or behavioral specializations. However, if two species have identical ecological requirements, they will not be able to coexist because of competition for limited resources. Competition is difficult to study and demonstrate in nature because it is such an ephemeral phenomenon.

The fundamental role of an organism in the community is its **niche** (Elton, 1927). The niche is the occupational status of the species in the community—what it does and its relation to its food, its competitors, and its enemies. It is an abstract concept that has not yet been defined and fully measured. A niche should not be confused with a habitat, the physical place where an organism lives. The niche is partially defined by characteristics of the habitat, but also by what the organism eats; how, when, and where it finds and captures its food; the time of the year and time of the day when it is most active; the optimal and extreme climatic factors (heat and cold, sun and shade, wet and dry) it can withstand; its parasites and predators; where, how, and when it reproduces; and so forth. Every aspect of an organism’s existence helps define that organism’s niche. Interspecific competition may play an important role in shaping a species’ niche.

Niches of different species may overlap either temporally or spatially. Niche overlap may promote interspecific competition, but the special adaptations that each species has for its own specific niche should protect it from extinction. For example, downy woodpeckers (*Picoides pubescens*) and hairy woodpeckers (*P. villosus*) are found in similar habitats from Newfoundland to the Gulf of Mexico. Although they often feed on the same tree at the same time, downies feed among the upper and smaller branches, while hairies locate their food on the trunk and larger branches. Niche overlap may occur on the medium-sized branches, but competition is minimized because the *primary* foraging microhabitat is slightly different.

If there is complete niche overlap between two or more species, intense competition for the niche will occur, and one species will outcompete the others. The unsuccessful species will either be excluded from the habitat or forced to shift its niche—usually to a suboptimal habitat. This concept is often known as **Gause's Rule** after the Russian biologist G. F. Gause, who published a study in 1934 showing that when cultured together, one species of *Paramecium* drove a second, competing species to extinction. Hardin (1960) proposed the name **competitive exclusion principle** for this phenomenon. Although competitive exclusion has been demonstrated clearly in the laboratory, it probably is rare in nature because different species seldom compete for precisely the same niche in the same habitat (Mares, 1993).

Fishes may adapt to different foods and to water of different depths, temperatures, salinities, and oxygen contents. Terrestrial species use elevational, macrohabitat, and microhabitat differences as well as food-size partitioning. Studies of plethodontid salamanders in the Appalachian Mountains, for example, have revealed habitat partitioning based on elevation and moisture gradients (Hairston, 1949, 1980, 1983; Dumas, 1956; Jaeger, 1971). Daily (diel) and seasonal activity cycles, differences in microhabitats (terrestrial, arboreal), and characteristics of the environment like temperature or moisture are used by anurans to partition the environment. Within a breeding pond, the difference in time of breeding, egg development, and larval development of different species avoids direct competition with other species. Natural selection favors those individuals that breed at such a time as to avoid competition. Adaptive modifications of salamander larvae and tadpoles, including distinct interspecific differences in mouth structure and whether they inhabit still or flowing water, permit them to gather food in different macrohabitats and microhabitats (see Fig. 5.20).

Anoles of the Greater Antilles (Cuba, Hispaniola, Jamaica, and Puerto Rico) illustrate a classic case of adaptive radiation (Losos and de Queiroz, 1998). Each of six species is adapted to its own ecological niche, in particular, to the substrate on which it lives and moves. Anoles that live in the grass have slender bodies and very long tails, whereas a closely related species that must maintain its balance on narrow twigs has evolved a short body and stubby legs. A shorter-limbed species with large toe pads inhabits the upper trunk and canopy of trees, whereas a large species with large toe pads lives high in the crowns of trees. Some prefer shade; others seek out sunny basking sites. Although some overlap occurs, each species consumes differing food items.

Garter snakes and ribbon snakes (both members of the genus *Thamnophis*) often inhabit the same general area (sympatric). Competition between them, however, is reduced by differences in food requirements. Garter snakes feed extensively on earthworms; ribbon snakes usually shun earthworms, but are fond of salamanders, frogs, and small fish.

Interspecific competition is evident among introduced starlings (*Sturnus vulgaris*) and house sparrows (*Passer domesticus*) and native species in North America. Both European species compete with native American hole-nesters like eastern bluebirds (*Sialia sialis*) and purple martins (*Progne subis*) for suitable nest sites. Due to their aggressiveness, both introduced species often usurp or evict the native species from their nest sites.

MacArthur's (1958) study of five species of warblers revealed they all fed on the same species of caterpillar prey, but they partitioned spruce trees into preferred foraging regions (Fig. 14.1). Although some overlap occurred, competition was minimal, and all five species were able to coexist during the breeding season.

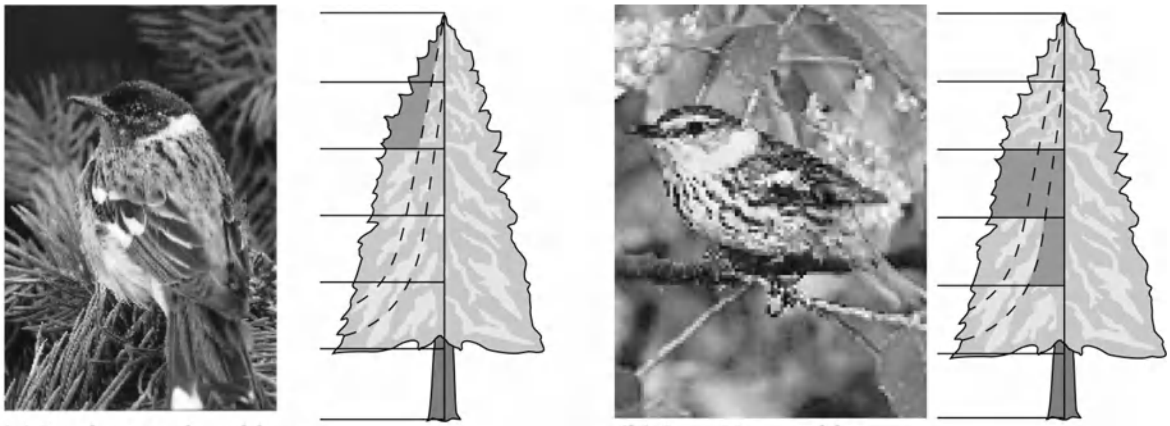
Among mammals, interspecific competition occurs in some areas between black bears (*Ursus americanus*) and grizzly bears (*Ursus arctos*), between red squirrels (*Tamiasciurus*) and gray squirrels (*Sciurus*), and between southern flying squirrels (*Glaucomys volans*) and northern flying squirrels (*G. sabrinus*) (Weigl, 1978; Flyger and Gates, 1983). This competition may be a function of territorial behavior (Layne, 1954; Ackerman and Weigl, 1970; Flyger and Gates, 1983). In the southern Appalachians, four closely related species of mice (*Peromyscus leucopus*, *P. maniculatus*, *P. gossypinus*, and *Ochrotomys nuttalli*) inhabited a 6 hectare (14.8 acres) study area (Linzey, 1968). The mice partitioned the habitat by means of spatial orientation (terrestrial versus arboreal) and by food preference.

Both native and domestic mammals may be affected by indirect competition, a more subtle type of interspecific interaction. Small mammals, like mice, rabbits, prairie dogs, ground squirrels, gophers, and others, affect the growth of forage plants without competing directly with livestock or game animals for some of the aerial parts of plants. These small mammals consume the roots and early growth of grasses and forbs, and their presence can result in lower forage yields above ground. Long-term investigations of the interactions among rodents, birds, and plants in the Chihuahuan desert of southeastern Arizona have shown a persistent and steady competition among species despite the importance of climatic effects on the numbers of individuals (Brown et al., 1986). Brown et al. (1986) stated: “Our experiments suggest a view of community organization in which virtually all species affect each other through a complex web of direct and indirect interactions. These relationships are highly asymmetrical, nonlinear, and influenced importantly by the physical environment as well as by other species.”

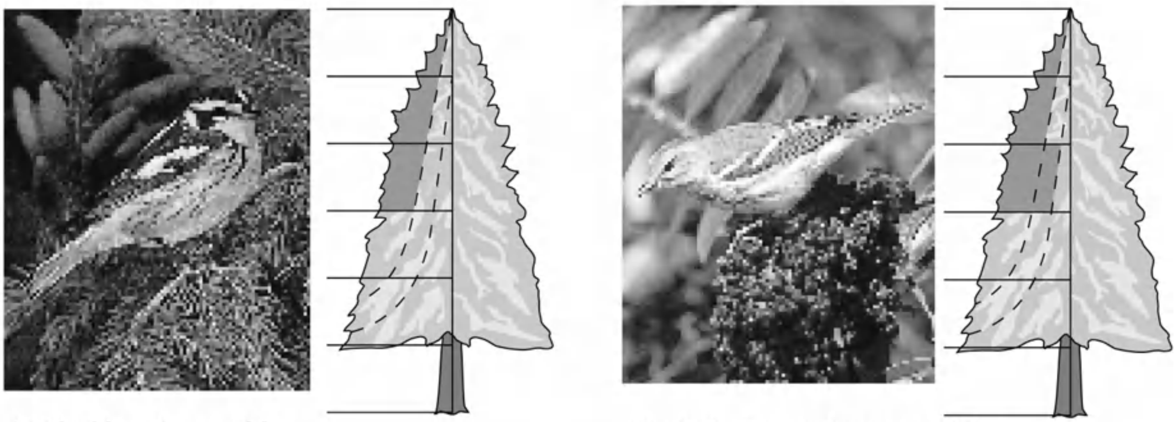
A Competitive Interaction

An interesting example of competitive interaction was reported between bluebirds (*Sialia*) and chickadees (*Parus*). A pair of chickadees began building a nest of green moss in a bluebird house. The next day, the bluebirds entered the house and carried some of the moss away. These actions were repeated. Then the chickadees deposited a single egg on the nearly bare floor. The male bluebird went inside the box and came out with the egg in his beak. He flew to a large tree limb, where the egg balanced momentarily, before falling to the ground below. This action was repeated a second time, after which the chickadees left and did not return.

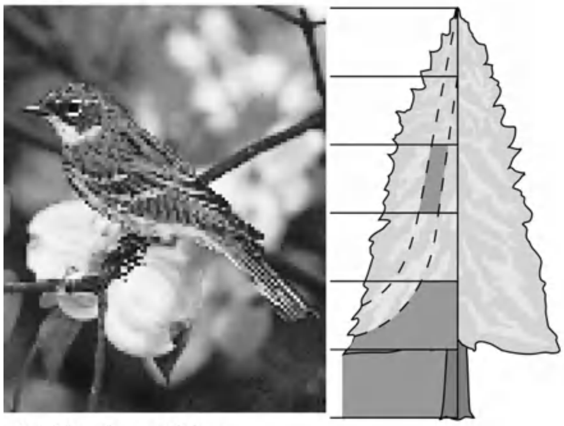
Reed, 1989



(a) Bay-breasted warbler **(b) Cape May warbler**



(c) Blackburnian warbler **(d) Black-throated green warbler**



(e) Myrtle warbler

Figure 14.1. Coexistence of competing species. Robert MacArthur found that five species of warblers were able to coexist by partitioning spruce trees into preferred foraging regions: (*a*) bay-breasted warbler (*Dendroica castanea*), (*b*) Cape May warbler (*D. tigrina*), (*c*) Blackburnian warbler (*D. fusca*), (*d*) black-throated green warbler (*D. virens*), (*e*) myrtle warbler (*D. coronata*).

SYMBIOSIS

Symbiosis (Gr. *sym*, together, + *bios*, life) is the term applied to an intimate relationship between members of different species. Such interactions may be beneficial to one or more members (commensalism, mutualism); other interactions may be detrimental (parasitism). Participants in symbiotic associations often have coevolved with one another and continue to do so.

Commensalism

A **commensal** relationship exists when one member of the association benefits while the other is neither helped nor harmed. Some fishes, like jackfish (*Caranx*) and pilot fish (*Naucrates*), seek protection in the vicinity of larger fishes like barracudas, sharks, and rays (Moyle and Cech, 2004). In most cases, the larger fishes derive no advantage from their companions. A commensal relationship exists between gopher tortoises and many amphibians, reptiles, and mammals that inhabit their burrows (Lips, 1991) (Table 14.1) (Fig. 14.2). Woodchuck (*Marmota monax*) burrows also are used by a wide variety of vertebrates and invertebrates (Fig. 14.3). Woodchucks and red foxes have been known to coexist in the same burrow system (Linzey, 1998). Turtles often deposit their eggs in alligator nests. The eggs presumably benefit from the alligator's defense of the nest from predators. Aquatic turtles may hibernate inside a beaver lodge. Small birds sometimes construct their nests among the branches and twigs of an eagle's nest.

A unique commensal relationship exists between a bird and a lizard in New Zealand (Carr, 1970). Sooty shearwaters (*Puffinus griseus*) often share their burrows with tuataras (*Sphenodon*) (Fig. 14.4). The diurnal shearwaters occupy their burrows at night while the nocturnal tuatara is out foraging. The tuatara occupies the burrow during the day while the shearwater is fishing. When the bird migrates, the tuatara hibernates in the burrow.

Table 14.1. Summary of Captures of Amphibians, Reptiles, and Mammals in Gopher Tortoise Burrows in Four Habitats in South-Central Florida

	Habitats				
Species	Turkey Oak	Sand Pine Scrub	Scrubby Flatwoods (burned)	Scrubby Flatwoods (unburned)	Total
Amphibians					
Southern toad (*Bufo* [*Anaxyrus*] *terrestris*)	0	1	0	0	1
Greenhouse frog (*Eleutherodactylus planirostris*)	101	70	12	27	210
Narrow-mouthed toad (*Gastrophryne carolinensis*)	0	1	1	0	2
Gopher frog (*Rana areolata* [*Lithobates capito*])	9	5	1	0	15
Subtotal	*110*	*77*	*14*	*27*	*228*
Reptiles					
Green anole (*Anolis carolinensis*)	1	0	6	1	8
Six-lined racerunner (*Cnemidophorus sexlineatus*)	1	5	4	0	10
Black racer (*Coluber constrictor*)	3	2	2	1	8
Eastern indigo snake (*Drymarchon* [*couperi*] *corais*)	0	2	0	0	2
Southeastern five-lined skink (*Eumeces inexpectatus*)	18	3	0	3	24
Eastern coachwhip snake (*Masticophis flagellum*)	1	1	2	0	4
Eastern coral snake (*Micrurus fulvius*)	0	0	1	0	1
Pine snake (*Pituophis melanoleucus*)	0	0	1	0	1
Fence lizard (*Sceloporus woodi*)	3	6	8	5	22
Subtotal	*27*	*19*	*24*	*10*	*80*
Mammals					
Florida mouse (*Podomys floridanus*)	1	1	7	0	9
Cotton rat (*Sigmodon hispidus*)	1	0	0	0	1
Spotted skunk (*Spilogale putorius*)	0	0	1	0	1
Subtotal	*2*	*1*	*8*	*0*	*11*
Total	**139**	**97**	**46**	**37**	**319**

Source: From Lips, 1991. Copyright © Society for the Study of Amphibians and Reptiles, Oxford, Ohio. Used by permission.

Various birds and mammals are known to heed the warnings of other species. The ability to recognize and respond to the alarm calls of heterospecifics, however, has previously been described only in species with vocal communication. Marine iguanas in the Galápagos Islands, which are nonvocal, have been found to respond to the alarm calls of Galápagos mockingbirds when they spot a Galápagos hawk (Vitousek et al., 2007). Researchers suggest that alarm calls may share acoustical features that provoke reactions across species. Either the iguanas instinctively know what the bird calls mean, or they can learn over time that the calls announce the imminent arrival of a predator.

An unusual commensal relationship exists between fossorial blind snakes (*Leptotyphlops dulcis*) and screech owls (*Otus asio*). The snakes feed on insect larvae in the owl nests, thus potentially reducing larval parasitism on nestling owls (Gehlbach and Baldridge, 1987). Nestling owls in such nests had a higher survival rate, grew 19 percent faster, and fledged earlier than those in nests without snakes (Table 14.2). Owls transport live snakes to their nests and gain a benefit. There is no evidence, however, that the snakes gain any benefit by being in the nests rather than in the soil.

Squirrel monkeys (*Saimiri sciureus*) find it advantageous to associate with capuchin monkeys (*Cebus*) because the latter provide a better predator warning system than squirrel monkeys possess (Terborgh, 1985). The reciprocal benefit for the capuchins is minimal or nonexistent. Rats (*Rattus rattus* and *R. norvegicus*) and house mice (*Mus musculus*) have benefited by using structures built by humans and reach their highest densities in agricultural and urban areas. Large grazing animals like zebras, cattle, buffalo, and horses stir up insects as they feed. Birds, like cattle egrets (*Bubulcus ibis*) (see Fig. 12.9) and cowbirds (*Molothrus ater*), live among these mammals and feed on the grasshoppers, leaf hoppers, and other insects disturbed by the grazing animals.

Mutualism

In the type of symbiotic relationship known as **mutualism**, both partners benefit from the association. Clownfishes live among anemones. They are not affected by the anemone's sting, which serves to provide them a protected habitat. In turn, the clownfishes defend their homesite from other species that feed on anemones and also provide anemones with scraps of food. Many other species of fishes allow themselves to be cleaned by cleaner fishes (Fig. 14.5). Some even change color, a procedure that indicates a safe time to be cleaned and also makes parasites more easily visible against a contrasting background. Some pilot fish clean the mouths of manta rays. Reef fishes have been recorded cleaning algae or ectoparasites from sea turtles, and blacknose dace (*Rhinichthys atratulus*) have been observed apparently cleaning wood turtles (*Clemmys insculpta*) (Kaufmann, 1991). Kühlmann (1966) observed a toothed carp (*Gambusia*) cleaning the mouth of a crocodile (*Crocodylus acutus*). Cleaning symbioses were reviewed and discussed by Feder (1966).

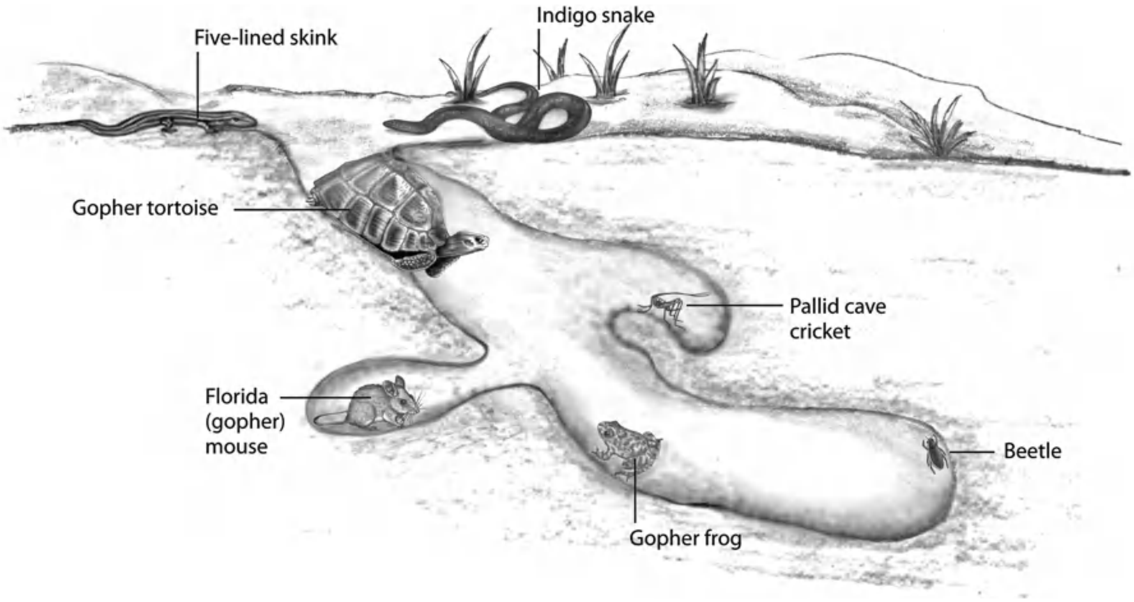


Figure 14.2. The long, cool burrow of the gopher tortoise (*Gopherus polyphemus*) in Florida provides refuge for a variety of vertebrate and invertebrate species. The tortoise derives neither benefit nor harm from these commensal relationships. Slender beetles feed on tortoise dung; cave crickets eat beetle dung as well as fungus. Gopher frogs (*Rana capito*) eat insects that wander or fall into the burrow. The nocturnal gopher mouse (*Podomys floridanus*) may excavate a side burrow in which it constructs its nest. Even the sandy dump pile may provide refuge for a five-lined skink (*Eumeces inexpectatus*). Sometimes, the gopher tortoise defends its burrow against a predatory snake by blocking the entrance with its shell.

Figure 14.3. Woodchuck burrows are used by many other vertebrates and invertebrates.

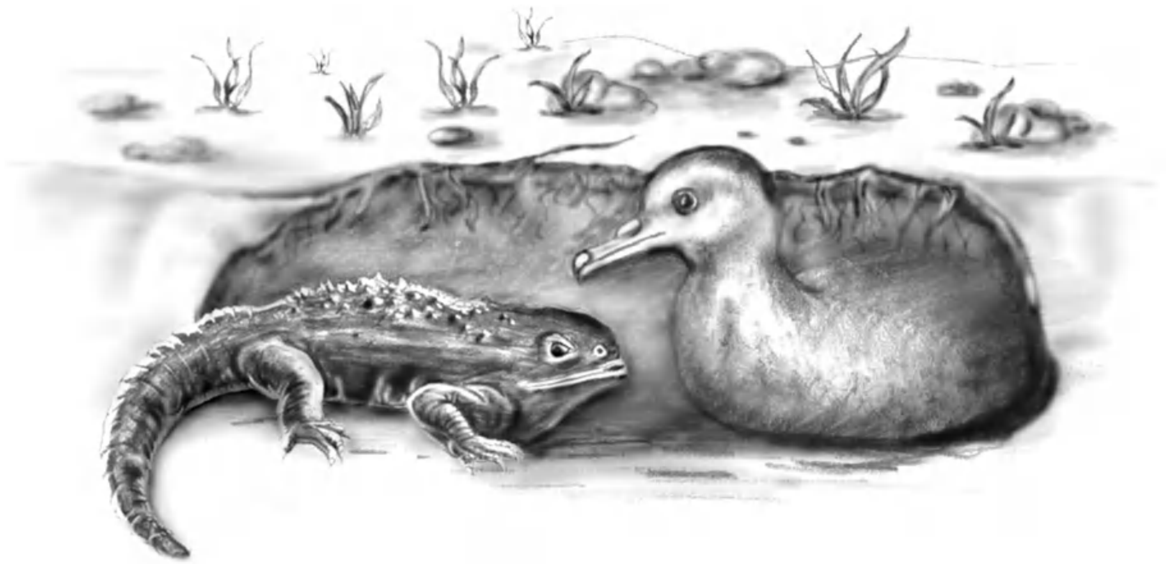
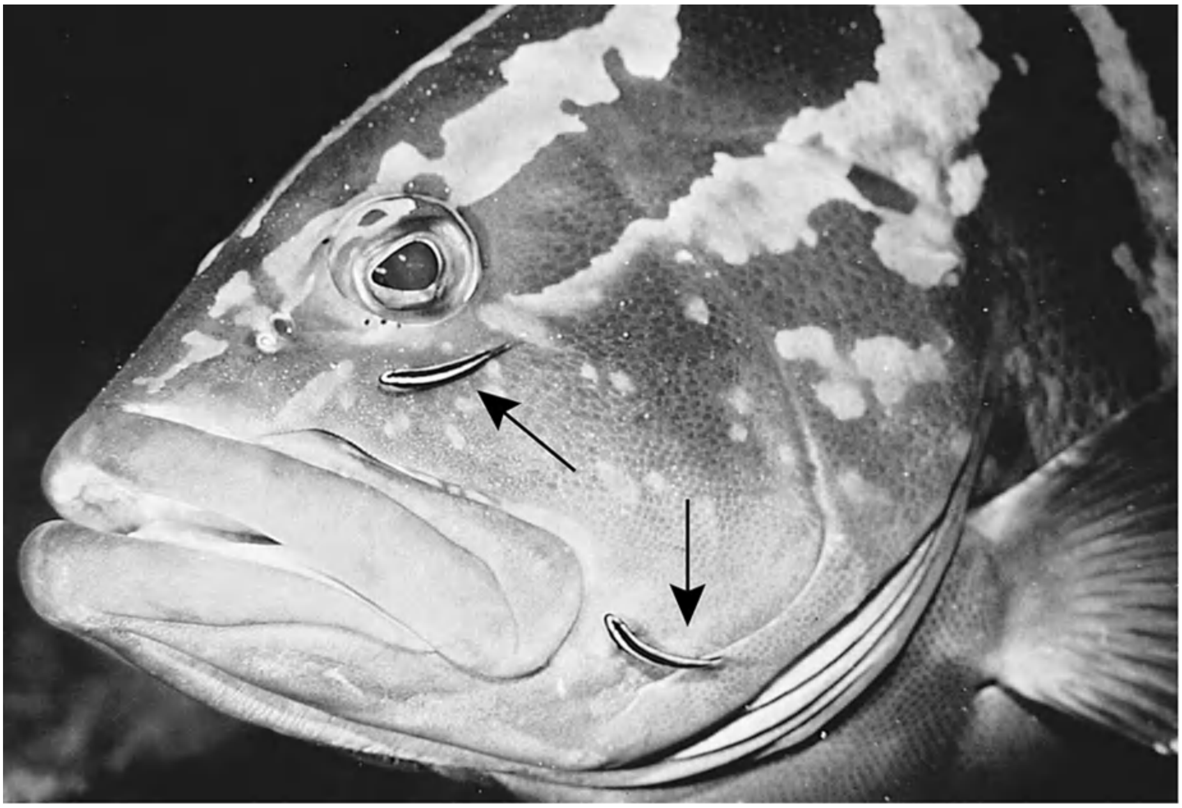


Figure 14.4. Sooty shearwaters (*Puffinus griseus*) often share their burrows with tuataras (*Sphenodon*). This unique commensal relationship allows the diurnal shearwaters to occupy their burrows at night while the nocturnal tuatara is out foraging. The tuatara occupies the burrow during the day while the shearwater is fishing. When the bird migrates, the tuatara hibernates in the burrow.

The small ground finch (*Geospiza fuliginosa*) of the Galápagos Islands searches for ticks on marine iguanas. Oxpeckers (*Buphagus africanus*) remove ticks, botfly larvae, and other parasites from zebras, rhinoceroses, and other large mammals (Fig. 14.6).

Table 14.2. Nestling Growth Dynamics in Eastern Screech Owl Nests with One, Undisturbed (by Us), Live Blind Snake at Fledging Time versus Same-Season Nests without Blind Snakes but Same-Size Broods



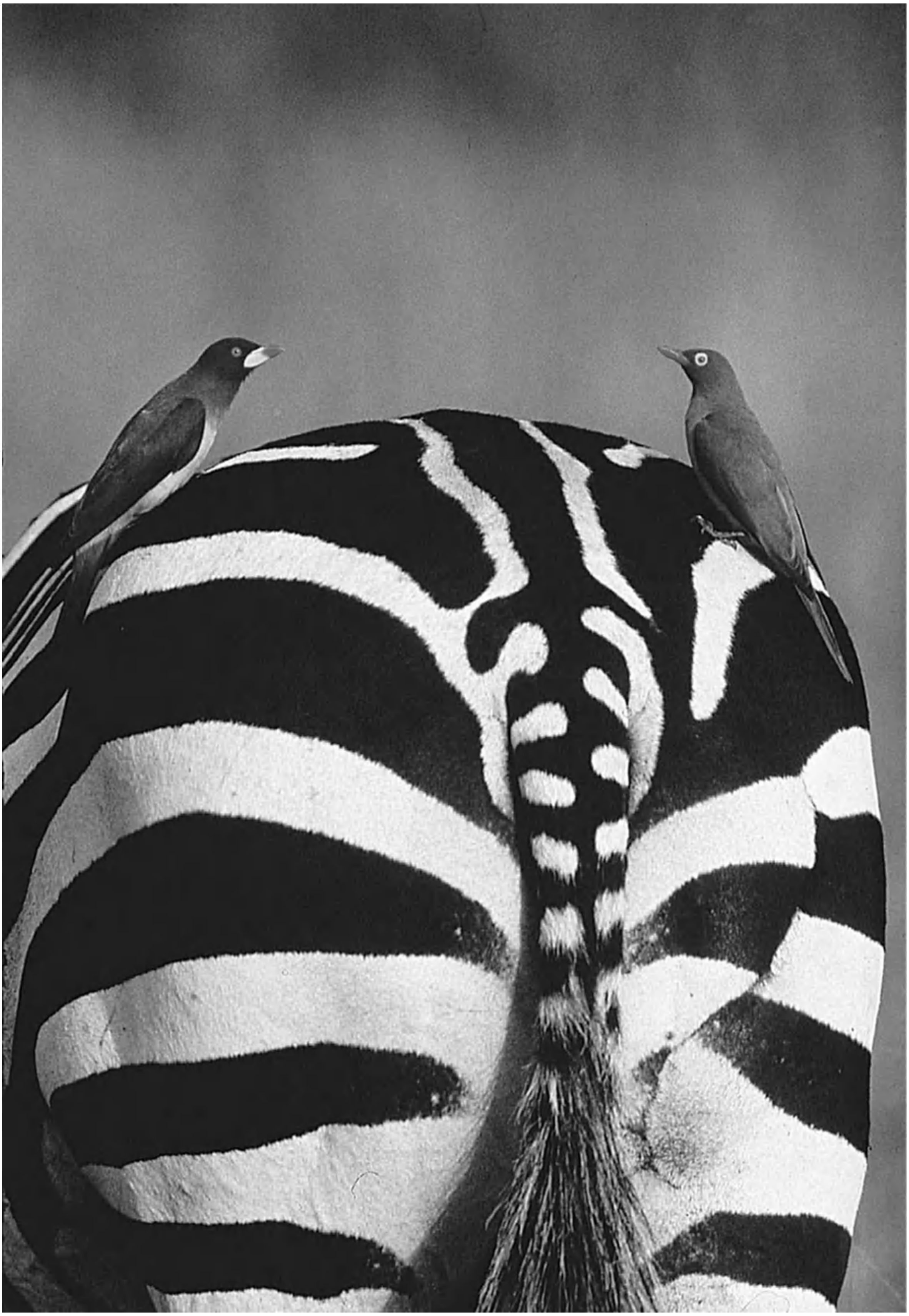
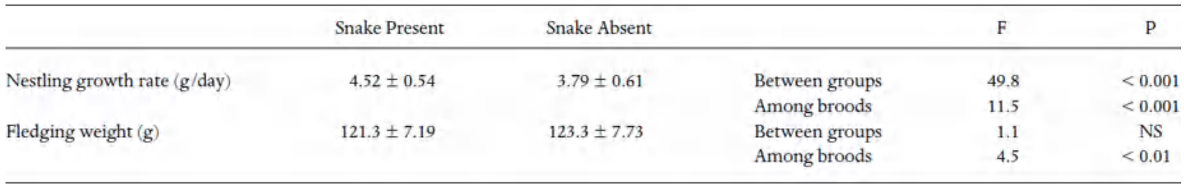


Figure 14.5. This Nassau grouper (*Epinephelus striatus*) is being cleaned by two gobies (*see black arrows*). Cleaning symbiosis is a common mutualistic relationship between marine animals.

Twenty species of trees in Madagascar’s dry forests depend largely on lemurs, especially the brown lemur, to eat their fruit and disperse their seeds. Researchers compared sapling numbers at plots in extended forests with plots in forest fragments where much of the largest wildlife had disappeared. In the fragments without the brown lemur, significantly fewer saplings of the 20 tree species dependent on lemurs were sprouting than in the larger areas. Saplings from trees dispersed by other animals thrived in both locations (Ganzhorn et al., 1999).

The ravaging of Guam’s bird life by the brown tree snake (see Chapter 11, Invasion of the Brown Tree Snakes, page **364**) has had a serious effect on the surrounding tree population since birds are primary seed dispersers. With more than two-thirds of Guam’s trees relying on animals to distribute and germinate their seeds, the impact of the reduction is expected to be a devastating drop of between 61 and 92 percent in seedling recruitment.

In the mountains of Borneo, the pitcher plant *Nepenthes lowii* has traps shaped like broad toilet bowls (Fig. 14.7). Tree shrews (*Tupaia montana*) defecate in them, and the plant assimilates the feces’ nitrogen. The adult plants dangle reinforced, nonslippery pitchers from their leafy vines. The lids exude a sweet secretion highly attractive to tree shrews. While licking the sweet secretion, the tree shrews often defecate into the trap. Using isotopic analysis, researchers confirmed that between 57 and 100 percent of the plant’s nitrogen originated from tree-shrew feces. The pitcher plant only grows where tree shrews live (Clarke et al., 2009).



	Snake Present	Snake Absent		F	P
Nestling growth rate (g/day)	4.52 ± 0.54	3.79 ± 0.61	Between groups	49.8	< 0.001
			Among broods	11.5	< 0.001
Fledging weight (g)	121.3 ± 7.19	123.3 ± 7.73	Between groups	1.1	NS
			Among broods	4.5	< 0.01

Figure 14.6. Yellow-billed and red-billed oxpeckers (*Buphagus* sp.) perch on the rump of a plains zebra (*Equus* sp.) in Masai Mara National Reserve. The birds help zebras by plucking off ticks and other pests.

Source: From Gehlbach and Baldridge, 1987. Copyright © Springer-Verlag, New York. Reprinted with permission.

Note: Mean + SD and F values are from two-way ANOVAs, N = 6 each group, N = 10 per group in a comparison without brood-size equality; however, mean number of nestlings is no different (3.3 ± 0.7 versus 2.8 ± 1.0, F = 1.6, NS) and results are the same; F = 54.8, 7.2 ($p < 0.001$) for growth rate and F = 0.8 (NS), 2.5 ($p < 0.02$) for fledging weight, between groups versus among broods, respectively.

The intestines of most vertebrates, including humans, provide a suitable environment for beneficial bacteria that aid in food digestion and synthesize certain vitamins. Herbivores, like cattle, sheep, and deer, depend on bacteria and protozoans to help them digest the tough cellulose cell walls of the plant material on which they feed.

Figure 14.7. The pitcher plant *Nepenthes lowii* and the tree shrew (*Tupaia montana*) in Borneo—a unique example of mutualism where both partners benefit from the association.

Dickman (1992) noted: "Commensal and mutualistic associations among terrestrial vertebrates are clearly dynamic, and form and dissolve under different conditions of predator risk, resource levels, competition, and many other factors. An important assumption is that these associations are favoured only when the benefits to individuals exceed the costs."

Parasitism

Parasitism is a vital interspecific interaction in which one member—the **parasite**—benefits while the other member—the **host**—is harmed in some way. Lampreys parasitize fish by sucking out their blood and body fluids (see Fig. 3.13). Cowbirds of the New World and cuckoos of the Old World are social parasites (Milius, 1998a) (Fig. 14.8). They both lay their eggs in nests of other bird species, often removing one egg from the host's nest prior to laying their own. Female cuckoos usually lay an average of eight eggs a year. Eggs are laid on alternate days and usually in two batches, separated by several days' rest (Davies and Brooke, 1991). Their deception involves surveillance, stealth, surprise, and speed. In less than 10 seconds, the female cuckoo alights on a nest, lays her own egg, removes one host egg, and is gone. The eggs often mimic the appearance of the host's eggs (Fig. 14.9). Cuckoo eggs have been found in nests of at least 125 bird species in Europe (Wyllie, 1981).

Figure 14.8. The brown-headed cowbird (*Molothrus ater*) is a social parasite.

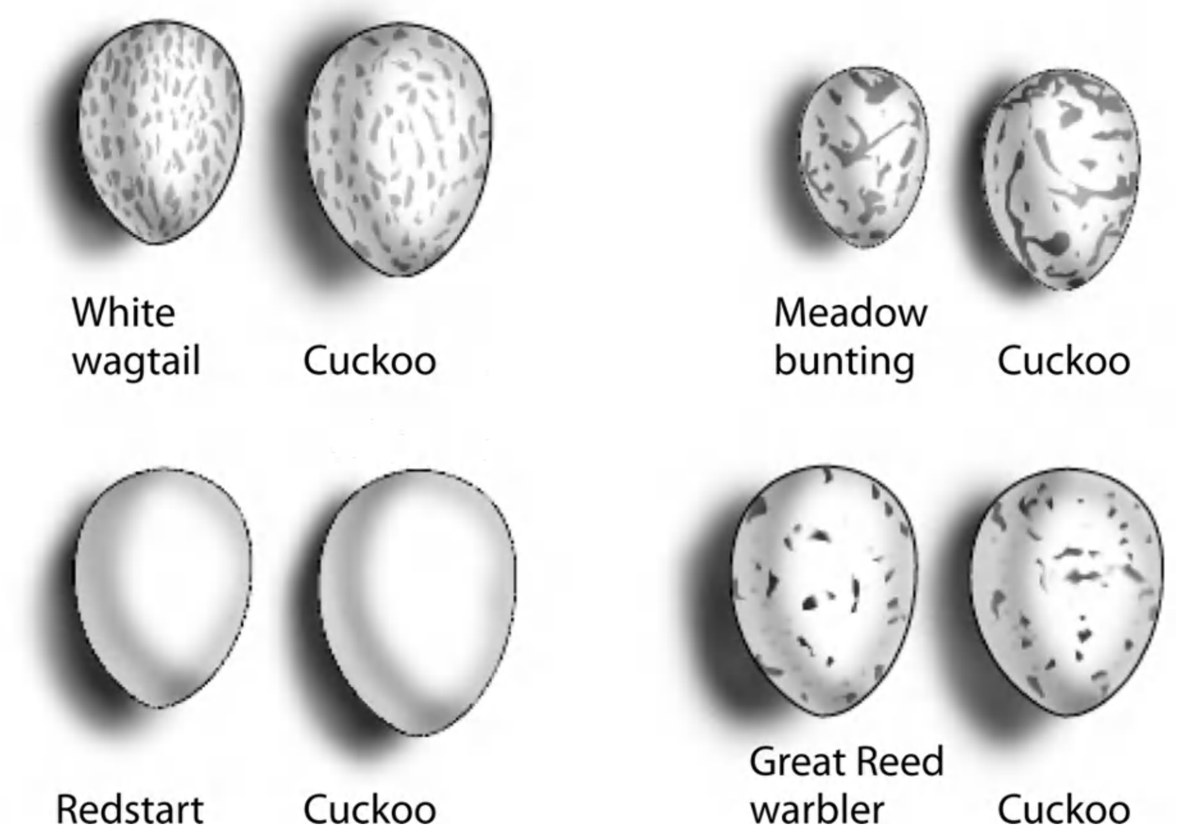


Figure 14.9. Cuckoo eggs often mimic the appearance of the host's eggs.

Many researchers have thought that cuckoos imprint on their foster parents and, when adult, choose to parasitize the same host species. However, studies in which newly hatched cuckoos were transferred into nests of other species failed to demonstrate host imprinting (Brooke and Davies, 1991).

Besides having a shorter incubation period than their host species, cowbirds (*Molothrus ater*) hatch before many hosts by disrupting incubation of smaller eggs and, possibly, hatching in response to stimuli from host eggs (McMaster and Sealy, 1998). In addition, young cowbirds and cuckoos are usually larger than the natural young in the parasitized nest, and they either take the lion's share of the food or eject the host young from the nest (see Fig. 8.43). Friedmann and Kiff (1985) recorded 220 species as having been parasitized by brown-headed cowbirds, with 144 species actually rearing young cowbirds. This difference in the number of species parasitized versus those actually rearing cowbirds is due to host recognition and counter-strategies: deserting the nest, rejecting the cowbird egg, or depressing the egg into the bottom of the nest. A 2017 study (Lynch et al., 2017) demonstrated that cowbird brains are wired to respond to the vocalizations of other cowbirds, allowing young cowbirds to find and join flocks of their own species once they leave the nest.

In Virginia, 39 percent of dark-eyed junco (*Junco hyemalis*) nests contained at least one cowbird egg (Wolf, 1987). Cowbirds laid an average of 1.7 eggs per nest and removed an average of 1.2 junco eggs per nest. Smaller species like cedar waxwings (*Bombycilla cedrorum*), Baltimore orioles (*Icterus galbula*), and warbling vireos (*Vireo gilvus*) remove the cowbird egg by puncture-ejection (entire cowbird egg removed or pieces of shell removed after egg contents are consumed) (Sealy, 1996). Larger species generally remove cowbird eggs by grasp-ejection.

In the early 1980s, half of all nests of the least Bell's vireo (*Vireo bellii pusillus*) on the Camp Pendleton military base in southern California were parasitized by cowbirds, and the vireo population was near extinction (Holmes, 1993). When a cowbird-trapping program reduced parasitism to near zero, the vireo population increased tenfold. Cowbird populations are being controlled by trapping at Camp Pendleton as well as in the breeding grounds of several endangered songbirds, including the Kirtland's warbler (*Dendroica kirtlandii*) in northern Michigan and the black-capped vireo (*Vireo atricapillus*) in central Texas (Holmes, 1993).

American goldfinches (*Spinus tristis*) are regularly parasitized by cowbirds, but cowbirds do not survive the nestling period because the granivorous diet of the goldfinch provides inadequate protein (Middleton, 1991). It is rare among birds for the diet of nestlings to be composed mainly of seeds, because seeds are relatively low in protein.

Although most foster parents fail to recognize the foreign cuckoo chick in their nest, such is not always the case with Australia's superb fairy-wren (*Malurus cyaneus*). Researchers found that if a chick of Horsfield's bronze cuckoo (*Chrysococcyx basalis*) hatches in a superb fairy-wren nest and heaves out the rightful chicks, about 40 percent of mother fairy-wrens desert the nest. The cuckoo chick is left to starve while the mother starts another nest (Langmore et al., 2003, 2009). Fairy-wrens abandon 100 percent of nests containing a lone shining bronze cuckoo (*Chrysococcyx lucidus*) nestling. The cuckoos lay eggs that usually fool the fairy-wrens, so an ability to detect phony chicks may have evolved as a countermeasure.

The only known parasitic mammals are vampire bats, which feed on the fresh blood of sleeping or resting birds and mammals, including humans (Fig. 14.10). Their teeth are sharp, so that the incision is virtually painless and the victim is not awakened or disturbed as blood is “lapped up” rather than “sucked out.” The saliva may contain an anticoagulant, so that blood may continue to flow from the wound for several hours. The bitten animal may contract virally caused diseases like rabies, or secondary infections may develop at the site of the wound.

Male Asian elephants with longer tusks have been found to have fewer internal parasites (Bagla, 1997). Males carrying genes for resistance to parasites are healthier and in a better condition to develop secondary sexual characteristics. These better-fit males are then more likely to be chosen by females as mates. Since ivory hunters are likely to poach the best males because of their larger tusks, it is feared that poaching may weaken the elephant gene pool by removing the most fit males and their parasite-resistant genes from the population.

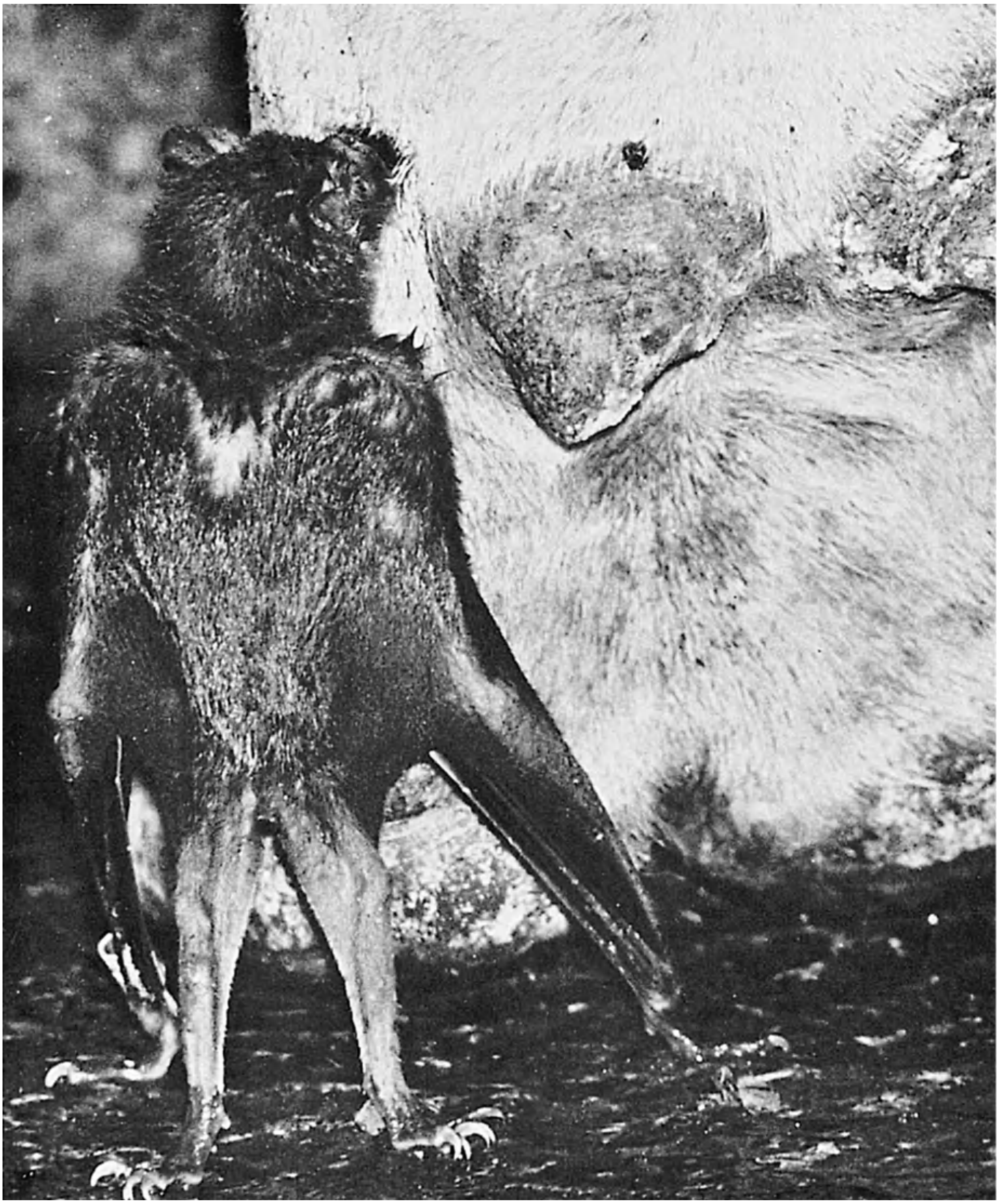


Figure 14.10. Vampire bat (*Desmodus rotundus*) feeding on the foot of a cow. Observations of vampire bats indicate that this stance and area of assault illustrate the most frequent method of attack.

Parasitism of reintroduced and captive endangered species by external (ticks, mites, lice, fleas) and internal (nematodes, trematodes, cestodes) parasites may be a critical danger to their well-being and reestablishment (Phillips and Scheck, 1991). Potential parasites need to be considered when designing and implementing restoration projects.

PREDATION

Predation is an interaction in which one species—the **predator—** benefits from killing and eating a second species—the **prey**. Predators and prey coevolve, with predators becoming specialized to capture their prey, and prey species becoming adapted to evade their predators.

Each vertebrate class has a large number of predaceous species. Sharks feed on other fishes and marine mammals. Largemouth bass (*Micropterus salmoides*) feed primarily on smaller fishes.

Amphibians and reptiles feed on a wide variety of invertebrates and vertebrates, with the choice of food being primarily determined by the size of the mouth opening—amphibians and reptiles are gape-limited predators. Amphibians feed primarily on invertebrates, although some larger forms like bullfrogs will eat almost any suitably sized animal that moves within striking range. Many aquatic turtles feed on invertebrates, as well as on small fish and amphibians. Snapping turtles are known to consume amphibians, snakes, small turtles, birds, and small mammals. Most marine turtles are omnivorous. Juvenile green turtles (*Chelonia mydas*), however, are more carnivorous than adults, which subsist mainly on plants. Most lizards feed on invertebrates, although some, like the Gila monster and the Komodo dragon, include mammals in their diet. Crocodilians prey on fishes, reptiles, and birds, as well as on mammals as large as antelopes. All snakes are predaceous, feeding on prey ranging from larger invertebrates, birds, and bird eggs (Fig. 14.11) to mammals.

Carnivores, in general, have a more difficult time obtaining food than herbivores. Once a carnivore captures its prey, however, the meal is far higher in nutrition because of its protein and fat content. Thus, meat eaters spend considerably less time eating than plant eaters (Fig. 14.12). In addition, the larger the herbivore, the more time it needs each day to obtain sufficient food.

Many birds and mammals are insectivorous; others feed on a wide variety of fishes, amphibians, reptiles, birds, and mammals. Hawks, eagles, ospreys, and owls feed on fishes, lizards, snakes, other birds, and mammals up to the size of skunks, monkeys, and sloths. Most predatory birds consume their smaller prey whole, later regurgitating the indigestible hair, bones, feathers, scales, or insect parts as pellets (Fig. 14.13). Predatory mammals include such groups as bears, raccoons, cats, wolves, foxes, and weasels. Black bears and raccoons, for example, are major predators on American alligator eggs and young (Hunt and Ogden, 1991).

Figure 14.11. A black rat snake (*Elaphe obsoleta*) homes in on a clutch of northern cardinal eggs. Snakes strongly prefer to forage along forest edges. Eggs and nestlings are normally only a minor part of the snake's diet.

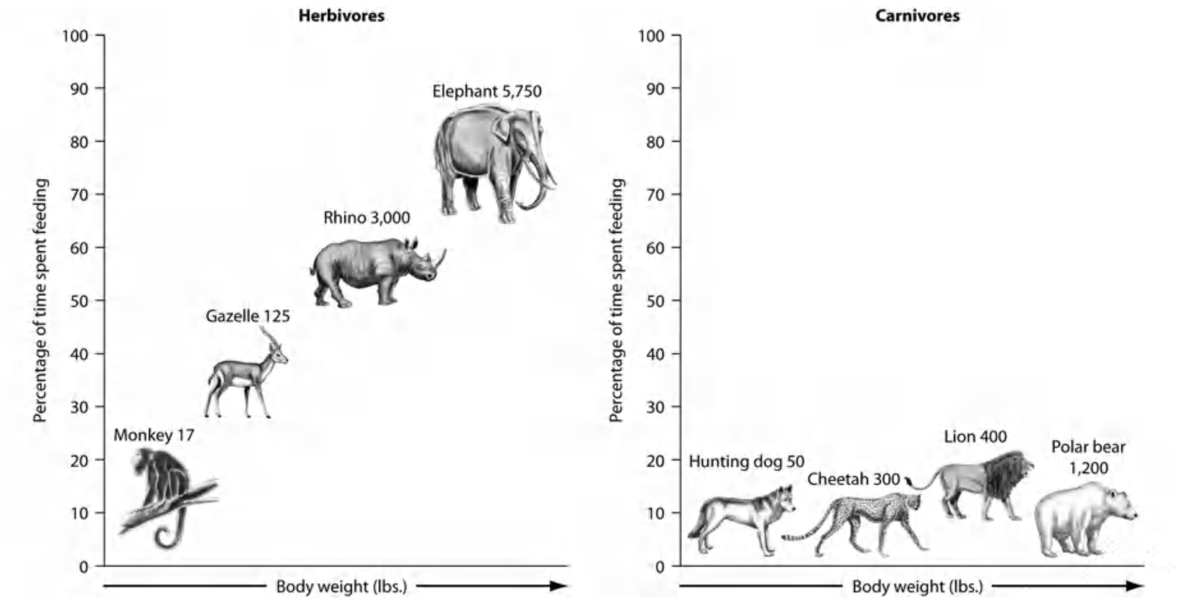


Figure 14.12. Although carnivores must work harder than herbivores to find a meal, a carnivore's meal is higher in nutrition than an herbivore's. Thus, carnivores spend much less of their time eating than herbivores. In addition, the larger the herbivore, the more time it needs each day simply to stay fed.

Figure 14.13. A life-size regurgitated pellet from a short-eared owl (*Asio flammeus*). The pellet contains the remains of a small rodent.

Predators in certain regions have preferred prey (cougar, deer; wolf, moose; fox, rabbit), but most are opportunistic and will kill a variety of prey. They frequently capture older, weaker, and/or debilitated animals, thus acting as selective agents promoting the genes of those prey animals able to evade capture.

Predators may differentially consume individuals based on age or sex within populations of prey species and thus may have subtle effects on prey-population dynamics. On an island off the coast of western

Australia, adult house mice (*Mus musculus*) foraged primarily in dense cover; juveniles, especially females, used areas of open vegetation more than adults and were potentially most at risk of predation (Fig. 14.14a) (Dickman et al., 1991). Barn owls (*Tyto alba*) took a greater number of young female house mice than any other size or sex class. Correlations between the hourly number of hunting owls and the overall hourly capture rates of mice were significant for juvenile females ($r = \pm 0.84$, $p < 0.001$), almost significant for juvenile males ($r = +0.57$, $p \sim 0.05$), and not significant for adults (males: $r = -0.10$; females: $r = +0.51$) (Fig. 14.14b). These data strongly support the hypothesis that juvenile mice, especially females, which use more open vegetation than adults face a higher risk of predation from hunting owls.

Some predators and their prey have developed complex interrelationships. For example, moose (*Alces alces*) colonized Isle Royale in Lake Superior, probably swimming from nearby Ontario in the early part of the twentieth century (Mech, 1966) (Fig. 14.15). With no effective predators and an abundant food supply, the population grew to very high levels by the late 1920s. Murie (1934) estimated 1,000 to 3,000 moose present in 1929 and 1930. Significant mortalities from malnutrition apparently reduced the population to several hundred animals by the mid-1930s (Hickie, 1936). The population again increased, until direct mortality from malnutrition was observed in the late 1940s. In 1947, a population of 600 moose was estimated by aerial strip count (Krefting, 1951). Mech (1966) estimated the 1960 population at 600 animals. The moose population apparently increased during the 1960s (1,300 to 1,600 from 1968 to 1970) and leveled off, or perhaps even declined, from 1970 to 1974. Mid-winter aerial censuses in 1972 and 1974 produced estimates of 818 ± SE 234 and 875 ± SE 260 moose, respectively (Peterson, 1977).

During the winter of 1948–49, timber wolves (*Canis lupus*) managed to cross the ice from the mainland of Ontario and became established on Isle Royale. Their population increased and fluctuated between 20 and 50 animals during the period 1960–80. Thus, predator and prey had reached a dynamic equilibrium—a stabilization of numbers such that each species could survive without having a detrimental impact on the other. Sufficient resources were available to support the moose population, which was maintained at healthy levels by selective culling of old and weak individuals by the wolves. In 1958, wildlife biologist Durward Allen began tracking the changing population numbers in what has become the longest-studied system of natural predator-prey dynamics in existence.

After the wolf population on Isle Royale reached an all-time peak of 50 animals in 1980, it experienced a decline in the early 1980s, from which it still has not recovered (see Fig. 14.15). Only 14 wolves were present in 1982. Only four pups were born, to the same female in one wolf pack, between 1991 and 1993 (Mlot, 1993). As of August 1993, the other two packs were down to just a pair of wolves each. The moose population, which had steadily increased, reached a record high of about 2,442 animals in 1995. As of 2005, the population of the two species was 540 moose, which is the lowest recorded, and 30 wolves, which is considered rather high. By 2017, there were 1,600 moose but only 2 wolves—a father and daughter—remaining. Without wolves and depending on the weather (severe winters), the moose population could double in the next three to four years. With climate change, there are fewer ice bridges forming from the mainland to the island which was the route by which wolves initially got to the island. Therefore, in the fall of 2017, the National Park Service issued a final decision to reintroduce 20 to 30 wolves over three to five years with the goal of establishing a genetically diverse, reproducing population of 20 to 30 wolves to control the booming moose population.

The decline of the wolves was probably the result of two factors: an encounter with canine parvovirus in 1981 and low genetic variability (Mlot, 1993). Because the start of the wolves' decline coincided with a 1981 parvovirus outbreak in nearby Houghton, Michigan, it is thought that the virus could have been carried to Isle Royale on the hiking boots of visitors to the US national park on the island. Restriction enzyme analysis of the wolves' mitochondrial DNA (mtDNA) revealed that they were all descended from a single female and had only about half the genetic variability of mainland wolves (Mlot, 1993). Whenever a small number of individuals manage to cross an already existing barrier and find a new geographically isolated colony, they generally carry with them in their own genotypes only a small percentage of the total genetic variation present in the gene pool of the parental populations. Thus, the new colony likely will have allelic frequencies very different from those of the parental population. This is a special form of genetic drift, called the **founder effect**. For these reasons, some biologists believe the wolf population is on its way to being extirpated, although others feel it will make a comeback.

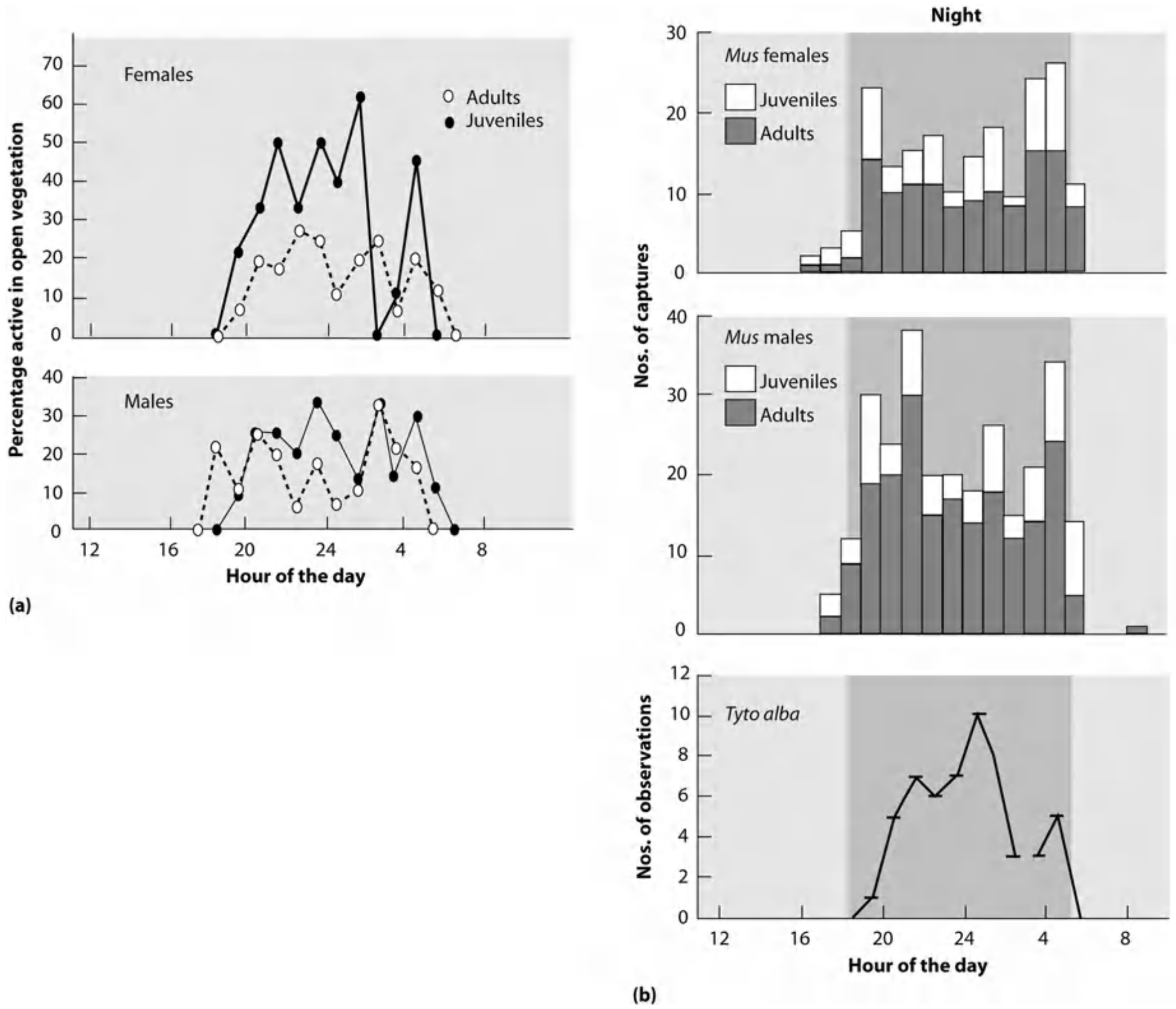


Figure 14.14. (*a*) Hourly number of captures of *Mus musculus* in open vegetation by barn owls (*Tyto alba*), expressed as percentages of the total numbers of captures in different sex and size categories; (*top*) females, (*bottom*) males. Results for three periods of 24 hours are combined. (*b*) Comparison of hourly numbers of captures of *Mus musculus* by sex and size, and numbers of observations of *Tyto alba*. Results for three periods of 24 hours are combined.

Probably the best-known predator-prey oscillation is that between lynx (*Lynx canadensis*) and snowshoe hares (*Lepus americanus*) (see Fig. 11.11). Hare populations have a cyclic fluctuation of 8 to 11 years. As the hare population increases in size, so does the lynx population. When the hare population suffers a dramatic decrease, it is followed shortly thereafter by the lynx population. The cycle of the lynx, as well as other predators like coyotes, great horned owls, and goshawks, lags a year or more behind that of the hare. Various theories have been proposed over the years to explain this predator-prey interaction. Recent evidence has suggested that the hare population size may be limited by their plant food and *not* by a predator (see Cycles, Chapter 11).

Some predators, like bears (Fig. 14.16), lynx, cougars, owls, and snakes, hunt singly. Others, like wolves and lions, usually hunt in groups. Female lions normally make the kill, after which food is shared with the rest of the pride, consisting of several males and the young.

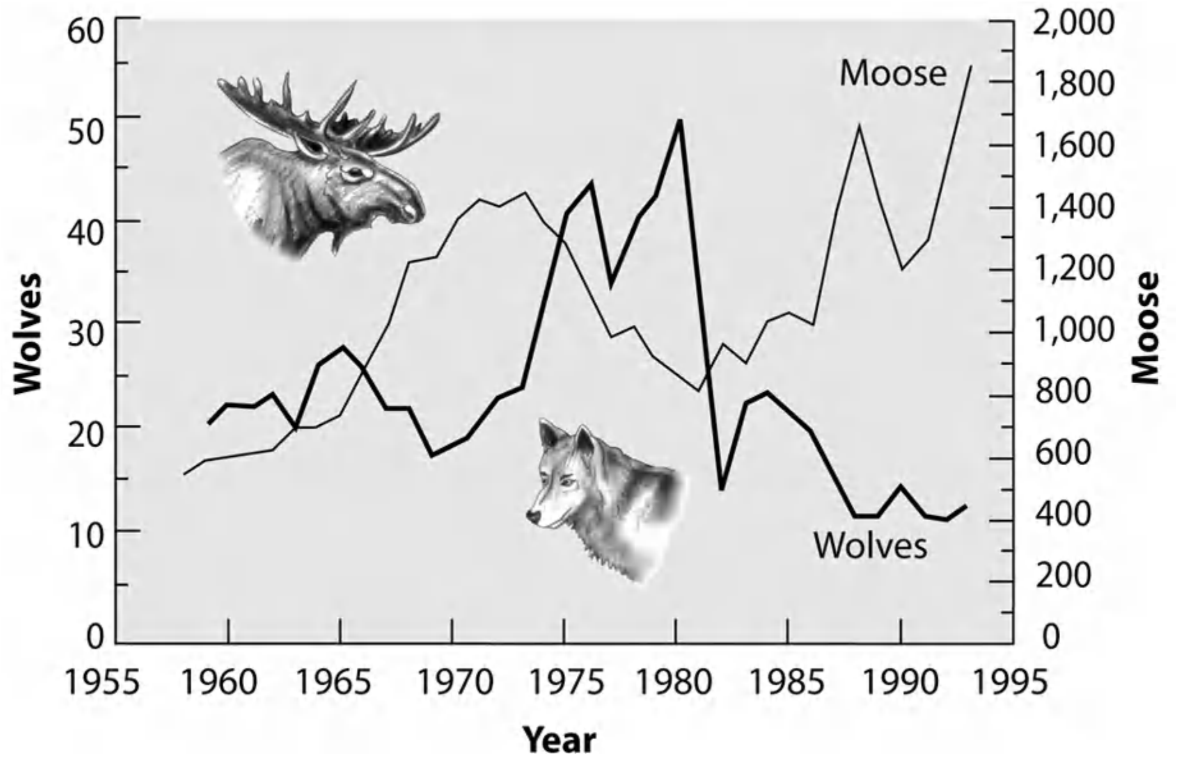


Figure 14.15. Comparison of wolf (*Canis lupus*) and moose (*Alces alces*) populations on Isle Royale, 1957 to 1993.

Grasshopper mice (*Onychomys* spp.), whose primary diet consists of invertebrates and small mammals, are the only predominantly carnivorous rodents in North America. They are extremely aggressive toward other species of small mammals and often include them in their diet. They have a rich repertoire of vocalizations and are reputed to "bay" in pursuit of their prey. When giving this call, the animal often stands on its hind legs with its nose pointed upward. The shrill call is often repeated several times and has been compared to a miniature wolf howl in its qualities of smoothness and duration and in the posture of the animal when it is calling (Nowak, 1999).

Prey species have developed a variety of antipredator defenses. The schooling of fishes, flocking of birds, and herding of mammals are all adaptations that protect individuals from their predators. Schooling behavior confers considerable antipredator benefit to individual group members through a dilution effect (Morgan and Godin, 1985). The risk of predation is greater for those individuals that stray from a school. Grazing herbivores are almost always alert for predators. If one senses danger, others are alerted by vocalizations or by the display of special patches of hair like the white rump patch and underside of the tail in white-tailed deer and the white rump patch of elk and pronghorn antelope.

Crucian carp (*Carassius carassius*) exposed to pike (*Esox lucius*) predation develop deeper bodies—as measured from backbone to belly—than carp that live without pike (Bronmark and Miner, 1992). Over a period of several weeks, carp develop "potbellies," making them too large to fit into the predators' mouths, thus reducing their susceptibility to predation. Although some fish like the pufferfish (Tetraodontidae), many toads, lizards like the chuckwalla, and snakes can inflate their lungs and thereby enlarge their bodies to intimidate a potential predator, this discovery marks the first known instance in which natural selection brings about a change in body dimensions through growth over time in order to avoid predators.

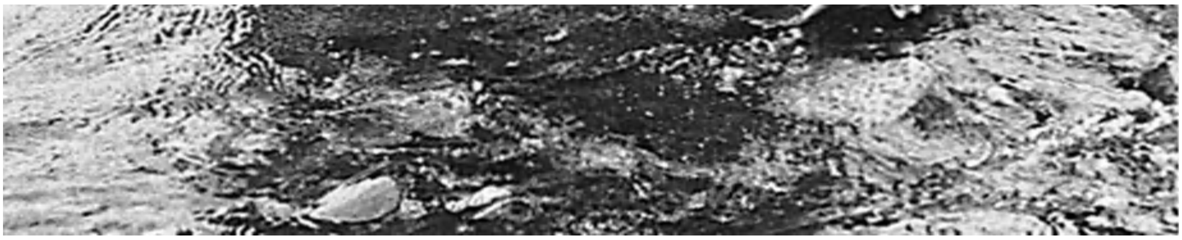


Figure 14.6. The solitary grizzly bear (*Ursus arctos*) is classified as an omnivore. In coastal regions of the bear's range, salmon become an important component of the diet.

The protective coloration of many species renders them inconspicuous in their normal habitat, whereas some, like the striped skunk (*Mephitis mephitis*), which have a powerful defensive weapon in their spray, are boldly marked—called **aposematic coloration**—as a warning to potential predators. Some poisonous species also are brightly colored, which serves as a warning to those that might prey on them. The coral snake (*Micrurus fulvius*) of the southern United States is one example. The poison dart frogs of South America are brilliantly patterned with reds, blues, yellows, and blacks. The fire-bellied toad (*Bombinator igneus*) assumes a unique "warning" position when threatened (Fig. 14.17). It exposes its bright red or yellow belly coloration in an attempt to discourage a potential predator.

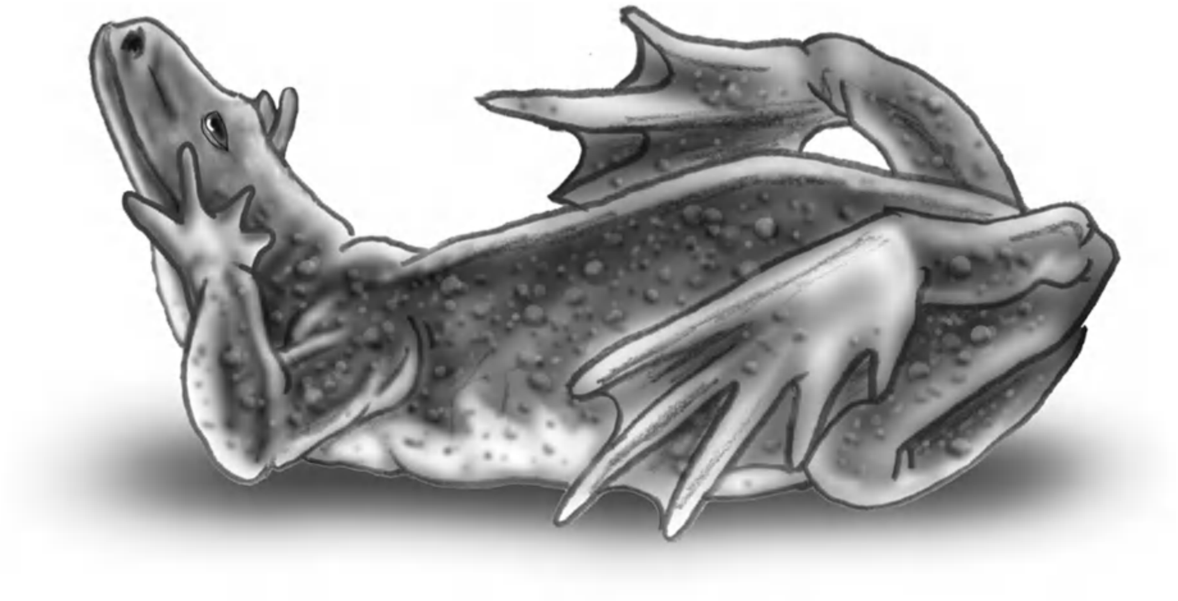


Figure 14.17. The fire-bellied toad (*Bombinator igneus*) assumes a unique “warning” position when threatened. It exposes its bright red or yellow belly coloration in an attempt to discourage a potential predator.

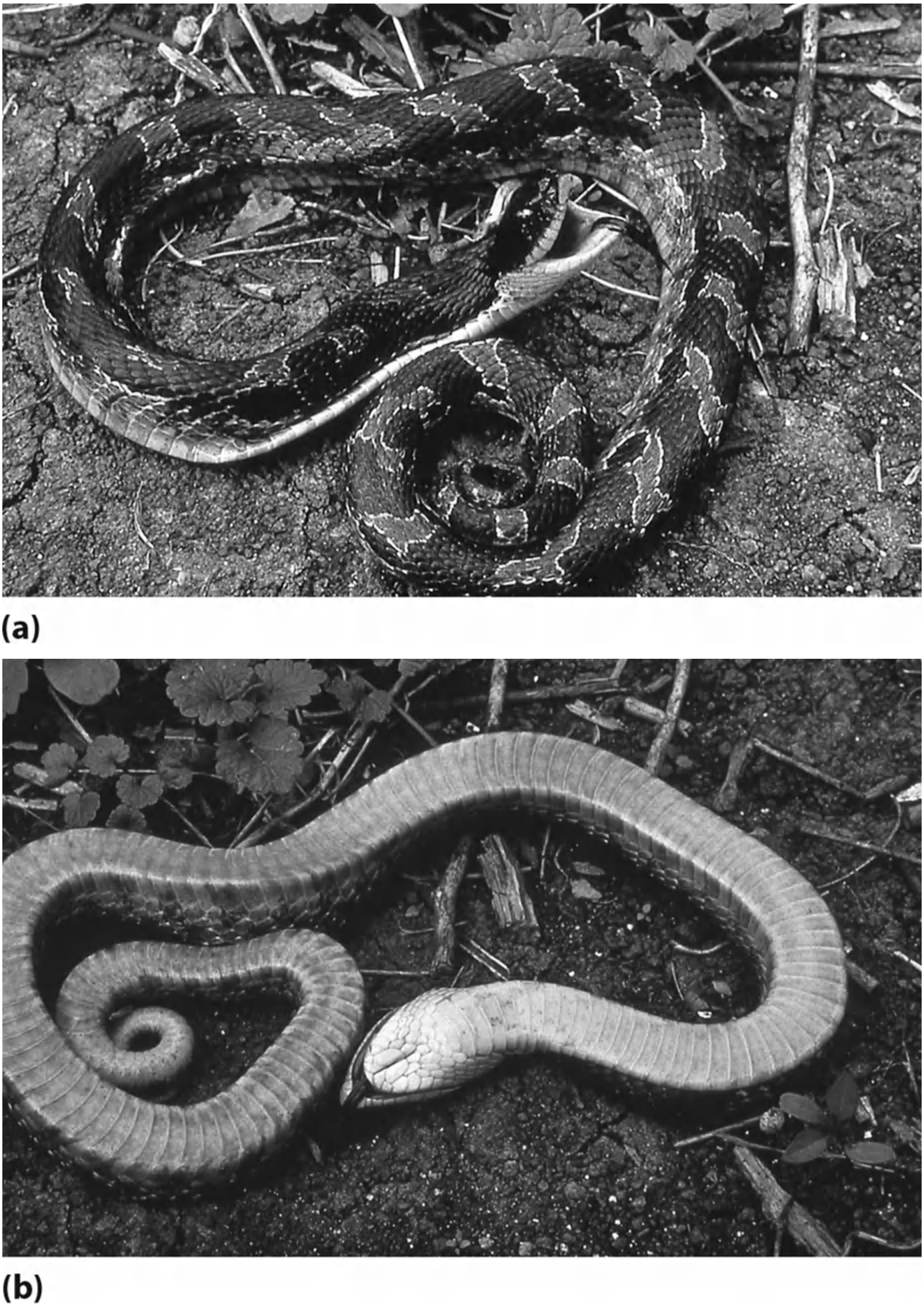


Figure 14.18. (*a*) Eastern hognose snake (*Heterodon platirhinos*). (*b*) An eastern hognose snake feigning death.

The frilled lizard of Australia can open up folds of skin around its neck, a behavior that makes it appear much larger and serves as a unique predator-avoidance strategy. In contrast, newly metamorphosed green frogs and leopard frogs crouch and cease to move in the presence of active snakes (Heinen and Hammond, 1997). When confronted by a potential predator, an eastern hognose snake (*Heterodon platirhinos*) will “die” (Fig. 14.18a, b). It turns itself upside down, becomes motionless, and opens its mouth. Most predators are not interested in a dead snake and leave. After several minutes, the snake rights itself and continues on its way. This death-feigning act can occur numerous times in succession, if necessary. Green herons (*Butorides striatus*) attempt to conceal themselves by looking like straight tree branches. American bitterns (*Botaurus lentiginosus*) stick their beaks in the air and sway from side to side in an attempt to appear like just another reed in the marsh (Fig. 14.19). Musk oxen form a circular defensive ring when threatened (Fig. 14.20).

Figure 14.19. Camouflage behavior of the American bittern (*Botaurus lentiginosus*). The bill is pointed upward in an attempt to be just another "reed" in the marsh.

Certain plants have evolved effective antiherbivore chemical defenses. During the winter, snowshoe hares are highly selective in their feeding habits in response to such chemical defenses. They often ignore large areas of potential food, even though snow cover puts extreme limitations on the browse available (Sinclair and Smith, 1984). One shunned food source is the Alaskan balsam poplar (*Populus* *balsamifera*). Buds are ignored, and twigs of juvenile poplar are fed upon only to a slight extent. These poplars produce specific plant metabolites that act as antifeedants. Buds are defended from hares by cineol, benzyl alcohol, and bisabolol, whereas internodes are defended by 6-hydroxycylohexenone and salicylaldehyde (Jogia et al., 1989; Reichardt et al., 1990b). The major component of the oil of Labrador tea (*Ledum groenlandicum*), a slow-growing evergreen, consists of germacrone, which also has been shown to be a potent antifeedant to snowshoe hares. Labrador tea has very low palatability for hares, and so this chemical serves as an effective antiherbivore defense (Reichardt et al., 1990a).

Figure 14.20. Musk oxen (*Ovibos moschatus*) forming a defensive circle with the females and young in the center. Predation pressure can favor the evolution of social life when members of the group are safer than solitary animals.

Food preferences of wild voles are influenced by the presence of phenolics in certain plants (Bergeron and Jodoin, 1987). Phenolics in the bark of coniferous trees like white pine (*Pinus strobus*) and white spruce (*Picea glauca*) have been shown to act as deterrents against debarking by meadow voles (*Microtus pennsylvanicus*) (Roy and Bergeron, 1990b).

Voles often cut the branches of young trees and leave them lying in the snow for two days or longer before eating them completely. This behavioral manipulation of a potential food source results in a decrease in the concentration of secondary metabolites to a level similar to that found in preferred summer food sources (Roy and Bergeron, 1990a).

Australian koalas (*Phascolarctos cinereus*) feed almost exclusively on the leaves of about a dozen of the 650 native varieties of eucalyptus trees (Stix, 1995) (Fig. 14.21). The leaves are hard to digest and provide one of the least nutritious diets of any mammal. Eucalyptus trees growing in poor soil produce more toxins than trees in good soil. Thus, the trees have evolved leaves that are foul-tasting and toxic, but koalas have evolved complex digestive systems to deal with the poisons.

At times, even biological researchers are unwittingly responsible for the predation of the species upon which they are working. Moen (1973) noted that intrusions by biologists in the process of marking animals, attaching radios, checking nests, and counting eggs may result in increased predation. The effect of human activity depends on the type and amount of cover used by prey species and on the abilities of predators to capitalize on human research activities to locate prey. Moen (1973) noted that crows (*Corvus brachyrhynchos*) have been known to locate nests by watching biologists working at nest sites, and that merely flushing a bird from a nest leaves the eggs exposed to crow predation. Significant losses of ruffed grouse (*Bonasa umbellus*) may have been caused by tags attached to the backs of the grouse, which made them easier to see under field conditions.

Figure 14.21. Australian koalas (*Phascolarctos cinereus*) feed almost exclusively on the leaves of eucalyptus trees. However, these trees, which provide homes for koalas, are being increasingly destroyed to provide space for urban development.

HUMAN INTERACTIONS

Humans have had a major impact on many vertebrate species; such effects include the alteration of habitat, the introduction of competitor species into new areas, and the extirpation and extinction of many groups (see Chapter 16). Possibly the greatest impact of humans on other species will be from global warming. In January 2018, several scientific agencies around the world, including the National Aeronautics and Space Administration (NASA) and the National Oceanic and Atmospheric Administration (NOAA) in the United States, named 2017 as the third-warmest year recorded. The average global temperature was 1.12°C (2.02°F) above a 1881–1910 baseline. Using this older period as a baseline gives a better indication of how much warming has taken place since the start of the industrial period. The 2015 Paris Climate Agreement aims to limit warming well below 2°C (3.6°F) of that period. The average global temperature for 2016 was 14.8°C (58.69°F), beating the previous year by 0.04°C (0.07°F)—a difference that actually is one of the largest NOAA has seen between record years. This was the fifth time in a dozen years that the globe has set a new annual heat record. Records have been set in 2016, 2015, 2014, 2010, and 2005. The 2016 record marked the third consecutive year reaching a new record temperature, the first time since the current warming trend began in the 1970s that three years in a row were record highs.

Combining the data sets from NOAA and NASA finds:

- The 5 warmest years in the global record have all come in the 2010s.
- The 10 warmest years on record have all come since 1998.
- The 20 warmest years on record have all come since 1995.

In the last 10,000 years through the nineteenth century, the Earth’s average temperature appears not to have varied by more than 1°C (1.8°F). However, in just the last 100 years, the average surface temperature has risen by about 0.28°C to 0.62°C (0.5°F–1.1°F). (See more detailed discussion of global warming in Chapter 20).

As a result of human impact, populations of some vertebrates have had to be managed to prevent overexploitation and possible extinction. Such is the case with bear, elk, antelope, deer, moose, squirrels, rabbits, muskrats, waterfowl, turkeys, quail, and many other species. Federal and state agencies have been established to propose and enforce legislation defining certain species as "game" animals and establishing open and closed hunting and fishing seasons. Size limits as well as the numbers and kinds (e.g., bucks, does) that can be harvested legally are written into law. Age limits are set for hunting and fishing, and licenses (in-state, out-of-state) are required.

As a result of these measures, fish hatcheries and game farms have been established to propagate certain species for stocking in order to increase populations of prey for sports hunting and fishing. In some areas, the protective measures begun in the early part of the twentieth century have yielded populations of certain species approaching and/or exceeding the carrying capacities of their natural ranges, resulting in damage to crops and ornamental plantings. White-tailed deer in parts of the eastern United States are an excellent example of a species whose population has grown beyond the carrying capacity of its range.

Seal Die-Offs and Global Warming

Human predation has all but eliminated several regional populations of seals, including harbor seals (*Phoca vitulina*), Mediterranean monk seals (*Monachus monachus*), and Caribbean monk seals (*Monachus tropicalis*). Thousands more seals have succumbed to viral plagues like phocine distemper virus, which is caused by a morbillivirus (family Paramyxoviridae). Chemical pollutants known to disarm seal immune systems have been suggested as a possible contributing factor.

Lavigne and Schmitz (1990) proposed two other factors that could explain the twentieth century's most conspicuous seal die-offs: unusually warm weather and overcrowding within the seal herd. They note that "four of the six documented mass mortalities in seal populations have occurred in the past 12 years, a period that includes some of the warmest years in the 20th century." They also point out that recent die-offs of dolphins and whales followed unseasonably warm temperatures. Bacteria, algae ("red tide"), and other organisms harmful to this species often flourish as temperatures rise.

The apparent global warming resulting from human activities will have the most far-reaching effects of any of humanity's interactions with other species. Predictions of global temperatures rising as much as 3°C (5°F) within the next century carry profound implications for the future. Lavigne stated: "Our data show that a 1°C to 3°C increase in average temperature can trigger very significant ecological events." Noting a recent rash of die-offs among seabirds, fish, coral reefs, and sea turtles, Lavigne added: “If the record of the past 12 years is anything to go by, we probably have much more to worry about than seal deaths.”

The most recent die-off occurred during the summer of 2018 along northern New England beaches. Since July 1, 2018, nearly 600 seals (mostly pups) had been found stranded or washed ashore with the majority of fatalities in Maine. As of September 10, 2018, the state breakdown was Maine—455, New Hampshire—100, and Massachusetts—106 for a total of 661 fatalities. An additional 177 seals were stranded alive but most later died. The National Oceanic and Atmospheric Administration (NOAA), declaring the die-offs an “unusual mortality event,” reported that dead seals had tested positive for avian flu and phocine distemper. Both are spread through direct contact between animals, including between a mother and her pups. The illnesses can also be absorbed through the inhalation of respiratory particles, as well as through the eyes, mouth, stomach, and skin wounds, according to NOAA. The declaration of the marine die-off as an unusual mortality event means the deaths will be prioritized for investigation and response.

Lavigne and Schmitz, 1990; Osterhaus et al., 1997; Higgins, 2018; National Oceanic and Atmospheric Administration, 2018

Review Questions and Topics

1. Differentiate between the habitat and the niche of a species.
2. Discuss the competitive exclusion principle. Why does it rarely occur in nature?
3. Differentiate between commensalism and mutualism. Give examples.
4. Discuss factors involving the eggs and nestling young of cowbirds that allow them to outcompete the natural young of their host parents.
5. Differentiate between parasitism and predation. Why is it advantageous for parasites not to kill their host?
6. What is the founder effect? How would this affect a population of frogs introduced onto an island devoid of their species?
7. Discuss several antipredator defenses developed by prey species.
8. List several specific pieces of evidence in support of the occurrence of global warming. What effects is global warming having on vertebrate populations?

Supplemental Reading

Byers, J. A. 1997. *American Pronghorn: Social Adaptations and the Ghosts of Predators Past*. Chicago: University of Chicago Press.

Keddy, P. A. 1989. *Competition*. London: Chapman and Hall.

Soler, M., ed. 2017. *Avian Brood Parasitism*. New York: Springer.

Vertebrate Internet Sites

1. Nearctica—Commensalism

   https://web.ma.utexas.edu/users/davis/375/LECTURES/L22/Commensalism.pdf

   Discusses commensalism using cattle egret, anemonefish, several invertebrates, and a plant as examples.

2. Symbiosis

   www.marietta.edu/~biol/biomes/symbiosis.htm

   Discusses parasitism, commensalism, and mutualism with many excellent photographs. Includes table of effects of interactions.

3. Interspecies Communication

   www.interspecies.com

   Interspecies communication between humans and particularly cetaceans, like orca and sperm whales; sounds of orcas; information about *The Interspecies Newsletter*; links to other sites.

4. Predation and Competition

   www2.nau.edu/~gaud/bio326/class/predat/pred.htm

   An online course with lessons and information on competition, predation, and coevolution from Northern Arizona University.

15 | Techniques for Ecological and Behavioral Studies

> Birds were flying from continent to continent long before we were. They reached the coldest place on Earth, Antarctica, long before we did. They can survive in the hottest of deserts. Some can remain on the wing for years at a time. They can girdle the globe. Now, we have taken over the earth and the sea and the sky, but with skill and care and knowledge, we can ensure that there is still a place on Earth for birds in all their beauty and variety—if we want to. And surely, we should.
>
> Sir David Attenborough, 1998

INTRODUCTION

Discovery and problem-solving in all fields of science employ techniques of gathering, coordinating, organizing, and evaluating information as it relates to a specific subject. In a scientific approach to any problem, the researcher must first ask a question or identify a problem based on observations of objects or events. Then, a hypothesis or potential answer to the question being asked is proposed, and the investigator predicts what the consequences might be if the hypothesis is valid. The investigator then devises ways to test the hypothesis by making observations, developing models, or performing experiments. Hypotheses must be testable; those that are not testable are inadmissible in science. Observations and/or tests should be repeated as often as necessary to determine whether results will be consistent and as predicted. Hypotheses that are found upon testing to be contradicted by the evidence must be modified or abandoned. The investigator must then report objectively on the results and on conclusions drawn from them, presenting both the data and his or her interpretation of the information as it relates to the hypothesis. This mode of action is known as the **scientific method**. Critical evaluation of the techniques—or methodology—used in any scientific investigation is extremely important. Thus, scientists must constantly be concerned with the selection and application of the best techniques for use in each of these steps. A deficiency in any of these steps will hinder the interpretation of the results.

Limitations inherent in field and laboratory investigations of animal populations make it even more critical that researchers choose most carefully the techniques to be used. The mobility, secretiveness, and constant fluctuation in numbers of practically all wild animals make precise data difficult to secure. For these reasons, census work often requires a major portion of the time in many field investigations. The secretive nature of most wild animals makes the determination of the influence of pathology, disease, and related factors especially difficult to examine for any species of animal in nature.

Because the objective of any investigation is to gather and evaluate accurate data, the investigator must always bear in mind that the techniques used should yield data that are objective and reliable. If the investigator's approach to the problem is not scientifically sound—if the techniques are inadequate or flawed—the results will be of little value. Critical appraisal of the investigational techniques should be made at the beginning, not at the termination, of the research project.

The difficulties mentioned above highlight the need for careful planning and equally careful collection of data on the part of fish and wildlife investigators. Inexperienced investigators often propose to collect data that, due to field conditions or the characteristics of the animal being investigated, are impossible to secure. Thus, detailed planning, including critical scrutiny of all the proposed techniques to be employed, is necessary to ensure that insurmountable problems are not encountered in the proposed study. Long-term studies are needed to learn these limitations and to collect the necessary information; yet, this is rarely accomplished, since most studies are short-term (and are *financed* as short-term projects).

Many studies do not require the capture of individual animals. Noninvasive wildlife surveying techniques employing simple observation, aerial photography, aerial censusing, transect counts, hair snag stations, actual counting of individuals like fishes and hawks that pass a certain point on their migratory journeys, and identification of signs like tracks and scats can provide valuable data. Scat samples offer a wealth of information about a species' distribution, relative abundance, diet, and even individuals' health, habitat use, and home-range size. The hormones and DNA extracted from scats can provide insight on the sex and reproductive status of individuals, which in turn can be used to determine population size, home range, paternity, and kinship—information that is critical to the success of management and conservation initiatives. For some purposes, animals like amphibians, reptiles, and mammals killed by vehicles (DOR, or dead on road) can yield useful data. Many behavioral studies can be done in the animal's natural habitat.

Other studies, however, do require direct contact between animal and investigator. Such studies include those dealing with the collection of anatomical data like weight, length, condition of molt, or the like, or those dealing with age determination, sex ratios, genetic analyses, home ranges, and parasites.

CAPTURE TECHNIQUES

A wide variety of techniques are used for capturing vertebrates. Humane capture techniques should always be employed. These techniques should not injure or increase the mortality of the animals, and they should not cause more than minimal disruption to the animals' normal behavior patterns.

Dip-netting, seining, the use of trap- and gill-nets, and the use of immobilizing chemicals and electroshocking (Fig. 15.1) are among the capture methods utilized by fish biologists. Most amphibians can be captured either by hand or with the use of a net. Some terrestrial reptiles also can be taken by hand, although nets, nooses, and tongs are frequently used for some species. Aquatic turtles may be secured through the use of turtle traps, commercial fish trap-nets, and trawls.

Figure 15.1. Electroshocking temporarily stuns fish so that they can be captured, examined, and then released.

Nestling birds can be removed from the nest by hand for weighing, sexing, and tagging. Fine-mesh mist nets are often used to capture small flying birds, which become entangled in the mesh and can be removed uninjured for study. Live traps placed on the ground and baited with seeds are used successfully for some granivorous species. The projection, or cannon, net trap is widely used for turkeys and waterfowl (Fig. 15.2). It consists of a large, light net that is carried over the baited birds by mortar projectiles or rockets. Funnel-entrance traps are used commonly for waterfowl. Hawks can be trapped by using traps baited with live prey. Some carrion-eating species have been immobilized by consuming drug-laden meat.

Many small-mammal researchers employ traps. These should be live traps suitable for the species, although snap traps were extensively used in the past. Traps may be placed on the surface of the ground or in tunnels, or they may be affixed to the branches of trees.

(a)

(b)

Figure 15.2. (*a*) The cannon net is an effective way of taking gamebirds, unharmed, for scientific purposes. The birds are prebaited at the site; the net is then carefully folded and camouflaged in front of the “cannons.” (*b*) When properly deployed, the net is highly effective. The birds are snow geese (*Chen hyperborea*).

Shrews are taken most effectively in pitfall traps in which a series of containers (cans, plastic cups, etc.) are buried with their tops flush with the ground and loosely covered by a piece of wood or some other object. Due to the shrews’ high metabolism, this method of collection will yield live shrews only if the cans are checked several times each day. If the cans cannot be checked frequently, they can be partially filled with a preservative liquid/fixative to kill and preserve animals for future study. All cans should be removed and the holes filled at the conclusion of the study.

Small-mammal distribution studies can be augmented by examining discarded bottles and aluminum cans along roadsides. Shrews are the most abundant small mammals found in these discarded containers (Morris and Harper, 1965; Glegg, 1966; Pagels and French, 1987; Benedict and Billeter, 2004; Dealy et al., 2015; Hamed and Laughlin, 2015; and others). An 18-month study in Great Britain found mice, shrews, and voles in 8 percent of bottles and almost 5 percent of cans (Moates, 2018). Examination of owl pellets also can yield valuable distributional and population data on shrews, voles, and other small mammals.

Bats usually are captured with mist nets positioned at cave entrances or along watercourse flyways. Nets must be monitored continually and bats removed as soon as possible in order to prevent injury.

Although mammals as large as bears can be trapped successfully with snares and culvert traps (Fig. 15.3), most large mammals are shot with a tranquilizer-containing dart (Fig. 15.4). Fairly accurate estimation of weights of animals in the field must be made for proper dosages to be administered.

Drift fences and traps are used for studies on a wide range of terrestrial vertebrates, including amphibians, reptiles, and mammals. This method requires the erection of one or more fences with openings at periodic intervals. The object is to direct the movement of an animal into a trap at one of the openings.

IDENTIFICATION TECHNIQUES

To study the movements and behavior of animals in the wild, there must be a means of identifying specific individuals. In some cases, this can be accomplished by noting unique individual characteristics like distinctive coloration, scars, deformities, injuries, or some aberrant behavior. For example, Schaller (1963) found that the noses of mountain gorillas appeared distinctive and served as the best single character for recognizing individuals. “Chessie,” the Chesapeake Bay manatee, was positively identified almost 11 years after his last sighting by distinctive markings and scars on his body (Chapter 12).

In most cases, however, it is not possible to distinguish individuals visually. Therefore, some appropriate method of marking or tagging each individual animal must be devised. In deciding on a particular technique, consideration must be given as to whether the study in question is short-term or long-term and how many animals will be involved. The method selected should not injure the animal, alter the animal’s behavior or locomotion, or cause increased susceptibility to predation. Many identifying techniques have been devised, including marking, tagging, photography, use of radio transmitters, and satellite tracking.

Figure 15.3. Culvert trap used for capturing bears in Great Smoky Mountains National Park.

Figure 15.4. Tranquilizer-containing darts used for temporarily immobilizing large mammals.

Marking

Marking usually refers to changing a part of the animal's body so that it can be discerned readily from all other members of the population. Moyle and Cech (2004) summarized fish-marking methods as follows: "Marks may consist of clipped fin rays, liquid nitrogen 'cold brands,' pigmented epidermis from high-pressure spray painting, or fluorescent rings on bones or scales (visible under ultraviolet light) from incorporation of tetracycline or 2, 4-*bis*(*N*, *N*′-dicarboxymethylaminomethyl) fluorescein (DCAF) in the diet." Juvenile salmonids have been marked chemically by feeding them dissolved strontium, a biologically rare element, which is then incorporated into their scales (Snyder et al., 1992).

Amphibians usually are marked by toe-clipping—that is, excising the terminal phalanx of one or more toes in a specific pattern. They also may be marked by branding and by the use of dyes and phosphorescent powders. Larval (tadpole) stages may be semipermanently marked by injecting an acrylic polymer dye into the fin. A detailed discussion of marking and tagging techniques suitable for amphibians may be found in Heyer et al. (1994).

Lizards and snakes may be marked by toe-clipping, by excising specific scales in a prearranged manner, by branding, or by using a latex-based house paint. Marking methods for reptiles have been reviewed by Dunham et al. (1988). Individual turtles can be identified by having an identifying mark painted on their shells or by notching specific marginal scutes. Birds may be marked by dyeing their feathers.

Mammals may be marked by toe-clipping, fur-clipping, ear-notching, tattooing, branding, dyeing, painting, or bleaching. In the case of toe-clipping, smoked paper affixed to plywood or cardboard can be placed throughout the study area so that whenever a marked animal crosses the surface, it will leave its own distinctive identifying imprint.

Commercial dyes have been employed in various ways to identify mammals. In some species, the dye is applied to the captured animal prior to its release. In other studies, a marking device may be placed in the animal’s normal habitat (designed in such a way that the animal triggers the device in its typical pattern of activity). Once triggered, the device discharges a quantity of the dye onto the animal’s body. The use of a dye in this manner will provide visual identification until the animal undergoes its next molt. Fluorescent powders have also been used successfully. A detailed discussion of marking and tagging techniques suitable for mammals may be found in Wilson et al. (1996).

Petit et al. (2012) injected UV fluorescent tattoo ink subcutaneously into the tail of eight small mammal species and into the ventral area of seven lizard species. Recaptures indicated that the animals were healthy and the marks had not moved.

Tagging

Tagging requires the attachment of a metal, plastic, or cloth device to the body of an animal or by the implantation of a tag to allow for future identification (Fig. 15.5). Any tagging device must anticipate the growth of the animal and must not impede its movements or other normal behavior.

Fishes

Tagging of fishes can be done by externally and internally attached disks, microtags, dart tags, plates, streamers, and small, implantable metal rods detectable in a magnetic field (Moyle and Cech, 2004). Electronic tags that record depth, water temperature, and light intensity weigh as little as 16 g (0.56 oz.) and can store more than 500,000 data samples (Metcalfe and Arnold, 1997). Data on plaice (*Pleuronectes platessa*) have been recorded continuously by electronic tags for more than 200 days.

Figure 15.5. A biologist tags a hawksbill turtle (*Eretmochelys imbricata*) in an effort to gather more information on the species' movements and habitat needs. The threats facing this species include habitat destruction and commercial demand for stuffed juveniles and products made out of its shell.

Amphibians

Amphibian studies have used tags and radioactive isotopes for identifying individual animals. The use of isotopes allows the continuous monitoring of an individual without recapture. Passive integrated transponder (PIT) tags are small, glass-encapsulated diodes, 0.1 g (0.004 oz.) and do not require batteries (Camper and Dixon, 1988). When activated by a detector, they transmit a unique code back to the receiver. PIT tags must be implanted in the animal (thus, infection is a major consideration), and current transponder systems have a very short range. Ingested radio transmitters also have been successful in yielding short-term data on amphibians like the common frog (*Rana temporaria*) and the common toad (*Bufo bufo*) (Oldham and Swan, 1992), as well as on snakes. Visible implant elastomer tags (VIE), visible implant alpha tags (VI Alpha), and coded wire tags (CWT) offer alternatives for identifying both amphibians and reptiles. All three tag types are injected beneath the skin with little effect on the host animals. VIE and VI Alpha tags can usually be seen in ambient light, but tag detection may be greatly enhanced by fluorescing the tags (Sapsford et al., 2015). VIE tags, a UV fluorescent polymeric material, offer a large number of individual codes if colors and body locations are combined. A total of 255 individual codes were created using three colors and four body locations in a study of salamanders (Jung et al., 2000). VIE tags have been used in studies of both adult and larval amphibians (Grant, 2010; Brannelly et al., 2014; Iannella et al., 2017; and others) and in a caecilian (*Gegeneophis ramaswamii*) (Measey et al., 2001). VI Alpha tags were initially developed for fishes, but since 2006 have been used on caecilians (Measey et al., 2001; Gower et al., 2006), salamanders (Osbourn et al., 2011) and anurans (Chelgren et al., 2006; Heard et al., 2008; Pittman et al., 2008; Courtois et al., 2013).

The thread-bobbin technique proved effective for large anurans, medium-large terrestrial snakes, and one chelid turtle in a study of the ecology of herpetofauna in a tropical rain forest (Waddell et al., 2016). The thread trail revealed the exact movements of the tracked animal, providing detailed information on activity and microhabitat use that many alternative tracking methods cannot provide.

Reptiles

Several unique methods of tracking turtles have been employed. Stickel's (1950) attachment of a spool of thread to the carapace of a box turtle yielded valuable data on the movements of this species. The attachment of helium-filled weather balloons to marine turtles allows tracking of their movements for short periods of time. Galdino et al. (2014) described a bead-tagging method for permanently marking live lizards (*Tropidurus* sp. and *Eurolophosaurus nanuzae*).

Birds

For years, ornithologists have been studying migration in birds, as well as many other aspects of avian biology, by using aluminum, stainless, or monel alloy leg bands (Figs. 15.6a, b and 15.7). These tags are numbered and contain the address of an agency to which the finder should mail them. In the United States, the agency is the US Fish and Wildlife Service. Bands come in a variety of sizes, and future growth in the diameter of the leg must be carefully anticipated prior to attachment of the band. These bands have provided valuable data on the migratory habits of many species of birds, but a bird must either be recaptured or found dead in order to be positively identified. A toll-free telephone number (1-800-327-BAND) is now available to report any bird band identified or recovered in North America. This recording service, developed in cooperation with the National Biological Survey, the US Fish and Wildlife Service, and the Canadian Wildlife Service, can be called from anywhere in the United States, Canada, and most parts of the Caribbean.

Colored leg bands, neck bands, or plastic streamers are used in behavioral or home-range studies so that individual birds can be identified without recapture (see Fig. 15.7). Patagial tags and feather grafts also have been used as field identification tags (Figs. 15.8 and 15.9).

Researchers studying Western European populations of the white stork (*Ciconia ciconia*) implanted electronic PIT tags, 30 mm (1.18 in.) long, 3 mm (0.12 in.) in diameter, 0.8 g (0.28 oz.) mass, beneath the stork’s skin (Michard et al., 1995). The tag, which permits automatic individual identification, is long-lasting because it does not require a battery. Body condition can also be assessed, as the birds weigh themselves on scales coupled with tag-identification systems at feeding sites. The tags are read by an antenna-recorder from a distance of approximately 1 m (3.28 ft.).

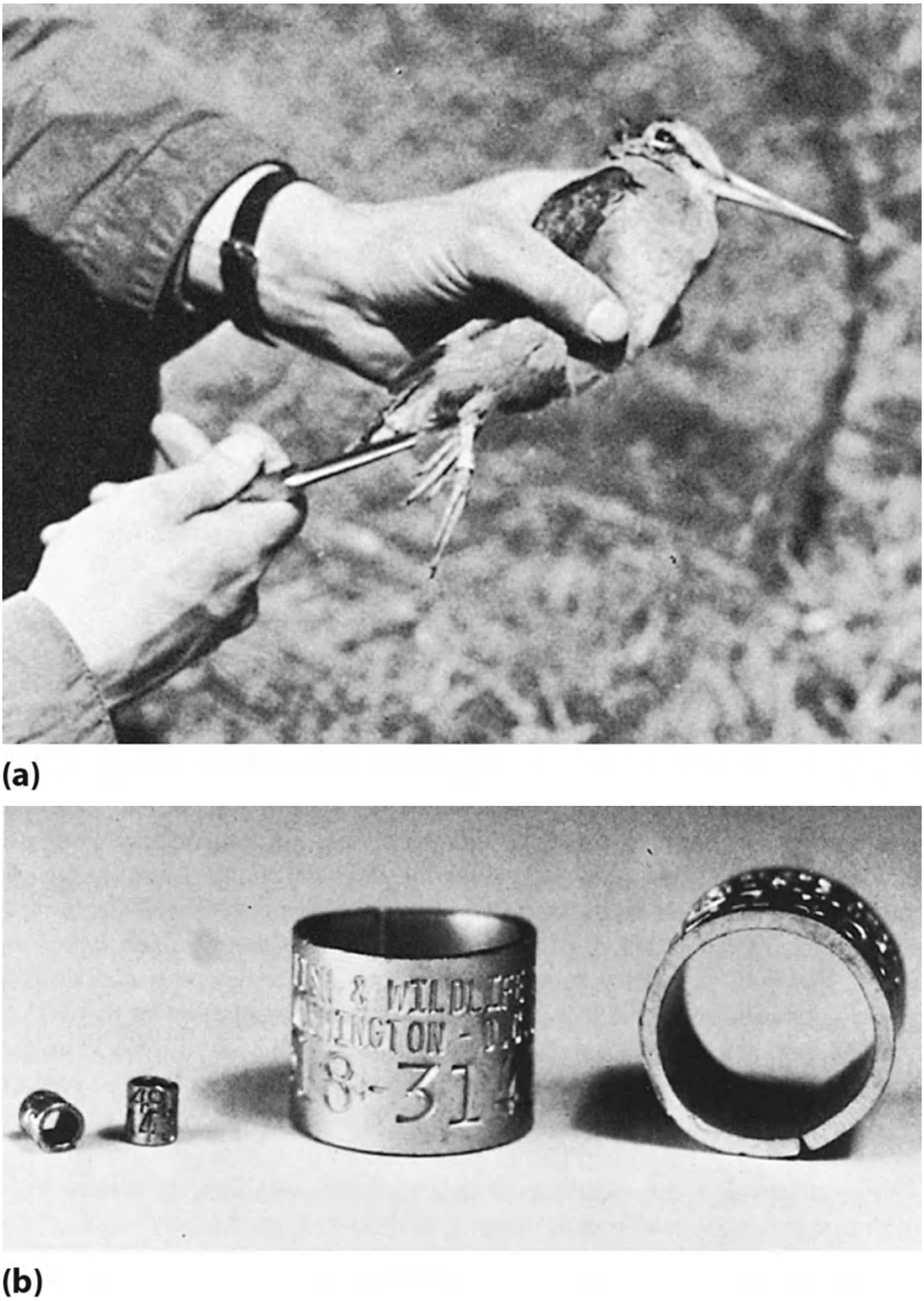


Figure 15.6. (*a*) Banding a woodcock (*Philohela minor*). Future growth of the leg must be anticipated when selecting the proper size band. (*b*) Bands of various sizes, made of soft, lightweight metal, are provided by the US Fish and Wildlife Service for bird-banding to determine the migratory movements of various species.

Mammals

Mammals may be tagged in a variety of ways. Studies involving bats utilize lightweight aluminum bands similar to those used for birds. These bands are numbered and are affixed to the forearms of the bats. In some studies, 2.54 cm (1 in.) long luminous Cyalume rods have been attached to the backs of bats for easier tracking at night. Metal or plastic ear tags have been used on mammals of all sizes (Fig. 15.10). In some cases, colored plastic streamers have been attached to the tags so that visual identification can be made at a distance. Neck collars are used on larger mammals. Unfortunately, all tags are subject to loss; Siniff and Ralls (1991), for example, reported an estimated annual tag loss rate of 26 percent in California sea otters (*Enhydra lutris*).

Spool-and-line tracking has been employed in several mammal studies. This technique utilizes a spool of thread attached to the animal's body. The spool continuously releases thread as the animal moves, thus providing a fairly accurate representation of the animal's travels. For example, Hawkins and Macdonald (1992) used spools attached to webbed collars to investigate the movements of badgers (*Meles meles*). One disadvantage of this method is that it yields only one or two nights of potentially high-quality data per capture.


C4T5

Figure 15.7. The neck collars on these parent Canada geese (*Branta canadensis*) make it possible to keep track of eggs and young up to the migratory stage, yielding information on daily and seasonal habitat preferences.

Dyes have been incorporated in food in order to stain the feces. In small-mammal studies, dropping boards are placed throughout the study area in order to facilitate the recovery of dyed fecal pellets. This is a temporary technique that depends on the rate of passage of the food material through the animal's alimentary canal.

Radioactive isotopes in the form of wires and pellets have been inserted under the skin of various species of mammals. This method of tagging permits continuous location of the animal with minimal disturbance. Radioactive materials injected into animals will render their feces identifiable.

The use of genetic tagging has revealed individual local and migratory movements and yielded estimations of abundance in humpback whales (*Megaptera novaeangliae*) (Palsboll et al., 1997). Genetic tagging consists of collecting skin samples, removing the DNA, and determining the sex and genotype at six Mendelian-inherited microsatellite loci for each sample. More than 2,300 unique genotypes were identified. Genetic tracking has also allowed the tracking of an individual whale from fishery to market (Cipriano and Palumbi, 1999). This technique, as well as similar genetic tools, will allow new management efforts to focus on the individual, rather than the species, and to distinguish individual "legal" whales (those of a particular sex and size that can be legally harvested) from all others.

G9
G9

Figure 15.8. Colored patagial tags have been used to study the breeding behavior of mourning doves (*Zenaidura macroura*).

Tagging frequently requires specific federal and/or state permits, as well as approval from university and institutional animal care and/or ethics committees in many instances, particularly when dealing with species whose travels cross international boundaries, like most birds. Researchers must be qualified in identification and handling of particular species, as well as in the tagging/marking techniques to be employed.

Photography

Photography is useful for making a permanent record of the location and/or behavior of a marked or tagged animal. Approximately 80 percent of the manatees (*Trichechus manatus*) in the Homosassa and Crystal rivers in Florida are distinctively scarred, primarily from boat strikes. These scar patterns have been used to identify individual manatees. Photographs were taken at regular intervals (twice a week, weekly, biweekly), both from the water's surface and from beneath the surface, and were incorporated into an identification catalog (Powell and Rathbun, 1984; Rathbun et al., 1990). Resightings of humpback whales (*Megaptera novaeangliae*) returning to their summer feeding grounds have been verified photographically. Photoidentification of cetaceans is a worldwide ongoing endeavor with regional catalogs and specific repositories of all photographed whales.

Figure 15.9. Feather graft of an immature wing feather onto the head of a great black-backed gull (*Larus marinus*). Best results are obtained when the graft is made on immature birds. The grafted feather is permanent and molts with other body feathers, thereby serving as a permanent field identification “tag.”

Photography has been increasingly used by researchers to verify the presence of an animal in a specific area. Infrared motion-sensitive cameras allow an unsuspecting animal to trigger a mechanism and take its own picture. This not only provides a record of the animal’s presence but may also identify food brought to the nest and the frequency and length of absence from the nest. A clock or timing device can be positioned so that it is included in the photograph and records the time the photograph was taken.

Small video systems and data loggers that were mounted on the heads of four adult Weddell seals (*Leptonychotes weddellii*) at McMurdo Sound in Antarctica have revealed some aspects of the secret lives of diving animals (Davis et al., 1999) (Fig. 15.11). The video system recorded images of the seal’s head and the environment immediately in front of the animal. Filming was accomplished in near-infrared light emitted from the camera like a flashlight. The light, which was invisible to the seal’s eye and its prey, should not have altered either one’s behavior. The data logger recorded time, depth, water speed, and compass bearing once per second. Flipper stroke frequency and ambient sound were recorded continuously on the audio channels. Several unknown tactics used by the seals to extract prey from their refuges in the ice were revealed.

Figure 15.10. Affixing an ear tag to a black bear.

Figure 15.11. A Weddell seal (*Leptonychotes weddellii*) surfaces in McMurdo Sound, Antarctica, with an 18 kg (40 lb.) cod in its mouth and a video camera strapped to its head. Filming was accomplished in near-infrared light emitted from the camera. The video camera and data logger revealed heretofore unknown behavior and tactics used by the seals to secure their food beneath the ice.

Biologists studying tool use in a New Caledonian crow (*Corvus moneduloides*) have fastened tiny video cameras to the birds and recorded their search for food (Rutz et al., 2007). The cameras were attached to the tail feathers so that the devices look forward between the birds' legs. The system, which can transmit video to a receiver several hundred meters away, appears to let the crows forage normally in their rugged forest habitat. Videos included scenes of the birds probing for food with plant stems.

Radio Transmitters

One of the earliest reports on the use of radio telemetry to locate free-ranging animals was their use on woodchucks (*Marmota monax*) by LeMunyan et al. (1959). The use of radio transmitters has met with considerable success since that time, as transmitters continue to be miniaturized and receiving equipment continues to be improved. In many ways, the use of radio transmitters has revolutionized the study of animal movements. They have been used in studies involving all of the vertebrate groups.

This technique uses the transmission of radio signals to locate a transmitter attached to the animal of interest. It provides the ability to locate the transmitter regularly, both day and night, and to check on the location and condition of the carrier. Radio telemetry is valuable in obtaining location data on the animal's preferred habitat, home range, individual behavior patterns, as well as to understand population dynamics and to study predation. Several telemetry techniques have been designed specifically for detecting mortality in free-ranging animals. For example, transmitters may contain temperature sensors that detect the drop in body temperature upon the death of the animal.

The different types of radio telemetry techniques include very high frequency (VHF) transmitters, global positioning system (GPS) tracking, and satellite tracking. The basic components of a radio-tracking system consist of (1) a transmitting subsystem consisting of a radio transmitter, a power source and a propagating antenna; and (2) a receiving subsystem including a "pick-up" antenna, a signal receiver with reception indicator (speaker and/or display) and a power source. VHF tracking is relatively low cost and has reasonable accuracy. However, it is labor intensive. GPS uses a radio receiver (rather than a transmitter) in an animal's collar. It may store data and drop off the animal when expired to allow data retrieval, transmit the data to another set of satellites that deliver it to the researchers, or send the data on a programmed schedule to biologists who must be in the field to receive them. It is highly accurate, suited for studies where intensive and frequent data are needed, and may not require frequent field visits. However, it is relatively short-lived and has higher initial costs. Satellite tracking (Argos System) uses a higher-powered transmitter attached to an animal. It is ideal for studying long-distance movements in remote areas (marine animals). Its disadvantages are a higher initial cost and less accuracy—mean accuracy is 480 m (1,575 ft.).

Researchers have successfully employed radio tracking in a wide range of amphibians, including *Ambystoma maculatum*, *A. tigrinum*, *Cryptobranchus alleganiensis*, and *Lithobates* [*Rana*] *clamitans* and *Rana pretiosa* (McAllister et al., 2004; and others). Madison (2010) reviewed both implant and external attachment procedures for amphibians. Rowley and Alford (2007) found that tag attachment in frogs did not affect distance moved or number of times moved. They also determined that measures of movement and habitat use did not differ significantly between radio telemetry and harmonic radar direction finding. The effects of tag attachment and harmonic direction finding versus radio telemetry in amphibians was investigated by Rowley and Alford (2007).

Limosa harlequin frogs (*Atelopus limosus*) in Panama are especially sensitive to the amphibian chytrid fungus. Ninety individual harlequin frogs resulting from a captive breeding program were released in 2017 into the Mamoni Valley Preserve in Panama. Each was wearing a mini radio transmitter and had a small numbered tag inserted under its skin so researchers could tell individuals apart and track whether they acquired the fungus. Researchers also gave each frog an elastomer toe marking that glows under UV light to easily tell this cohort of frogs apart from any future releases.

Transmitters may be strapped to the body, attached by means of a collar placed around the neck (Fig. 15.12), wired to the carapace of turtles, or implanted intraperitoneally or subcutaneously (Ralls et al., 1989; Rowe and Moll, 1991; Werner, 1991; and others). For example, surgically implanted temperature-sensitive radio transmitters revealed daily variations in the body temperatures of free-ranging garter snakes (*Thamnophis elegans vagrans*) in eastern Washington (Peterson, 1987) (Fig. 15.13). Collars may be designed to deteriorate after a certain length of time, or, in long-term studies, the animal may need to be recaptured and refitted with a new collar. Intraperitoneal radio-transmitter implants were found to have no effect on reproductive performance (copulation, embryonic and fetal development, and lactation) in river otters (Reid et al., 1986). Snakes have been fitted with internal transmitters that still allow the snake to move through small openings and to shed its skin.

Figure 15.12. Male elk (*Cervus canadensis*) with a radio transmitter, permitting movement and behavioral studies of animals of known age and sex, even though they may be located several kilometers away.

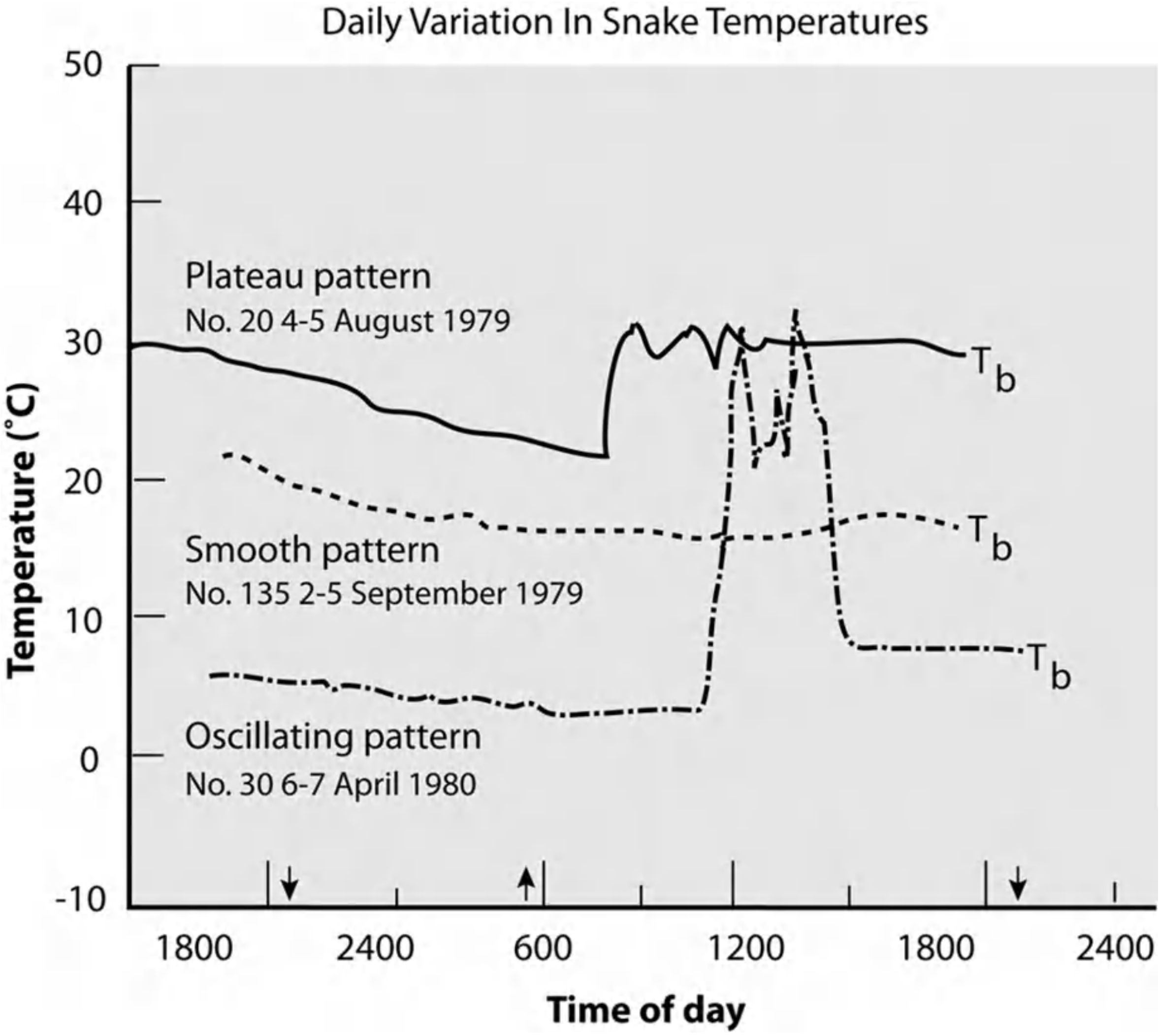


Figure 15.13. Surgically implanted temperature-sensitive radio transmitters have been used to reveal daily variations in the body temperatures of free-ranging vertebrates, including garter snakes (*Thamnophis elegans vagrans*) in eastern Washington. The daily body temperature patterns shown here are classified as plateau pattern, smooth pattern, and oscillating pattern. Sunrise (↑) and sunset (↓) are indicated on the time axis.

Transmitters have been glued to the bony shells of some species of turtles, but the oily, flexible skin that covers the thin, loosely fused, bony plates in a leatherback sea turtle's carapace resists adhesives. In an experimental technique, the bone is pierced with 1.27 cm (1/2 in.) long screws made of a synthetic polymer that slowly dissolves (Raloff, 1998). A nylon suture is threaded through each screw and serves to firmly attach the transmitter. As the screws dissolve, they are replaced by bone that continues to anchor the sutures until they weaken and release the transmitter.

Radio contact with naturally migrating whooping cranes (*Grus americana*) traveling between their wintering site off the coast of Texas and their breeding site in Canada has been maintained by means of leg-band radio transmitters, antennas attached to aircraft struts, and radio receivers carried in the aircraft (Kuyt, 1992). Radio signals, which could be picked up from distances up to 155 km (96 mi.), have allowed researchers to follow the cranes. Visual contact has been maintained for up to 50 percent of the migration, enabling air crews to obtain data on flight behavior.

The miniaturization of tracking devices has allowed researchers to gather data on smaller birds. Miniature light loggers (geolocators) with a mass of just 1.4 grams (0.05 oz.), which is less than a paper clip, were attached to plastic leg rings of Arctic terns (*Sterna paradisaea*) at their breeding grounds in Greenland and Iceland (Egevang et al., 2010). The combined weight of the logger, ring, tape, and cable tie was 2.0 g (0.07 oz.), approximately 1.9 percent of the average 125 g (4.4 oz.) size of an adult bird. The loggers work by recording and storing ambient light intensity, which in turn reveals information on sunrise and sunset. When this data is combined with time recordings, two geographical positions per day can be calculated, which adds up to a record of the entire migration route including stopover sites and wintering areas. While light loggers are much lighter and cheaper than conventional satellite transmitters, they do not transmit their data, so the only way it can be retrieved is by recapturing each bird and removing the device. DeLuca et al., (2015) affixed dime-sized devices that record daylight and time to the backs of 20 blackpoll warblers that weighed just 12 g (0.42 oz.) apiece. Results showed that blackpolls fly about 2,500 km (1,550 mi.) over water, stopping off in the Caribbean en route to Venezuela—one of the longest nonstop overwater flights ever recorded for a songbird.

A male wolverine that researchers radio-collared in Wyoming's Teton Mountains in 2002, and monitored for almost two years, ranged widely through mountain terrain. In one 19-day stint, the wolverine made a round-trip of 412 km (256 mi.) between Grand Teton National Park and Pocatello, Idaho—an average of 21.7 km (13.5 mi.) a day. A few days later, he made a round-trip between the Tetons and Mount Washburn, in Yellowstone National Park, averaging 32.1 km (20 mi.) a day for a solid week. He generally stayed in forests above 2,134 m (7,000 ft.) and covered an estimated area of some 59,570 km^2 (23,000 mi.^{2}), suggesting that this rarely seen species may need a huge amount of suitable habitat in order to survive.

In studies of marine species, specific problems arise because of diving and because of the effect of high electrolyte concentrations on the radio signals. A floating transmitter tethered to a swivel strapped to the tail stock was devised and successfully used in studies of manatees (Rathbun et al., 1987). Baits containing acoustic transmitters have been consumed by deepsea fishes. In conjunction with an automatic tracking system and cameras on the seafloor, this technique has allowed the tracking of the speed and direction of travel in deepsea scavenging fishes (Priede et al., 1991).

Summaries of standard radio-tracking techniques have been presented by Mech (1983), Godfrey and Bryant (2003), Cooke et al. (2013), and Lopez-Lopez (2016). Mech and Barber-Meyer (2002) present a critique of wildlife radio tracking in national parks. *Radio Tracking and Animal Populations* (Millspaugh and Marzluff, 2001) is a succinct synthesis of technologies and their applications to the problems of population assessment.

A 16-year effort to detect from space the movements of small animals tagged with radio transmitters got a boost in August 2018 when Russian cosmonauts unfurled an antenna on the International Space Station. The 3 m (9.8 ft.) by 2 m (6.6 ft.) device was set to become fully operational in 2019, giving animal researchers more comprehensive movement data over larger areas than they can monitor with handheld receivers in the field. Members of the International Cooperation for Animal Research Using Space (ICARUS) group have designed 5 g (0.18 oz.) tags that can send the space-based antenna many kinds of data, including an animal’s location and acceleration and the temperature and magnetic field in its surrounding environment. The antenna can scan 120 such tags over a 30 to 800 km (18.6–497 mi.) area every three seconds. Among many planned projects, the ICARUS team will test whether the behavior of goats on Italy’s Mount Etna predicts its eruption and track African fruit bats to better understand Ebola’s spread.

Investigating wild animals while minimizing human disturbance remains an important challenge. To gather data on nesting emperor penguins in Antarctica, LeMaho et al. (2014) created a remote-control rover disguised as a chick to approach shy penguins while researchers watch from more than 198 m (650 ft.) away (Fig. 15.14). The rover is covered in gray fur, sports black arms, and has a black-and-white painted face and black beak. At times, the rover crowds in with a group of chicks, acting as “a spy in the huddle.” It is equipped to make radio-frequency identifications in order to read signals from radio tags on the adult birds. Penguins had significantly lower and shorter stress responses (determined by heart rate and behavior) than when approached by humans. The rover did not disorganize colony structure, and stress rapidly ceased. LeMaho has also used a rover without any animal disguise to gather data on king penguins and elephant seals.

Figure 15.14. Remote control rover gathering data on nesting emperor penguins in Antarctica.

Satellite Tracking

Satellite tracking is one of the latest tools in the repertoire of wildlife biologists. It allows for monitoring of an individual by providing an update with every pass of the satellite. Satellite tracking is best used in situations where conventional tracking techniques are not useful, like for animals that range widely or are in habitats where they cannot be followed. Compared with conventional radio tracking, satellite tracking is less accurate and more expensive.

Satellite tracking has been used successfully on a variety of species, including sea turtles, penguins, whales, elephant seals, polar bears, elephants, caribou, bears, musk oxen, ocelots, and manatees (Mate, 1989; Reynolds, 1989; Rathbun et al., 1990; Holden, 1992; Stewart and DeLong, 1995; Reid, 1997). One of the first successful tracking experiments of a bird using satellite telemetry was reported by Jouventin and Weimerskirch (1990), who showed that wandering albatrosses (*Diomedea exulans*) remain active at night, fly at speeds of up to 80 km (50 mi.) per hour, and range over distances of up to 900 km (550 mi.) per day. Albatrosses covered from 3,600 to 15,000 km (2,200–9,300 mi.) in a single foraging trip during the time their mates had taken over the duties of incubation. Most studies of albatrosses and petrels have recorded extended trip durations and, in some cases, high rates of nest desertion following transmitter attachment. Phillips et al. (2003), however, found that while only a few black-browed (*Thalassarche melanophris*) and gray-headed (*T. chrysostoma*) albatrosses may have slightly extended their foraging trips, overall there was no significant difference in trip duration, meal mass, breeding success, or rate of return in the next season between birds with transmitters and controls. In order to minimize effects, they suggested that transmitter loads be reduced to a minimum, the use of harnesses be avoided (particularly for breeding season deployments when tape attachment to feathers is an effective alternative), and that careful attention be given to limiting handling times during incubation when some species are particularly sensitive to disturbance.

Figure 15.15. Trumpeter swans (*Cygnus buccinator*) following an ultralight aircraft, a method designed to teach birds the ancient migratory route of their ancestors.

Teaching Birds to Migrate

Migration is important because birds that do not fly south for the winter are more likely to exhaust their food supply, become a nuisance to people, get sick, or freeze to death. Many waterfowl learn to migrate from their parents, but if the older birds in a flock are killed by hunters, the young do not know where to migrate and the knowledge is forever lost.

Beginning in the early 1990s, motorized ultralight aircraft have been used to guide a variety of species of waterfowl to wintering areas. In 1993, an ultralight piloted by Bill Lishman led a Canada goose migration from Ontario, Canada, to the Airlie Environmental Center in Warrenton, Virginia—a trip depicted in the 1996 movie *Fly Away Home*. In October 1995, an ultralight led eight sandhill cranes on an 11-day, 1,204 km (930 mi.) trip from Idaho to the Bosque del Apache National Wildlife Refuge in New Mexico. In October 1997, an ultralight painted to look like a whooping crane guided two of the endangered white birds and six sandhill cranes on a nine-day flight from Idaho to New Mexico. The first time that an ultralight aircraft was used with an endangered species occurred in 2001 when a flock of seven whooping cranes was led south from the Necedah National Wildlife Refuge in central Wisconsin to the Chassahowitzka National Wildlife Refuge on Florida's Gulf Coast (see details in Chapter 17).

Trumpeter swans (*Cygnus buccinator*) vanished from the Chesapeake Bay nearly 200 years ago. These swans are white with a black beak, weigh up to 13.5 kg (7.5 lb.), have a 2.5 m (8 ft.) wing span, and can stand up to 1.8 m (6 ft.) tall with neck outstretched. Beginning in 1997, scientists working with Defenders of Wildlife, a conservation organization based in Washington, DC, and the US Fish and Wildlife Service have attempted to restore America's largest waterfowl to the mid-Atlantic region by reteaching the birds to migrate by using a bright yellow ultralight plane with an overarching white wing (see Fig. 15.15). The goal of this project was to reestablish a migration route between upstate New York and Maryland's Eastern Shore. As of 2018, despite repeated attempts, this project has not met with success.

In October 2000, a single-propeller ultralight led a flock of 11 sandhill cranes on a month-long, 2,013 km (1,250 mi.) flight from central Wisconsin to Florida. This was the longest human-led bird migration in history. In January 2001, 10 trumpeter swans followed an ultralight from New York to the Horseheads Wetland Center operated by Wildfowl Trust of North America on Chesapeake Bay near Grasonville, Maryland. Projects involving Canada geese, trumpeter swans, and ultralight aircraft from 1990 to 2001 have been reviewed by Sladen et al. (2002).

In an effort to find a method that is less time-consuming than using an ultralight aircraft and that could be used to train more birds to migrate, wildlife researcher William Sladen, Director of Environmental Studies at Airlie Environmental Center, is experimenting with helium balloons and passive migration. On December 22, 2017, 10 Canada geese in crates suspended from a helium balloon were launched from the Airlie Center in an attempt to see whether birds can learn a migration route passively by being carried over it in crates, rather than actually flying the route themselves behind an ultralight. The geese were transported 113 km (70 mi.) south and released. As of April 2018, none of the geese had returned.

Lewis, 1996; Lishman et al., 1997; Sladen et al., 2002

In 2005, a frigatebird was tracked with a global positioning device. The bird made a nonstop journey of just more than 26 days and covered nearly 1,550 km (960 mi.) before returning to her chick on Christmas Island. This represents the longest known nonstop journey for this species.

Several widely used tags for tracking marine vertebrates are pop-up archival transmitters (PAT) tags, satellite-linked transmitters (SAT) tags, and smart positioning or temperature-transmitting (SPOT) tags (Hart and Hyrenbach, 2010; Cyr and Nebel, 2013). PAT tags accurately record and store information about water depth, temperature, and ambient light levels. Frequently used for monitoring large-scale movements, they have preprogrammed detachment dates, usually between 30 and 90 days. Upon floating to the surface, they transmit a data summary to passing Argos satellites. The raw data can be obtained upon retrieval of the tag. SAT tags accurately determine geographical locations via Doppler-shift calculations and transmission to orbiting Argos satellites. They are designed to be long-lasting, transmitting signals until they run out of batteries or become detached. SPOT tags are highly accurate devices for recording small-scale movements. They track movements at near-real time, and are particularly useful for tracking horizontal movements of individuals, which can be analyzed at much higher resolution than those obtained from PAT tags. SPOT tags contain a saltwater switch, which initiates transmission only when it surfaces. The collection of geological positioning data is dependent on passing satellites, which may require the tagged animal to surface for long periods of time, which is one of the major disadvantages of using SPOT tags. Satellite and data logging technology is continually improving with recent modifications such as fast-GPS tags, tri-axial accelerometer tags, mobile phone telemetry, acoustic “business card” tags, and satellite-relayed data loggers (SRDLs). Satellite and data logger telemetry will continue to yield data that can be used in the field of ecological conservation and management of marine vertebrates.

High-Tech, Humane Ways Biologist Can Identify Individual Animals

In the past, researchers have relied on externally imposed methods of identifying individual animals, such as leg or arm bands, collars, toe clippings, ear notching, brands, or tattoos. Such methods are often invasive and can alter behavior, injure the animals or increase susceptibility to predators by impeding movement or camouflage. Capture-recapture methods that include no increased mortality or alterations of behavior may still be employed.

Within the past decade, biologists have developed new high-tech ways of using animals’ unique features to differentiate between individuals with minimal physical interference. Researchers are starting to rely on a combination of biometric technologies (the use of biological characteristics to identify individuals) and animals’ unique characteristics to remove the need for invasive or disruptive tagging techniques, allowing conservationists to monitor individuals without putting undue stress on the animals. Individuals can be recognized based upon various morphologies and phenotypic variations including pelage patterns, tail flukes, and whisker arrangement. Biometric systems use four biologic measurement criteria: universality, distinctiveness, permanence, and collectability.

Whales

High-resolution satellite images have provided unprecedented details of individual whales, a step toward making comprehensive, automated population counts of whales worldwide. Satellites can survey more of the ocean than boats and planes can. In the past, low resolution meant whales appeared more like blobs.

The high resolution of the new images—31 cm^2 (5 $in.^2$) on a side—allows specialists to distinguish body sizes, shapes, and features such as flukes and fins, which are useful for identifying species. By examining images from the new, privately owned WorldView-3 satellite of four ocean patches where fin, gray, humpback, or southern right whales congregate, researchers counted 200 whales seen in enough detail to assign them to one of those species.

Zebras

Each zebra has a unique configuration of stripes, which allows conservationists to keep track of zebra populations without physically tagging the animals. In 2011, a joint project between Princeton University and the University of Illinois at Chicago created StripeSpotter, a computer program to identify the animals in the wild. The software converts digital photos of zebra’s flanks into a series of horizontal, black-and-white pixelated bands, which creates a unique “StripeCode” for each animal, similar to a barcode. The software is currently being used to build a zebra-print database for plains and endangered Grévy’s zebras in Kenya.

Bats

A new noninvasive technique for identifying individual bats involves examining patterns of collagen-elastin bundles on the bats' fibrous wings. Differentiation of individuals of little brown bats (*Myotis lucifugus*), northern long-eared bats (*M. septentrionalis*), big brown bats (*Eptesicus fuscus*), and tricolor bats (*Perimyotis subflavus*) have proven highly effective with a 96 percent success rate using photographs taken at previous times, even when identifying bats with wings damaged by fungus.

Koalas

Patterns of pigmentation on the large, leathery noses of these marsupials has been used as a method of identification for many years. It does not require researchers to actively capture and individually tag the animals.

Lemurs

Researchers at Michigan State University created a database, LemurFaceID, that modifies human facial recognition software (used to detect passport fraud and to catch shoplifters) to study endangered lemur populations in Madagascar. The software breaks down lemur facial characteristics to the pixel, allowing researchers to create a database of lemur faces to use while tracking population changes. Future modifications may enable conservationists to identify other primates facing extinction.

Amelon et al., 2017; Crouse et al., 2017; Cubaynes et al., 2018; White, 2019

Elephant seals carrying satellite transmitters have been found to dive more frequently and deeper than previously thought—some 60 times a day, routinely as far down as 600 m (1,970 ft.), and sometimes as deep as 2,000 m (6,500 ft.) (Pala, 2006).

Kenya is the first country to try elephant texting as a way to protect both a growing human population and the wild animals that now have less room to roam (Houreld, 2008). The Kenyan Wildlife Service and the conservation group known as Save the Elephants place mobile phone SIM cards in elephant collars, then set up a virtual "geofence" using a GPS that mirrors the conservatory's boundaries. When an elephant approaches the virtual fence, its collar texts rangers, who speed to the site in jeeps bristling with spotlights to frighten the elephant back onto the conservancy's property and away from neighboring farms. The experiment is in its infancy. It requires full-time staff and a standby vehicle to respond when a message flashes across a ranger's screen. It is hoped that the project, which thus far has been a success, will help resolve some of the many complaints about elephants raiding and destroying crops.

MAPPING TECHNIQUES

Geographic information systems (GIS) technology is the computerized recording of data for a region, using geographic coordinates as the primary indexing system. The kinds of data that can be stored include presence or absence of a species, abundance of that species where it is present, ecosystem type, soil type, geology and physiography, land protection status, and many other variables. For example, most home-range studies have focused only on the horizontal component of the landscape (planimetric area), where the slope of the terrain is assumed to be zero. Topography adds an important element to landscape because the slope of the terrain often fluctuates throughout the home range, and because changes in topography can increase the surface area. A GIS that incorporates topography can account for topographic changes and yield more accurate estimates of home-range size (Stone et al., 1997).

GIS systems are well adapted to using data from remote sensing sources. Detailed data on the actual vegetation of a geographical area are difficult to obtain from traditional vegetation maps, which often show the potential climax vegetation thought to characterize a region rather than the vegetation actually present. With improved satellite imagery and analysis, detailed data on the vegetation that actually exists can be determined on a grid scale and entered into the indexing system. Ideally, a GIS system permits data on a particular feature to be stored for all the geographic units included in the indexing system. With modern GIS systems, it should be possible to develop much more comprehensive databases than previously available for researchers and conservationists.

CENSUSING TECHNIQUES

The word *census* is defined as a count, which usually includes details as to sex and age. A **true census** is a count of all individuals present in a given area. Because such counts of wild animals are rarely possible, estimates usually are made based on some sampling procedure. **Sampling estimates** are derived from counts made on sample plots or a portion of a population. These estimates have variability, but still permit inferences about the population. An **index** is a count of some object that is related in some numerical way to the animal, like tracks, feces, call counts, or nests. For example, Richard and Karen Barnes developed the first standardized method for gauging elephant populations by counting dung piles along previously identified routes and inserting the results into a mathematical formula that considers rates of defecation and dung decay (Tangley, 1997). Similar methods have been developed for jackrabbit indexing (Blackburn, 1968).

For population estimates to be valid, all members of a population must have an equal probability of being counted, or the relative probabilities of counting different categories of individuals (e.g., sex and age classes) must be known. Animals must not group by sex or age, they must mix randomly, and they must not develop "trap-shyness" or "trap-happiness" if grid live-trapping is being employed (see Chapter 12). In addition, during the period when data are collected, either mortality or recruitment must be negligible, or the estimates must be corrected for these effects.

Data may be gathered by visual observation or by evidence of an animal's presence (tracks, calls, etc.). For instance, haypiles of pikas (*Ochotona*) may be found in late summer and fall and can be used as an index. The average distance between the haypiles of adjacent pikas is approximately 30 m (100 ft.) (Smith, 1982). Another method of gathering data is by the use of a transect. **Transects** are predetermined routes that are covered in an effort to estimate a population. All animals that are sighted or heard are recorded. Transect data from different seasons and years provide relative estimates of population size.

Many territorial species can be observed easily within their territories and counted for a specific area. The result usually is expressed as animals per hectare. However, nonterritorial individuals in these species often are hard to count. Animals that congregate in groups or flocks (e.g., coveys of quail, flocks of turkeys and other birds, herds of antelope and bison) are relatively easy to count either on the ground or by means of aerial photographs. In those species of frogs and birds that call or sing, the vocal members of the population can be counted. The National Audubon Society's annual Christmas Bird Count provides an index of species' abundance nationwide. The North American Breeding Bird Survey has provided valuable data on the sizes of breeding bird populations since 1965, especially those of neotropical migrants. Such databases are revealing steady population declines of breeding birds for many species in North America (see Chapters 16 and 19).

Fecal DNA analysis is potentially a powerful method for identifying species, population size, sex ratio, home range, paternity, and kinship. However, finding enough samples for this approach is difficult and time-consuming in many habitats, like dense vegetation. Trained scenting dogs, however, can find many times as many scats as an experienced person searching for scats visually—because they possess the extraordinary ability to detect odors at concentrations 100 million times lower than what humans can smell. Dogs have been trained to specifically detect the scats of a particular species—bobcat, lynx, cougar, jaguar, kit fox, coyotes, grizzly bears, black bears, giant anteater, giant armadillo, orcas, and others—and ignore the scats of any other species (Smith et al., 2003; Wasser, 2008). Since species identification based on mitochondrial DNA (mtDNA) currently costs about $40 per sample, the use of scent-detection dogs to distinguish scats from species of interest could provide a cost-effective alternative to laboratory methods in some conservation applications.

Figure 15.16. The author and his dog, Brandi, whose training and keen sense of smell have aided in locating mammal scats along trails.

Statistical estimates of population size based on sample plots, indices, rates of capture, changes in sex or age ratios, recaptures, or home-range data can be calculated by many different methods (Mosby, 1963). The Lincoln Index (also known as the Petersen-Jackson Method because it was first used on wild populations of plaice by Petersen [1896]), for example, is based on the recapture of marked individuals where the population (N) is related to the number marked and released (M) in the same way as the total caught at a subsequent time (n) is related to the number of marked individuals captured (m).

Censusing methods, along with capture and marking techniques, have been discussed for game birds and mammals by Mosby (1963), for terrestrial vertebrates by Davis (1982), for amphibians by Heyer et al. (1994), and for mammals by Wilson et al. (1996).

AGING TECHNIQUES

Many fishes, amphibians, and reptiles grow throughout their lives. This **indeterminate** growth is most rapid in younger individuals; it may speed up when food and environmental conditions are favorable and slow down when conditions are more stressful, like during periods of cold, drought, and food shortage.

Birds and mammals generally experience a steady increase in size until they reach maturity, after which growth slows and essentially ceases for the remainder of their lives. This is known as **determinate** growth.

Various methods of determining the age of vertebrates have been developed. Animals that are captured shortly after hatching or birth and that are marked and recaptured at periodic intervals provide the most accurate means of determining age under natural conditions. In some cases, direct observation of an animal’s life stage, physical features, and size can give an approximation of its age. Lifecycles of most amphibians, for example, involve two, and sometimes three, distinct stages (larval or tadpole, and adult). Few long-term age-determination studies have been reported. In one long-term reptilian study, three-toed box turtles (*Terrapene carolina triunguis*) studied for 25 years had estimated ages ranging from 27 to 59 years at the conclusion of the study (Schwartz and Schwartz, 1991).

Working Dogs for Conservation

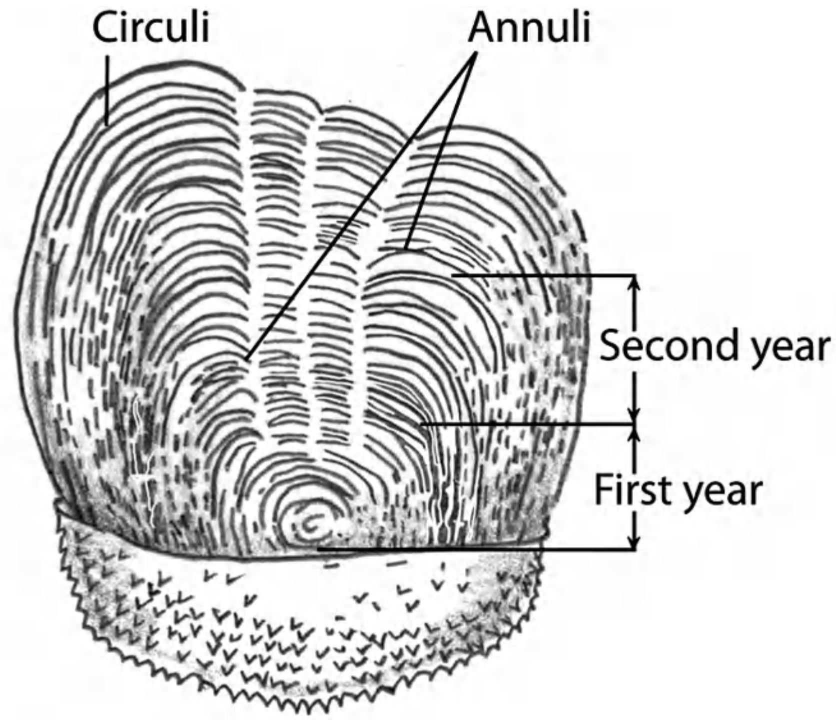
Working Dogs for Conservation (https://wd4c.org) is a nonprofit organization founded in 2000 and headquartered in Bozeman, Montana, with three main aims: monitoring endangered wildlife, defining wildlife corridors, and helping eradicate damaging invasive species. Over the past 18 years, their dogs have been trained to detect a variety of wildlife scat (ranging from grizzly, black, and moon bear, wolf, cougar, kit fox, blunt-nosed leopard lizard, moose, wolverine, and fisher), as well as live wildlife (including black-footed ferrets, brown tree snakes, and desert tortoises) and invasive plants. Partnerships with 50 conservation groups (universities, local and international nongovernmental organizations, state and federal agencies, and private researchers) have taken them to five continents to collect data on over 30 plant and animal species. Individual researchers have used dogs to locate scat and signs of many species including gibbons, monkeys, and jaguars. The author of this book trained his dog, Brandi, to help locate potential mountain lion scats in Great Smoky Mountains National Park (see Fig. 15.16).

Most young birds have several distinct juvenile and subadult plumages as they mature, like natal down, juvenal plumage, first winter plumage, and nuptial plumage (see Chapter 8 for detailed discussion of molts and plumages). Some birds, like bald eagles, may not attain their full adult plumage until they are 3, 4, or even 5 years old. The pelage of many young mammals also differs from the adult pelage and is known as the **juvenal** pelage. When molting occurs, this pelage usually is replaced by the **postjuvenal** pelage and then by the **adult** pelage.

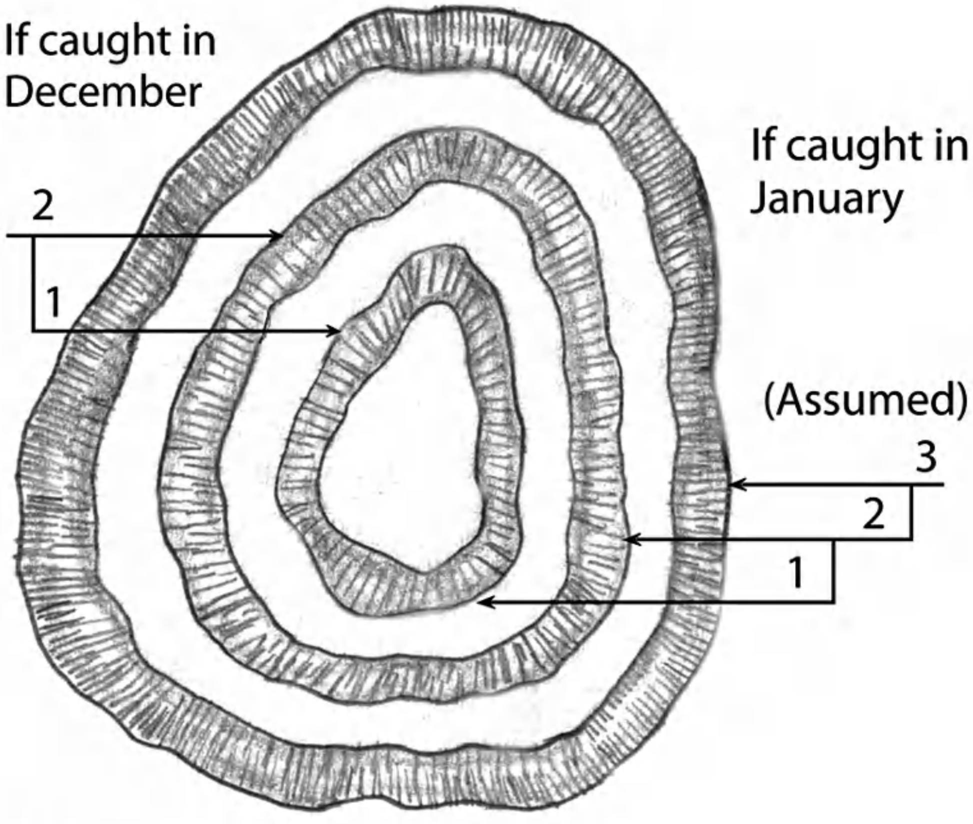
More precise age-determination techniques vary among the vertebrates and involve features of the integumentary, skeletal, and even the nervous systems. Some techniques are useful in field investigations with live animals, whereas others can only be used on dead specimens. For example, temperate-zone fishes can be aged by examining the annuli on scales (Fig. 15.17a), bones, and ear-stones (otoliths) (Fig. 15.17b), and in cross sections of fin rays, fin spines, and vertebral centra. Many fish deposit otolith growth increments with a 24-hour periodicity (Panella, 1971; Prince et al., 1991; Kingsmill, 1993). In some species, like Atlantic salmon (*Salmo salar*), the scales may contain spawning marks. Examination of such scales can provide information about when the fish first went to sea, its age when it first spawned, how many times it has spawned, and its age at capture. Because growth accelerates in the sea, annuli are more widely spaced.

Annuli also are evident on the scutes of some turtles. Most juvenile turtles add single growth rings each year, whereas rings are added less frequently as adults (Galbraith and Brooks, 1989) (see Fig. 15.17c). Moll and Legler (1971) reported that multiple growth lines were added each year in a population of neotropical sliders (*Pseudemys scripta*) in Panama. Annual bone rings in the phalanges and femurs of lizards have been used to age such species as tuataras (*Sphenodon*) (Castanet et al., 1988). Klinger and Musick (1992) injected tetracycline into juvenile loggerhead turtles (*Caretta caretta*) in the Chesapeake Bay area and found annular deposition in bone layers.

The condition of teeth is useful for establishing the age of mammals. Both the deciduous and permanent dentitions usually erupt in a definite sequence and at definite times in different species. Patterns of wear, particularly of the permanent dentition, provide a fairly accurate means of determining age, particularly in large herbivores (Fig. 15.18). In addition, roots of teeth in some mammals form annual growth ridges on their surfaces. The roots of teeth also may be sectioned to reveal the presence of growth rings or annuli. Many studies involving game species, like bears, use data obtained from an extracted premolar removed at a checking station. In addition to being used as an aging technique, the incremental layering of the dental cementum can be used to reconstruct the reproductive histories of female black bears (Coy and Garshelis, 1992).


Circuli
Annuli
Second year
First year

(a)


If caught in December
2
1
If caught in January
(Assumed)
3
2
1

(b)

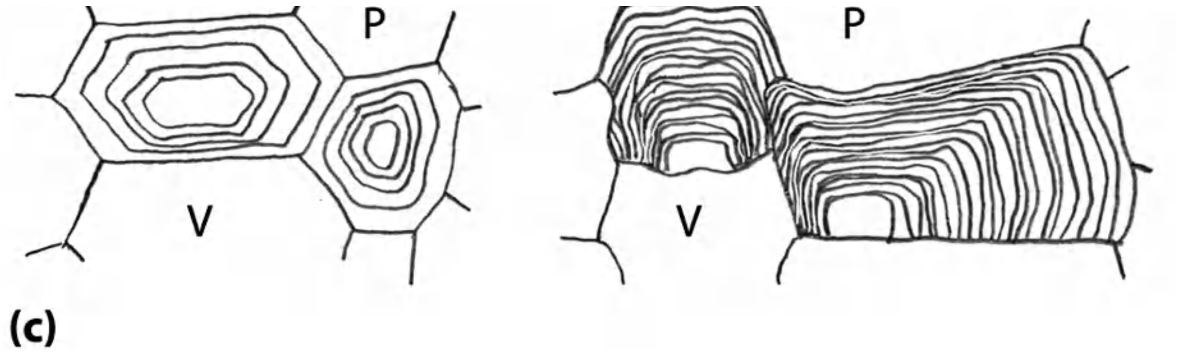


Figure 15.17. (*a*) A typical ctenoid scale, showing groups of concentric rings that can be classified into annuli and interpreted as seasonal growth marks. (*b*) A fish otolith showing annuli. A year class and/or birthdate can be assigned, using the time of year the fish was collected. (*c*) Growth lines (annuli) on the vertebral (V) and the pleural (P) shields of the terrapin (*Malaclemys*) (*left*) and the box turtle (*Terrapene*) (*right*). In *Malaclemys*, embryonic shield areas are near the center of the shields; in *Terrapene*, they are eccentrically located, and growth proceeds primarily anteriorly and laterally.

Mammals with permanent horns, like sheep and goats, often possess ridges on their horns (Fig. 15.19). These ridges are the result of periods of good (summer) and poor (winter) food conditions. When forage is good, the horns grow rapidly; when forage is poor, the horns stop growing. The stoppage is marked by a ridge that has proved to be a valuable aging tool in these mammals.

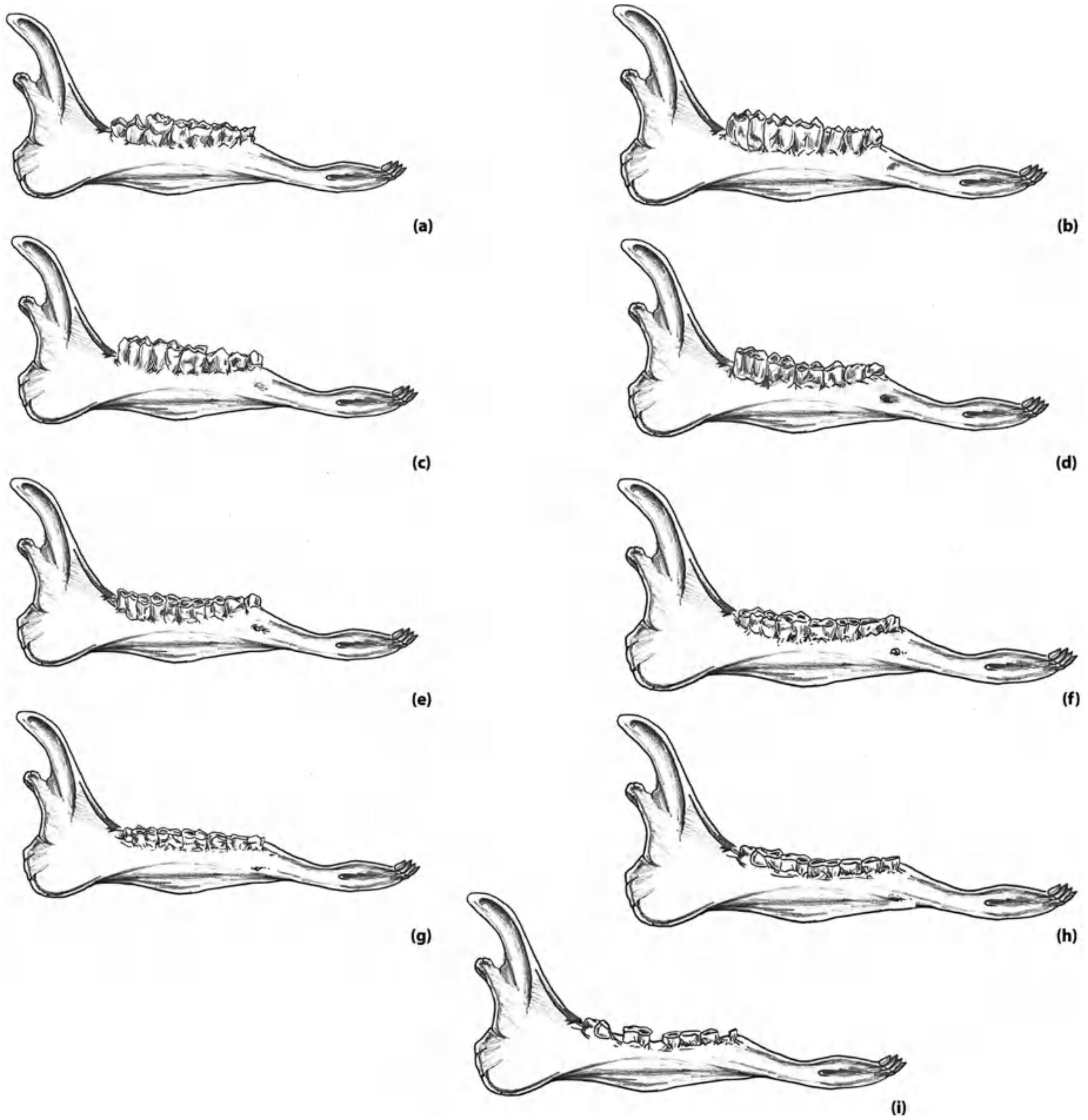


Figure 15.18. Progressive wear on the molars is used to determine the age of white-tailed deer (*Odocoileus virginianus*): (*a*) 1 year, 7 months; (*b*) 2.5 years; (*c*) 3.5 years; (*d*) 4.5 years; (*e*) 5.5 years; (*f*) 6.5 years; (*g*) 7.5 years; (*h*) 8.5–9.5 years; (*i*) 10.5 or older.

As a mammal grows, its long bones lengthen from the tips. While it is growing, each long bone has a cartilaginous zone: the **epiphyseal plate** near each end covered by a bony cap, the **epiphysis**. Bone is deposited at the inner side of the cartilaginous zone, pushing the cap farther out as the bone grows. When growth is complete, the cartilage ossifies (is replaced by solid bone), so that the cap and the shaft are fused firmly together. The only remaining evidence of the epiphyseal plate is a line known as the epiphyseal line. Thus, examination of the ends of long bones often can provide an indication of the age of a mammal. In many bats, the joints of the bones in the wing remain swollen until ossification is complete.

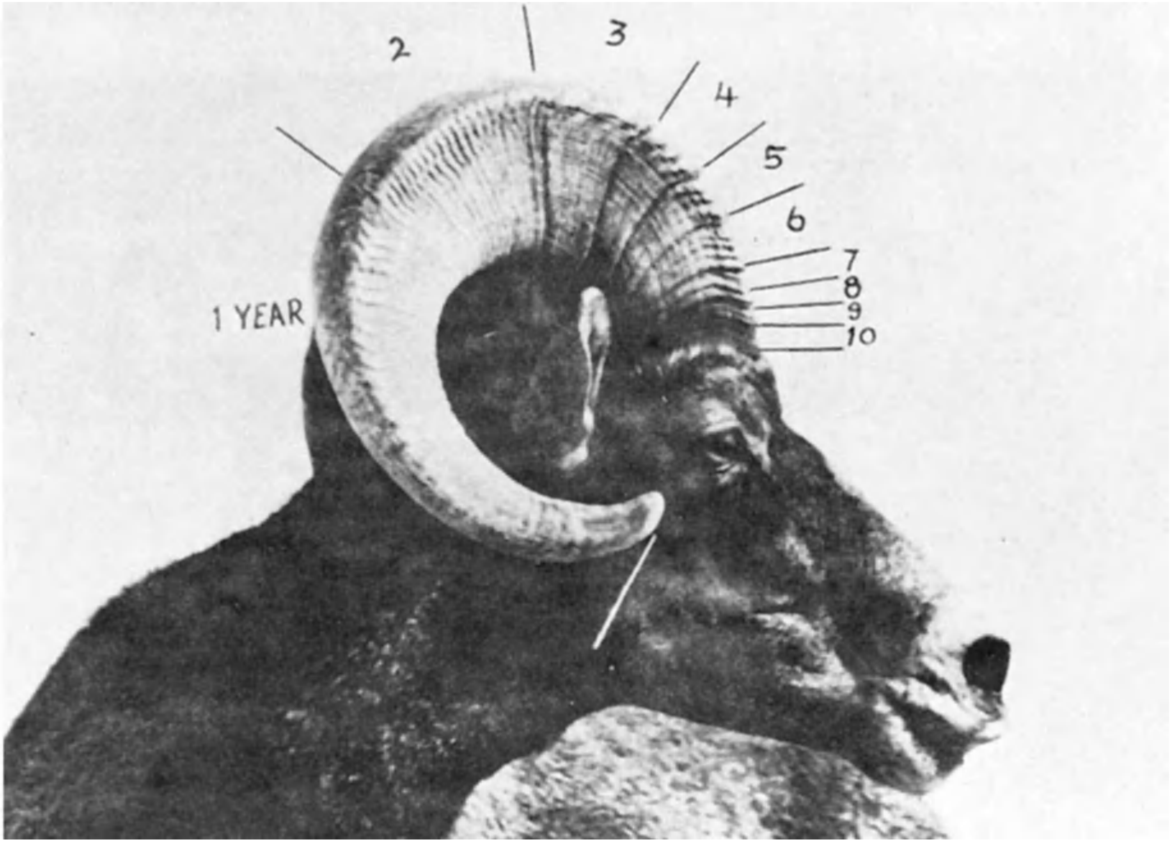


Figure 15.19. Annual rings in the horn of a 10-year-old desert bighorn sheep (*Ovis canadensis*).

Other methods of measuring age include the weight of the eye lens, the condition of the baculum (os penis) in those mammals in which it is present, and the development of prominent crests and ridges on the skull, particularly in male mammals.

In addition, a number of species-specific aging techniques have been employed. Among these are leg coloration in coots (*Fulica*), the size of spurs on ring-necked pheasants (*Phasianus colchicus*), and the presence of lateral suprasesamoid tubercles on the femurs of adult mink (*Mustela vison*) (Gullion, 1952; Lechleitner, 1954; Godin, 1960).

Review Questions and Topics

1. What factors must be taken into consideration when designing a research program for a wide-ranging species like a cougar? How would this differ from a prairie dog research study?
2. Discuss several techniques for capturing small mammals alive and uninjured.

3. List several techniques for marking reptiles and mammals for short-term studies.
4. List several techniques used to tag birds and mammals so that individuals can be recognized at a distance.
5. List several advantages and several disadvantages of attaching external radio transmitters to vertebrates.
6. What are some advantages and some disadvantages of satellite tracking as compared with the use of radio transmitters?
7. List several ways of censusing vertebrate populations. Which methods would provide the greatest amount of data for the spotted salamander (*Ambystoma maculatum*), which lives underground most of the year but migrates to a breeding pond in late winter?
8. Differentiate between determinate and indeterminate growth. Give several examples.
9. List several techniques used to determine the age of vertebrates.
10. Which methods of age determination would be most appropriate for studying a population of marine toads (*Bufo marinus*) whose life expectancy may be as much as 8 years?

Supplemental Reading

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Vertebrate Internet Sites

1. Tracking Sea Turtles

   www.gma.org/space1/turtles.html

   Students can plot actual turtle migration paths. Links to sensory remote sensing, satellite tracking, visible and infrared satellite images.

2. Geographical Information System (GIS)

   www.gis.com/content/environmental-management-and-conservation

   Environmental management and conservation and natural resource sections with maps and links.

3. Bird Banding

   www.usgs.gov/centers/pwrc/science/bird-banding-laboratory

   Website of the US Geological Survey Bird Banding Laboratory at the Patuxent Wildlife Research Center. Administers the North American Bird Banding Program, which manages more than 77 million archived banding records. Information about securing a federal banding permit, how to report a banded bird, and information about the history of bird banding.

   Excellent discussion of capture and marking methods. Bibliography.

4. Working Dogs for Conservation

   www.workingdogsforconservation.org

   Learn more about scat detector dogs.

5. Sea Turtles

www.noaa.gov/topic-tags/sea-turtles

Much information about sea turtles including many short videos on marking, rescues, potential effects of global warming, designation of critical habitat, and more.

6. Seaturtle.org: Satellite Tracking

   www.seaturtle.org/tracking

   Sea turtle tracking projects online. Many satellite tracking links with daily project updates.

16 | Extinction and Extirpation

Natural and Human-Caused

> What is man without beasts? If all the beasts were gone, men would die from a great loneliness of the spirit. For whatever happens to the beasts soon happens to man.
>
> Chief Seattle, 1854

INTRODUCTION

Extinction is the most obscure and local of all biological processes. We usually do not see the last individual of a species as it dies or is captured by a predator. We hear that a certain animal or plant is imperiled, perhaps already gone. We return to the last known locality to search, and when no individuals are encountered there year after year, we pronounce the species extinct.

After a six-year series of forest surveys in the high-canopy forests (rain forests) in Ghana and Ivory Coast, scientists pronounced a type of large West African monkey presumably extinct in 2000 (Oates et al., 2000). The International Union for Conservation of Nature (IUCN) Red List notes this monkey, Miss Waldron's red colobus, as critically endangered. It is hard to prove that an animal is extinct, but the team was confident that they would have found the noisy, conspicuous monkeys had they still been around. The last confirmed sighting of Miss Waldron's red colobus (*Piliocolobus badius waldronae*) was in 1978 in Ivory Coast. It was listed as endangered in 1988. Scientists blame its demise on hunting for bush meat and the disruption of habitat by logging, road-building, and farming. It would be the first primate to become extinct in more than a century, the last being the giant aye-aye (*Daubentonia robusta*), a lemur that lived in Madagascar until the nineteenth century. Discovered in 1933, the red colobus monkeys are popular targets for hunters who supply local markets with game meat because they weigh 20 pounds or more and live in large, noisy social groups.

Several months after the initial article declaring the species extinct was published, a hunter in Ivory Coast showed a scientist the tail of a monkey he had recently killed. DNA tests proved the tail came from a Miss Waldron's red colobus. In 2002, a monkey hide containing freshly dried blood was observed hanging on a clothesline in an Ivory Coast village. The hide had red fur on its thighs and brow, unmistakable Miss Waldron's markings. In 2003, a recent photo surfaced of a monkey carcass that appeared to be a Miss Waldron's. Thus, even though scientists are unable to find a live specimen, some members of the species apparently still survive (McGraw, 2005). A similar situation occurred in 1962 involving the Bavarian pine vole (*Microtus bavaricus*). It was declared extinct, but in 2000 a small population was found living in Austria.

* * *

Populations decline whenever deaths and emigration exceed births and immigration. The elimination of a species or subspecies from a region, although it continues to exist elsewhere, is known as **extirpation**. The cougar (*Puma concolor*) is thought by many to be extirpated from most of the eastern United States, but cougars remain in Florida and many western states as well as in Canada, Central America, and South America. **Extinction** is the total disappearance of a species. Extinction has been the fate of most species since the origin of life. Dinosaurs, passenger pigeons, heath hens, dodos (Fig. 16.1), mastodons, and saber-toothed tigers are among the many vertebrates that have become extinct. Disappearance of entire species or even entire families, orders, or classes has occurred at times of extreme environmental change or, more recently, because of human action.

With or without human interference, extinction has always occurred. The last dinosaurs disappeared 65 Mya, more than 60 million years before humans evolved. Judging from the fossil record, Peter Raven, director of the Missouri Botanical Gardens, calculated the average life span of a species at about 4 million years (Raven, 1995). If there are about 10 million species in the world, Raven calculated the normal rate of extinction at about four species a year. Many scientists believe that humans now have increased the pace of extinction far beyond natural levels, so that species are now becoming extinct at rates 1,000 to 10,000 times the natural rate that occurred before our ancestors first appeared on Earth. Raven predicted that animal and plant species will likely become extinct at the rate of 50,000 species a year during the next few decades (Raven, 1995). If Raven is correct, it will be the greatest mass extinction ever, far surpassing the die-off of the dinosaurs. These extinctions—and the loss of biodiversity—are irreversible.

Figure 16.1. The flightless dodo (*Raphus cucullatus*) is classified in the family Raphidae in the order Columbiformes, which includes pigeons and doves. It was twice as large as a goose, with thick, stubby legs, a poodle-like tail (complete with curls), tight, pigeon-like body plumage, a tremendous skull equipped with a stout, heavily plated and deeply hooked bill, a naked face, and a dog-sized mouth. It was perhaps the most unbird-like bird that ever lived. The true dodo lived on the island of Mauritius in the Indian Ocean, about 805 km (500 mi.) east of Madagascar. It was first discovered by the Portuguese in 1507 and last seen alive in 1681. Dodos lived in deep forest, walked with a ludicrous waddle, and laid one large egg, which both parents incubated. They swallowed gizzard stones as large as chicken eggs. Most people took a skeptical view of the early sketches and accounts that depicted so preposterous a creature—even though a number of live dodos were brought to Europe early in the seventeenth century. Most of what we know of these birds comes from about 400 remains and from written records, like this 1848 account: “These birds were of large size and grotesque proportions, the wings too short and feeble for

flight, the plumage loose and decomposed, and the general aspect suggestive of gigantic immaturity… . So rapid and complete was their extinction that the vague descriptions given of them by early navigators were long regarded as fabulous or exaggerated, and these birds, almost contemporary of our great-grandfathers, became associated in the minds of many persons with the Griffin and Phoenix of mythological antiquity." Dodos were no match for the pigs that were introduced by early settlers. The pigs are thought to have feasted on the eggs and young birds, and the phrase "dead as a dodo" soon became a tragic reality.

NATURAL EXTINCTION

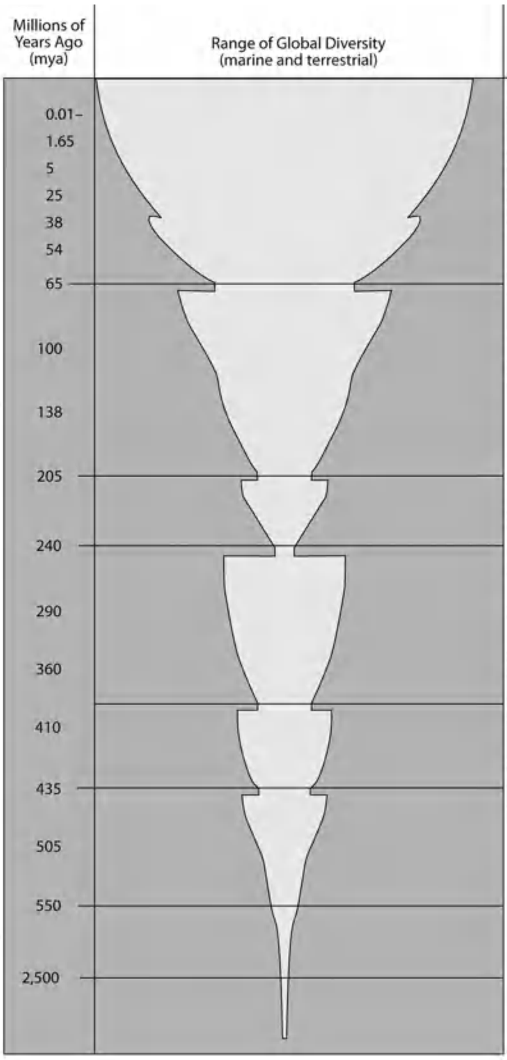
More than 99 percent of all plant and animal species that have ever lived are extinct (Romer, 1949; Simpson, 1952). Little is known, however, about the immediate causes of extinction, even of species that have become extinct in historic times (Simberloff, 1986).

Natural extinction, a normal ongoing process with a certain number of species steadily disappearing over time, is somewhat balanced with the natural process of speciation. This background extinction usually is localized and may be caused by overspecialization, climatic or other environmental changes, or competition with more adaptable forms. A species must evolve continually to keep pace with a constantly changing environment, simply because other species are also evolving, thus altering the availability of resources and the patterns of biotic interactions. Species that cannot keep pace with this change become extinct.

Mass extinctions, on the other hand, were worldwide events in which a large number of species, and even entire higher taxonomic groups, disappeared within an interval of just a few million years. They have occurred throughout the history of the Earth. Afterward, remaining groups are apt to undergo adaptive radiations as they spread out and fill niches vacated by those that have become extinct. The greatest mass extinctions occurred during Late Ordovician, Late Devonian, Late Permian, Late Triassic, and Late Cretaceous periods (Fig. 16.2a, b). The latter three had significant impacts, particularly on terrestrial vertebrates. Whether mass extinctions have followed a periodic pattern over the past 250 million years has not been resolved (Raup and Sepkoski, 1986; Sepkoski and Raup, 1986; Benton, 1995).

A leading extinction theorist, David Jablonski of the University of Chicago, believes that selection pressures are changed by mass extinctions (Jablonski, 1986). Often it is the most fortunate, not necessarily the most fit, that survive such an event. Groups that had been healthy may suddenly be at a disadvantage when their environment is disrupted. Other species that had been barely surviving somehow manage to survive the event, find conditions more favorable, and proceed to “inherit the Earth.”

Mammals are a good example of the latter scenario. Dinosaurs and mammals originated within 10 million years of each other, about 220 Mya; however, for 140 million years, dinosaurs were the dominant terrestrial vertebrates, while mammals stayed relatively small and inconspicuous. Most early mammals were shrewlike or squirrel-like, and no larger than woodchucks. Some mammalian relatives, however, such as *Lisowicia bojani*, an elephant-sized dicynodont, walked on Earth in the Late Triassic just when dinosaurs were evolving to giant sizes (Sulej and Niedzwiedzki, 2019). Mammals probably began their radiation to fill ecological niches left vacant by the demise of the dinosaurs about 65 Mya, and within 10 million years, there were mammals of all shapes and lifestyles ranging from moles and bats to elephants and whales (see Fig. 9.1).



Times of Major Geological and Biological Events

1.65 mya to present. Major glaciations. Modern humans evolve. Starting with hunters of most recent ice age, their activities set in motion the most recent **mass extinction**.

65–1.65 mya. Colossal mountain building as continents rupture, drift, collide. Major shifts in climate. First tropical and subtropical conditions extend to polar regions. Woodlands, then grasslands emerge as climates get cooler, drier. Major **radiations** of flowering plants, insects, birds, mammals. Origin of earliest human ancestors.

65 mya. Apparent asteroid impact causes **Cretaceous mass extinction** of all dinosaurs and many marine organisms.

135–65 mya. Pangea breakup continues, broad inland seas form. Major **radiations** of marine invertebrates, fishes, insects and dinosaurs. Origin of angiosperms (flowering plants).

181–135 mya. Pangea starts to break up. Major **radiations** of dinosaurs.

205 mya. Asteroid impact? **Triassic mass extinction** of many species in seas, some on land: some dinosaurs, mammals survive.

240–205 mya. Recoveries, **radiations** of fishes, dinosaurs. Gymnosperms the dominant land plants. Origin of mammals.

240 mya. **Permian mass extinction**. Nearly all species on land and in seas perish.

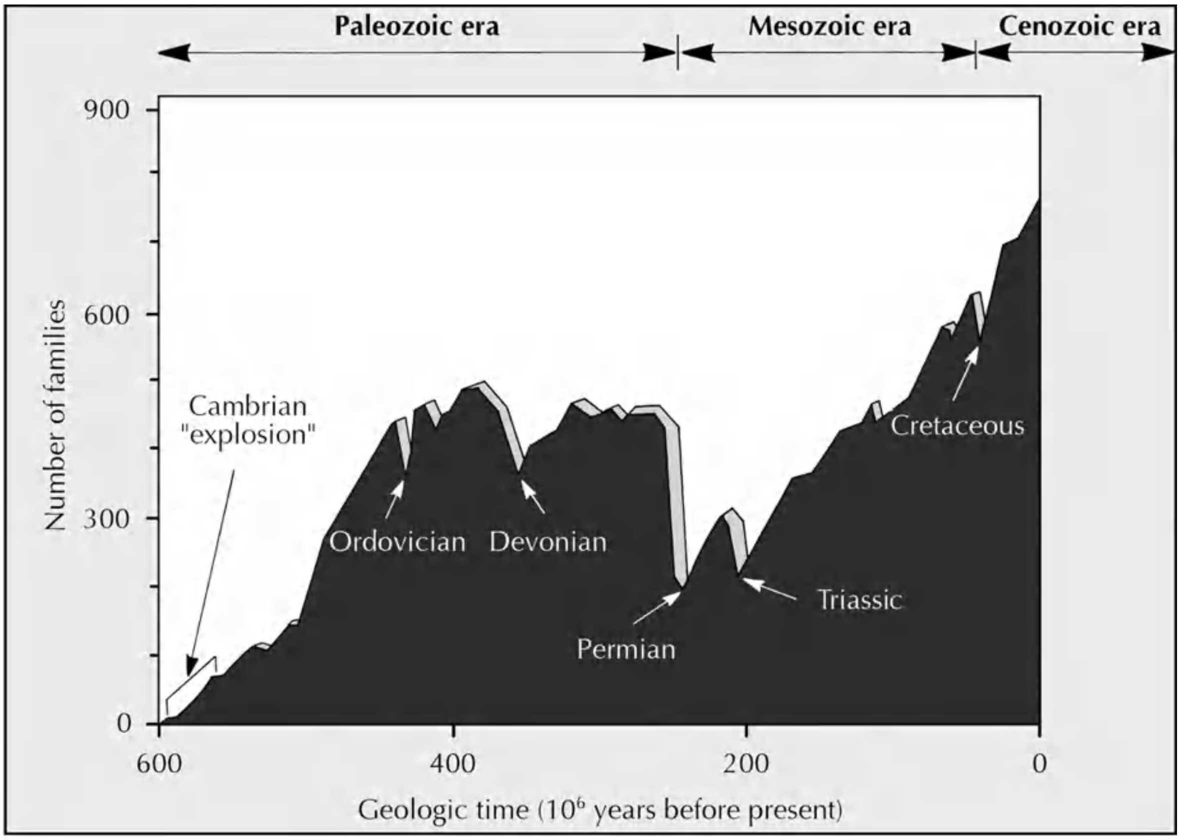
280–240 mya. Pangea and worldwide ocean form. **Radiation** of reptiles.

360–280 mya. Major **radiations** of insects, amphibians on land. Origin of reptiles.

370 mya. **Devonian mass extinction** of many marine invertebrates, most fishes.

435–360 mya. Laurasia forms. **Mass extinctions** of many marine species. Gondwana drifts north. Vast swamps, first vascular plants. **Radiations** of fishes continue. Origin of amphibians.

(a)



(b)

Figure 16.2. (*a*) Summary of major extinction events in the evolution of the Earth and of life. (*b*) Changes in the numbers of families of marine animals through time from the Cambrian period to the present. The five major extinctions of skeletonized marine animals caused sharp drops in diversity during the Ordovician, Devonian, Permian, Triassic, and Cretaceous periods. Despite the extinctions, the overall number of marine families actually has increased to the present.

In contrast, Hedges et al. (1996) suggest that the continental fragmentation that took place in the Mesozoic may have been a more important mechanism in the diversification of orders of birds and mammals than the Cretaceous-Tertiary (K-T) extinction event of 65 Mya. The adaptive radiations of birds and mammals occurred rapidly after the K-T extinction event. Nuclear gene comparisons of four bird orders (galliform, anseriform, columbiform, and struthioniform) and three mammal species (human, *Homo sapiens*; house mouse, *Mus musculus*; and cattle, *Bos taurus*) reveal molecular estimates of divergence averaging 50 to 90 percent earlier than fossil-based estimates. The use of molecular time estimation of evolutionary divergence assumes that genera evolve at a relatively constant rate. All molecular estimates of divergence occurred during the Mesozoic rather than the Cenozoic and are considerably older than divergence times suggested by fossil evidence. Hedges et al. (1996) conclude that fragmentation of land areas during the Cretaceous, not the relatively sudden availability of ecological niches following the K-T extinction event, was the mechanism responsible for the diversification of avian and mammalian orders.

Tooth fossils (family Zhelestidae) found in 85-million-year-old sediment in Uzbekistan in Asia bear the marks of animals that grazed, and they could be from the ancestors of modern-day horses, cows, elephants, and other hooved animals (Archibald, 1996). The teeth had flat, squared, grinding surfaces similar to those found in herbivores' teeth. The ancestors of hooved mammals may have evolved *during* the time of the dinosaurs—about 20 million years earlier than previously believed—and the evolution of ungulates probably was well under way before the dinosaurs were gone.

Permian

The Permian extinction was the first to affect terrestrial life significantly and was easily the greatest extinction event of all time. The death toll was three times worse than the later event that ended the dinosaur age. The known genera of tetrapods represented by fossils decreased from 200 in the Late Permian to 50 in the Early Triassic. Between 80 and 95 percent of all marine *species* and about 70 percent of vertebrate *families* on land disappeared (Gore, 1989; Erwin, 1994; Stanley and Yang, 1994; Renne et al., 1995). Among vertebrates, 78 percent of reptile and 67 percent of amphibian families disappeared during the Late Permian (Erwin, 1996). Benton (1995) calculated a mean familial extinction rate of 60.9 percent for all life, 62.9 percent for continental organisms, and 48.6 percent for marine life.

Although the Permian-Triassic (P-T) extinction was once thought to have lasted for 8 million years, it now appears to have occurred in a geological heartbeat—perhaps even instantaneously. Many paleontologists now presume it had a single, abrupt cause: a mega-volcanic eruption, a catastrophic release of toxic chemicals from the ocean's depths, or an impact. Researchers have used isotopic dating to show that extensive volcanic activity in Siberia was contemporary with the Permian extinction. The Siberian traps (after the Swedish word for "stairs," which describes the steplike edges of the deposits) are solidified layers of ancient lava ranging from 400 to 3,700 m (1,300–12,000 ft.) in thickness (Erwin, 1996). At least 45 separate flows cover an area of at least 1.5 million km^2 (579,000 mi.^{2}). Periodic outpourings of magma occurred for 600,000 to 1 million years (Renne et al., 1995; Erwin, 1996). The world's oceans also became anoxic (depleted of oxygen) in the Late Permian, a condition that could have suffocated some marine life and might have contributed to the extinction of marine organisms (Wignall and Twitchett, 1996). Reductions in oxygen levels occurred throughout a range of depths and extended into shallow waters that served as critical nurseries for many marine organisms. Wignall and Twitchett (1996) concluded that while oxygen solubility declines in warmer waters, the most probable cause of oxygen-deficient waters was the decline in oceanic circulation as the waters warmed and the equator-to-pole temperature gradient declined. Ogden and Sleep (2012) present a physical analysis of explosive eruption of coal and basalt, demonstrating that it is a viable mechanism for global extinction. Recent evidence suggests that the flood basalts may have mobilized carbon in thick deposits of organic-rich sediments.

Other scientists have a modified mega-volcanic explanation. They have determined that exactly 254.1 Mya the Earth's thin crust sprang a leak (Muller et al., 2001). The crack allowed a vast flood of molten rock to gush over 2.6 million km^2 (1 million mi.^{2}) in Siberia. This scalding lava from deep within the Earth belched sulfurous fumes that poisoned the air and sea, while great clouds of carbon dioxide altered the global climate, rendering the world uninhabitable for most organisms more complex than a bacterium. The huge mass of lava was heavy enough to make the world wobble on its axis, shifting the North and South poles from their normal orientation. This could also have contributed to global climate disruption.

Jin et al. (2000) analyzed in detail fossil occurrences in the Meishan marine section in South China. The data are consistent with a sudden extinction (within a few hundred thousand years) rather than a series of extinction steps. The marine extinction coincides with an abrupt decrease in carbon isotope values, although the specific cause of the extinction remains unknown. Two studies suggest the extinction was caused by a meteorite. Becker et al. (2001, 2004) analyzed rock cores from the 200 km (125 mi.) wide Bedout crater off the northwest coast of Australia and found meteorite fragments, "shocked" quartz, and other impact evidence from the time of the Permian-Triassic extinction. Some scientists believe the crater was caused by a 10 km (6 mi.) wide meteorite. The melted rock filling the crater likely released soot and sulfur that polluted the atmosphere and the oceans, triggering catastrophic climate change. Rocky fragments recovered on Graphite Peak in Antarctica were found at a geological horizon, or layer, which also was laid down at the start of the Permian-Triassic extinction (Basu et al., 2003). Analysis shows the fragments have chemical ratios that are unique to meteorites. Basu et al. (2003) suggest that the asteroid was probably bigger than the 10 km (6 mi.) wide space rock that is thought to have killed the dinosaurs. Such an impact could cause a huge fireball and send billions of tons of dust into the atmosphere, enough to darken the sun for months. It also would have laid down a layer of dust bearing the same chemical composition as the meteorite.

Hoffman (2018) examines a variety of aspects and theories concerning the Permian extinction.

Triassic

At the family level, the Triassic extinctions were greater than those of the Permian, with an estimated 80 percent of all families becoming extinct at or near the end of the Triassic. Colbert (1986) believed that the Triassic extinctions were caused largely by the loss of long-established taxa, perhaps in part as a result of the appearance and rapid development of new groups better adapted to the warmer environment during the Mesozoic. In addition, some of the Triassic extinctions were the result of the evolution of some lines of therapsid reptiles into early mammals and of some thecodont reptiles into more advanced archosaurian reptiles.

Mollusks, like the chambered shelled ammonoids, and bivalves, like mussels, clams, scallops, and oysters, were decimated, and conodonts finally disappeared during the Late Triassic extinctions. On land, several families of reptiles disappeared, particularly the last of the basal archosaurs (thecodontians), the group that includes the ancestors of dinosaurs and crocodilians, and some mammal-like reptiles (therapsids), the group that includes the ancestors of the mammals (Benton, 1993).

Cretaceous

An estimated 61 percent of all tetrapod families became extinct at the end of the Cretaceous period (Jablonski and Raup, 1995). This extinction event caused a 70 to 80 percent reduction in marine biodiversity at the species level and a 50 percent reduction at the generic level.

As in previous mass extinctions, some Cretaceous extinctions were the result of the development of better-adapted groups and the evolution of ancestral groups into more derived groups. Others were the result of evolutionary attrition—the disappearance of “experimental” groups like certain groups of Mesozoic mammals (symmetrodonts, pantotheres, multituberculates) during the early stages of their evolutionary development. However, Cretaceous extinctions were marked largely by the rather sudden disappearance of many members of well-established and seemingly highly successful groups like microscopic foraminiferans (protozoans), bivalves, gastropods, and cephalopods, as well as dinosaurs, pterosaurs, and many marine reptiles.

The extent of terrestrial vertebrate extinctions at the end of the Cretaceous is poorly understood, and estimates have ranged from a mass extinction of many avian and mammalian lineages to limited extinctions of specific groups (Gibbons, 1997a). Colbert (1986), for example, noted that 35 orders of tetrapods lived during Mesozoic times (4 amphibians, 15 reptiles, 7 birds, and 9 mammals). Orders that became extinct during the Mesozoic are designated by an asterisk:

Amphibia

*Temnospondyli (labyrinthodont amphibians)

*Proanura (ancestral to the anurans—frogs and toads)

Anura (frogs and toads)

Urodela (salamanders)

Reptilia

*Cotylosauria (stem reptiles)

Eosuchia (the first and most primitive diapsids)

Rhynchocephalia (“beaked reptiles,” represented today by the tuatara)

Chelonia (turtles)

Squamata (lizards and snakes)

*Thecodontia (Triassic archosaurs)

*Pterosauria (archosaurs, flying reptiles)

Crocodilia (archosaurs, crocodilians)

*Saurischia (archosaurs, saurischian dinosaurs)

    *Ornithischia (archosaurs, ornithischian dinosaurs)

    *Protorosauria (a “wastebasket group” of Triassic reptiles)

    *Sauropterygia (marine nothosaurs and plesiosaurs)

    *Placodontia (marine, mollusk-eating reptiles of Triassic age)

    *Ichthyosauria (ichthyosaurs, of fishlike form)

    *Therapsida (mammal-like reptiles)

  Aves

    *Archaeopterygiformes (*Archaeopteryx*, the first bird, Jurassic)

    *Hesperornithiformes (loonlike toothed birds, Cretaceous)

    *Ichthyornithiformes (ternlike birds, Cretaceous)

Gaviiformes (the divers, loons and grebes)

Columbiformes (doves and pigeons)

Ciconiiformes (waders, storks, and herons)

Charadriiformes (gulls and terns and their relatives)

  Mammalia

    *Multituberculata (earliest herbivores, with specialized teeth)

    *Triconodonta (small carnivores with sharp-cusped teeth)

    *Docodonta (Jurassic mammals with expanded tooth crowns)

    *Symmetrodonta (ancient mammals with triangular-shaped cheek teeth)

    *Eupantotheria (possible ancestors of later mammals)

Marsupialia (pouched mammals)

Prototheria (very primitive eutherian mammals)

Primates (today the lemurs, monkeys, apes, and man)

    *Condylarthra (primitive hooved mammals)

Of the 35 orders, 21 (2 amphibians, 10 reptiles, 3 birds, and 6 mammals) became extinct during the Mesozoic. During the same period, plants, turtles, crocodiles, fishes, birds, and placental mammals were comparatively unaffected, a fact that has not yet been fully explained (Dodson and Dodson, 1985).

Cooper and Penny (1997) used molecular and paleontological data to show that modern bird orders started diverging in the Early Cretaceous, and that at least 22 avian lineages of modern birds survived the K-T boundary. Using the combined data for other terrestrial vertebrates, Cooper and Penny (1997) estimated that a minimum of 100 terrestrial vertebrate lineages survived the end-Cretaceous extinctions. Incremental changes probably occurred during a Cretaceous diversification of birds and mammals, rather than an explosive radiation in the Early Tertiary.

Various theories have been proposed to explain the K-T event. In a period of time variously estimated from weeks to 50,000 years or more, life on Earth was totally devastated by what probably was the greatest catastrophe in the history of our planet. Theories for the demise of the dinosaurs include racial senescence, bodily disorders, stress, disease, climatic change, an extraterrestrial impact, cosmic radiation, extensive volcanism, major regression of the seafloor from the land, geochemical changes, predation by mammals, and the rise of new flowering plants to which the highly specialized herbivorous dinosaurs could not adapt (Stanley, 1987; Norman, 1991; Rampino and Self, 1992; Renne et al., 1995; Wignall and Twitchett, 1996). At one time or another, almost every conceivable catastrophe—terrestrial or extraterrestrial—has been advanced to explain mass extinctions.

Based on paleobotanical evidence (comparisons of modern leaf sizes and shapes with those of fossil leaves), the Cretaceous was a time of global warmth (Herman and Spicer, 1996). The Arctic Ocean was relatively warm, remaining above 0°C (32°F) even during the winter months. The ocean’s warmth implies that there was significant heat transport toward the poles during all seasons of the year. Normal geological events (mountain-building, massive volcanic activity, and especially, a major regression of sea level that eliminated the epicontinental seas) also occurred at that time.

The K-T extinction was widespread geographically, but selective in the groups that it affected. Norman (1991) noted the general disappearance of any land-living animal more than 1 m (3.28 ft.) long, and the extinction of nearly all large marine reptiles, including marine crocodiles (but excluding marine turtles). All of the ammonites disappeared, as did most brachiopods and clams. All flying reptiles vanished, but birds and freshwater crocodiles survived with few apparent effects. Most bony fishes, sharks, and mammals also seemed to be unaffected. Although some early flowering plants were lost, the majority of plant species seem to have survived. Following the K-T event, however, there seems to have been a brief, extraordinarily diverse flora of ferns.

The Jurassic was characterized by uniform tropical conditions with abundant rainfall and lush vegetation. These conditions continued into the Cretaceous, but, beginning about 100 Mya (Middle Cretaceous), a gradual worldwide cooling trend began. By the early part of the Late Cretaceous, average yearly temperatures were in the range of 18°C to 20°C (64°F–68°F). Norman (1991) noted that periods of prolonged cool temperatures could have caused a fatal drain on the body temperature of large ectotherms, from which they would have had little chance of recovering. Even though small endothermic dinosaurs apparently could generate heat, they may not have been able to control the loss of their body heat during cooler periods because they lacked an insulating layer of fur or feathers.

The end of the Cretaceous was marked by a sudden cooling and drying trend, which resulted from the lowering of sea levels. These climatic changes may have significantly affected the distribution of plant populations that served as food for herbivorous dinosaurs. Some believe the demise of the dinosaurs was an indirect effect of such a climate-induced change in vegetation.

Other researchers (Renne et al., 1995; Wignall and Twitchett, 1996) believe massive volcanism was the cause of the extinction. Ash, sulfur, and sulfate aerosols, along with chlorine and other acidic compounds, are emitted into the stratosphere by volcanic eruptions. Sulfur dioxide eventually becomes small droplets of sulfuric acid, which condense and remain in the stratosphere as a mist of fine particles that eventually return to Earth in the form of acid precipitation (rain, snow). These particles also reflect the sun's radiation and cool the lower atmosphere while the reflected radiation warms the upper atmosphere. The chlorine interacts chemically with ozone molecules (O_3), breaking them apart and hastening the depletion of the planet's ozone shield. Destruction of the ozone layer has been linked to increased volcanic activity at the end of the Cretaceous. Increased ultraviolet radiation striking the Earth could have destroyed animals living on land and the plankton in the upper layers of the ocean. For example, the eruption of Toba in Sumatra 73,500 years ago was the largest known explosive volcanic event in the Late Quaternary. It could have sent huge quantities of fine ash and sulfur gases to heights of 27 to 37 km (17–23 mi.), creating dense stratospheric dust and aerosol clouds (Rampino and Self, 1992). The volcanic dust could have caused a “volcanic winter” and several years of decreased surface temperatures.

Significant eruptions continue to occur. Air waves generated by the eruption of Indonesia’s Krakatoa in August 1883 traveled around the world four times (Flannery, 1996). Dust from the explosion circled the globe, producing brilliant-colored sunsets for as long as two and a half years following the eruption (Alvarez et al., 1980). The associated explosion was estimated to be 10,000 times more powerful than the Hiroshima bomb and was heard by people as far away as central Australia, who thought it was a distant cannon. More recently, eruptions of Mount St. Helens (1980) in North America, Mount Pinatubo (1991) in the Philippines, and southern Iceland’s Eyjafjallajökull glacier (April 2010) spewed great quantities of debris into the stratosphere (Fig. 16.3). Material from these eruptions circled the Earth many times. In the case of Mount Pinatubo, scientists believe that the eruptions are the cause of a temporary cooling of the Earth’s climate—at least 1°C (1.8°F) over one to two years—and ozone decreases of 30 percent in certain areas.

Figure 16.3. The eruption of Mt. Pinatubo in the Philippines in 1991 spewed hundreds of millions of tons of ash, rocks, and molten lava. An estimated 18.1 million metric tons (20 million US tons) of sulfur from the volcano created an acidic aerosol that circled the Earth for two years and cooled the average global temperature by at least 1°C (1.8°F).

Other scientists believe that a supernova explosion or other extraterrestrial event is the most likely explanation of the extinction, with the ensuing cosmic radiation killing off the large, unprotected dinosaurs. The explosion could have triggered a chain reaction of major changes in the Earth's climate. Many mammals and birds, protected by fur or feathers, survived. Among ectothermic reptiles, only those that could hibernate or seek refuge in riverbanks or under rocks escaped death. To explain the multiple stages of extinctions that occurred near the K-T boundary, some believe Earth was hit not by one great object but by a shower of comets that bombarded the planet over several million years. The movements of the comets or asteroids through the atmosphere could have ionized molecules in the air, which would have fallen to the ground as acid rain. The rain could have made the ocean's surface acidic enough to kill off many tiny marine animals (and, thus, the animals that feed on them) by dissolving their calcium-based shells. This would help explain why species with calcium-based shells suffered at the K-T boundary far more than those with silica-based shells.

Relatively close approaches of asteroids happen frequently. For example, a 5 m (16 ft.) long space rock passed by Earth in May 2012 at a distance of 14,400 km (8,950 mi.) from the Earth's surface. In February 2013, a megarock asteroid measuring 46 m (150 ft.) passed within 27,360 km (17,000 mi.) of Earth—the closest known approach ever for an object of this size. Asteroid DX110 hurtled between the moon and Earth on March 5, 2014. It passed an estimated 350,000 km (217,000 mi.) from Earth. On September 1, 2017, an asteroid named Florence, 4.5 km (2.8 mi.) in width, flew past Earth at a distance of about 7.1 million km (4.4 million mi.). It was the largest asteroid to pass so close to our planet since 1890.

Some scientists believe that a meteor impact caused a huge cloud of dust, water droplets, and other debris to ascend into the air (Fig. 16.4). Such a cataclysmic event might have darkened the entire globe for three to nine months and interrupted plant photosynthesis, created acid rain, caused a greenhouse effect that warmed the air and the seas, and burned huge forests, thus causing the extinction of vulnerable species both on land and in the sea. Researchers who study isotopes from the rocks of the seafloor believe that a period of global warming coincided with the downfall of the dinosaurs. The discovery of an apparent global soot layer at the K-T boundary provides evidence that global wildfires might have been ignited by energy radiated from reentering ejecta from the impact (Wolbach et al., 1985, 1988; Melosh et al., 1990). Solar transmission was reduced to 10 to 20 percent of normal for a period of 8 to 13 years (Pope et al., 1994). This reduction also may have caused a cooling of the climate that far exceeded the greenhouse warming caused by the increase in carbon dioxide through the vaporization of carbonates and, therefore, produced a decade or more of freezing and near-freezing temperatures. Several decades of moderate warming followed the decade of severe cooling. The prolonged impact-winter may have been a major cause of the K-T extinctions.

The impact hypothesis originated in 1978, when a team from the University of California and Lawrence Livermore Laboratory discovered a clay layer a few centimeters thick in a 66-million-year-old layer of rock from Italy (Alvarez et al., 1980; Alvarez, 1983). The clay layer contained a relatively high concentration of the element iridium, which is rare on Earth but relatively common in meteors and asteroids. At present, deposits of iridium dating back approximately 65 million years have been found in more than 100 locations around the world. Its distribution over the Earth may have resulted from fallout from a great cloud of dust following the explosive impact of a meteorite. Because the iridium deposits are 65 to 66 million years old, they are coincident with the worldwide die-off of many species at the K-T boundary. Considerable evidence has been cited both for and against this hypothesis (Clemens et al., 1981; Van Valen, 1984; Jablonski, 1984, 1986).

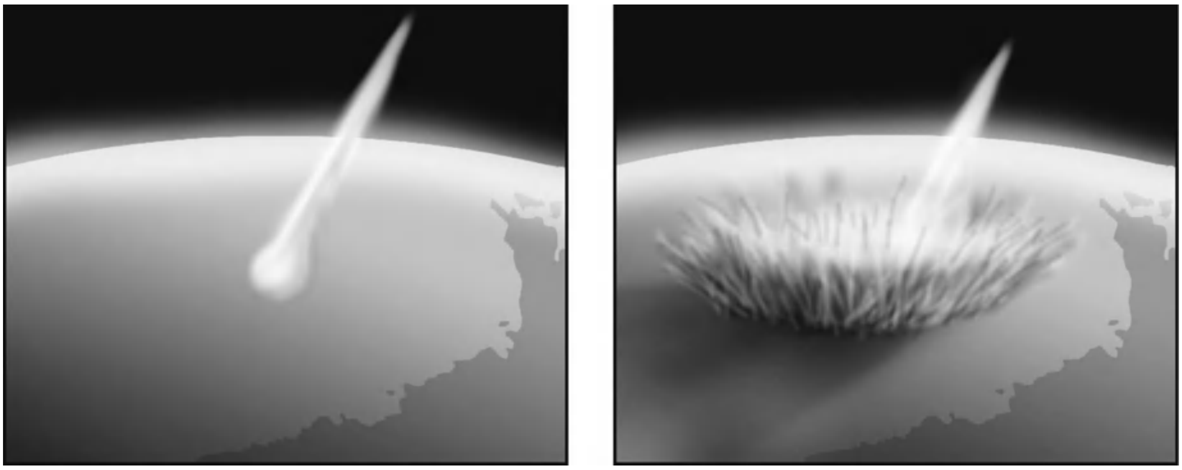


Figure 16.4. An artist/astronomer's interpretation of what might have happened during the last few minutes of the Cretaceous. Note the angle of impact is 20° to 30°.

The search for a crater big enough (approximately 200 km [120 mi.] in diameter) and old enough to explain the demise of the dinosaurs has focused on several sites. Glassy rock from the center of a huge crater with a diameter of at least 100 km (62 mi.) in northern Siberia is 66.3 million years old. Because the crater is so large, it could be the point where a meteorite 8 to 16 km (5–10 mi.) in diameter hit the Earth. More recently, however, researchers have focused on a potential site beneath the coast of the Yucatan Peninsula in Mexico (Chicxulub), where an impact crater 180 km (112 mi.) in diameter was discovered and dated (Kerr, 1992; Kring and Boynton, 1992; Swisher et al., 1992; Alvarez et al., 1995; Hildebrand et al., 1995; Schulte et al., 2010). Tiny fragments of glass (shocked quartz) in nearby sediments are thought to be hardened droplets of rocks (melted by the impact and ejected into the atmosphere) that cooled into glass as they rained down. Using radioisotopic dating, Swisher et al. (1992) revealed the crater to have a reported age of 64.98 million years, ± 0.06 million years. Impact debris has been dated at 65.06 million years, ± 0.18 million years. Based on argon-argon dating, Paul Renne of the Berkeley Geochronology Center dated the impact at 66.043 ± 0.011 Mya (Renne et al., 2013). Renne et al. (2013) further posits that the mass extinction occurred within 32,000 years of this date. Thus, the ages of impact, impact debris, and the heart of the mass extinction are essentially indistinguishable. In addition, a 2.5 mm (0.1 in.) chip of rock rich in iridium and thought to have been thrown from the crater was found in a sediment core taken from the North Pacific (Kerr, 1996a; Kyte, 1998).

The meteor's impact angle was from the southeast to the northwest at a 20° to 30° angle from the horizontal (Schultz and D'Hondt, 1996). Chemical and mineralogical signs in the sediments surrounding the rock chip put it at the base of a 10 cm (4 in.) thick layer rich in debris particles thrown from the impact crater. Cores of ancient seafloor sediment, taken off the eastern coast of the United States in early 1997, provide additional evidence that the impact occurred precisely at the time of the extinction of many marine microfossils (Kerr, 1997a). Because the asteroid hit in the shallow waters surrounding the Yucatan Peninsula rather than plunging into deep ocean, it created a giant sulfur cloud from the underlying gypsum, which led to the global winter that killed plant and animal life.

In 2016, the International Ocean Discovery Program (IODP) and International Continental Scientific Drilling Program (ICDP) Expedition 364 sponsored a deep-coring expedition to remove and examine material from the Chicxulub crater's center to better understand peak ring formation and the impact's environmental effects (Betz, 2016). The team drilled 1,334.7 m (4,380 ft.) down from the seafloor over a period of nearly two months at a cost of about $75 per centimeter. A summary of Expedition 364 is presented by Gulick et al. (2017).

Some scientists point out that the dinosaurs dwindled slowly over a period of many thousands of years, and that the end of the Cretaceous simply marked the end of a long decline (Clemens et al., 1981; Officer and Drake, 1983). An intensive study and analysis of dinosaur bones from the last 2.5 million years of the Cretaceous period in North Dakota and Montana, however, revealed no evidence of a gradual decline (Sheehan et al., 1991). Eight families were represented in lower, middle, and upper portions of the rock formation, and relative strengths of the families remained constant from the earliest portion to the latest. Past studies of pollen fossils also revealed that many species of plants in the same region died out at the end of the Cretaceous.

Excavation of a 300 m (980 ft.) long ravine in the Chinese countryside near Zhucheng, China, is believed to be the largest dinosaur fossil site in the world. The fossils—more than 15,000 fractured, mangled, and blackened bones from about 65 Mya—support theories of a catastrophe like global fires, explosions, or climate change. In order to understand why there are so many dinosaurs dead in one place, researchers theorize that the dinosaurs were killed by the force of an explosion from a volcanic eruption or a meteor impact and then were caught in a flash flood, landslide, or even a tsunami that threw them together. There are seven distinctive “floors,” or layers, of dead dinosaurs in the pit, presumably showing that perhaps several such disasters occurred over a period of years.

Most geologists agree that an extraterrestrial body struck the Earth at the end of the Cretaceous and that at least some major groups of organisms became extinct rather abruptly; but there is still no clear consensus on whether or not an extraterrestrial impact was the principal cause of the entire mass extinction (Futuyma, 1986). While most paleontologists agree that impacts have occurred, many believe that a combination of normal biological, climatic, and geological processes provides the most plausible explanation for the observed faunal changes (Hallam, 1987; Kerr, 1988).

Discoveries in Ukraine and in the North Sea have given support to the idea that objects from outer space may have sometimes arrived in pairs or even swarms. In Ukraine, a well-known but smaller crater, some 9 km (6 mi.) wide, is actually 65 million years old. A British team found a crater at the bottom of the North Sea dating to the same era and stretching approximately 8 km (5 mi.) in a series of concentric circles.

Paleobotanical evidence for a marked temperature increase following the K-T boundary is consistent with inferred greenhouse heating. Wolfe (1990) stated:

> An oceanic impact site, resulting in the injection of large amounts of water vapour into the stratosphere and the formation of a humid greenhouse is suggested in one model; however, the stratospheric residence time for this water vapour would be of the order of months or years. Because warmth and wetness continued for a far longer time, complex feedback mechanisms in the earth’s ocean-atmosphere system may have altered the carbon cycle and may have involved factors such as production of large amounts of carbon dioxide by the bolide impact.

Bakker (1986), however, believes the extinction was a natural event preceded by the draining of shallow seas, like the Bering Strait, and the emergence of land bridges as described by Osborn as long ago as 1925. The exchange of species across continents brought new combinations of predators and prey together. In addition, Bakker speculates the exchange also may have transmitted parasites and disease organisms to species that possessed little or no resistance. When two continents mix their faunas, each group is challenged by enemies for which they are unprepared. During the Late Cretaceous, many Asian dinosaurs crossed the Bering land bridge into North America, and many North American species crossed into Asia. Foreign predators might have thrived unchecked until they succumbed to a disease for which they had no immunity. The constantly warm tissue of warm-blooded creatures with high metabolic rates could have provided an ideal habitat for pathogenic organisms. Thus, Bakker speculates that dinosaurs with high metabolic rates would have been at much greater risk of mass extinction during intercontinental exchange than would have been the giant, ectothermic reptiles.

In March 2010, an international panel of 41 geologists, paleontologists, and other researchers met to review all of the data (Schulte et al., 2010). Their conclusion: it was a giant asteroid striking Chicxulub that blasted a cloud around the world that led to the end of the dinosaurs. They stated that the argument for multiple impacts was not supported by worldwide data, and the eruption of volcanoes, known as the Deccan Traps, in India actually began 400,000 years before the end of the dinosaurs.

HUMAN IMPACTS ON EXTINCTION AND EXTIRPATION

How and when the Americas were populated remains contentious (Zorich, 2016). For decades, there was a consensus that the earliest Americans came from Asia across the Bering Strait “land bridge” (Beringia) near the end of the Ice Age about 14,000 years ago, settling first in the North American high plains, then moving into South America down the Andean chain (Martin, 1973; Patrusky, 1980; Brown and Gibson, 1983) (Fig. 16.5a). Goebel et al. (2008) stated:

> They [humans] occupied western Beringia by 32,000 years ago, and no glacial ice sheets would have blocked passage through western Canada during this relatively warm time. However, there is still no unequivocal archaeological evidence in the Americas to support such an early entry. The most parsimonious explanation of the available genetic, archaeological, and environmental evidence is that humans

colonized the Americas around 15,000 years ago, immediately after deglaciation of the Pacific coastal corridor. Monte Verde, Schaefer, and Hebior point to a human presence in the Americas by 14,600 years ago. Human occupations at Meadowcroft, Page-Ladson, and Paisley Cave also appear to date to this time. Together these sites may represent the new basal stratum of American prehistory, one that could have given rise to Clovis. Most mtDNA and Y-chromosome haplogroup coalescence estimates predict a 15,000 year ago migration event, and it may correlate to the post-LGM [last glacial maximum] dispersal of microblade-producing populations into northern Siberia and their eventual appearance in Beringia during the last glacial. The first Americans used boats, and the coastal corridor would have been the likely route of passage since the interior corridor appears to have remained closed for at least another 1,000 years. Once humans reached the Pacific Northwest, they could have continued their spread southward along the coast to Chile, as well as eastward along the southern margin of the continental ice sheets, possibly following traces of mammoth and mastodon to Wisconsin. Clovis could have originated south of the continental ice sheets, and the dense Clovis quarry-campsites in the southeastern United States may be the result of a longer occupation there than in other regions. Alternatively, Clovis could be the result of a second dispersal event from Beringia to America—from the same ancestral gene pool as the first dispersing population—when the interior ice-free corridor opened, about 13,500 years ago.

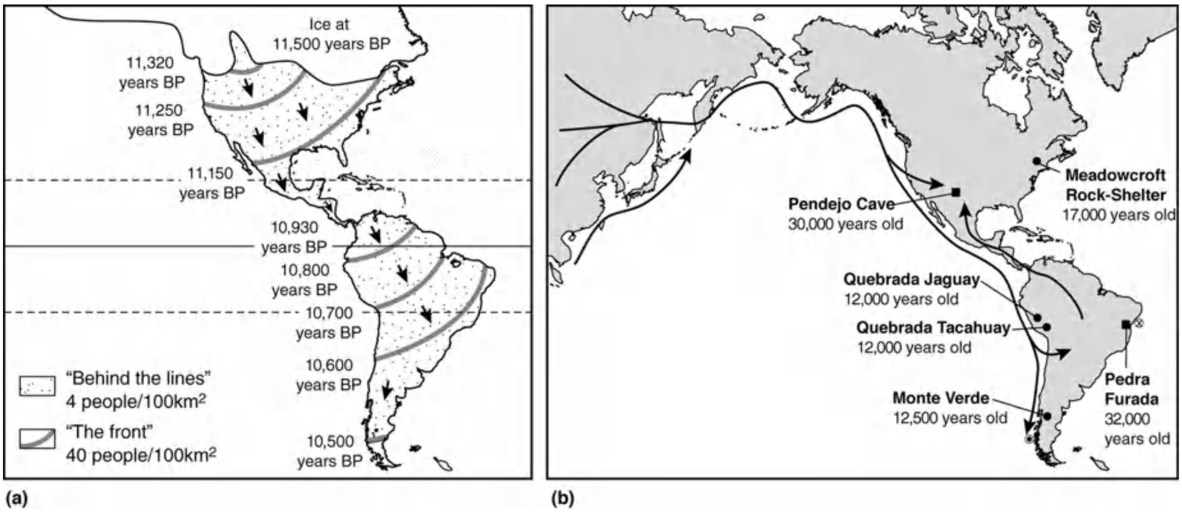


Figure 16.5. (*a*) One theory concerning the progressive extinction of the large Pleistocene mammal species suggests a correlation with advancing populations of big game hunters who crossed the Bering Strait and moved southward, maintaining a relatively dense front population that subsisted on large mammals. (*b*) Old view of land route into the New World some 11,500 years ago (*top*). New evidence from various sites (*black circle is probable site*; *black square is possible site*) suggests that migrants might have arrived more than 11,500 years ago, perhaps by sea.

Mitochondrial DNA (mtDNA) studies suggest that Native Americans are descended from people who migrated from Beringia to the Americas sometime after 16,500 years ago across the now-submerged 1,610 km (1,000 mi.) wide land bridge that connected Asia to North America (Politis, 2010). Some researchers believe that the ancestors of the first Americans holed up in Beringia for 8,000 to10,000 years during the Last Glacial Maximum (a period of intensely cold temperatures from about 17,000 to 28,000 years ago) before continuing into North America (Pringle, 2014; Raghavan et al., 2015). Around 16,000 years ago, they began moving south, but ice sheets then covered much of the North American interior, so the only route available was along the coastlines (Pedersen et al., 2016). A study of 13,600-year-old bison bones found on Vancouver and Orcas Islands in the Pacific Northwest, just off Washington State, identified cut marks suggesting that people had butchered some of the animals. These herds were able to colonize the islands after the glacial ice retreated around 15,000 years ago and before the sea level rose to swamp the land. New World immigrants appear to have hunted large mammals both on land and in the sea. Researchers turned up feces that proved to be unequivocally human—and 14,000 years old—from Paisley Five Mile Point Caves in Oregon (Gilbert et al., 2008). Extractions of mtDNA from the sample links it to an ancestor of modern-day Native Americans. The findings support early entry into the Americas via a route that skirted the coast (Fig. 16.5b).

McLaren et al. (2018) discovered a total of 29 footprints of at least three different sizes impressed into a 13,000-year-old paleosol beneath beach sands on Calvert Island, British Columbia. These are believed to be the earliest found so far in North America and provide evidence that people were inhabiting the region at the end of the last Ice Age. They add support to the idea that some ancient humans from Asia ventured into North America by hugging the Pacific coastline, rather than by traveling through the interior. Since Calvert Island would only have been accessible by watercraft 13,000 years ago, it implies that the people who left the footprints were seafarers who used boats to get around, gather and hunt for food, and live and explore the islands.

Scientists have recently found artifacts from the Cooper’s Ferry site in western Idaho indicating that people were living there approximately 16,000 years ago, providing new evidence that the first Americans entered their new home by following the Pacific coast before an inland ice-free corridor had opened approximately 14,800 years ago (Davis et al., 2019). The site is between 15,280 and 16,560 years old, for an approximate age of 16,000 years. Cooper’s Ferry represents the oldest radiocarbon-dated record of human presence in North America and was occupied repeatedly over time.

For decades, researchers believed the Western Hemisphere was settled by humans roughly 13,500 years ago, a theory based largely upon the widespread distribution of Clovis artifacts dated to that time. Clovis artifacts are distinctive prehistoric stone tools so named because they were initially found near Clovis, New Mexico, in the 1920s, but have since been identified throughout North and South America. Williams et al. (2018), however, have dated a significant assemblage of stone artifacts to 16,000 to 20,000 years of age, pushing back the timeline of the first human inhabitants of North America before Clovis by at least 2,500 years. The research team identified a previously unknown, early projectile-point technology unrelated to Clovis at the Gault site in central Texas, an extensive archaeological site with evidence of continuous human occupation. The presence of Clovis technology at the site is well-documented, but excavations below the deposits containing Clovis artifacts revealed well-stratified sediments containing artifacts distinctly different from Clovis.

Pre-Clovis projectile points found at the Debra L. Friedkin site in central Texas date from approximately 13,500 to 15,500 years ago (Waters et al. 2018). Among the 100,000 stone artifacts were 12 spearpoints whose shapes show a progression from stemmed points to a short triangular blade. Researchers believe that this progression means the artifacts may have been precursors to long, triangular Clovis points.

The skull of a young child was discovered near Wilsall, Montana, in 1968 along with more than 100 stone and bone tools. Known as the Anzick-1 child, archaeologists concluded that the skull was about 12,700 years old—the oldest known burial in North America—and that the tools belong to the Clovis culture. A complete sequence of the Anzick child's nuclear genome shows that the 1- to 2-year-old boy is directly ancestral to today's native peoples from North, Central, and South America (Rasmussen et al. 2014). The findings refute the hypothesis that postulates that ancient migrants from Western Europe founded the Clovis culture. The data also undermine contentions that today's Native Americans descend from later migrants to the Americas, rather than from the earlier Paleo-Americans.

Moreno-Mayar et al. (2018) sequenced 15 ancient human genomes recovered from sites spanning from Alaska to Patagonia. All genomes were most closely related to ancestral Native Americans who diverged from Siberians and East Asians approximately 23,000 years ago. Results also showed that Native American dispersal gave rise to complex serial splitting and early population structure.

Dating of stone tools shows the presence of humans from Montana to Mexico between 12,500 and 11,000 years ago. The 1926 discovery of a fluted stone projectile tip between the ribs of an extinct bison in Colorado has been dated as being about 12,500 years old and was the first definitive proof that humans lived in the Americas during the Ice Age. Fluted points found among the bones of mammoths near the town of Clovis, New Mexico, in 1932 have been dated at 13,500 to 12,900 years old and long have been accepted as the continent's oldest known human artifacts. In 2009, a landscaper excavating a pond in Boulder, Colorado, unearthed a cache of 83 ancient stone tools buried by the Clovis people. The tools, dated at 13,000 years old, contained blood and protein residue. Biochemical analyses revealed the tools were used to butcher camels, horses, sheep, and bears. Halligan et al., (2016) reported that a stone knife and mastodon bones with cut marks found in a Florida sinkhole were about 14,500 years old. Canadian researchers studied

5,600 bone fragments from caribou and other mammals found in a Yukon cave (Bourgeon, 2015; Bourgeon et al., 2017). The vast majority of the scrapes, cuts, and other marks on them were the work of carnivores scavenging meals from the remaining gristle and marrow. But at least two of the bone fragments bore clear indications of having been modified by human hands that the researchers date back 24,000 years.

Scientists investigating the DNA of two prehistoric human infants, who lived 11,500 years ago at a site known as Upward Sun River in Alaska, suggest the region was settled by people crossing from Asia 25,000 years ago (Moreno-Mayar et al., 2018). The scientists have called this new population the Ancient Beringians. Comparison of the number of genetic similarities and differences with those of other ancient and contemporary humans allowed the scientists to roughly time the movement of ancient people from Asia to North America to a much earlier data. Their analysis suggested Ancient Beringians and the ancestors of other Native Americans all descend from a single founding population that split decisively from East Asians around 25,000 years ago.

Other sites in southern Patagonia and in the Brazilian Amazon date back 11,500 years (Roosevelt et al., 1996, 1997; Barse, 1997; Haynes, 1997; Reanier, 1997) (see Fig. 16.5b).

Roughly 12,900 years ago, massive global cooling kicked in abruptly, along with the end of the line for some 35 different mammal species, including the mammoth, as well as the so-called Clovis culture of prehistoric North Americans. Various theories have been proposed for the die-off, ranging from abrupt climate change to overhunting. But now magnetic grains with iridium above background levels and glass-like carbon containing nanodiamonds found in the sediment from this time period point to an alternative: a massive explosion or explosions by a fragmentary comet (Firestone et al., 2007). Sediments from six sites across North America—Arizona, Oklahoma, Michigan, South Carolina, Manitoba, and Alberta—yielded tiny diamonds, which only occur in sediment exposed to extreme temperatures and pressures, such as those from an explosion or impact. The authors suggest that the catastrophic event and associated biomass burning led to abrupt cooling, contributed to the late Pleistocene megafaunal extinction, and led to immediate decline in some post-Clovis human populations. New evidence and support for the 2007 theory was presented by Kennett et al. (2009) and LeCompte et al. (2012).

A 130,000-year-old archaeological site in Southern California was reported by Holen et al. (2017). The authors' claim of prehistoric hominid involvement is based on four lines of evidence: a reliable radiometric age, the presence of stone artifacts, clear evidence of tool-imparted percussion damage to the remains of a mastodon, and an undisturbed geological context. Some experts were intrigued by the research, but many archaeologists strongly criticized it, saying the evidence did not come close to supporting such a profound conclusion (Ferraro et al., 2018). If early humans did smash those mastodon bones 130,000 years ago, scientists will have to rethink how humans came to the Americas.

A study that examined the bone structure of nearly 10,000 human skulls concluded that descendants of an ancient people who once lived in Japan may have been the first to cross a land bridge from Asia and settle in the Americas (Brace et al., 2001). The conclusions are based on a detailed analysis and measurement of 21 bone characteristics. A computer analysis of the thousands of measurements revealed a pattern of similarity that enabled researchers to connect peoples from different parts of the world. The study suggests that the first Americans were most closely related to the Jomon, a prehistoric people who lived in Japan thousands of years ago, and to a later group, the Ainu. Evidence suggests the members of the Jomon-Ainu group crossed the Bering land bridge and migrated throughout the Americas, from Alaska to the tip of South America. Those first migrants reached the Americas about 15,000 years ago and within about 1,000 years, there were people living near South America's tip. There is strong evidence to suggest that the Jomon peoples in Japan were skilled boat builders and probably used boats to move down the west coast of the Americas, settling wherever game and food plants were plentiful. Characteristics of the first migrants are now clearly seen in many of the Native American tribes, including the Blackfoot, Sioux, and Cherokee. A second migration came some 3,000 to 4,000 years ago, but these people were a mix of Chinese, Southeast Asian, and Mongolian. They probably came by boat, paddling across the Bering Strait. These people became the Inuit and Aleut, with some migrating south and being represented today by the Navajo.

Recent evidence, however, indicates that early humans—*Homo erectus*—may have reached Siberia 500,000 years ago (Morell, 1994). Descendants of *Homo erectus* could have pushed from Siberia through Beringia (a continent-sized land mass linking Asia and North America) and into America long before the currently accepted colonization date of around 14,000 years ago. Paleontologists continue to present evidence showing that unspecialized hunters and gatherers may have been present in the New World at least 25,000 years ago and possibly more than 40,000 years ago (see Fig. 16.5b) (Patrusky, 1980; Adovasio and Carlisle, 1986; Bower, 1990). For example, burned wood found with tools at a Virginia site called Cactus Hill, south of Richmond, was dated to 18,000 years ago. Spear points and bone found in a rock-shelter at Meadowcroft, Pennsylvania, near Pittsburgh, were up to 19,000 years old. All such finds, however, have been controversial. The presence of butchered mammoth bones at an archaeological site in Wisconsin hints that people inhabited the area between 14,700 and 14,100 years ago, just as the populations of large herbivores were disappearing. The Page-Ladson site in Florida (from approximately 14,550 years ago) is currently the oldest radiocarbon-dated site in North America with artifacts of the first Americans, including a bifacial knife, found among the bones of extinct animals (Waters, 2019).

An archaeological site in Siberia—long thought to be the original jumping-off point for crossing the Bering land bridge into North America—is actually much younger than previously believed, shaking the theory that the first Americans migrated over land during the final cold snap of the last great Ice Age (Goebel et al., 2003). Using radiocarbon dating, scientists found that the Ushki site (the remains of a community of hunters clustered around Ushki Lake) appears to be only about 13,000 years old—4,000 years younger than originally thought. The new date places the Ushki settlement in the same time period as the Clovis site in New Mexico, making it highly unlikely that people could have traversed the thousands of kilometers from Siberia in such a short period.

Linguists say the diversity of native languages in the Americas—more than 140 language families, each as different as English and Arabic—also attests to a much longer period of occupation, probably at least 30,000 years or more. Evidence has been accumulating that the Clovis people may have shared the Americas with people of a different culture—one based on gathering fruits and nuts, fishing, and hunting small animals rather than felling mammoths (Gibbons, 1996b).

Other theories suggest that the first Americans may have used boats to skip across Atlantic ice floes from Europe, entering North America perhaps as early as 20,000 years ago. Some archaeologists believe that early humans from the Japanese archipelago followed whales and other marine food sources across the Pacific Ocean to North America. A growing list of ancient Pacific coastal sites—Paisley caves (14,300 years ago), Channel Islands (13,000 years ago), Cedros Island, Mexico (12,600 years ago), Huaca Prieta, Peru (15,000 years ago), and Monteverde, Chile (14,500+ years ago)—supports the idea (Wade, 2017).

America's Lost Dogs

Dogs were present in the Americas before the arrival of European colonists, but the origin and fate of these precontact dogs are largely unknown. Researchers sequenced 71 mitochondrial and 7 nuclear genomes from ancient North American and Siberian dogs from time frames spanning approximately 9,000 years. Analyses indicate that American dogs were not derived from North American wolves. Rather, American dogs form a monophyletic lineage that likely originated in Siberia and dispersed into the Americas alongside people. After the arrival of Europeans, these dogs almost completely disappeared.

Leathlobhair et al., 2018.

Luzia

The skull of "Luzia," the oldest skull in the New World, was a celebrity in Brazil's National Museum in Rio de Janeiro. A major fire destroyed most of the museum's collections on September 2, 2018. Along with Luzia, the museum's archaeological material included the oldest skeletons found in Brazil, excavated in the Lagoa Santa region; the country's largest collection of skeletons from the coastal shell midden tradition known as Sambaqui; and a rich variety of precolonial Amazonian material culture and Andean pottery. Fortunately, the Luzia skull was in a metal case, within a metal cabinet, which protected it during the fire. When researchers recovered the skull in the scorched rubble, it was broken and scarred, but in good enough shape to be reconstructed.

Matacic, 2018

From 1977 to 1985, a site adjacent to a small creek between the Andes and the Pacific Ocean was excavated by an international team led by Dr. Tom D. Dillehay of the University of Kentucky (Dillehay, 1989, 1997). The site, known as Monte Verde, is about 800 km (500 mi.) south of Santiago, Chile. As a result of these excavations, Dillehay concluded that tool-using humans lived in southern Chile at least 12,500 years ago—more than 1,000 years earlier than most scientists had believed possible. Remains of a 14,700-year-old campsite represents the oldest known site of human habitation anywhere in the Americas. Later research using radiocarbon and luminescence dating methods uncovered new evidence of stone artifacts, faunal remains, and burned areas dated between ~18,500 and 14,500 years ago (Dillehay et al., 2015). In January 1997, a team led by Alex Barker, curator of archaeology at the Dallas Museum of Natural History, worked at Monte Verde and reached a similar conclusion. A study of dietary material at Monte Verde supports a coastal migration. Nine kinds of seaweed, including two used for medicine, have been found; some may have been collected seasonally along the shore (Dillehay et al., 2008). Their use indicates a sustained knowledge of coastal resources.

In the same area, Dillehay has also found preliminary evidence—charcoal, stone tools, and clay-lined pits that could be hearths—of an even more ancient settlement in a soil layer more than 30,000 years old (Wright, 1999). Consequently, researchers may have to radically revise their ideas of how and when humans migrated into the New World. The possibility has been raised that some early inhabitants of Chile may have crossed the Pacific from Southeast Asia. The discovery in southeastern Brazil of an 11,500-year-old skull ("Luzia")—the oldest in the New World—may help to rewrite the theory of how the Americas were settled. Excavations in central-west Brazil at the Santa Elina rock-shelter revealed remains of hearths, stone artifacts, and bones of giant sloths (Vialou et al, 2017). The sloth remains included small, bony plates from the skin that humans apparently made into ornaments by adding notches and holes. Three different dating methods indicate that people reached Santa Elina over 20,000 years ago.

Diamond (1987) believed many vertebrate species were quickly exterminated—possibly within just 10 years at any given site—by Paleo-Americans arriving in North America from Asia toward the end of the last Ice Age. Evidence of excessive human predation of mammals (overkill) has been shown by computer simulation to be possible. Mosimann and Martin (1975) hypothesized that, perhaps, a new wave of humans immigrated from Asia some 13,000 years ago (Fig. 16.6). Alroy (2001) programmed a computer to run a large-scale simulation of virtual hunters moving into virgin territory in Late Pleistocene North America, starting 14,000 years ago. The model, which simulated the population dynamics of humans and 41 large herbivores, showed that mass extinctions were unavoidable once people showed up. No matter how he adjusted the variables—how quickly the invaders traveled, how efficiently they hunted, how various prey species competed with one another for food—mass extinctions ensued. Ross MacPhee of the American Museum of Natural History, however, points out that the relevant archaeological record contains barely a dozen examples of stone points embedded in mammoth bones (and none are known from other megafaunal remains). Furthermore, some of these species had huge ranges—the giant Jefferson’s ground sloth, for example, lived as far north as the Yukon and as far south as Mexico—which would have made slaughtering them in numbers sufficient to cause their extinction rather implausible. MacPhee suggests that people may have introduced hyperlethal disease, perhaps through their dogs or hitchhiking vermin, which then spread wildly among the immunologically naive species of the New World. Populations of large mammals would have a harder time recovering because they have longer gestation periods than smaller mammals and their young require extended care. Thus far, MacPhee has no evidence for the hyperlethal disease hypothesis.

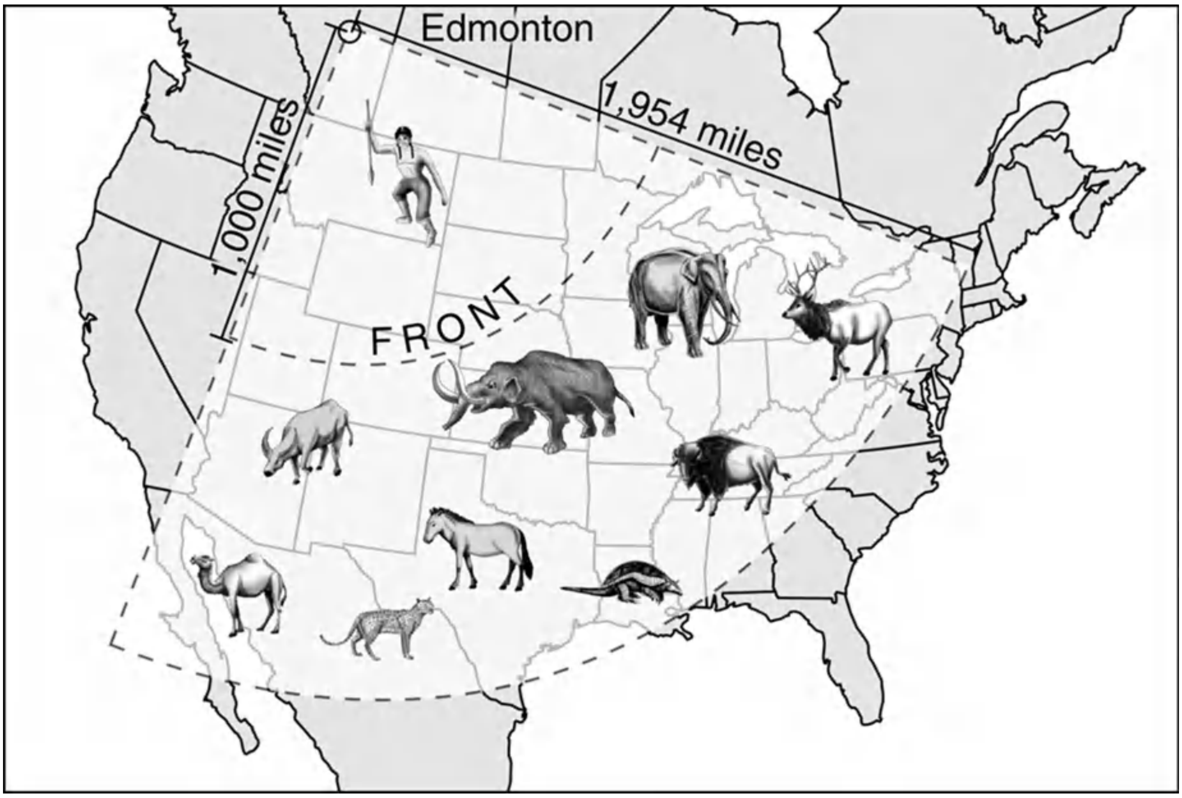


Figure 16.6. An essential feature of the overkill scenario is the concept of the “front.” Upon reaching a critical density, the population of hunters, newly arrived in the New World, expands southward in a quarter-circle. As long as some prey remains in the area of human occupation, the front advances smoothly. When the local herds are exhausted, it advances in a jump. The range available to the hunted is steadily reduced. The width of the front prevents survivors from “leaking” back into unoccupied areas behind the front. By the time the front has reached the gulfs of Mexico and of California, the herds of North America have been hunted to extinction.

Many paleontologists blame the extinctions of America’s megafauna on drastic changes in climate and habitat at the end of the Ice Age rather than on human predation. With deglaciation, deserts expanded northward, wiping out huge areas of grassland once used for foraging (Patrusky, 1980). Diamond (1987) points out, however, that ice-free habitats for mammals expanded rather than contracted as glaciers yielded to grass and forest. In addition, big American mammals already had survived the ends of many glaciations without such an extinction event, and there were far fewer extinctions in Europe and Asia when the glaciers of those continents melted at around the same time.

The spores of a fungus from the genus *Sporormiella*, which thrived in and on the dung of large herbivores like mammoths, suggest that changes in habitat did not cause the extinctions. Digestive processes in large herbivores are an integral part of the lifecycle of these fungi. Studies suggest that when the number of *Sporormiella* spores in a sample of lake sediment is less than 2 percent of the number of grains of tree pollen, it is a sign that the surrounding area is home to few if any herbivores producing the large quantities of dung required for the fungi to thrive. Analyses of sediments from a lake in northeastern Indiana reveal that the numbers of *Sporormiella* spores began to decline about 14,800 years ago. But it was not until 13,700 years ago, more than a millennium later, that the spore-to-pollen ratio dropped below 2 percent, signaling a disappearance of the megafauna from the local area (Gill et al., 2009). Also around 13,700 years ago is precisely when pollen grains from broad-leaved trees like ash and ironwood began to show up in lake bottom sediments in substantial numbers. These presumably tasty trees could flourish only when the megafauna that ate them were no longer present in large numbers. Thus, in at least some regions, megafaunal populations apparently began to wane several centuries before changes in vegetation that have been linked to a climatic shift occurred.

Extinction of Island Megafauna

Humans have greatly increased the rate of vertebrate extinction through many of their activities. Some investigators believe that humans were at least partially responsible for the extinction of such Late Quaternary species like mammoths, mastodons, saber-toothed cats, pygmy hippos, dodos, elephant birds, and many others (Martin, 1973; Mosimann and Martin, 1975) (Fig. 16.7). Diamond (1991) noted that Madagascar and several Mediterranean islands are yielding fossil evidence that human arrival on islands has always been accompanied by selective extinction of island megafauna (large animals), irrespective of whether this arrival was around 1,000 (New Zealand), 1,500 (Madagascar), 3,600 (New Caledonia), 10,000 (Mediterranean islands), or 30,000 (Bismarcks) years ago. He suggests that, whenever anatomically and behaviorally modern *Homo sapiens* reached land previously unoccupied by humans—whether it be a continent like Australia or the Americas, or an island—many of the native large prey have become extinct. Among the spectacular species that have disappeared from Madagascar were the elephant birds, including a species that grew to be 2.7 m (9 ft.) tall and weighed 450 kg (992 lb.); at least two species each of hippo and giant tortoise; an aardvark; and 8 genera and a minimum of 15 species of lemurs. The latter were giants compared with today’s lemurs. One looked superficially like a huge koala, another acted like a large tree sloth, and yet another was bigger than an adult male gorilla (Mittermeier, 2005).

The recent discovery of ancient butchered bones of massive lemurs, hippos, giant tortoises, and crocodiles show humans made their home on Madagascar 10,500 years ago, an astonishing eight millennia earlier than once thought (Hansford et al., 2018). The authors argue that by showing that humans coexisted with megafauna for as long as nine millennia, it eliminates the rapid extinction hypothesis or blitzkrieg for Madagascar. Only after farming populations had expanded across the island, altering the environment and increasing hunting pressure, did creatures like the elephant bird finally go extinct. Many scientists remain skeptical.

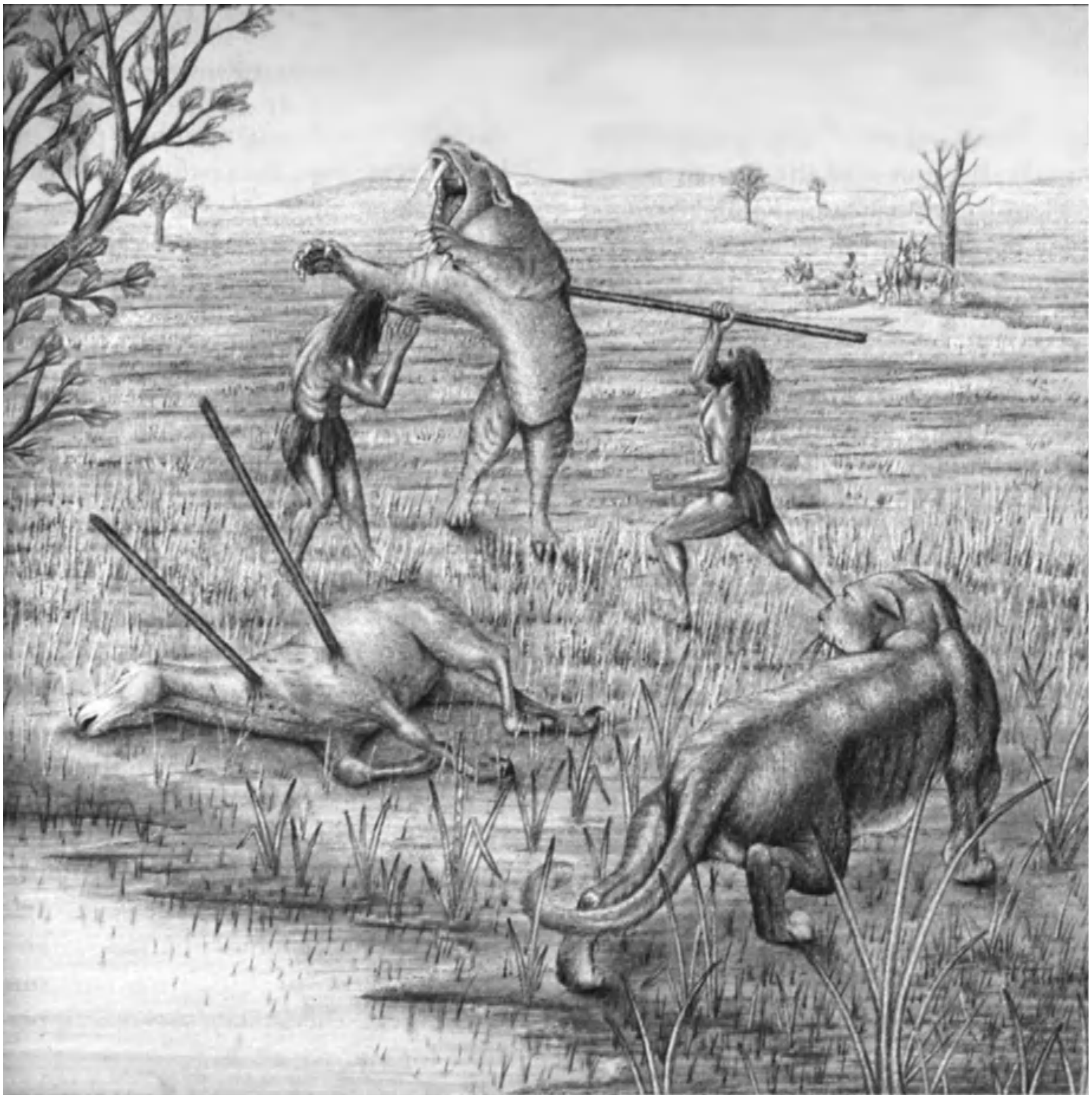


Figure 16.7. A Pleistocene scene. The fact that large herbivores (like mastodons, mammoths, giant sloths, peccaries, beavers, bears, deer, and antelope) hunted by humans who were making their way south from Alaska became extinct suggests that the two events may be related. If true, this last round of extinction may be attributable to our own species.

Miller et al. (1999) concluded that human impact, not climate, was responsible for the sudden disappearance 47,000–50,000 years ago of the large flightless mihirung (*Genyornis newtoni*) in Australia. This was about the same time that humans arrived in Australia. Miller et al. (2016) showed that diagnostic burn patterns on eggshell fragments found at over 200 sites across Australia were created by humans discarding eggshells in and around transient fires, presumably made to cook the eggs. Harvesting of their eggs by humans would have decreased *Genyornis* reproductive success, contributing to the bird's extinction. Roberts et al. (2001) used optical and thorium-uranium methods to get ages for rocks and sediment associated with large-animal remains. Dates show that large animals at 28 sites were buried between 51,200 and 39,800 years ago, just as human beings were spreading across Australia. Twenty-eight genera and 55 species of vertebrates are estimated to have vanished—including fearsome claw-footed kangaroos that weighed in at 300 kg (650 lb.) and the 100 kg (220 lb.) *Genyornis*, the heaviest bird ever known. Roberts and his colleagues think the lethal blow was indirect. They believe that Aborigines changed vegetation by burning the landscape, possibly to make hunting and traveling easier. The result was less food for big browsing animals; hunting and climate fluctuations may then have tipped them to oblivion.

Tasmania became reconnected to Australia and accessible to human settlement about 43,000 years ago. Seven megafaunal species recorded on Tasmania were still present in deposits from 56,000 years ago—strong evidence against the cause of their extinctions being climatic and vegetational changes before humans arrived. The seven now-vanished giants consisted of two 500 kg (1,100 lb.) marsupial equivalents of a rhinoceros and a ground sloth, three antelope-like kangaroos weighing 100 to 150 kg (200–330 lb.) and standing 2 m (7 ft.) tall, a leopard-like marsupial predator, and a giant echidna (not a marsupial but a monotreme).

Steadman (1995) estimated that the prehistoric (2,000–30,000 years before present) loss of bird life on tropical Pacific islands may have exceeded 2,000 species, many of which were pigeons, doves, parrots, flightless rails, and passerines. If accurate, this represents a 20 percent worldwide reduction in the number of species of birds. Instead of 10,730+ species alive today, there probably would have been about 12,400+ species if these extinctions had not occurred. The loss of island birds was mainly due to predation by humans and the non-native mammals (rats, dogs, pigs) brought with them, removal of native forests and plants, introduction of non-native plants, and erosion of the soil.

Other factors may have been responsible for the extinctions on Madagascar. Some species may not have been able to adapt to the natural wet-to-dry oscillations of the climate. Clearly, whenever humans invade new territory, many megafauna vanish (Diamond, 1991; Steadman, 1995). Direct competition for space and resources could have been responsible for their demise. A most intriguing, but still unsupported, theory is that early humans carried a lethal pathogen to the vulnerable island communities (Culotta, 1995a). A lethal pathogen could have swept rapidly through native animals that had never been exposed to the disease. Because illness usually affects young animals hardest, and because larger species have fewer offspring, the megafauna could have been pushed to extinction. Those species that survived the pandemic would be resistant to future outbreaks. Culotta's theory explains why first contact with humans seems to be the deadliest. It also might be applicable to the North and South American extinctions that occurred 10,000 to 12,000 years ago. During this time, North America lost 73 percent and South America 80 percent of their genera of big mammals (Diamond, 1987). North American losses included 3 genera of elephants, 6 of giant edentates, 15 of ungulates, and various giant rodents and carnivores (Martin, 1967). Culotta (1995a) points out that more than 70 species of large mammals became extinct; since that time, in contrast, no large mammals have been lost.

* * *

Since 1500, more than 200 extinctions have been documented among vertebrates, mostly birds and mammals. Approximately 90 of these have been mammals (Fig. 16.8) (MacPhee and Flemming, 1997); undoubtedly, more have disappeared without a recorded history. In some cases, overhunting resulted in the extirpation of some species from former areas (bison) or in total extinction (Steller's sea cow, passenger pigeon, great auk, dodo; see Fig. 16.1). Passenger pigeons (Fig. 16.9) formerly traveled in dense flocks numbering in the millions. Ornithologists have estimated that passenger pigeons in precolonial America numbered 2 billion to 3 billion, making them perhaps the most abundant bird species on the Earth at the time. By 1890, they had virtually disappeared due to overhunting for food and feathers. The last passenger pigeon died in the Cincinnati Zoo in 1914. The dusky seaside sparrow (*Ammospiza maritima nigrescens*) (Fig. 16.10), which formerly resided on Merritt Island and on the adjacent mainland along the St. John's River in East Central Florida, became extinct in the wild in the late 1970s after the habitat was altered for mosquito and flood control.

The thylacine (*Thylacinus cynocephalus*) (see Fig. 10.1; Plate 1), a marsupial also known as the Tasmanian tiger and/or Tasmanian wolf, was the largest carnivorous Australian marsupial to survive into the modern era. Once occurring throughout Australia and New Guinea, it was common in Tasmania prior to European colonization. Since they preyed on livestock, among other large prey, they soon came into conflict with humans (Wroe et al., 2005). Thylacine populations rapidly declined throughout the 1800s and early 1900s because of predator control, habitat loss, and competition with the dingo (Johnson and Wroe, 2003). The Australian government placed a bounty on thylacines in 1888 with the last wild animal being shot in 1930. The last captive thylacine died in the Hobart Zoo in 1936. The species was eventually declared extinct in 1982. By extracting DNA from the soft tissue of a 108-year-old, alcohol-preserved young specimen in the pouch of a thylacine, DNA fragments have been isolated and sequenced (Feigin et al., 2018). The sequencing of the genome of the Tasmanian tiger provides insights into the evolution and demography of this extinct marsupial carnivore.

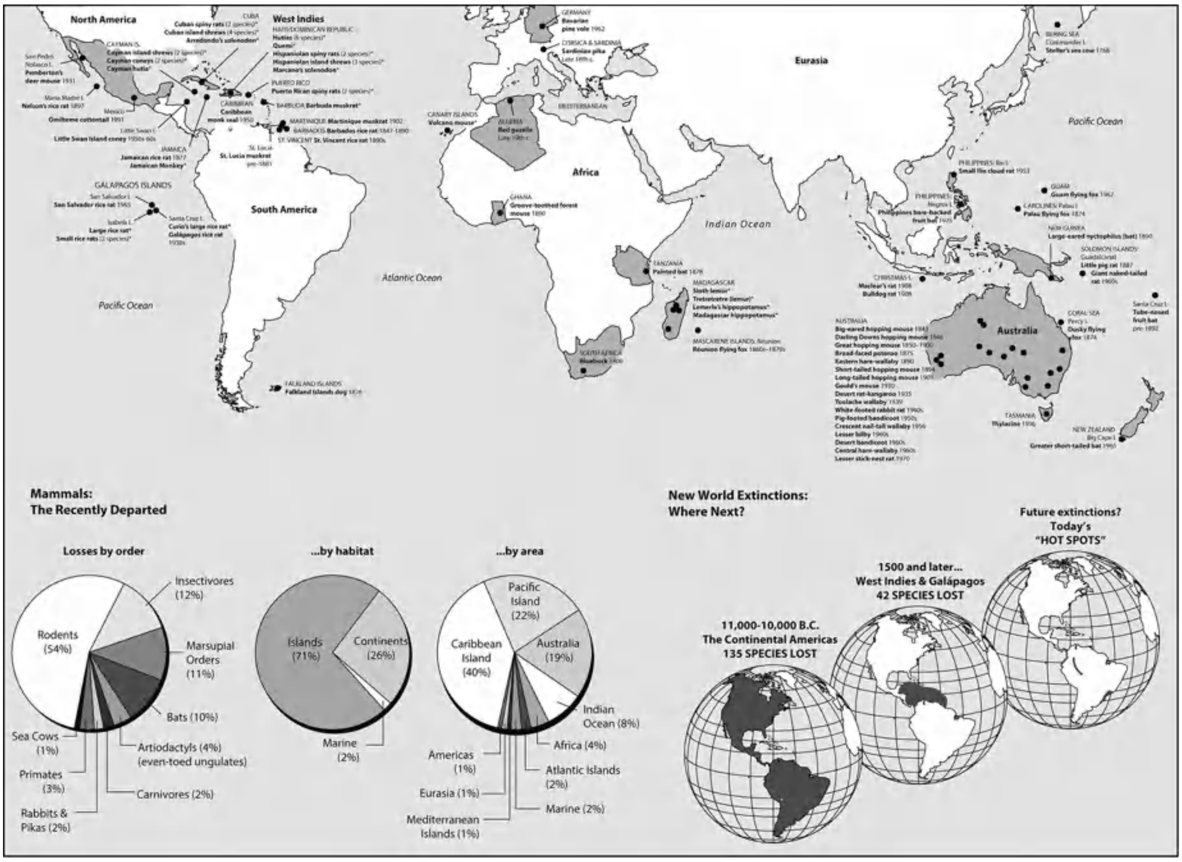


Figure 16.8. Recently departed mammals. The world has suffered two well-documented waves of mammal extinction since the arrival of humans at least 15,000 years ago. The first wave, striking between 12,000 and 13,000 years ago, affected the mainland areas and resulted in the extinction of at least 135 species. The second hit thousands of years later, in the West Indies and the Galápagos. In the West Indies, more than 80 percent of the land mammal fauna was lost. Rodents, bats, and insectivores have been the groups hardest hit by extinctions in the last 500 years. (*Asterisk (*) indicates species which became extinct after the year 1500; precise date not known.*)

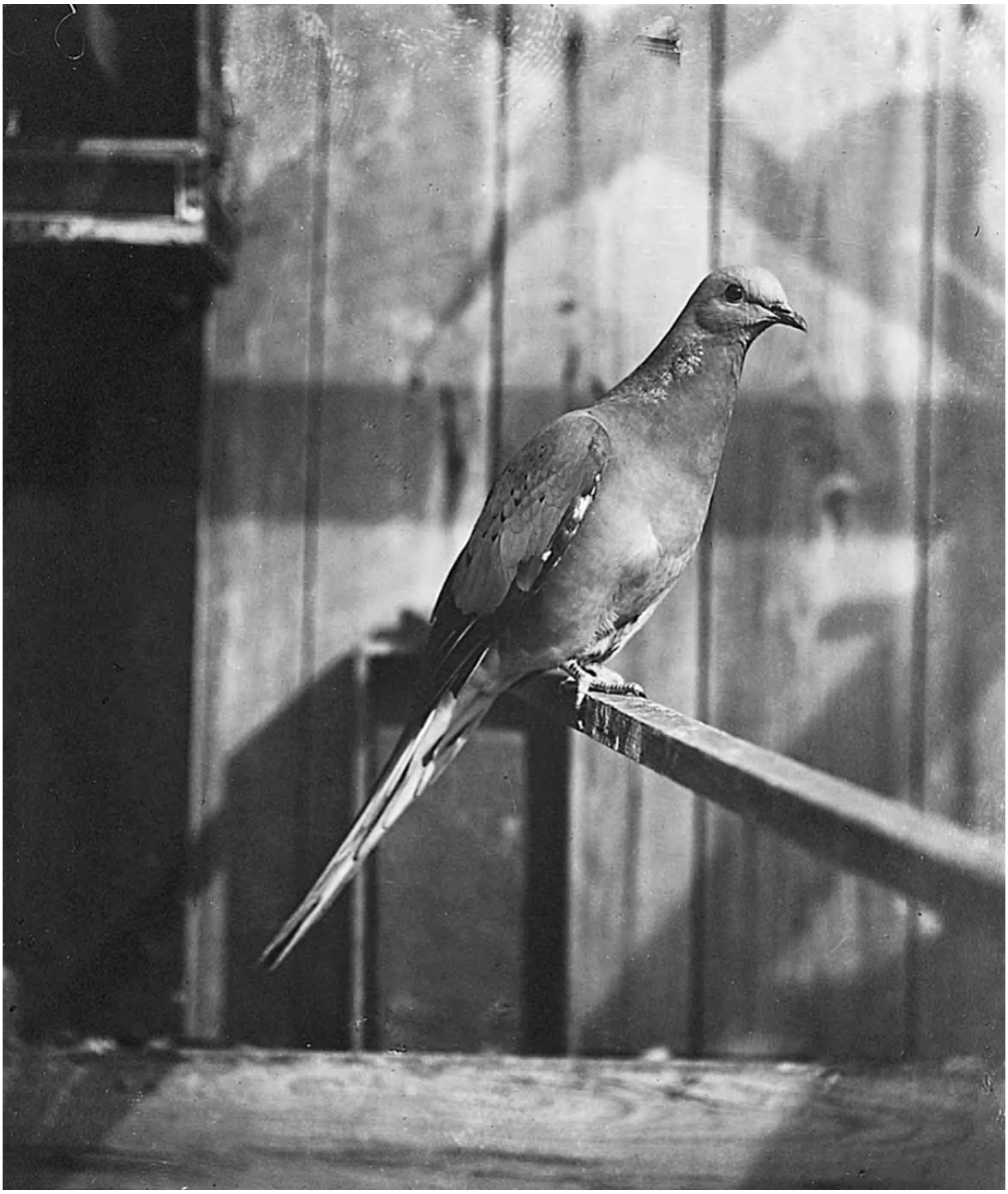


Figure 16.9. The extinct passenger pigeon (*Ectopistes migratorius*). In 1605, the French explorer Samuel de Champlain observed passenger pigeons in “infinite numbers” in Maine. These birds perched on trees in such dense groups that they often broke the branches by their sheer weight. Migratory flocks, kilometers long, darkened the sun and took hours to pass a given point. Alexander Wilson, the “Father of American ornithology,” estimated that one such throng observed by him near Frankfort, Kentucky, about the year 1808, contained more than 2 billion passenger pigeons. Humans mass-slaughtered passenger pigeons for food for themselves and for their pigs. It was fantastically easy to shoot the birds, but it was cheaper and quicker to blind them with torches and club them to death, or suffocate them by burning sulfur under their roosts. The last known passenger pigeon died in the Cincinnati Zoo in 1914.

In 2006, a rare, nearly blind white dolphin, the baiji (*Lipotes vexillifer*) (Fig. 16.11), which had survived for millions of years, was declared effectively extinct by the IUCN following a fruitless six-week search of its Yangtze River habitat in China. (Under scientific rules, however, it takes up to 25 years before an extinction is ratified.) The baiji represents the first large aquatic mammal to be driven to extinction since the Caribbean monk seal in the 1950s. It succumbed to a degraded habitat—ship traffic (which confounds the sonar the dolphin used to find food), overfishing, and pollution. This particular species was the only living representative of a whole family of mammals. Thus, this is the end of a whole branch of evolution.

Figure 16.10. The dusky seaside sparrow (*Ammospiza maritima nigrescens*) was a resident on Merritt Island and on the opposite mainland along the St. Johns River in East Central Florida. It is now extinct because the habitat has been altered for mosquito and flood control.

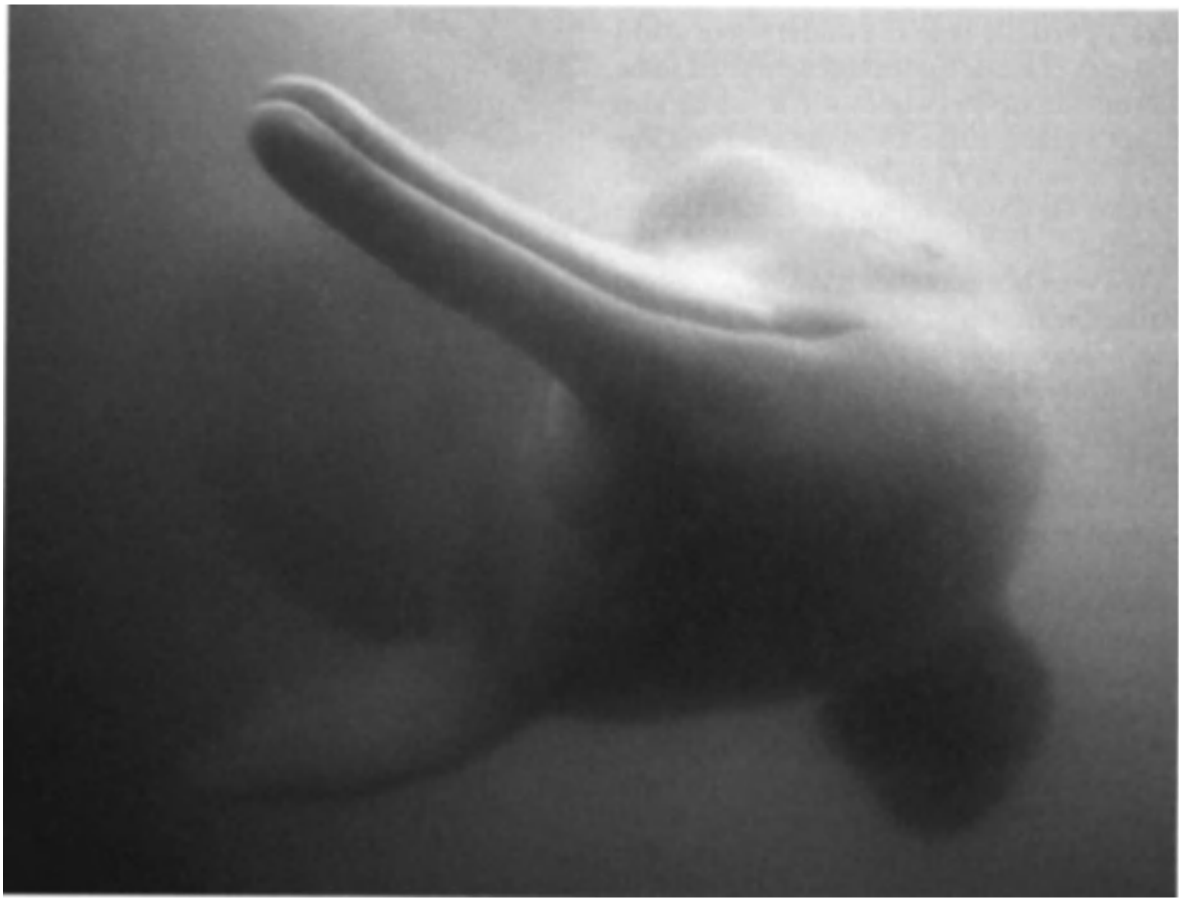


Figure 16.11. A rare photograph of the baiji river dolphin (*Lipotes vexillifer*). The baiji river dolphin has recently been declared extinct.

The Christmas Island pipistrelle (*Pipistrellus murrayi*) was listed as officially extinct according to the September 2017 IUCN Red List of Endangered Species (Matacic, 2017). The pipistrelle was the sole echolocating species on Australia's Christmas Island, some 350 km (215 mi.) south of Java, making it easy for scientists to detect the bats using ultrasonic devices that record their calls. It is unknown what led to the decline, which accelerated in the 1990s, but researchers suspect invasive predators such as snakes and giant centipedes. A survey in January 2009 had indicated that just 20 bats were left.

The Yangtze giant softshell turtle (*Rafetus swinhoei*) is listed as critically endangered by the IUCN. Threats to its existence include habitat loss caused by humans' excessive hunting for food and trade, resource competition, climate change, disease, and genetic stochasticity. On April 14, 2019, the only known female *Rafetus swinhoei* died in China, leaving one captive male in China and two known wild males in Vietnam. Unless another female is found in the wild, the species is now functionally extinct (Liu et al., 2019).

Desert pupfish (*Cyprinodon macularis*) (see Plate 2) are found in shallow water of desert springs, small streams, and marshes below 1,500 m (5,000 ft.) elevation. Naturally occurring populations have been extirpated in Arizona but still occur in the Salton Sink Basin of California, the Colorado River Delta, and the Laguna Salada Basin in Mexico (California Department of Fish and Wildlife, 2019). They tolerate high salt content and high water temperatures. A number of species of desert pupfish (*Cyprinodon* sp.) have become extinct due to the introduction of predatory and competitive fishes, the construction of bathhouses over the sources of thermal springs, stream channelization, and the filling or draining of springs for agricultural purposes (Brown, 1971). Pumping of water from natural underground reservoirs lowers the water level in the springs and is threatening the extinction of seven additional species (US Fish and Wildlife Service, 1990). The desert pupfish was listed as endangered by the US Fish and Wildlife Service on March 31, 1986.

Effects of Introduced Species

Introduced species, whether their introduction has been accidental or planned, are well known for their negative impacts on native species. Many, however, have provided benefits to humans in the form of aquaculture, sport fishing, forestry, horticulture, and game hunting. The economic value of many exotic species provides a strong incentive to their further introduction, despite the potential ecological risks.

Marine islands are home to a disproportionately large number of endangered species, and eradicating invasive predators on 169 of them could protect 9.4 percent of the world’s most at-risk vertebrate species. There are approximately 465,000 islands in the world (UNEP-WCMC, 2015), and though they make up just 5.3 percent of the Earth’s terrestrial area, they have hosted 75 percent of known amphibian, reptile, bird, and mammal extinctions since 1500 and currently support 36 percent of species in these groups that are classified as critically endangered on the IUCN Red List (Tershy et al., 2015). During the past 25 years, conservationists have succeeded in 85 percent of attempts to rid 792 marine islands of invasive mice and rats and feral goats and cats. Island Conservation, an environmental organization based in Santa Cruz, California, evaluated the potential for eliminating invaders that remain on 1,279 marine islands, taking into account the number of endangered species, the severity of the invasive mammal infestations, and political and economic considerations (Holmes et al 2019).

Vertebrates that have been introduced either into North America or elsewhere that have had negative impacts on native species include such well-known examples as rainbow trout, English sparrow, starling, cane toad, Nile monitors, Argentine tegu lizards, green anacondas, brown tree snake, nutria, mongoose, and many others. The Florida Fish and Wildlife Conservation Commission has identified 50 types of non-native lizards, turtles, crocodilians, and snakes just within Florida—more than anywhere else in the world (Sweeney, 2018). Some lesser-known examples in North America include Asian carp, red lionfish, northern snakehead, and Burmese python.

Asian Carp

Carp are a family of fish native to Europe and Asia (see Plate 3). Seeking a natural weed killer, the US Fish and Wildlife Service brought "Asian carp" to the United States. Collectively known as "Asian carp," the newest carp invaders are the bighead carp, black carp, grass carp, and silver carp. In the 1970s, catfish farmers in the Southeast began importing them as a natural pond cleaner. But floods in the Mississippi caused the ponds to overflow, and the carp swam into the river. In some parts of Mississippi, Asian carp have been known to dominate entire steams, effectively pushing out the native species. They feed by filtering plankton from the water and compete with native species for food and living space. They are thought to lower water quality, which can kill off sensitive organisms like native freshwater mussels. They can weigh up to 100 pounds and can consume 40 percent of their body weight daily. They have no natural predators, and are so bony that US consumers do not want to eat them. Carp were recently discovered in the Chicago Sanitary and Ship Canal, an artificial body of water connecting the Mississippi River to the Great Lakes. The Army Corps of Engineers has an electronic barrier at the canal to stop the fish from entering the Great Lakes. But Michigan authorities are complaining that the electronic barrier—which costs $40,000 a month to power—is not enough to keep the carp from the Great Lakes. They want the Corps to close the canal and protect Michigan's $7 billion tourism/recreational fishing industry. But closing the canal would disrupt a huge amount of interstate commerce, so the Corps is planning to erect another barrier to further insulate the lakes. In July 2012, Congress included the Stop Invasive

Species Act as an amendment to a transportation bill it approved. The act requires the US Army Corps of Engineers to speed up implementation of strategies to protect the Great Lakes from Asian carp. Part of the Corps Action Plan for 2018 was to develop several new deterrents such as using carbon dioxide and underwater sound to keep the carp from moving through locks or other types of chambers. The proposed Brandon Road Lock and Dam near Joliet, Illinois, will feature electrical barriers, a bubble barrier, acoustic deterrents, and a final flushing lock. In less than 50 years, the Asian carp has gone from a helpful pond cleaner to a multimillion-dollar nuisance.

Red Lionfish

The red lionfish (Fig. 16.12; see also Plate 4), a native of the South Pacific, Indian Ocean, and Red Sea, has been found in Atlantic waters from south Florida to North Carolina, and its presence is causing scientists concern. Found near the sandy bottom of the warm Gulf Stream waters, it is the first non-native ocean fish to successfully invade the Atlantic in North America in documented maritime history. A voracious predator, the 30 cm (12 in.) long lionfish has the potential to upset the ecosystem, preying unchecked on other fish and displacing native top-level species. Lionfish devour small reef fish whole, competing aggressively for the food of larger native Atlantic fish. Native reef fish take an average of three to four years to reach reproductive maturity, while lionfish take about six months. Female lionfish spawn monthly during the summer with egg sacks containing up to 20,000 eggs. The fish also presents a threat to humans. Lionfish, which are members of the scorpionfish family, carry a painful—and in rare cases, deadly—venom in the spines on their fins. There are several scenarios by which this fish could have entered coastal waters. A popular aquarium fish, it is thought that there could have been several deliberate lionfish releases into US waters by aquarium owners when their pet lionfish outgrew their aquariums. Another possibility is that dive-boat operators may have released red lionfish, perhaps purchased at a pet store, to establish a population for their customers to observe. The earliest sighting was during the mid-1980s, when a red lionfish was caught from a pier in Lake Worth, Florida. Many biologists point to Hurricane Andrew in 1992 as the agent behind a later release. The hurricane destroyed an aquarium that had housed six red lionfish in a Miami home on Biscayne

Bay. Several of the vividly striped survivors were spotted in the bay shortly thereafter.

Figure 16.12. The red lionfish is the first known non-native ocean fish to invade the Atlantic Ocean in North America. It is native to the South Pacific, Indian Ocean, and Red Sea.

National Oceanic and Atmospheric Administration (NOAA) researchers have concluded that invasive lionfish populations will continue to grow and cannot be eliminated using conventional methods. Marine invaders are nearly impossible to eradicate once established. Local Florida dive shops and other organizations host lionfish derbies and lionfish removal days where people compete to catch the most lionfish. Dive shops show you how to catch, clean, and cook your own lionfish. Even grocery stores are now carrying lionfish. The lionfish's arrival comes on the heels of another high-profile invasion caused by humans releasing their fish—the northern snakehead invasion in a Maryland lake.

Northern Snakehead

The northern snakehead (*Channa argus*) is a type of snakehead fish that is native to China, Russia, and Korea. In the United States it is considered to be a highly invasive species. Several were found in a pond in Crofton, Maryland, in the summer of 2002. Since a heavy rain could wash the fish into the nearby Little Patuxent River and the fish was considered a threat to the Chesapeake Bay watershed, officials poisoned and drained the pond in an attempt to destroy the species. Two adults and more than 100 small fish were captured and destroyed. A man admitted to having released two adults that he had purchased from a New York market into the pond. In 2004, 19 adults were captured in the Potomac River. It was later confirmed that they had become established by breeding. As of 2009, scientists have discovered hundreds of them in the Potomac and several of its Northern Virginia tributaries. The northern snakehead has also been found in Florida, New York, Pennsylvania, Massachusetts, California, North Carolina, and Arkansas.

Northern snakeheads are top-level predators and pose a threat to native fish populations. Not only can they breathe air, but they can also survive on land for up to four days, provided they are wet, and are known to migrate up to 400 m (1,312 ft.) on wet land to other bodies of water by wriggling with their bodies and fins. These fish reach sexual maturity at 2 to 3 years of age. Each spawning female can release up to 15,000 eggs at once. Since they can mate as often as five times a year, a single female could potentially release up to 150,000 eggs in just two years.

Burmese Python

Several large exotic snakes and lizards currently live in Everglades National Park, Florida. The Burmese python (*Python molurus bivittatus*) (see Plate 5), however, is the only one known to be breeding. The snake is an invasive species that now numbers in the tens of thousands in the southern part of Florida, with the core of the population centered in the park. It feeds on such native wildlife as alligators (Fig. 16.13), great egrets, limpkins, white ibises, magnificent frigate birds, cotton rats, round-tailed muskrats, bobcats, and endangered Key Largo wood rats. Road surveys by researchers have recorded staggering declines in animal sightings: a drop of 99.3 percent among raccoons, 98.9 percent for opossums, 94.1 percent for white-tailed deer, and 87.5 percent for bobcats. One of the largest snakes in the world, the Burmese python can grow to more than 6 m (20 ft.) long and weigh as much as 91 to 113 kg (200–250 lb.). Although the size of the wild population is not known, it has been estimated to be in the thousands (Snow et al., 2007). Such animals, popular in the pet trade, were released into the state by their owners when the reptiles became too big to handle. They have many young (Fig. 16.14) and grow very quickly. A 50 cm (20 in.) long hatchling can often reach 3 m (10 ft.) within three years. Exotics like the python have the potential to greatly alter the landscape of the Everglades by pushing out native plants and animals, making control of these invaders one of the greatest challenges in Everglades restoration. In addition, yellow anacondas, reticulated pythons, green iguanas, and Nile monitors have also been found in subtropical Florida. The iguanas and monitors may reach lengths of 1.8 to 2.1 m (6–7 ft.) long, with the monitors eating just about anything, including burrowing owls, gopher tortoises, and domestic pets.

Figure 16.13. An American alligator and a Burmese python locked in a struggle. Alligators eat pythons, but pythons also eat alligators.

University of Florida researchers are using radio telemetry to determine how pythons are using the habitat and the extent and timing of their movements. In an effort to control them, researchers are using "Judas snakes"—captured pythons that are implanted with radio transmitters and then released back into the wild. In the spring, when the reptiles come together in breeding aggregations, one radio-tagged snake can lead scientists to many others. In addition, state-sanctioned hunts are held periodically to help control the pythons.

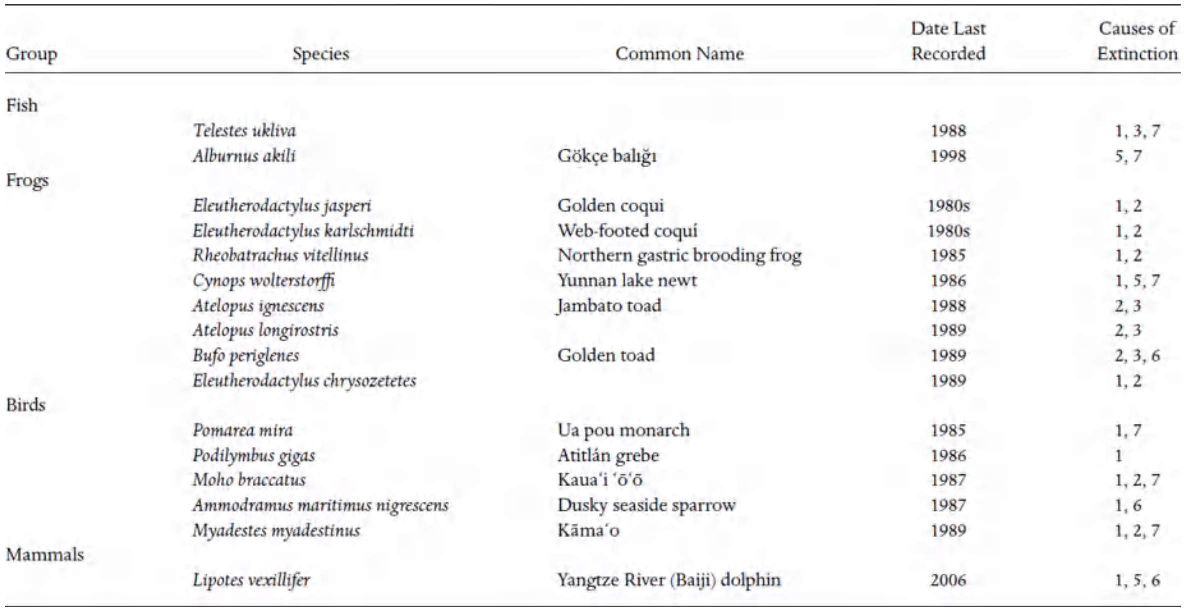
Extinction

The IUCN was 70 years old in 2018 and is the oldest global conservation organization. Since 1964, it has been compiling and publishing the *IUCN Red List of Threatened Species*, which documents extinctions that have occurred globally since the year 1500. As of 2018, it covered over 93,500 species, with a 2020 goal of 160,000 species. A species is listed in the Red List Categories of "possibly extinct" and "possibly extinct in the wild" (but not "extinct") until their extinction can be confirmed. A species is declared extinct after exhaustive surveys of all potential habitats eliminate all reasonable doubt that the last individual of a species, whether in the wild or in captivity, has died and that all local or unconfirmed reports have been investigated and discounted. The 2016 edition of the *IUCN Red List* documented 306 possibly extinct and/or possibly extinct in the wild species (28 mammals, 22 birds, 41 reptiles, 128 amphibians, and 89 fishes).

Since 1500, roughly 90 mammal species and 190 species of birds have become extinct. Ninety percent of the bird extinctions have been of insular species with the major causes being invasive species (46 percent) and hunting/trapping (26 percent) (Butchart et al., 2018). However, results of a recent study by BirdLife International (2018) confirm that there is a growing wave of extinctions sweeping across the continents, driven mainly by habitat loss and degradation from unsustainable agriculture and logging. Some recent extinctions are listed in Table 16.1. Half of Hawaii’s 140 native bird species and subspecies are extinct. Of the 69 that remain, half are endangered. Some have not been seen for so long that naturalists believe they are gone. Others, like the Hawaiian crow, or ‘alalā, survive only in captivity.

Figure 16.14. Burmese pythons breed in the early spring, with females laying clutches of 12–36 eggs in March or April. Females remain with the eggs until they hatch.

Table 16.1. Some Documented Species Extinctions from 1984 to 2009



Group	Species	Common Name	Date Last Recorded	Causes of Extinction
Fish				
	Telestes ukliva		1988	1, 3, 7
	Alburnus akili	Gökçe balığı	1998	5, 7
Frogs				
	Eleutherodactylus jasperi	Golden coqui	1980s	1, 2
	Eleutherodactylus karlschmidti	Web-footed coqui	1980s	1, 2
	Rheobatrachus vitellinus	Northern gastric brooding frog	1985	1, 2
	Cynops wolterstorffi	Yunnan lake newt	1986	1, 5, 7
	Atelopus ignescens	Jambato toad	1988	2, 3
	Atelopus longirostris		1989	2, 3
	Bufo periglenes	Golden toad	1989	2, 3, 6
	Eleutherodactylus chrysozetetes		1989	1, 2
Birds				
	Pomarea mira	Ua pou monarch	1985	1, 7
	Podilymbus gigas	Atitlán grebe	1986	1
	Moho braccatus	Kauaʻi ʻōʻō	1987	1, 2, 7
	Ammodramus maritimus nigrescens	Dusky seaside sparrow	1987	1, 6
	Myadestes myadestinus	Kāmaʻo	1989	1, 2, 7
Mammals				
	Lipotes vexillifer	Yangtze River (Baiji) dolphin	2006	1, 5, 6

Note: Key to causes of extinction: 1 = habitat loss; 2 = disease; 3 = climate change/pollution; 4 = natural disaster; 5 = exploitation/persecution; 6 = restricted range; 7 = invasive species (not disease).

The World Wildlife Fund (WWF) publishes the *Living Planet Report* every two years. The 2016 Report stated that populations of vertebrates had declined by 58 percent between 1970 and 2012. More specifically, terrestrial vertebrate populations had declined by 38 percent, freshwater populations had declined by 81 percent, and marine species showed a 36 percent overall decline between 1970 and 2012 (World Wildlife Fund, 2016).

The US Census Bureau forecasts that the world's population of humans will be nearly 9.1 billion by 2050—a nearly 50 percent increase from 6.2 billion in 2002. The global population grew 1.2 percent from 2001 to 2002, or about 74 million people, but growth is expected to slow to 0.42 percent by 2050. The world's population growth is slowing because women are having fewer children and more people are dying from AIDS, especially in Africa. Both of these factors are susceptible to future changes.

Many scientists believe that humanity is in the midst of Earth's sixth mass extinction (Ceballos et al., 2017). In a sample of nearly half of known vertebrate species, 32 percent were found to be decreasing; that is, they have decreased in population size and range. Nature is being annihilated by a massive and escalating assault on living things, not only because of the human population explosion but also as a result of massive commercial endeavors and public apathy. Dwindling population sizes and range shrinkages amount to a massive anthropogenic erosion of biodiversity and of the ecosystem services essential to civilization. It has been difficult to quantify the real extent of the current extinction episode, either for a given taxonomic group at the continental scale or for the worldwide biota, largely because comparisons of pre-anthropogenic and anthropogenic biodiversity baselines have been unavailable. Carrasco et al. (2009) computed those baselines for mammals of temperate North America.

Paul Ehrlich (1986) noted that the Earth's biota appears to be entering an era of extinction that may rival or greatly surpass in scale the extinction that occurred at the end of the Cretaceous.

> As far as is known, for the first time in geologic history, a major extinction episode will be entrained by a global overshoot of carrying capacity by a single species—*Homo sapiens*. The episode, if it culminates as projected, will produce a crash in the population size of the species that caused it. Unfortunately, few laypeople are aware of the utter dependence of our species on the free services provided by natural ecosystems—and thus on other organisms that are key components of those systems. Ironically, for the first time, a species engendering its own collapse has the knowledge necessary to avoid its fate but may not be able to disseminate that knowledge and act on it in time.

Plant Extinction

Since the mid-1700s, researchers have identified a total of 571 plant species that have disappeared. Plant extinctions endanger other organisms, ecosystems, and human well-being and must be understood for effective conservation planning.

Humphreys et al., 2019

Many scientists feel that there are disturbing analogies between what happened in the Pleistocene and today's world (Barnosky, 2009):

1. Human contributions to global warming are causing potentially harmful climate change, threatening the survival of many species.
2. Intercontinental travel rapidly spreads diseases like AIDS, tuberculosis, cholera, and pandemic flu.

3. In the Amazon, expanding populations are cutting down rain forests where more than 600 species, including jaguars, tapirs, and giant otters, are listed as endangered.
4. In Africa, rogue hunters are slaughtering apes and monkeys to eat as "bushmeat."

Although eminent ecologists warn that humans are causing a mass extinction event (the sixth mass extinction) of a severity not seen since the age of dinosaurs came to an end 65 Mya, some paleontologists and statisticians have called such comparisons into doubt (Gibbs, 2001). Attempting to project future extinction rates is complex. Factors that must be considered are the natural (or "background") extinction rate, the current rate, and whether the pace of extinction is steady or changing. Attempts to quantify these factors are controversial.

Mark Urban, ecologist at the University of Connecticut, found that extinction risk accelerates with every degree of temperature rise, as habitats become uninhabitable. He stated: "If we continue on our current trajectory of greenhouse gas emissions, we face losing one in six species" (Urban, 2015). In 1999, E. O. Wilson cited current estimates that between 1 and 10 percent of species are extinguished every decade—at least 27,000 a year. Novacek and Cleland (2001) wrote that "figures approaching 30 percent extermination of all species by the mid-21st century are not unrealistic." In a 1998 survey of biologists, 70 percent said they believed that a mass extinction was underway, and an equal number predicted that up to one-fifth of all living species could disappear within 30 years (Warrick, 1998).

Extirpation

The September 2018 IUCN Red List recorded the following percentages of threatened vertebrates: sharks and rays (31 percent), selected bony fishes (7.5 percent), amphibians (41 percent), selected reptiles [marine turtles, sea snakes, chameleons, and crocodilians] (35 percent); birds (13 percent); and mammals (25 percent). Rhodin et al. (2018) looked at the conservation status of all 360 species of turtles and tortoises and found that the Order Testudines is among the most endangered of all vertebrate orders. The epicenter of the threat is Asia, where trade in turtles for meat and traditional medicine has driven large declines across species. Further harm to this group is inflicted by habitat loss and degradation, disease, invasive species, and climate change.

Although one in four of the world's mammal species is currently threatened with extinction, an estimated 36 percent of the marine mammals are at risk, according to the IUCN (Schipper et al., 2008). (This is the same percentage as reported by the WWF. See Chapter 16, page **467**). Populations are declining in half of all mammal species, with some experiencing an extreme decline; Tasmanian devil (*Sarcophilus harrisii*) numbers plummeted by 60 percent over the past decade, for example. The survey placed 188 species in the most severe, "critically endangered" category, including the Iberian lynx (*Lynx pardinus*), which has a wild population estimated at 84 to 143 adults. The greatest threats that mammals face are deforestation, habitat loss, freshwater and marine pollutants, and hunting, with the most dramatic population declines occurring in Southeast Asia, where approximately 79 percent of primates are threatened with extinction.

Many predators (gray wolf, *Canis lupus*; red wolf, *Canis rufus*; cougar, *Puma concolor*; and grizzly bear, *Ursus arctos*) have been extirpated from large parts of their former ranges. Overhunting has also greatly reduced populations of alligators, sea turtles, and whales. The American alligator (*Alligator mississippiensis*) benefited from its protection under the Endangered Species Act and has recovered to the point where its status has been changed from endangered to least concern. In some areas, it is being legally harvested for its meat and skin.

Iberian Lynx

The Iberian lynx (*Lynx pardinus*) (see Plate 6), once prevalent from the Pyrenees south to the Mediterranean, now survives in just two fragmented pockets in Andalusia. In the 1980s, a small but sustainable population of about 1,100 animals existed, but an outbreak of two diseases killed up to 90 percent of the region's wild rabbits—the lynx's primary prey. In addition, new roads, high-speed trains, and tourism infrastructure have reduced the lynx's habitat. Only 200 individuals are left. If the Iberian lynx does not survive, it would be the first documented feline extinction since the saber-toothed tiger. A captive breeding program is under way with the goal of releasing animals into currently lynx-free areas. As one researcher stated: "If we're breeding but there is no habitat, we're not saving the species" (Vogel, 2006).

Asiatic Cheetahs

The Asiatic cheetah (*Acinonyx jubatus venaticus*) (see Plate 7) once ranged over the grasslands of India, Pakistan, Russia, Iran, and the Middle East, but it was extirpated from most of its range during the twentieth century. Today, the critically endangered cheetah subspecies survives only in Iran. The cats have been nearly wiped out by excessive hunting, habitat degradation, and scarcity of medium-sized herbivore prey such as gazelle, wild sheep, wild goats, and cape hares.

Between 2001 and 2012, 42 different cheetahs were found dead. Illegal anthropogenic killing, mainly by herders (and their dogs) or poachers, was the greatest cause of death, accounting for 21 individuals (50 percent), followed by road mortalities, which killed 12 cheetahs (29 percent, ten adults and two cubs), with almost equal sex ratios. Seven cases (17.5 percent) were due to suspected natural causes, including one individual that was killed by other carnivores (Farhadinia et al., 2017).

The last wild Asiatic cheetahs in Iran numbered between 70 and 110 individuals in 2013, with all of them occupying three main population nuclei in the remote and arid central plateau. Iran considers their cheetah an important part of their natural and cultural heritage, and Asiatic cheetah has now become a symbol of the country's conservation efforts. Iran's Department of the Environment partnered with Panthera and various other groups, including the Wildlife Conservation Society and the United Nations Development Program, to create a comprehensive conservation program.

Tigers

The Switzerland-based World Wide Fund for Nature announced in 1996 that tigers (*Panthera tigris*) (see Plate 8) that once roamed much of Asia are dying at a rate of perhaps one a day because of deforestation and poaching. As of 2016, the WWF and Global Tiger Forum announced the number of tigers remaining in the wild, mostly in Asia, was an estimated 3,890, up from an estimate of "as few as 3,200" in 2010. For the first time after decades of constant decline, tiger numbers appear to be on the rise. The countries that showed increases in their wild tiger count (estimated) included India (2,226), Russia (433), Nepal (198), and Bhutan (103). The number in 1996 could have been as low as 4,600, down from 5,000 in 1994. Tigers numbered approximately 100,000 in 1900. Numbers have been shrinking not only because of hunting and poaching, but also loss of habitat, such as deforestation (particularly in

Sumatra) for palm oil and paper and pulp industries. Another major threat to Asian tigers is an increased illegal trade in tiger bones, skin, and other parts for traditional Chinese medicines. Illegal trading is also a threat to many other vertebrates, especially reptiles, birds, and primates.

Primates

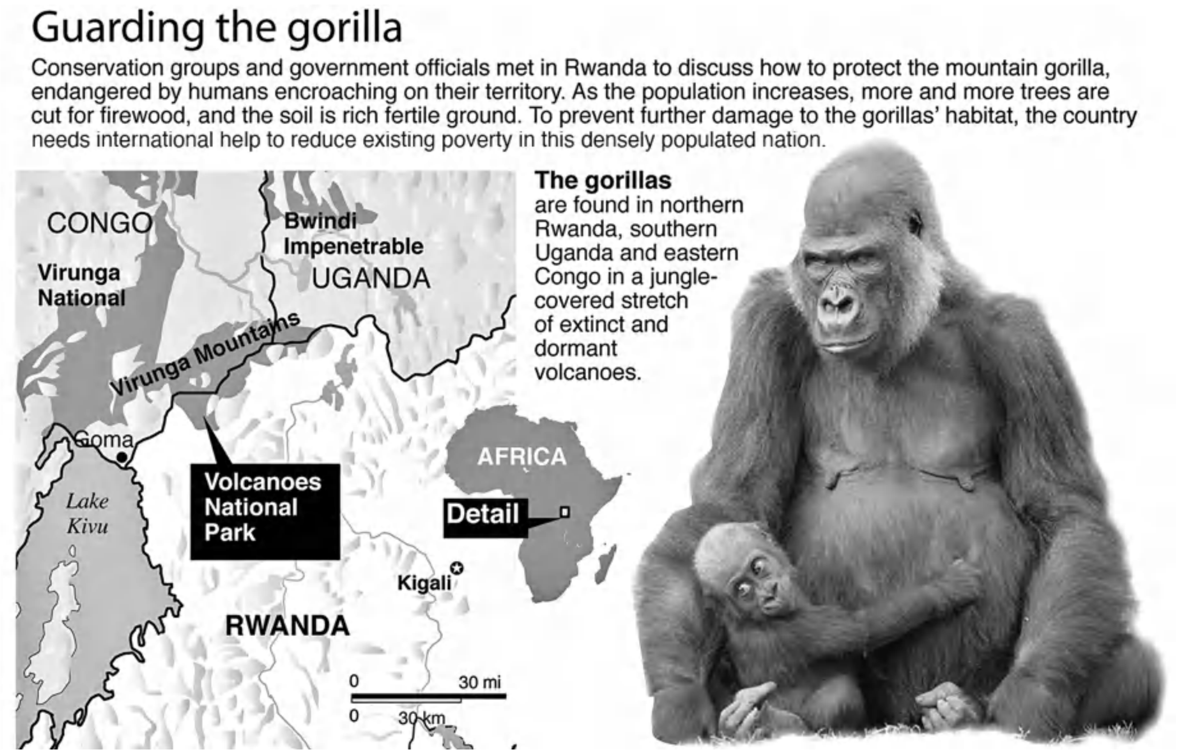
In 2003, Conservation International and the IUCN released a report stating that, after surviving a century with no extinctions, 25 species of apes, monkeys, lemurs, and other primates now were at risk of disappearing forever. Of the top 25 most endangered, 11 are found in Asia, 8 in Africa, and 3 each in Madagascar and the Neotropics (Central and South America). The population of one Madagascar lemur, the silky sifaka (*Propithecus candidus*) (see Plate 9), is estimated at only 100 to 1,000 animals. The bone-white animal, weighing between 5 and 6.5 kg (11 and 14 lb.) and measuring up to 1.1 m (3.5 ft.) long, is called silky because of its luxurious fur. Illegal logging, burning, and hunting are the main threats to its continued existence.

Of the 418 primate species considered on the 2012 IUCN Red List, 207 (49.5 percent) were rated as vulnerable, endangered, or critically endangered. Trade in primates is seen as a significant impediment to their conservation (Nijman, V., et al. 2011).

Primates in China and Vietnam are the most vulnerable. Vietnam hosts 20 percent of the most endangered primates, and China harbors another 16 percent. Several primates in China and Vietnam now number only in the dozens or hundreds of individuals. Two gorilla species live in equatorial Africa; each has a lowland and upland subspecies. The western lowland gorilla (*Gorilla g. gorilla*) (see Plate 10) is the most widespread, possibly numbering 100,000; the Cross River gorilla (*Gorilla* g. *diehli*) is currently the world’s rarest great ape with a population of only around 250–300; the population of the eastern lowland gorilla (*Gorilla beringei graueri*) has crashed in recent decades and is now under 4,000; and the total population of the mountain gorilla (*Gorilla b. beringei*) (Fig. 16.15) is around 1,000 individuals, split into two separate groups (World Wildlife Fund, 2018). Strindberg et al. (2018) presented the largest survey data set ever assembled for the western lowland gorilla and estimated its overall abundance at more than 360,000 individuals. They estimated the annual population decline at 2.7 percent with the main causes of decline being tropical forest habitat destruction, disease, and poaching (local bushmeat hunting). Live capture for the pet trade and export for biomedical research also threaten some species, as does civil unrest in some areas.

In 2005, Conservation International issued a report on primates based on an analysis of computer databases and field studies at universities and government institutions around the world. The report stated that, globally, 25 percent of the 625 primate species and subspecies were now at risk of extinction, with habitat loss and bushmeat hunting as the primary causes. Nearly 45 percent of the most endangered primates are native to Asia. One scientist reported that orangutans on Borneo and Sumatra could be extinct in the wild within 20 years.

The term *bushmeat hunting* no longer applies only to starving villagers needing meat. Today, the term is applied by conservationists to the heavily organized commercial poaching where money is the motivation. The bushmeat trade is a global problem, affecting primates and other protected species in Asia, South and Central America, and Africa. Trucks loaded with armed men are paid by businessmen to kill everything in sight. The meat of everything from small game to monkeys, gorillas, and even rodents is in high demand back in the cities. A 12-month study in Brazzaville counted 15,000 animal carcasses at bushmeat markets, including 293 chimpanzees. A conservationist in Yaounde, Cameroon, estimated that 1 metric ton (2,205 lb.) of smoked bushmeat was unloaded at the railway station every day to supply the bushmeat markets. The big money is in western lowland gorillas, prized by restauranteurs and wealthy patrons who regard gorilla meat as a symbol of status and power. Poaching in the once remote regions of Cameroon, Central African Republic, Equatorial Guinea, Gabon, and Republic of Congo has become the most immediate threat to the survival of lowland gorillas. Based on a 2002 survey, approximately 100,000 lowland gorillas live in groups in the former remote regions. No one is certain how many are being killed, but experts agree the number is in the thousands per year. A 2009 undercover investigation in the Republic of the Congo found that a single group of poachers halved a local gorilla population in 12 months; an estimated 300 gorillas, the investigators said, were sold in the country in the course of a year (Guarino, 2015). Most of the countries already have laws banning poaching, but enforcement is difficult. If nothing is done immediately, the 2002 report estimated that only 10 percent of gorillas would remain by 2030. For additional information, refer to the website Ape Alliance (www.4apes.com) listed under Vertebrate Internet Sites at the end of this chapter. Information about a 2010 bushmeat documentary by the Canadian Ape Alliance can be found at https://great-apes.com/2010/10/11/bushmeat-documentary. A joint report from the United Nation's Environmental Program and Interpol issued in March 2010, entitled "The Last Stand of the Gorilla," stated that the 2002 estimate appeared too optimistic. The 2010 report states that gorillas may become extinct from most parts of their range in perhaps 15 years. One of the dangers gorillas now face is a large increase in logging for timber that is mostly destined for Asia, particularly China.



Guarding the gorilla

Conservation groups and government officials met in Rwanda to discuss how to protect the mountain gorilla, endangered by humans encroaching on their territory. As the population increases, more and more trees are cut for firewood, and the soil is rich fertile ground. To prevent further damage to the gorillas' habitat, the country needs international help to reduce existing poverty in this densely populated nation.

The gorillas are found in northern Rwanda, southern Uganda and eastern Congo in a jungle-covered stretch of extinct and dormant volcanoes.

Figure 16.15. Approximately 1,000 mountain gorillas are estimated to be surviving in the wild.

In addition to suffering from poaching, gorilla (and chimpanzee) populations have been ravaged by Ebola virus (EBOV). Among gorillas, the virus has up to a 95 percent mortality rate, compared with roughly 50 percent for humans, according to the World Health Organization. One of the earliest "die-offs" came in 1994, when an EBOV outbreak in the Minkebe region of Gabon decimated the region's entire gorilla population—once the second largest in the world. In 2002, an outbreak in the Democratic Republic of Congo wiped out 95 percent of the region's gorilla population. The population dropped from about 380 gorillas before the outbreak to fewer than 40 after the outbreak, which spreads by physical contact. An equally brutal attack broke out in 2006, when EBOV in Gabon killed 254 people and claimed more than 5,500 gorillas (Bermejo et al., 2006). Following the epizootic, no loss in genetic diversity was detected (Le Gouar, et al. 2009). Genton et al. (2012) investigated the recovery capacity of the gorillas following the 2002 outbreak. They found that the surviving females paired up with big silverback solitary males, which were less likely to be infected with the virus because they do not live in groups. The population stayed at about 40 individuals for the next six years, but the demographics—the age and relationships between the gorillas—changed drastically. The several solitary males that survived the outbreak disappeared, and new adult females moved into the area, forming new breeding groups. The adult females left in the population gave birth to several new gorillas—positive signs that this group will recover and repopulate the area. Even so, the researchers note that it could be more than 130 years before the population reaches 300 gorillas again—and their habitat must be protected.

A new oral vaccine to protect wild chimpanzees (see Plate 11) and gorillas against EBOV is undergoing its final trials (Walsh, 2017). Studies are underway to determine the dosage and to see if lacing sweet treats with the vaccine or using remotely operated sprays or darts could help to immunize wild animals. The vaccine must remain effective and stable in the heat of the forest.

After decades of protection and conservation efforts, the numbers of the critically endangered mountain gorilla (*Gorilla b. beringei*), a critically endangered gorilla subspecies in Virunga National Park, located in the eastern part of the Democratic Republic of Congo, bordering Rwanda and Uganda (see Fig. 16.15)., are the highest ever recorded (International Gorilla Conservation Programme, 2018). Numbers in the Virunga massif have increased from an estimated 480 individuals in 2010 to 604 as a minimum count as of June 2016. Combined with the 2011 results from the Bwindi Impenetrable Forest in Uganda, the other area inhabited by the mountain gorilla, the global population estimate now stands at 1,004. Despite this success, the mountain gorilla's status remains fragile. War has been waged in areas around the park, with gorillas subject to related threats like poaching and loss of habitat.

Increasingly steep population declines over the past century or two have imperiled the Bornean orangutans' (*Pongo pygmaeus*) (see Plate 12) survival in northeastern Borneo (Goossens et al., 2006), according to a DNA analysis. Results indicate that populations decreased by more than 95 percent over the past 100 to 200 years. Just from 1999 to 2015, an estimated 100,000 Bornean orangutans were lost (Voigt et al. 2018). In addition to illegal hunting, this trend coincides with extensive forest clearance that began in the 1890s. Forest destruction has accelerated during the past 50 years in order to develop palm oil and acacia plantations. As of 2015, Borneo's estimated orangutan population stands at approximately 65,700 animals (Western Schwaner population = 40,700; Eastern Schwaner population = 16,800; and Karangan population = 8,200). Orangutans were declared “critically endangered” by the IUCN in 2016.

Rhinoceroses

At the beginning of the twentieth century, 500,000 rhinos roamed many places in Africa and Asia. But today very few rhinos survive outside national parks and reserves due to persistent poaching and habitat loss over many decades. Most rhino horns find their way into the illegal market in Vietnam, where criminal networks grind up the horns for use in traditional medicines or sell them as high-value gifts. China is an important consumer market, as well, where rhino horns enter art and antique markets and are sometimes acquired as an investment purchase.

The smaller black rhino (see Plate 13) remains critically endangered, with about 5,000 left. Asian species of rhino have suffered even more, with 3,500 Indian one-horned rhinos left in Nepal and India, fewer than 100 Sumatran rhinos, and only about 60 Javan rhinos left in the world. The only two remaining northern white rhinos (see Plate 14) are kept under 24-hour guard in Ol Pejeta Conservancy in Kenya (Chutel, 2018). Both are females. The last male northern white rhinoceros, named Sudan, passed away at the age of 45 in March 2018. Neither female is able to conceive naturally. The only option is to harvest sex cells from the living northern white rhinos and use in vitro fertilization to impregnate southern white rhino surrogates. The technology to accomplish this is still being perfected, and there is no guarantee that it will work.

In 2013, another rhino subspecies, the western black rhino, was declared extinct. The eastern black rhino, numbering around a thousand, could be the next rhino species facing extinction. Conservationists are continuing to focus on saving this species in addition to the southern white rhino, a species numbering around 20,000.

A sharp upsurge in rhinoceros poaching in South Africa and Zimbabwe by organized crime gangs has devastated Zimbabwe’s rhino population and threatens to wipe out South Africa’s critically endangered black rhinos by 2030. About 1,500 rhino horns were traded illegally between 2006 and 2009, despite a long-standing ban on international trade (International Union for Conservation of Nature, 2010). The number of rhinos poached steadily increased each year from 2007 (13) to a high in 2014 (1,215) (Save the Rhino International, 2018). A total of

1,028 rhinos (approximately three rhinos every day) were poached in South Africa in 2017, a slight decline (26) from the 1,054 animals killed in 2016 and the 1,174 killed in 2015. In just a decade, more than 7,245 African rhinos have been lost to poaching. In Kenya, the worst year for poaching was 2013, when 59 animals were killed (more than 5 percent of the national population). In 2015, both Zimbabwe and Namibia suffered losses: Namibia lost 80 rhinos to poaching, up from 25 in 2014 and just two in 2012, while in Zimbabwe at least 50 rhinos were poached in 2015, more than double the previous year. For Africa as a whole, the total number of rhinos poached during 2015 was the highest it had been in two decades. While poaching is down in Kruger National Park, it is significantly up in other provinces, particularly KwaZulu-Natal. Rhino population growth continues to be severely impacted, and poachers are proving adept at changing their target sites and trafficking strategies.

Elephants and Lions

In May 2019, Botswana made it legal once again to kill elephants, lions, and other large mammals commonly sought by trophy hunters. The country is home to the world’s largest elephant population, estimated at more than 130,000. A government report recommended allowing hunting, citing increases in human-elephant conflict, loss of livestock to predators, and economic hardship on communities that had been supported by hunting revenue before a ban went into effect in 2014. Conservationists have broadly condemned the reversal, with some arguing that it is an attempt by the current president to win over rural voters in an election year. A poll by Humane Society International suggests the resumption of hunting could deter tourists wanting only to observe wild animals. Tourism accounts for one-fifth of Botswana’s economy.

Diseases

While concern about newly evolving diseases has focused on humans, scientists warn that wildlife faces the same threats as animals are forced into more crowded areas and moved to new locations. Globalization of the planet leads to the spread of diseases as animals are taken abroad from one country to another. Emerging infectious diseases (EIDs) can cause the extirpation of local populations of wild animals and even lead to extinction of a species (Daszak et al., 2000). Such diseases not only threaten wildlife, but also may form a reservoir of germs that could harm humans and domestic animals.

Peste des petits ruminants (PPR), a viral disease that affects domestic small ruminants with high morbidities and mortalities across more than 70 countries, has become a wildlife conservation challenge (Aguilar et al., 2018). PPR has spread from its historic range of Africa, West Asia, and the Middle East to the vast and remote steppes and mountains of East Asia, threatening even more wildlife. The mass mortality event affecting more than two-thirds of the critically endangered Mongolian saiga (*Saiga tatarica mongolica*) population in 2017 is one example of PPR's reach. In 2018, multiple PPR-related mortalities of the Siberian ibex (*Capra sibirica*) were recorded in Mongolia. Its impact on other steppe and mountain ungulates of Asia is unknown. The inaccessibility of their habitats, together with the lack of wildlife health surveillance programs across large areas, contributes to underestimating and underreporting of PPR mortality events. PPR is of special concern for the conservation of the susceptible markhor (*Capra falconeri*), argali (*Ovis ammon*), and goitered gazelle (*Gazella subgutturosa*), considered vulnerable by the IUCN, and for the survival of the snow leopard (*Panthera uncia*), which relies on prey abundance.

The virus that causes AIDS spread from chimpanzees and mangabeys to humans. Researchers have determined that a type of herpes virus that is harmless to African elephants can be fatal to Indian elephants. Measles contracted from humans threatens wild mountain gorillas habituated to tourists, and poliovirus has killed chimpanzees in Gombe National Park in Tanzania. Western lowland gorillas have been hit hard by the EBOV in Africa (Vogel, 2007). During the last 15 years, it has wiped out about a third of the gorillas found in protected areas. Some scientists think that the population has been depleted to a point where it might be impossible for the gorillas to recover. Frogs and other amphibians have been dying in record numbers, apparently because of a fungal disease. In Florida, the endangered scrub jay, which is not found in any other state, has been shoved closer to extinction by new diseases. West Nile virus is another avian danger. It has sharply reduced some bird populations in Costa Rica and has drastically affected populations of some species like crows and chickadees in the Midwest.

Declining Amphibians

In recent years, many amphibian populations throughout the world have been declining (Doyle, 1998; Houlihan et al., 2000). In 2004, the first worldwide assessment of amphibian populations, the Global Amphibian Assessment, found that 32 percent of species were globally threatened, at least 43 percent were experiencing some form of population decrease, and that between 9 and 122 species had become extinct since 1980 (Stuart et al., 2004). However, only 34 species have been officially declared extinct, due to the difficulty in proving that there are no individuals left.

Frogs living in highland and northern areas seem to be the most drastically affected species. Wake (1991) summarized some of the most dramatic declines. Frogs of the genus *Rana* have almost disappeared from Southern California. By the late 1980s, *Rana muscosa*, a montane frog, had disappeared from 98 percent of the ponds in which it had been studied in the mid-1970s in Sequoia and Kings Canyon National Parks. Populations of *Rana cascadae* monitored since the mid-1970s have suffered about an 80 percent disappearance in Oregon. The golden toad (*Bufo periglenes*), endemic to the Monteverde Cloud Forest Preserve in Costa Rica, has not been seen since 1989. During this same period, many other species of frogs in the same region have experienced declines and possible extirpation. The gastric brooding frog (*Rheobatrachus silus*) (see Fig. 5.35), which inhabited rivers in relatively undisturbed regions of Queensland, Australia, has not been seen since 1979, and several other sympatric species of frogs now are thought to be extinct. Sometime after 1981, 8 of 13 species of frogs that had been present in Brazil’s Atlantic Forest Biosphere Reserve disappeared. Do these declines represent normal population fluctuations, or can they be the result of habitat destruction, large-scale climate changes, or a new disease? The answer: probably a combination of some or all of these factors.

A devastating disease (chytridiomycosis), caused by the microscopic chytrid fungus *Batrachochytrium dendrobatidis* (*Bd*), is sweeping the planet, wiping out entire populations of amphibians. Various factors already have combined to cause more than 120 amphibian species to vanish between 1980 and 2015, in what one biologist has called “one of the largest extinction spasms for vertebrates in history.” A third of the world’s nearly 7,000 species of anurans are threatened—their populations weak and susceptible to disease. If they go, ecosystems will tilt out of balance and potential medical breakthroughs—like potent painkillers or HIV inhibitors—could be lost. It is hard to determine how many species have been affected by the fungus, but it has factored into most of the recent extinctions and declines. When this fungal disease came along, anurans already faced significant stress from global warming, pesticides and herbicides, acid rain, and habitat destruction. In Costa Rica, researchers found that species tended to vanish during years with the warmest average temperatures (Pounds et al., 2006). Warm periods enhance cloud formation over the tropics, which makes days cooler and nights warmer. Temperatures thus stay in the narrow range in which the fungus thrives, which could explain massive amphibian die-offs.

Scheele et al. (2019) reconstructed the biodiversity impact of the global spread of pathogenic *Bd*. They compiled a detailed dataset of chytridiomycosis-associated declines from both published records and interviews with regional experts around the world, presented a global, quantitative assessment of the chytridiomycosis panzootic, and demonstrated its role in the decline of at least 501 amphibian species over the past half-century, including 90 presumed extinctions. The effects of chytridiomycosis have been greatest in large-bodied, range-restricted anurans in wet climates in the Americas and Australia. Declines peaked in the 1980s, and only 12 percent of declined species show signs of recovery, whereas 39 percent are experiencing ongoing decline. Of the 292 surviving species for which population trends are known, 60 (20 percent) have shown initial signs of recovery. The authors note, however, that recoveries generally represent small increases in abundance of individual populations, not complete recovery at the species level. Although there is risk of further chytridiomycosis outbreaks in new areas, the authors conclude that the severity of declines may be dwindling over time. It remains unclear whether this is a sign of hosts and pathogen achieving a stable co-existence or merely a lull after the first of many waves of outbreaks. The authors state that the chytridiomycosis panzootic represents the greatest recorded loss of biodiversity attributable to a disease.

Chytridiomycosis was first identified in 1998 and even now is not well understood. As it moves around the globe, it has caused massive anuran deaths in Australia and hit the population of boreal toads in the Rocky Mountains. In the Sierra Nevada, one researcher found “piles” of mountain yellow-legged frogs dead from the disease. The disease filtered down Central America—one of the most biologically diverse areas on the planet—at a rate of about 27 km (17 mi.) a year. Researchers have traced the source of *Bd* to the Korean peninsula, where one lineage, BdASIA-1, exhibits the genetic landmarks of an ancestral population that seeded the panzootic (O'Hanlon et al., 2018). They date the emergence of this pathogen to the early twentieth century, coinciding with the global expansion of commercial trade in amphibians. By sequencing the genomes of 29 *Bd* strains, Rosenblum et al. (2013) discovered that many of the strains had arisen well before the epidemic started and that they differ significantly. So far, the disease is not believed to have reached areas of great amphibian diversity like Madagascar, India, and Indonesia.

Vredenberg et al. (2013) added weight to a prevailing theory that humans helped to spread the fungus by importing and releasing the African clawed frog, used 60 years ago for human pregnancy testing. The researchers found *Bd* in clawed frog museum specimens from California and Africa, suggesting that imported infected frogs carried the fungus from Africa to California, where it spread to other species.

The chytrid fungus lives in water and moist soil, but the disease is specific to anuran amphibians, invisibly feeding on their skin's keratin and causing it to thicken (Fig. 16.16). Animals that live primarily in cool, moist environments are the perfect target for the deadly pathogen. Until recently, the exact mode of death was unknown—it was thought that the fungus may produce a toxin or that it may impair the amphibian's ability to breathe and absorb water through its skin. An amphibian's existence depends on the physiological interactions of the skin with the external environment. Recent studies show that the fungus causes such severe electrolyte imbalances that the frog's heart stops. Electrolyte transport across the epidermis was inhibited by more than 50 percent, plasma sodium and potassium concentrations were reduced by approximately 20 percent and 50 percent, respectively, and cardiac arrest resulted in death (Voyles et al., 2009). Analyzing the timing of losses in relation to changes in sea surface and air temperatures, Pounds et al. (2006) concluded with "very high confidence" that large-scale environmental warming is a key factor in the disappearances. They proposed that temperatures at many highland localities are shifting toward the growth optimum of *Bd*, thus encouraging outbreaks.

Figure 16.16. The skin of a frog infected with the chytrid fungus.

Researchers have also found that certain skin bacteria can protect against fungal infections. The bacterium *Janthinobacterium lividum* makes an antifungal compound that stops the fungal infection in its tracks (Harris et al., 2009). The composition of symbiotic bacteria on their skin predicted survival in Panamanian golden frogs and American bullfrogs infected with *Bd* (Becker, et al., 2015; Walke et al., 2015).

A second fungus, *Batrachochytrium salamandrivorans* (*Bsal*) was discovered during baffling die-offs of rare fire salamanders in the Netherlands in 2013 (Martel et al., 2013). In laboratory tests, the fungus seemed unable to attack frogs, toads, or caecilians, but it literally eats the skin off susceptible salamanders. The salamander fungus appears to have originated in Asia and is hitchhiking around the world in the pet trade. As of 2015, there is no evidence that the new fungus has reached North America, home to a quarter of the world's known salamander species. In order to protect North American salamanders, the US Fish and Wildlife Service issued an interim rule effective January 28, 2016 that prohibits the import and interstate transport of 201 salamander species.

While the extinction of frogs and salamanders might seem unimportant, this could not be farther from the truth. These animals regulate their local ecosystems, consume and control populations of mosquitoes and other insects that spread disease, and potentially point the way to new drugs for fighting diseases like cancer and HIV/AIDS. Vanderbilt University Medical Center researchers reported in 2005 that compounds secreted by an Australian red-eyed frog's skin appear to inhibit HIV infection (VanCompernolle et al., 2005). Also in 2005, scientists isolated short proteins called antimicrobial peptides from frog skin and found that the peptides not only killed bacteria directly, but also ramped up the host immune system to help clear infections more quickly (Conlon et al., 2005). One peptide killed five bacterial species. Among the affected microorganisms were three that commonly cause deadly hospital-acquired infections, including *Staphylococcus aureus* and two emerging bacterial pathogens, *Stenotrophomonas maltophilia* and *Acinetobacter baumannii*, which are a growing cause of infections in hospital intensive-care units. Poison dart frogs long have provided venom used by hunters in Central and South America, but pharmaceutical companies are researching a compound found in the frogs that could yield a painkiller 200 times more potent than morphine. Thus, the fate of amphibians is inexorably linked to our own. Many researchers feel that amphibians could be serving as "indicator" species, warning of serious environmental changes brought about by pesticide pollution, increased ultraviolet radiation, acid precipitation, and/or global warming.

Captive breeding programs for rare frogs have been established in numerous places, including the Baltimore Aquarium, the Atlanta and Houston Zoos, and the Amphibian Research Centre near Melbourne, Australia. One concern is that captive-bred frogs may become genetically adapted to domesticated life, rendering them less able to live in the wild. Inbreeding, one cause of reduced fitness, must be avoided. A problem of equal complexity is what will happen to an amphibian's native ecosystem in the amphibian’s absence. It may be that the organisms it ate will immediately increase in number and the animals that fed on it will become fewer. Such adjustments may lead to other changes in an unpredictable cascade through the ecosystem. Depending on how long the amphibian is gone, its ecological niche might not be there when it returns. In addition, climate change is reshuffling where species are found, especially on mountains. Thus, amphibians that are reintroduced after decades in captivity may encounter an alien world.

Snake Fungal Disease

Lorch et al. (2015) established a causal relationship between the fungus *Ophidiomyces ophiodiicola* and an emerging skin infection, documented in at least 23 species of wild snakes in eastern and midwestern North America, known as snake fungal disease (SFD), which causes swelling, lesions, and crusty scabs. First described in 2006, the disease has been confirmed as infectious and pathogenic. Snakes pick up the fungal spores from soil. In less than a decade, the fungus has been identified in at least nine eastern states, and although it affects a number of species, it is especially threatening to rattlesnakes that live in small, isolated populations with little genetic diversity, such as those found in Vermont, New Hampshire, Massachusetts, and New York. The eastern massasauga (*Sistrurus catenatus*) is an endangered rattlesnake that is highly susceptible to SFD. Studies of this species in central Illinois found the disease altered the skin biome of affected snakes (Allender et al., 2018). On infected snakes, researchers found the fungal pathogen present even at locations on the snakes’ bodies far from their open sores, indicating that their entire skin biome was affected.

White-Nose Syndrome in Bats

An emerging threat to American bats was first reported at four sites during the winter of 2006–07 near Albany, New York, and caused massive mortality among hibernating bats (Blehert et al., 2009; Zimmerman, 2009). White-nose syndrome (WNS) is named for the white fungus *Pseudogymnoascus destructans* evident on the nose, ears, and wing membranes of affected bats (see Fig. 16.17). The fungus thrives in the cold and humid conditions characteristic of caves and mines used by bats. In March 2009, laboratory tests confirmed that a bat found in France carried the same fungus as that identified in the United States. More recently, *Pseudogymnoascus destructans* has been documented widely across Europe and Asia on multiple species of bats (Puechmaille et al., 2011; Zukal et al., 2014; Hoyt, et al., 2016). Although the definitive source for introduction into the North American population has not been conclusively identified, phylogenetic studies by Drees et al. (2017) support the origin of the North American invasion by *P. destructans* from Europe rather than Asia.

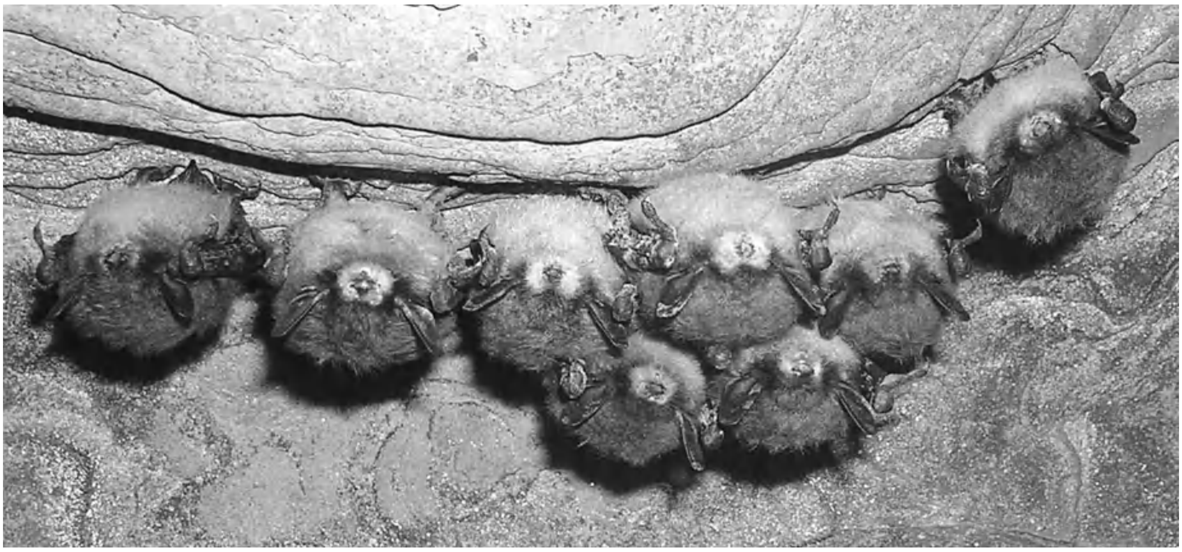


Figure 16.17. White-nose syndrome (WNS) is named for the white fungus present on the nose, ears, and wing membranes of affected bats. It was first discovered near Albany, New York, during the winter of 2006–07.

Bats affected with WNS do not always have obvious fungal growth, but they display abnormal behavior within and outside of their hibernacula. Signs of WNS include bats losing their fat reserves long before winter is over, bats flying outside during the day in temperatures at or below freezing, bats clustered near the entrance of hibernacula, and dead or dying bats on the ground or on buildings, trees, or other structures. Once aroused, the bats burn energy at a much faster rate, depleting stored fat. Typically, once the disease is established in a colony, 90 percent of the bats are gone by the second year.

A 2014 study by the US Geological Survey (USGS) and the University of Wisconsin (Verant et al., 2014) found that bats with WNS used twice as much energy (due to frequent arousals) as healthy bats during hibernation and had potentially life-threatening physiologic imbalances that could inhibit normal body functions. With no food source available during the winter, the bats soon die.

More than 6 million hibernating bats have died in the United States over the past decade from WNS. The fungus has rapidly spread to multiple sites throughout the Northeast and as far south as Mississippi and west to Missouri. It was recorded in Virginia for the first time in 2009. Tennessee's first case was from a cave in upper East Tennessee in February 2010. In April 2010, the National Wildlife Health Center in Madison, Wisconsin, confirmed the first case of WNS in a little brown bat from White Oak Blowhole Cave in the Great Smoky Mountains

National Park. This cave contains the largest known Indiana bat hibernacula in Tennessee. The Indiana bat is a federally endangered species and, thus far, no individuals have been found with the fungus. Also in April 2010, the fungus was confirmed for the first time in a Missouri cave, about 480 km (300 mi.) from the next closest known site of infestation in Tennessee. By 2017, the fungus had been confirmed through testing in 31 states and 5 Canadian provinces (National Fish and Wildlife Foundation, October 2017). New states are added each year. The fungus was detected in 2017 in Texas and Nebraska, and in March 2018 an infected little brown bat was found by hikers at the edge of the Cascade Mountains in Washington—approximately 2,000 km (1,240 mi.) farther west than previously seen. Parallels can be drawn between WNS and the lethal fungal skin infection that has caused precipitous global amphibian population declines.

Laboratory studies by the USGS and the University of Wisconsin (Rocke et al., 2019) have shown that vaccination with virally vectored *Pd* antigens induced antifungal immunity in little brown bats (*Myotis lucifugus*). Ongoing studies will reveal whether such vaccinations can protect other species and will develop practical methods of application.

Rabies in Bats

Since 1960, bats have caused about 70 percent of the 89 deaths from rabies exposure that occurred in the United States, according to a US Center for Disease Control and Prevention (CDC) report issued June 12, 2019. Approximately two people die from rabies in the United States every year.

In 2015, the CDC noticed that bats had surpassed raccoons to become the animal with the greatest number of positive tests for rabies. However, the vast majority of bats tested (about 94 percent) do not have rabies, and the CDC estimates that less than 1 percent of bats overall are infected.

Worldwide, bats play critical ecological roles in insect control, plant pollination, and seed dissemination. The decline of North American bat populations would likely have far-reaching ecological consequences. Current information concerning the disease can be found at www.whitenosesyndrome.org.

Cape Buffalo and Lions

Cape buffalo in Kruger National Park in South Africa contracted bovine tuberculosis (*Mycobacterium bovis*) by mingling with infected cattle herds in the 1950s near southern Kruger before the park’s boundary was fenced off. The spread of the disease is slow among buffalo, with many of those affected being able to live out a normal life span. However, African lions feeding on infected buffalo, their natural prey, get a massive dose of tuberculosis. Approximately 1,300 of Kruger's estimated 2,000 lions live in the southern sector of the park. Researchers reported that more than 90 percent of the lions tested during 1998 in the southern part of the park were infected with the incurable disease, which causes the lions to develop intestinal lesions before the disease spreads to lymph nodes and other organs. A lion that contracts bovine tuberculosis can take several years to die from the disease itself, but its weakened condition makes it an easier target for rival lions. Scientists believe that most of the infected lions will die, and that the entire lion population is at risk. Field studies to detect antibodies to tuberculosis antigens in free-ranging lions are showing positive results (Miller et al., 2012).

* * *

The world continues to face a biodiversity crisis, with the sources of current extinction patterns all around us. The most important and undoubtedly the number one modern-day cause of species population declines is habitat alteration and habitat destruction. In 2008, Carlos Nobre, a meteorologist and biosphere scientist at Brazil's National Institute for Space Research in Sao Paulo, predicted that, for the next 30 years, the combination of deforestation, degradation, and fire will be the greatest threat to Amazon rain forests (Fig. 16.18). For the second half of the twenty-first century, global warming will become the big menace.

Figure 16.18. Ground-level view of tropical rain forest destruction in the Amazon basin in Brazil.

Many conservationists are fearful that entire ecosystems will fail once a few "keystone" species are removed. A single parasitic wasp variety pollinates all 900 species of fig trees in the tropics. Almost 80 percent of canopy-level trees in the Samoan rain forests depend on flying foxes in order to reproduce. Other scientists, however, say that there is redundancy in ecosystems and that the loss of one species will not cause an entire ecosystem to collapse.

Living in a world with fewer species creates a human crisis as well as an ecological one, researchers warn. Paul Ehrlich notes that biodiversity is essential for human health, economies, food production, and cultures: "We're sawing off the limb that we are sitting on."

On August 24, 2011, the Census of Marine Life announced a new estimated total number of species on Earth—the most precise calculation ever offered—at 8.7 million (give or take 1.3 million). This includes 6.5 million species on land and 2.2 million (about 25 percent of the total) dwelling in the ocean depths. The figure is based on an innovative, validated analytical technique that dramatically narrows the range of previous estimates. Until now, the number of species on Earth was said to fall somewhere between 3 million and 100 million.

Education of the public and politicians is critical. To make the best decisions on protecting plant and animal life, we need to know how to protect the most species at the lowest cost. However, a poll in 2000 found that fewer than one-quarter of Americans recognized the term *biological diversity*. Because science knows so little about many of the species that inhabit the Earth, let alone what complex roles each one plays in the ecosystems it inhabits, it may never be possible for economics to come to the aid of endangered species. Some scientists even suggest that rare species should not be the focus of conservation efforts, but that efforts should be made to save relatively pristine—and inexpensive—land where evolution can proceed unaffected by human activity.

Clearing of forest areas for agriculture, subdivisions, shopping centers, and roads destroys the habitat of many species. Such practices have caused the destruction of vast areas of tropical rain forests, as well as temperate forests, worldwide. The forested habitat of gorillas (*Gorilla gorilla*), orangutans (*Pongo pygmaeus*), and other primates, as well as giant pandas (*Ailuropoda melanoleuca*) and many tropical birds, is decreasing at an alarming rate. In addition, civil unrest in parts of Africa and the resettling of hundreds of thousands of refugees have put the mountain gorilla and the chimpanzee in great peril, according to the WWF.

The tiger, the orangutan, and megavertebrates on every continent are living on borrowed time and may find their final refuge in zoos. Forms of life that developed over eons, entire complexes of life, are winking out like birthday candles—up to three species an hour gone (an estimated 15 to 40 percent of all species by 2050), not to malice, not necessarily by design, but all by human hands (Houck, 2017).

Review Questions and Topics

1. Differentiate between extirpation and extinction. Give two examples each of extirpated and extinct species.
2. Discuss several theories for the Cretaceous extinctions.
3. Give several pieces of evidence in support of the meteor impact theory.
4. List several species of vertebrates whose extinction is believed to have been at least partially caused by humans.

5. What do you think would have happened if extinction had never occurred during evolutionary history? Do you think there would be a greater or a lesser number of species on Earth than are currently present? Why?
6. What are some of the theories concerning the cause of declining amphibian populations?
7. Prepare a brief research proposal outlining the methods you would employ in an attempt to determine the cause(s) of a regional amphibian decline.

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Vertebrate Internet Sites

1. Bushmeat: US Fish and Wildlife Service

   www.fws.gov/international/wildlife-without-borders/global-program/bushmeat.html

   Extent and effects of bushmeat hunting; global website links.

2. Illinois State Museum Ice Age Exhibit

   http://iceage.museum.state.il.us

   Visit the Ice Ages and their late fauna at the Illinois State Museum's online exhibits. Animations show ice sheets waxing and waning, and text describes such matters as Milankovitch factors—shifts in Earth's elliptical orbit that partly explain Earth's eight glaciations over the past 750,000 years. In a section on the US Midwest 16,000 years ago, check out a saber-toothed cat skeleton and a discussion of whether people killed off such big mammals.

3. Avoiding Deforestation in Madagascar—Conservation International

   www.conservation.org/projects/Pages/avoiding-deforestation-in-madagascar.aspx

   Learn about the efforts of Conservation International's highest-priority biodiversity hotspot.

4. White-Nose Syndrome

   www.whitenosesyndrome.org

   Interagency website with up-to-date information about white-nose syndrome—what it is, current control efforts, funding projects, good management practices, and more.

5. The International Union for Conservation of Nature (IUCN)

   www.iucn.org and www.iucnredlist.org

   This organization was founded in 1948 and currently includes some 10,000 experts from 181 nations. Its mission is providing advice for nature conservation. The IUCN produces the famous Red Lists of threatened species.

6. Jane Goodall

   www.janegoodall.org

   Learn about the work of famed primatologist Jane Goodall, whose specialty is the chimpanzee.

17 | Restoration of Endangered Species

Every creature is better alive than dead, men and moose and pine trees, and he who understands it aright will rather preserve its life than destroy it.

Henry David Thoreau, 1848

INTRODUCTION

The previous chapter discussed the deleterious effects that humans have imposed on many vertebrates, including the extinction of species and families. This is a chapter about the efforts of researchers and conservationists in bringing some species back from the brink of extinction. While some well-known endangered species, given protection, have prospered enough to be removed from the endangered species list, for example, American alligators (2007), gray whales (1994), bald eagles (2007), Aleutian Canada geese (2001), brown pelicans (2009), and peregrine falcons (1999), this chapter focuses on some that are either less well known and/or that have required extensive efforts on the part of humans to bring about an increase in their populations.

SPECIES ACCOUNTS

Komodo Dragon

The Komodo dragon (*Varanus komodoensis*) (see Plate 15) of Indonesia is the world's largest lizard with adults reaching a length of over 2.7 m (9 ft.) and a weight of nearly 91 kg (200 lb.). Normal life expectancy is 30 to 50 years, although they can live as long as 62 years (see Table 7.2). Their saliva contains a hemotoxic venom that prevents the blood of their prey from clotting. Listed as vulnerable by the Encyclopedia of Life, Komodo dragon populations appear to have declined over the past 50 years due to environmental changes as well as human encroachment (fires to clear land for gardens and pastures, feral dogs, etc.). In 1980, much of the Komodo dragon's habitat was turned into Komodo National Park, which encompasses all of Komodo, Rinca, and other smaller islands. Later, three nature reserves were added, two of them on Flores Island. Approximately 5,000 animals remain. In Indonesia, Komodo dragons have been breeding in captivity since 1965. In 1992, the first baby Komodo dragon was born outside the homeland, at the National Zoo in Washington, DC. Today, about 400 Komodo dragons live in zoos worldwide.

Bermuda Cahow (Bermuda Petrel)

The Bermuda cahow (*Pterodroma cahow*) (Fig. 17.1a), the highly endangered relative of the petrel and the albatross, was thought to be extinct for 330 years until 18 surviving pairs were found in Castle Harbour, Bermuda, by David Wingate in 1960. That was when Wingate began his lifelong campaign to save the birds, although many believed it was impossible to halt their impending extinction. Besides providing protection, Wingate constructed artificial nesting burrows for the birds (Fig. 17.1b). As of May 2010, 95 pairs of adult cahows nested on six small islands off the coast of eastern Bermuda with a fledgling crop of more than 50 birds (Wingate, pers. comm.). The 2017 nesting season saw the cahow nesting population increase to a record number of 117 established breeding pairs with a record number of 61 chicks successfully fledged out to sea (Madeiros, 2017). In addition, a record number of over 10 newly established, prospecting pairs was recorded, most of which were expected to produce their first eggs as breeding pairs during the next breeding season. These numbers have probably not existed since the 1600s when the formerly abundant cahow was decimated by the arrival of human colonists on Bermuda, by overhunting, and by predation from human-introduced mammal predators such as pigs, rats, cats, and dogs.

Once the chicks emerge from their nests, they leave Bermuda and go to sea for a period of three to four years. There are a handful of locality records from the Gulf Stream off North Carolina (Wingate et al., 1998). During that time, they do not return to land but roam above the ocean, even sleeping in spiral wind currents above thermal areas of the sea. When they return to Bermuda, they are mature adults ready to create nests of their own. Cahows mate for life and return to their same nesting ground—within meters—year after year. Beginning in 2002, chicks were banded before departing their nests in order to accumulate data on their habits. In 2009, geolocator bands were placed on 12 adults. Results show that the cahow ranges across the Atlantic in the Gulf Stream from Cape Hatteras to the west and to the Azores and the continental shelf off Ireland to the east. They also were found to range far north of the Gulf Stream into the Gulf of Maine and the Newfoundland banks.

Figure 17.1. (*a*) An adult Bermuda cahow (petrel). (*b*) Dr. David Wingate inspecting the nest-chamber of one of the many cahow burrows that he has constructed.

Hurricane Fabian destroyed many nesting burrows in 2003. Hurricane Nicole hit Bermuda directly in October 2016, submerging two of the smaller nesting islands but causing only limited damage. One of the main objectives of the Cahow Recovery Program has been to establish new cahow nesting colonies on larger islands that are safe from hurricane erosion and have more room to enable the cahow population to grow. The increased risk from sea level rise and more intense hurricanes caused by climate change inspired a plan to attract cahows to nest on Nonsuch Island, Bermuda, a larger island that is higher and safer from hurricane overwash events. This was done by a combination of audio attraction (playing courtship calls from amplifiers at artificial burrows built on Nonsuch) and translocation of chicks to these burrows at a critical stage of their development so that they imprint on the translocation site when they depart and return to that new site first when ready to breed. A total of 102 chicks were translocated between 2005 and 2009. A total of 49 of the original 102 translocated birds had been confirmed as returning to the nesting islands by 2015, of which 29 had returned to Nonsuch Island itself. In 2009, the first pair established on Nonsuch. The first chick was born on Nonsuch in 2009. This project has been successful in establishing a new nesting colony on Nonsuch, which by 2016 had grown to 15 nesting pairs. This colony produced 46 successfully fledged chicks between 2009 and 2016.

The islands must be constantly managed to eradicate predators, such as rats, and to control human access to prevent disturbance. Although the cahow population is increasing (a record number of 124 breeding pairs produced a record number of 71 fledglings on Nonsuch and surrounding islands in 2018), it would need to increase to at least 1,000 pairs before the species could be removed from the endangered species list.

California Condor

The California condor (*Gymnogyps californianus*) (see Plate 16) is a New World vulture and the largest North American land bird. It has the largest wingspan of any North American bird. It is listed by the International Union for Conservation of Nature (IUCN) as critically endangered.

The last wild condor was trapped by biologists in 1987 (Fig. 17.2). At that time, only 27 birds remained as genetic "founders" for a breeding program. By December 1991, the program had produced 25 additional birds, including the first two freed in January 1992. As many populations decline, they often experience a significant loss in genetic variation that may decrease fitness, limit the long-term capacity of the population to respond to environmental challenges, and allow chance environmental and demographic events to pose a more immediate threat. Using DNA fingerprinting, researchers found that the 52 living condors comprised three distinct ancestral groups (Hedrick, 1992). The existing condor gene pool is more diverse than some had believed, and this has proven invaluable in developing successful reintroduction plans for the condor into its native habitat.

By November 1996, three captive breeding flocks contained 104 California condors. These flocks are maintained for propagation at the Los Angeles Zoo, San Diego Wild Animal Park, and World Center for Birds of Prey in Boise, Idaho. In addition, another 17 condors were flying free in California.

Figure 17.2. California condor (*Gymnogyps californianus*) breeding pair in captivity at the San Diego Zoo. When biologists trapped the last remaining California condor in 1987, only 27 birds remained as genetic "founders" for a breeding program.

On October 29, 1996, six captive-reared condor chicks were transferred to a release site located at Vermilion Cliffs, approximately 48 km (30 mi.) north of Grand Canyon National Park in northern Arizona. These birds were released in December 1996, and they became the first free-flying California condors in Arizona since 1924. This was the eighth release of captive-bred condors since 1992, and the first release outside California. A series of releases of captive-reared condors at the Vermilion Cliffs has occurred each fall in hope of establishing a population of approximately 150 condors. Released birds are approximately 6 months old and are monitored through the use of radio transmitters and wing markers. If this reintroduction project is successful, it will achieve one of the primary goals of the California Condor Recovery Plan: to establish a second self-sustaining population in the wild. The population of wild and captive individuals was 162 by September 1999. This included 49 condors in the wild—29 in California and 20 in northern Arizona. A total of 19 chicks were hatched from the captive breeding flocks during 1998. The first condor to be born in the wild in California in 17 years was hatched in June 2001 in the Los

Padres National Forest. In May 2003, the first condor chick to be born in Arizona in nearly 100 years was hatched in the Grand Canyon.

A third reintroduction area, added in 2002, is located in a remote area of Baja California, Mexico. As of July 2009, there were a total of 356 California condors (180 wild and 176 captive). The wild population was comprised of the California population (89), the Arizona population (75), and the Baja population (16). By 2017, there were 463 condors living wild or in captivity.

In 2000, four of the condors that had been released into the wild died of lead poisoning. The birds may have feasted on the carcass of a cow or another animal killed with a shotgun. Seventeen lead shotgun pellets were found in one dead condor's digestive system. High concentrations of lead have also been found in the shells of chicks that have died.

Whooping Crane

The International Whooping Crane Recovery Team, a partnership of 10 Canadian and US experts, was formed in 1995 to write the game plan to restore the whooping crane (*Grus americana*) (see Plate 17) population and protect whooping crane habitat. The Whooping Crane Eastern Partnership was established in 1999 to be an umbrella for government and nonprofit groups dedicated to the restoration of the species.

The original wild whooping crane flock overwinters on the Aransas National Wildlife Refuge on the Texas coast during the winter and migrates 4,000 km (2,500 mi.) to Wood Buffalo National Park in the Northwest Territories of Canada where they nest and rear their young. During the fall season, the whooping cranes, or whoopers, migrate south to Aransas where they spend the winter and early spring. During the winter of 1995–96, a total of 158 whoopers wintered on Aransas, up from 15–16 in 1941 (Collar et al., 1993). A US Fish and Wildlife Service (USFWS) count in early 2017 estimated that 505 whooping cranes, including 49 juveniles, had arrived at Aransas that season. Surveys from the whooping cranes' nesting grounds in Wood Buffalo National Park showed record reproduction in 2017, with a new record of 98 whooping crane nests and a total of 63 young fledged. The previous record was 82 nests in 2014. A March 2018 USFWS report counted an additional 161 whooping cranes in captivity at 12 different sites, and an estimated 177 in three reintroduced flocks, putting the total population in 2018 at over 800. Even though the whooping crane population has steadily increased in size, they remain one of the most critically endangered species in the world.

Climate change appears to be affecting whooping cranes' migration patterns (Richter-Ryerson, 2017). Whooping cranes are migrating earlier in the spring and later in the fall in association with higher average temperatures. The study, which analyzed USFWS data on whooping crane sightings between 1942 and 2016, found migration shifted as many as 22 days earlier in the spring and 21 days later in the fall, indicating that patterns are more closely tied to temperature than previously thought. The shift in timing appears to have accelerated since about 2000. It is unclear what impact this change will have on whooping crane populations. Ornithologists are concerned that migrating through the Midwestern states in March and November—as opposed to April and October—could leave the birds more vulnerable to being exposed to snowstorms.

An attempt to establish a separate nonmigrating flock of whooping cranes in Florida in January 1993 failed when the 14 birds were killed by bobcats and other predators. However, after that, an average of 20 chicks, hatched and reared in captivity, were released at the Florida site each year. By April 1997, a nonmigratory population was in the process of being established in central Florida's Kissimmee Prairie. It consisted of approximately 29 cranes in 1999. Older birds began showing territorial behavior characteristic of sexual maturity and during the spring of 1996, a pair constructed a nest and were observed copulating and defending a several-hundred-acre marsh. It was not until April 1999, however, that the first eggs were observed. The first whooping crane chick hatched in Florida in 2000, but was killed by a bobcat. The first chick to be successfully fledged was hatched in 2002. A total of 289 captive-bred birds were released between 1993 and 2004. However, by 2005, this nonmigratory flock was no longer receiving released captive-reared chicks due to its high mortality and low reproduction. All studies of the population were discontinued in 2012. As of March 2018, the population had dwindled to just 14 cranes. The USFWS has proposed a plan to relocate the few surviving Kissimmee cranes to join the newer Louisiana reintroduced nonmigratory flock.

Attempts to establish a third whooping crane flock was initiated in 2001. This was to be a migratory flock. As part of Operation Migration, a flock of seven whooping cranes was led south in 2001 by an ultralight aircraft from the Necedah National Wildlife Refuge in central Wisconsin (where they fledged in 2000) to the Chassahowitzka National Wildlife Refuge, an isolated marsh north of Tampa on Florida's Gulf Coast. This was the beginning of the eastern migratory population (EMP). Operation Migration is a not-for-profit organization cofounded by Joe Duff and Bill Lishman. The fall journey, which began in October, covered 1,960 km (1,218 mi.), included 26 stopover locations, and took 50 days to complete. It was the first time that the ultralight technique had been used with an endangered species. (In 1993, two Canadian ultralight aircraft, flown by Bill Lishman and Joe Duff, successfully led 18 Canada geese from Ontario to Virginia. Of the 16 geese that survived the winter, 13 returned to Ontario the next year—without needing a human guide.) On April 9, 2002, five of the cranes departed their Florida winter home. On the first day of their unassisted return migration, they flew 350 km (220 mi.) north to Wilcox County, Georgia. Within 10 days, the cranes had returned to the Necedah National Wildlife Refuge in Wisconsin—the first wild whooping cranes in Wisconsin following an absence of more than 100 years.

Annual ultralight-led migrations continued until 2016. Eggs were incubated and chicks were hatched at the Patuxent Wildlife Research Center in Laurel, Maryland. When approximately 2 months old, the chicks were placed in crates and flown to Wisconsin, where they were taught to fly behind an ultralight aircraft. Then, come fall, the ultralight led them south. In 2006, 18 chicks began the journey and all arrived safely at Chassahowitzka. In early February 2007, storms moved through central Florida and churned up a surge of water that drowned the birds in their net-covered pen. Only one bird survived, but several weeks later it was found dead in a Gulf Coast salt marsh. Thus, the entire Class of 2006 was wiped out. The loss of a generation will have a ripple effect. It takes four to five years for the birds to reach sexual maturity, so in 2010–11, there was a break in the reproduction cycle. As of October 2018, there were 101 surviving whooping cranes (45 females, 50 males, 6 unsexed) in the EMP (Ray, 2018). This included five fledged wild-hatched chicks. At the same time, there were at least 80 whooping cranes in Wisconsin, 3 in Michigan, possibly 3 in Illinois, and 1 in Minnesota.

A major hurdle to this and other introduced populations is illegal hunting. Over a period of two years, 5 of the approximately 100 whooping cranes in the EMP were illegally shot and killed. The International Crane Foundation estimates that approximately 20 percent of the deaths of reintroduced cranes are due to illegal shootings. Illegal shootings have also been a significant source of mortality for the Louisiana population (see below).

Sixteen young whooping cranes released in 2017 in Wisconsin successfully migrated south to Florida for the winter on their own along with older cohorts. Since 2011, the Whooping Crane Eastern Partnership has focused on placing birds in an area of Wisconsin that includes Horicon Marsh and White River Marsh. Prior to that, the focus was in Juneau County in central Wisconsin, until it was discovered that biting black flies contributed to whooping cranes abandoning their nests.

A population must be able to produce young and grow to a self-sustaining level. Unfortunately, of the over 240 birds released into the migratory flock in Florida through Operation Migration, only 10 chicks have survived to fledge. The causes are unknown. Could it be the inattentiveness of the parents? Could it be methods used in hand rearing? Could captive specimens have undergone genetic changes that might have weakened their ability to persist in the wild? The answers are unknown at the present time. Although the adult birds in the population survive, migrate, and pair, and they are wild, the near-total failure of the hand-raised and guided birds to reproduce in the wild led the USFWS in January 2016 to discontinue the ultralight program in favor of alternatives with reduced human interaction.

The USFWS is attempting to establish a second nonmigratory population in Louisiana’s White Lake Wetlands Conservation Area where there had historically been a nonmigratory population of whooping cranes. In March 2011, 10 cranes were released, but all but three had been lost by the time a second group were released in December 2011. Subsequent annual cohorts followed, ranging in size from 10 to 27 birds. The flock has established a range centered on southwestern Louisiana but also including central and northeastern Louisiana, southeastern Arkansas and southeastern Oklahoma, and east Texas. None of the first group survived to full maturity, but in the spring of 2014 the second cohort began to form pairs and nest, producing the population’s first eggs. However, since the parents were still juveniles, these eggs were infertile. The next year saw fertile eggs, but none survived to hatching. In April 2016, a pair of reintroduced whooping cranes hatched two chicks, one of which survived to fledge, representing the first fledgling in the wild in Louisiana since 1939. Starting in 2017, a novel strategy was introduced: eggs in the process of hatching, taken from captive birds, were swapped into Louisiana nests in place of infertile eggs, allowing the chicks to be raised by substitute whooping crane parents in the wild. In 2018, a combination of naturally laid and substituted eggs added five wild-raised juveniles to the population, which all survived to fledge. As of August 2018, 125 birds had been released, with at least 65 surviving.

For more than 50 years, the Patuxent Wildlife Research Center in Maryland raised whooping cranes in captivity with the ultimate goal of increasing the birds' numbers and releasing juveniles into the wild when possible. Patuxent's whooping crane program began with just 12 eggs in 1967 and ultimately grew to more than 60 adult whooping cranes. Patuxent's biologists and dedicated volunteers successfully raised more than 30 chicks each year. Unfortunately, the $1.5-million-a-year breeding program has been eliminated because the 2018 US presidential administration decided to stop funding the program. Nearly half of the Patuxent whooping cranes were to be shipped to Louisiana in October 2018. The remaining captive cranes were to be sent to other facilities. Breeding programs are scattered across North America—at zoos in Texas, Oklahoma, Nebraska, and Canada and at wildlife centers in Wisconsin, Louisiana, and Florida.

Peregrine Falcon

Peregrine falcons (*Falco peregrinus*) (see Plate 18) were once so rare that there were no breeding pairs east of the Mississippi River. The use of dichlorodiphenyltrichloroethane (DDT) as a pesticide during the 1940s, 1950s, and 1960s resulted in a precipitous decline of peregrine falcons in North America. During this period of DDT use, eggshell thinning and nesting failures were widespread, and in some areas, successful reproduction virtually ceased. DDE, a metabolite of DDT, prevents normal calcium deposition during eggshell formation, resulting in thin-shelled eggs that are susceptible to breakage during incubation. After DDT was banned, however, populations rebounded from a low of 324 nesting pairs in 1975 to between 2,000 and 3,000 breeding pairs in the United States, Canada, and Mexico in 2013, well above the overall recovery goal of 631 pairs (Hoffman, 1998; Reichhardt, 1998). The species has recolonized most of its former range and has even expanded into some new areas.

Bald Eagle

The resurgence of bald eagle populations (see Plate 19) from Virginia to Alaska allowed the US Department of the Interior to remove this species from the threatened species list in June 2007. It had been reclassified from endangered to threatened in 1995. As of 2019, there were over 5,000 nesting pairs in the contiguous 48 states, compared with a documented 417 in 1963, when the bird was on the verge of extinction everywhere except in Alaska and Canada, where it had continued to thrive. There are about 70,000 bald eagles in the whole of North America (including Alaska and Canada).

Grizzly Bear

When Lewis and Clark explored the West in the early 1800s, an estimated 50,000 grizzly bears (see Plate 20) roamed between the Pacific Ocean and the Great Plains, across vast stretches of open and unpopulated land. However, when pioneers moved in, bears were persecuted and their numbers and range drastically declined. Of 37 grizzly populations present in 1922, 31 were extirpated by 1975. In 1975, there were between 100 and 300 bears occupying less than 2 percent of their historical range. The grizzly bear was listed as a threatened species by the USFWS in 1975. Since then, the bears have thrived under government protection and management (US Fish and Wildlife Service, 2018b). Today, with the western United States inhabited by millions of Americans, only a few small corners of grizzly country remain, supporting about 1,700 wild grizzly bears in Idaho, Montana, Washington, and Wyoming.

The Yellowstone grizzly population, which has been increasing by 4 to 7 percent a year, now stands at 650 bears and has spilled beyond the park into areas that were bear-free for decades. As of September 2018, an estimated 718 bears lived in the Greater Yellowstone Ecosystem. In 2007 and 2017, the USFWS delisted the Greater Yellowstone Ecosystem distinct population from the endangered species list. In each instance, federal judges ruled that the bears should remain on the threatened species list because their delisting did not adequately consider the impacts of climate change on their food supply. The most recent ruling came in September 2018.

Ecologists at the University of Saskatchewan have found all three North American bear species—polar bears, black bears, and grizzly bears—ranging in the same subarctic region in Canada’s Wapusk

National Park on Hudson Bay (Clark et al. 2019). This has never been documented anywhere else. Evidence indicates that grizzlies are undergoing a substantial range expansion in northern Canada. Wapusk lies at the convergence of three ecosystems: boreal forest, tundra, and ocean. All three ecosystems are increasingly showing effects of climate change. Thus far, there is no evidence that the three bear species are interacting in the region.

Mountain Gorilla

After facing near-extinction, mountain gorillas are slowly rebounding. There are now just over 1,000 animals in the wild, up from an estimated population of 680 a decade ago. In November 2018, the IUCN updated mountain gorillas' status from critically endangered to endangered, a more promising, if still precarious, designation.

Giant Panda

The giant panda (see Plate 21), China's national symbol, is one of the world's rarest animals. With the protection afforded them beginning in the early 1990s, however, the number of pandas in the wild has increased by 40 percent. A 1988 survey found 1,110 pandas in the wild. A survey in 2004 found 1,590 animals living in the wild in China. A 2007 report showed 239 pandas living in captivity in China and another 27 outside the country. The Fourth National Giant Panda Survey released by China in February 2015 showed the following: 1,864 estimated minimum population of wild pandas, 16.8 percent increase in wild panda numbers over the previous decade, and an 11.8 percent increase of giant panda geographic range since 2003 (World Wildlife Fund, 2015). Giant pandas are found only in China's Sichuan, Shaanxi, and Gansu provinces. There are currently 67 panda nature reserves in China (compared to just 13 reserves two decades ago) with 1,246 wild pandas living within nature reserves. The approximately 33 percent that live outside protected areas face higher risks to their survival as major infrastructure projects cause large-scale habitat loss.

In recent years, captive breeding programs have taken place both in China and in a few zoos throughout the world. The China Wildlife Conservation Association rents pandas to zoos with the stipulation that the offspring be returned to China after approximately two years so that they can participate in the panda breeding program. In 2019 in North

America, giant pandas resided at the National Zoo in Washington, DC, the San Diego Zoo in California, Zoo Atlanta in Georgia, the Memphis Zoo in Tennessee, the Calgary Zoo in Alberta, and the Chapultepec Zoo in Mexico City. These zoos typically pay the Chinese government $1 million a year per pair in fees, as part of a typical 10-year contract. A recent transfer occurred in February 2010, when Tai Shan, a panda born at the National Zoo on July 9, 2005, was returned to China. He will take part in the panda breeding program at Bifengxia Panda Base. Prior to that, Mei Sheng, born at the San Diego Zoo on August 19, 2003, was returned to China on November 5, 2007; Hua Mei, born at the San Diego Zoo on August 21, 1999, was returned in February 2004; and Mei Lan, born at Zoo Atlanta on September 6, 2006, was returned in 2010. By the end of 2007, Hua Mei had given birth to three sets of twins.

In April 2006, Xiang Xiang, a 4-year-old giant panda weighing about 180 pounds, was released on a Sichuan Province mountainside. He became the first panda born in a laboratory from an artificially inseminated mother, raised in captivity in China, and released into nature to fend for himself. Unfortunately, he died as the result of a fall in 2007. Another setback to the program occurred in 2008 when the Sichuan earthquake damaged much of the giant panda facility at Wolong, where Xiang Xiang was born.

Giant pandas are no longer an endangered species; as of September 2016, they are considered vulnerable to extinction by the IUCN. The IUCN says that, in the next 80 years, climate change could destroy more than 35 percent of bamboo forests, where pandas live on a bamboo-only diet. In addition, even with protection, pandas are still threatened by hunters and logging in their isolated mountain habitat of southwestern China.

The 2008 Sichuan earthquake damaged much of the giant panda facility at Wolong. It has been rebuilt at a safer location in Gengda Town 23 km (14 mi.) away and is now complete. The Gengda Wolong Panda Center is still within the large Wolong Nature Reserve but is divided into two sections. The area in Shengshuping is for captive breeding, and in Huangcaoping the concentration is on reintroduction training. Updated information can be accessed at: www.pandasinternational.org/panda-reserves.

Elephant

Africa’s elephant population has plummeted from millions around 1900 to approximately 415,000 in 2019 (Figs. 9.62, 13.4 and 13.11). Intelligent and emotional, with highly developed social behavior, elephants have been hunted for their ivory for centuries. A ban on commercial trade in ivory across international borders went into effect in 1990, but many countries continued to allow the domestic buying and selling of ivory. Increased demand from consumers in China fueled a new wave of killings. In Tanzania alone, the elephant population declined by 60 percent to 43,000 between 2009 and 2014. The fight against the illegal ivory trade has been likened to squeezing a balloon—when gains are made in one area, such as Tanzania, the killings intensify in another spot, like Mozambique’s Niassa Game Reserve to the south. After reaching a peak in 2011, however, elephant poaching has declined to pre-2008 levels, according to the Convention on International Trade in Endangered Species (CITES). There is evidence of increased processing of ivory tusks into jewelry and trinkets within Africa, instead of the old method of shipping raw ivory out of the continent. This allows traffickers to transport ivory in smaller quantities that are hard to detect and avoids increased scrutiny of ivory-carving operations in Asia.

Two decades ago, American conservation biologist Sam Wasser, from the University of Washington, began working on a geographic map of elephant genetics using DNA extracted from dung (Kolbert, 2017). Populations from different regions carry different mutations, and Wasser’s map shows where each mutation can be found. When he analyzes a piece of ivory, he can find its specific mutation and match it up with his dung map, locating the spot where the animal was slaughtered. His sampling efforts have shown that most illegal ivory is coming from just two “hotspots.” This has provided a powerful tool for law enforcement officials deciding where to focus their resources.

A collaring program has been funded by the World Wildlife Fund. The collars are designed to allow rangers to track the movement of elephant herds, and then mobilize to protect them if they move into poaching hotspots. By receiving satellite-transmitted data on mobile phones, rangers can also intercept elephants that drift into a human settlement or fields of crops. In Kenya, an undercover project in 2014 employing drones decreased poaching by 96 percent, prompting the government to deploy drones in all 52 national parks and reserves. The drones have the capacity to spot poachers before they have the opportunity to kill an animal.

Black-Footed Ferret

One of the last known populations of black-footed ferrets (see Plate 22) was extirpated in South Dakota during the early 1970s. The species was feared to be extinct until a small population of approximately 120 animals was found at Meeteetse in northwestern Wyoming in 1981. Before the wild population disappeared, six animals from the Wyoming population were caught for a captive breeding program that began in October 1985. Two of these ferrets were infected with canine distemper; this spread to the other four and all six died. Intensive efforts were then launched to capture as many of the last remaining free-living black-footed ferrets as possible. These were vaccinated against distemper soon after capture, and all 18 captured ferrets survived to form the sole captive breeding population for the species. No young were born in the population's first year in captivity, but in the second year two females produced a total of eight kits, of which seven survived. These were followed by 34 kits in 1988, 58 in 1989, and 66 in 1990. Successes in the captive breeding program allowed reintroductions at a south-central Wyoming site from 1991 until 1995, but disease and other factors caused that program to be suspended. Beginning in 1994, reintroduction efforts were begun in Montana and South Dakota. In March 1996, Arizona became the recovery program's fourth reintroduction site when 44 captive-bred ferrets were sent to Aubrey Valley for acclimation. They were released into the wild between September 5 and November 19, 1996. Each animal had a surgically implanted passive integrated transponder tag; nine adults and seven kits also had radio collars affixed to track their movements (Reading et al., 1996). Between 1996 and 1999, 147 ferrets were released in the Conata Basin (part of the Buffalo Gap National Grassland) in South Dakota. The Conata Basin population was estimated at approximately 250 ferrets in 2007—the largest wild population among the 18 sites where reintroduction of the species has been attempted to date (Grenier et al., 2007). Reintroductions have also taken place in Kansas and Utah. By 2010, black-footed ferrets were living in the wild in eight US states (Wyoming, Montana, South Dakota, Arizona, Colorado, Utah, Kansas, and New Mexico), as well as at one site in Mexico and one in Canada (US Fish and Wildlife Service, 2013). Another 250 to 300 existed in captivity.

As of November 2013, the USFWS estimated that the average minimum number of breeding adults in the wild were 418 animals, with a minimum of those animals at four of the most successful sites to date

(Aubrey Valley, Arizona; Cheyenne River Indian Reservation, South Dakota; Conata Basin, South Dakota; and Shirley Basin, Wyoming). Approximately 280 additional animals are managed in captive breeding facilities. The overall downlisting goal is to have 1,500 ferrets in 10 locations, with at least 30 breeding adults in each population. The Second Revision of the Black-Footed Ferret Recovery Plan (November 2013) states: "At this time, the downlisting criteria may be 40 percent complete with regard to establishing 10 successful populations and approximately 24 percent complete with regard to the goal of 1,500 breeding adults at successful sites. The species remains vulnerable to several threats, including sylvatic plague and inadequate regulatory mechanisms."

Each year, 150 to 250 young ferrets are reintroduced into the wild after a period of preconditioning and vaccination against canine distemper and plague. By 2010, more than 7,000 ferret kits had been born in captivity and, since 1991, more than 2,500 had been reintroduced at the 18 sites in the United States, Canada, and Mexico (US Fish and Wildlife Service, 2013a).

Black-footed ferrets are one of the most specialized carnivores in the world. They eat, sleep, and raise their young in prairie dog burrows. To thrive, they need large prairie dog towns. Not only the ferret, but dozens of other animals and plants depend on prairie dog habitat for survival. However, due to political pressure and ranchers' complaints, prairie dogs continue to be poisoned and black-footed ferret habitat continues to shrink.

Southern (California) Sea Otter

The sea otter (*Enhydra lutris*) (see Plate 23) has a historic range that forms an arc across the North Pacific Ocean, stretching from the shores of Baja California, up the west coast to Alaska, across the Bering Strait to the Kamchatka Peninsula, and down to the islands of northern Japan. Southern sea otters (*Enhydra lutris nereis*) make up a subspecies of sea otter that ranges along the central California coast from San Mateo to Santa Barbara, California. They were listed as a threatened species in 1977.

Sea otters have the densest pelage of any mammal in the world. It was their fur that led to their demise as it was prized across the globe. The average human head has about 100,000 hairs in total. A sea otter, by comparison, can have close to a million hairs per square inch. That is ten human heads of hair for every square inch of their 1.2 m (4 ft.) frames. Sea otters are true tool-users, employing rocks to smash open the tough abalone and urchins that are among their main sources of food.

The sea otter is considered a keystone species—one that has a disproportionately large effect on its environment relative to its abundance. Sea otters feed on sea urchins, playing a critical role in maintaining the health of kelp forest ecosystems. They also consume filter-feeding benthic invertebrates, resulting in the removal of contaminants and disease-causing pathogens from near-shore waters. Thus, sea otters are highly effective sentinels of the health of our oceans.

In 1938, only approximately 50 sea otters existed off the California coast. Populations have slowly recovered, although they still face threats such as poachers, oil pollution, and orca predation. As of 2017, their number had increased to 3,090.

Hawaiian Monk Seal

Fewer than 1,100 Hawaiian monk seals (*Monachus schauinslandi*) (see Plate 24) remain, making it the most endangered marine mammal in US waters. For generations, Hawaiians have called the monk seal ‘Ilio-holo-i-ka-uaua, or “dog running in the rough sea.” Most of the remaining seals live on the rocky shoals and beaches of Hawaii’s Northwestern Islands, where the population decreased 4 percent a year since 2010 and an estimated 60 percent from the late 1950s. Although these animals can live up to 30 years, not more than one in five makes it past the age of 5 and into adulthood. The primary cause in the islands’ French Frigate Shoals, where at least a quarter of the seals live, has been that the pups and juveniles are just not getting the food they need. Researchers suspect that, in addition to some marine species being overfished, rising ocean temperatures and the resulting changing ocean currents have not brought the influx of algae and plankton needed to support the fish, octopus, crustaceans, and other animals the seals eat. In addition, a few rogue Galápagos sharks on two of the shoals’ islets have developed a startling hunting tactic of lunging into shallow water and onto beaches to snatch resting pups. Galápagos sharks have injured or killed more than 200 of the estimated 800 pups born on the shoals since about 2005. Scientists with the Hawaiian Monk Seal Research program of the National Oceanic and Atmospheric Administration’s National Marine Fisheries Service are relocating some seals to safer shores. Although full recovery of the species is a long way off, overall species population growth of 3 percent each year occurred between 2014 and 2016.

West Indian Manatee

The West Indian manatee, or "sea cow" (see Figs. 9.10 and 11.7; Plate 25), is the largest surviving member of the aquatic mammal order Sirenia, which includes the dugong and the extinct Steller's sea cow. Historically, West Indian manatees were found along the US Atlantic and Gulf of Mexico coasts, throughout the Caribbean, and as far south as Brazil's Atlantic coastline. However, due to hunting, habitat fragmentation and loss, and other factors, manatees have disappeared from various parts of their range. For example, manatee hunts were common until the early 1900s, and as a result, the species is no longer found in Guadeloupe and other islands in the Lesser Antilles.

When aerial surveys were begun in 1991, there were an estimated 1,267 manatees in Florida. By 2017, there were more than 6,300 in Florida, representing a significant increase over a 25 year period. The range-wide population is estimated to be at least 13,000 manatees, with more than 6,500 in the southeastern United States and Puerto Rico.

Manatees cannot tolerate temperatures below 20°C (68°F) for extended periods of time. During the colder winter months, these cold temperatures keep the population concentrated in peninsular Florida where many manatees rely on the warm water from natural springs and power plant outfalls. During the summer, manatees expand their range, and on rare occasions are seen as far north as Massachusetts on the Atlantic coast and as far west as Texas on the Gulf coast.

Their preferred habitats include areas near the shore featuring underwater vegetation like seagrass and eelgrass. They feed along grass bed margins with access to deep water channels, where they flee when frightened. (See Red Tide and Manatees in Chapter 11 and Wandering Manatees in Chapter 12.)

A relative of the manatee, the dugong (*Dugong dugon*) is one of four extant herbivorous marine mammal species in the Order Sirenia. Dugongs are listed as endangered by CITES and vulnerable by the IUCN. Dugongs and their habitats—coastal waters in limited areas of the Indian and Pacific Oceans—are threatened by environmental pollution, fishing, habitat destruction, and coastal economic development, putting the species at risk of extinction.

Gray Wolf

In 1973, the USFWS listed the northern Rocky Mountain wolf (*Canis lupus irremotus*) (see Plate 26) as an endangered species and designated Greater Yellowstone as one of three recovery areas. In January 1995, a restoration project was begun to reestablish gray wolves (*Canis lupus*) in the ecosystem of Yellowstone National Park (National Park Service, 2017). Fourteen wolves from Canada were released into the park. They formed the first wolf packs in the park in more than 60 years and began the most celebrated ecological experiment in history. Seventeen more wolves were released the following winter. These reintroduced wolves thrived and, along with their offspring, established a strong foothold in the region. Between 1995 and 1997, 41 wild wolves from Canada and northwest Montana were released in Yellowstone National Park. In general, wolf numbers have fluctuated between 83 and 108 wolves from 2009 to 2016. A population high of 174 wolves was recorded in 2003, and a population of 171 was recorded in 2007. There were at least 108 wolves in 11 packs, including nine breeding pairs, in the park as of December 2016. This was an increase from 95 wolves in 10 packs during 2013. Pack size in 2014 ranged from 2 to 14 and averaged 9 wolves. Forty pups survived to year-end. For the first time, the size of a wolf pack was estimated via genetic sampling methodology, using scat samples from a den site.

The pack is a complex social family, with older members (often the alpha male and alpha female) and subordinates each having individual personality traits and roles within the pack. Packs defend their territory from other invading packs by howling and scent marking with urine.

From 1995 to 2000, in early winter, elk calves comprised 50 percent of wolf prey and bull elk comprised 25 percent. That ratio reversed from 2001 to 2007, indicating changes in prey vulnerability and availability.

Disease periodically kills a number of pups and old adults. Outbreaks of canine distemper occurred in 2005, 2008, and 2009. In 2005, distemper killed two-thirds of the pups within the park. Infectious canine hepatitis, canine parvovirus, and Bordetella have also been confirmed among Yellowstone wolves, but their effect on mortality is unknown. Sarcoptic mange, caused by a mite, reached epidemic proportions among wolves on the northern range in 2009. By the end of 2011, the epidemic had largely subsided, but it is still present at a lower prevalence throughout the park (National Park Service, 2017).

The presence of wolves in the Yellowstone ecosystem is causing a trophic cascade of ecological change among animals and plants that will take decades of research to understand (Boyce, 2018). When the gray wolf was reintroduced into the Greater Yellowstone Ecosystem in 1995, there was only one beaver colony in the park. As of 2011, the park is home to nine beaver colonies. Predatory pressure from wolves keeps elk on the move so they do not have time to intensely browse young willow, aspen, and cottonwood trees, especially during the winter months. As a result, willow stands recovered from intense browsing, and beaver rediscovered an abundant food source that had not been there earlier. Beavers have exerted multiple effects on stream hydrology with their dams and ponds. The dams even out the seasonal pulses of runoff; store water for recharging the water table; and provide cold, shaded water for fish, while the now robust willow stands provide habitat for songbirds.

The goal of the wolf restoration program is to maintain 30 breeding wolf pairs with an equitable distribution throughout the three Rocky Mountain recovery areas, including Greater Yellowstone, central Idaho, and northwest Montana. Once 30 pairs were established and had reproduced for three successful years, the gray wolf was considered for removal from the list of endangered species in Idaho, Montana, and Wyoming. As of 2017, Wyoming’s wolf numbers reveal an enduring healthy population with approximately 377 wolves in 52 packs with 25 breeding pairs (US Fish and Wildlife Service, 2017c). The northern Rocky Mountain wolf population as a whole continues to be self-sustaining, with numbers well above federal management levels. Wolves have continued to expand their range westward into Oregon, Washington, northern California, and Nevada. As of 2017, the USFWS estimated 5,691 gray wolves in the contiguous United States.

According to the USFWS, “recovery of the gray wolf in the Northern Rocky Mountains is one of our nation’s greatest conservation success stories.” The gray wolf was removed from the endangered species list in 2011 in Idaho and Montana, but is currently protected as an endangered species in the state of Wyoming. Wolves are hunted in Idaho and Montana under state hunting regulations. That success was affirmed by the USFWS filing a notice in 2012 delisting the gray wolf as endangered in the state of Wyoming. Wolves had already been delisted throughout the rest of the northern Rockies population. A US District Court vacated the notice, but the ruling was overturned by the US Court of Appeals for the DC Circuit on April 25, 2017, which recognized the recovered status of gray wolves and affirmed the USFWS's determination that the state's regulatory mechanisms are sufficient for conserving wolves under its authority. The USFWS planned to continue to monitor the population for five years to ensure recovery criteria were met (US Fish and Wildlife Service, 2017c). In March 2019, the USFWS proposed a plan to lift protections for gray wolves across the lower 48 states, reigniting a legal battle over a predator that is running into conflicts with farmers and ranchers as its numbers rebound in some regions. The proposal would give states the authority to hold wolf hunting and trapping seasons. Wildlife advocates and some members of Congress promised to challenge any final decision in court.

At the end of 2009, at least 96 to 98 wolves in 14 packs (six breeding pairs), 1 non-pack grouping, and 2 loners occupied Yellowstone National Park (National Park Service, 2009). This represented a 23 percent decline from 124 wolves in 2008. Intraspecific strife, food stress, and mange were likely causes for the decline. Pack size ranged from 3 to 17 and averaged 7.1, down from the long-term average of 9.8 wolves per pack. During 2009, 22 wolves were captured and collared. At year's end, 32 of 96 (35 percent) wolves were collared. The size of the Yellowstone wolf population varies over the years. As of December 2018, there were 80 wolves in nine packs. A biological count on April 1, 2019, revealed 61 wolves in eight packs (National Park Service, 2019). As one biologist stated, "Wolf restoration is evidence of a new way of thinking that will lead to protection of ecosystems, biological diversity, and humankind."

Thousands of Mexican gray wolves (*Canis lupus baileyi*) once lived in the wild. As of 2018, only 114 survived. On January 26, 1998, federal wildlife officials drove three Mexican wolves to a remote corner of southeastern Arizona, where they soon became the first wild wolves to roam the US Southwest in nearly 30 years. During the remainder of 1998, 31 additional wolves were reintroduced into southeastern Arizona in an attempt to reestablish a population that was hunted to near-extinction about 50 years ago. During the first year of reintroduction, five wolves were shot, one was hit by a vehicle, one disappeared, and five others were returned to captivity. Releases have continued with a goal of building a population of about 100 wild wolves within approximately 10 years. Their number surpassed 100 only recently, but the population is highly inbred. In 2011, scientists devised a science-based definition of "recovery" for Mexican wolves. It would require at least three connected populations of at least 200 animals each and a total population of approximately 750 individuals, a reintroduction effort that prioritizes genetic health, and two more populations in the Southern Rockies and Grand Canyon ecosystems.

In June 2017, 19 years after the initial release in Arizona, the USFWS announced its draft plan for reestablishing a viable population (Carswell, 2017). The draft recovery plan was met with extensive criticism from qualified wildlife biologists who claim that it is politically based because of pressure from Arizona, New Mexico, Colorado, and Utah, which objected to expanding wolf territory. It departs dramatically from the science team's recommendations. It concludes that expanding the current population to just over 300 wolves and establishing a population of 170 wolves in Mexico will be enough to ensure recovery. Biologists are skeptical about the plan to build a new wolf population in Mexico, where most habitat is on private land, cattle are plentiful, and data on natural prey are unreliable. A final version of the plan (Mexican Wolf Recovery Plan, First Revision) was released in November 2017. It states: "Our recovery strategy for the Mexican wolf is to establish and maintain a minimum of two resilient, genetically diverse Mexican wolf populations distributed across ecologically and geographically diverse areas in the subspecies' range in the United States and Mexico."

Red Wolf

By 1970, the entire population of the red wolf (*Canis rufus*) (see Plate 27) consisted of fewer than 100 individuals roaming a small coastal strip of Louisiana and Texas. Because the wolves were interbreeding rapidly with much more common coyotes—diluting the endangered animals' gene pool—the red wolf was on the verge of extinction. Between 1975 and 1980, the USFWS captured more than 400 animals. Each was screened for genetic purity and only 14 were determined to be pure red wolves. These wolves formed the basis for an ambitious captive breeding and reintroduction project. The USFWS declared red wolves extinct in the wild in 1980. When a pair of radio-collared red wolves was released into North Carolina's Alligator River National Wildlife Refuge in 1987, the event marked the first time a carnivore extinct in the wild had been reintroduced to its native range. Since then, the experimental population area has expanded to include three national wildlife refuges, a

Department of Defense bombing range, state-owned lands, and private property, spanning a total of 687,965 hectares (1.7 million acres). This population eventually expanded up to 130 wolves roaming their native habitats in five northeastern North Carolina counties. On April 19, 2018, USFWS completed its Species Status Assessment and five-year review (https://www.fws.gov/southeast/wildlife/mammals/red-wolf). The Assessment reported that only 40 red wolves remain on the North Carolina range. The wild population is in crisis and could go extinct within eight years. Gunshot wounds have been the number one cause of death, but automobile collisions also contribute to the red wolf's mortality.

Although the red wolf recovery program once served as a model for successful recovery of wolves, political barriers and consistent mismanagement by the USFWS have seriously threatened the continued existence of this highly imperiled species. In 2014, the USFWS stopped reintroducing captive-born red wolves into the wild, ceased implementing the Red Wolf Adaptive Management Plan that limited hybridization with coyotes, and even began issuing kill permits to landowners—even if wolves were not threatening people or causing problems. In its most recent proposal announced in 2016, the agency called to place most of the last remaining wild red wolves in captivity.

However, in November 2018, US District Court Judge Terrence Boyle found that the changes violated the Endangered Species Act and ruled that the USFWS must do a better job of protecting the endangered red wolf. The decision overturns several controversial management decisions that wolf advocates say would have doomed the 40 or so remaining red wolves.

Termination of the recovery program will inevitably result in the loss of the last population of red wolves, rendering the species extinct in the wild, and reducing it to a "museum curio." As of April 2018, there were over 200 red wolves in the Species Survival Plan captive breeding program in sites across the United States (www.fws.gov/redwolf).

In 1990, an experimental reintroduction effort in the Great Smoky Mountains National Park, which straddles the border of North Carolina and Tennessee, was begun. A total of 37 red wolves were introduced in the park between 1991 and 1998. Eight litters consisting of 33 pups were born in the park, but only two pups were confirmed to have survived into the fall. Many wolves left the park presumably in search of prey, and some of those that remained succumbed to disease, parasites, and starvation. The lack of survival of wild litters, and the difficulty of keeping wolves within the park, caused the USFWS to terminate the Smokies project in October 1998.

Ocelot

The ocelot (*Leopardus pardalis*) (see Plate 28) is a medium-sized American wild cat. The ocelot, jaguar, and jaguarundi, all of which are endangered cats, still roam the Mexican–US border area, but only the ocelot still breeds on the northern side (Tangley, 2006). It is estimated that between 50 and 75 ocelots survive in two isolated populations at the southernmost tip of Texas—one in Laguna Atascosa National Wildlife Refuge and the other on private ranchland some 48 km (30 mi.) away. Although scientists believe that the ocelot once ranged across the southern United States as far north as Arkansas and Arizona, much of the cat's habitat has been destroyed to make way for farms, ranches, subdivisions, and shopping malls over the past 60 years. Today, the automobile is the greatest cause of mortality. Ocelots inhabit many ecosystems from tropical rain forest to dry deciduous forest, but they must have at least 75 percent woody cover. Thick vegetation provides ocelots with an abundance of mice, rabbits, and other food, as well as camouflage from prey and from predators like coyotes and humans. In Texas, less than 5 percent of the dense native brush that once sheltered the ocelot still stands. Normally, a pair of ocelots will occupy a home range of more than 809 hectares (2,000 acres); in Texas, most pairs have 32 hectares (80 acres) or much less. Private conservation efforts to provide landowners with tax breaks or other incentives if they will protect the cat's habitat are being actively pursued.

The proposed construction of a border wall by the US government would have catastrophic implications not only for the ocelot but for hundreds of vertebrate species including the cactus ferruginous pygmy owl, desert cottontails, jaguars, jaguarundis, Mexican gray wolves, mountain lions, javelinas, and black bears that rely on borderland habitat (Schlyer, 2018). Peters et al. (2018) presented an analysis showing that the border bisects the geographic ranges of 1,506 native terrestrial and freshwater animal (n=1,077) and plant (n=429) species, including 62 species listed as critically endangered, endangered, or vulnerable by the IUCN Red List. More than 180 species of wildlife in the region are already listed as endangered or threatened. A border wall in the 2,028 km (1,260 mi.) long Rio Grande floodplain would cause unnatural and significant flooding, cause erosion and debris build-up post flood, divert the natural water flow, and keep animals from their natural crossings. Unfortunately, the Department of Homeland Security is authorized to waive any existing law in order to build border walls. Along 24 km (15 mi.) of border near San Diego, 33 laws have been waived to build a wall, including the Clean Water Act, the Endangered Species Act, and the Clean Air Act.

Jaguar

The jaguar (*Felis onca*) (see Plate 29) is the world's third largest feline, behind tigers and lions. It is the only big cat in the Western Hemisphere that roars. Biologists confirmed only seven jaguars in southern Arizona and southwestern New Mexico over two decades—including media sensations Macho B (who died in 2009 and had been photographed around the Arizona-Mexico border since 1996) and El Jefe (who was last captured on a trail camera a few years ago) (Grant, 2016). Once roaming as far north as the Grand Canyon, jaguars were common in Texas and may even have claimed territory in California and Louisiana. But by the early twentieth century, they had largely disappeared, killed off by government predator-control agents, livestock producers, and hunters. Today, jaguars, which are protected under the Endangered Species Act, may be ready to return, particularly given that populations of their favorite prey (deer and javelinas) are more abundant than they were 100 years ago when jaguars still mated and raised young in the United States. But obstacles remain. Jaguar mortality, including deaths caused by guns and vehicles and the indirect mortality associated with mining and other activities that destroy habitat, must be prevented. The USFWS and state agencies must champion jaguar recovery in the United States. There is also the problem of the potential border wall (see discussion above under Ocelot).

Florida Panther

Genetic analyses of the Florida panther (*Puma concolor coryi*) population (see Plate 30) show that it was nearly wiped out in the early twentieth century, dropping to a population size of as little as six animals. The Florida population was declared endangered under 1967's predecessor law to the Endangered Species Act. At that time, only 12 to 20 known individuals were living in less than 5 percent of their historical range. Even as late as the early 1990s, the population was in desperate straits. Habitat was shrinking, highway deaths were common, and the population size was only about 30 animals. Many of the remaining cats were closely related, sporting the kinked tails and cowlicks that are considered signs of inbreeding. Many of the males had undescended testes and low sperm counts. In 1995, amid considerable controversy, the USFWS captured eight female cougars in the Big Bend region of Texas and brought them to Florida. Six were released just east of Naples, and two were released into the Everglades. Five of the eight Texas cougars produced a total of at least 20 kittens. In 1990, 88 percent of the Florida population had kinked tails. By 2000, not a single first- or second-generation kitten born to the Texas females had the characteristic 90° crook in the last five tail vertebrae. At the same time, the population expanded from about 30 cats to more than 80, and they entered habitats once thought unsuitable for panthers. In addition, the installation of wildlife underpasses beneath Interstate 75 in 1991 has significantly decreased road kills, not only for panthers but also for many other animals, including bears, otters, raccoons, deer, and wild turkeys.

None of the eight original Texas cougars remain in the wild population today: five died from various causes and the remaining three were removed from the wild and placed in captivity after they had produced a sufficient number of offspring. Subsequent analyses have documented the beneficial impact of genetic restoration on the genetic health of the population, as well as the coinciding increase in panther abundance since 1995.

Automobiles are still a problem for the Florida panther. Sixteen panther deaths from cars were confirmed in 2009, and an additional animal was suspected of having died from injuries due to a car. The mortality rate due to cars alone depleted the population by more than 15 percent. In 2014, 25 panthers were killed by vehicles. Unfortunately, a record number of Florida panthers died during 2015 and 2016, the two worst years on record, due to car collisions. In each of those years, vehicular fatalities claimed 42 panthers.

As of 2017, the population was estimated to be between 120 and 230 animals (US Fish and Wildlife Service, 2017b). These population estimates do not include kittens that are still dependent on their mothers. Additionally, a female was confirmed to have crossed the Caloosahatchee River (once thought to form a natural barrier to the species’ expansion to the north) for the first time in over 40 years and was using lands in Charlotte County. In 2017, it was confirmed that this female had mated and produced two litters of kittens. Male panthers continually disperse out of the breeding range and have been confirmed as far north as Georgia.

Under the current Recovery Plan, established in 2008, the USFWS will consider delisting the Florida panther when three populations of at least 240 individuals each (excluding dependent-aged kittens) have been established and sufficient habitat to support these populations is secure in the long-term. These recovery goals cannot be met without establishing additional populations outside of southern Florida, which requires support from private landowners. But even as efforts are undertaken to increase the population, southern Florida appears to be running out of room. Even lands that have been identified by scientists as "essential panther habitat" are disappearing at a rate of 1 percent a year. The Florida panther currently occupies only 5 percent of its historic range.

Humpback Whale

The humpback whale (see Plate 31) was very nearly extinguished from the planet during the eighteenth and nineteenth centuries due to human hunting, with population levels dropping to 10 percent of pre-hunting days. But over the past half-century, laws protecting humpback whales have boosted survival. Those that live below the equator have fared so well since whaling regulations were enacted that they are no longer considered to be endangered.

It appears that climate change is helping humpback whales rebound even more. From 2010 to 2016, researchers used dart guns to take blubber samples of humpbacks near the Western Antarctic Peninsula (Pallin et al., 2018). Blubber samples can be tested for progesterone levels and also gender. The team tested 268 females and 239 males and reported that 60 percent of the females tested appeared to be pregnant. The percentage rose as the years passed, suggesting a relatively constant upswing in pregnancy rates. The researchers suggested that part of the reason for the increase in pregnancy rates is global warming, which has provided an average of 80 more ice-free days per year, allowing the whales to feed on krill more easily. However, on a long-term basis, a reduction in sea ice due to global warming will also mean a reduction in krill populations because krill feed on the zooplankton that resides on the underside of the ice. Less krill to go around will make it more difficult for all of the creatures, like humpback whales, that feed on the tiny crustaceans.

American Plains Bison

One of the first successful restorations of an endangered species involved the bison (*Bos bison*) (see Figs. 9.21 and 10.25). Originally numbering around 30 million, bison were slaughtered by European settlers in such unbelievable numbers that by 1888 only 541 plains bison remained in the United States. Some of these had been bred with cattle and were no longer considered wild. However, 23 wild bison remained in Yellowstone National Park in 1900, holed up in Pelican Valley. Bison were saved from total destruction by a handful of far-sighted individuals and organizations. In 1907, the New York Zoological Society donated 15 bison to the first national preserve for bison, near Cache, Oklahoma. That preserve is now called the Wichita Mountains National Wildlife Refuge.

Yellowstone has done its job so well that the herd now consistently exceeds 4,000 bison, a number large enough to provoke fears of overgrazing in the park and of bison roaming beyond its boundaries. To keep from rounding up "excess" bison for slaughter or watching them be hunted outside park boundaries, the National Park Service decided to manage the herd by periodically relocating animals. Recently, two small herds of pure, wild Yellowstone bison were reintroduced to the Fort Peck and Fort Belknap Indian Reservations in northeastern Montana. A small herd of Yellowstone bison has been thriving at Fort Peck since a modest 2012 feasibility experiment. The plan is to build up that herd and to create a bison pipeline. As more animals arrive from Yellowstone, the Fort Peck tribes will gradually export bison to start protected herds on other reservations and conservation lands. Bison are totally dependent upon conservation actions and protected lands.

Ranchers and others have long maintained that Yellowstone bison spread brucellosis, a bacterial infection that is devastating to cattle, when they roam outside park boundaries. A 2017 study by the National Academies of Sciences, Engineering, and Medicine, however, determined that every case of brucellosis in cattle in the Yellowstone region over the past 20 years came from infected elk, not bison. That finding has made it harder to argue that wild bison should not be allowed out of the park.

Current bison herds contain more than 250,000 animals and are found in all 50 states and many foreign countries. Currently, 6 of the 20 wild herds, representing approximately 12,000 animals (64 percent), are anchored by national parks, refuges, or sanctuaries, with Yellowstone National Park having the largest population.

Review Questions and Topics

1. Do you feel that it is advantageous or disadvantageous for one species to control the destiny of all plants and animals on the Earth? How might this affect future efforts to establish colonies on other planets?
2. The over 240 birds released into the migratory flock of adult whooping cranes in Florida survive, migrate, pair, and are wild, but these hand-reared and ultralight-aircraft guided birds have fledged only ten chicks. What steps would you take to seek a solution?
3. Do you favor delisting the Greater Yellowstone Ecosystem population of grizzly bears from the endangered species list? Support your answer.
4. Should China's program of loaning pandas to zoos throughout the world with the stipulation that any offspring be returned to China to participate in the panda breeding program be a model for other endangered species? If so, name several specific species that might benefit from such a program.
5. Can you think of any method(s) other than collars and drones to prevent poachers from killing elephants?
6. Speculate on what might happen to the ecosystem if southern sea otters were to become extinct.
7. Taking into consideration both the human and wildlife situations, how would you resolve the problem of constructing a border wall along the US–Mexico border?

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Vertebrate Internet Sites

1. Red Wolf

   www.fws.gov/redwolf

   Red wolf website maintained by the US Fish and Wildlife Service. History of breeding and reintroductions, project reports, current red wolf facts, refuge finder, etc.

2. Cahow Conservation

www.audubon.bm/conservation/cahow

Discusses conservation efforts for the Bermuda cahow. Includes videos of nesting burrows on Nonsuch Island.

3. Bermuda Petrel

   https://en.wikipedia.org/wiki/Bermuda_petrel

   Includes taxonomy, history of decline, current world population, current nesting areas, and conservation efforts.

4. Florida Panther

   www.floridapanthernet.org

   Official website of the Florida Fish and Wildlife Conservation Commission. Current news, regular updates about the current Florida panther population, photos, genetic studies, natural history, identification of panther signs, range, diet, life expectancy, and more.

5. Patuxent Wildlife Research Center, Laurel, Maryland

   www.pwrc.usgs.gov

   This site provides access to hundreds of ongoing studies, including amphibian surveys based on vocalizations, breeding bird censusing, and endangered species. It includes biological monitoring information databases, as well as information concerning many other baseline studies, images, and links.

6. Save the Manatee Club

   www.savethemanatee.org

   Established in 1981 by former Florida Governor Bob Graham and singer/songwriter Jimmy Buffett. Save the Manatee Club was started so the public could participate in conservation efforts to save endangered manatees from extinction.

18 | Regulatory Legislation Affecting Vertebrates

National parks and reserves are an integral aspect of intelligent use of natural resources. It is the course of wisdom to set aside an ample portion of our natural resources as national parks and reserves, thus ensuring that future generations may know the majesty of the earth as we know it today.

John F. Kennedy, 1962

INTRODUCTION

Conservation of plants and animals is a global concern. Although the conservation movement did not start in the United States, this country has been the leader in the realm of conservation both within North America and throughout the world.

LEGISLATION

Efforts to regulate hunting in the United States can be traced back to the seventeenth century. Virginia, for example, was one of the earliest colonies to offer a bounty for wolf control. This law was adopted by the Grand Assembly at Jamestown on September 4, 1632 (Green, 1940). The first major federal legislation in the area of animal conservation, however, came with the passage of the Lacey Act of 1900. This law, among other things, prohibited the interstate transportation of "any wild animals or birds" killed in violation of state laws. It also authorized the secretary of agriculture to adopt all measures necessary for the "preservation, distribution, introductions, and restoration of game birds and other wild birds" subject to the laws of the various states. In 1916, a Convention of Migratory Birds produced a treaty adopting a uniform system of protection for certain species of birds that migrate between the United States and Canada. The Migratory Bird Treaty Act of 1918 implemented the treaty of 1916, providing for regulations to control the taking, selling, transporting, and importing of migratory birds for their feathers. The Act played an important role in protecting many species like the snowy egret (*Egretta thula*) (Fig. 18.1).

The Migratory Bird Conservation Act of 1929 provided for the acquisition and development of land for migratory bird refuges and also authorized investigations and publications on North American birds. The Act, however, provided no funds for these purposes. Funding was not provided until 1934 when the Migratory Bird Hunting and Conservation Stamp Act (commonly known as the Duck Stamp Act) was passed. This legislation requires all waterfowl hunters 16 years of age or older to possess a valid federal hunting stamp. Receipts from the sales of this stamp are set aside in a special account known as the Migratory Bird Conservation Fund. From this, funds are appropriated for the acquisition and management of migratory bird refuges and waterfowl production areas. These two Acts have played an important role in protecting such birds as the trumpeter swan (*Olor buccinator*) and the whooping crane (*Grus americana*).

The Fish and Wildlife Coordination Act of 1934 was the first major federal statute to employ the strategy of requiring consideration of humanity's impact on wildlife. This forward-looking legislation authorized federal water resource agencies to acquire lands or interests in connection with water-use projects specifically for the protection and enhancement of fish and wildlife.

In 1936, a Convention between the United States and Mexico for the Protection of Migratory Birds and Game Mammals was held. This meeting was similar to the Convention with Canada in 1916, and it was similarly implemented under the Migratory Bird Treaty Act of 1918. This Convention was amended in 1972 to add 32 additional families of birds, including eagles, hawks, owls, and members of the family Corvidae (jays, magpies, and crows).

The federal Aid in Wildlife Restoration Act (commonly referred to as the Pittman-Robertson Act) was passed in 1937. This Act provides federal aid to states for wildlife restoration work with funds being raised by an excise tax on sporting arms and ammunition. Funds are apportioned to the states on a 75 percent–25 percent matching basis and can be used for approved land acquisition, wildlife research, and development and management projects. Amendments in 1970 and 1972 added excise taxes on pistols, revolvers, bows, arrows, parts, and accessories used in wildlife projects or hunter safety programs. The majority of all wildlife refuges have been purchased through funding provided by the Pittman-Robertson Act.

Figure 18.1. Snowy egret (*Egretta thula*) in breeding plumage. The Migratory Bird Treaty Act of 1918 played an important role in protecting many species, including the snowy egret.

The Bald Eagle Act of 1940 was designed to provide for the protection of bald and golden eagles. The Convention on Nature Protection and Wildlife Preservation in the Western Hemisphere produced a 1940 treaty that stated that the government of the United

States and 11 other American republics wished to “protect and preserve in their natural habitat representatives of all species and genera of their native flora and fauna, including migratory birds.” This treaty covers the wintering grounds of many birds that nest in the United States.

The federal Aid in Fish Restoration Act (commonly referred to as the Dingell-Johnson Act) was passed in 1950. It provides federal aid to the states on a 75 percent–25 percent matching basis for approved land acquisition, research, and development and management projects involving fish (Fig. 18.2). Funds are obtained by means of an excise tax on certain items of sport fishing tackle. Most fish hatcheries, including those now used to raise endangered species, were built using funds from the Dingell-Johnson Act. People who buy Duck Stamps, hunting licenses, and hunting and fishing equipment have been indirectly responsible for most of the species management and protection efforts in this country.

Figure 18.2. The Aid in Fish Restoration Act (commonly known as the Dingell-Johnson Act) passed in 1950 and provides funds for management projects involving fishes—for example, fish ladders that provide access around a dam for fish migrating upstream. Fish ladders are often constructed with a 10 percent-graded flume interrupted with vertical, slotted partitions. The maximum 30 cm (1 ft.) drop in water level at each partition produces a flow that fishes instinctively pursue. Setting the slots at an angle directs the flow exclusively into the pools behind the partitions, so that the dropping water never has more energy than the fish can resist. Changes in water level do not disrupt the ladder. Higher water increases the flow through the slots as well as the amount of energy-absorbing water in the pools.

The Fish and Wildlife Act of 1956 established a comprehensive national fish and wildlife policy. It directs a program of continuing research, extension, and information services on fish and wildlife matters of national and international importance. This Act was responsible for the establishment of Cooperative Fisheries and Wildlife Units at many of the nation's universities. It designated a US Fish and Wildlife Service (USFWS) made up of the Bureau of Sport Fisheries and Wildlife (BSFW) and the Bureau of Commercial Fisheries. This Act was amended in 1970 to transfer the Bureau of Commercial Fisheries to the National Oceanic and Atmospheric Administration (NOAA). A 1974 amendment redesignated the BSFW as the USFWS under the US Assistant Secretary for Fish and Wildlife and Parks.

In an effort to accelerate the acquisition of migratory waterfowl habitat, Congress passed the Wetlands Loan Act in 1961, which authorized $100 million to be added to the Migratory Bird Conservation Fund. Advances were to be repaid to the Treasury using Duck Stamp receipts.

The Wilderness Act of 1964 provided for the formal preservation of wilderness areas. Areas within the National Wildlife Refuge System and areas within the National Parks and National Forests were to be reviewed for wilderness designation and recommendations submitted to Congress. Also in 1964, the Land and Water Conservation Act enabled a federal lands purchase program that has helped protect Yellowstone National Park, the Appalachian Trail, and Central Park in New York City. The program has steered billions of dollars from federal offshore oil and gas leasing revenues to conserve millions of acres of land at more than 40,000 parks, monuments, and historic sites.

Additional environmental protection under such laws as the National Wild and Scenic Rivers Act (1968), the National Environmental Policy Act (1969), the Marine Mammal Protection Act (1972), the Endangered Species Act (1973), the Fishery Conservation and Management Acts (1976, 1978, 1982), the Whale Conservation and Protection Study Act (1976), the Fish and Wildlife Improvement Act (1978), and the Fish and Wildlife Conservation Act (Nongame Act) (1980) has helped preserve habitats of endangered species as well as other wildlife. This protection, however, has been insufficient for many species.

The Habitats Directive of the European Union (EU), enacted in 1992, is a bold conservation law containing a master list of threatened

European habitat types that the 27 member nations are supposed to identify and protect. It is one of the EU's two directives in relation to wildlife and nature conservation, the other being the Birds Directive. The Habitats Directive aims to protect 220 habitats and approximately 1,000 species (listed in the Directive's Annexes), other than birds, that are considered to be endangered, vulnerable, rare, and/or endemic. Due to differences in nature conservation traditions, national problems have arisen in the implementation of the directive. Since member states in the south and east of Europe participated less in nature policies, these states experienced misfits in promoting the new EU-originating provisions.

ENDANGERED SPECIES IN THE UNITED STATES

In January 1964, the BSFW circulated a tentative list of rare and endangered fish and wildlife among some 300 knowledgeable persons and organizations. Comments and suggestions were solicited. A revised list based on these suggestions was reviewed further and the additional comments incorporated into the first edition of the "Red Book," as the Federal List of Rare and Endangered Fish and Wildlife of the United States was popularly known. This was issued in July 1966 and revised in 1968. Species were classified as **endangered, rare, peripheral**, or **status undetermined.**

A second revision of the Red Book in March 1973 combined endangered and rare species into a single category termed **threatened.** This change was made primarily to indicate that the Red Book did not comprise the official list of endangered species. The official list is found in the US Department of the Interior's list of endangered native fish and wildlife, published annually in the *Federal Register*.

In 1966, the BSFW began a special research program for endangered species. This program was centered at the Patuxent Wildlife Research Center in Laurel, Maryland, and had two primary objectives: (1) to learn how to propagate certain species in captivity, and (2) to seek, through field studies, key factors that threatened the existence of certain species. With enactment of the Endangered Species Preservation Act of 1966, which authorized use of land and water conservation funds for the acquisition of endangered species habitat, refuge lands began to be purchased specifically for endangered species.

In 1969, Congress passed the Endangered Species Conservation Act (Public Law 91-135). This Act provided broad authority to the federal government to establish a comprehensive program for the conservation, restoration, and propagation of selected fish and wildlife in the United States that are threatened with extinction. The Act also provided assistance on an international level for the preservation of wild animals in other nations.

The Endangered Species Act of 1973 (Public Law 93-205; 87 Stat. 884), signed into law by President Richard Nixon, became effective on December 28, 1973, and thereby supplanted the Endangered Species Conservation Act of 1969. The new law sought "to provide a means whereby the ecosystems upon which endangered species and threatened species depend may be conserved, to provide a program for the conservation of such endangered species and threatened species, and to take such steps as may be appropriate to achieve the purposes of the treaties and conventions" in which the United States had pledged its support for the conservation of wild flora and fauna worldwide. This law encompasses all species of the animal and plant kingdoms, with the term *species* including any species, any subspecies, and any smaller taxonomic unit of plant or animal, and also any viable population segment thereof. Furthermore, the law established two categories of endangerment:

1. *Endangered species:* Those species in danger of extinction throughout all or a significant portion of their range.
2. *Threatened species:* Those species that are likely to become endangered within the foreseeable future throughout all or a significant portion of their range.

This law also emphasized the need to preserve critical habitats on which endangered species depend for their continued existence. Individual states were encouraged to establish guidelines to complement the goals outlined in the 1973 Act.

Also in 1973, the United States was one of 44 nations attending the Convention on International Trade in Endangered Species of Wild Fauna and Flora. The treaty and species lists negotiated at the Convention were implemented by the United States on February 22, 1977. The scientific authority for the United States is an autonomous committee of representatives of six federal agencies. Known as the Endangered Species Scientific Authority (ESSA), this committee's primary responsibility is to establish biological criteria on which to base findings for individual species protected by the Convention so that it may advise the management authority (Federal Wildlife Permit Office of the USFWS) on the issuance of appropriate US export and import permits.

In mid-1978, the US Supreme Court handed down a decision upholding the applicability of the Endangered Species Act of 1973 in a case involving the Tennessee Valley Authority. Following this decision, Congress subsequently amended the Act (the Endangered Species Act Amendments of 1978), reauthorizing administration of the Endangered Species Act of 1973 and, among other things, providing for a review board and a cabinet-level committee to act as the final decision-making authorities in those cases where a seemingly irresolvable impasse has been reached regarding approval of a project that might destroy the habitat and last remaining members of an endangered species. Whether this amendment permitting exemptions from the Act's stringent requirements will seriously weaken the Endangered Species Act remains to be seen. The Endangered Species Act was re-authorized in 1988 and 1995.

As of March 14, 2019, a total of 444 native species and subspecies of vertebrate animals were listed as endangered and/or threatened in the United States and/or trust territories. These include 94 mammals, 101 birds, 46 reptiles, 36 amphibians, and 167 fishes (US Fish and Wildlife Service, 2019). The numbers change as species are added or removed from the list.

The polar bear (Fig. 18.3) was officially listed in the "threatened" category in May 2008, becoming the first species listed with climate change as the main threat. Nearly 4,000 other dwindling species, most of them little-known plants and invertebrates, are awaiting classification. Appendix B of the Endangered Species Act contains a complete listing of the vertebrates currently classified as endangered by the USFWS. Each listed species has a Recovery Plan—a species management plan developed by a Recovery Team that is designed to restore habitats or do whatever else is necessary to enhance the survival of the species.

In 1998, the US Department of the Interior announced that 29 species of fishes, reptiles, birds, and mammals had recovered enough to be seriously considered for removal from the endangered list over a two-year period. Some of the species (13) were downgraded to threatened and others (16) were removed from the law's protection altogether, although states may still regulate them. The American alligator was delisted in June 1987. In 1999, the American peregrine falcon (*Falco peregrinus anatum*) (see Plate 18) was removed. The American bald eagle (*Haliaeetus leucocephalus*) (see Plate 19) was delisted in July 2007. Another 14 species were removed after they either disappeared or new information was uncovered indicating they never should have been included on the list in the first place. In February 2014, the USFWS announced that populations of the Oregon chub (*Oregonichthys crameri*) were healthy enough to remove the 9 cm (3.5 in.) long fish from the list of threatened and endangered species. The delisting became official on February 17, 2015. It marks the first time an endangered fish has recovered enough to be delisted.

Figure 18.3. The polar bear (*Ursus maritimus*), the first species added to the US Fish and Wildlife Service Threatened Species list as a primary result of climate change.

Resource allocation poses a problem for agencies responsible for species recovery. Should resources be allocated toward species facing imminent extinction or species whose long-term survival can most benefit from investment? Some argue that the latter strategy is ethically unsound because it may abandon species with little hope of long-term recovery. Resource allocation is not about saving some species and letting others go extinct; it is about finding a way to better order the work so that as many species as possible are recovered given the limited resources available (Cornwall, 2018; Gerber, et al., 2018).

In addition, most states have held one or more endangered species symposia. Statewide symposia allow researchers to pool the most accurate and up-to-date information about the endangered and threatened species that reside within their borders. The author of this book organized the first endangered species symposium in Virginia in 1978 (Linzey, 1979).

Since January 2017, more than 75 bills and amendments have been introduced in the US Congress that would simplify, restrict, or outright weaken the Endangered Species Act, ranging from attempts to delist individual species to defunding specific projects. As of November 2018, none of the legislation had passed. In 2018, the presidential administration proposed changes allowing agencies deciding whether to list a species to be allowed to cite potential economic losses from missed development. As well, some federal units undertaking projects that could impact protected species—such as floodplain control or a border wall—would no longer be required to consult with wildlife experts from other agencies. Additionally, threatened plants and animals would no longer by default be entitled to the same protections as endangered species.

SANCTUARIES AND REFUGES

The establishment of wildlife refuges, parks, and sanctuaries has been a major component in the survival of many species. Protected areas allow species to breed, rest during migration, or winter with minimum disturbance. Some refuges have been established specifically to provide critical habitat for endangered species.

The first US federal wildlife refuge was established at Pelican Island in Florida in 1903. Its purpose was to protect a large heronry from plume hunters. The USFWS lands include national wildlife refuges consisting not only of wildlife refuges but also wildlife ranges, wildlife management areas, game preserves, and conservation areas. The refuge system has grown to more than 59 million hectares (146 million acres), including more than 22 million hectares (54 million acres) of submerged lands and waters in refuges within marine national monuments. Over 50 percent of the land area of these refuges is located in Alaska. Many refuges permit sport and commercial fishing, hunting, trapping, mining, oil and gas development, timber harvesting, farming, and livestock grazing. Regulations usually prohibit such activities on refuges during periods of the year when protected species are present. Approximately 25 percent of the land within national wildlife refuges is protected as wilderness, a designation that prohibits all of the above activities. The USFWS also oversees 210 waterfowl production areas along with 38 wetland management districts (www.fws.gov/refuges, September 2017) (Fig. 18.4).

Yellowstone National Park, established in 1872, was the first public national park in the world. The National Park System now consists of 417 individual units covering more than 54 million acres in all 50 states.

Among the individual units are 60 major parks and 357 national recreation areas, monuments, battlefields, historic sites, parkways, trails, rivers, seashores, and lakeshores (National Park Service, 2018b). Although open to the public for certain types of recreational activities, these areas, to some extent, preserve and protect wildlife and its habitat. Sport fishing is allowed in all units, but hunting is prohibited except in national recreation areas. Approximately 50 percent of the land is protected as wilderness.

The National Wild and Scenic Rivers Act was passed by Congress in 1968. It prohibits development along portions of rivers that have unique and outstanding wildlife, geological, scenic, historical, or cultural values. As of September 2018, there are 5 national rivers and 10 national wild and scenic rivers administered as distinct units of the National Park System. These encompass only 0.2 percent of the nation's 6 million km (3.7 mi.) of rivers. In contrast, 17 percent of the length of wild rivers in the United States have been modified by dams (Miller, 1999).

The US Forest Service oversees 154 national forests, 76.2 million hectares (188.2 million acres), and 20 national grasslands, 1.5 million hectares (3.8 million acres), comprising a total of 77.7 million hectares (192 million acres) (US Forest Service, 2018). These areas are managed under the concepts of sustained yield and multiple use. Uses include timber harvesting, fishing, hunting, grazing, mining, and oil and gas development. Only about 15 percent of national forest lands are protected as wilderness.

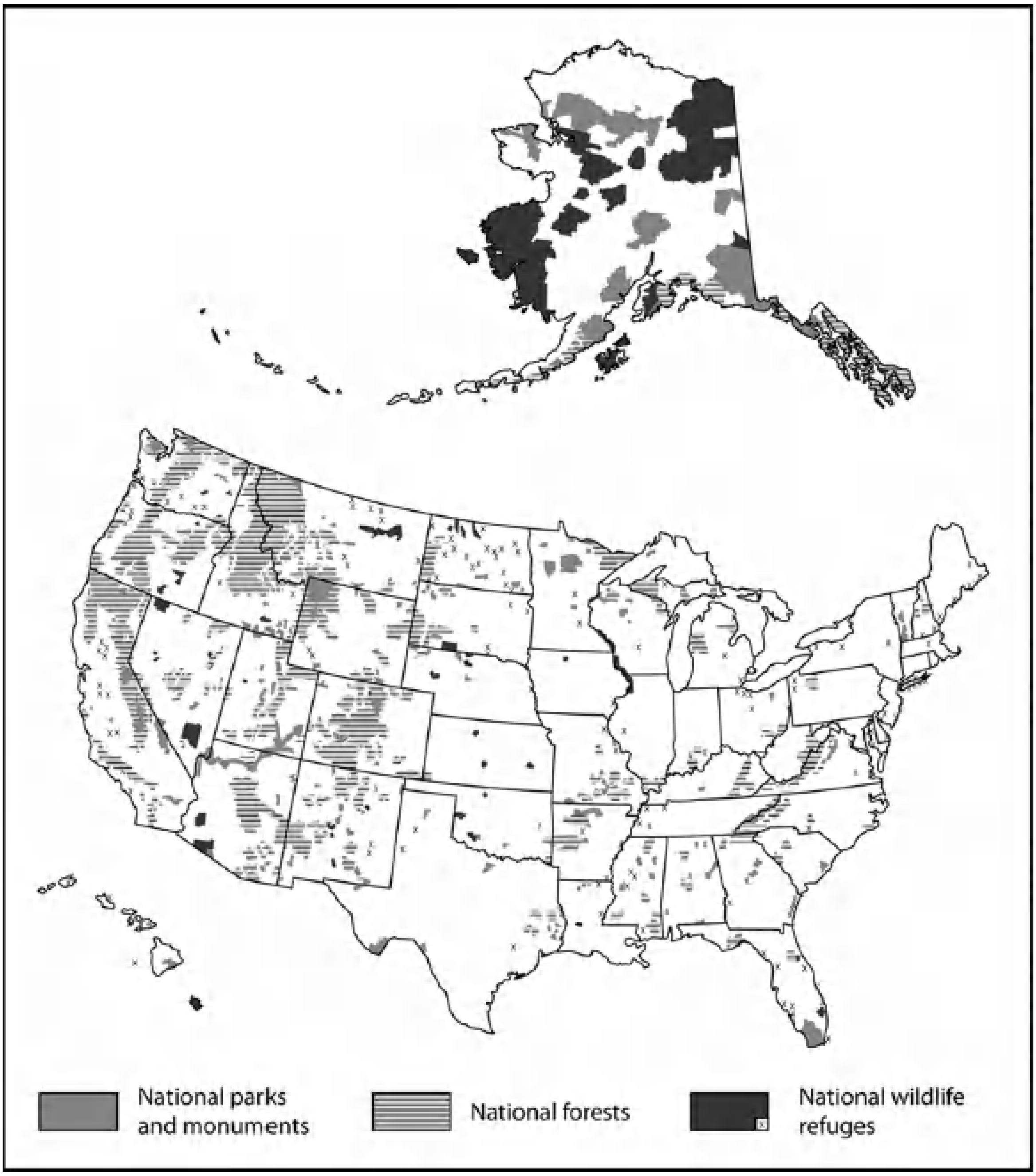


Figure 18.4. As of September 2017, the National Wildlife Refuge system consisted of 566 units. The National Park Service consisted of 60 major parks and 357 national recreation areas, monuments, battlefields, historic sites, parkways, trails, rivers, seashores, and lakeshores. The US Forest Service oversaw 154 national forests and 20 national grasslands.

The National Wilderness Preservation System is the most protective and restrictive of all federal lands. Wilderness areas are located within national wildlife refuges, parks, and forests. They are managed by the agency that oversees the area in which they are located. At present, 765 wilderness areas have been designated, 44.5 million hectares (110 million acres), in 44 states and Puerto Rico. Alaska contains more than half (52 percent) of America's wilderness. These areas are roadless and, generally, have little or no evidence of human intrusion or presence (www.wilderness.net/nwps, October 2018). In 1980, the passage of the Alaska National Interest Lands Conservation Act added 22.7 million hectares (56 million acres) of wilderness to the system, the largest addition in a single year. Overall, only about 5 percent of the entire United States—an area slightly larger than the state of California—is protected as wilderness. Because Alaska contains just over half of America's wilderness, only about 2.7 percent of the contiguous United States—an area about the size of Minnesota—is protected as wilderness.

Although not managed primarily for wildlife, many federal military installations provide habitat for numerous species. In addition to federal lands, there are numerous state wildlife management areas, parks, and forests that provide protection for many species. These are generally smaller than their federal counterparts and place more emphasis on managed human recreational activities like hunting, fishing, timber management, and camping.

The Nature Conservancy (TNC), a private nonprofit environmental organization formed in 1951 with headquarters in Arlington, Virginia, has done more than any other private organization to preserve unique and fragile habitats. TNC acquires land either through donation or purchase and sets it aside to protect endangered wildlife and plants and to provide future generations with opportunities to enjoy the out-of-doors. It has pioneered new land preservation techniques such as the conservation easement and debt-for-nature swaps. Since 1951, TNC has protected more than 48 million hectares (119 million acres) of land and thousands of miles of rivers worldwide. Some tracts are maintained and managed by TNC; others are donated to appropriate government agencies or universities. In 2007, TNC organized the protection of 65,154 hectares (161,000 acres) of forest in the Adirondacks of New York and recently negotiated a debt-for-nature swap to protect the tropical forest in Costa Rica. In December 2015, TNC announced the finalization of the first ever debt swap in Seychelles aimed at ocean protection. TNC's Plant a Billion Trees campaign is an effort to restore 1,011,714 hectares (2,500,000 acres) of land and plant one billion trees in the Atlantic Forest of Brazil. The Plant a Billion Trees campaign has been identified as a tool to help slow climate change, as the Atlantic Forest—one of the biggest tropical forests in the world—helps regulate the atmosphere and stabilize global climate.

Two private organizations, Ducks Unlimited and Trout Unlimited, have played extremely important roles in purchasing critical wetland habitats and protecting them from development. Both organizations also sponsor research on species management.

The National Audubon Society also maintains a network of refuges. Many colleges and universities maintain research stations and protected areas for faculty and student research. The American Museum of Natural History maintains two research stations and sanctuaries in Florida and Arizona. The Smithsonian Institution has a primary research station in Panama and others in various locations around the world.

Debt-for-Nature Swaps

On a global basis, many countries are seeing the value of setting aside areas as sanctuaries and refuges. The debt-for-nature swap, a unique program that began in 1987, was designed to help less developed countries preserve vital habitat. International nongovernmental organizations like TNC, the World Wildlife Fund (WWF), and Conservation International purchase part of the debt of a foreign country from the bank to whom the debt is owed. Many banks are willing to sell these debts for between 5 cents and 60 cents on each dollar owed. In exchange for not having to repay a portion of its debt, the country enters into an agreement with the conservation organization whereby the country agrees to protect a portion of its tropical forest and the inhabitants of that forest.

Bolivia was the first country to participate in a debt-for-nature swap when the government agreed to protect 1.5 million hectares (3.7 million acres) of tropical forest surrounding its Beni Biosphere Reserve. Conservation International purchased $650,000 of debt at an 85 percent discount. Implementation of the plan was delayed for several years, however, due to internal opposition and Bolivia’s tight financial resources. By 2004, 10 other countries had participated in debt-for-nature swaps, with Costa Rica, Ecuador, Madagascar, and the Philippines having accounted for 95 percent of the funds expended (Miller, 2004). Colombia is one of the five most biologically abundant nations on Earth, harboring 1 of every 10 species of animals and plants. Safeguarding this rich environment was the driving force behind a 2004 debt-for-nature swap involving the United States, Colombia, and three conservation groups—Conservation International, WWF, and TNC. The United States contributed $7 million in support of the Colombia swap, while Conservation International's Global Conservation Fund and its partners added another $1.4 million. With additional monies, approximately $10 million will flow into Colombian conservation efforts over the 12 years after 2004. The funds will be primarily directed toward conservation of 4.45 million hectares (11 million acres) of tropical forest and freshwater habitat.

Some countries have been much more successful than others with this program. Costa Rica, for example, has made great strides in protecting its remaining tropical forests and restoring ecologically damaged areas. Guanacaste National Park in Costa Rica is designated an International Biosphere Reserve. Debt-for-nature swaps represent just one way of protecting biodiversity.

Ecotourism

Although problems remain, like human encroachment, overpopulation, and poaching, many countries are recognizing the economic benefits of attracting wildlife tours and expeditions. This is **ecotourism.** The International Ecotourism Society (TIES) defines ecotourism as "responsible travel to natural areas that conserves the environment, sustains the well-being of the local people, and involves interpretation and education." An ecotourist travels in a way that shows respect to nature and does not contribute to its degradation. Ecotourism is a highly consumer-centered activity that uses environmental conservation as a means to further economic growth for the local people so that their quality of life can be improved. With the promotion and regulation of ecotourism, people gain from the creation of jobs, countries see increases in their economies, and wildlife benefits because of the preservation of habitat and the improvement of human awareness.

Bolivia is among the countries with the most biological diversity in the world, with more than 40 percent of the bird species of South America being found within its boundaries. In late 1994, the Bolivian government teamed with private investors to build a program of "ecological tourism" it hoped would bring in $1 billion a year. An important part of the plan involved Noel Kempff Mercado National Park, a huge wilderness park the size of West Virginia, carved out of a remote area on the border with Brazil. The park was designated a United Nations Educational, Scientific and Cultural Organization (UNESCO)

World Heritage site in 2000. It contains more than 600 species of birds—as many as in all of North America. The project was financed by TNC of Arlington, Virginia, and the Parks in Peril program of the US Agency for International Development. The government of Bolivia provided the basic infrastructure needed for tourism, while the private sector supplied the basic services.

Researchers have found that average human population growth rates on the borders of 306 protected areas in 45 countries in Africa and Latin America were nearly double average rural growth, suggesting that protected areas attract, rather than repel, human settlement (Wittemyer et al., 2008). Higher population growth on the edges of protected areas is correlated positively with international donor investment in national conservation programs and an index of park-related funding. Such findings provide insight on the value of protected areas for local people, but also highlight a looming threat to the effectiveness of protected areas and biodiversity conservation—threats like potential increases in water pollution, air pollution, and pesticide usage.

Top ecotourism regions and/or countries in alphabetical order are Alaska, the Amazon rain forest, Antarctica, Blue Mountains of Australia, Borneo, Botswana, Costa Rica, Dominica, Galápagos Islands, Himalayas (Nepal), Iceland, Kenya, Norway, and Palau.

Tourism has become the salvation for mountain gorillas in Rwanda and Congo (former Zaire), and ecotourism has funded the Monteverde Cloud Forest Preserve in Costa Rica. (However, recent internal strife in Rwanda, including a civil war, has created a potentially disastrous problem for continued survival of the gorillas.) Some countries, however, have been lax about monitoring the impact of tourism, and in some cases, unregulated ecotourism has led to habitat destruction. Ecuador, for instance, has tripled the number of tourists permitted to visit the Galápagos Islands, and in Nepal, forests have been devastated to provide firewood and lodging for trekkers.

Giant Panda Reserve

The Wolong Nature Reserve in southwestern China was set aside as the largest protected area designated for conserving endangered giant pandas (see Plate 21). It contains approximately 10 percent of the wild panda population. Following its establishment in 1963, economic activities within the reserve included agriculture, fuelwood collection, timber harvesting, road construction and maintenance, Chinese herbal medicine collection, and tourism. As a result, the reserve became more fragmented and less suitable for giant panda habitation (Liu et al., 2001). The rate of loss of high-quality habitat after the reserve's establishment was much higher than before the reserve was created, and the fragmentation of high-quality habitat became far more severe. Local people in the reserve were the direct driving force behind the destruction of the forest and of panda habitat. A management plan in 2002 aimed to ensure that the "biodiversity, ecosystem and habitat of the giant panda will be effectively protected in the World Heritage site and social and economic development of the human population in the area will be harmonized with the natural environment guidelines for the area and for management of different types of use." The management plan provides a sound framework for site management and conservation. Wolong was placed on the UNESCO Man and Biosphere Reserve Network in 1980. Prior to a devastating earthquake in 2008, Wolong was a major ecotourism site, getting up to 200,000 visitors every year. Long-term distribution and habitat changes of giant pandas in the Wolong Nature Reserve were reported by Bai et al. (2018).

The region, including the Panda Research Center, was largely devastated by the catastrophic May 12, 2008 Sichuan earthquake. Most of the captive pandas survived, although several escaped after their enclosures were damaged. All pandas were temporarily relocated to the Bifengxia Base of the China Panda Protection and Research Center until a new panda center (Shenshuping Panda Center) was built on the Wolong Nature Reserve and put into use on October 30, 2012. It opened to visitors in May 2016. As of 2018, it housed 74 captive pandas. It consists of 59 colony houses and a research center, which is a world leader in propagating the panda species.

Antarctic Marine Reserve

On October 28, 2016, at a meeting of the Commission for the Conservation of Antarctic Marine Living Resources in Hobart, Australia, 24 countries and the EU agreed to establish , in the Ross Sea off Antarctica, the world's largest marine reserve. The deal bans commercial fishing in the 1.55 million km^2 (600,000 mi.^{2}) swath of international waters, but allows research in 28 percent of the preserve. The reserve opened on December 1, 2017, and will exist for at least 35 years. The reserve, which borders a major ice shelf, includes two biologically rich seamounts and is home to an estimated one-half of the world's South Pacific Weddell seals, one-third of Adélie penguins and Atlantic petrels, and one-quarter of emperor penguins.

Review Questions and Topics

1. In your opinion, has the Endangered Species Act been beneficial or detrimental to (a) wildlife species, and (b) landowners? Explain your answer.
2. Do you feel that the provision for a review board and a cabinet-level committee to act as a final decision-making authority for issues regarding certain endangered species will strengthen or weaken the Endangered Species Act? Why?
3. Define ecotourism. How can it benefit the wildlife, the people, and the country?

Supplemental Reading

Bean, M. J., and M. J. Rowland, eds. 1997. *The Evolution of National Wildlife Law*. 3rd ed. Westport, Connecticut: Greenwood Publishing.

Riley, L., and W. Riley. 2005. *Nature's Strongholds: The World's Great Wildlife Reserves*. Princeton, New Jersey: Princeton University Press.

Vertebrate Internet Sites

1. US Fish and Wildlife Service Endangered Species Homepage

   www.fws.gov/endangered

   Species information, laws, policies, grants, habitat conservation, plans, listings, publications, recovery. Publishes the *Endangered Species Bulletin*.

2. The Endangered Species Act

   www.natureserve.org/explorer/statusus.htm

   Listings, status, and definitions.

19 | Wildlife in a Modern World

Threats and Conservation

A nation that destroys its soils destroys itself. Forests are the lungs of our land, purifying the air and giving fresh strength to our people.

Franklin Roosevelt, 1937

INTRODUCTION

Vertebrates, which have been a part of the Earth's fauna for more than 500 million years, have evolved into many different groups that have successfully adapted to virtually every habitat. They can swim, crawl, walk, run, climb, glide, and fly. Insects (phylum Arthropoda: class Insecta) are the only other group in the Animal Kingdom whose evolution surpasses that of the vertebrates in terms of global distribution and adaptation to such a wide variety of habitats.

Humans are vertebrates and represent one of the most recent products in the evolution of placental mammals. Although the first modern humans—*Homo sapiens sapiens* (as "Cro-Magnon" man)—appeared only about 165,000 years ago in Africa, the impact that our species has made has been greater than that of any other species in the history of the Earth. Not only have humans had a direct impact on many other species (extirpation, extinction, propagation, and dispersal), but indirect actions by humans may ultimately threaten the continued existence of vertebrates and even life as we know it. Activities that threaten biodiversity, like population growth, destruction of the rain forests, damaging of the ozone layer, climate change, production of acid rain, and pollution of waterways, are major global concerns. Humanity ultimately may determine whether *Homo sapiens* and all other organisms on Earth will continue to survive. The fate of 500 million years of vertebrate evolution seemingly rests in the hands of one species.

HUMAN POPULATION GROWTH

Earth's capacity to support humans is determined both by natural constraints and by human choices concerning economics, environment, and culture. Human choice is not governed by ecological factors like those that affect the carrying capacity of nonhuman populations; therefore, human carrying capacity is more dynamic and uncertain. The expanding human population requires increasing amounts of space, food, and resources—all to the detriment of other vertebrate species. Thus, emphasis must be placed on controlling human population growth. According to the United Nations and the US Census Bureau, the December 2018 world population was 7.2 billion individuals with approximately 5.23 billion in developing countries and 1.5 billion in developed nations (Fig. 19.1). As of 2018, the world's overall growth rate was approximately 83 million annually, or 1.09 percent per year, with the population of less developed regions growing at an average of 1.9 percent per year, and that of more developed regions growing at 0.3 to 0.4 percent per year. This growth equals approximately 414,085 live births per day or 17,254 live births per hour. There is an average of 162,545 deaths per day. The world population was projected to increase by 92,157,695 people in 2018, which was an increase of 252,487 persons daily. The United Nations predicts that the human population will reach 8.6 billion by mid-2030, 9.8 billion by mid-2050, and 10.9 billion by 2100.

Global population growth is predicted to stop—or even decrease—by 2100, according to the United Nations. The biggest cause: declining birth rates across both developed and developing nations. Currently, the global fertility rate is about 2.5 births per woman—well above the 2.1 births necessary to maintain the existing population. By 2100, that number is expected to drop to 1.9. Fewer births mean the world's population is steadily getting older, putting increased pressure on health care, pension, and social welfare systems.

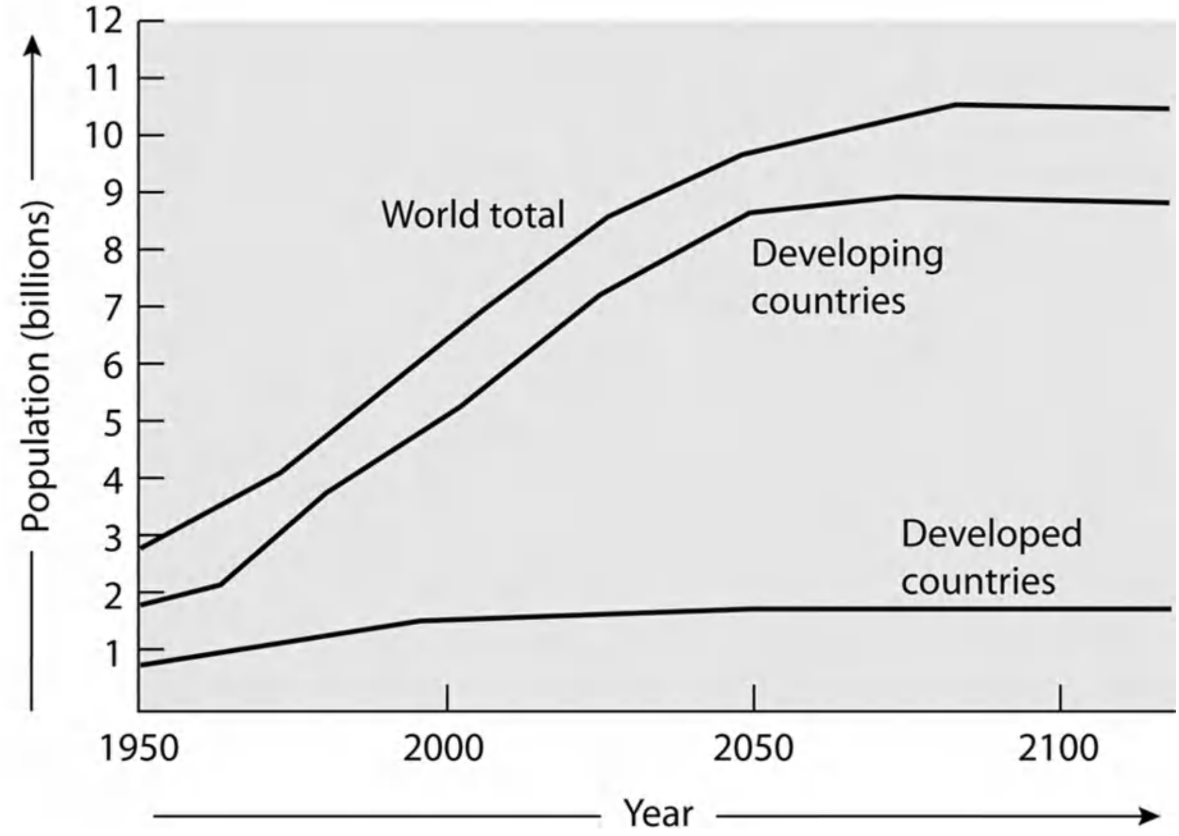


Figure 19.1. The United Nations broadly classifies the world's countries as "developing" or "developed." Developed countries are highly industrialized and usually have a high gross national product (GNP) per capita, whereas developing countries have low to moderate industrialization and GNPs per capita. Past and projected population sizes for developed countries, developing countries, and the world for the period 1950–2120 are shown.

The Top 10 Countries with the Greatest Populations (2019)

Below are the top ten countries in the world by population (with percentage of world population noted).

China: 1,418,000,000 (18.4%)

India: 1,362,000,000 (17.7%)

United States: 328,000,000 (4.3%)

Indonesia: 269,000,000 (3.5%)

Brazil: 212,000,000 (2.8%)

Pakistan: 203,000,000 (2.7%)

Nigeria: 199,000,000 (2.6%)

Bangladesh: 168,000,000 (2.2%)

Russia: 144,000,000 (1.9%)

Mexico: 132,000,000 (1.4%)

https://www.census.gov/popclock

It is estimated that a total of approximately 106 billion people have been born since the dawn of the human species, making the population currently alive roughly 6 percent of all people who have ever lived on planet Earth.

Asia accounts for approximately 59 percent of the world population, with almost 4.5 billion people. China and India together have about 36 percent of the world population. Africa follows with approximately 17 percent of the world's population (1.3 billion people). Europe's 743 million people make up 9.6 percent of the world's population. North America is home to 366 million (4.8 percent), Latin America and the Caribbean to 658 million (8.5 percent), and Oceania to 42 million (0.5 percent).

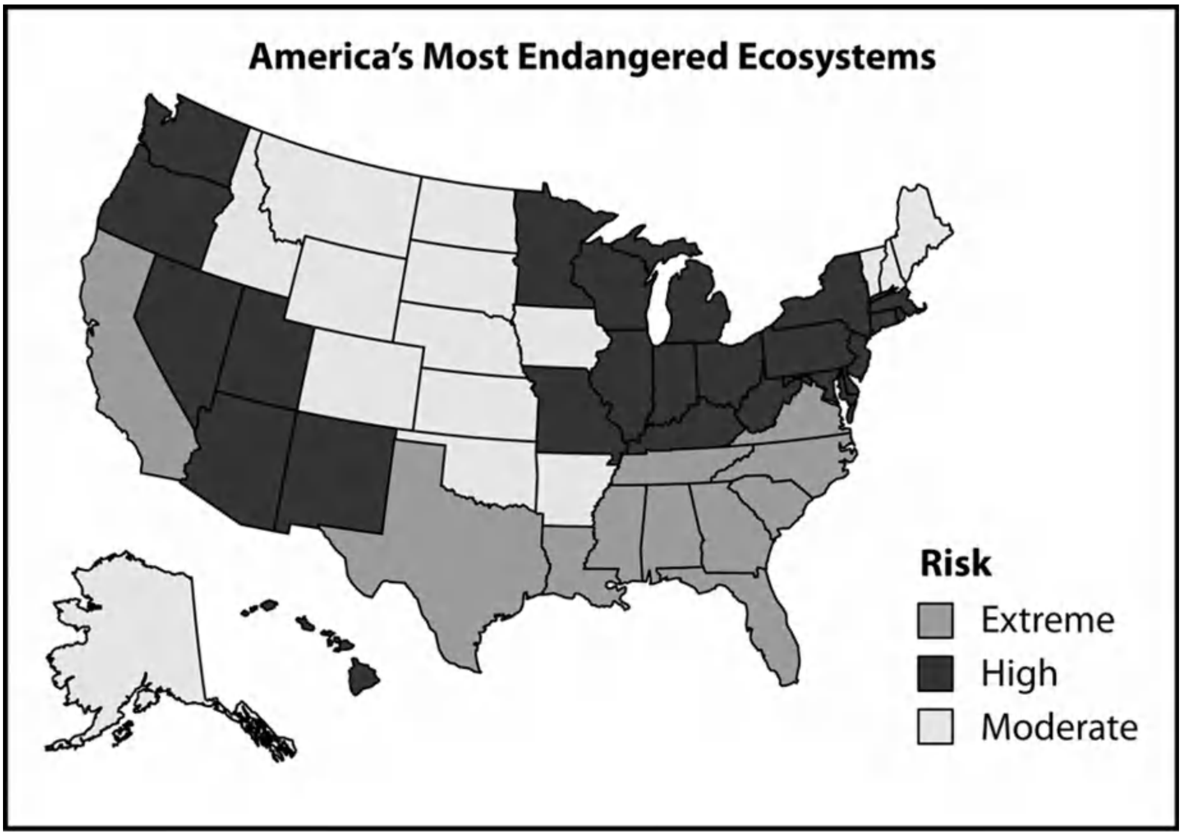


Figure 19.2. The Defenders of Wildlife, a national conservation organization, assessed the health of ecosystems state by state in 1995. They factored in the number of endangered ecosystems, numbers of endangered species, and the rates at which both are losing ground. Florida was the hands-down leader. Despite conservation efforts, advances are being overwhelmed by rapid population growth and development. The Southeast, from its longleaf pine forests to its coastal wetlands, is in particular jeopardy.

If human population growth can be brought under control, many of the problems facing other species of vertebrates would resolve themselves. Unilateral efforts by only a few countries, no matter how well intentioned, will not be sufficient to preserve Earth's vital habitats and species. The coordinated efforts of most, if not all, countries will be required to sustain life as we know it.

BIODIVERSITY

Biodiversity is the total of all plants, animals, and micro-organisms in the biosphere or in a specified area. The year 2010 was the International Year of Biodiversity with the world's nations attending October's Convention on Biological Diversity meetings in Nagoya, Japan. The planet's biological storehouse is so unexplored that researchers cannot even say for sure how many species exist: the total could be 10 million or as many as 100 million. Yet global biodiversity continues to decrease, primarily because of the loss of habitat.

Emphasis must be placed on biodiversity and on preserving and/or restoring entire ecosystems (Fig. 19.2). A major goal must be to educate people about the meaning of biodiversity. In a recent poll, more than 75 percent of the respondents did not know what the term *biodiversity* meant.

The first attempt to build a comprehensive method to assess the cost of human activity borne by nature was published in 2002 (Wackernagel et al., 2002). It is part of a body of work that attempts to calculate the cost to the environment of human activities. The reason the world is only now waking up to the real cost of the degradation of the Earth's wildlife and resources—commonly referred to as biodiversity loss—is because, before now, no one has had to pay for it. Drivers for biodiversity loss include land-use change (e.g., cutting down forests that provide essential water regulation, flood protection, and carbon storage to make way for agriculture), overexploitation (e.g., overfishing or intensive farming that leads to soil degradation), invasive species (e.g., the introduction of nonindigenous species that crowd out endemic species), and climate change (e.g., rising temperatures that cause more extreme weather conditions). Businesses and individuals have largely operated on the basis that the natural resources and services that the planet provides are infinite. But, of course, they are not. And only when the value of protecting them, and in some cases replacing them, is made evident does their vital role in the global economy become clear. The impact of biodiversity loss is felt hardest by the world's poor. Biodiversity is valuable for everyone, but it is an absolute necessity for the poor.

Humans now consume more of the Earth's natural resources than the planet can replace, raising doubts about the long-range sustainability of modern economies. For the last several decades, people have been depleting natural resources, including fish, forests, and arable land, at a rapid rate. Humans are no longer living off nature's interest; instead, we are living off nature's capital. In estimating the "ecological footprint" of humanity, Wackernagel et al. (2002) looked at six activities over the past 40 years and calculated how much land and biological production was devoted to those activities and how much is needed to sustain them. The researchers looked at growing crops for food and other products; grazing animals for meat, milk, and wool; logging; fishing; providing space and materials for houses, highways, dams, and industries; and fossil-fuel burning. According to their analysis, human demand has been outstripping nature's ability to resupply since the early 1980s. Since 1961, the human demand on resources has nearly doubled and today exceeds the Earth's replacement capacity by 20 percent. Critics note that technological breakthroughs and better land-use practices can make farms, factories, and power plants, among others, more efficient. In addition, the study does not factor in the large holdings of natural resources effectively kept in reserve.

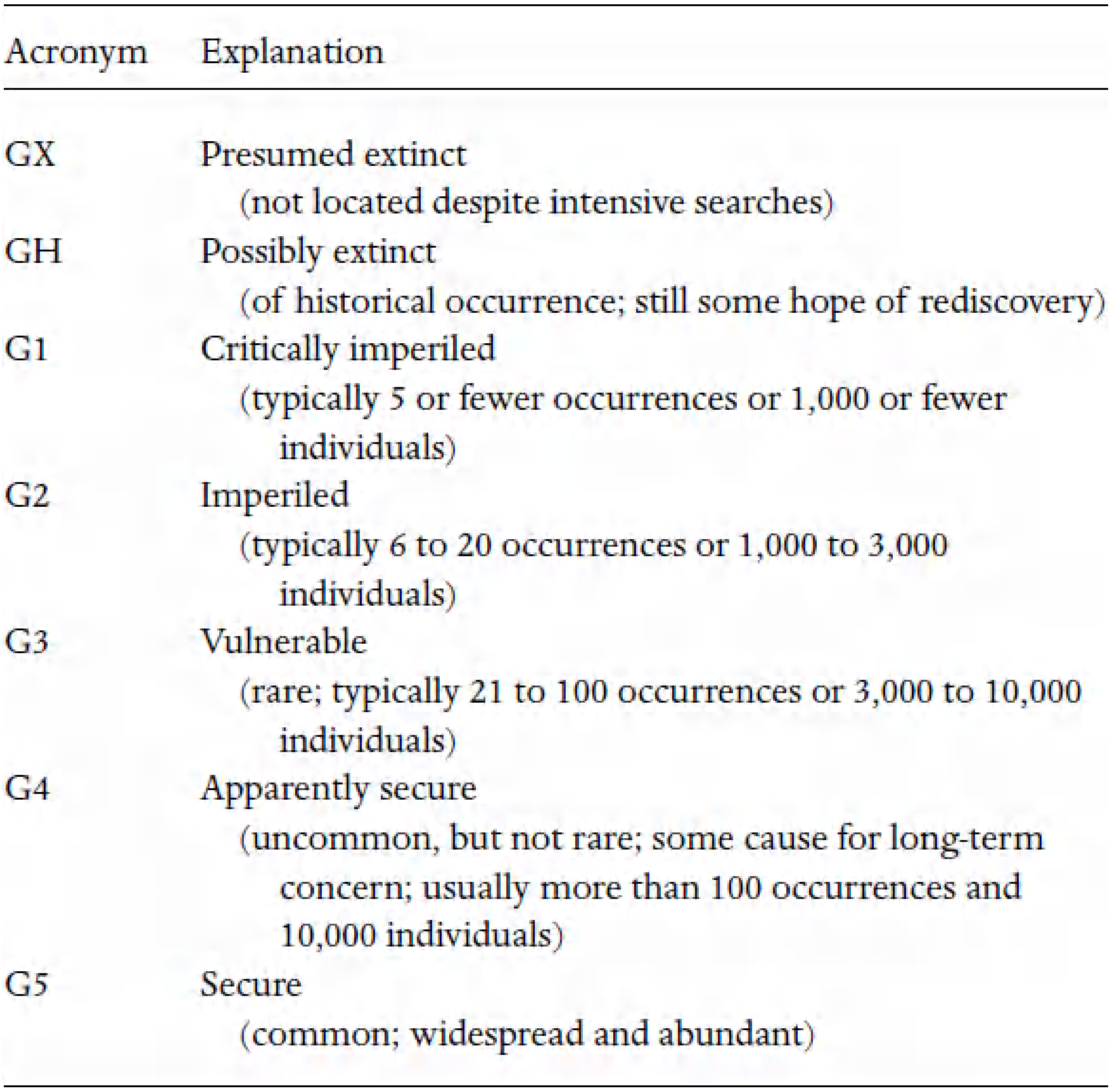
Worldwatch Institute's annual *State of the World* (Flavin, 1997) reported that five years after the 1992 Earth Summit in Rio de Janeiro, millions of acres of tropical and deciduous forest were still disappearing every year, carbon dioxide emissions were at record highs, and population growth was outpacing food production. The report noted that governments lagged badly in meeting goals set at the Rio summit: "Unfortunately, few governments have even begun the policy changes that will be needed to put the world on an environmentally sustainable path," the report declared. On the positive side, the report found hope in increasing numbers of grassroots groups, particularly in Bangladesh and India, and in the fact that more than 1,500 cities in 51 countries had adopted local plans and rules—often more stringent than their national governments proposed at Rio de Janeiro.

Three years in the making, a $2.4 million assessment of Earth's biodiversity and ecosystems (Global Assessment Report on Biodiversity and Ecosystem Services) was published by the United Nations Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Systems on May 6, 2019. The report found that, due to human impact on the environment in the past half century, the Earth's biodiversity has suffered a catastrophic decline unprecedented in human history. An estimated 82 percent of wild mammal biomass has been lost, while 40 percent of amphibians, almost a third of reef-building corals, more than a third of marine mammals, and 10 percent of all insects are threatened with extinction. Experts from 50 nations participated in a review of scientific literature and government data. The report, the first since a similar effort in 2005, forecasts the future of species on the planet under business-as-usual and other scenarios. A new assessment, due in 2020, is intended to inform the next generation of biodiversity targets.

The Community Environmental Legal Defense Fund (CELDF) is a nonprofit, public-interest law firm, spearheading a movement to establish rights for humankind and nature over the systems that control them (www.celdf.org). Since 1995, CELDF has assisted hundreds of communities to advance rights to a healthy environment, a right to climate, and other issues. Over 200 communities have now adopted CELDF-drafted laws that stop shale gas drilling and fracking, factory farming, corporate water withdrawals, land application of sewage sludge, and other harms. CELDF's International Center for the Rights of Nature is working in the United States, Nepal, India, and other countries, partnering with civil society, communities, indigenous peoples, and governments to recognize legally enforceable rights of ecosystems. In 2008, CELDF assisted Ecuador to become the first country in the world to enshrine those rights in its national constitution. In April 2018, the Colombian Supreme Court declared that the "Colombian Amazon is recognized as an entity, a subject of rights," including the right to "legal protection, preservation, maintenance and restoration." This decision builds on the precedent set by Colombia's Constitutional Court in November 2016 when it ruled that the Atrato River possessed legal rights to "protection, conservation, maintenance, and restoration" (Community Environmental Legal Defense Fund, 2018). Countries such as India have recognized that rights of nature exist for rivers and other ecosystems. In 2016, CELDF assisted the Ho-Chunk Nation, based in Wisconsin, to advance the first rights of nature tribal constitutional amendment.

The National Heritage Network of The Nature Conservancy has developed a consistent method for evaluating the health and condition of species and ecological communities. Using this method, it is possible to rank their conservation status. Conservation status ranks are based on a scale from 1 to 5, ranging from critically imperiled (G1) to demonstrably secure (G5) (see Table 19.1 for more details). Species known to be extinct (or missing and possibly extinct) are also recorded. In general, species classified as vulnerable (G3 or rarer) may be considered to be at risk.

Table 19.1. Definition of Conservation Status Ranks



Acronym	Explanation
GX	Presumed extinct (not located despite intensive searches)
GH	Possibly extinct (of historical occurrence; still some hope of rediscovery)
G1	Critically imperiled (typically 5 or fewer occurrences or 1,000 or fewer individuals)
G2	Imperiled (typically 6 to 20 occurrences or 1,000 to 3,000 individuals)
G3	Vulnerable (rare; typically 21 to 100 occurrences or 3,000 to 10,000 individuals)
G4	Apparently secure (uncommon, but not rare; some cause for long-term concern; usually more than 100 occurrences and 10,000 individuals)
G5	Secure (common; widespread and abundant)

Source: From Stein and Flack, 1997b. Reprinted with permission.

Note: “G” refers to the global or range-wide status of a species. Both national (N) and state (S) status ranks are also assessed.

The year 2010 was supposed to be a milestone. A United Nations Convention on Biological Diversity was attended by 193 nations in 1992. Article 1 of the Objectives stated: “The objectives of this Convention, to be pursued in accordance with its relevant provisions, are the conservation of biological diversity, the sustainable use of its components and the fair and equitable sharing of the benefits arising out of the utilization of genetic resources, including by appropriate access to genetic resources and by appropriate transfer of relevant technologies, taking into account all rights over those resources and to technologies, and by appropriate funding.” They adopted a treaty in which they agreed to “achieve by 2010 a significant reduction of the current rate of biodiversity loss at the global, regional and national level as a contribution to poverty alleviation and to the benefit of all life on Earth” (Milius, 2010b). The Convention met in 2010 in China to review progress during the past decade and agreed on a new set of targets and a revised indicator framework (2011–2020 Strategic Plan). Although most of the original targets were not achieved, conservationists and trend watchers noted a few bright spots among worsening losses. Policy has achieved little for biodiversity, but scientists have fared better in coming to understand just what biodiversity means for the fundamental workings of an ecosystem.

A celebration of 25 years of the Biodiversity Convention was held on May 23, 2018, in Montreal. A total of 196 parties have now ratified the agreement. Almost all parties have created National Biodiversity Strategies and Action Plans that are the focus of national efforts to implement the Convention. Significant areas of the world are now being conserved as part of protected areas. Improvements have been made in governance models and sustainable use approaches to manage key natural resources. It was noted at the Convention that the value of biodiversity for society—our social and economic needs as well as our own health and well-being—are now widely recognized. A post-2020 global biodiversity framework is being developed and discussed at the next United Nations Biodiversity Conference in Egypt in late 2018.

Fish

Logging removes trees from forests adjoining streams, increasing stream temperatures and covering fish spawning beds in eroded dirt. Cattle, if not fenced out of streams, can accelerate erosion and stir up sediments.

The construction of dams and the straightening and channelization of rivers have destroyed habitats for many fish species. Today about 800,000 dams operate worldwide, 45,000 of which are large, that is, greater than 15 m (50 ft.) tall. Most were built in the past century, primarily after World War II. The United States, with some 74,000 dams (most of which are relatively small), has perhaps the most active dam-removal movement. In many states, dam removals are becoming increasingly popular. Dams do not live forever. Many no longer serve any purpose. Decommissioning dams (particularly small ones) is becoming a regular occurrence as structures age, provide an inconsequential share of a region’s power, become unsafe or too costly to repair, or as communities decide that they want their rivers wild and full of fish again. Some are the remnants of mills that rotted away decades ago or canals long since overgrown by trees and weeds. For example, in February 2004, the US Corps of Engineers, working with the City of Fredericksburg, Virginia, blasted away a 40 m (130 ft.) section of a dam on the Rappahannock River so that fish can now migrate to spawning grounds nearly 160 km (100 mi.) upriver in the foothills of the Blue Ridge Mountains. The dam, built in 1910, was last used for hydroelectric power generation in the 1960s. Thus, the river had been closed to fish migration for nearly 150 years. The demolition of the dam was completed in 2006 and opened up 114 km (71 mi.) for fish spawning in the Rappahannock River, 56 km (35 mi.) on the Rapidan River, and as much as 1,448 km (900 mi.) on smaller tributaries. It was a major contribution toward the Chesapeake 2000 agreement goal of opening 2,184 km (1,357 mi.) of new fish passages. More than 1,931 km (1,200 mi.) of streams were opened between 2011 and 2017 in Maryland, Pennsylvania, and Virginia—a nearly 50 percent increase in the number of stream miles opened to fish migration in the preceding 22 years, according to the Chesapeake Bay program. Between 2013 and 2018, 12 dams were removed in Rhode Island, Connecticut, New Jersey, and Massachusetts, helping restore fishes such as American shad, river herring, and alewives in six rivers.

The 31 m (102 ft.) high Elwha Dam and 70 m (230 ft.) high Glines Canyon Dam, both on the Elwha River and now within the borders of Olympic National Park, were built in the 1910s and 1920s and all but wiped out the river’s once-rich runs of steelhead trout and salmon, fisheries to which the Elwha S’Klallam tribe had been guaranteed rights “in perpetuity.” These two large dams were demolished in 2012 (Elwha) and 2014 (Glines Canyon) as part of the Elwha River Ecosystem Restoration Project. The restored, free-flowing river is expected to sustain as many as 400,000 salmon and steelhead within 30 years. As of 2015, the Glines Canyon Dam was the tallest dam ever to be intentionally breached. The largest dam-removal project in US history is set to begin in 2020 on the Klamath River in Northern California and southern Oregon. Following site work in 2020, deconstruction of the four dams—J. C. Boyle, Copco No. 1, Copco No.2 and Iron Gate—will begin in 2021 (Arthur, 2018).

Criteria from the International Union for Conservation of Nature (IUCN) have been used to classify marine fish species as endangered since 1996, but deepsea fish have not so far been evaluated—despite their vulnerability to aggressive deepwater fishing. Deepsea fish are highly vulnerable to disturbance because of their late maturation, extreme longevity, low fecundity, and slow growth. At one time it was presumed, from the vastness of the oceans, that fishing would not drive species to extinction. There have, however, been recent sharp declines in the numbers of oceanic cod, sharks, rays, tuna, marlin, and swordfish.

Commercial fishing has wiped out 90 percent of the world's populations of large fish. This is the conclusion of a 10-year study using industry data from over five decades to look at fisheries from the North Atlantic to the Antarctic Ocean (Myers and Worm, 2003). Popular species in danger include tuna, cod, swordfish, marlin, halibut, skate, flounder, and shark. And scientists fear that the damage may be beyond repair. Excessive fishing already may have reduced some fisheries to unrecoverable levels. At present rates of fishing, some species will disappear from supermarket shelves and some sharks, like the hammerhead, may become extinct. Scientists suggest that international efforts to manage coastal and deep-ocean fisheries have not kept up with advances in commercial fishing and oversized fishing fleets.

Sea Turtles

Populations of sea turtles continue to decrease. Large numbers of adults of some species, like the green sea turtle (*Chelonia mydas*), are killed illegally every year and are served as a delicacy. It has been estimated that as many as 30,000 green turtles are killed every year just in Baja California, even though killing them has been strictly prohibited by the US Endangered Species Act since 1978 and by Mexican law since 1990. In addition, massive efforts are undertaken in many countries to protect nesting beaches from poachers and predators.

Birds

More than one in four US bird species is declining in numbers or is at risk of disappearing. In 2002, the National Audubon Society estimated that 201 species of birds in the continental United States, Hawaii, and Alaska were menaced by habitat destruction, pollution, diseases, and other threats. Among the most imperiled was the short-eared owl, which had seen a nearly 70 percent population decline since the 1960s because of grassland destruction and the ingestion of poisoned rats and mice. The cerulean warbler (*Dendroica cerulea*), a deep-blue bird once found throughout the Ohio and Mississippi River valleys, had suffered more than a 70 percent decline, and it is unknown how many are left. Habitat destruction combined with an extremely low reproductive rate (one egg every other year) were key factors in the almost complete loss of California condors (*Gymnogyps californianus*) (see additional discussion in Chapter 17).

The overall health of bird populations, worrisome on its own, should be taken as a broader indication of the health of the country's ecosystem. Birds warn us about disease, as well as about the quality of the coasts, oceans, and forests.

Over the past 500 years, people have killed, crowded out, or otherwise made normal life impossible for close to 500 bird species worldwide (Pimm et al., 2006). During the twenty-first century, 10 species a year—of about 10,000 known worldwide—are likely to meet the same fate. While none of this spells the end of life on Earth, it is one more clue to the rate at which expanding human populations threaten wildlife. This report came not long after a United Nations report warned against a coming wave of plant and animal extinctions unmatched since dinosaurs were wiped out 65 Mya.

Birds at Risk

A major study by the International Union for Conservation of Nature (IUCN) and BirdLife International indicates that 1,107 bird species, approximately 11 percent of the world's total, are at risk of dying out. They list 168 bird species that are critically endangered—meaning they face an extremely high risk of extinction in the wild in the immediate future. Like other animal groups, birds are most threatened in island habitats. Of the 104 bird species that became extinct in the past 400 years, approximately 90 percent lived on islands. Island species often are found nowhere else on Earth and therefore cannot be replenished from outside. They have few defenses against introduced predators, and they are vulnerable to introduced diseases. Hawaii, at 33 percent, currently has the highest proportion of threatened bird species. Significant threats to bird life also exist in continental areas due to such factors as population pressure, exploitation of tropical forests, and habitat destruction in nesting areas. Continental species with small ranges are most vulnerable.

Doyle, 1997; Manne et al., 1999

In 2007, the National Audubon Society issued a report stating that the populations of 20 common American birds—northern bobwhite, evening grosbeak, northern pintail, greater scaup, boreal chickadee, eastern meadowlark, common tern, loggerhead shrike, field sparrow, grasshopper sparrow, and others—had seen their populations drop by at least half over 40 years (1967–2007). The bobwhite had the biggest drop (82 percent) with the evening grosbeak (78 percent), chickadee (73 percent), and meadowlark (72 percent) not far behind. Many of these species depend on open grassy habitats that are disappearing. Suburban sprawl, climate change, and other invasive species are largely to blame.

While many common birds are in decline, others are taking their place. The wild turkey is growing at a rate of 14 percent a year. The double-crested cormorant is growing at a rate of 8 percent a year, and populations of the Canada goose increase by 7 percent yearly. Many of the birds that are disappearing are specialists, while the thriving ones are generalists that do well in urban sprawl and all kinds of environments. Robins, Carolina wrens, blue jays, and crows are doing fine. These species thrive in suburban habitats; most of them even like city parks, so they are not as susceptible to the human changes in environment.

The North American Breeding Bird Survey (BBS), launched in 1966, is designed to provide a continent-wide perspective of population change. Data from the survey, an important source for the range maps found in field guides, are valuable in evaluating the increasing and decreasing range of bird populations, which can be a key point to bird conservation. As of 2017, the BBS counted approximately 3,700 active routes in the United States and Canada. A summary of results and analysis from 1966 through 2015 can be found in Sauer et al. (2017).

Deforestation of tropical wintering habitats and drought are the biggest threats to the breeding birds of North America. Robbins et al. (1989) analyzed data from the BBS and reported that, although populations of neotropical migrants throughout eastern North America were stable or increasing before 1978, there has been a general decline since then that has not been paralleled in residents or short-distance migrants. Chiefly, those species that winter in tropical forests have been affected. In addition, many migratory species winter in countries that continue to use dichlorodiphenyltrichloroethane (DDT) and other biologically harmful pesticides. La Sorte et al. (2017) stated that, within 40 years, migratory songbirds will face greater danger where they overwinter in Central America than where they nest.

Cocaine trafficking is destroying Central America’s forests (Sesnie et al. 2017). Cocaine trafficking accounts for between 15 percent and 30 percent of annual forest loss in Honduras, Guatemala, and Nicaragua.

Traffickers in the region had to figure out a way to funnel their money into the legal economy, and land clearing—in the form of cattle ranching, agro-industrial plantations, and timber extraction—is the preferred way to do it.

The populations of long-distance, migrating songbirds have declined in recent years. The excessive fragmentation of forests that has occurred throughout the United States and elsewhere results in the loss of nesting sites and food and also increases the exposure of bird nests to predators like raccoons, cats, opossums, blue jays, and parasitic birds like the brown-headed cowbird (Wilcove, 1985; Terborgh, 1992; Robinson and Wilcove, 1994). Predation is especially intense in woodlots near suburban neighborhoods compared to woodlots in isolated rural areas. Ivory-billed woodpeckers (*Campephilus principalis*), red-cockaded woodpeckers (*Picoides borealis*), Kirtland's warblers (*Dendroica kirtlandii*), Bachman's warblers (*Vermivora bachmanii*), and spotted owls (*Strix occidentalis*) are examples of species whose habitats have almost disappeared. Hopes that the ivory-billed woodpecker (Fig. 19.3) had survived in flooded lowlands of Arkansas's Big Woods rose in 2005 when a Cornell University-led team released sound recordings and a blurry four-second video as corroboration of their reported ivory-billed sightings (Fitzpatrick et al., 2005). Other bird experts have disputed the evidence, claiming the image is that of a pileated woodpecker. Other researchers claim to have found this species in the swamplands of the Choctawhatchee River in the Florida Panhandle.

Figure 19.3. Young ivory-billed woodpecker taken from the nest by Dr. James Tanner for banding in the late 1930s.

The Fifth Waterbird Population Estimates (Wetlands International, 2012) found that, of all populations for which trend information was available, 38 percent were declining, 20 percent were increasing, 39 percent were stable, and 3 percent were fluctuating. In 2007, the populations of 44 percent of the 900 global species had fallen in the previous five years, 17 percent were rising, and 34 percent were stable. In 2012, 41 percent of waterbird populations worldwide were found to be decreasing. Most declining populations in the 2012 survey could be found in the Neotropics (59 percent), followed by a 50 percent decline in Asia, 38 percent decline in Oceania, 36 percent in Africa, 32 percent in Europe, and 33 percent in North America.

The US Fish and Wildlife Service (USFWS) report on 2018 Trends in Duck Breeding Populations (US Fish and Wildlife Service, 2018a) showed that overall duck numbers in the survey area remained high. Total populations were estimated at 41.2 million breeding ducks in the traditional survey area, 13 percent lower than last year's estimate of 47.3 million and 17 percent above the long-term average.

Coffee beans were traditionally grown in shade under a canopy of trees that protected the plants and offered sanctuary for more than 150 species of migratory birds. For many years, however, agriculture experts encouraged large coffee plantations in Latin America to grow more beans at a faster pace by cutting down trees shading the coffee trees and growing high-yield, sun-tolerant hybrid trees that need high doses of pesticides and chemical fertilizers. As the canopy trees disappeared, so did the birds—in some cases by as much as 97 percent. In 1996, the Smithsonian Institution, National Audubon Society, Rainforest Alliance, and other conservation groups began encouraging farmers to cultivate shade-grown coffee, which they hoped would save the tall trees where US and Canadian migratory birds seek refuge from the cold. Shade trees yield benefits not only for migratory birds (increased numbers and species of birds and corridors for migrating birds to make their way through dwindling forests), but also for the farmer and the consumer. For example, shade-tree fruit, like walnuts, palm fruits, oranges, bananas, lemons, and avocados, together with other products grown beneath the trees, can provide farmers with additional food and supplemental income. The trees also provide firewood, soil protection/erosion control, carbon sequestration, natural pest control, and improved pollination. For the consumer, a slower-ripening red coffee fruit, known as a cherry, retains more natural sugars and results in better-tasting coffee. Several

US companies have developed coffee brands that are certified as shade-grown by independent monitors. By reviewing more than 50 studies on shade-grown coffee farms in regions ranging from Central and South America to Indonesia over 15 years, the Smithsonian Migratory Bird Center concluded that shade-grown coffee is the next best thing to a natural forest (Rice, 2010).

Climate change is projected to drive hundreds of bird species to extinction and greatly reduce the ranges of others (see Chapter 20). As climate change makes the seasons less predictable, birds are struggling to time their migrations with the greenery. Mayor et al. (2017) confirmed a growing disconnect between birds' internal clocks and the changing seasons. Although birds adjusted their arrival dates, 9 of 48 songbird species did not keep pace with rapidly changing green-up, and across all species the interval between arrival and green-up increased by over half a day per year. Changing climate alters avian food resources that drive fitness. To maximize fitness, birds must time their breeding phenology (including arrival on breeding grounds, breeding, egg-laying, and fledging) to coincide with optimal habitat conditions and food availability. This means there is evolutionary incentive to correctly anticipate breeding conditions while birds are still at their winter grounds, often thousands of kilometers away.

THREATS TO WILDLIFE

Habitat Fragmentation

For a species to survive, its habitat must provide all of its needs. When a habitat is divided or decreased in size, a process known as **fragmentation**, it may no longer be large enough to meet the needs of all the species that formerly occupied it. Fragmentation is generally a consequence of land use: agricultural activities, road building, suburban housing developments, and shopping centers all break up existing habitat (forests, fields, wetlands, etc.). Mitigation efforts attempt to replace destroyed habitat, but many of these are only partially successful.

When a habitat faces fragmentation, it triggers an edge effect in the resulting smaller and isolated fragments. The edges of these fragments become less suitable for some or many of the species and organisms. The edges of a habitat are usually the least populated areas, and when that habitat divides into many fragments, they become challenging and competitive areas for their inhabitants. Even moderate habitat destruction can cause time-delayed, but predictable, extirpation of the dominant species in the remaining patches (Tilman et al., 1994). As habitat continues to be destroyed, additional species may be extirpated, especially territorial species.

One example of the negative effects of habitat fragmentation is that fragmented landscapes disrupt ecological checks and balances that limit interaction between vertebrates and ticks. And the life cycle of ticks takes advantage of wildlife species that thrive in edges. Shrews and plentiful rodents like white-footed mice—many already infected by the Lyme bacteria or another pathogen—are often the first blood meal for tick larvae after they hatch in summer. When the larvae molt into nymphs in their second spring, they are already host to the pathogen and may pass it on as they feed on larger animals, including humans. More deer and rodents increase the number of ticks possible. Habitat that is good for rodents such as mice, along with overabundant deer, is a recipe for lots of ticks.

Turtles are an example of a species greatly affected by habitat fragmentation. Even without road mortality, many turtle populations are declining as habitat is fragmented or destroyed. Some of these are now known as “ghost populations,” made up of old turtles just hanging on with little or no recruitment. With consistent losses, they will reach a breaking point and crash. In addition to alerting drivers with “turtle crossing” signs, some localities are designing safe passages to steer turtles away from danger. A 2012 fencing project in Massachusetts that kept turtles off a heavily trafficked road reduced mortality there by 90 percent. Tunnels and culverts beneath roadways are employed in some areas.

Traveling through one fragment to another becomes dangerous for many species, as it involves having to cross roads, rail tracks, and even fences. Because some extirpations may occur generations after fragmentation, they represent a debt—a future ecological cost of current habitat destruction. The ecological consequences of habitat fragmentation were discussed by Didham (2010). Recent research suggests that indirect and interaction effects may be the dominant driver of the ecological changes often attributed to habitat loss alone (Didham et al., 2012).

Habitat loss and fragmentation have long been considered to have negative effects on biodiversity. A recent review by Fahig (2017), however, argues that in fact habitat fragmentation has largely positive effects on biodiversity. His arguments are refuted by Fletcher et al. (2018).

Hanks (1996) noted that biodiversity is related to the size of an area. For example, an area of 10 hectares (25 acres) generally contains twice as many species as an area of 1 hectare (2.5 acres). If an area is reduced to one-tenth of its original size, half of the species in that area will no longer be able to live there. Loss of biodiversity has insidious consequences. Ecosystems with fewer species tend to be less stable in the long term, and in the event of climatic changes, diversity will help determine which ecosystems collapse and which ones flourish. In a long-term study of grasslands, Tilman and Downing (1994) showed that primary productivity in more diverse plant communities was more resistant to, and recovered more fully from, a major drought. Thus, preservation of biodiversity is essential for the maintenance of stable productivity in ecosystems (Naeem et al., 1994; Wilson et al., 2016). Fossil evidence suggests that ponderosa pine, now prevalent throughout America’s Rocky Mountain forests, was a marginal species at the end of the last Ice Age. Thus, some of today’s rare and apparently “insignificant” species may be the ones best able to cope with the climate of the next century.

Forests

In terms of water quality, forests are, hectare for hectare where they naturally occur, the most beneficial land use because they help regulate stream flow, control runoff, filter nutrients, and create the stream environment needed by many fish and other aquatic species. In addition, forests improve air quality. One hectare of trees can remove more than 86 metric tons (95 US tons) of carbon dioxide annually, while producing enough oxygen to sustain more than 1,000 people during the year. Woodlands also provide much of the watershed’s habitat for animal and plant life (http://coloradotrees.org/plant).

Global forest loss amounted to 18.7 million hectares (46 million acres) in 2014, a decline of about 9 percent relative to 2013 and 20 percent compared to 2012 (Petersen et al., 2015). The data reflects changes in tree cover, including deforestation, harvesting of tree plantations, fire damage, and forest die-off from disease and pests. This loss is equal to 27 soccer fields every minute, according to the World Wildlife Fund (WWF). Countries topping the 2014 list were Russia, Brazil, Canada, Indonesia, and the United States. Coming in at number six was the Democratic Republic of the Congo, which surpassed a million hectares of forest loss for the only time in the 14-year data set. Annual forest loss in the Central African nation has roughly doubled since the early 2000s. Madagascar—a country that does not have much forest left to lose—lost almost two percent of its total forest cover in 2014. Among the planet's biomes, the tropics accounted for the largest share of loss at 10 million hectares in 2014.

TROPICAL FORESTS

Tropical forests, which grow near the equator in Latin America, Africa, and Asia, cover about 6 percent of the land surface of the Earth. Initially, Earth had 18 million to 23 million km^2 (7–9 million mi.^{2}) of tropical forest, half of which has disappeared in the past 50 years. Three countries—Brazil, Zaire, and Borneo—contain more than half of the world's tropical forests.

About 14 percent of the Amazon's 5 million km^2 (2 million mi.^{2}) is already deforested, and up to 40 percent of the forest suffers from the damaging effects of fragmentation. If current development trends go unabated, it is estimated that the Amazon basin's forest will lose 2.1 million km^2 (811,000 mi.^{2}) of its 5.3 million km^2 (2 million mi.^{2}) by 2050. Currently, about 3 to 4 percent of the Amazon is protected, with plans to protect 10 percent. In 2003, Conservation International and the Brazilian government created the 3.9 million hectare (9.6 million acre) Tumucumaque Mountains National Park, Earth's largest tropical forest park. Scientists estimate that at least 8 primate species, 350 bird species, and 37 lizard species live in Tumucumaque's forests. Among these are several species threatened elsewhere, including the jaguar, giant armadillo, and white-faced saki monkey.

In Borneo, the situation is even more dire. About 80 percent of forest cover has been allocated to commercial logging and industrial plantations.

Some forests receive almost daily rainfall and are known as **tropical rain forests**; others have one or two dry seasons each year and are known as **tropical seasonal deciduous forests**.

Rain forests are the Earth’s oldest living ecosystem, and yet, where once these tropical forests covered 14 percent of the Earth’s surface, they now cover just 6 percent. They are often referred to as the “lungs of the Earth” because they remove vast amounts of carbon dioxide from the atmosphere and add vast quantities of oxygen. The Amazon basin contains the world’s largest rain forest (roughly the size of the continental United States) and covers about 40 percent of South America. Nearly two-thirds of the Amazon rain forest lies within the borders of Brazil. The second largest rain forest is found in Central Africa’s Congo basin. Next is the rain forest of New Guinea (Butler, 2018).

A recent satellite-imagery study of 34 countries that make up 80 percent of forested tropical lands found that, for the period of 1990 to 2000, yearly net forest loss was 4 million hectares (9.9 million acres) per year for all countries in the study. The figures rose for the period covering 2000 to 2010, with 6.5 million hectares (16 million acres) being lost yearly for all countries in the study, an increase of 62 percent (Kim et al., 2015). This is comparable to losing a tract of forest the size of West Virginia or Sri Lanka each year. The countries showing the largest losses due to deforestation were led by Brazil, where 607,000 hectares (1.5 million acres) of rain forest are lost every year. Following in Brazil’s footsteps is tropical Asia with 801,000 hectares (2 million acres) lost in Malaysia, Cambodia, Thailand, and the Philippines. Tropical Africa showed the smallest net loss of tropical forests—with the exception of Democratic Republic of Congo and Madagascar, where a steady increase was shown. An in-depth evaluation of deforestation of the Brazilian Amazon has been presented by Fearnside (2017).

The World Resources Institute reported that 2017 was the second-worst year on record for tropical tree cover loss (Weisse and Goldman, 2018). In total, the tropics experienced 15.8 million hectares (39 million acres) of tree cover loss: an area the size of Bangladesh. That is the equivalent of losing 40 football fields of trees every minute for an entire year.

As fast as the trees go, the chance of slowing or reversing climate change becomes slimmer. Tropical deforestation caused carbon dioxide, the main greenhouse gas, to linger in the atmosphere and trap solar radiation. This raises temperatures and leads to climate change. The consensus of the world’s atmospheric scientists is that about 12 percent of all climate emissions caused by humans—nearly as much as the world’s 1.2 billion vehicles—now comes from deforestation, mostly in tropical areas.

Tropical rain forests have the highest species diversity of any biome. Each hectare may contain from 100 to 300 different tree species, as opposed to generally fewer than 10 species in a hectare of temperate forest.

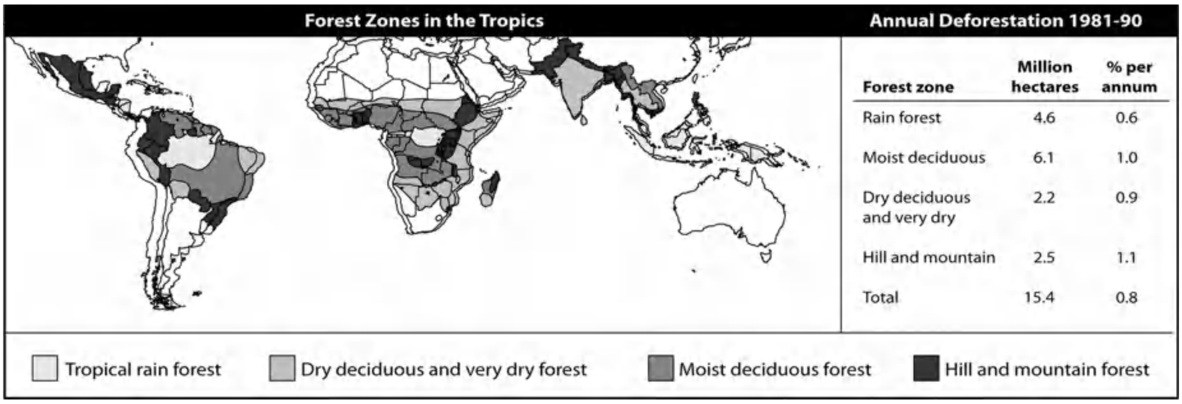
At least half of the world’s species—and perhaps up to 90 percent—inhabit tropical rain forests, which, according to the Food and Agriculture Organization of the United Nations (FAO), are being destroyed at the rate of 7.3 million hectares (18 million acres) a year, either from logging, burning, or other destructive methods. Upwards of 32,000 hectares (80,000 acres) of tropical rain forest are lost daily with another 32,000 hectares (80,000 acres) being significantly degraded every day on top of that. This is equivalent to losing an area the size of the country of Panama every year. Other examples equate the destruction to 34 city blocks per minute or to the area of two football fields each second (Miller, 1995). Along with this loss and degradation, we are losing some 135 plant, animal, and insect species every day—or about 50,000 species a year—as the forests fall.

As the species in rain forests disappear, so do many possible cures for life-threatening diseases. While 25 percent of Western pharmaceuticals are derived from ingredients found in rain forests, scientists have tested less than 1 percent of the tropical trees and plants in rain forests. The US National Cancer Institute has identified 3,000 plants that are active against cancer cells, with 70 percent of these plants being found in the rain forest. Twenty-five percent of the active ingredients in today’s cancer-fighting drugs come from organisms found only in the rain forest (Taylor, 2019).

Landsat satellite imagery covering the entire forested portion of the Brazilian Amazon basin showed an increase in annual deforestation from 78,000 km^2 (30,000 mi.^{2}) in 1978 to 230,000 km^2 (89,000 mi.^{2}) in 1988 (Skole and Tucker, 1993). The FAO estimated that 11.3 million hectares (28 million acres) of tropical forest had been lost each year during the 1970s (FAO, 1982); the destruction jumped by nearly 40 percent in the 1980s, reaching an average of 15.4 million hectares (38 million acres) per year (FAO, 1993); 10.16 million hectares (25 million acres) were lost each year during the 1990–2000 period; and 10.4 million hectares (26 million acres) of tropical forest were permanently destroyed each year in the period from 2000 to 2005 (Food and Agriculture Organization, 2010) (Fig. 19.4). FAO data show that primary forests are being replaced by less biodiverse plantations and secondary forests. South America accounted for the largest absolute losses—6.2 million hectares (15 million acres) a year—which translates to an annual deforestation rate of 0.6 percent, but continental Southeast Asia is losing a staggering 1.6 percent and Central America 1.5 percent a year. A Brazilian-American study is currently under way to determine minimum effective reserve areas for wildlife species (Fig. 19.5).

As population demands have increased in areas containing tropical rain forests, trees have been harvested for lumber and the land used for agriculture. However, converting tropical rain forests to agricultural land is not sustainable because the soils are nutrient-poor, erode easily, and are compacted by heavy machinery. Approximately 95 percent of the nutrients in tropical forests are in the biomass and only 5 percent are in the soil, just the opposite of a temperate forest. Thus, these soils can produce food for only three or four years before becoming unusable. Clear-cutting of tropical rain forests exposes the soil to intense rains that wash it away, filling nearby streams and rivers with sediment.

The Brazilian government plans to repair and pave 3,500 km (2,170 mi.) of roads as part of an economic development program known as “Advance Brazil.” These projects could destroy up to 186,000 km^2 (72,000 $mi.^2$) of rain forest over the next 25 to 30 years. The pending completion of a new highway through the Brazilian Amazon is alarming tropical ecologists, who fear it will open the way to increased habitat destruction as well as illegal hunting and development. The 870 km (540 mi.) road, known as BR319, connects Manaus, Brazil, in central Amazonia to Porto Velho, Brazil, in southern Amazonia. The project has been on the books for almost a decade, but recently work accelerated such that as of January 2018 only the central section remained to be paved. If that occurs, BR319 and a second highway will slice the Amazon in half along a north-south axis.



Forest zone	Million hectares	% per annum
Rain forest	4.6	0.6
Moist deciduous	6.1	1.0
Dry deciduous and very dry	2.2	0.9
Hill and mountain	2.5	1.1
Total	15.4	0.8

Figure 19.4. Annual deforestation in tropical forest zones, 1981–1990. Deforestation reached an average of 15.4 million hectares (38 million acres) per year by 1990. A satellite-based imagery study of 34 countries making up 80 percent of forested tropical lands found a yearly net forest loss of 4 million hectares (9.9 million acres) for the period 1990–2000. The figures rose to 6.5 million hectares (16 million acres) per year for the period 2000–2010, an increase of 62 percent over the previous decade.

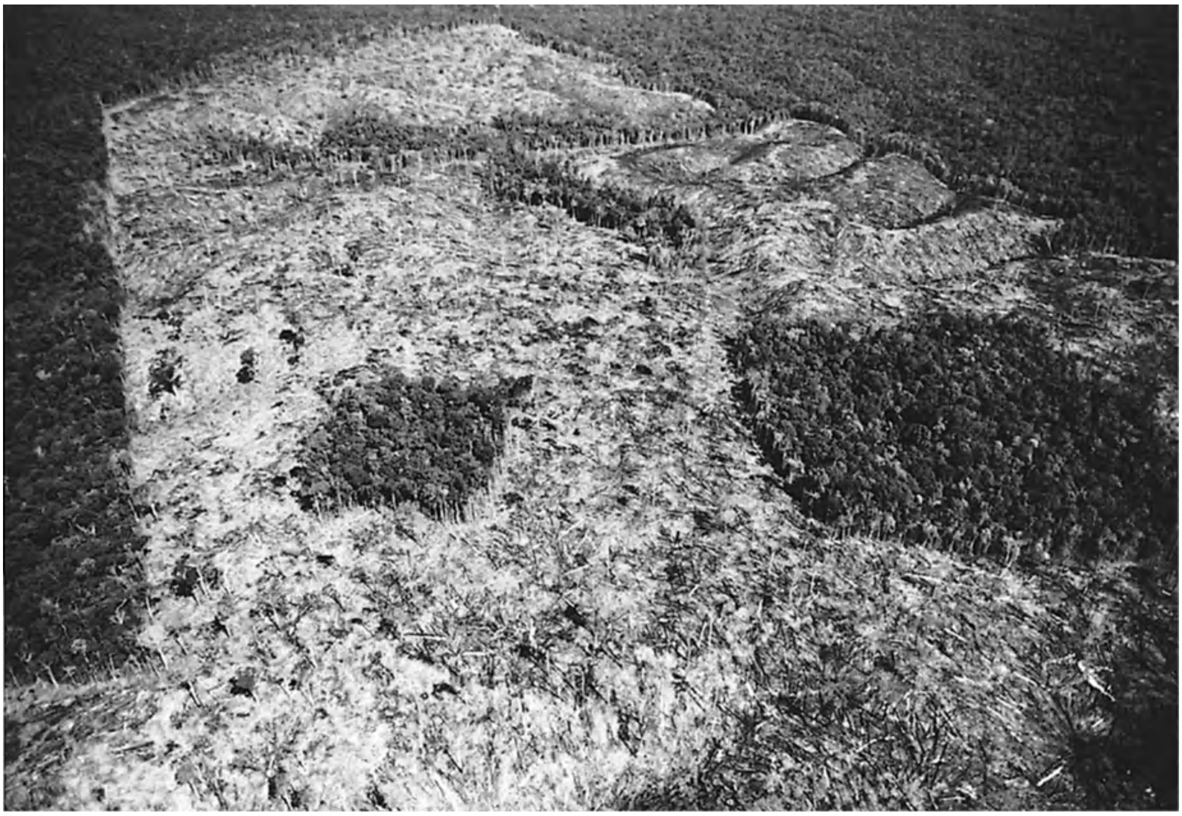


Figure 19.5. A joint Brazilian-American study sponsored by the World Wildlife Fund is attempting to determine the minimum effective reserve sizes for both plants and animals. These plots of 1 hectare (2.5 acres) and 10 hectares (24.7 acres) in Amazonia are surrounded by clear-cut areas. Some plots are linked to virgin forest by corridors.

Deforestation increased sharply in May 2019, with 740 km^2 (286 mi.^{2}) of land newly cleared, according to the Real-Time Deforestation Detection System (DETER), a satellite monitoring program run by the National Institute for Space Research in São José dos Campos. That is 35 percent more than in May 2018 and twice as much as in May 2017. Stricter regulations and monitoring led annual deforestation rates in the Brazilian Amazon to drop by 83 percent between 2004 (when DETER operations began) and 2012, but they trended upward in the following years because of political and economic pressures. Protecting the Amazon has been at the heart of Brazil's environmental policy for much of the past decade. At one point, Brazil's success in slowing the deforestation rate made it an international example of conservation and the effort to fight climate change. However, many scientists fear that Brazilian president Jair Bolsonaro's loosening of environmental policies and enforcement will embolden loggers, farmers, and land developers to encroach further on the forest. (See below for more details about Bolsonaro's potential environmental impact.)

Brazil has established a network of protected areas currently encompassing 1,743 units covering roughly 25 percent of Brazil's territory and protecting 39 percent of the remaining area of native vegetation. The Amazon biome houses the largest extent (49 percent) of the protected areas. Soares-Filho et al. (2010) examined the role of Brazil's protected areas in climate change mitigation, while Oliveira et al. (2017) assessed biodiversity conservation and knowledge gaps in the protected areas. The Brazilian Blue Initiative enables Brazil to manage existing and new coastal and marine protected areas (Maretti, 2018). In 2018, two large mosaics of marine protected areas, approximately 920,000 km^2 (355,000 $mi.^2$) were designated as well as areas including Amazon mangroves and coastal sea areas.

A major factor for environmental protection in Brazil was the election of a far-right president in 2018. President Jair Bolsonaro has vowed to withdraw Brazil from the 2015 Paris Agreement. He planned to eliminate the Ministry of the Environment and fold its duties into the Ministry of Agriculture, Livestock, and Supply, but scrapped the plan under pressure from the nation's agriculture sector, which feared the move would incite a boycott of Brazilian products (Casado and Londono, 2019). He has brushed off international criticism of his positions, arguing that calls to preserve large parts of Brazil are part of a global plot to hamper his country's development. He has stated that Brazil has "too many protected areas" that "stand in the way of development." He has promised to promote more agriculture and mining in the Amazon. One of his policy developers said that he missed the days when road builders could cut down trees in the Amazon without being bothered by environmental authorities (Escobar, 2018). However, at the World Economic Forum in Davos, Switzerland, in January 2019, Bolsonaro promised to stay in the Paris Agreement and stated: "The environment must go hand-in-hand with development efforts: One should not of course emphasize one more than the other. We plan to work in harmony with the world, and in sync with the whole world, in terms of decarbonizing the economy, reducing CO_2 emissions, and of course preserving the environment." In July 2019, Bolsonaro called the preoccupation with the Amazon a form of "environmental psychosis" and argued that its use should not concern outsiders (Casado and Londono, 2019).

Biosphere Reserves

The United Nations Educational, Scientific and Cultural Organization organized the first intergovernmental conference on “the rational use and conservation of the resources of the biosphere” in 1968. Out of this pioneering gathering emerged the Man and the Biosphere Programme (MAB), an ongoing international research and training effort. The MAB, which is supervised by an international coordinating council, was designed to address three major objectives. The first was to reinforce the extent and relevance of the conservation of biological diversity, including genetic resources, through a world system of protected areas. The second objective was to ensure the harmonious coexistence of rural populations and the ecosystems from which they derive their subsistence and income. The third was to provide basic and applied researchers with a number of permanent field sites that could be used as a network of information exchange.

Biosphere reserves are areas comprising terrestrial, marine, and coastal ecosystems. Each reserve promotes solutions reconciling the conservation of biodiversity with its sustainable use.

These basic objectives corresponded with the three basic functions of what came to be known as a **biosphere reserve** (see Fig. 19.6). Each reserve consists of three zones (see Fig. 19.7). A **core area** is devoted to long-term protection. One or more **buffer zones** surround the core area. Only activities compatible with the conservation objectives (research, education, nondestructive recreation, tourism, resource use) may take place in the buffer zone. A **transition area** is a flexible outer region where sustainable resource management practices are promoted and developed, and where local communities cooperate in managing the biosphere reserve, possibly deriving some benefits from it. These three areas vary considerably depending on geographic conditions and local constraints.

As of 2017, there were 686 biosphere reserves in 122 countries, including 20 transboundary sites. They are distributed as follows:

- 79 sites in 28 countries in Africa
- 33 sites in 12 countries in the Arab States
- 152 sites in 24 countries in Asia and the Pacific
- 292 sites in 37 countries in Europe and North America
- 130 sites in 21 countries in Latin America and the Caribbean

Although the biosphere reserve concept has been successful, continual monitoring is necessary to ensure that they fulfill their functions properly and that each country continues to afford them legal protection. In cooperation with local communities, biosphere reserves should be key components in maintaining biodiversity.

Composed of more than 202,000 hectares (500,000 acres) of wilderness, and serving as a refuge for some of the richest and most diverse communities of life in the temperate world, the Great Smoky Mountains National Park was designated an International Biosphere Reserve and a World Heritage Site in 1976 and 1983, respectively. A large-scale biodiversity survey, known as the All Taxa Biodiversity Inventory, began in 1998 and seeks to locate and identify every species living in the park. As of October 2018, scientists had discovered 1,000 new species to science and 10,566 new to the park. During the past 20 years, the number of all species known to inhabit the park has doubled from about 9,300 to 19,866 species. The author of this book serves as Chair of the Mammal Taxonomic Working Group for this project and has compiled an exhaustive database on the mammals. The data resulting from this project allow for park management attention to be focused on organisms and habitats with special needs, as well as on more efficient maintenance of healthy populations of species and their ecological surroundings. It also provides a baseline record for the examination of global factors like acid rain, climate change, and pollution—knowledge that is essential for this park's biodiversity to be preserved for future generations to enjoy. Additional information about this world-renowned project can be found at www.dlia.org.

Batisse, 1997; Linzey, 2016a, b; United Nations Educational, Scientific and Cultural Organization, 2017

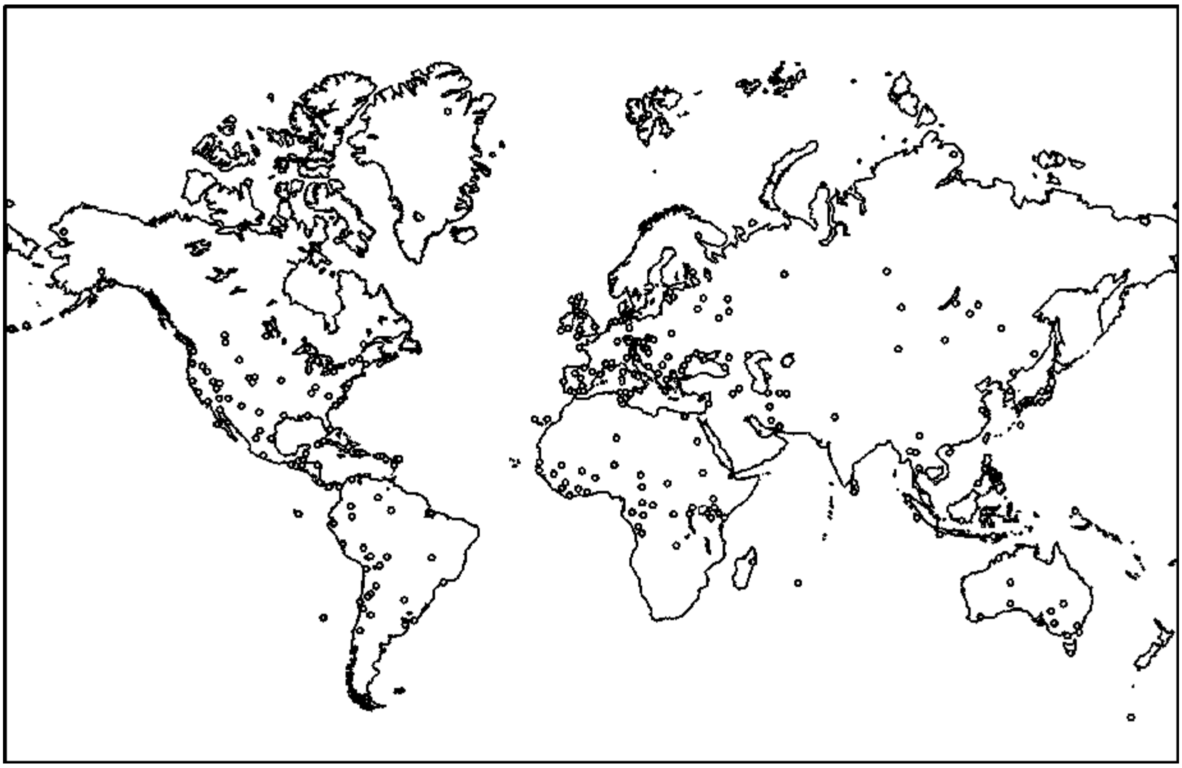


Figure 19.6. World network of biosphere reserves. The dots mark specific biosphere reserves.

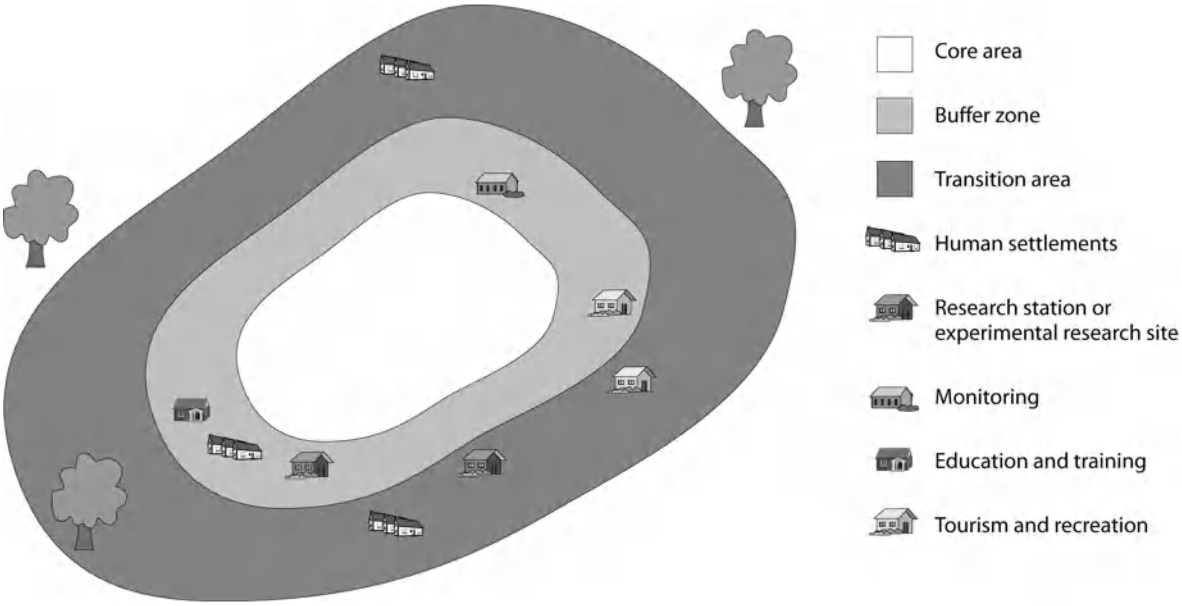


Figure 19.7. Pattern of zoning for a biosphere reserve.

The Colombian Amazon, which is also threatened by rampant deforestation, got a boost on July 2, 2018, when the country's government expanded Serranía de Chiribiquete National Park from 2.8 million to 4.3 million hectares (6.9 million to 10.6 million acres), making it the world's biggest national park in a tropical rain forest. The park was created in 1989 by Carlos Castano, then the director of the national parks system. The park's forests shelter thousands of plant and animal species, including lowland tapirs, jaguars, seven primate species, and more than 200 fish species. The newly expanded park will be managed through Heritage Colombia, an initiative using an innovative funding model to increase Colombia's protected areas and ensure they are well managed for generations to come. Heritage Colombia is led by the government of Colombia and supported by WWF, the Gordon and Betty Moore Foundation, the Protected Areas and Biodiversity Fund, Wildlife Conservation Society, and Conservation International (Anonymous, 2018).

In addition to providing a unique habitat and playing a significant role in maintaining biodiversity, tropical forests are a critical component in the global recycling of oxygen and carbon dioxide. An estimated 13 percent of the world's annual increase in carbon dioxide is brought about by global deforestation (Miller, 1997). Although efforts are being made to protect the remaining tropical forests, their destruction continues to proceed at a rate much faster than their protection.

Fires are common in Brazil during the annual dry season, but during 2019 they were much more widespread than normal. From January to September 2019, Brazilian state experts reported nearly 77,000 wildfires across the country, up 85 percent over the same period in 2018. Many of those were set by people clearing land for cultivation or pasture.

TEMPERATE FORESTS

Temperate forests also suffer from overharvesting and deforestation (Fig. 19.8). During the nineteenth century in the United States, more than 80 percent of hardwood forests were destroyed. Many pine forests were also destroyed, along with most of the prairie ecosystems (Smith, 1996). Ninety percent of the old-growth forests in the northwestern United States have already been logged (Hanks, 1996). This massive deforestation in the United States is thought to have played a role in the extirpation and/or extinction of some wildlife species, including passenger pigeons (*Ectopistes migratorius*) and ivory-billed woodpeckers (*Campephilus principalis*). In May 2016, Audubon scientists published a study revealing that one-third of wintering North American bird populations have declined since 1966 (Soykan et al., 2016). Also in May 2016, the North American Bird Conservation Initiative (NABCI) reported that more than one-third of North American bird species were at risk of extinction unless significant conservation actions were taken.

The Forested Wetlands of the Mississippi River

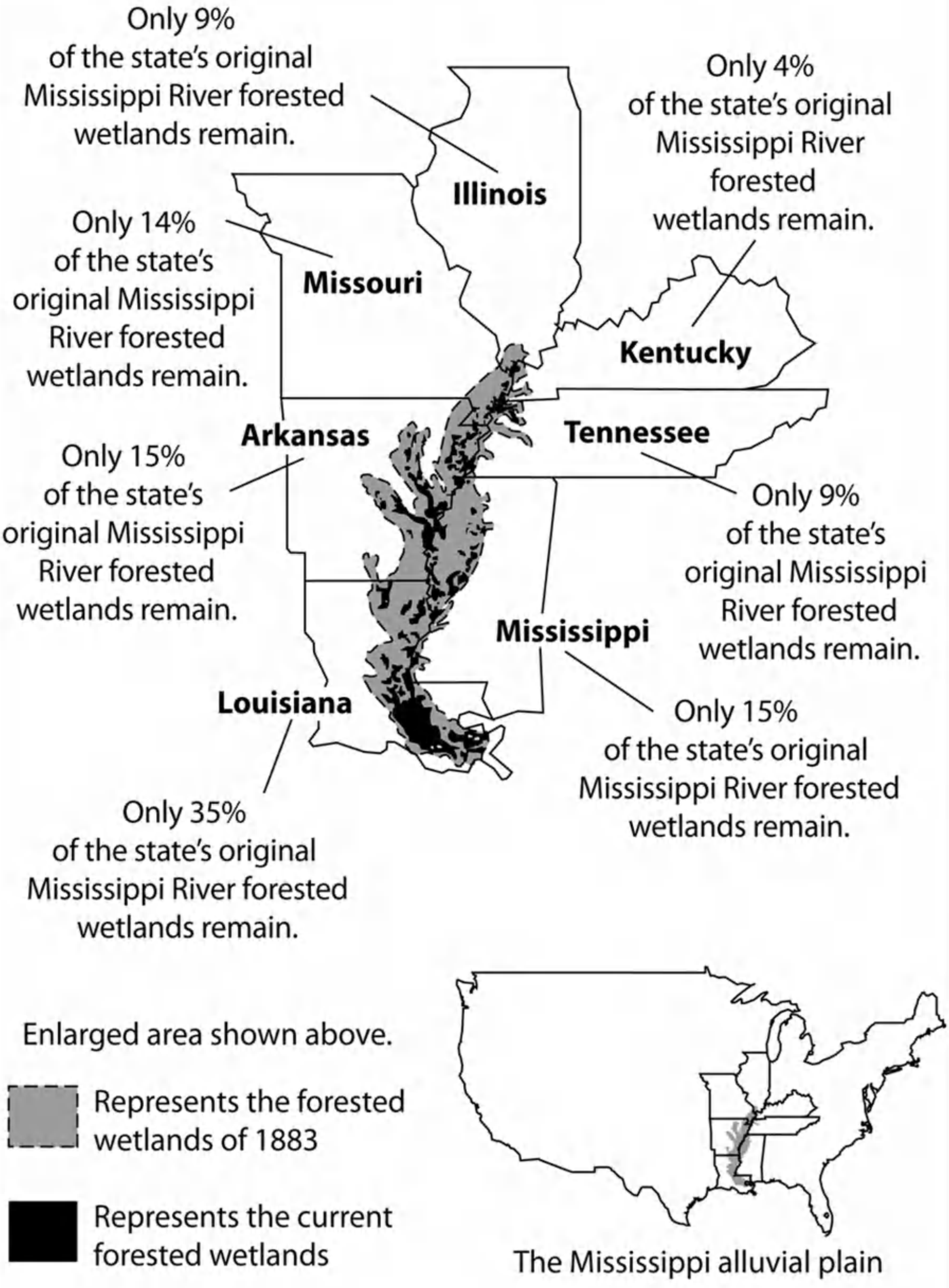


Figure 19.8. Temperate forests, like those along the Mississippi River, also suffer from overharvesting and deforestation. During the nineteenth century in the United States, more than 80 percent of hardwood forests were destroyed.

Every spring, more than half of the 650 bird species that breed in the United States return to North America from their wintering grounds in Central and South America. These neotropical migrants include such familiar species as the ruby-throated hummingbird (*Archilochus colubris*), gray catbird (*Dumetella carolinensis*), purple martin (*Progne subis*), chimney swift (*Chaetura pelagica*), red-eyed vireo (*Vireo olivaceus*), scarlet tanager (*Piranga olivacea*), hooded warbler (*Setophaga citrina*), and wood thrush (*Hylocichla mustelina*) (Fig. 19.9a, b, c). Many are strictly forest-nesters, whereas others—like the Tennessee warbler (*Vermivora peregrina*), eastern meadowlark (*Sturnella magna*), and dickcissel (*Spiza americana*)—prefer scrub or grasslands. They are some of our best insect controllers, eating tons of immature and adult insects annually.

Over recent years, scientists have noticed an alarming drop in the numbers of neotropical migrants—particularly in the populations of forest-nesting birds (Terborgh, 1992; Askins, 1995; Robinson et al., 1995). Although threats to these populations are many and complex, habitat loss throughout North, Central, and South America has had the greatest impact on their decline (Temple, 1998).

(a)

(b)

(c)

Figure 19.9. (*a*) Scarlet tanager; (*b*) wood thrush; (*c*) hooded warbler. Three species affected by deforestation of their tropical wintering habitats.

Overwintering habitats for migratory birds in Central and South America are being altered and are disappearing, in some cases faster than the breeding habitats of the birds. Robbins et al. (1989) analyzed data from the BBS, which was begun in 1965. Although populations of neotropical migrants throughout North America were stable or increasing before 1978, they have declined since. In contrast, residents or short-distance migrants have maintained stable populations. Species wintering in tropical forests have been affected chiefly, whereas those overwintering in scrub remain common. Some of the species most affected in the northeastern United States include the American redstart (*Setophaga ruticilla*), black-and-white warbler (*Mniotilta varia*), black-throated blue warbler (*Dendroica caerulescens*), Canada warbler (*Wilsonia canadensis*), magnolia warbler (*Dendroica magnolia*), Kentucky warbler (*Oporornis formosus*), crested flycatcher (*Myiarchus crinitus*), northern waterthrush (*Seiurus noveboracensis*), ovenbird (*Seiurus aurocapilla*), Swainson's thrush (*Catharus ustulatus*), wood thrush (*Hylocichla mustelina*), veery (*Hylocichla fuscescens*), scarlet tanager (*Piranga olivacea*), summer tanager (*Piranga rubra*), and the yellow-billed cuckoo (*Coccyzus americanus*).

Many biologists who study migratory songbirds have concentrated their efforts on northern breeding grounds rather than southern wintering areas. In a study of American redstarts (*Setophaga ruticilla*), however, Marra et al. (1998) showed for the first time that the quality of a migratory songbird's tropical wintering grounds can affect its survival and breeding success when it arrives in the north. For many migratory species, males arrive at breeding habitats before females, and breeding success and physical condition decline the later the arrival date. Thus, early arrival and physical condition are important determinants of reproductive success and fitness. Through the use of a carbon isotope marker (birds incorporate habitat-specific carbon isotopes into their tissues from the plant-eating insects they consume) in the bird's blood that is keyed to winter habitat type, Marra and his team showed that wet forest birds—which were 65 percent male—maintained or gained weight during the winter months, whereas the scrub-dwellers—which were 70 percent female—had lost up to 11 percent of their body mass and had elevated levels of the stress hormone corticosterone. Wet forest birds—mostly males—were the earliest arrivals at the breeding grounds. Dry-scrub females and younger males arrived later. The wet forest habitat in this study consisted of mangroves, which shelter large numbers of migratory species, but which are declining worldwide. Thus, as prime habitat grows scarce, more and more birds will be forced into the scrub or other suboptimal habitat. Marra's study has provided a crucial piece of information for conservation.

A similar problem involves the golden-winged warbler (*Vermivora chrysoptera*) whose population has declined by as much as 68 percent since the BBS began in 1966. Today, the remaining 400,000 breeding adults make up one of the smallest populations of any songbird outside the endangered species list. Two populations exist. Along the Great Lakes, where the birds nest beneath grasses near forest edges, the population has remained stable. But the only other population—found summering in young forests of the Appalachian Mountains—has declined by 98 percent. Kramer et al. (2018) used tiny tracking devices to locate the birds' nonbreeding habitat in Central and South America. Researchers found that the birds face quite different conditions where they winter. The Great Lakes birds migrate to Central America, a region with less habitat loss, whereas the warblers that breed in Appalachia—which have long been in decline—spend nonbreeding months in a region of Venezuela that shows signs of both current and historic exploitation. Because migration is based in genetics, and evolution takes hundreds (if not thousands) of years, the warblers that breed in Appalachia are unlikely to change their migration route to seek better habitat in Central America.

Though some of the annual decreases in bird populations may seem small, a steady trend of population decrease over several years can be devastating. For instance, a bird species declining 2 percent per year translates into a 50 percent decline in that population over 35 years. Since 1965 in the Chesapeake Bay watershed, the BBS has recorded yellow-billed cuckoos, gray catbirds, scarlet tanagers, least flycatchers (*Empidonax minimus*), and barn swallows (*Hirundo rustica*) declining at less than 1 percent per year. Wood thrushes, whip-poor-wills (*Caprimulgus vociferus*), wood pewees (*Contopus virens*), chipping sparrows (*Spizella passerina*), and Baltimore orioles (*Icterus galbula*) have been declining at a rate of 1 to 3 percent annually. Warblers, however, have been affected most drastically. Populations of prothonotary (*Protonotaria citrea*) and black-throated blue warblers are declining by more than 3 percent, the cerulean warbler (*Dendroica cerulea*) is declining by 4 percent, the black-and-white warbler by more than 5 percent, and the golden-winged warbler (*Vermivora chrysoptera*) by an average of 7 percent per year.

Sydney Gauthreaux, a Clemson University biologist, has studied bird migrations using radar for nearly 30 years. He and his students used the US Navy's weather radar on Dauphin Island off the coast of Alabama to monitor neotropical migrants flying over the Gulf of Mexico (Watson, 1992). By comparing radar pictures from a three-year period in the 1960s with images taken over a three-year span in the 1980s, Watson concluded that migrants from the tropics appeared to have declined by 40 to 50 percent.

Emerging Infectious Diseases

Emerging infectious diseases are known to cause significant changes in bird populations. These changes can potentially lead to marked changes in community composition and ecosystem functioning. LaDeau et al. (2007) demonstrated significant changes for 7 of 20 species of North American birds (American crow, blue jay, tufted titmouse, American robin, house wren, chickadee, and eastern bluebird) following the introduction of West Nile virus in New York City in 1999. The primary hosts of the virus are birds, in which the virus numbers are amplified before the virus is transmitted by mosquitoes to the next victim. Besides birds, the virus can infect other vertebrates, including humans. In just seven years, the American crow population had declined by up to 45 percent. Immune responses of wild birds to emerging infectious diseases (EIDs) has been reviewed by Staley and Bonneaud (2015). (For a discussion of other vertebrates, see Diseases in Chapter 16.)

Cell Towers

The ever-increasing number of communication towers (cell towers) also constitute a risk. Almost 200,000 towers loom above the tree line (Fig. 19.10). Roads and utilities have to be built to them, dividing open space and fragmenting habitats. Cell towers create major obstacles for flying birds, especially at night. According to the American Bird Conservancy, as many as 40 million birds die each year from tower-related collisions.

The Federal Communications Commission and the Federal Aviation Administration have been studying the design of communications towers to reduce the estimated more than 6 million birds killed each year in collisions with the towers and their guy wires (the heavy cables that anchor the masts to the ground). They either hit the poles directly, or become so disoriented by the towers' lights that they crash into the guy wires or each other. Studies have shown that the steadily glowing red lights seem to confuse flying birds, causing them to crash into the towers or to fly in circles until they drop from exhaustion. Replacing these lights with flashing strobe lights could cut bird mortality by as much as 75 percent without compromising aircraft safety. Similar problems exist for bats.

Wind Turbines

Renewable energy production is expanding rapidly despite mostly unknown environmental effects on wildlife and habitats. At a time of growing concern over the rising costs and long-term environmental impacts of the use of fossil fuels and nuclear energy, wind energy has become an increasingly important sector of the electrical power industry. Although promoted as being emission-free and as being "green" or environmentally friendly, wind turbines kill hundreds of thousands of birds and bats every year at utility-scale wind-energy facilities, especially along forested ridgetops in the eastern United States (Piorkowski, 2006; Kunz et al., 2007; Miller, 2008; Grodsky, 2010;

Piorkowski and Connell, 2010; Cryan, 2011; Hayes, 2013; Smallwood, 2013; White, 2013; Bryce, 2016; and others) and in Europe (Rydell et al., 2010, 2012; Wellig et al., 2018; and others). A literature synthesis and annotated bibliography of bats and wind energy was compiled by Ellison (2012).

Figure 19.10. Cell towers are responsible for the deaths of large numbers of birds and bats every year.

And yet, wind turbines are one of the most rapidly expanding renewable energy industries with more than 49,000 individual wind turbines now existing across 39 states (Bryce, 2016). Thousands of bird deaths continue to occur even though the Migratory Bird Treaty Act makes it illegal to kill any bird protected by the Act, even if the death is "incidental" (meaning it occurs unintentionally on the part of the wind farm), and the Bald and Golden Eagle Protection Act recommends that to avoid eagle deaths, specifically, companies seriously consider where they site their wind developments, and that they also limit turbines' impact using techniques like radar to detect incoming birds. Katzner et al. (2016) reported on the continental-scale consequences of local wind-energy generation on golden eagles in California.

A number of retrofits for wind turbines are in the process of evaluation. Some ideas include cameras, radar, and GPS to detect incoming flocks of birds, purple wind turbine blades (white blades attract insects and insects attract foraging birds), bright lights, vertical axis turbines, and smart blades that can recognize approaching birds. The American Bird Conservancy and other groups support proposed regulations that would keep wind turbines away from migration routes, wetlands, wildlife refuges, and similar areas likely to be frequented by birds.

Bats represent a substantial contribution to mammalian diversity and ecosystem processes, including their role in performing important economic service functions. Effects of wind turbines on bats first came to the notice of researchers in the mid-1990s when a study monitoring bird fatalities at a facility in Minnesota reported 13 bat fatalities in the first two years of operation (Osborn et al. 1996). The death of over 1,000 bats at Mountaineer Wind Energy Center in West Virginia in 2003, followed by additional deaths in 2004, triggered research efforts to determine how to minimize both bird and bat windmill collisions. Arnett et al. (2008) synthesized information on patterns of bat fatalities from a review of 21 fatality studies conducted at 19 facilities in five US regions and one Canadian province. A consistent theme in most of the studies in the United States, Canada, and Europe has been the predominance of migratory tree-roosting species—some of which migrate long distances in spring and late summer to autumn—among the fatalities (Cryan et al., 2014).

Bats are being struck and killed by the turning rotor blades of wind turbines. Kunz et al., (2007) listed 11 hypotheses as to why bats are attracted to wind turbines, including the following: bats mistake large monopoles for roost trees, bats are attracted to sites that provide rich foraging habitats, bats are attracted to the sounds produced by the wind turbines, the complex electromagnetic fields produced by wind turbines create interference with bat receptors that are sensitive to magnetic fields, and bats may become trapped in blade-tip vortices and experience rapid decompression due to changes in atmospheric pressure as the turbine blades rotate downward.

Arnett et al. (2011) examined the effectiveness of raising wind turbine cut-in speed—defined as the lowest wind speed at which turbines generate power to the utility system, thereby reducing turbine operation during periods of low wind speeds—to decrease bat mortality. Relatively small changes to wind turbine operation resulted in nightly reductions in bat mortality, ranging from 44 percent to 93 percent. Similar results were reported by Wellig et al. (2018) in Europe. Arnett et al. (2013) evaluated the effectiveness of an ultrasonic acoustic deterrent. They concluded that broadband ultrasound broadcasts may reduce bat fatalities by discouraging bats from approaching sound sources, although the effectiveness of ultrasound deterrents is limited by distance and the area that ultrasound can be broadcast, in part due to rapid attenuation in humid conditions. Cryan et al. (2014) utilized thermal video-surveillance cameras supplemented with near-infrared video, acoustic detectors, and radar to study the behavior of bats at wind turbines in Indiana.

Reimer et al. (2018) tested the echolocation activity of migratory bats at a wind-energy facility in Southern Alberta, Canada, to explain bat fatalities. Their results do not support the feeding attraction hypothesis for hoary and silver-haired bats, and suggest that while some bats forage in the vicinity of wind turbines, they are not specifically attracted to turbines to feed.

Light Pollution

Over the last 150 years, the natural nighttime environment has been drastically altered by the proliferation of artificial lighting. In 2001, it was estimated that almost a fifth of the Earth's land surface was polluted by light (Cinzano et al. 2001), and subsequently the amount of artificial light has been increasing at approximately 6 percent annually (Holker et al. 2010).

The ecological impacts of nighttime light pollution have been a longstanding source of concern, accentuated by realized and projected growth in electrical lighting (Gaston, 2018). As human communities and lighting technologies develop, artificial light increasingly modifies natural light regimes by encroaching on dark refuges in space, in time, and across wavelengths. A wide variety of ecological implications of artificial light have been identified with primary research to date being largely focused on the disruptive influence of nighttime light on higher vertebrates, particularly migrating birds and bats. In many urban areas, skyglow even obscures lunar light cycles, which are used by many organisms as cues for biological activity. Many sea turtle hatchlings emerge from their shells and nests at night on ocean beaches. In order to quickly reach the ocean, they normally orient toward the reflected light coming off the water. In some areas, however, the overpowering light coming from inland urban sources causes them to become disoriented and to travel in the opposite direction from the ocean. By doing so, most succumb to predators or dehydration. Many communities and towns in these areas now ban or greatly decrease artificial lighting during sea turtle breeding seasons.

Recent studies have shown that light pollution is changing plant phenology (earlier tree burst, earlier flowering, etc.) (ffrench-Constant et al., 2016).

Highways

The rapid increase in animal-vehicle collisions on roadways is a growing concern not only in terms of human safety, property damage, and injury costs, but also in the viability of wildlife populations. Large highways act as effective genetic barriers, much the same as rivers and mountains (Gerlach and Musolf, 2000; Rico et al., 2007) (Fig. 19.11). Many animals, especially vertebrates, alter their behavior to avoid roads, shifting home ranges, feeding sites, and nesting areas away from them. But most animal groups still attempt to cross these barriers with some frequency, often by making use of culverts and other potential crossing points. These crossing points may be specifically designed for animal dispersal, like large vegetated overpasses or underpasses, or they may be unintentional dispersal corridors where highways cross rivers, canyons, or other roads. Wildlife crossing structures are gaining national recognition by transportation agencies as effective measures to reduce animal-vehicle collisions and connect wildlife habitat across transportation corridors (van der Ree et al., 2015). Crossing poles served as a rapid method to reconnect endangered flying squirrel habitat isolated by a roadway corridor in North Carolina (Kelly et al., 2013). Scientists in Canada's Banff National Park have seen ungulate fatalities drop by 80 percent in areas where wildlife bridges, underpasses, and fences have been employed. In 2012, along a 2.1 km (1.3 mi.) stretch of Route 41 in Florida that has proven to be particularly deadly for Florida panthers, transportation workers installed a $450,000 system of motion-activated sensors linked to flashing bright LED lights on six warning signs that alert motorists of the presence of a large animal.

One study found that vole populations living on each side of a four-lane highway were genetically distinct. In a study of coyotes and bobcats in California, Riley et al. (2006) found that most home ranges abutted the highway but did not cross it. Such limited DNA transfer makes small populations vulnerable to extinction. Roads also play a role in the worldwide decline of reptiles (Gibbons et al., 2000; Shepard et al., 2008). Road ecology has been described as a "sleeping giant" among environmental biologists. There is not a lot of information concerning genetic fragmentation in animal populations separated by roadways, and what data are available are not encouraging. An overview of transportation impacts on wildlife movement and populations has been presented by Jackson (2000).

Discarded Bottles

Discarded bottles and cans along roadways and roadside pull-offs are a source of mortality for shrews and other small mammals by acting as traps (Morris and Harper, 1965; Benedict and Billeter, 2004; Brannon et al., 2010, 2017; Brannon and Bargett, 2013; and others). Pagels and French (1987) reported a total of 378 dead shrews at 64 different sites in Virginia. A 2-liter (2.1-quart) soda bottle found in Spain in 2014 contained a total of 54 small mammals—the highest number ever recorded from a single discarded bottle (Arrizabalaga et al., 2016). Mammals appear to become trapped in bottles because of their differential abilities to enter and exit through the neck. Entry is probably in response to feeding or exploratory drives. Escape is often not possible because of the steep angle of incline, slippery interior surface, and narrow neck. Hamed and Laughlin (2015) noted that glass disproportionately trapped more small mammals than plastic or aluminum containers. Containers with an upslope orientation greater than 15° were significantly more likely to be associated with mortality than containers in other orientations. Hamed and Laughlin's study estimated a mean of 25.6 small mammals per kilometer killed in discarded containers.

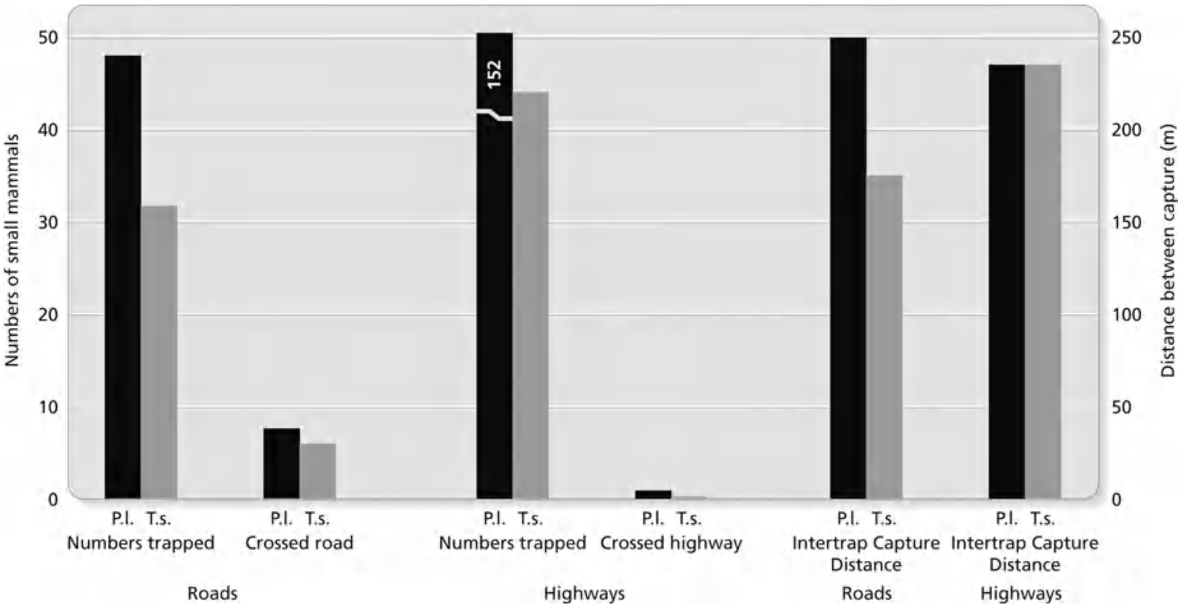


Figure 19.11. Roads as possible barrier to genetic exchange. Relatively few white-footed mice (*Peromyscus leucopus* = *P.l.*) and eastern chipmunks (*Tamias striatus* = *T.s.*) cross country roads and highways. This is true even though the ranges of their movements, as determined from data on intertrap capture distances, indicate that they travel more than sufficient distances to cross such "barriers." For the four pairs of histograms on the left, use the left axis; for the two pairs of bars on the right, use the right axis.

Wetlands

The Prairie Pothole Region of North America is vital for much of North America's waterfowl (Fig. 19.12a, b). Commonly referred to as the "duck factory of North America" because of its critical importance to breeding waterfowl, this area is annually responsible for producing 50 percent of the total number of ducks for 8 of the 12 most common species. The Prairie Pothole Region extends from central Iowa to north of the Canadian border, encompassing a large portion of eastern North Dakota and eastern South Dakota as well as smaller portions of western Minnesota, northwestern Iowa, and northeastern Montana. The region is important because of the tremendous density and diversity of wetland habitats. Retreating glaciers carved out nearly 25 million prairie pothole wetlands. This amazing density—an average of 83 potholes per square acre—is unparalleled in North America. Duck breeding-pair densities in this area approach 120 pairs per square mile. Besides water, the birds also require upland cover in which to nest.

Wetland loss is a major concern. Many wetlands have been drained or filled and much of the native grasslands have been converted to cropland. Iowa lost 98 percent of its wetlands during the past century. In other states, the losses amounted to 90 percent in Minnesota, 49 percent in North Dakota, 35 percent in South Dakota, and 27 percent in Montana. Landowners are learning that not only are these pothole wetlands important to ducks, but also to people. Pothole wetlands help to retain water, control flooding, and improve water quality. And the surrounding grasslands provide forage for livestock. These wetlands also provide opportunities for fishing, hunting, wildlife watching, and outdoor education. Most prairie wetlands are privately owned. Through cooperative landowner agreements, existing wetlands and grasslands are being protected and restored (Tolmé, 2018).

The National Wildlife Federation calls climate change “the most serious threat this century facing America’s migratory birds.” Changing precipitation patterns in the midwestern Prairie Pothole Region could cause the loss of significant breeding habitat for ducks, including mallards and pintails. The benefits of wetlands conservation have been discussed by James and Herbert (2018).


Alberta
Saskatchewan
Manitoba
Canada
United States
Minnesota
North Dakota
Montana
South Dakota
Iowa

(a)

(b)

Figure 19.12. (*a*) Prairie pothole regions. (*b*) Aerial view of potholes.

Predation

The excessive fragmentation of forests that has occurred throughout the United States increases the exposure of bird nests to predators like raccoons (*Procyon lotor*), opossums (*Didelphis virginiana*), cats, blue jays (*Cyanocitta cristata*), and crows (*Corvus brachyrhynchos*), as well as to parasitic birds like the brown-headed cowbird (*Molothrus ater*). Fewer chicks survive to adulthood to replace the adults killed by natural causes.

Domestic cats are not native to America. They were introduced as early as 1614 and have had a serious effect on many vertebrates, including amphibians, reptiles, birds, and mammals. Several million free-roaming felines have taken, and continue to take, a huge toll on wildlife. Some wildlife organizations warn that entire populations of birds and other wildlife are declining or even being pushed toward extinction by domestic cats. The culprits are not just feral cats (those that avoid humans and most domestic food sources and reproduce in the wild) and tame strays—both frequently found in colonies provisioned by people—but also household pets allowed to roam free. Though these felines are simply following natural instincts, their toll on wildlife is tremendous. Loss et al. (2013) estimated that domestic cats, considered a global invasive species, kill 1.3 billion to 4 billion birds and 6.3 billion to 22.3 billion small mammals in the lower 48 states each year. The authors state: "Our findings suggest that free-ranging cats cause substantially greater wildlife mortality than previously thought and are likely the single greatest source of anthropogenic mortality for US birds and mammals." Carey (2017) estimated their toll on wildlife at more than one billion birds and billions more small mammals a year in the United States.

Recognition of the extent of predation by free-ranging domestic cats on native animals by the general public is not widespread. Doherty et al. (2016) reported that cats have played a role in the extinction of 63 bird, mammal, and reptile species worldwide. Cat predation or diseases spread by cats are threatening 430 additional species. Some researchers suspect that toxoplasmosis from cat feces flushes into coastal areas and poses a hazard to seals and other marine mammals. Doherty et al. stated: "We found that cats have contributed to a massive 26 percent of [modern-day] bird, mammal, and reptile extinctions—a figure that had never been quantified before for the entire globe."

In a suburban study in Athens, Georgia, employing KittyCam video cameras to monitor hunting by house pets, Loyd et al. (2013) found that almost half of the cats hunted wildlife with an average of 2.4 kills per week. In addition, these authors showed that domestic cats brought home fewer than one in four kills, a finding that greatly increases previously reported mortality estimates.

Some communities have developed a trap-neuter-return (TNR) program whereby feral and free-roaming stray cats are humanely trapped, spayed or neutered, vaccinated against rabies, marked by having the tip of one ear surgically removed (a "tipped" cat is the universally recognized sign of a cat that has been spayed or neutered), and then returned to their colony. Such programs reduce the number of cats having to be euthanized and, in some areas, feral colonies have been completely eradicated. But even spayed or neutered cats, unable to reproduce, can still kill many birds and mammals during the remainder of their lives.

Air and Water Pollution

In addition to the steps that need to be taken regarding population control, preservation of biodiversity, and the conservation of tropical and temperate forests, air and water pollution laws must be significantly strengthened and enforced worldwide.

Environmental pollution—from filthy air to contaminated water—kills more people every year than all war and violence in the world. Pollution has been studied extensively, but it has never received the resources or level of attention as issues like AIDS or climate change. What affects humans also affects many other species of vertebrates, but these effects have largely been ignored. Few studies have been published on the impact of pollution on species other than humans. Those studies that have been done in the past have dealt primarily with the effects of organochlorine pesticides, mercury, and lead contamination, most of which have now been banned or have levels in the environment that are legally controlled. Even so, they still have not disappeared from the environment. Lead, for example, has been removed from gasoline, but what about the fragments of lead ammunition that are scavenged from deer carcasses or other animals that have been shot? A lead fragment the size of a grain of rice can kill a bald eagle. What about toxic particulates in the air from coal-burning power plants? What about the potentially toxic wastes from mines and coal-burning power plants that leak into groundwater and nearby rivers? While the number of human deaths and welfare costs are continually calculated, no one knows the effects of environmental pollution on the vast majority of other vertebrates.

The nation’s waterways are awash with traces of painkillers, caffeine, antibiotics, and other products commonly passed through humans and farm animals. Lawn pesticides and benign-looking home detergents, artificial fragrances, and germicides that are sent down millions of drains and rivers contribute to the deaths of vital plankton and fishes. Perfumed household detergents, drier sheets, shampoos, lotions, and deodorants usually contain dozens of unlisted neurotoxic petrochemicals, hidden by the nonthreatening generic code word “fragrance.” Used as produce-preservatives, they are deadly to the microbial life comprising the human immune system and to the oceans alike.

Contraceptives, insect repellants, perfumes, and nicotine were among the 95 substances that were detected in US waterways in a 2002 US Geological Survey (USGS) study. These are substances that generally go untreated at wastewater treatments plants but may pose threats to the aquatic environment. Pharmaceuticals and personal care pollutants, or

PPCPs, could pose risks not only to aquatic life, but also to downstream water users. Many such substances fall through the cracks of existing clean water laws. They generally are not defined as pollution—the Environmental Protection Agency (EPA) has no water quality criteria for 81 of the 95 chemicals examined by the USGS. Also, the Food and Drug Administration (FDA) does not review pharmaceuticals for potential environmental impacts. Studies have suggested that hormones released into the waterways may alter sexual characteristics in fishes and other wildlife exposed to the chemicals. For more information on the impact of environmental chemicals on wildlife vertebrates, see Bernanke and Kohler (2009).

The popular impotence drug, Viagra, may be reducing demand for traditional Chinese impotence remedies, many of which contain ground-up animal parts (von Hippel and von Hippel, 2002). Sales of seal penises and reindeer antlers dropped sharply about the same time Viagra came on the market in 1998. While those two products were studied because they are legally traded and easy to monitor, there is some indication that the Viagra effect also holds true for endangered and threatened species, ranging from sea horses to green turtles. Thus, Viagra may be one part of the answer to helping save world wildlife.

Regarding our oceans, Sylvia Earle, award-winning ocean researcher stated: "Most of the oxygen in the atmosphere is generated by the sea. The ocean drives climate and weather, stabilizes temperature … forms clouds that return to the land and the seas as rain, sleet and snow, and provides home for about 97 percent of life in the world, maybe in the universe." Oxygen concentrations in both the open ocean and coastal waters have been declining since at least the middle of the twentieth century (Breitburg et al. 2018). Within just the past few decades, humans have destroyed 90 percent of the big ocean fishes and have been responsible for population declines in numerous other vertebrate species, including cetaceans and marine carnivores.

Increasing quantities of diverse litter are being discarded in the world's freshwater and marine environments. With more than 7.1 metric tons (8 million US tons) of plastic entering the ocean each year, humanity must urgently rethink the way we make and use plastics (MacArthur, 2017). The production of cheap, light, and versatile plastics are the dominant materials of our modern economy. Their production is expected to double over the next two decades. Yet only 14 percent of all plastic packaging is collected for recycling after use, and most quantities escape into the environment. MacArthur (2017) points out that “if the current trend continues, there could be more plastic than fish by weight in the oceans by 2050.” As one small step, in 2019 Maryland legislators adopted the nation’s first statewide ban on polystyrene foam food and drink containers.

Marine Debris from Land and Sea

The follow list gives estimated timelines for the breakdown of various products. These estimates depend on production composition and environmental conditions.

Paper towel: 2 to 4 weeks

Newspaper: 6 weeks

Waxed milk carton: 3 months

Plastic grocery bag: 1 to 20 years

Foam plastic cup: 50 years

Tin can: 52 years

Aluminum can: 200 years

Plastic beverage holder: 400 years

Disposable diaper: 450 years

Plastic bottle: 450 years

Monofilament fishing line: 600 years

Glass bottles and jars: undetermined

South Carolina Sea Grant Consortium (https://www.scseagrant.org); South Carolina Ocean & Coastal Management (OCRM) (https://scdhec.gov/environment/your-water-coast/ocean-coastal-management-ocrm); National Oceanic and Atmospheric Administration (NOAA) (https://www.noaa.gov)

Dirty Dozen Endocrine Disruptors

According to the Environmental Working Group (EWG), here are 12 of the worst hormone disruptors together with the problems they cause:

BPA—Linked to breast and other cancers, reproductive problems, obesity, early puberty, and heart disease; 93 percent of Americans have BPA in their bodies.

Dioxin—Can disrupt delicate ways that signaling of both male and female sex hormones occurs in the body; dioxins are powerful carcinogens.

Atrazine—Low levels can turn male frogs into females that produce completely viable eggs; linked to breast tumors, delayed puberty, and prostate inflammation in animals; some research has linked it to prostate cancer in humans.

Phthalates—Linked to hormone changes, lower sperm count, less mobile sperm, birth defects in the male reproductive system, obesity, diabetes, and thyroid irregularities.

Perchlorate—Alters thyroid hormone balance.

Fire retardants (Polybrominated diphenyl ethers, or PBDEs)—Disrupt thyroid hormone activity.

Lead—Harms almost every organ system in the body, including causing permanent brain damage, lowered IQ, hearing loss, miscarriage, premature birth, increased blood pressure, kidney damage, nervous system problems, and lower sex hormone levels.

Arsenic—Large amounts may kill outright; smaller amounts can cause skin, bladder, and lung cancer as well as interfere with normal hormone functioning in the glucocorticoid system, which regulates how our bodies process sugars and carbohydrates, leading to weight gain or loss, protein wasting, immunosuppression, insulin resistance (which can lead to diabetes), osteoporosis, growth retardation, and high blood pressure.

Mercury—Can interfere with fetal brain development; known to bind directly to one particular hormone that regulates women's menstrual cycle and ovulation, interfering with normal signaling pathways; may play role in diabetes.

Perfluorinated chemicals (PFCs)—Linked to decreased sperm quality, low birth weight, kidney disease, thyroid disease, and high cholesterol; 99 percent of Americans have these chemicals in their bodies.

Organophosphate pesticides—Interfere with the way testosterone communicates with cells, lowering testosterone and altering thyroid hormone levels.

Glycol Ethers—Blood abnormalities and lower sperm counts; may damage fertility or the unborn child.

Environmental Working Group, www.ewg.org/research/dirty-dozen-list-endocrine-disruptors

Ingestion of human-related debris causes the deaths of many aquatic animals each year. Monofilament fishing line, plastic bags, string, rope, fishhooks, wire, paper, cellophane, synthetic sponges, rubber bands, and stockings have been recovered from intestinal tracts of endangered Florida manatees (Beck and Barros, 1991). Additional deaths have resulted from entanglement in lines and nets. Nonbiodegradable plastics, in particular, have caused mortality in sea turtles, waterfowl, and various aquatic mammals when they become entangled in plastic products or ingest them (Wallace, 1985; Walker and Coe, 1990). In March 2019, a dead whale washed up on a beach in the Philippines; its stomach contained 40 kg (88 lb.) of plastic. In April 2019, an 8 m (26 ft.) sperm whale was found dead off Sardinia, Italy, with 22 kg (48.5 lb.) of plastic in its stomach. The whale's stomach contained a corrugated tube for electrical works, plastic plates, shopping bags, tangled fishing lines, and a washing detergent package with its bar code still legible.

Endocrine Disruptors

The endocrine system is made up of a number of glands in the body that do not have ducts and other similar structures. The endocrine system includes the thyroid, parathyroid, adrenal, and pituitary glands, the ovaries, the testes, the pineal body, and the pancreas. As well, it includes cells releasing hormones found in the gastrointestinal tract, kidney, heart, and placenta. What distinguishes endocrine glands from other glands is that endocrine glands secrete certain chemicals called hormones.

Many plants and animals produce substances that can have endocrine effects. Some of the substances are toxic, but certain effects have proven beneficial in some circumstances. For example, some "endocrine disruptors" have been used to control fertility (birth control pills), to treat cancer (corticosteroids), and to treat psychiatric disorders and other medical conditions. Natural substances, such as sex hormones or phytoestrogens (plant chemicals having estrogen-like effects), can become concentrated in industrial, agricultural, and municipal wastes. Exposure to these wastes may produce reactions in humans, wildlife, fishes, or birds.

Endocrine disruptors are also found in synthetic chemicals used as industrial solvents, lubricants, and their byproducts. These include polychlorinated biphenyls (PCBs), polybrominated biphenyls (PBBs), and dioxins. Other examples of endocrine disruptors include bisphenol A (BPA) from plastics, dichlorodiphenyltrichloroethane (DDY) from pesticides, vinclozolin from fungicides, and diethylstilbestrol (DES) from pharmaceutical agents. Certain metals such as cadmium, mercury, arsenic, lead, manganese, and zinc also disrupt endocrine systems. Many consumer products like cosmetics, personal care products, and cleaners (especially fragranced products), contain complex mixtures of chemicals that have endocrine disruption properties.

Certain synthetic compounds, like the estrogen DES, widely used before it was banned in 1971, can mimic the activity of naturally occurring hormones and act as endocrine and reproductive disruptors in various species (Smolen and Colborn, 1997). At least 51 chemicals disrupt hormones in one way or another (Raloff, 1995; Colborn et al., 1996). Some mimic estrogen, as DES does, and others interfere with different parts of the endocrine system, like thyroid and testosterone metabolism. These substances in fishes, reptiles, and birds can potentially have drastic consequences, including sterility, sperm abnormalities, a reduction in sperm count, and the alteration of male genitalia (Sharpe, 1995; Colborn et al., 1996; Dold, 1996). They also cause the development of oviducts in male carp during sexual differentiation (Gimeno et al., 1996).

Intersex is when one sex develops characteristics of the opposite sex, such as the presence of immature eggs in the testes (testicular oocytes) of male fishes. While its exact causes are unknown, it has been linked to artificial environmental chemicals that mimic or block sex hormones. Scientists from the USFWS and the USGS studied largemouth and smallmouth bass in 19 national wildlife refuges in the northeastern United States for evidence of estrogenic endocrine disruption. Intersex in male smallmouth bass was observed at all sites and ranged from 60 to 100 percent; in male largemouth bass the range was 0 to 100 percent (Iwanowicz et al., 2016). High levels of vitellogenin, a plasma protein involved in producing egg yolk, was found in many smallmouth bass. In male fish, the gene that tells the body to produce vitellogenin is usually "turned off." That gene only switches on in the presence of estrogen, a female sex hormone. When vitellogenin is found in the blood, it is a pretty clear indication that those male fishes were exposed to extra estrogens of some kind. Intersex was first discovered in smallmouth bass in the Chesapeake Bay watershed in 2003. Studies of bass in the upper Potomac River and its tributaries, including the Shenandoah River, revealed germ cells (oocytes) in the testes of 82 to 100 percent of the male smallmouth bass and in 23 percent of the males from the single largemouth bass collection near the Blue Plains Wastewater Plant in Washington, DC (US Fish and Wildlife Service, 2009). A study by the USGS in 2009 (Hinck and Puckett, 2009) found fish in rivers across the United States to exhibit both male and female sex characteristics. They found intersex fish at about one-third of sites tested in the Apalachicola, Colorado, Columbia, Mississippi, Mobile, Pee Dee, Rio Grande, Savannah, and Yukon river basins. The condition affected one-third of male smallmouth bass and one-fifth of all male largemouth bass at those sites. The condition was found in populated areas and agricultural regions, as well as in more remote locations where a likely culprit—like pollution from wastewater or runoff—does not occur. Lab studies are under way to isolate potential causes, but a solution to the mystery could be years away.

Over the past decade, feminized male fish have been discovered in 37 species in lakes and rivers throughout North America, Europe, and other parts of the world (Bahamonde et al. 2013). These discoveries in protected wildlife refuges is worrisome because it suggests that pollution may be even more pervasive than previously thought. Worldwide, intersex conditions caused by hormonal disruption have occurred in an array of aquatic animals, including alligators, turtles, and frogs.

Environmental estrogens have been found to have a surprising effect on male starlings (*Sturnus vulgaris*)—like turning them into better singers, thus duping female starlings into choosing mates that may be less fit because of compromised immune systems (Markman et al., 2008). Researchers compared starlings raised in aviaries and fed a controlled diet with those living at sewage treatment plants and feasting on earthworms that survive on microbes that degrade the sewage. By feeding on the earthworms, the treatment plant starlings consumed natural estrogen along with three estrogen mimics: DEHP (Di-2-ethylhexyl phthalate phthalate), used to manufacture polyvinyl chloride; DBP (dibutyl phthalate), found in nail polish; and bisphenol A, common in hard plastic bottles. When spring mating season arrived, estrogen in the male brain surged in both groups, triggering an expansion of the vocal center and a burst of song. But for birds consuming the estrogen cocktail, the vocal center grew even larger—and they sang five times as long as uncontaminated birds and composed more complex songs. In the lab, female starlings showed a preference for those songs, perching near a loudspeaker that was playing them. Blood tests, however, showed that the doped male starlings had compromised immune systems.

Hormone-disrupting chemicals may have synergistic effects, and seemingly insignificant quantities of individual chemicals can have a major cumulative effect. At present, 100,000 synthetic chemicals are on the market, with approximately 1,000 new substances being introduced each year. Many of these are ingredients in pesticides that are applied worldwide—not only to agricultural fields, but in areas around parks, schools, homes, gardens, restaurants, and supermarkets. Besides pesticides, these substances include certain detergent breakdown products and various plastics additives and stabilizers. The hormonal activity of these chemicals usually bears little relationship to their intended function. There is no known way of predicting—based on structure or function—which compounds will mimic naturally produced hormones.

Atrazine is the most commonly detected pesticide contaminant of ground water, surface water, and precipitation. It is also an endocrine disruptor that, among other effects, alters male reproductive tissues when animals are exposed during development. When atrazine was present in the water, four times as many snails developed as did in water free of the weed killer. As snail populations climbed, so did the number of incubating trematodes (which are any parasitic flatworms of the class

Trematoda, especially flukes, having hookers or suckers). In northern leopard frogs (*Rana pipiens*) and green frogs (*Rana clamitans*), trematode infections were significantly higher when atrazine was present (Rohr et al., 2008). The same was not true for pickerel frogs (*Rana palustris*), but this species did experience a high rate of mortality when trace quantities of atrazine laced the water. Hayes et al. (2011) found demasculinization and feminization of male gonads by atrazine to have consistent effects across all vertebrate classes examined. It demasculinizes male gonads, producing testicular lesions associated with reduced germ cell numbers in teleost fishes, amphibians, reptiles, and mammals, and induces partial and/or complete feminization in fishes, amphibians, and reptiles.

Pesticides and heavy metals are present in the blubber, muscle, liver, and brains of many vertebrate species. After spending most of their lives in the ocean, where they absorb widespread industrial chemicals like PCBs, sockeye salmon flock to Alaska’s interior lakes in huge numbers to spawn and then die. Each salmon accumulates just a small quantity of PCBs, but the thousands of decaying carcasses produce a sevenfold increase in the PCB concentrations of the spawning lakes (Krummel et al., 2003). Lakes with the highest numbers of spawning salmon had the highest concentrations of PCBs. Previous studies had shown that orcas in the northwest were among the most contaminated marine mammals in the world. Salmon and grayling fishes form a major part of the killer whale’s diet. A 2006 study of Florida’s top saltwater predators, like sharks, as well as marine mammals, revealed high concentrations of PCBs and polybrominated diphenyl ethers (PBDEs); these concentrations are increasing rapidly. Calculations suggest that concentrations of these two contaminants are doubling every two to four years in bull sharks and bottlenose dolphins. Mercury pollution from power plants and other industrial sources is causing mammals like river otters to suffer from impaired motor function, which hinders their ability to hunt and find food.

Why PCBs Persist

Polychlorinated biphenyls (PCBs), a group of 209 artificial organic chemicals, were widely used beginning in the 1930s as insulators in electrical equipment, engine oil, caulk, paint, and fluorescent lights, among other things. By the time the United States banned their manufacture in 1979, nearly 680,388,550 kg (1.5 billion lb.) had been produced and disseminated nationwide. The same durability that made them useful in commerce and industry has allowed them to stick around and spread. Some equipment containing the compounds is still in use. And while the Environmental Protection Agency did clamp down on the storage and disposal

> of remaining PCBs, many have leaked or been unwittingly dumped in sewers or unlined landfills. Used oil containing the chemicals was for a time even sprayed on some unpaved roads to control dust. The manufacturing ban has not been airtight, either—PCBs are still an inadvertent byproduct in making the yellow paint used to mark highways and parking lots.
>
> Wheeler, 2018

Many male salmon in the Columbia River have become female, perhaps because of pesticides and other chemicals that mimic estrogen. Male frogs exposed to very low doses of atrazine, a common weed killer, can develop multiple sex organs—sometimes both male and female (Hayes et al., 2002, 2010). Male frogs exposed to 2.5 parts per billion (ppb) developed few sperm and had very low testosterone levels. Ten percent of these males transformed into functional "females" who encouraged the advances of healthy males, and in two cases were found to have produced eggs that hatched into viable young. The effects on the frogs results from atrazine causing cells to produce the enzyme aromatase, which is present in vertebrates and converts the male hormone testosterone to the female hormone estrogen. The EPA permits up to 3 ppb of atrazine in drinking water, but the study team found that it affected frogs at doses as small as 0.1 ppb. Atrazine was found to alter the activity of a liver enzyme and thyroid hormones in *Lithobates* [*Rana*] *pipiens* tadpoles (Langlois et al., 2009). Atrazine-exposed tadpoles proved only about half as likely to metamorphose as those raised in clean water. Beattie and Tyler-Jones (1992) reported that increasing aluminum concentrations and low pH reduced the fertilization success of European common frogs (*Rana temporaria*), increased embryonic mortality, and decreased larval body length.

Little is known about the effects of pollutants on reptiles. Noteworthy exceptions are studies of pollution-caused alterations of sex hormones in alligators of Florida's Lake Apopka and effects of organic contaminants on snapping turtles around the Great Lakes. Some species live up to 60 years, so they could yield valuable information on cumulative exposure to toxins. The effects of environmental contamination on the development of snapping turtle eggs was reported by Bishop et al. (1991).

Some species literally have almost been poisoned out of existence, like California condors (*Gymnogyps californianus*) (see Fig. 17.2), Utah prairie dogs (*Cynomys parvidens*), and black-footed ferrets (*Mustela nigripes*) (see Plate 22), while others ingested and accumulated such high quantities of chlorinated hydrocarbon compounds like DDT and

PCBs that they could no longer reproduce and maintain viable populations in certain areas, like brown pelicans (*Pelecanus occidentalis*), bald eagles (*Haliaeetus leucocephalus*) (see Plate 19), and peregrine falcons (*Falco peregrinus*) (see Plate 18). Organochlorine pesticides like DDT, which are insoluble in water but soluble in fat, accumulate in food chains and food webs, a process called **biological amplification** (Fig. 19.13). Ingested compounds caused thinning of eggshells, which frequently cracked prior to hatching (Fig. 19.14a). Although the use of DDT and other organochlorines in the United States has been legally banned since 1970, the United States is still the largest producer of DDT, which is exported to developing countries that use it to kill mosquitoes and prevent malaria. Environmental groups have suggested alternatives to DDT that are also as cheap and have proven successful in experiments in killing malaria-carrying mosquitoes. However, the chemical is still endorsed by the World Health Organization for killing malaria-carrying mosquitoes, despite a ban in 34 countries and severe restrictions in 34 others.

Green (1998) documented widespread declines in eggshell thickness beginning in 1850 for several species of thrush (*Turdus* sp.) in Britain. These declines, well before the introduction of DDT in 1947, may have been an early consequence of industrialization. Acid deposition, caused by anthropogenic emissions of sulfur dioxide, nitrogen oxides, and ammonia, may have altered soil or water chemistry, affecting the availability of those invertebrates like snails (or their shells) that are an important source of calcium during eggshell formation (Fig. 19.14b). Decreased availability of dietary calcium is known to adversely affect egg-laying and eggshell integrity in birds as well as the growth of hatchling birds and neonatal mammals. Scheuhammer (1991) reviewed the effects of acidification of the environment on the availability of toxic metals and calcium to wild birds and mammals.

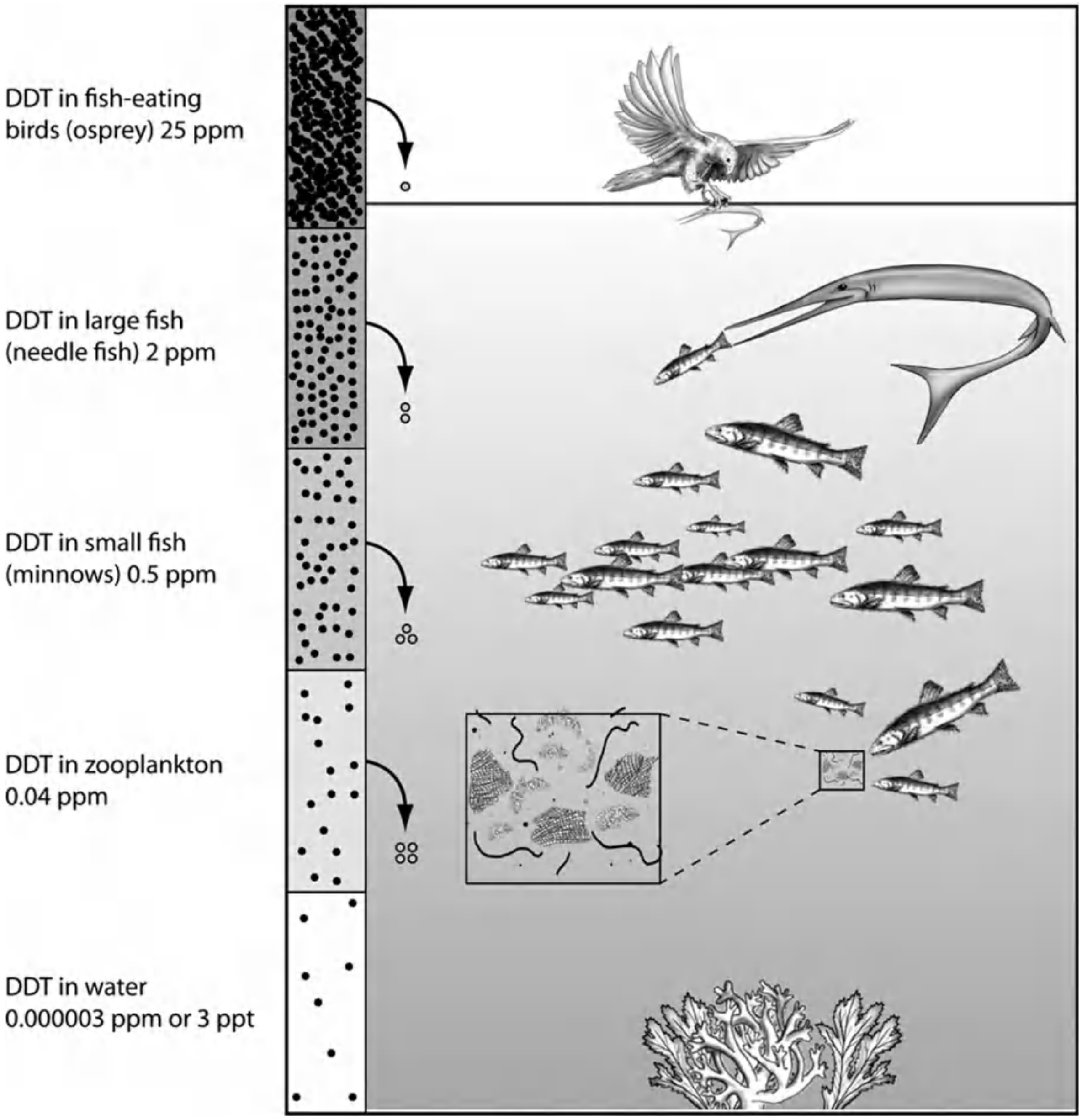
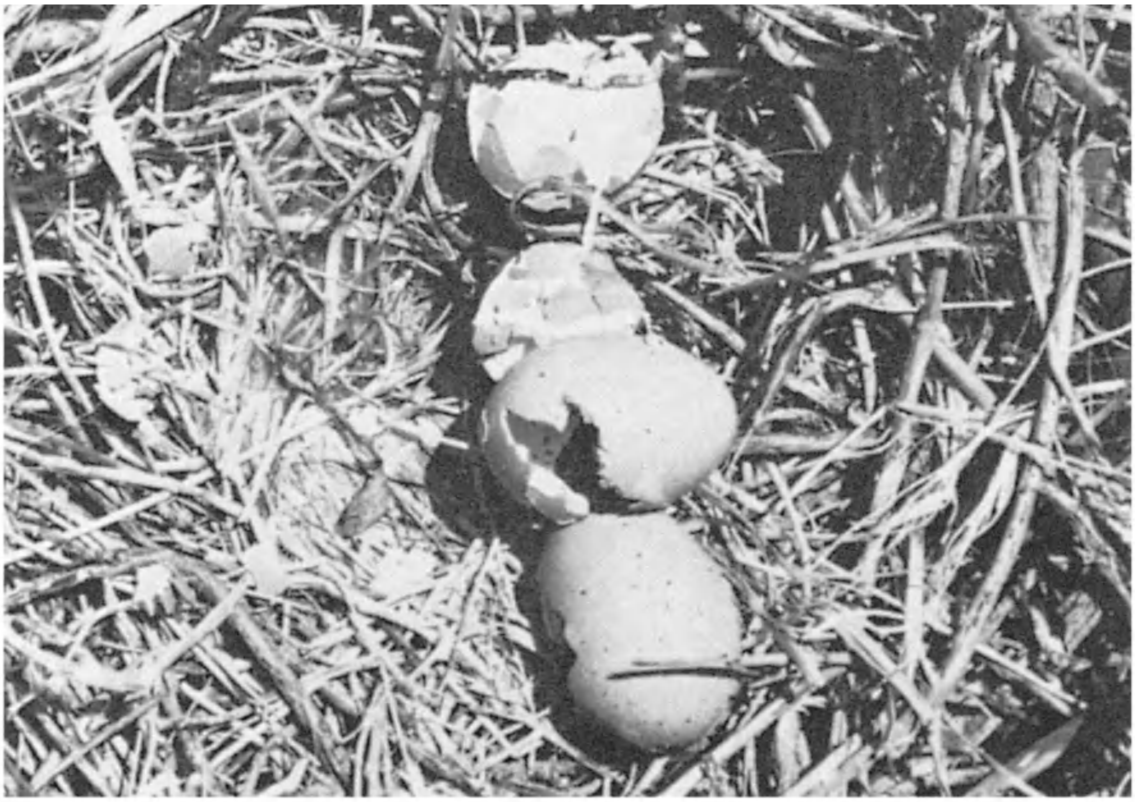
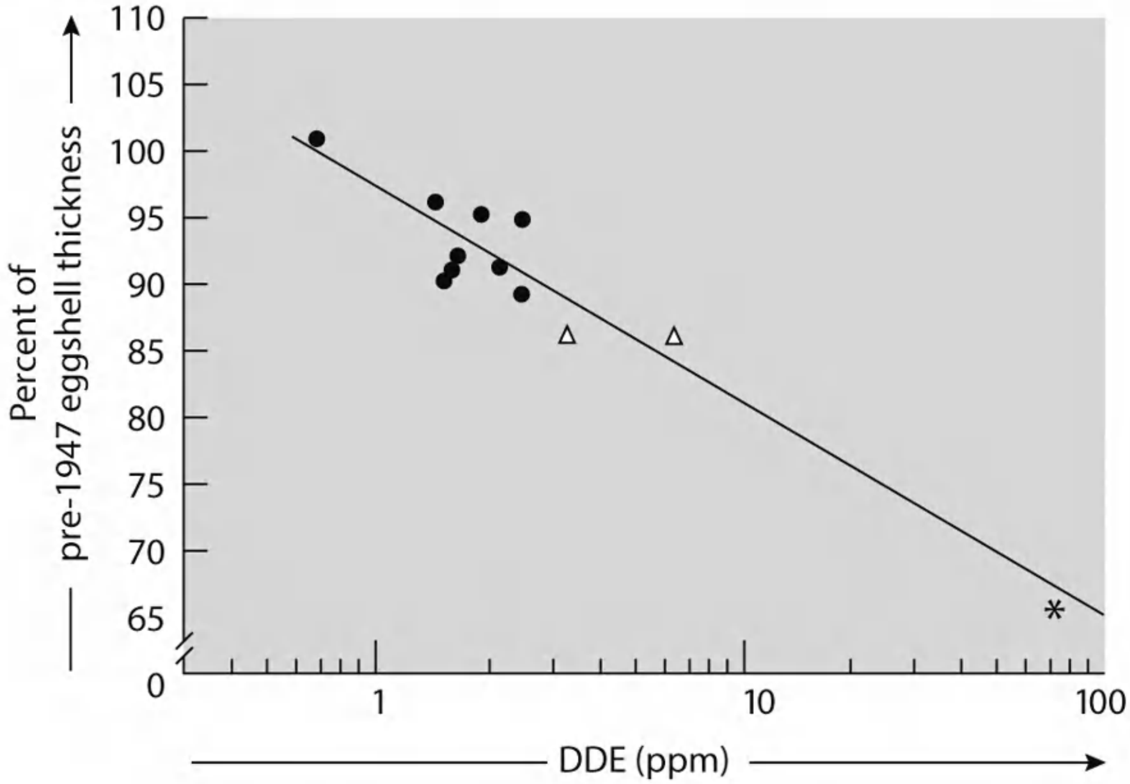


Figure 19.13. Biological amplification. The concentration of DDT (dichlorodiphenyltrichloroethane) in the fatty tissues of organisms was biologically amplified about 10 million times in this food chain of an estuary adjacent to Long Island Sound, near New York City. Dots represent DDT, and arrows show small losses of DDT through respiration and excretion. Concentrations measured in parts per million (ppm) or parts per trillion (ppt).

Pollution of water by oil or other toxic chemicals is detrimental to many marine species as well as to shorebirds (e.g., *Exxon Valdez* spill of 1989, BP Deepwater Horizon spill of 2010, and others) (Fig. 19.15a, b). Mead (1997) reviewed European and American studies on the fate of seabirds cleaned and released after being caught in oil slicks. The best efforts to clean up oiled birds are not very successful. Fishes living in polluted water often develop lesions due to bacterial or viral infection. Viruses have been identified as the pathogen in mass mortalities of seals in Antarctica in 1955, in northwestern Europe in 1988, in Lake Baikal in 1989, and in West Africa in 1997, as well as porpoises in Ireland in 1988 and dolphins in the western Mediterranean in 1990 (Harvell et al., 1999).



(a)



Association of DDE residues in brown pelican eggs from nine colonies in Florida (●), two colonies in South Carolina (△), and one colony in California (⁎)

(b)

Figure 19.14. (*a*) Abandoned ibis nest with broken thin-shelled eggs. (*b*) DDE (dichlorodiphenyldichloroethylene) content and eggshell thinning of brown pelican eggs from Florida, South Carolina, and California are strongly correlated.

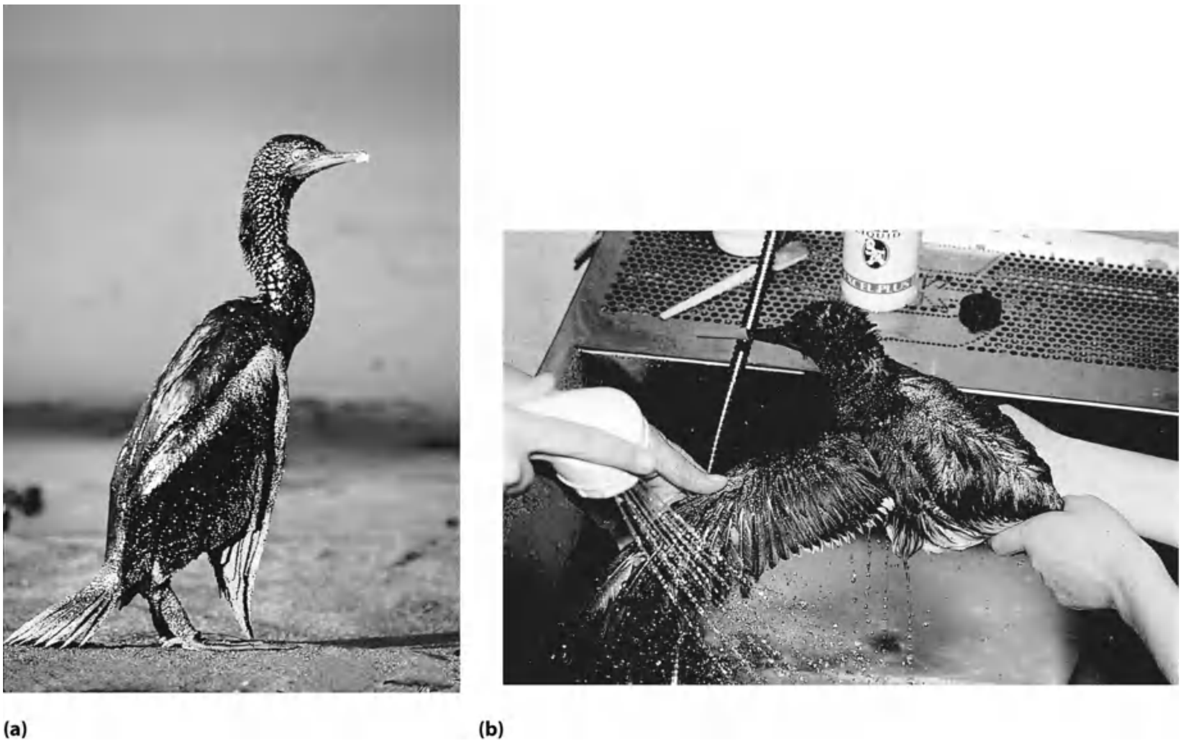


Figure 19.15. (*a*) A seabird coated with crude oil from an oil spill. (*b*) Oil-soaked birds die unless the oil is removed with a detergent solution. Even when the oil is removed, many do not survive.

Most people know about the BP disaster, but most are unaware of the continuing pollution caused in 2004 when Hurricane Ivan toppled a Taylor Energy Company drilling platform in the Gulf of Mexico. In the 14 years following this incident, the US federal government estimates that up to 111,000 liters (29,400 US gallons) of oil were leaking into the Gulf *each day* from the site; oil slicks often stretch for miles off Louisiana's coast. On November 22, 2018, the US Department of the Interior's Board of Land Appeals made public their October 30 decision refusing to excuse the company from requirements to permanently plug the oil wells that were the source of the leaks. Taylor Energy was required to cap each of the more than two dozen leaking wells that broke open, and the government was determined to hold the company to the agreement.

The BP Deepwater Horizon oil disaster fouled more than 2,092 km (1,300 mi.) of coastline, caking seabirds and killing sea creatures and other wildlife. Pockets of methane caused marine life to smother. Large numbers of fish kills were reported in the area. Pregnant dolphins in the Gulf of Mexico were found to have a higher incidence of in utero infections, fetal issues, and late-term pregnancy failures. Between 2010 and 2016, over 170 stillborn and stranded juvenile dolphins were found in Gulf waters, according to the National Oceanic and Atmospheric Administration (NOAA). But the oil's impact on microbes, each measuring just a fraction of a millimeter, could prove even more significant given their foundational role at the base of the ocean food chain. Deepsea microbes regulate carbon in the atmosphere and recycle nutrients. The environmental effects of the Deepwater Horizon oil spill have been reviewed by Beyer et al. (2016).

Unfortunately, ocean conservation measures put in place by a former US president in the wake of the Deepwater Horizon calamity were being dismantled by the 2018 US presidential administration. In June 2018, the president issued an executive order that essentially revoked a previous directive that established the National Ocean Council to "ensure the protection, maintenance and restoration" of the oceans and the Great Lakes.

Penguins and alcids are more vulnerable to oil spills than are flying birds because they must swim through any oil that occurs between their breeding colonies and feeding grounds. Resting Adélie penguins (*Pygoscelis adeliae*) contaminated with oil have reductions in heart rate, body temperature, and energy expenditure. In the water, the swimming speed of oiled penguins is lower, their heart rates are increased, and their metabolic rates are 50 percent higher while swimming than in control penguins (Culik et al., 1991).

The oil tanker *Jessica* ran ashore on San Cristóbal Island in the Galápagos Natural World Heritage Site on January 17, 2001. Several days later, 2.8 million liters (750,000 US gallons) of diesel and bunker oil spilled throughout the archipelago. Although few animals died immediately, the long-term effects of oiling indicated that losses might be severe. Conservationists feared that the fuel would sink to the ocean floor, destroying algae vital to the food chain and threatening marine iguanas, sharks, and birds that feed off fish, invertebrates, and plants (Fig. 19.16). Ten days after the oil spill, oil patches were visible in tide pools and, of 170 individual marine iguanas examined, 70 percent had oil residue on their skin. In addition, plasma levels of corticosterone, the species-specific stress hormone, were highly elevated in iguanas sampled after the oil spill. Researchers felt that corticosterone was elevated because iguanas ingested oil residues while feeding in polluted intertidal areas. Marine iguanas, which are extremely sensitive to environmental perturbations like El Niños, have corticosterone levels that are linearly related to survival rates. During an El Niño event, only individuals that died within two to four weeks after sampling had levels elevated to the same degree as oiled iguanas; thus, marine iguanas appear to be extremely sensitive to oil contamination (Romero and Wikelski, 2001; Wikelski et al., 2001).

Evans (1987) reviewed contaminant levels and their biological effects in cetaceans. Concentrations of DDT up to 2,700 ppm and up to 850 ppm of PCBs have been reported (Gaskin, 1982).

Commercial Fisheries (Gill Nets and Shrimp Nets)

The most serious danger to dolphins, porpoises, sea turtles, and other marine species around the world is the threat from various methods of gill-net fishing. More than 80,000 small cetaceans are killed annually in coastal waters around the world. Active acoustic alarms spaced 92 m (300 ft.) apart, and emitting a broadband signal with a frequency of 10 kHz and a source level of 132 dB, have proven effective in reducing the number of deaths of harbor porpoises (*Phocoena phocoena*) in gill nets along the coasts of New Hampshire and Maine (Kraus et al., 1997). The signal lasted for approximately 300 milliseconds and was repeated every 4 seconds.

NOAA and the USFWS proposed elevating the status of the loggerhead turtle to the nation's list of endangered animals (2010). Although their food supply (horseshoe crabs, blue crabs, menhaden, and croakers) keeps dwindling and their beach nesting habitats (particularly in Florida, their primary nesting area) have been mostly destroyed by coastal development, the principal source of mortality is commercial fisheries (Fig. 19.17). Although the National Marine Fisheries Service has required that shrimp nets have turtle excluder devices, more than 50 countries engage in the longline tuna fishery industry. Hundreds of thousands of hooks are baited with squid and are set in the middle of pelagic nurseries. Turtles die when they swallow the hooks.

Sea otters (*Enhydra lutris*) living off the Alaskan coast play a major role in marine ecosystems by limiting the distribution and abundance of sea urchins, thereby promoting kelp forest development. By feeding on sea urchins, otters help preserve kelp forests that provide food for a wide range of species, from barnacles to bald eagles. Since 1990, however, Estes et al. (1998) have documented a 90 percent decline in sea otter populations in western Alaska's Aleutian Islands. Evidence points to increased predation by orcas (*Orcinus orca*). Orcas, whose usual food sources are seals and sea lions, have begun feeding on sea otters, whose numbers have plummeted from about 53,000 in the 1970s to 6,000 in 1998 along an 800 km (500 mi.) span of coastline. As sea otter numbers decline, sea urchin density and kelp deforestation increase. Estes et al. (1998) believe that whales are feeding on otters because of a decline in the numbers of sea lions and seals. The reason for the seal and sea lion decline is controversial. It may be due to intensified trawler fishing in the Bering Sea, which has sharply curtailed or altered the food supply for the whales, or changes in fish populations could also be related to warmer ocean temperatures and/or the local extirpation of baleen whales, which has allowed pollock, a fish low in fat, to flourish.

Figure 19.16. The oil tanker *Jessica* after running aground on San Cristobal Island in the Galápagos Islands in January 2001.

Figure 19.17. Turtle in trouble. A loggerhead turtle trapped in the loops and folds of a drifting net near Barcelona, Spain. After being lifted on board and spending 20 minutes being cut free, the turtle was released and quickly swam away.

A separate population of southern sea otters lives off the coast of central California. This population was listed as threatened in 1977 under the US Endangered Species Act. The population currently consists of 2,000 to 3,000 animals. This population is especially susceptible to oil spills and shootings. They can become entangled in fishing nets and drown, although gill-net closures in Monterey Bay have reduced entanglements and drowning. The USGS's National Wildlife Health Center has investigated southern sea otter deaths since 1992 and reports that approximately 40 percent of these deaths were due to disease. Since sea otters are sentinels of ocean health, if they are getting sick, chances are, so are the oceans. Scientists are working to determine the possible effects of contaminants, stress, and disease on sea otter immune systems and overall health.

The baiji (*Lipotes vexillifer*) (see Fig. 16.11) was the first cetacean to succumb to human pressures, and many people fear that the vaquita (*Phocoena sinus*) (see Fig. 9.63 and page 301) will soon be number two. The vaquita is not only the rarest of the cetaceans, but also the smallest (Pitman and Rojas-Bracho, 2007). The 1.5 m (5 ft.) long vaquita has been known to science only since 1958, when three skulls were found on a beach in the Gulf of California (Sea of Cortez). The entire world population lives in the northernmost portion of the Gulf. Its range is now the smallest of any marine mammal. Nearly the entire population lives in a region less than 64 km (40 mi.) across. Scientists surveyed the vaquitas in 1997, counting 567. The estimated population in 2012 was approximately 100 animals, and by 2016 only about 60 remained. Every year, 20 to 30 vaquitas get caught in gill nets and drown. Since the vaquita's maximum population growth rate is assumed to be like that of other porpoises, only 4 percent a year, the vaquita may have only a few more years left before it goes the way of the baiji.

Whaling

The 1946 International Convention for the Regulation of Whaling established the International Whaling Commission (IWC) as the international body charged with the conservation of whales and the management of whaling. It currently has 89 member governments. Uncertainty over whale numbers led to the introduction of a moratorium on commercial whaling in 1986. This remains in place, although the Commission continues to set catch limits for aboriginal subsistence whaling.

Already among the world's most endangered whale species, North Atlantic right whales have suffered an unusually high number of deaths since early June 2019. At least eight have been reported dead in Canada's Gulf of St. Lawrence—about 2 percent of their estimated total population of about 400. At least three died from trauma after being struck by vessels, and others may have been lethally entangled in fishing gear. Few right whales were born during 2019, and several of the dead whales were females of reproducing age, which makes the high mortality of this period a disaster.

Unfortunately, the moratorium included a clause that allows taking whales for scientific research. Japan has used the clause as the basis for continuing to support its whaling industry. The clause effectively provides a loophole to allow its scientists to catch and analyze hundreds of minke whales each year as part of an ongoing study of whale stocks. Japan recoups slightly more than half of its $75 million operating budget by selling the whales it captures, a sore point among environmentalists who see the income as proof of the program's commercial focus. Between 2005 and 2013, Japan's fleet killed nearly 4,000 minke whales and 18 endangered fin whales. The meat from the whales is sold at fish markets and high-end restaurants. Whale meat became a staple of school lunches in Japan in the postwar era, an action that raised criticism due to allegations of toxic methyl mercury levels in the whale meat.

Norway respected the IWC ban until 1993, then used a loophole to declare itself exempt. Norway has since lifted its annual kill quota of 425 in 1996 and increased it to over 1,200, though whalers usually catch only half that many. Iceland declared itself exempt from the moratorium in 2004. In 2013, Iceland set a quota of hunting 184 fin whales every year for the next five years. Greenland historically has been given permission for its native Inuit to hunt whales for subsistence needs, currently set at 207 kills per year. Critics say the quota is too high; therefore, the surplus will continue to be sold commercially and to tourists. Indigenous peoples living along Alaska's coast have been hunting bowhead whales for thousands of years. The Alaskan Natives were set an overall quota of 306 bowheads from 2013 to 2018; catches are shared among the whole community.

The IWC meets every two years. The September 2018 meeting was in Florianopolis, Brazil. A request from Japan's Institute of Cetacean Research to re-establish commercial whale hunting was rejected, as was a proposal to create a South Atlantic Whale Sanctuary.

Japan's Institute of Cetacean Research operates a program in the Antarctic and, beginning in 1994, a second program in the North Pacific Ocean. The quota for the North Pacific program for 2008 was 340 minke whales, 50 Bryde's whales, 100 sei whales, and 10 sperm whales. The IWC established a Southern Ocean Sanctuary in 1994 (Japan was the only member nation that voted against it), but since then, Japan has continued to take all of its annual catch of Antarctic minke whales from within the sanctuary boundary. In 2000, Japan announced that it would also begin hunting Bryde's and sperm whales. During the 2009–10 season, the Japanese fleet included a factory ship, four harpoon ships, and two security patrol vessels. The Japanese-set quota during the 2009–10 season included 935 minke whales, 50 fin whales, and 50 humpback whales. The total is more than all other countries kill for scientific, commercial, and subsistence purposes combined. Every year there are increasingly violent confrontations between conservationists and Japanese whaling vessels. The International Court of Justice ruled against Japan's whaling operations in the Antarctic in 2014.

In 1999, the Australian government established the Australian Whale Sanctuary to protect dolphins and whales from being hunted in waters within the Australian government's jurisdiction. In 2008, the Federal Court of Australia found Japan in contempt for killing protected whales within the Sanctuary. In 2015, a Japanese fishing company was found guilty of willful contempt and fined $1 million. The International Court of Justice ordered Japan to halt their whaling operations in the Antarctic in 2014. Japan canceled their program for 2015, but then resumed under new programs it deemed compliant with the court's ruling. Japan then developed a brand-new research plan that would allow its ships to kill nearly 4,000 minke whales over the following 12 years (2016–2028). In March 2016, Japan announced that its whaling boats had returned from Antarctic waters hauling the carcasses of 333 minke whales—including some 157 pregnant females (Plumer, 2016). On December 26, 2018, Japan announced that it will withdraw from the IWC and resume commercial whaling in its own waters (Normile, 2019). Japan intends to continue to participate in IWC as an observer, but it will no longer contribute to the group's budget.

New regulations from the International Maritime Organization (IMO), which took effect in July 2011, make it illegal for Japan's *Nisshin Maru*, the world's only whaling factory ship, to operate below 60° south, but all of the Japanese pelagic whaling is done inside the area. The new rules prohibit ships using heavy oil in the Antarctic Treaty System area because of the harm a spill would cause. Furthermore, the IMO's *Guidelines for Ships Operating in Ice-Covered Waters* put requirements on safety and hull-strength that the *Nisshin Maru* does not fulfill. Nevertheless, a helicopter from the conservation organization Sea Shepherd photographed the *Nisshin Maru* with a slaughtered whale on its deck within the Australian Whale Sanctuary in January 2017.

International Trade

The 175-nation Convention on International Trade in Endangered Species met in Qatar in March 2010. Fishing nations, especially Japan, won a victory over environmentalists when a US-backed proposal to ban export of the Atlantic bluefin tuna was rejected, even though scientists report that populations of the fish are down 75 percent—primarily because Japan imports 80 percent of the Atlantic bluefin tuna to satisfy the appetites of Japanese sushi lovers. In another blow to conservationists, a proposal to ban the international sale of polar bear skins and parts failed to pass. Proponents argued that the sale of polar bear skins was compounding the loss of the animals' sea ice habitat because of climate change. They cited projections that the bear's numbers, which are estimated at 20,000 to 25,000, could decline by two-thirds by 2050. Fortunately, African governments voted to uphold the 21-year-old ban on ivory sales on the grounds that sales would hurt already declining African elephant populations by encouraging illegal hunting.

Noise Pollution

There is heated debate over the threat that human-made noise poses to whales and other sea life. All whales are acoustically active and may be affected by vessel strikes, geophysical surveys, construction, and operations associated with offshore energy installations. Many researchers feel that the pinging noises produced by some underwater sonars can deafen and daze some kinds of whales, leaving them vulnerable to stranding and shark attack.

The US Navy has developed and, beginning in 2003, deployed a dangerous low frequency active (LFA) sonar system across 75 percent of the world's oceans. In 2004, the Navy acknowledged that vessels on maneuver off Hawaii used their sonar periodically in the 20 hours before a large pod of almost 200 melon-headed whales unexpectedly beached themselves on the shoreline of a Kauai bay. The submarine protection system operates by blasting hundreds of thousands of square miles of ocean habitat with extremely loud sound. Its shock waves can maim, deafen, or kill whales at close range and, even at a distance of 483 km (300 mi.), can interfere with behaviors essential to the whales' very survival. The Navy itself has conceded that warships carrying LFA sonar may harm thousands of marine mammals—the kind of impact normally prohibited by the Marine Mammal Protection Act. Warships towing underwater loudspeakers flood the ocean with an effective noise level of 235 decibels—comparable to a dynamite blast. The resulting shock waves can destroy eardrums, cause lungs to hemorrhage, and even kill. In 2000, the testing of high-intensity Navy sonar in the mid-frequency range caused a mass stranding of whales in the Bahamas. Whales from at least three different species died, their inner ears bleeding from the extraordinary power of the sonar signal. After the stranding, the area's entire populations of rare Cuvier's beaked whales simply disappeared. Scientists believe that they either abandoned their habitat or died at sea.

At longer ranges, LFA sonar noise dissipates, but is still extremely dangerous. At 180 decibels, the sound can cause permanent hearing loss in marine mammals after a single transmission. At 64 km (40 mi.) from the source, LFA noise registers 165 decibels—more intense than the 160-decibel level documented by the Navy to cause disorientation, memory loss, and seizures in human divers. At 483 km (300 mi.) from the source, the Navy has calculated that LFA noise may still reach 140 decibels—hundreds of times more intense than the level at which gray whales begin swerving from their migration path to avoid sonar noise. In addition, the noise from LFA transmitters travels in the very same low-frequency range that many large whales, including humpbacks, use for communicating. The highly evolved systems of communication—based on an acute sense of hearing—of these whales enable them to find food, follow migratory routes, locate one another over great distances, and care for their young. By jamming their communication channels, LFA sonar is tampering with critical activities—feeding, breeding, migrating—in ways that we simply do not understand. Whale biologists have cautioned that the resulting impacts could threaten the survival of entire whale populations—including endangered species whose numbers are already depleted. The Navy has provided a group of acoustics engineers and whale biologists with ample funds, ships, and state-of-the-art equipment to conduct some of the first large-scale, meaningful, controlled experiments on the effects of sound on marine mammals. On January 28, 2010, 14 conservation groups filed a court suit challenging the US Navy's decision to build its $100 million Undersea Warfare Training Range next to the only known calving ground for the critically endangered North Atlantic right whale. The project threatens the already precarious survival of right whales by introducing multiple known threats—ship strikes, entanglement, and noise disturbances—into an area critical to mothers and calves. Construction of the facility was completed with a ribbon cutting on April 26, 2016. Several studies investigating the impacts of sonar on marine mammals are currently in progress.

In January 2018, the US Department of the Interior proposed opening formerly protected United States coastal waters to hazardous offshore drilling, further imperiling our own fragile marine ecosystems. Preliminary plans call for a five-year draft proposal (2019–2024) for offshore oil and gas leasing programs that would put nearly all of the United States' coastal waters on the table for drilling on its outer continental shelf. The National Marine Fisheries Service says that it has authorized permits under the Marine Mammal Protection Act for five companies to use seismic air guns to find oil and gas formations deep beneath the Atlantic Ocean floor from Delaware to Central Florida There have been no sales in the Atlantic since 1983, and there are no existing leases.

In March 2019, however, a US District Court judge restored President Obama's restrictions. In 2015, President Obama halted exploration in coastal areas of the Beaufort and Chukchi seas and the Hanna Shoal (an important area for walruses). In late 2016, he withdrew most other potential Arctic Ocean lease areas—about 98 percent of the Arctic outer continental shelf. The bans were intended to protect polar bears, walruses, ice seals, and Alaska Native villages that depend on the animals. In the Atlantic, Obama banned exploration in 15,375 km^2 (5,937 mi.^{2}) of underwater canyon complexes, citing their importance for marine mammals, deepwater corals, valuable fish populations, and migratory whales.

Whales have acute underwater hearing, but they might not be able to pick up the sounds of a rapidly approaching cargo ship soon enough to move out of the way. The underwater background noise of busy ports is such that whales may grow inured to it and be unable to distinguish the threat of an oncoming ship. Large ships cannot slow or alter course easily, and whales cannot necessarily hear oncoming ships. The front of a ship can block the engine noise coming from the propeller on back of the ship, a phenomenon known as acoustic masking or Lloyd's mirror effect. Under a federal rule first imposed in 2008 to protect endangered right whales, all ships 20 m (65 ft.) or longer are limited to speeds of 10 knots or slower within 32 km (20 mi.) of ports. Experiments with alarms, forward-facing sonar, and thermal detection have not proven useful.

The governing council of the Galápagos Islands has banned noisemaking fireworks to protect the sensitive and unusual species living there (Brainard, 2019). In its December 2018 decision, the council said pyrotechnic bangs had harmed local animals, inducing rapid heart rates, cardiac diseases, and stress that threatened their survival. Fireworks that produce light but not sound are permitted.

Mountaintop-Removal Coal Mining

Scientific evidence has proven that mountaintop-removal coal mining destroys forests and streams and threatens human health. The consequences of this mining in eastern Kentucky, West Virginia, and southwest Virginia are pervasive and irreversible. As of 2017, Appalachian Voices reported that mountaintop removal has already destroyed more than 500 mountains encompassing more than 405,000 hectares (1 million acres) of Central and Southern Appalachia. This method of coal mining contaminates well water and produces toxic dust and fishes that are tainted with the chemical selenium (Biello, 2010). A study published by the USGS reveals that the number of fish species present in the streams of West Virginia have dropped by half as the result of mountain top mining (Hitt and Chambers, 2014). They found no evidence that fish communities have recovered over time, and instead observed persistent effects of mountaintop mining associated with water quality degradation. Hendryx and Luo (2014) documented an increase in the number of human cardiovascular and respiratory illnesses in areas of West Virginia where mountaintop removal and other forms of coal mining were prevalent. One positive outcome has been that some flattened regions have been reseeded in grasses and are being utilized for elk reintroduction in southwestern Virginia and eastern West Virginia.

Hunting

Human activities are driving population declines across species, but identifying actual sources of individual mortality from human activities is challenging. Between 1970 and 2018, Hill et al. (2019) documented 42,755 mortalities of known cause from 120,657 individuals representing 305 vertebrate species in 1,114 studies. They found that 28 percent of individual mortalities were caused directly by humans, with larger species of birds and mammals most affected. Predation (55 percent) and legal harvest (17 percent) were the leading sources of mortality. Although most of the mortality was due to natural processes, that humans directly cause more than a quarter of the mortality for animals in the wild emphasizes the degree to which we affect natural systems.

CONSERVATION

Value of Museum Collections

Vertebrate collections range in size from those large collections maintained by such institutions as the American Museum of Natural History and the Smithsonian Institution (Fig. 19.18) to collections of only a few specimens maintained by single individuals. The curatorial care provided ranges from excellent to nonexistent. Professional societies, like the American Society of Mammalogists and the American Society for Systematics Collections, have attempted to develop standards for curatorial care. Properly maintained collections are inspected at intervals and are certified by the appropriate society. In cases where a collection cannot be maintained, the institution is encouraged to donate the collection to an organization that can provide the necessary curatorial care to prevent the possibly irreplaceable loss of data.

Figure 19.18. Museum collections serve as permanent repositories for voucher specimens and provide reference collections for researchers who need to examine a large series of specimens from a given area. The collection shown here is part of the mammal collection in the Museum of Natural History at the Smithsonian Institution in Washington, DC. These specimens are available for a variety of studies.

Vertebrate collections are used in many ways (Suarez and Tsutsui, 2004; Clemann et al., 2014; Museum of Vertebrate Zoology at Berkeley, 2015). They serve as a permanent repository for voucher specimens—that is, type specimens, locality records, and so forth. They also provide a reference collection for researchers needing to examine a large series of specimens from a given area or areas. In the case of extinct species, like passenger pigeons (*Ectopistes migratorius*), museums often retain the only evidence of their existence. In 2013, researchers discovered the first new species of American carnivore described in 35 years—the olinguito—which had been stored at The Field Museum in Chicago since the early 1900s, but had been misidentified as an existing sister species (Helgen et al., 2013; McDermott, 2013). Natural history collections are absolutely essential to biodiversity research. Creating a complete inventory of life on Earth is impossible without reference to museum specimens, and the associated taxonomy and systematics is needed to make rational decisions about conservation.

The Biological Survey Unit (BSU) is administered by the USGS and is located in the Smithsonian Institution's National Museum of Natural History (NMNH). Since 1889, the BSU has managed the North American collections of nonfish vertebrates. The BSU has been instrumental in tracking biotic diversity in North America and beyond, as well as anthropogenic impacts on plant and animal life. This mission is more timely now than ever before—we face likely future extinctions linked to human activities, and the conversion of natural habitats for human use places a premium on understanding the distributions and dynamics of wild taxa. BSU activity has included collection of many thousands of specimens from multiple states and foreign countries, loans of scientific specimens to institutions in the United States and abroad, hosting visiting researchers, and publication of seminal scientific contributions. This small unit collects and curates foundational resources upon which untold future discoveries will be based.

During the 1960s, populations of several species of fish-eating birds, including the bald eagle, brown pelican, osprey, and others, became seriously threatened because of the birds' inability to fledge young. Although the birds were breeding and females were laying eggs, a high percentage of eggshells broke, resulting in the loss of young prior to hatching. By measuring the thickness of eggshells collected prior to 1940 in museum collections and comparing them with recent shells from broken eggs in nests, researchers showed that eggshells had become much thinner and, thus, more susceptible to breakage. Further investigation linked the manufacture and use of the chlorinated hydrocarbon DDT to the eggshell thinning. In 1939, entomologist Paul Mueller had discovered that DDT was a potent insecticide, and it soon became the world's most-used pesticide. Birds at the top of the food chain were subject to the cumulative effects of all the chlorinated hydrocarbons previously ingested by their prey. This discovery was critical in the successful effort to ban DDT and either restrict or ban other chlorinated hydrocarbons, like aldrin, dieldrin, chlordane, mirex, and Kepone, in the United States. These broad-spectrum insecticides kill insects by causing convulsions, paralysis, and death, and they persist in the environment for up to 15 years. The discovery of the cause of eggshell thinning undoubtedly saved a number of species from extirpation, if not extinction. Unfortunately, chlorinated hydrocarbons are still widely used in many other parts of the world, especially in less developed countries.

By means of the polymerase chain reaction (PCR), molecular biologists are now able to extract DNA from many parts of museum specimens, including dried skin, bone, hair, feathers, and eggshells. DNA can be extracted, amplified, and sequenced from archaeological and museum specimens in order to study the relationships of extinct and extant forms. In addition, researchers now can compare modern and historical specimens of the *same* extant species in terms of individual and geographical variation in mitochondrial DNA (mtDNA) (Thomas et al., 1990). Thus, historical trends of genotype frequencies can be directly measured. Museum collections could be untapped troves of genetic material.

Concerning the value of museum collections, Diamond (1990a) stated: “Old specimens constitute a vast, irreplaceable source of material for directly determining historical changes in gene frequencies, which are among the most important data in evolutionary biology. Until PCR became available, those data were lost forever as soon as the gene-bearing individual died. Now, however, museums with large, well-run collections of specimen series large enough for statistical analysis will be at the forefront of research in molecular evolution.”

A survey and directory of mammal collections of the Western Hemisphere were reported by Dunnum et al. (2018).

Ecoregions

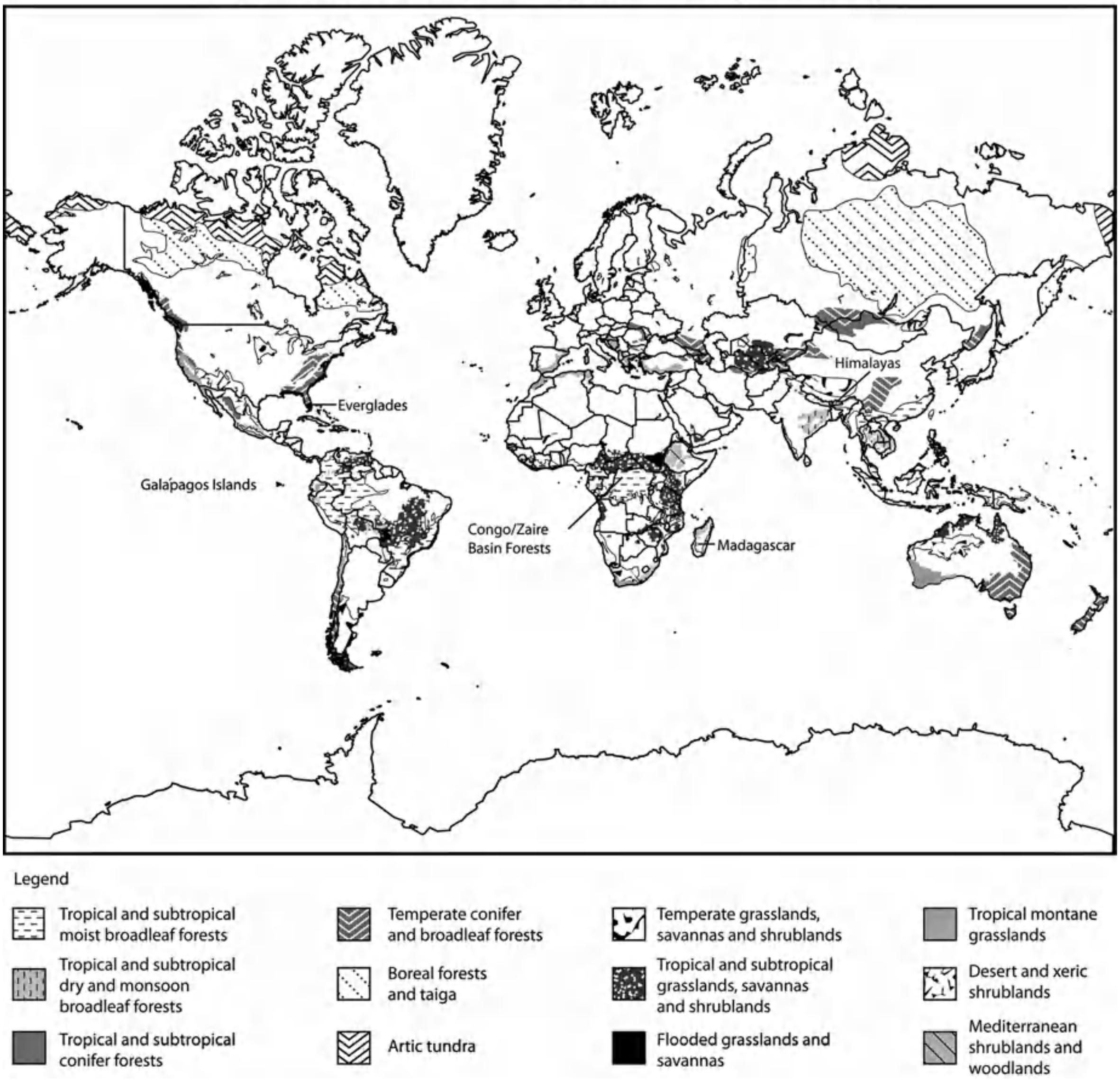
WWF scientists have identified approximately 200 key “ecoregions” that are all important for their rich diversity of species and other unique biological features (Fig. 19.20a, b). The “Global 200” is a centerpiece in the WWF’s campaign to stimulate public action aimed at protecting the Earth’s most valuable harbors of biological diversity. A critical feature is the emphasis on conserving a full representation of the world’s diverse ecosystems, including not only tropical rain forests and coral reefs, but also tundra, tropical lakes, and temperate broadleaf forests. **Ecoregions** define geographically distinct assemblages of natural communities that share a large majority of their species, ecological processes, and environmental conditions. Ecoregions function efficiently as conservation units at regional scales because they encompass similar biological communities and roughly coincide with the regions over which key ecological processes most strongly interact. They can be defined for marine, freshwater, and terrestrial ecosystems. The Global 200 will hopefully serve as a powerful tool for conservation-planning and priority-setting.

World Heritage Sites

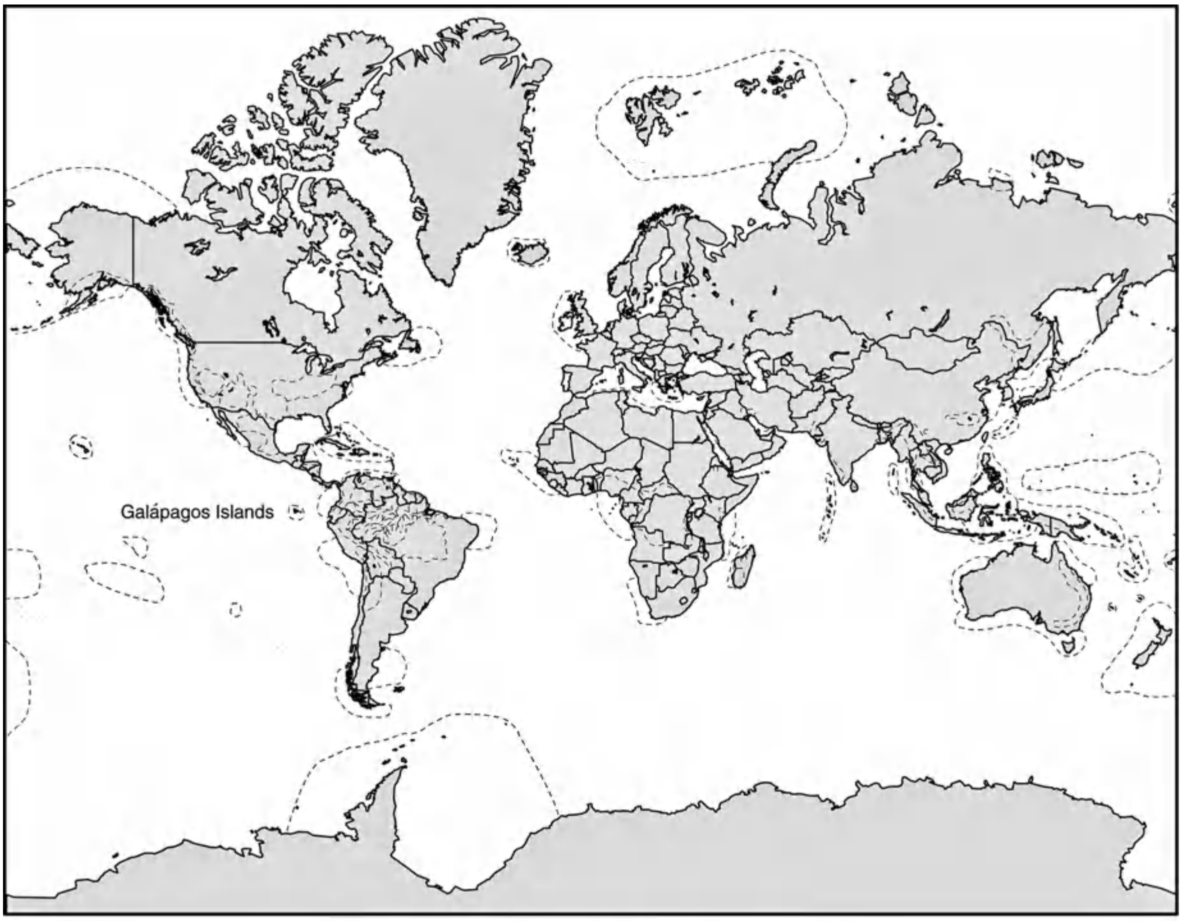
The United Nations has identified over 200 Natural World Heritage Sites (NWHS). These sites, which span the globe, are considered to have outstanding universal values that transcend national boundaries. They are globally recognized as containing some of the Earth's most valuable natural assets. Allan et al. (2017) found that 63 percent of the sites that could be analyzed had experienced an increase in human pressures, including encroaching roads, agriculture, infrastructure, and settlements, since 1993. Human pressure on NWHS increased on all continents except Europe, where it decreased significantly. Komodo National Park in Indonesia (home to about 5,700 Komodo dragons, which live nowhere else in the world outside of zoos), underwent one of the biggest increases in human pressure. Of those sites that contain forests, 91 percent of those analyzed had experienced some loss of those forests since 2000. The worst losses were in North America and Australia. The Waterton-Glacier International Peace Park, crossing the Canadian and US border, lost about a quarter of its forested area, while Wood Buffalo National Park in Canada lost 12 percent and Yellowstone National Park lost 6 percent. The researchers found that, on average, human pressure increased faster and more forest loss occurred in areas surrounding NWHS, suggesting they are becoming increasingly isolated and are under threat from processes occurring outside their borders.

Endangered Species

Studies of the geographic distribution of endangered species in the United States were undertaken by Dobson et al. (1997) to determine whether significant correlations exist in the geographic distributions of different groups of endangered species, and whether such correlations, if present, could be used as indicators for identifying potential areas to protect for other poorly known taxa. These studies revealed "hot spots" of threatened diversity, where the ranges of many endemic species overlap with intensive urbanization and agriculture, but no consistent correlations existed in the distributions of endangered species from different taxa. However, the presence of endangered birds, amphibians, and reptiles provided a more sensitive indication of overall endangered biodiversity within any region. Conserving plant species maximizes the incidental protection of all other species groups. The greatest number of endangered species in the United States occur in Hawaii, Southern California, the southeastern coastal states, and southern Appalachia (Fig. 19.20). Two counties were hot spots for three groups: San Diego, California (fish, mammals, and plants), and Santa Cruz, California (arthropods, amphibians, reptiles, and plants). Nine counties were found to be hot spots for two groups: Hawaii, Honolulu, Kauai, and Maui, Hawaii; Los Angeles and San Francisco, California; Highlands and Monroe, Florida; and Whitfield, Georgia. Except for these locations, the key areas for most groups overlap only weakly, which suggests that the endangered species hot spots of one group do not necessarily correspond with those for other groups.



(a) Terrestrial ecoregions (approximate original extent)

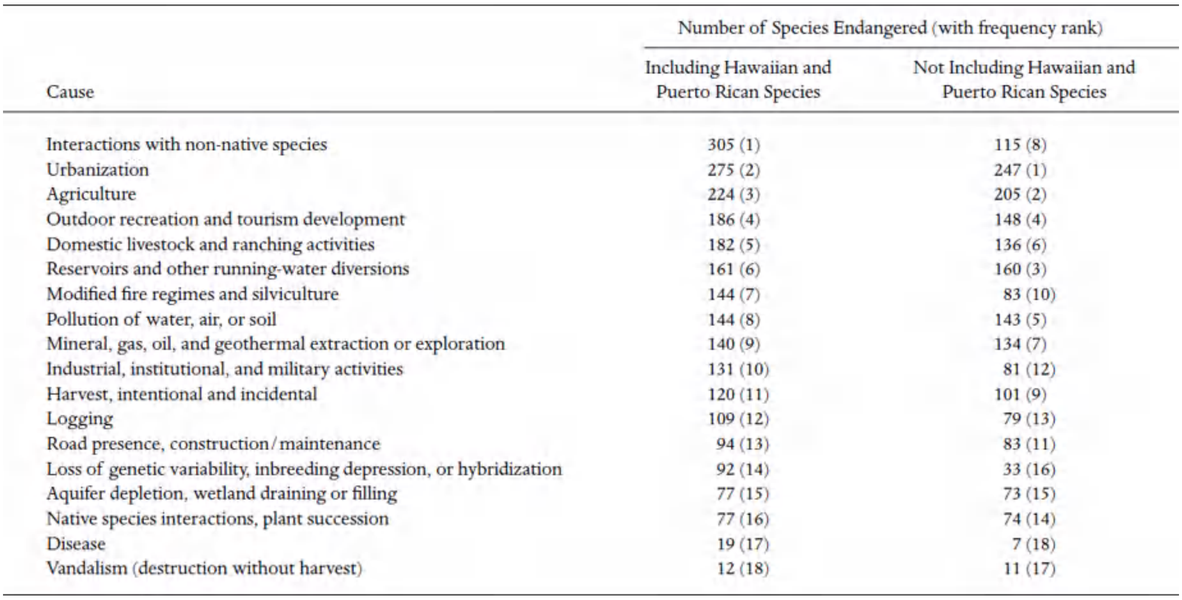


(b) Marine and freshwater ecoregions

Figure 19.19. (*a*) Terrestrial ecoregions identified by World Wildlife Fund scientists. Ecoregions were selected on the basis of their rich diversity of species and other unique biological features. (*b*) Marine and freshwater ecoregions identified by World Wildlife Fund scientists.

Figure 19.20. "Hot spots" of threatened diversity, as determined by Dobson et al. (1997). These are areas where the ranges of many endemic species overlap with intensive urbanization and agriculture. The counties shown contains 50 percent of the listed species for each taxonomic group. The analysis identified two counties that contain large numbers of endangered species from three groups and nine counties that contain large numbers of species from two groups. (Hawaii not to scale).

Table 19.2. Causes of Endangerment for Species Classified as Threatened or Endangered by the US Fish and Wildlife Service



	Number of Species Endangered (with frequency rank)	
Cause	Including Hawaiian and Puerto Rican Species	Not Including Hawaiian and Puerto Rican Species
Interactions with non-native species	305 (1)	115 (8)
Urbanization	275 (2)	247 (1)
Agriculture	224 (3)	205 (2)
Outdoor recreation and tourism development	186 (4)	148 (4)
Domestic livestock and ranching activities	182 (5)	136 (6)
Reservoirs and other running-water diversions	161 (6)	160 (3)
Modified fire regimes and silviculture	144 (7)	83 (10)
Pollution of water, air, or soil	144 (8)	143 (5)
Mineral, gas, oil, and geothermal extraction or exploration	140 (9)	134 (7)
Industrial, institutional, and military activities	131 (10)	81 (12)
Harvest, intentional and incidental	120 (11)	101 (9)
Logging	109 (12)	79 (13)
Road presence, construction/maintenance	94 (13)	83 (11)
Loss of genetic variability, inbreeding depression, or hybridization	92 (14)	33 (16)
Aquifer depletion, wetland draining or filling	77 (15)	73 (15)
Native species interactions, plant succession	77 (16)	74 (14)
Disease	19 (17)	7 (18)
Vandalism (destruction without harvest)	12 (18)	11 (17)

Source: From Czech and Krausman, 1997. Used with permission.

Czech and Krausman (1997) compiled a database of the 877 American threatened and endangered species listed by the USFWS up to 1995 and the causes of their endangerment that have been operational since passage of the Endangered Species Act. Eighteen causes of endangerment were identified and ranked (Table 19.2). Most of these result from habitat destruction caused by human activities.

* * *

These are the factors that must be taken into consideration by conservationists, scientists and researchers, governmental organizations, and others if we are going to avoid losing vertebrates through extirpation and extinction. Education of the public and politicians is critical. Should the focus be on specific species or on preserving and saving critical habitats? As noted earlier in this chapter, biodiversity is essential for human health, economies, food production and cultures. We DO NOT want to saw off the limb that we are sitting on.

Review Questions and Topics

1. Will a baby born in a developed country have more or less impact on the world's resources than a baby born in a developing country?
2. Give several reasons that human population growth is causing many of the problems that are facing other vertebrate species.

3. Define biodiversity. Why is it important to maintain biodiversity?
4. What do you think would have happened to biodiversity if extinction rates occurred throughout evolutionary history at the same rate they have been occurring during the past 50 years?
5. Define fragmentation in ecological terms. What are its effects?
6. Give several reasons why tropical forests are vital to the world's ecosystem.
7. Give several reasons for the alarming decline in the numbers of many species of neotropical migrating birds.
8. What difference could the loss of essentially all the remaining old-growth tropical forests and old-growth forests in North America have on your life and the lives of your descendants?
9. Discuss the major features of a biosphere reserve. What is the significance of each?
10. Is a protected area "useless" because it does not add significantly to economic growth? Explain. Describe the usefulness of an area in ecological terms.
11. List several ways in which vertebrate museum collections are valuable to researchers.
12. How does the ecoregion approach differ from previous efforts to preserve a particular species?
13. List 10 activities you engage in each day that harm the environment. List 10 ways in which you might reduce the harmful effects of these activities.

Supplemental Reading

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Vertebrate Internet Sites

1. National Grasslands

www.fs.fed.us/grasslands

Website for the National Grasslands. History of grasslands, resources, descriptions of the 20 grasslands, Grassland Ecosystem Services, and more.

2. Community Environmental Legal Defense Fund (CELDF)

   www.celdf.org

   Nonprofit, public-interest law firm assisting communities to advance rights for a healthy environment. CELDF's International Center for the Rights of Nature works with communities, indigenous peoples, and governments to advance rights of nature legal frameworks.

3. Conservation International

   www.conservation.org

   Conservation International works to find funding to ensure that the most critical areas on Earth remain intact. Since 1987, it has helped protect more than 6 million km^2 (2.3 million mi.^{2}) of land and sea in 77 countries.

4. TRAFFIC

   www.traffic.org

   World's largest wildlife trade monitoring program. A global expert on wildlife trade issues. TRAFFIC is an international network with a culturally diverse staff in 21 offices on five continents, and conducts ongoing research worldwide.

5. Ducks Unlimited Canada

   www.ducks.ca

   Mission is to conserve wetlands and associated habitats for the benefit of North America's waterfowl, which in turn provides healthy environments for other wildlife and people.

20 | Climate Change

Humankind has not woven the web of life. We are but one thread within it. Whatever we do to the web, we do to ourselves. All things are bound together. All things connect.

Chief Seattle, 1855

INTRODUCTION

The subject of climate change has been referred to in several chapters. It is of such overwhelming significance that a discussion of its possible ramifications, including global warming, greenhouse gases, melting of glaciers, rising sea levels, desertification, northward migration of plants and animals, as well as its effects on plant blooming and migratory species (**phenology**), warrants special consideration.

GLOBAL WARMING

Scientists no longer doubt that global warming is occurring. Although some researchers dispute specific aspects of global warming, most of the world's leading climate scientists have concluded that global warming is real and that carbon dioxide is largely to blame.

Given the size and tremendous heat capacity of the global oceans, it takes a massive amount of accumulated heat energy to raise Earth's average yearly surface temperature even a small amount. Behind the seemingly small increase in global average surface temperature over the past century is a significant increase in accumulated heat. That extra heat is driving regional and seasonal temperature extremes, reducing snow cover and sea ice, intensifying heavy rainfall, and changing habitat ranges for plants and animals—expanding some and shrinking others.

The National Aeronautics and Space Administration (NASA) recognized 2009 as the second-warmest year on record and the end of the warmest decade (Voiland, 2010). However, the average annual US temperature for 2012 was 12.96°C (55.32°F), 0.5°C, or one full degree Fahrenheit, higher than the old record set in 1998. According to the National Oceanic and Atmospheric Administration (NOAA), July 2019 was the hottest month measured on Earth since records began in 1880—the latest in a long line of peaks that scientists say backs up predictions for human-caused climate change. July was 0.96°C (1.71°F) warmer than the twentieth century average of 15.8°C (60.4°F) for the month. According to NOAA's records, 9 out of the 10 hottest Julys on record globally have occurred since 2005, and July 2019 was the 43rd consecutive July above the twentieth century average. The first seven months of 2015 were the hottest January-to-July span on record. The warmest year on record for the Earth's land and oceans was 2016. That is followed by 2015, 2017, and 2018. Depending on the source, the year 2017 was either the second hottest, according to NASA, or the third hottest, according to NOAA, year on record. The global average temperature in 2017 was 14.73°C (58.51°F), which is 0.84°C (1.51°F) above the twentieth century average and just behind 2016 and 2015, according to NOAA.

Global warming is thought to be caused primarily by an increase in the amounts of **greenhouse gases**, like carbon dioxide, methane, and some industrial gases like chlorofluorocarbons (CFCs), spewed into the atmosphere through human activities. Carbon dioxide is increasing in the atmosphere as a result of the burning of fossil fuels (coal, oil, and natural gas) (Fig. 20.1), the destruction of forests, and some agricultural activities. The top two CO_2 emitters are coal-fired power plants in Georgia. Other coal-fired power plants in the top 10 are located in Indiana, Alabama, Texas, Arizona, Tennessee, and Minnesota. These greenhouse gases warm the planet by trapping heat in the atmosphere, thus causing the so-called greenhouse effect. Most experts agree that the accumulation of greenhouse gases in the atmosphere is warming the

Earth’s climate at an unprecedented rate (Ramanathan, 1988; Schneider, 1989) (Fig. 20.2). Just exactly how fast is still controversial. Some climate models are predicting that within 100 years the Earth will not only be warmer than it has been during the past million years, but the change will have occurred more rapidly than any on record. In April 2010, the National Research Council reported that ocean chemistry was changing faster than it had in hundreds of thousands of years because of the carbon dioxide being absorbed from the atmosphere. Nearly a third of carbon dioxide emissions end up in the oceans, triggering a chemistry change that makes the water more acidic, dissolving the shells of sea creatures. The ocean is almost 40 percent more acidic than it used to be.

Figure 20.1. Pollutants, including carbon dioxide and particulates, entering the atmosphere as a result of burning fossil fuels.

In addition, since 1978 an upward trend in total solar irradiance of 0.036 percent per decade has been verified (Willson, 1997). If sustained, this upward trend could also result in rising global temperatures. Large wildfire activity in the western United States increased suddenly and markedly in the mid-1980s with higher large wildfire frequency, longer wildfire durations, and longer wildfire seasons (Westerling et al., 2006). These increases are strongly associated with increased spring and summer temperatures and an earlier spring snowmelt.

Climate change will have a rapidly increasing effect on the structure of global ecological communities over the next few decades, with amphibians and reptiles being significantly more affected than birds and mammals (Newbold, 2018). It is predicted to overtake land use as a major threat to global diversity. Wildlife in even the best-protected and best-managed reserves could be depleted in a few decades if such climate changes take place.

Male sensitivity to heat is recognized in endotherms, but ectotherms have received limited attention, despite comprising most life forms on Earth and being more influenced by temperature variation. Using a flour beetle model system, Sales et al. (2018) found that heatwave conditions —5°C to 7°C (41°F–45°F) above optimum for five days—damaged male but not female reproduction. Heatwaves reduce male fertility and sperm competitiveness, and successive heatwaves almost sterilize males. Heatwaves reduce sperm production, viability, and migration through the female. Transgenerational impacts were also reported with reduced reproductive potential and lifespan of offspring when fathered by males, or sperm, that had experienced heatwaves. This male reproductive damage under heatwave conditions provides one potential driver behind biodiversity declines and contractions of both vertebrates and invertebrates through global warming.

Figure 20.2. Blackberry leaf showing ozone damage (60 percent stippling).

Growing seasons are getting longer, glaciers are disappearing from mountaintops around the globe, sea levels are rising, and drought is affecting many areas. Severe drought during the summer of 2016 was partially responsible for the devastating fire that burned over 6,880 hectares (17,000 acres), destroyed 2,500 structures, and killed 14 people in Great Smoky Mountains National Park and surrounding areas in eastern Tennessee in November 2016. It was the state's deadliest wildfire in a century. Rising sea levels will mean the potential loss of coastal wetlands worldwide, together with their valuable fish and wildlife species. Australian scientists recently announced the first documented extinction of a mammal owing to human-caused climate change. Their report said rising sea levels "almost certainly" wiped out the Great Barrier Reef's only endemic mammal species, a rodent known as Bramble Cay melomys (Howard, 2019). Last seen by researchers in 2009 and declared extinct by the Queensland Government and University of Queensland researchers in 2016, it was formally declared extinct by the International Union for Conservation of Nature (IUCN) in May 2015 and the Australian government in February 2019.

Weather Patterns

Climate change can disrupt long-standing weather patterns. It is linked to heavier precipitation, including snowstorms. For example, around the Great Lakes region during warmer winters, the lakes are less likely to freeze over or are freezing later; therefore, surface water evaporation is recharging the atmosphere with moisture. The result is increased snowfall. Warmer air holds more water vapor than cold air does. The increased evaporation from land and sea leads to more drought but also to more precipitation, since what goes up eventually comes down. Global warming has added 4 percent more moisture to the atmosphere since 1970 (McKibben, 2010). Higher temperatures may cause not only growth in the number of violent storms, like hurricanes and typhoons, but also an increase in their strengths. The number of "extreme events" like downpours and floods has grown steadily; the most intense storms have increased by 20 percent across the United States in the past century.

Rising Sea Levels

Prior to the twentieth century, global sea levels had been stable for about 3,000 years. Sea levels began rising during the twentieth century with the rising being accelerated due to global warming. As the world warms, oceans are getting hotter, causing them to expand. Rising sea levels due to melting of sea ice and polar ice caps and expansion of water will flood some of the coastal areas where most of the world's population resides. Storm surges will be capable of much greater damage. Sea levels have risen nearly 21 cm (8 in.) worldwide since 1880, but they do not rise evenly. According to tide gauge data collected by NOAA, sea levels have climbed about 30.5 cm (12 in.) or more in some US cities because of ocean currents and land subsidence—46 cm (18 in.) in Norfolk, Virginia; 30.5 cm (12 in.) in Charleston, South Carolina; and 63.5 cm (25 in.) in Galveston, Texas. At the current rate, the world's oceans, on average, will be at least 61 cm (2 ft.) higher by the end of the century compared to today. Iconic locations from American history—from Jamestown to Cape Hatteras to Charleston—could be underwater by the end of the century (Anderson et al., 2017). Some homeowners have already begun raising their homes to prevent flooding (Fig. 20.3).

The predicted changes could drastically affect ecosystems and the distribution and existence of many vertebrate species (Poiani and Johnson, 1991). The impact of climate change on marine vertebrates, including marine fishes, mammals, turtles, and seabirds, and their potential for adaptation has been reviewed by Sydeman et al. (2015). In the Chesapeake Bay region, for instance, the projected relative sea level rise is at least between 61 cm (2 ft.) and 152 cm (5 ft.) by the year 2100. Species like the diamondback terrapin face a loss of crucial beach nesting sites when rising water levels cause beaches to erode and disappear. When rivers get too warm, fishes can experience slower growth rates, lower oxygen levels in the water, and greater susceptibility to toxins, parasites, and disease. If pollution from fossil fuels like coal and oil continues to increase (causing temperatures to rise), as much as 20 percent of the Columbia River and Snake River basins and coastal watersheds of Washington and Oregon could become too warm for many cold-water fish populations by the 2040s. Higher regional temperatures could also change the timing and volume of runoff coming from snowpack and glaciers in nearby mountains, affecting stream flows that fish populations have historically depended on. Earlier peak spring flows and lower-than-normal summer flows can make it more difficult for adult fishes returning from the ocean at their usual time to negotiate obstacles like falls as they navigate upstream to spawn. Excessively high flows in winter, which can result from rapid melting of snowpack or increased rainfall, can cause “scouring” events in which the gravel beds that salmon and other fishes use as nesting sites wash away. Since the mid-1900s, peak snowfall and snowmelt-derived stream flow across the Pacific Northwest have already shifted 10 to 30 days earlier, and snow pack has decreased 11 percent over the same period (Glick, 2005).

Figure 20.3. Some homeowners have begun raising their homes to prevent flooding.

For nearly 30 years, India and Bangladesh argued over control of New Moore Island, a tiny island in the Bay of Bengal. Rising sea levels have resolved the dispute for them: the island is gone. What these two countries could not achieve from years of talking has been resolved by global warming.

Effects on Salamanders

Over the past decade, scientists have documented several population declines in amphibians, including salamanders. But the causes of these declines have been hard to uncover—disease, habitat loss, invasive species, or something else.

One family of salamanders (Plethodontidae), unique because they respire entirely through their skin, play a key role in the ecosystems of the Southern Appalachian Mountains, consuming insects that are too tiny for most other vertebrates. Dr. Karen Lips from the University of Maryland and her colleagues analyzed more than 9,000 salamanders from a dozen plethodontid species—some from museum specimens collected as early as 1950 and others from 85 current locations across the southern Appalachians. Although they did not find widespread evidence of disease, they did notice another trend: the salamanders had gotten smaller. Salamanders collected after 1980 were 8 percent smaller than those from previous decades. The trend was most significant in places that had seen the largest shifts in climate during that time: low elevations with an increase in temperature and a decrease in rain (Caruso et al., 2014).

Lungless salamanders are highly sensitive to changes in their surrounding environment because of the way they breathe through their skin. When the temperature rises, their body speeds up. Using computer modeling, Lips and her collaborators showed that temperature increases in the areas of the Appalachians that have warmed over the past 50 years could speed the salamanders' metabolisms by more than 7 percent.

Lips and her team have not yet confirmed the mechanism by which the change in body size has occurred, although they hypothesize that it is driven by the salamanders' metabolisms. Lips stated: "If it's a little bit warmer, the animal is going to burn through its calories much faster. If availability of extra calories or extra time to forage is limited, the salamanders will grow to a smaller adult size due to this increased calorie burn. And smaller salamanders lay fewer eggs and are more susceptible to predators."

The research team has not yet confirmed that the salamanders' smaller size is behind the documented population declines, though they are confident that climate change is what is driving the shrinkage in body size. An increasing number of ongoing studies are examining the effects of climate change on a variety of species. One such study is examining the effects of climate change on the Flatwoods Salamander (*Ambystoma cingulatum*), particularly in relation to the hydrology of wetlands embedded in fire-maintained longleaf pine stands in Florida.

Effects on Breeding Birds

A comparison of breeding distributions of British birds from 1968 to 1991 revealed that the northern margins of many species moved farther north by an average of 18.9 km (11.8 mi.) (Thomas and Lennon, 1999). Robins are arriving each spring in Wisconsin several days earlier than they did a decade ago. Endangered woodpeckers in North Carolina are laying their eggs about a week earlier than they did 20 years ago. A

National Audubon Society report released in February 2009 found that the purple finch now spends the winter 644 km (400 mi.) farther north than it used to. The report's study of the migration habits of 305 species of birds from 1966 through 2005 found that 177 species had moved northward.

"The State of the Birds: 2010 Report on Climate Change" was issued by the US Department of the Interior in March 2010. According to the report, global climate change poses a significant threat to migratory bird populations, which are already stressed by the loss of habitat and environmental pollution. The report says oceanic birds, like petrels and albatrosses, are at particular risk from a rapidly changing marine ecosystem and rising sea levels. Birds in arid regions and forests show less vulnerability to climate change, but the report says many species struggling in arid regions now, including the endangered golden-cheeked warbler and black-capped vireo in Texas, could be further imperiled by shifting climate conditions.

Phenology

The yellow-bellied marmot—one of the nation's longest hibernating mammals—wakes up in Colorado 42 days earlier on average than it did 17 years ago. Since 1985, red squirrels in the southern Yukon have advanced their birth dates, on average, about 18 days—enabling them to take advantage of the larger spring bloom of spruce cones. And the cherry trees in Washington, DC, bloom about a month earlier than they did a half-century ago (Root et al., 2005). On a global average, signs of spring appear 9.6 days earlier than they did 30 years ago. Europe's spring moved ahead 15 days, while North America's has advanced 6 days, on average. Areas north of 45° north latitude—from Maine to Washington state—saw spring species arriving more than 13 days earlier.

The global environment is changing so fast that the slow evolutionary process of species adaptation may not be able to keep up. Matching the timing of breeding with the local peak in food abundance is crucial to reproductive success in many birds. By advancing the timing of budding, leaf production, and food supply (phenology), climatic warming exacerbates such mismatching. Pied flycatcher numbers in the Netherlands are crashing in places where climate change has knocked the birds' spring migration out of sync with the food bonanza on the breeding ground. In some places, the warming trend has moved up the timing of a short-lived banquet of caterpillars that adult flycatchers feed to their ravenous chicks. The flycatcher numbers in those locations have dropped by about 90 percent (Both et al., 2006).

Northward Movement of Plants and Wildlife

Large and extraordinarily rapid climate-induced changes in the ranges and distribution of small mammals in Michigan have been documented by Myers et al. (2009). Changes consistently reflect increases in species of primarily southern distribution (white-footed mice, eastern chipmunks, southern flying squirrels, and opossums) and declines by northern species (woodland deer mice, southern red-backed voles, woodland jumping mice, least chipmunks, and northern flying squirrels). White-footed mice and southern flying squirrels have expanded their ranges northward over 225 km (140 mi.) since 1980.

The Virginia opossum successfully invaded the United States despite the cold winters and physical barriers to range expansion. A slow but steady migration northward has been underway for several hundred years. In the 1960s, opossums were becoming common in central New York, but most had lost the tips of their ears and the tip of their tail to frostbite. Currently, opossums are found as far north as Toronto, Canada. They are now quite common in most counties bordering Lake Erie, in the Niagara Peninsula, and north to Guelph and the Kitchener-Waterloo area. At least one opossum has been observed crossing the Rainbow Bridge at Niagara Falls.

Nine-banded armadillos and other small mammals are on the move in the United States, expanding into terrains biologists thought highly unlikely just a few years ago. Armadillo expansion in the United States appears to be limited primarily by temperature and rainfall. They have very little body fat and are not good at conserving heat. Taulman and Robbins (1996) stated: “They may be expected to continue their advance up the East Coast to about the region of 41° North Latitude, decreasing to 39° North Latitude across the Midwestern states.” This means that the nine-banded armadillo could establish stable populations from Nebraska to New York, and northeast to Cape Cod. Their current range already encompasses most of Tennessee.

High-mountain species are particularly susceptible to global warming. Computer models show some alpine regions in the western United States heating up an additional –15°C to –10°C (4.5°F to 14.4°F) during the next 100 years. If temperatures warm by 3°C (5°F), researchers estimate the tree line would rise 366 m (1,200 ft.). Trees are already on the move. The low-elevation distribution of Engelmann spruce, which thrives in the subalpine zone, moved 175 to 198 m (575–650 ft.) upslope in three of four watersheds studied in Nevada's Great Basin National Park between 1992 and 2001. Trapped at the top, alpine wildlife is vulnerable to vegetation changes, the invasion of new predators and pests, reduced winter snowpack, and increases in extreme weather events. Pikas (see Fig. 9.54), white-tailed ptarmigan, and even Dall sheep could be adversely affected. Birds like American pipits, horned larks, and rosy finches, all of which are considered "alpine specialists" because they breed atop mountains but migrate to warmer climates during winter, could face breeding challenges. In the East, disjunct populations of the northern flying squirrel (*Glaucomys sabrinus*) (Fig. 20.4a), red squirrel (*Tamiasciurus hudsonicus*) (Fig. 20.4b), southern red-back vole (*Clethrionomys gapperi*) (Fig. 20.4c), and northern water shrew (*Sorex palustris*), which occur in the Appalachian Mountains south to Tennessee and North Carolina, could potentially see their habitat disappear (Burns et al., 2003).

On the other hand, beaver (*Castor canadensis*) (Fig. 20.5) were hard to find in northwestern Alaska several decades ago. Now, there are lots of beavers, lodges, and dams (Perkins, 2018). Beavers may be infiltrating the region for the first time in recent history as climate change makes conditions more hospitable, or the expansion may be a rebound after trapping reduced beaver numbers to imperceptible levels in the early 1900s. Nobody knows for sure. James Ross, an ecologist at the University of Manitoba in Winnipeg, Canada, notes that the biggest effects of the beaver on Arctic ecosystems may come from the added biodiversity within the ponds they create. These "oases on the tundra" will not only provide permanent habitat for fishes and amphibians, but will serve as seasonal stopover spots for migratory waterfowl. Physical changes to the environment could be just as dramatic, thawing permafrost decades faster than climate change alone would (Perkins, 2018).

A study of 171 forest species in Western Europe showed that most of them were shifting their favored locations to higher, cooler spots (Lenoir et al., 2008). Comparing the distribution of species between 1905 and 1985 with their distribution between 1986 and 2005 showed a shift upward of 29 m (95 ft.) per decade. Unlike animals, plants can't just pick up and move in search of a better home. But plant species do move, as seeds and spores that are spread tend to grow better in one place than another—in this case, at higher elevations in preference to lower ones. The quickest to relocate, not surprisingly, were plants with shorter life spans and faster reproduction cycles, like herbs, ferns, and mosses. Not so swift were large, woody plants that reproduce more slowly. In fact, long-lived plants like trees, which reproduce slowly, are more threatened by climate change because they cannot relocate quickly. Threats from climate change to terrestrial vertebrate hotspots in Europe have been discussed by Maiorano et al. (2013). Their study covered a total of 1,149 species of terrestrial vertebrates. Results of the study suggest that the main hotspots of biodiversity of terrestrial vertebrates may be extensively influenced by the climate change projected to occur over the coming decades, especially in the Mediterranean bioregion, posing serious concerns for biodiversity conservation.

(a)

(b)

(c)

Figure 20.4. Disjunct populations of (*a*) the northern flying squirrel (*Glaucomys sabrinus*), (*b*) American red squirrel (*Tamiasciurus hudsonicus*), (*c*) southern red-backed vole (*Myodes gapperi*), and northern water shrew (*Sorex palustris*) in the southern Appalachian Mountains could potentially see their habitats disappear due to global warming.

Over a period of 11 years, the active growing season of plants had advanced by approximately 8 days in northern latitudes (Crick et al., 1997). Fei et al. (2017) analyzed 86 tree species/groups across the eastern United States spanning the last three decades and showed that more tree species have experienced a westward shift (73 percent) than a poleward shift (62 percent) in their abundance. The observed shifts were associated with changes in moisture availability and successional processes in response to climate change.

Crick et al. (1997) presented data from 65 species of birds in the United Kingdom for a 25-year period from 1971 to 1995, showing a significant trend toward earlier laying dates for 20 species (31 percent), with only one species laying significantly later. The shift toward earlier laying for the 20 species averaged 8.8 days.

Species' responses to climate change are individualistic, that is, species in the same communities do not show identical responses. In addition, climate change effects on species residing in flatland systems are more pronounced than previously thought (International Union for the Conservation of Nature, 2003).

Desertification

Hotter, drier tropics may cause some rain forests to become grasslands, whereas cold tundra areas may warm enough to grow forests. Most deserts are likely to become hotter and drier (although the Sahara is expected to get more rain), and agricultural areas will shift.

Figure 20.5. Beaver (*Castor canadensis*) populations have rebounded in many areas after regulations were passed to control their trapping.

ARCTIC

Rising temperatures are wreaking havoc in the Arctic and Antarctic, melting once pristine ice sheets and killing wildlife. A study by NOAA found that 2018 was the second-warmest year on record in the Arctic and the second-worst for sea ice. In winter 2018, ice cover in the Bering Sea reached its lowest extent since constant satellite monitoring began in 1978. The world's northernmost region is now so warm that it sheds ice even in the Arctic winter. The Bering Sea lost an area of ice the size of Idaho during two weeks in February 2019. Toxic algae blooms, typically a warm-water phenomenon, are increasingly common in the region, fatally poisoning seals, walruses, and whales.

Scientists reconstructed the Arctic temperature record of the past 2,000 years, using evidence from tree rings, ice cores, and lake sediment, and found a steady cooling trend in Arctic summer temperatures of about –17°C (0.9°F) during the first 1,900 years (Kaufman et al., 2009). The cooling was caused by a slow natural cycle in Earth’s orbit that continues in this century. The summer cooling would likely be continuing today were it not for the increase of greenhouse gases from fossil fuel burning. One of the most important findings of the study was that it matched the National Center for Atmospheric Research’s climate-system computer model.

The Arctic is warming at a rate twice as fast as the rest of the planet. In September 2007, government scientists predicted that two-thirds of the world’s polar bears (*Ursus maritimus*) will be killed off by 2050—including the entire population in Alaska—because of thinning sea ice from global warming in the Arctic (Fig. 20.6). Polar bears along Hudson Bay are also threatened with starvation because the pack ice season (the time when they feed on seals) is dwindling. The pack ice season has been reduced by three weeks over the past two decades, according to a study by the Canadian Wildlife Service. Polar bears hibernate or fast for up to eight months a year and depend on hunting on the pack ice to sustain themselves and bring up their weight. The reduced ice season has resulted in polar bears returning to the mainland in worse shape, with females giving birth less often. Starving bears will also become progressively more likely to enter areas of human habitation in search of food, threatening human life and property. Northern Canada’s indigenous people, the Inuit, could find their hunting prey out of reach, their water supplies contaminated, and their coastal communities subjected to erosion from seas no longer covered by ice. Eventually, forests could spread much farther north, taking range land from some of the world’s biggest caribou herds. The polar bear was declared a threatened species in May 2008.

Walruses prefer sea ice for molting, mating, nursing, and resting between dives for food. In 2007, thousands of Pacific walruses above the Arctic Circle were killed in stampedes after the disappearance of sea ice caused them to crowd onto the shoreline in extraordinary numbers. Unlike seals, walruses cannot swim indefinitely. They typically clamber onto the sea ice to rest or haul themselves onto land for a few weeks at a time. As a result of the disappearance of the sea ice, walruses came ashore earlier and stayed longer, congregating in extremely high numbers, with herds as big as 40,000 at Cape Schmidt on the Russian side of the Bering Strait. Walruses are vulnerable to stampedes when they gather in such large numbers. The appearance of a polar bear, a hunter, or a low-flying airplane can send them rushing to the water. Many of the youngest and weakest animals, mostly calves born in the spring, are crushed during these stampedes. In the Chukchi Sea between Alaska and Russia, where females and juveniles spend their summer, ice could be absent during that season by 2060 or sooner, according to the US Fish and Wildlife Service. Since 1981, an area more than double the size of Texas—1.6 million km^2 (610,000 $mi.^2$)—has become unavailable to Arctic marine mammals by summer's end. By late August, as sea ice recedes beyond the shallow continental shelf, female walruses and their calves face a choice: stay on ice over water too deep to reach the ocean floor for feeding or come ashore for rest periods where the smallest animals can be crushed in stampedes. In addition, more open water means more ship traffic and human intrusion. Former President Obama permanently withdrew most Arctic waters from offshore drilling lease sales, but the Trump administration is reversing that decision with a proposed five-year offshore leasing plan that includes sales in the Chukchi Sea.

Melting ice in the Arctic Circle is helping some pathogens disperse throughout the world's oceans. When wildlife pathologists arrived at Hay Island off the coast of Nova Scotia in March 2012, thousands of silver and black-speckled gray seals were laying on the rocky outcrop. To their amazement, approximately 20 percent of the seals were dead, despite showing no outward signs of disease. After extensive laboratory investigation, researchers discovered that they were infested with a moon-shaped parasite, a new strain named *Sarcocystis pinnipedi*, which completely destroys the architecture of their liver (Underwood, 2014). It is a close relative to *Sarcocystis canis*, which can cause hepatitis or encephalitis in young dogs. The parasite is known to be harmless to ring seals who have long lived with the microbe with little ill effect. Because ring seals depend on ice to build caves for their young, they have historically remained isolated from gray seals, which inhabit warmer waters. But as ice covering the Arctic disappears, gray seals have entered the ring seals' territory. The new mixing of species exposed them to new diseases.

SOURCES: IUCN/SSC Polar Bear Specialist Group; US Geological Survey

Figure 20.6. Census of polar bear populations (2008).

Permafrost

The melting of Arctic permafrost has the potential to amplify global climate change because gases trapped in the soil are bubbling out of the thawing permafrost in amounts much higher than previously thought (Walter et al., 2006). Scientists worry about a global warming vicious cycle that was not part of their already gloomy climate forecast. Warming already under way thaws permafrost—soil that has been continually frozen for thousands of years. The world's permafrost is getting warmer, with temperatures increasing by an average of 0.3°C (0.54°F) between 2007 and 2016 (Biskaborn et al., 2019). Thawed permafrost releases methane and carbon dioxide. Methane remains in the atmosphere about 10 to 15 years after release and traps heat at least 20 times more effectively than carbon dioxide, the primary greenhouse gas. About 60 percent of the methane currently going into the atmosphere comes from human sources, like the burning of fossil fuels, but methane also arises from natural sources, like bacterial decomposition of plants and from termites. A massive amount of natural methane—363 billion metric tons (400 billion US tons)—has been trapped for millennia in the frozen Arctic tundra. Melting permafrost could release that methane; the methane would enter the atmosphere, increase the rate and intensity of global warming, and spur the release of yet more methane from ocean bottoms. The trapped heat thaws more permafrost and so on. The higher the temperature gets, the more permafrost melts, and the more likely it is that a more vicious cycle will develop. Once global warming reaches a level that speeds methane into the atmosphere, there may be no turning back.

Glaciers

Glaciers are retreating at an alarming pace. Glaciers are defined as slowly moving bodies of snow and ice larger than 10 hectares (25 acres) (Fig. 20.7). A new study shows that glaciers are losing 355 billion metric tons (369 billion US tons) of snow and ice each year, more than half of that in North America (Zemp et al. 2019). The world's glaciers are shrinking five times faster now than they were in the 1960s. One-third to one-half of the mountain glaciers and polar ice caps are predicted to disappear by 2050, in some cases changing river flows.

In April 2010, Glacier National Park in Montana officially lost two more of its namesake moving ice fields to climate change, which is shrinking the rivers of ice until they grind to a halt. Montana is warming nearly twice as quickly as the global average (Milman, 2017), and changes in precipitation patterns are eroding away glaciers. Warming winters are bringing more rain, rather than glacier-forming snow. Even when there is plenty of snow, the increasing heat of spring and summer is melting it away more quickly. Spring snow melts are now occurring at least two weeks earlier than they were in the 1960s. The latest two glaciers to fall below 10 hectares (25 acres) were Miche Wabun and Shepard. Each had shrunk by roughly 55 percent since the mid-1960s. When naturalists first hiked through Glacier National Park in Montana more than a century ago, 150 glaciers graced its high cliffs and jagged peaks. As of May 2017, there are 25 named glaciers in the park, and they continue to shrink. The largest remaining glacier is Harrison Glacier, at about 188 hectares (465 acres). Glaciers remaining in the park are disintegrating so fast that scientists estimate that the rest of them could be gone within 10 years. Experts predict that glaciers in the high Andes, the Swiss Alps, and even Iceland could disappear in coming decades as well. More than a quarter of the ice cover on Tanzania's Mount Kilimanjaro in the year 2000 had disappeared by late 2007. At current melting rates, permanent ice fields could disappear from Kilimanjaro by 2022. Glaciers in the Himalayas are retreating faster than in any other part of the world and they could disappear completely by 2035.

The island of Greenland is almost entirely covered in ice that is more than a mile thick in some areas. That is roughly 8 percent of all ice on Earth. And since the early 1990s, it has been melting, adding about 0.69 mm (0.027 in.) a year to global sea levels.

Since the early 1990s, melting of the West Greenland Ice Sheet has been at the highest levels in at least 450 years (Graeter et al., 2018). In 2005, one of Greenland's largest glaciers, Kangerlussuaq, was moving about 14.5 km (9 mi.) a year compared to 4.8 km (3 mi.) a year in 2001. Another glacier, Helheim, was retreating at about 11 km (7 mi.) a year—up from 6.4 km (4 mi.) a year during the same period (Hamilton, 2005). According to NASA data, the year 2007 shattered numerous records in the Arctic. During 2007, 501 billion metric tons (552 billion US tons) of ice melted from the Greenland ice sheet—15 percent more than the annual average summer melt, beating 2005's record. A record amount of surface ice was lost over Greenland, 12 percent more than the previous worst year, 2005. The surface area of summer sea ice floating in the Arctic Ocean was nearly 23 percent below the previous record. The Northwest Passage was open to navigation. The remaining sea ice was the thinnest on record.

During the summer of 2010, a 259 km^2 (100 mi.^{2}) chunk of ice—more than four times the size of Manhattan—broke off from a glacier in Greenland and began drifting across the Arctic Ocean. This is the biggest ice island in the Northern Hemisphere since 1962.

Figure 20.7. Holgate Glacier in Kenai Fjords National Park near Seward, Alaska. This glacier, along with many others, is decreasing in size due to global warming.

Glaciers play a major role in discharging water into oceans. Land beneath a disappearing ice sheet will rebound (today the Nordic countries and northern Canada bounce back almost 1 cm (0.39 in.) per year from the load of an ice sheet that disappeared more than 15,000 years ago), and the sea level will rise differentially, depending on the water temperature and the source of the water. Sea levels have swelled globally an estimated 10 to 20 cm (4–8 in.) during the past century due to melting glaciers and polar ice. In addition, rising temperatures cause ocean waters to warm and expand, like water heated in a teakettle. Loss of ice from Greenland is one of the largest contributors to global sea level rise. Melting of Greenland ice and calving of icebergs from glaciers is responsible for about 7 percent of the annual rise in global sea level. Coastal areas, especially along the East Coast, are experiencing increased beach erosion. As salt water pushes farther upriver, some rivers are widening into estuaries, tidal bodies of water where fresh water and salt water mix. The soil, exposed to salt, gradually disintegrates and releases carbon dioxide into the atmosphere, adding to global warming. As the trees die, a freshwater swamp changes into a salt marsh.

Alaska’s Columbia Glacier—about the size of Los Angeles—one of the fastest-melting glaciers in North America, has already reached the halfway point of disintegration and will continue to retreat for another two decades. It has shrunk 20 km (12 mi.) since the early 1980s. It is expected to lose an additional 14.5 km (9 mi.) in the next 15 to 20 years before the bed of the glacier rises above sea level. The glacier, which moves about 24 m (80 ft.) a day, currently releases about 8.3 km^3 (2 $mi.^3$) of ice every year into Prince William Sound on the south coast of Alaska. Some scientists say that current climate change warming trends do not directly explain the shrinking Columbia Glacier and other tidewater glaciers (see Fig. 20.7). Instead, they think the retreat is triggered by a slow warming trend that began five centuries ago. As Alaska's pervasive permafrost begins to thaw, the consequences are dramatic and alarming: sagging roads, crumbling villages, sinking pipelines, the proliferation of insects that are destroying spruce forests, and the possible disruption of marine wildlife.

Even if global temperatures did not continue to rise, many scientists anticipate that Arctic ice would eventually disappear. The reason is that ice and snow, like any light-colored surface, reflect heat from the sun. As the ice shrinks, it leaves more open, darker water to absorb the sun's heat. More open water slows the formation of fresh ice in the fall and leads to a still earlier, more extensive melt the following summer. It is a self-reinforcing feedback process.

Antarctica

While temperatures in the Arctic are increasing two to three times as fast as the global average, the pace of warming has been thought to be much slower in Antarctica. The Arctic has warmed at a rate of 0.6°C (1°F) per decade over the last 30 years, while the average temperature of Antarctica as a whole has risen by around 0.12°C (0.2°F) per decade. Part of the reason for this slower pace of warming is because Antarctica is much colder than the Arctic, which means it takes more warming to get ice melting in the first place. It is also because Antarctica's ice sheets are hundreds of meters thick—compared to Arctic sea ice of a few meters. This means a lot more ice needs to melt to uncover the dark land surface beneath. The most recent theory is that the high land surface of the Antarctic might be an "important piece of the puzzle" (Salzmann, 2017). The soaring mountain ranges and thick ice sheets put Antarctica's average elevation at more than 2 km (1.2 mi.) above sea level. In contrast, the Arctic is predominately ocean, covered by sea ice a few meters thick. Researchers have also suggested that the hole in the ozone layer above Antarctica has helped limit warming by strengthening the winds over the Southern Ocean, thus cooling the surface. Central West Antarctica, however, revealed a linear increase in annual temperature between 1958 and 2010 by 2.4°C ± 1.2°C (4°F ± 2°F), establishing this region as one of the fastest-warming regions globally (Bromwich et al., 2013). There is clear evidence that the West Antarctic Ice Sheet is contributing to sea level rise. An assessment of the Antarctic Ice Sheet from 1992 to 2017 using satellite observations is presented by Shepherd et al. (2018).

East Antarctica, which has 10 times as much ice as the continent's western half, was long thought to be insulated from climate change because it rests on land, largely protected from warming ocean waters. However, using aerial photographs, satellite measurements and computer models, a study of four decades of Antarctic Ice Sheet mass balance (from 1979 to 2017) shows that Antarctica is losing ice six times faster today than in the 1980s (Rignot et al., 2019). Since 2009, Antarctica has lost almost 252 billion metric tons (278 billion US tons) of ice per year. In the 1980s, it was losing 40 billion metric tons (44 billion US tons) a year. The recent melting rate is 15 percent higher than the Shepherd et al. (2018) study.

The Southern Ocean around Antarctica is warming at an alarming rate—twice that of the rest of the world's oceans. Researchers have shown that greenhouse gas emissions and the depletion of ozone in the atmosphere—both human causes—have led to the warming of the Southern Ocean and an increase in its freshwater content (Swart et al., 2018).

Three of Antarctica's largest glaciers are rapidly thinning, and between 1991 and 2001 lost up to 46 m (150 ft.) of thickness in some places. The three glaciers in western Antarctica collectively have lost 157 km^3 (37.6 mi.^{3}) of ice to the ocean, according to a decade of measurements. In May 2002, an iceberg (C-18) 75 km (47 mi.) long and 7 km (4.6 mi.) across broke off the Ross Ice Shelf in the Antarctic. It is the 18th iceberg to be tracked in that section of the Antarctic since 1976, when record-keeping began. Also in May 2002, another new iceberg (D-17)—56 km (34.5 mi.) long and 11 km (6.9 mi.) wide—broke off from the Lazarev Ice Shelf, a large sheet of glacial ice and snow extending from the Antarctic mainland into the southeastern Weddell Sea. These came just a month after a much larger iceberg (B-22)—64 km (40 mi.) by 85 km (53 mi.)—broke away from another part of Antarctica. In March 2002, a large, floating ice shelf in Antarctica collapsed. The 3,237

km^2 (1,250 $mi.^2$) section of the Larsen Ice Shelf collapsed during a five-week period that ended March 7, 2002. It splintered into a plume of drifting icebergs. As of 2018, there have been nine major Antarctic ice shelf collapses in the past 40 years, after some 400 years of relative stability.

A NASA report in 2019 identified significant melting in a group of glaciers in East Antarctica, a region previously deemed stable and unaffected by climate change. Satellite imagery suggests that the height of glaciers feeding Vincennes Bay, an area due south of Australia, has dropped by nearly 3 m (10 ft.) since 2008—and the speed of melting is accelerating. The Vincennes Bay glaciers are crucial because they block the inland Aurora and Wilkes ice basins from falling into the sea; if both basins collapsed, sea levels could rise by up to 28 m (92 ft.), submerging coastal communities around the world.

The globe's southernmost continent has not always been ice-bound. The discovery of fossil ferns, pines, and ginkgoes from the Cretaceous Era shows that it was once a warm place and that many plant and animal species lived quite comfortably very near to the South Pole. Today, the majority of the Antarctic continent is covered by permanent ice and snow leaving less than 1 percent available for colonization by plants. Most of this ice and snow-free land is found along the Antarctic Peninsula, its associated islands, and in coastal regions around the edge of the rest of the Antarctic continent. There are no trees or shrubs, and there are only two species of flowering plants: Antarctic hair grass (*Deschampsia antarctica*) and Antarctic pearlwort (*Colobanthus quitensis*). In addition, there are approximately 100 species of mosses, 25 species of liverworts, 300 to 400 species of lichens, and about 20 species of macro-fungi. The greatest diversity of species is found along the western side of the Antarctic Peninsula where the climate is generally warmer and wetter than elsewhere in the Antarctic continent (Natural Environment Research Council, 2018).

Using NASA and Defense Department satellites (2003), researchers measured the loss from two Patagonian ice fields in southern Argentina and Chile. They found the melting rate doubled from 1995 to 2000 when compared with earlier measurements. Factors were higher temperatures, lower snowfall, and a more rapid breaking of icebergs.

Analysis of a 3.2 km (2 mi.) long ice core from the Antarctic in 2005 revealed tiny air bubbles in the ice that confirm that current levels of carbon dioxide are higher than anything experienced at least in the last 650,000 years. This evidence should prove beyond any reasonable doubt that this unprecedented increase in global warming is due to industrial activity that dumps billions of tons of greenhouse gases into the atmosphere every year.

East Antarctica as a whole warmed about 0.1°C (0.2°F) between 1957 and 2006. The largest rate of warming showed up in West Antarctica, where the average temperature increased about 0.17°C (0.3°F) per decade during the same period. For comparison, global average temperature has increased about 0.12°C (0.2°F) per decade since 1957. Researchers are suggesting that the 4°C to 5°C (7.2°F to 9°F) mid-winter warming of the western Antarctic Peninsula climate observed over the last five decades may be a factor in the significant decrease in the Adélie penguin population (Kaiser, 1997).

In a comprehensive assessment of Antarctica's ice sheet mass, combining data from two dozen satellite surveys, an international research team found that the continent lost an estimated 2,720 billion metric tons (300 billion US tons) of ice from 1992 to 2017. Much of that loss occurred in recent years, particularly in West Antarctica. Before 2012, the continent shed ice at an average rate of 68.9 billion metric tons (76 billion US tons) each year. From 2012 to 2017, the rate increased to 198 billion metric tons (219 billion US tons) yearly. Combined, all that water raised global sea levels by an average of 7.6 mm (0.3 in.), with two-fifths coming from the Antarctic melting between 2012 and 2017. Melting Antarctic ice is a major driver of the sea level rise, which threatens to flood coastal communities and ecosystems around the world as the climate changes.

Since 1950, ornithologists in eastern Antarctica have kept careful track of when nine species of seabirds arrive and lay their eggs (Barbraud and Weimerskirch, 2006). Data show that these birds migrated to the region an average of nine days later in 2004 than they had in the early 1950s, and they laid their eggs an average of two days later. Since the 1950s, total sea ice around eastern Antarctica has decreased by 12 to 20 percent. At the same time, winters are lasting longer. Sea ice shelters krill and other marine organisms on which the birds feed. Less sea ice means less krill, so the birds may need to fatten up before they arrive to breed. And as the sea ice breaks up later because of delayed yearly springs, the birds may also have to wait longer to reach their colonies.

Pacific Coast

Based on an analysis of temperature measurements taken daily since 1916 along the Pacific coast, researchers have recorded a trend of warmer water that may signal a climate change deeper than just a temporary El Niño effect (McGowan et al., 1998). Within just 10 months in 1977, sea surface temperatures suddenly jumped upward, and the average has remained about 2°C (3.6°F) warmer than it was previously. The whole temperature range shifted upward, so that the lows are not as low as they used to be and the highs are higher. Rising sea surface temperatures, which are affecting the entire eastern half of the northern Pacific and the Gulf of Alaska, are causing severe declines in fish, birds, seaweed, and mammals. Biological changes linked to the warmer water since 1977 include a 70 percent decline in zooplankton and a 90 percent decline in sooty shearwater (*Puffinus griseus*) populations. As well, warm-water fishes and other animals have migrated northward and are now common in places they once shunned; nearshore species like abalone, sea urchins, and kelp plants have been severely affected; warm surface waters are blocking the upwelling of nutrient-rich cold waters, resulting in the warmer surface waters lacking some of the chemicals that support plankton, which is at the base of the food chain; and fish populations have declined about 5 percent per year since 1986. According to a recent analysis, changes in winds over the eastern Pacific Ocean explain most of the warming trend along the West Coast of North America in the last century (Johnstone and Mantua, 2014).

Ozone, Chlorine, Bromine, UV-B Radiation

Ozone (O_3) is a gas that filters out harmful ultraviolet radiation and keeps it from reaching the Earth's surface. However, increasing amounts of human-made CFCs and other chemicals in the atmosphere have caused the destruction of ozone molecules, resulting in ozone holes over certain regions of the planet. An ozone hole is not technically a "hole" where no ozone is present, but is actually a region of exceptionally depleted ozone in the stratosphere over the Earth's polar regions that happens at the beginning of Southern Hemisphere spring (August–October) and Northern Hemisphere spring (April–June). When a CFC molecule absorbs ultraviolet light, it gives up a chlorine atom. The chlorine can react with ozone to form an oxygen molecule and a chlorine monoxide molecule. When the chlorine monoxide reacts with a free oxygen atom, another chlorine atom is released that can attack another ozone molecule. Each chlorine atom released in the reaction can convert as many as 10,000 molecules of ozone to oxygen.

Ozone holes are areas of severe ozone loss, but losses are occurring throughout the stratosphere (Rex et al., 1997). Between 1985 and 1995, the ozone holes over the Arctic and Antarctic regions increased in size, and concentrations of ozone fell to levels 10 to 20 percent lower than previously recorded over much of Central Asia, Western Europe, and the western United States. Overall, 1992 ozone levels north of the equator were 2 to 3 percent lower than ever before recorded. During late 1994, ozone levels were as much as 30 percent lower than normal over Finland and Siberia. According to measurements by a NASA satellite on September 19, 1998, the ozone hole over Antarctica grew to a record 27.3 million km^2 (10.5 million $mi.^2$)—larger than the North American continent (Monastersky, 1998b). The biggest previous ozone hole had reached 26 million km^2 (10 million $mi.^2$) in 1996. On October 2, 2015, a colder than usual stratosphere widened the hole to a peak of 28.2 million km^2 (10.9 million $mi.^2$)—bigger than Canada and Russia put together (CBC News, 2015). Ground-level measurements on three continents and on two Pacific islands indicated a reduction in the concentration of the group of industrial chemicals that erode the ozone layer (Montzka et al., 1996). A NASA study in 2018, using direct satellite observations of the ozone hole, provided the first direct proof of ozone hole recovery, an indication that the 1987 ban on gases that damage the fragile high-altitude screen was beginning to be successful (Reiny, 2018). Although the World Meteorological Organization (WMO) detected the first sign of ozone recovery in 2014 (CBC News, 2014), it will require many years to reduce the effect of the chemical molecules in the stratosphere.

Reactive chlorine and bromine were expected to reach a maximum in the stratosphere between 1997 and 1999, after which they were expected to gradually decline if all countries complied with their agreements in the revised Montreal Protocol signed in August 1987, which set limits on the manufacture and use of ozone-destroying chemicals. The treaty was ratified by 197 parties, which included 196 states and the European Union, making it the first universally ratified treaty in United Nations (UN) history. Due to its widespread adoption and implementation, it has been hailed as an example of exceptional international cooperation, with Kofi Annan quoted as saying that “perhaps the single most successful international agreement to date has been the Montreal Protocol.” As a result of the international agreement, the ozone hole in Antarctica is slowly recovering. Climate projections indicate that the ozone layer will return to 1980 levels between 2050 and 2070. This reduction, which was the first step toward the goal of eliminating ozone loss, meant that the holes could start closing within 10 years. It led, however, to a shift toward hydrofluorocarbons (HCFCs), which, like the ozone-depleting substances they replaced, are potent greenhouse gases that can be hundreds to thousands of times more potent than carbon dioxide in contributing to climate change. Amendments to the Montreal Protocol in 1997, 1999, and 2016 tightened controls on the production and consumption of HCFCs.

In the meantime, increasing amounts of biologically harmful ultraviolet-B (UV-B) radiation now reaching the Earth’s surface have disrupted plant growth and are damaging the health of animals by producing more severe sunburns, causing an increase in skin cancers and cataracts, as well as damaging the DNA within cells. Of special concern are those species of fishes and amphibians whose embryos develop in eggs directly exposed to sunlight. Researchers have also found that some whale species off the Mexican coast are showing signs of severe sunburn (Martinez-Levasseur et al., 2010). The sea-going mammals are particularly vulnerable, in part because they need to spend extended periods of time on the ocean’s surface to breathe, socialize, and feed their young. Because they do not have fur or feathers, that means they essentially sunbathe naked.

Conferences and Treaties

The Kyoto Protocol, announced in December 1997, was an attempt by governments to set legal, binding limits on greenhouse gas emissions. However, the binding commitments for nations to reduce carbon dioxide and other greenhouse gases—6 to 8 percent below 1990 levels—applies only to industrialized countries, including the United States, Japan, and the European Union. Although it is understood that at some point developing nations will also reduce emissions, they argued that they should not be required to take any action now because most of the gases in the atmosphere were put there by Europe and the United States. Much opposition from groups representing agriculture, manufacturing, transportation, and the coal-mining industries developed against the treaty. The US Senate approved a resolution to not accept a global warming treaty that does not also require developing countries (and economic competitors) like China and India to make a binding commitment to curtail greenhouse gases. Although the United States attempted to add limits on developing countries to the treaty when it came up for further review in November 1998, at the worldwide environmental conference in Brazil, the treaty had not been approved by the US Senate.

At the UN Climate Change Conference in Copenhagen in 2009, disputes between rich and poor countries and between the world's biggest carbon polluters—China and the United States—dominated the largest and most important UN meeting ever on fighting global warming. The final document included funds to aid poor nations and developing countries, a method for verifying each nation's reductions of heat-trapping gases, and a requirement that industrialized countries list their individual targets and that developing countries list what actions they will take to cut global warming pollution by specific amounts. The document said that carbon emissions should be reduced enough to keep the increase in average global temperatures below 1.9°C (3.5°F) above preindustrial levels. The Conference ended with a decision to "take note" of the final agreement instead of formally approving it. Some experts said that clears the way for the Accord to begin even though it was not formally approved by the Conference, although others have stated that the Copenhagen Accord is not legally enforceable. Since leaders failed to agree on a binding deal to reduce greenhouse gases, delegates scrapped a plan to protect the world's biologically rich tropical forests, which would have paid some 40 poor, tropical countries to protect their forests. Deforestation for logging, cattle-grazing, and crops has made Indonesia and Brazil the world's third- and fourth-biggest carbon emitters.

The UN Climate Change Conference in Paris (Paris Climate Accord) in 2015 culminated a four-year negotiating round by drafting a new treaty ending the strict differentiation between industrialized and developing countries, replacing it with a common framework that commits all countries to put forward their best efforts and to strengthen them in the years ahead. Among the final provisions, it reaffirms the goal of limiting global temperature increase well below 2°C (3.6 °F) above preindustrial levels, while urging efforts to limit the increase to 1.5°C (2.7°F). The 1.5°C (2.7°F) was at the urging of many vulnerable countries that called 2°C (3.6°F) a death sentence. The Accord requires all parties to report regularly on their emissions and implementation efforts, and to undergo international review. The United States pledged to cut its overall greenhouse gas emissions between 26 percent and 28 percent compared with 2005 levels by 2025. To reach this goal, the federal government passed rules aimed at curbing the nation's carbon output, including ones limiting greenhouse gases, emissions from existing power plants, oil and gas operations on federal land, and carbon emissions from cars and trucks. Many scientists warned that the target is not stringent enough to prevent major environmental changes.

At the time, scientists knew relatively little about how to compare the risks of a 1.5°C (2.7°F) warmer world with a 2°C (3.6°F) warmer world. The Intergovernmental Panel on Climate Change (IPCC) was asked to address these impacts. Stark differences are apparent. For instance, a half a degree Celsius less warming means about 10 cm (4 in.) less sea level rise on average by the next century. As a result, at least 10 million fewer people would be exposed to such risks as flooding, infrastructure damage, and saltwater intrusion into freshwater resources. Somewhere between 1.5°C and 2°C (2.7°F and 3.6°F), ice sheets may become increasingly unstable, further increasing the potential for sea level rise. In the 1.5°C (2.7°F) scenario, the Arctic Ocean is projected to be ice-free during the summer only once per century, whereas an ice-free Arctic would happen once a decade in the 2°C (3.6°F) scenario. For many plant and animal species, the lower temperature increase would mean less risk of habitat loss compared with 2°C (3.6°F) of warming. Other risks to these species, including forest fires and the spread of invasive species, would also be lower (Intergovernmental Panel on Climate Change, 2018). According to the 2018 report by the IPCC, climate emissions need to be cut by 20 percent by 2030 and then zeroed out by 2075 to keep warming from exceeding 2°C (3.6°F) above preindustrial levels. The IPCC report stated that, while it is possible to cap global warming at 1.5°C (2.7°F) by the end of the century compared to preindustrial times, this would require a dramatic overhaul of the global economy, including a shift away from fossil fuels. Due to objections by oil-exporting nations of the United States, Russia, Saudi Arabia, and Kuwait, the final text omits a reference to specific reductions in greenhouse gas emissions by

2030, and merely welcomes the "timely completion" of the IPCC report, not its conclusions.

According to a study published in October 2018, ocean temperatures have been warming 60 percent more than outlined by the IPCC, meaning the planet could have even less time to avoid catastrophic global warming (Resplandy et al., 2018). Sumner (2016b) examines some of the major areas where climate scientists have made significant progress since 2006.

Achieving either target (cutting greenhouse gas emissions and capping global warming at 1.5°C (2.7°F)) is daunting. The Paris Climate Accord faced a major setback in 2017 when the President of the United States announced his *promotion* of coal as a source of energy in the United States (a *repeal* of the rules governing the nation's carbon output). He also announced that the United States would pull out of the Paris Agreement. The United States is still technically in the Paris Agreement until 2020, which is why American officials participated in the Katowice talks.

Between 2014 and 2016, global emissions of carbon dioxide remained largely flat, leading to hopes that the world was beginning to turn a corner. However, just prior to the UN Conference in Poland in December 2018, these hopes were dashed when researchers with the Global Carbon Project reported that global emissions grew 1.6 percent in 2017 and the rise in 2018 is projected to be 2.7 percent. Researchers estimated that the expected increase, which would bring fossil fuel and industrial emissions to a record high of 33.7 metric tons (37.1 billion US tons) of carbon dioxide a year, is being driven by nearly 5 percent growth of emissions in China and more than 6 percent in India, along with growth in many other nations throughout the world. Emissions by the United States grew 2.5 percent, while emissions by the European Union declined by just under 1 percent.

Following two weeks of negotiations at the UN Climate Change Conference in Katowice, Poland, in December 2018, officials from almost 200 countries agreed to put into action the principles in the 2015 Paris Climate Accord. Negotiators delayed decisions on two key issues until 2019 in an effort to get a deal on them. Among the key achievements in Katowice was an agreement on how countries should report their greenhouse gas emissions and the efforts they are taking to reduce them. One climate policy expert stated: "The majority of the rulebook for the Paris Agreement has been created, which is something to be thankful for. But the fact countries had to be dragged kicking and screaming to the finish line shows that some nations have not woken up to the urgent call of the IPCC report on the dire consequences of global warming. A central feature of the Paris Agreement—the idea that countries will ratchet up their efforts to fight global warming over time—still needs to be proved effective."

Unfortunately, in December 2018, Brazil withdrew its offer to host the 2019 UN Climate Change Conference, signaling a shift in the country's stance on global warming. Newly elected President Jair Bolsonaro argued that the Paris Agreement threatens the country's sovereignty over the Amazon.

The National Climate Assessment was issued in Washington, DC, on November 23, 2018. The report is mandated by law every few years and is based on more than 1,000 previous research studies. It details how global warming from the burning of coal, oil, and gas is hurting each region of the United States and how it impacts different sectors of the economy, including energy and agriculture. "Climate change is transforming where and how we live and presents growing challenges to human health and quality of life, the economy, and the natural systems that support us," the report says.

The Trump administration no longer permits many United States government agencies to publish data concerning climate change. However, the United States Forest Service has continued to publish papers on how climate change is affecting wildfires, wetlands, and aquatic habitat across the country.

At the World Economic Forum in Davos, Switzerland, in January 2019, David Attenborough, famed British naturalist, voiced optimism that the Paris Climate Accord had shown a recognition that humanity and the natural world are interdependent. He said: "We are seeing that almost everything we do has its echoes and has its implications across the natural world. The mechanisms that we have for destruction are so wholesale and so frightening that we have actually exterminated whole ecosystems without even noticing."

Review Questions and Topics

1. What are some of the changes that are predicted to occur as global warming increases?

2. Do you feel that global warming is occurring? Why or why not? Support your reasoning.
3. Do you believe that global warming from an enhanced natural greenhouse effect caused at least partially by human activities is a serious problem or one that has been greatly exaggerated? Explain.

Supplemental Reading

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Vertebrate Internet Sites

1. Global Science Special Report

https://science2017.globalchange.gov

The Climate Science Special Report, Volume 1, of the Fourth National Climate Assessment (NCA4) assesses the physical science of climate change.

2. NOAA: Climate Change and Global Warming

   www.climate.gov

   Source of timely and authoritative scientific data and information about climate.

3. US Department of Energy

   www.energy.gov/science-innovation/climate-change

   Addressing the effects of climate change is a top priority of the Department of Energy.

4. NASA Global Climate Change Blog

   https://climate.nasa.gov/blog

   Underlines the sobering reality of climate change and the best ways to be proactive. Posts underline different climate change issues and also offer suggestions on how to overcome those opposed to climate change.

5. New Scientist: Climate Change

   www.newscientist.com/article-topic/climate-change

   New Scientist aims to find the truth in a myriad of climate change myths and to present truth to its readers. Site is broken down into environmental, tech, space, life, and other areas to best discern effects of climate change.

6. Science News: Climate Change

   www.sciencenews.org/topic/climate

   Underlines the increasing prevalence of climate factors and how they must be acknowledged to prevent further damage.

7. Climate Central

   www.climatecentral.org

   Independent organization of scientists and journalists who aim to provide objective information on climate change in order to have a more-informed America and preserve the world we live in.

21 | Wildlife Management in a Modern World

> Big animals, little animals, plants—right down to the sea itself. We need them, not just for their own sake, but because all this has to be here for everybody forever. There is no single, simple solution to the problems of continued existence for anything. Any answers are as complicated as life itself. Only one thing is certain: if we are to preserve our environment and save this priceless wildlife, we need much, much more knowledge.
>
> Henry Butler, 1977

Introduction

In 2002, more than 120 countries adopted a target to achieve a "significant reduction" in the rate of biodiversity loss by 2010. That aim was not met. But by just how much the world missed the target is difficult to calculate, because the target did not specify a baseline extinction rate from which to start counting. The next generation of targets will aim for a more positive outcome and set more easily measurable goals. The targets aim for a complete halt to biodiversity loss by 2050, and more modest interim targets are set for 2020. The new targets are designed to encourage countries to address the underlying drivers of biodiversity loss, like climate change and unsustainable land use. The new goals were discussed and agreed upon through a set of international negotiations, which culminated at the Convention on

Biological Diversity in Japan in October 2010. The new goals form the Strategic Plan for Biodiversity 2011–2020.

The manipulation and restoration of habitats and populations have been discussed in many chapters. Most endangered species require some form of habitat restoration for their survival. Wildlife management is a separate professional field of study with its own professional organization (the Wildlife Society) and a rigid certification requirement. Considerable effort has been devoted to restoring and/or maintaining wildlife populations.

Reintroduction of Species

Should wolves (see Plate 26) be reintroduced into suitable habitat in northern Maine, northern New Hampshire, Vermont, and Adirondack Park in northeastern New York, or should they be allowed to return on their own from Canada? Studies have shown that suitable habitat and sufficient prey exist for wolves in these areas and that the Northeast could support between 1,200 and 2,000 wolves (Defenders of Wildlife, www.defenders.org).

Should wolves be reintroduced to Isle Royale National Park by the National Park Service (NPS)? For more than 70 years, Isle Royale—a 53,000-hectare (132,000-acre) federally designated wilderness in Lake Superior—has been famous for its wolves and their role in keeping the island's moose population in check. Around 1949, wolves colonized the island by way of a winter ice bridge from Canada. It is believed that three animals established a population that, until recently, averaged around 25 and held moose numbers in check. By the summer of 2017, only an elderly, grossly inbred pair of wolves remained, incapable of reproduction. In the spring of 2018, the NPS made the decision to reintroduce up to 30 wolves from the Great Lakes region into Isle Royale over a five-year span so the population there can survive (Mihell, 2018). Should humans try to manipulate wilderness, especially now in an era of rapid climate change? Proponents and opponents of the NPS plan continue to debate the issue.

Should cougars (Fig. 2.1) be reintroduced into suitable areas in the southeastern United States to help control the burgeoning white-tail deer and wild hog populations? As one might suppose, these topics are highly controversial.

Reinvasion of Former Habitat

By felling trees and building dams, beavers (Fig. 20.5) capture water to expand their aquatic domains. European colonists to North America found as many as 400 million beaver, but fur trappers decimated their populations until conservationists began to help them recover. Today, approximately 15 million beavers swim in North America's waterways. Beavers create wetlands, prevent floods, store groundwater, and trap carbon in the form of organic sediment that settles to the bottom of their ponds. As well, beaver ponds prevent low-oxygen "dead zones" in the sea that are devoid of marine life by trapping runoff of synthetic fertilizers near their source and encouraging bacteria that convert nitrates to harmless gas. As beavers have rebounded, scientists have learned that beaver-built water features help address environmental problems, including drought, pollution, biodiversity loss, and climate change.

Aided by recent advances in technology, scientists have discovered new populations of several seriously imperiled species (Sachs, 2009). By employing hair traps and analyzing the hair samples for DNA, a researcher in Montana produced the first reliable census of the largest population of grizzly bears (see Fig. 14.16; Plate 20) in the lower 48 states. It revealed that the grizzly population in northwestern Montana now stands at 765, which is 2.5 times the previous government estimates. A previously unknown population of western lowland gorillas numbering more than 125,000 was discovered in a remote area of Congolese rain forest. This more than doubled some previous estimates of the entire world population. A population of black-footed ferrets (see Plate 22) in southeast Wyoming's Shirley Basin was all but wiped out by plague and distemper. Only five ferrets could be located in 1997. By 2003, however, researchers spotted approximately 50 ferrets at Shirley Basin, and by 2008 the rapidly expanding population yielded a count of 239 ferrets. Extrapolating from the study area, researchers estimate that the entire Shirley Basin may now be home to as many as 1,000 ferrets. As of 2007, one of the world's most endangered primates, the Tonkin snub-nosed monkey of Vietnam, had an estimated population of fewer than 150. However, in December 2008, a new group of 20 monkeys, including 3 babies, was discovered. Using satellite tracking combined with aerial surveys, the number of eastern bowhead whales is now estimated at between 6,000 and 14,000. Scientists had thought that the eastern population of bowhead whales was very small, even though they have been protected from commercial whaling since 1946. Enormous flocks of the social lapwing, a plover, once inhabited the grasslands of Eurasia. By 2003, however, scientists estimated that only 200 breeding pairs survived. In 2007, however, a lapwing tagged in Kazakhstan with an electronic device that broadcast its position via satellite led ornithologists to a flock of more than 3,000 birds on a remote Turkish steppe.

The scimitar-horned oryx (*Oryx dammah*) (see Fig. 21.1), which once roamed the northern borders of the Sahara, has been extinct in the wild for 25 years. By using animals raised in captivity, a team of zoo curators and animal researchers has brought 9 oryx and 13 addaxes (*Addax nasomaculatus*), another rare desert antelope, from US and European zoos to Tunisia and released them into two government wildlife preserves. Researchers hope to eventually release the antelopes into the wild.

Figure 21.1. The scimitar-horned oryx (*Oryx dammah*) has been extinct in the wild for 25 years. Researchers hope to release captive-raised animals into the wild.

Placed on the federal endangered species list in 1974, gray wolves began making a comeback in the 1980s when a few Canadian wolves crossed the border and settled in Montana. In the 1990s, the US Fish and Wildlife Service (USFWS) brought 66 Canadian and 10 Montana wolves to Yellowstone and to a separate area in Idaho. The reintroductions, which cost a total of $27 million over 33 years, have been hailed worldwide as great successes, particularly in Yellowstone National Park, where the wolves are helping to bring back a more balanced ecosystem.

Ongoing research raises concern for the future status of polar bear populations because recent analyses have shown that the permanent sea ice cover in the Arctic has been declining by almost 10 percent per decade since the late 1970s (see Fig. 18.3). Sea ice is critical for the survival of polar bears because it provides a platform for movement, breeding, and hunting. A major loss of sea ice habitat will result in a decline in the abundance of polar bears (see Fig. 20.6).

Effects of Climate Change on Distribution

Many wild species are already showing changes in their distributions that are, to varying degrees, tracking the shifting climatic zones. Although species translocations have been a frequent tool employed by conservation biologists to increase the numbers of populations of rare and endangered species, there is a consensus that more emphasis should be placed on some of the traditional conservation actions that could aid species in tracking the shifting climate, like improved connectivity of reserve networks through creation and preservation of dispersal corridors and "stepping-stone" habitats (small reserves placed in between large preserves). If and when the USFWS delists the grizzly bear in Montana, one requirement will be for the Montana Fish, Wildlife, and Parks Department to monitor the movements of bears to ensure widespread distribution throughout the Northern Continental Divide Ecosystem (NCDE) and *connectivity* between the NCDE population with other populations. Deference to climate change would give priority to corridors that encourage elevational and latitudinal movements and to reserve designs that emphasize elevational and latitudinal gradients, as well as topographic diversity in general.

If species within preserves (or other undisturbed habitats) experience degradation of their local climate, their natural dispersal abilities may be insufficient to allow them to cross agricultural lands and urban areas and successfully colonize newly formed habitats outside their current range. In these situations, it has been suggested that human-assisted translocation of individuals, often termed *assisted migration* or *assisted colonization*, may be necessary to ensure colonization of new geographic regions as parts, or all, of the historical species' range become climatically unsuitable (Hoegh-Guldberg et al., 2008; Parmesan, 2009). Debate on assisted movement is not just whether this should be undertaken, but on the details of when, how, and for which species this action should be considered. Should individuals be moved to new habitats that are still within the broad historic range of the species? A more controversial matter is whether species should be transplanted outside of the geographic region in which they have historically been documented. A third alternative would be to create suitable conditions for reproduction outside the current species' range, but to then allow natural colonization of the newly created sites. In considering whether assisted migration is a wise conservation measure, the most suitable scenario is when the risk of extinction of the target species in its historic range is high, but the risk to the community into which the species will be imported is low, and when the likelihood of successful colonization is high, but the time and cost to perform the transplantation is low.

Embryo Transplantation

In February 1989, a domestic cat gave birth to an endangered Indian desert cat, *Felis silvestris*, derived from an artificially fertilized embryo at the Cincinnati Zoo (Fig. 21.2). This was the first interspecies birth of a cat and the first birth of an exotic cat from a test-tube-fertilized egg. Additional breeding experiments have been undertaken as well as research into freezing embryos and sperm. On November 24, 1999, the first successful transplant of a frozen embryo from one species to another was recorded when a domestic cat delivered a prefrozen Indian desert cat at the Audubon Center for Research of Endangered Species in New Orleans (Holden, 1999). As one Cincinnati Zoo researcher stated: “Once they’re frozen, we can keep a species from going extinct” (Anonymous, 1989).

Cloning

In February 1997, researchers in Scotland reported the development of a “viable offspring” named Dolly, the first to be derived from the fusion of an adult sheep mammary gland epithelial cell and a fertilized egg cell from which researchers had removed the nucleus—a technique the researchers call nuclear transfer (Wilmut et al., 1997) (Fig. 21.3). Although the word *clone* is never used in the journal article, these researchers had cloned a lamb from the cells of an adult sheep. Dolly lived for six years and was euthanized on February 14, 2003, to prevent further suffering after she acquired a severe lung infection. Some researchers feel that cloning may be a useful technique for saving rare species (Cohen, 1997). Cells of rare species like Przewalski’s horse (*Equus caballus przewalskii*) and the Sumatran rhinoceros (*Dicerorhinus sumatrensis*) are banked at the San Diego Zoo’s Center for Reproduction of Endangered Species and at other sites and could be used to preserve and increase the genetic diversity of rare animals. A dairy cow in Iowa had the embryo of an endangered species known as a gaur (*Bos gaurus*), or wild ox, implanted in her uterus. When she gave birth on January 8, 2001, it marked the first time a member of an endangered species had been cloned, and the first time a mother of one species has given birth to the cloned offspring of another. While healthy at birth, the young gaur died within 48 hours of dysentery, likely unrelated to cloning. A similar procedure was used in Iowa to produce two banteng, a wild bovine species from the forests of Southeast Asia which is closely related to the domestic cow.

Figure 21.2. Desi, the black domestic cat, was a surrogate mom to Noah, a rare Indian desert cat. This was the first interspecies birth of a cat and the first birth of an exotic cat from a test-tube-fertilized egg.

A cloned Pyrenean ibex (*Capra pyrenaica pyrenaica*) was born on July 30, 2003, but died several minutes later due to physical defects in the lungs (Folch et al., 2009). This was the first, and so far only, extinct animal to be cloned.

Will cloning ever save endangered animals? Currently, cloning is not a viable conservation strategy, although some researchers remain optimistic that it will help threatened species in the future. Jabr (2013) discussed the history of cloning and the problems involved in cloning endangered species. Many animals have become endangered due to hunting and habitat destruction—problems that cloning does not address. In addition, current cloning techniques are too ineffective to make much of a difference.

Figure 21.3. Dolly, a lamb cloned from the cells of an adult sheep. The technique, known as nuclear transfer, was reported in February 1997 from Scotland. Since then, many other vertebrates have been cloned using similar techniques.

Numerous species have now been cloned, including crucian carp, cichlid fish, leopard frog, caecilian, New Zealand parrot, Arctic wolf, African wild cat, Canadian lynx, domestic cat, mouflon, dog, coyote, buffalo, deer, sheep, cow, horse, mule, camel, Pyrenean ibex, gaur, goat, pig, rabbit, monkey (Rhesus and crab-eating macaques), rat, mouse, and ferret species. Lambs cloned from fetal, rather than adult, cells have also been born (Pennisi, 1997b). In some of these lambs, the fetal-cell procedure has been combined with genetic engineering so that they carry extra genes, with a few even having a human gene. This achievement could aid efforts to develop livestock that produce human proteins, like blood-clotting factors, for therapeutic use. In December 2001, the first cloned house pet—a cat—was born in Texas (Shin et al., 2002). The lab managed to get one embryo to take hold and grow out of 87 that were implanted, a success rate typical of cloning work. Some private companies are offering to freeze pet DNA for future cloning, charging a one-time fee of approximately $1,000 plus $100 a year for storage. Genetically reproducing a pet is not cheap.

Researchers in the United States have successfully produced clones of cloned mice. In January 2000, Japanese scientists produced the clone of a cloned bull, the first time a large cloned animal has itself been cloned.

In October 2001, scientists at a laboratory in Massachusetts announced the first human embryos produced using the technique of nuclear transplantation, also known as cloning (Cibelli et al., 2002). This procedure was designed for therapeutic cloning for sick patients and not for reproductive cloning.

Ian Wilmut, the creator of Dolly the sheep, is now focusing his efforts on induced pluripotent stem cells (iPSCs) (Lehrman, 2008). This process restores adult cells back to an embryonic-like state called pluripotency, in which they regain the ability to develop into any kind of cell. Scientists use viruses to deliver three to four genes into an adult cell and reprogram it back to its unspecialized state, enabling it to grow into any type of cell in the body. This new approach may be the beginning of the end for embryonic cloning.

De-extinction

Should extinct animals be resurrected (i.e., de-extinction)? The biggest misconception about resurrecting extinct animals is that we would be creating clones. Cloning—the process of somatic cell nuclear transfer is a specific technology that requires cells that are harvested from a living individual. Instead of using this cloning technology, scientists who are working on mammoth de-extinction are using new molecular tools to edit the genomes of elephants so that some of their DNA sequences are changed to look like mammoth DNA sequences. The result is not a clone but a hybrid: a cell that contains DNA that is mostly elephant, but a little bit mammoth. If that cell is then used to create an embryo and eventually an animal, the result will be a hybrid animal with DNA that is mostly elephant and a little bit mammoth. Research on reviving the woolly mammoth and the passenger pigeon are well underway using genetic engineering techniques such as CRISPR-Cas9 and other gene-editing tools to swap relevant genes from the extinct animal into the living species and implant the hybrid genome into a surrogate or grow it in an artificial womb (Shultz, 2016). This approach does not produce genetically identical copies of extinct animals, but rather modern versions of an animal engineered to look and behave like its extinct relatives.

European scientists are attempting to revive the auroch (see Plate 32), a breed of "super cow" which died out in Poland in 1627, by breeding various cattle types and their offspring in an ambitious project launched in 2008. Using a combination of DNA extraction and selective breeding, a South African project is creating a herd of foals similar to those of the quagga (see Fig. 2.16), an ancient relative of the zebra that went extinct in 1883. Researchers hope to resurrect a species of giant tortoise from the Galápagos Islands (that was wiped out in the mid-nineteenth century) by breeding tortoises with a similar genetic makeup. Since the limit of DNA survival, which would be needed for de-extinction, is probably around one million years or less, it is not possible to recreate a dinosaur.

Captive Breeding

Captive breeding programs involving whooping cranes, California condors, black-footed ferrets, gray wolves, red wolves (see Chapter 17), and others have shown short-term success. But what about the long-term prospects for such species? What good does it do to produce condors in captivity if sufficient suitable habitat no longer exists into which they can be released? How much habitat currently exists for the red wolf? How much habitat remains for the desert cat? If the last remaining members of a species cannot be reestablished successfully in their native habitats, what then? Will an entire species be relegated to being maintained solely in captivity? We temporarily reached this level with three species—the California condor, the black-footed ferret, and the red wolf—although the ultimate goal was, and still is, the reestablishment of each species in its native range. Or will the species exist only in the form of frozen gametes? If either of these situations come to be, it will be a sad day in the history of humankind.

Research at the University of Exeter highlighted the low survival rates of captive carnivores that were released into their natural habitats (Jule et al., 2007). On average, only one in three captive-born carnivores survived in the wild, with most deaths related to human activities. Introduced captive-born carnivores were found to be particularly susceptible to starvation, unsuccessful predator/competitor avoidance, and disease.

The giant panda, China’s national symbol, is one of the world’s rarest animals (see Plate 21). In recent years, captive breeding programs have taken place both in China and in a few zoos throughout the world (See discussion in Chapter 17).

The Wildlands Network

The Wildlands Network (formerly known as Wildlands Project) was created in 1991 to stem the tide of species extinctions that were being recorded across North America. It is an organization of scientists and activists that advocates “Pleistocene rewilding” North America by restoring big carnivores and linking large wilderness areas and existing protected areas across North America (Kaiser, 2000; Jaffe, 2006; Donlan, 2007). A 220-page report entitled “The Sky Islands Wildlands Network” is a blueprint for protecting species across 4.2 million hectares (10.4 million acres) of Arizona, New Mexico, and Mexico by encouraging the return of wolves, jaguars, bears, and mountain lions. Sky Islands, for example, would establish corridors along a historic wolf and jaguar migration route. These connections are at the heart of the plan: a web of wilderness reserves with human "buffer zones." The plan, which would take decades to implement and comes without a cost estimate, is intended to guide the actions of government agencies and conservation groups. One key element is to enlarge wilderness areas. Dozens of conservation groups and a few ranchers have endorsed the plan. Ninety-five percent of the targeted lands are already managed for wildlife; only 5.5 percent are private. Some biologists are concerned because Sky Islands bucks the trend of focusing on habitat types; rather, it assumes that providing habitat for top predators will also protect other species. Other critics fear that rewilding could disrupt modern ecosystems just as easily as it could restore historic ones.

Some studies suggest that restoring caribou, rhinoceroses, and other large mammals around the world could help protect grasslands, forests, and tundra from catastrophic wildfires and other threats associated with global warming (Pennisi, 2018b). Other studies suggest grazers can help maintain tundra (Olofsson and Post, 2018). In the Arctic, rapidly warming temperatures are enabling trees and shrubs to invade the tundra. The woody plants amplify Arctic warming by absorbing heat and trapping a layer of snow that insulates the ground, keeping it warmer. The result is that the soil thaws and releases even more stored carbon and other warming gases. The authors state that there is a potential to reintroduce large herbivores in many Arctic locations, and that doing so would potentially reduce some of the unwanted effects of a warmer climate.

Continental Wildways

Wildlands Network identified four "Continental Wildways" traversing the Pacific and Atlantic coastlines, the Canadian Boreal Forest region, and the "Spine of the Continent" between Alaska and Mexico.

Eastern Wildway—This proposed corridor would connect the Adirondacks, the Great Smoky Mountains, the Appalachians, and the Everglades. In 2015, the Eastern Wildway Network was formed to advance and coordinate efforts.

Western Wildway—Also known as the Spine of the Continent Initiative, this is a proposed 9,650 km (6,000 mi.) swath that will stretch from the Brooks Range in Alaska, down the Rockies through Canada and the United States, to the Sierra Madre Occidental in Mexico.

Pacific Wildway—This proposal runs the length of the Pacific Coast from Baja, Mexico, to where the Coast Range converges with the Rockies, where it connects to the Western Wildway.

Boreal Wildway—Also known as the Canadian Boreal Initiative, this proposal would encompass most of the 485,622,770 hectares (1.2 billion acres) of the North American Taiga biome in Canada. This area is of particular importance due to its function as a carbon sink and its large swaths of unaltered landscapes from coast to coast.

Wildlands Network, www.wildlandsnetwork.org

Between 2000 and 2006, Wildlands Network scientists and associated conservation organizations mapped six regional "Wildlands Network Designs" within the corridors in the Rocky Mountains West and the Northern Appalachians. These conservation plans identified existing protected areas and proposed wildlife corridors that would connect them as pathways for wide-ranging (keystone) species in need of "room to roam." The plans also described the various positive ecological impacts that these species had on other flora and fauna.

Human Impacts

Data from 76 studies of 62 mammal species across the world—from opossums to deer to coyotes and from tigers to wild boar to elephants—revealed a marked increase in nocturnal activity (Gaynor et al., 2018)—an apparent universal behavioral adaptation of wildlife in response to humans. Overall, mammal nocturnality increased by a factor of 1.36 in areas or time periods of high human disturbance relative to nocturnality under low-disturbance conditions. Human activities of all kinds, even hiking, seem to drive animals to make use of hours when humans are not around. Such changes may provide some relief, but they may also have ecosystem-level consequences.

By 2050, rapid population growth will boost human numbers by nearly 50 percent, from 6.5 billion now to 9.1 billion. Virtually all of this growth will happen in existing or new cities in developing countries. During the same period, many richer nations will lose population. Falling fertility and increasing longevity worldwide will expand the proportion of potentially dependent elderly people. The peak population growth rate ever reached, about 2.1 percent a year, occurred between 1965 and 1970. Human population never grew with such speed before the twentieth century and is never again likely to grow with such speed. The dramatic fall since 1970 of the global population growth rate to 1.1 or 1.2 percent a year today resulted primarily from choices by billions of couples around the world to limit the number of children born. Rapid population growth has not ended. Human numbers currently increase by 74 million to 76 million people annually, the equivalent of adding another United States to the world every four years. But most of the increases are not occurring in countries with the wealth of the United States. Between 2005 and 2050, population will at least triple in Afghanistan, Burkina Faso, Burundi, Chad, Congo, Democratic Republic of the Congo, East Timor, Guinea-Bissau, Liberia, Mali, Niger, and Uganda. These countries are among the poorest on Earth.

For 12,000 years, humans lived through an epoch known as the Holocene, which provided a stable and relatively warm climate after the last ice age that allowed humans to develop everything from agriculture to atomic power. But that success remade the planet we live on through widespread deforestation, overfishing of the oceans, the extinction of countless species, and the altering of the planet's climate through the emission of greenhouse gases and sea level rise. Most telling is the spread of radioactive material across the Earth since 1950 as a result of the testing of nuclear bombs. Humans brought an end to the Holocene quickly—no other geological epoch lasted fewer than several million years.

On August 29, 2016, some scientists at a meeting of the International Union of Geological Sciences (IUGS) in South Africa said human activity has grown so powerful that it is forcing a change of the geological calendar: Earth has entered a new epoch, called the **Anthropocene**, defined by humans and our effect on the planet (Sumner, 2016a). The proposed beginning of the Anthropocene epoch is the year 1950. The IUGS gets the final vote on the geological calendar, and while scientists in its working group on the Anthropocene overwhelmingly recommended the new designation at the South Africa meeting, it has yet to be confirmed.

If the seas continue to rise, if the air and waters continue to warm, if the fires burn without end, if the rivers run dry, if the oceans further acidify, if vulnerable natural habitats are demolished for the sake of capital, if tribal lands are seized by extractive industries, if we create an environment that damns nonhuman life, we could bear witness, in the twenty-first century, to a catastrophic ecological and societal unfurling.

Figure 21.4. *The frog does not drink up the pond in which it lives.* —Native American proverb

Homo sapiens has emerged as the species that ultimately can control the fate of the Earth and all of its inhabitants. But saving the Earth is meaningless if there's nothing left to inhabit it. As Walt Kelly's cartoon character Pogo once said: "We have met the enemy and he is us." Only time will tell if we make the right decisions.

Review Questions and Topics

1. Should wolves be reintroduced into Isle Royale National Park by the National Park Service? Does this constitute human interference in a natural ecosystem?
2. Should cougars be reintroduced into the southeastern United States to help control the white-tail deer and wild hog populations? List five reasons that they should be reintroduced and five reasons why they should not.
3. Many mammals are adapting to human disturbance by increasing their nocturnal activity. What effect do you think light pollution (Chapter 19) will have on this behavior?
4. Why will the loss of sea ice result in a decline in the abundance of polar bears?
5. If techniques are perfected to allow an extinct animal to be brought back from extinction, are you in favor of such an action? Support your answer with several substantial reasons.
6. Are you in favor of maintaining a species, such as the red wolf, solely in captivity if no wild individuals of that species exist? Explain your answer.
7. Define cloning.
8. Are you in favor of "Pleistocene rewilding" of North America? Why or why not?

Supplemental Reading

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Wilmut, I., and R. Highfield. 2006. *After Dolly: The Uses and Misuses of Human Cloning*. New York: Norton.

Vertebrate Internet Sites

1. National Wildlife Federation (NWF)

   www.nwf.org

   NWF works to protect and restore wildlife and to provide a sustainable future for both wildlife and humans.

2. US Fish and Wildlife Service (USFWS)

   www.fws.gov

   Mission is to work with others to conserve, protect, and enhance fish and wildlife and their habitats for the continuing benefit of the American people.

3. Defenders of Wildlife

   www.defenders.org

Dedicated to the protection of all native wild animals and plants in their natural communities.

4. Wildlife Conservation Society—WCS

   www.wcs.org

   Works to save wildlife and wild lands throughout the world.

5. African Wildlife Foundation

   www.awf.org

   Working to conserve the wild animals of Africa.

6. Endangered Species International

   www.endangeredspeciesinternational.org

   Works to stop the trend of human-induced wildlife extinction.

7. Northern Prairie Wildlife Research Center

   www.usgs.gov/centers/npwrc

   Research and information on requirements for sustainable wildlife and wildlife habitats.

8. The Humane Society Wildlife Land Trust

   www.wildlifelandtrust.org

   The Humane Society of the United States Wildlife Land Trust works with landowners worldwide to protect wild animals by permanently preserving their natural habitats.

9. The Wildlife Society

   www.wildlife.org

   Represents wildlife conservation and management; ensures sustainable wildlife populations in healthy ecosystems.

10. Wildlife Management Institute (WMI)

    www.wildlifemanagement.institute

    WMI has worked to advance wildlife science since 1911. The Institute hosts the North American Wildlife and Natural Resources Conference each March.

PLATES

Plate 1. The now extinct thylacine or Tasmanian tiger (*Thylacinus cynocephalus*).

Plate 2. Desert pupfish (*Cyprinodon macularis*). Some species have become extinct due to the introduction of predatory and competitive fishes.

Plate 3. Asian (black) carp (*Mylopharyngodon piceus*) was brought to the United States as a natural weed killer.

Plate 4. Red lionfish (*Pterois volitans*), the first known non- native ocean fish to successfully invade the Atlantic Ocean in North America.

Plate 5. Burmese python (*Python molurus bivittatus*)—an invasive species that now numbers in the tens of thousands in southern Florida.

Plate 6. Iberian lynx (*Lynx pardinus*)—only approximately 200 individuals survive.

Plate 7. The Asiatic cheetah (*Acinonyx jubatus venaticus*) survives only in Iran.

Plate 8. Bengal tiger (*Panthera tigris*) populations are decreasing because of hunting, poaching, and deforestation of habitat for palm oil and pulp and paper industries.

Plate 9. The entire silky safaka (*Propithecus candidus*) population in Madagascar is estimated at only 100 to 1,000 animals.

Plate 10. The western lowland gorilla (*Gorilla g. gorilla*) is one of four gorilla subspecies and the most widespread, possibly numbering 100,000.

Plate 11. Chimpanzee (*Pan troglodytes*). In 1960, Jane Goodall began the first long-term study of wild chimpanzees. Her research in Tanzania at Gombe Stream National Park led to significant discoveries about social relationships and warfare in chimpanzee societies.

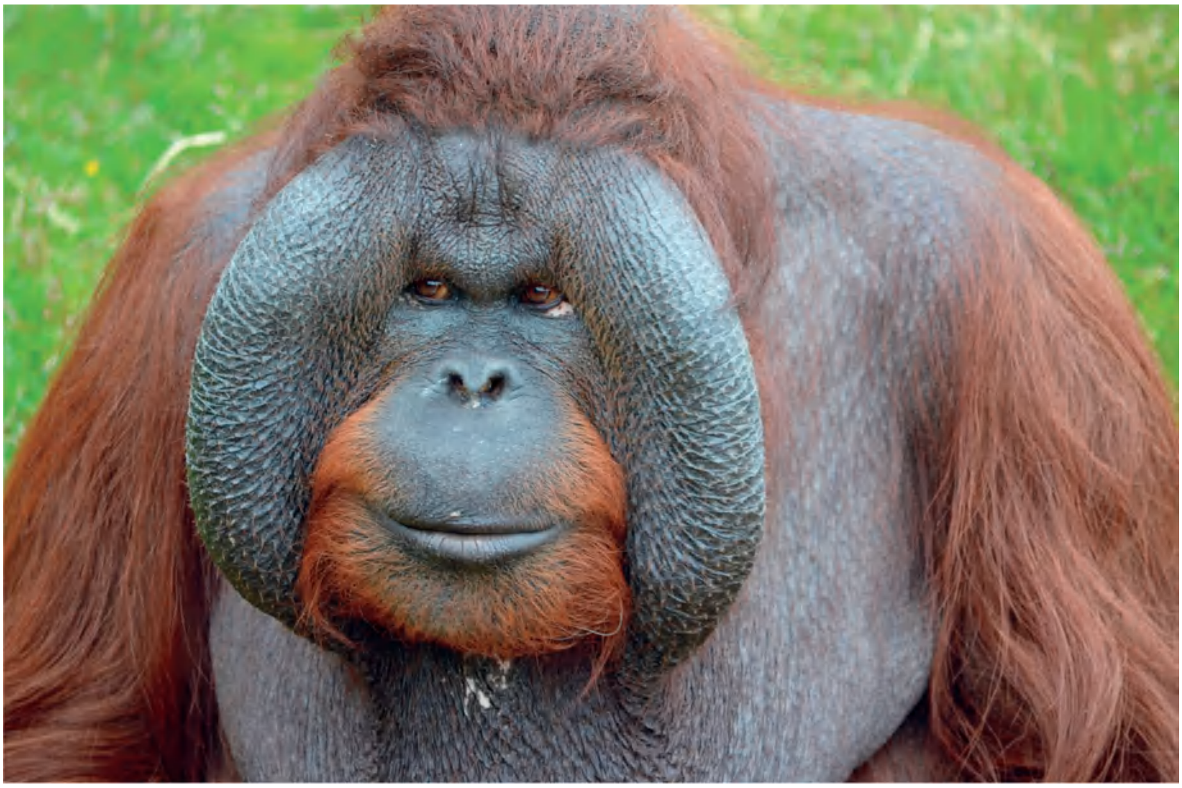

Plate 12. Orangutan (*Pongo pygmaeus*) populations in northeastern Borneo have decreased by more than 95 percent over the past 100 to 200 years.

Plate 13. The black rhinoceros (*Diceros bicornis*) is critically endangered with only about 5,000 individuals remaining.

Plate 14. White rhinoceros (*Ceratotherium simum cottoni*). Only two individuals (both female) exist.

Plate 15. The Komodo dragon (*Varanus komodoensis*) is the world's largest lizard with some adults reaching a weight of nearly 90 kg (200 lb.).

Plate 16. California Condor (*Gymnogyps californianus*). The largest North American land bird.

Plate 17. Whooping Crane (*Grus americana*). A US Fish and Wildlife Service count in early 2017 estimated that 505 whooping cranes had arrived at Aransas National Wildlife Refuge on the Texas coast.

Plate 18 and 19. Peregrine falcon (*Falco peregrinus*) and bald eagle (*Haliaeetus leucocephalus*—two species whose populations recovered sufficiently to allow removal from the US Fish and Wildlife Service list of endangered and threatened species.

Plate 20. The grizzly bear (*Ursus arctos*) was listed as a threatened species by the US Fish and Wildlife Service in 1975.

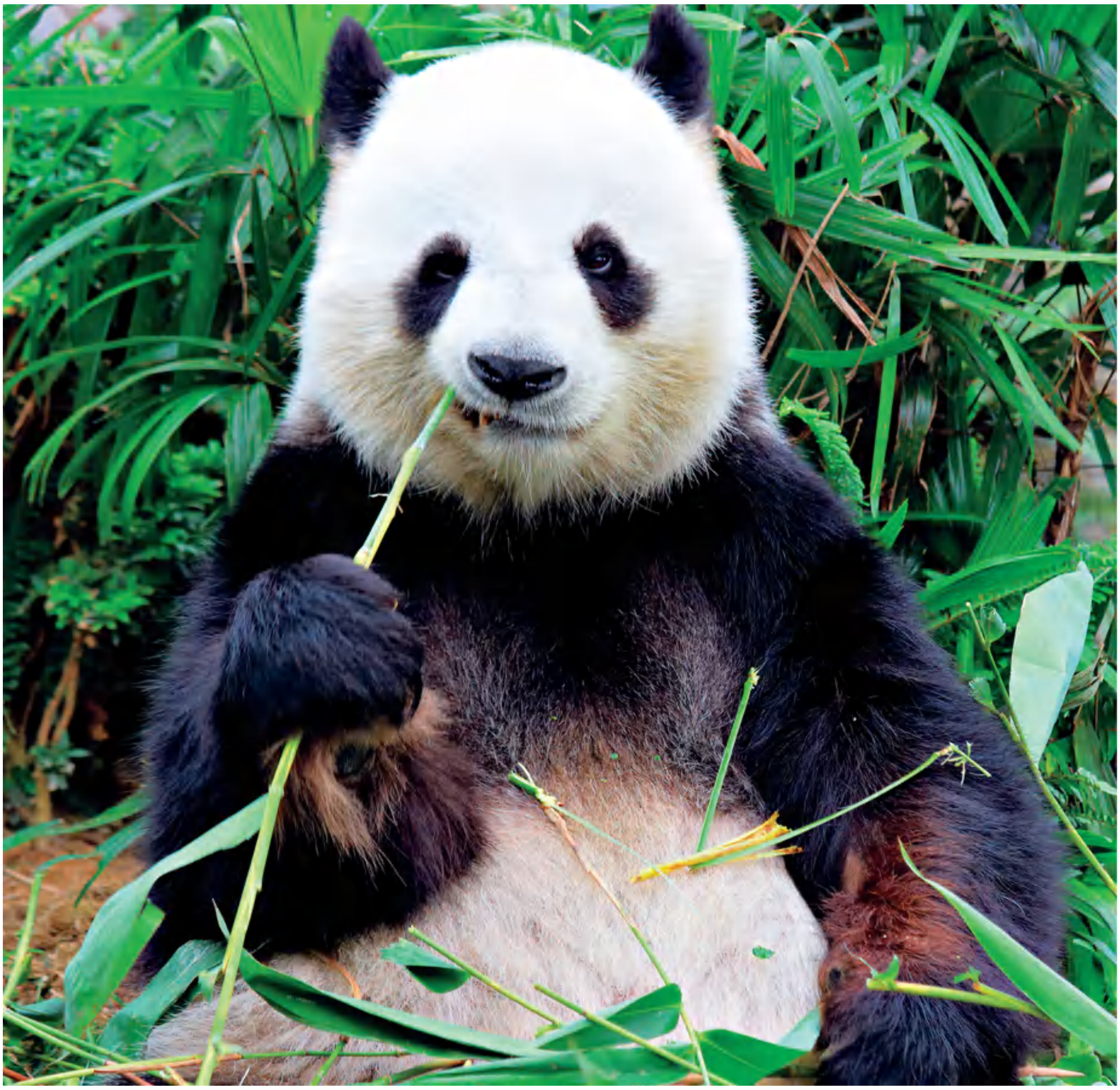

Plate 21. The existence of the giant panda (*Ailuropoda melanoleuca*), one of the world—s rarest mammals, continues to be threatened by hunters and logging in its isolated mountain habitat in southwestern China.

Plate 22. The black- footed ferret (*Mustela nigripes*) is one of the rarest mammals in North America.

Plate 23. The southern sea otter (*Enhydra lutris nereis*), which has the densest pelage of any mammal in the world, was listed as a threatened species in 1977.

Plate 24. The Hawaiian monk seal (*Monachus schauinslandi*) is the most endangered marine mammal in US waters.

Plate 25. The West Indian manatee (*Trichechus manatus*) is the largest surviving member of the aquatic mammal order Sirenia.

Plate 26. Gray wolf (*Canis lupus*). According to the US Fish and Wildlife Service, “recovery of the gray wolf in the Northern Rocky Mountains is one of our nation’s greatest conservation success stories.”

Plate 27. The red wolf (*Canis rufus*) was on the verge of extinction in the 1970s because the wolves were breeding with coyotes along the coasts of Louisiana and Texas. Today, through the efforts of the US Fish and Wildlife Service, an estimated 40 wolves roam their native habitat in several eastern North Carolina counties.

Plate 28. The ocelot (*Leopardus pardalis*) is a medium-sized American wild cat.

Plate 29. The jaguar (*Panthera onca*) is the only big cat in the Western Hemisphere that roars.

Plate 30. The Florida panther (*Puma [Felis] concolor coryi*) was declared endangered in 1967 when only 12 to 20 known individuals were living in less than 5 percent of their historical range. As of 2017, the population is estimated to be between 120 and 230 animals.

Plate 31. Humpback whale (*Megaptera novaeangliae*) populations have recovered due to protective legislation.

Plate 32. The auroch (*Bos primigenius*), a breed of "super cow," died out in Poland in 1627. Researchers are attempting to "revive" the species by breeding various cattle types and their offspring.

APPENDIX A

Classification of Living Chordates

Phylum Chordata

TUNICATES, LANCELETS, AND FISHES

The classification of fishes is based on the system presented by Nelson et al. (2016).

- **Subphylum Urochordata**—tunicates
- **Subphylum Cephalochordata**—lancelets
- **Subphylum Craniata**
  - **Infraphylum Myxinomorphi**
    - **Class Myxini**
      - Order Myxiniformes—hagfishes (78 species)
  - **Infraphylum Vertebrata**—vertebrates
    - **Superclass Petromyzontimorphi**
      - **Class Petromyzontida**
        - Order Petromyzontiformes—lampreys (40 species)
    - **Superclass Gnathostomata**—jawed vertebrates
      - **Class Chondrichthyes**—cartilaginous fishes (1,423 species)
        - Subclass Holocephali

      - Order Chimaeriformes—chimaeras
    - Infraclass Elasmobranchii
      - Order Heterodontiformes—bullhead sharks
      - Order Orectolobiformes—carpet sharks
      - Order Lamniformes—mackerel, thresher, and basking sharks
      - Order Carcharhiniformes—requiem, great white, and hammerhead sharks
      - Order Hexanchiformes—frill and cow sharks
      - Order Squaliformes—dogfish sharks
      - Order Echinorhiniformes—bramble sharks
      - Order Squatiniformes—angel sharks
      - Order Pristiophoriformes—saw sharks
      - Order Torpediniformes—electric rays
      - Order Rajiformes—skates
      - Order Pristiformes—guitarfishes and sawfishes
      - Order Myliobatiformes—sting, eagle, manta, and devil rays
- **Class Osteichthyes—**bony fishes (30,508 species)
  - Subclass Sarcopterygii—lobe-finned fishes (8 species)
      - Order Coelacanthiformes—coelacanths
      - Order Ceratodontiformes—lungfishes
  - Subclass Actinopterygii—ray-finned fishes (30,500 species)
    - Infraclass Cladistia
      - Order Polypteriformes—bichirs
    - Infraclass Chondrostei
      - Order Acipenseriformes—sturgeons and paddlefishes
    - Infraclass Holostei—gars, bowfins, and relatives
      - Order Lepisosteiformes—gars

    - Order Amiiformes—bowfins
  - Division Teleosteomorpha
- Cohort Elopomorpha
    - Order Elopiformes—tenpounders
    - Order Albuliformes—bonefishes
    - Order Notacanthiformes—halosaurs and deep-sea spiny eels
    - Order Anguilliformes—eels
- Cohort Osteoglossomorpha
    - Order Hiodontiformes—mooneyes
    - Order Osteoglossiformes—bonytongues
- Cohort Otocephala—Ostarioclupeomorpha, Otomorpha
  - Superorder Clupeomorpha
    - Order Clupeiformes—herrings and anchovies
  - Superorder Alepocephali
    - Order Alepocephaliformes—slickheads and tubeshoulders
  - Superorder Ostariophysi
    - Order Gonorynchiformes—milkfishes
    - Order Cypriniformes—carps, loaches, minnows, and relatives
    - Order Characiformes—characins
    - Order Siluriformes—catfishes
    - Order Gymnotiformes—Neotropical knifefishes
- Cohort Euteleostei
    - Order Lepidogalaxiiformes—salamanderfishes
  - Superorder Protacanthopterygii
    - Order Salmoniformes—trout, salmon, and whitefish
    - Order Esociformes—pikes and mudminnows
  - Superorder Osmeromorpha

- Order Argentiniformes—marine smelts
- Order Galaxiiformes—galaxiids
- Order Osmeriformes—freshwater smelts
- Order Stomiiformes—dragonfishes

Superorder Ateleopodomorpha
- Order Ateleopodiformes—jellynose fishes

Superorder Cyclosquamata
- Order Aulopiformes—lizardfishes

Superorder Scopelomorpha
- Order Myctophiformes—lanternfishes

Superorder Lampridiomorpha
- Order Lampriformes—opahs and oarfishes

Superorder Paracanthopterygii
- Order Polymixiiformes—beardfishes
- Order Percopsiformes—trout-perches and cavefishes
- Order Zeiformes—dories
- Order Stylephoriformes—tube-eyes or thread-tails
- Order Gadiformes—cods, hakes, and grenadiers

Superorder Acanthopterygii
- Order Holocentriformes—squirrelfishes
- Order Trachichthyiformes—roughies
- Order Beryciformes—beryciforms
- Order Ophidiiformes—cusk-eels
- Order Batrachoidiformes—toadfishes
- Order Kurtiformes—nurseryfishes and cardinalfishes
- Order Gobiiformes—gobies
- Order Mugiliformes—mullets
- Order Cichliformes—cichlids and convict blennies

Order Blenniiformes—blennies

Order Gobiesociformes—clingfishes

Order Atheriniformes—silversides and rainbow fishes

Order Beloniformes—needlefishes

Order Cyprinodontiformes—killifishes, four-eyed fishes, and rivulines

Order Synbranchiformes—swamp eels

Order Carangiformes—jacks

Order Istiophoriformes—barracudas and billfishes

Order Anabantiformes—labyrinth fishes

Order Pleuronectiformes—flatfishes

Order Syngnathiformes—pipefishes and seahorses

Order Icosteiformes—ragfishes

Order Callionymiformes—dragonets

Order Scombrolabraciformes—longfin escolars

Order Scombriformes—mackerels

Order Trachiniformes—swallowers, gapers, and relatives

Order Labriformes—wrasses and relatives

Order Perciformes—perches, bass, sunfishes, icefishes, and relatives

Order Scorpaeniformes—mail-cheeked fishes

Order Moroniformes—temperate basses

Order Acanthuriformes—surgeonfishes and relatives

Order Spariformes—breams and porgies

Order Caproiformes—boarfishes

Order Lophiiformes—anglerfishes

Order Tetraodontiformes—plectognaths, boxfishes, porcupinefishes, and puffers

AMPHIBIANS

Many classification schemes have been presented to portray the relationships of amphibians. The following classification system follows Amphibian Species of the World 6.0, an online reference (http://research.amnh.org/herpetology/amphibia). Appreciation is extended to Dr. Darrel Frost of the American Museum of Natural History for his assistance and advice.

Subphylum Craniata

Class Amphibia (7,904 species)

Subclass Lissamphibia

- Order Gymnophiona—caecilians (209 living species)
  - Family Caeciliidae—common caecilians
  - Family Chikilidae
  - Family Dermophiidae—Neotropical and Tropical African caecilians
  - Family Herpelidae—African caecilians
  - Family Ichthyophiidae—Asian aquatic caecilians
  - Family Indotyphlidae—Indo-African caecilians
  - Family Rhinatrematidae—beaked (tailed) caecilians
  - Family Scolecomorphidae
  - Family Siphonopidae
  - Family Typhlonectidae—Aquatic caecilians
- Order Caudata (Urodela)—salamanders (722 species)
  - Family Ambystomatidae—mole salamanders
  - Family Amphiumidae—amphiumas
  - Family Cryptobranchidae—giant salamanders
  - Family Hynobiidae—Asian salamanders
  - Family Plethodontidae—lungless salamanders
  - Family Proteidae—mudpuppys and olms
  - Family Rhyacotritonidae—torrent salamanders
  - Family Salamandridae—newts

- Family Sirenidae—sirens

Order Anura—frogs and toads (6,973 species)

- Family Allophrynidae
- Family Alsodidae
- Family Alytidae—painted frogs
- Family Aromobatidae
- Family Arthroleptidae—screeching (squeaker) frogs
- Family Ascaphidae—tailed frogs
- Family Batrachylidae
- Family Bombinatoridae—fire-bellied toads
- Family Brachycephalidae—saddle-backed toads
- Family Brevicipitidae—rain frogs
- Family Bufonidae—true toads and harlequin frogs
- Family Calyptocephalellidae—Chilean toads
- Family Centrolenidae—glass frogs
- Family Ceratobatrachidae—triangle frogs and others
- Family Ceratophryidae—horned frogs
- Family Conrauidae—goliath frog and relatives
- Family Craugastoridae—Middle American rain frogs
- Family Cycloramphidae—Austral frogs
- Family Dendrobatidae—poison dart frogs
- Family Dicroglossidae—Forked-tongue frogs
- Family Eleutherodactylidae—New World rain frogs
- Family Heleophrynidae—ghost frogs
- Family Hemiphractidae—horned and marsupial frogs
- Family Hemisotidae—shovel-nosed frogs
- Family Hylidae—American and Australian tree frogs
- Family Hylodidae—torrent frogs

Family Hyperoliidae—reed frogs

Family Leiopelmatidae—New Zealand primitive frogs

Family Leptodactylidae—neotropical grass frogs

Family Limnodynastidae—Australian ground frogs

Family Mantellidae—Madagascan frogs

Family Megophryidae—Asian toads

Family Micrixalidae—Indian frogs

Family Microhylidae—narrow-mouthed frogs

Family Myobatrachidae—Australian water frogs

Family Nasikabatrachidae—Western Ghats frog (purple pig-nosed frog)

Family Nyctibatrachidae—robust (night) frogs

Family Odontobatrachidae

Family Odontophrynidae

Family Pelobatidae—Old World spadefoot toads

Family Pelodryadidae

Family Pelodytidae—parsley frogs

Family Petropedetidae—African cascade (torrent) frogs

Family Phrynobatrachidae—puddle frogs

Family Phyllomedusidae

Family Pipidae—clawed frogs

Family Ptychadenidae—grassland frogs

Family Pyxicephalidae—Box-headed frogs and African bullfrogs

Family Ranidae—true frogs

Family Ranixalidae—leaping (dancing) frogs

Family Rhacophoridae—African and Asian treefrogs

Family Rhinodermatidae—Darwin’s frogs

Family Rhinophrynidae—Mexican burrowing toads

    Family Scaphiopodidae—North American spadefoot toads

    Family Sooglossidae—Seychelles frogs

    Family Telmatobiidae

REPTILES

The system of classification for reptiles is based on The Institute for Genomic Research (TIGR) database (http://www.reptile-database.org), which is now a part of the J. Craig Venter Institute (JCVI). The TIGR database is the new name for the former European Molecular Biology Laboratory (EMBL) reptile database.

Subphylum Craniata

Class Reptilia

- Subclass Anapsida
  - Order Testudines—turtles and tortoises (340 species)
    - Suborder Cryptodira
      - Family Chelydridae—snapping turtles
      - Family Emydidae—pond turtles/box and water turtles
      - Family Testudinidae—tortoises
      - Family Geoemydidae (Bataguridae)—Asian river turtles, leaf and roofed turtles, and Asian box turtles
      - Family Platysternidae—big-headed turtles
      - Family Carettochelyidae—pig-nosed turtles
      - Family Trionychidae—softshell turtles
      - Family Dermatemydidae—river turtles
      - Family Kinosternidae—mud and musk turtles
      - Family Cheloniidae—sea turtles
      - Family Dermochelyidae—leatherback sea turtles
    - Suborder Pleurodira
      - Family Chelidae—Austro-American side-neck turtles
      - Family Pelomedusidae—Afro-American side-neck turtles

- Family Podocnemididae—Madagascan big-headed and American side-neck river turtles

Subclass Diapsida (Lepidosauria)

- Order Rhynchocephalia—tuataras (2 species)
    - Family Sphenodontidae—tuataras
- Order Squamata—lizards, amphisbaenians, and snakes (9,400 species)
    - Suborder Sauria (Lacertilia)—lizards (5,810 species)
        - Infraorder Iguania
            - Family Agamidae—agamas
            - Family Chamaeleonidae—chameleons
            - Family Corytophanidae—casquehead lizards
            - Family Crotaphytidae—collared and leopard lizards
            - Family Dactyloidae—anoles
            - Family Hoplocercidae—wood lizards and clubtails
            - Family Iguanidae—iguanas and spinytail iguanas
            - Family Leiocephalidae
            - Family Leiosauridae
            - Family Leilaemidae
            - Family Opluridae—Madagascar iguanids
            - Family Phrynosomatidae—earless, spiny, tree, side-blotched, and horned lizards
            - Family Polychrotidae—anoles
            - Family Tropiduridae—Neotropical ground lizards
        - Infraorder Gekkota
            - Family Gekkonidae—spectacled geckos
            - Family Carphodactylidae—knob-tailed geckos
            - Family Diplodactylidae—Pacific geckos
            - Family Eublepharidae—eyelid geckos

- Family Phyllodactylidae—leaf-toed geckos
- Family Sphaerodactylidae—dwarf geckos
- Family Pygopodidae—legless (flap-footed) lizards

Infraorder Scincomorpha

- Family Cordylidae—spinytail lizards
- Family Gerrhosauridae—plated lizards
- Family Lacertidae—wall lizards and relatives
- Family Scincidae—skinks
- Family Xantusiidae—night lizards
- Family Alopoglossidae—largescale and shade lizards
- Family Gymnophthalmidae—spectacled lizards
- Family Teiidae—whiptails and tegus

Infraorder Diploglossa

- Family Anguidae—glass lizards, alligator lizards, and relatives
- Family Diploglossidae—galliwasps and South American glass lizards
- Family Anniellidae—American legless lizards
- Family Xenosauridae—knob-scaled lizards

Infraorder Dibamia

- Family Dibamidae—blind lizards

Infraorder Platynota

- Family Helodermatidae—Gila monsters and Mexican beaded lizards
- Family Lanthanotidae—earless monitor lizards
- Family Varanidae—monitor lizards
- Family Shinisauridae—Chinese crocodile lizards

Suborder Amphisbaenia—worm lizards (190 species)

- Family Amphisbaenidae—worm lizards

- Family Bipedidae—two-legged (mole-limbed) worm lizards
- Family Blanidae—Mediterranean worm lizards
- Family Cadeidae—Cuban worm lizards
- Family Rhineuridae—Florida worm lizards
- Family Trogonophidae—shorthead worm lizards

Suborder Ophidia (Serpentes)—snakes (3,400 species)

- Family Acrochordidae—file snakes
- Family Anomochilidae—dwarf pipe snakes
- Family Cylindrophiidae—Asian pipe snakes
- Family Uropeltidae—shield-tail snakes
- Family Loxocemidae—Mexican burrowing pythons
- Family Pythonidae—pythons
- Family Xenopeltidae—sunbeam snakes
- Family Boidae—boas
- Family Colubridae—colubrids
- Family Lamprophiidae—sometimes included under Colubridae
- Family Natricidae
- Family Pseudoxenodontidae
- Family Elapidae—cobras, coral snakes, and sea snakes
- Family Homalopsidae—Asian water snakes
- Family Pareatidae—Asian snail-eating snakes
- Family Viperidae—vipers and pit vipers
- Family Xenodermatidae—odd-scaled snakes
- Family Anomalepididae—dawn blind snakes
- Family Gerrhopilidae—blind snakes
- Family Typhlopidae—blind snakes
- Family Leptotyphlopidae—slender blind snakes

Family Xenotyphlopidae

Family Aniliidae—Neotropical pipe snakes

Family Bolyeriidae—Round Island (split-jaw) boas

Family Tropidophiidae—dwarf boas

Family Xenophidiidae

Subclass Archosauria

Order Crocodilia—alligators, crocodiles, and gavials (25 species)

Family Crocodylidae—crocodilians

Family Gavialidae—gharials

Family Alligatoridae—alligators

BIRDS

Many ornithologists in North America prefer to use the " Check-list of North American Birds" prepared by the American Ornithologists' Union (1998). This well-respected checklist includes " the species of birds of North America from the Arctic through Panama, including the West Indies and Hawaiian Islands." For the purposes of this text, however, it is necessary to use a worldwide checklist.

The following taxonomy is based on the World Bird List, version 8.2, maintained by the International Ornithological Congress (IOC) (Gill and Donsker, 2018). This site—http://www.worldbirdnames.org—provides a complete list of the extant bird species of the world. The list is updated regularly to include changes of names or classification, additions of newly described species, as well as proposed splits and lumps, and taxonomic comments. It supplements and virtually replaces the book Birds of the World: Recommended English Names *by Gill and Wright (Princeton University Press, 2006).*

Subphylum Craniata

Infraclass Eoaves—terrestrial, mostly flightless birds (60 species)

Order Struthioniformes—ostriches (2 species)

Family Struthionidae—ostriches

Order Rheiformes—rheas (2 species)

        - Family Rheidae—rheas
    - Order Casuariiformes—cassowaries and emus (4 species)
        - Family Casuariidae—cassowaries and emus
    - Order Apterygiformes—kiwis (5 species)
        - Family Apterygidae—kiwis
    - Order Tinamiformes—tinamous (60 species)
        - Family Tinamidae—tinamous
- Infraclass Neoaves (10,651 species)
    - Order Galliformes—megapodes, chachalacas, pheasants, and fowl (300 species)
        - Family Megapodiidae—megapodes and scrubfowl
        - Family Cracidae—chachalacas, curassows, and guans
        - Family Numididae—guineafowl
        - Family Odontophoridae—New World quail
        - Family Phasianidae—pheasants, turkeys, and grouse
    - Order Anseriformes—ducks, geese, swans, and screamers (177 species)
        - Family Anhimidae—screamers
        - Family Anseranatidae—magpie geese
        - Family Anatidae—ducks, geese, and swans
    - Order Gaviiformes—loons (5 species)
        - Family Gaviidae—loons
    - Order Sphenisciformes—penguins (165 species)
        - Family Spheniscidae—penguins
        - Family Oceanitidae—Austral storm petrels
        - Family Diomedeidae—albatrosses
        - Family Hydrobatidae—northern storm petrels
        - Family Procellariidae—petrels, shearwaters, and diving petrels
    - Order Podicipediformes—grebes (23 species)

Family Podicipedidae—grebes

Order Phoenicopteriformes—flamingos (6 species)

Family Phoenicopteridae—flamingos

Order Phaethontiformes—tropicbirds (3 species)

Family Phaethontidae—tropicbirds

Order Ciconiiformes—storks (19 species)

Family Ciconiidae—storks

Order Pelecaniformes—ibises, spoonbills, herons, pelicans, frigatebirds, gannets, cormorants, and anhingas (118 species)

Family Threskiornithidae—ibises and spoonbills

Family Ardeidae—herons, bitterns, and egrets

Family Scopidae—hamerkops

Family Balaenicipitidae—shoebills

Family Pelecanidae—pelicans

Order Suliformes—frigatebirds (61 species)

Family Fregatidae—frigatebirds

Family Sulidae—gannets and boobies

Family Phalacrocoracidae—cormorants and shags

Family Anhingidae—anhingas and darters

Order Accipitriformes—New World vultures, ospreys, hawks, and eagles (266 species)

Family Cathartidae—New World vultures

Family Sagittariidae—secretarybirds

Family Pandionidae—ospreys

Family Accipitridae—kites, hawks, and eagles

Order Falconiformes—caracaras and falcons (67 species)

Family Falconidae—caracaras and falcons

Order Otidiformes—bustards (26 species)

Family Otididae—bustards

Order Mesitornithiformes—mesites (3 species)

- Family Mesitornithidae—mesites

Order Cariamiformes—seriemas (2 species)

- Family Cariamidae—seriemas

Order Eurypygiformes—kagus and sunbitterns (2 species)

- Family Rhynochetidae—kagus
- Family Eurypygidae—sunbitterns

Order Gruiformes—rails, coots, cranes, and limpkins (189 species)

- Family Sarothruridae—flufftails
- Family Heliornithidae—finfoots
- Family Rallidae—rails, crakes, and coots
- Family Psophiidae—trumpeters
- Family Gruidae—cranes
- Family Aramidae—limpkins

Order Charadriiformes—stilts, plovers, snipes, gulls, terns, and auks (382 species)

- Family Turnicidae—buttonquail
- Family Burhinidae—stone-curlews and thick-knees
- Family Chionidae—sheathbills
- Family Pluvianellidae—Magellanic plovers
- Family Haematopodidae—oystercatchers
- Family Dromadidae—crab-plovers
- Family Recurvirostridae—stilts and avocets
- Family Charadriidae—plovers
- Family Pluvianidae—Egyptian plovers
- Family Rostratulidae—painted snipes
- Family Jacanidae—jacanas
- Family Pedionomoidae—Plains-wanderers

  Family Thinocoridae—seedsnipes
  Family Scolopacidae—sandpipers and snipes
  Family Glareolidae—coursers and pratincoles
  Family Laridae—gulls, terns, and skimmers
  Family Stercorariidae—skuas
  Family Alcidae—auks
Order Pterocliformes—sandgrouse (16 species)
  Family Pteroclidae—sandgrouse
Order Columbiformes—pigeons and doves (344 species)
  Family Columbidae—pigeons and doves
Order Opisthocomiformes—hoatzins (1 species)
  Family Opisthocomidae—hoatzins
Order Musophagiformes—turacos (23 species)
  Family Musophagidae—turacos
Order Cuculiformes—cuckoos (149 species)
  Family Cuculidae—cuckoos
Order Strigiformes—owls (222 species)
  Family Tytonidae—barn owls
  Family Strigidae—owls
Order Caprimulgiformes—frogmouths, oilbirds, potoos, and nightjars (116 species)
  Family Podargidae—frogmouths
  Family Steatornithidae—oilbirds
  Family Nyctibiidae—potoos
  Family Caprimulgidae—nightjars
Order Apodiformes—swifts and hummingbirds (481 species)
  Family Aegothelidae—owlet-nightjars
  Family Hemiprocnidae—treeswifts

  Family Apodidae—swifts
  Family Trochilidae—hummingbirds
Order Coliiformes—mousebirds (6 species)
  Family Coliidae—mousebirds
Order Trogoniformes—trogons (43 species)
  Family Trogonidae—trogons
Order Leptosomiformes—cuckoo rollers (1 species)
  Family Leptosomidae—cuckoo rollers
Order Coraciiformes—rollers, kingfishers, todies, motmots, and bee-eaters (177 species)
  Family Coraciidae—rollers
  Family Brachypteraciidae—ground rollers
  Family Alcedinidae—kingfishers
  Family Todidae—todies
  Family Momotidae—motmots
  Family Meropidae—bee-eaters
Order Bucerotiformes—hoopoes and hornbills (74 species)
  Family Upupidae—hoopoes
  Family Phoeniculidae—wood hoopoes
  Family Bucerotidae—hornbills
  Family Bucorvidae—ground hornbills
Order Piciformes—jacamars, puff birds, toucans, barbets, honeyguides, and woodpeckers (445 species)
  Family Galbulidae—jacamars
  Family Bucconidae—puffbirds
  Family Capitonidae—New World barbets
  Family Semnornithidae—toucan barbets
  Family Ramphastidae—toucans
  Family Megalaimidae—Asian barbets

  Family Lybiidae—African barbets

  Family Indicatoridae—honeyguides

  Family Picidae—woodpeckers

Order Falconiformes—caracaras and falcons (67 species)

  Family Falconidae—caracaras and falcons

Order Psittaciformes—parrots and cockatoos (398 species)

  Family Strigopidae—New Zealand parrots

  Family Cacatuidae—cockatoos

  Family Psittacidae—African and New World parrots

  Family Psittaculidae—Old World parrots

Order Passeriformes (6,468 species—This order contains 60 percent of the 10,711 species of birds recognized by the IOC)

  Family Acanthisittidae—New Zealand wrens

  Family Eurylaimidae—broadbills

  Family Pittidae—pittas

  Family Furnariidae—ovenbirds

  Family Thamnophilidae—antbirds

  Family Formicariidae—antthrushes

  Family Grallariidae—antpittas

  Family Conopophagidae—gnateaters

  Family Rhinocryptidae—tapaculos

  Family Melanoparaeiidae—crescentchests

  Family Tyrannidae—tyrant flycatchers

  Family Cotingidae—cotingas

  Family Pipridae—manakins

  Family Tityridae—tityras, becards, and sharpbill

  Family Menuridae—lyrebirds

  Family Atrichornithidae—scrubbirds

Family Ptilonorhynchidae—bowerbirds

Family Climacteridae—Australasian treecreepers

Family Maluridae—Australasian wrens

Family Meliphagidae—honeyeaters

Family Dasyornithidae—bristlebirds

Family Pardalotidae—pardalotes

Family Acanthizidae—Australasian warblers

Family Pomatostomidae—Australasian babblers

Family Orthonychidae—logrunners

Family Cnemophilidae—satinbirds

Family Melanocharitidae—berrypeckers and longbills

Family Paramythiidae—painted berrypeckers

Family Callaeidae—New Zealand wattlebirds

Family Notiomystidae—stitchbirds

Family Psophodidae—whipbirds, jewel-babblers, and quail-thrushes

Family Platysteiridae—wattle-eyes and batises

Family Malaconotidae—bushshrikes

Family Machaerirhynchidae—boatbills

Family Vangidae—vangas

Family Pityriasidae—bristleheads

Family Artamidae—woodswallows

Family Rhagologidae—mottled berryhunters

Family Aegithinidae—ioras

Family Campephagidae—cuckooshrikes

Family Mohouidae—whiteheads

Family Neosittidae—sitellas

Family Eulacestomatidae—ploughbill

Family Pachycephalidae—whistlers and allies
Family Laniidae—shrikes
Family Vireonidae—vireos, greenlets, and shrike-babblers
Family Oriolidae—figbirds, orioles, and pitohuis
Family Dicruridae—drongos
Family Rhipiduridae—fantails
Family Monarchidae—monarchs
Family Corvidae—crows and jays
Family Corcoracidae—Australian mudnesters
Family Melampittidae—melampittas
Family Ifritidae—ifrits
Family Paradisaeidae—birds-of-paradise
Family Petroicidae—Australasian robins
Family Picathartidae—rockfowl
Family Chaetopidae—rockjumpers
Family Eupetidae—rail-babblers
Family Bombycillidae—waxwings
Family Ptiliogonatidae—silky-flycatchers
Family Hypocoliidae—hypocolius
Family Dulidae—palmchats
Family Mohoidae—‘ō‘ōs
Family Hylocitreidae—Yellow-flanked or olive-flanked warblers
Family Stenostiridae—fairy flycatchers
Family Paridae—tits and chickadees
Family Remizidae—penduline tits
Family Nicatoridae—nicators
Family Panuridae—bearded reedling
Family Alaudidae—larks

Family Pycnonotidae—bulbuls

Family Hirundinidae—swallows and martins

Family Pnoepygidae—cupwings

Family Macrosphenidae—African warblers

Family Cettiidae—cettia bush warblers and allies

Family Scotocercidae—streaked scrub warblers

Family Erythrocercidae—yellow flycatchers

Family Incertae Sedis—*Graveria*, *Hylia*, and *Pholidornis*

Family Aegithalidae—bushtits

Family Phylloscopidae—leaf warblers and allies

Family Acrocephalidae—reed warblers and allies

Family Locustellidae—grassbirds and allies

Family Donacobiidae—black-capped donacobius

Family Bernieridae—Madagascan warblers

Family Cisticolidae—cisticolas and allies

Family Timaliidae—babblers and scimitar babblers

Family Pellorneidae—fulvettas and ground babblers

Family Leiothricidae—laughing thrushes and allies

Family Sylviidae—sylviid babblers

Family Zosteropidae—white-eyes

Family Modulatricidae—dapple-throats and allies

Family Promeropidae—sugarbirds and allies

Family Irenidae—fairy-bluebirds

Family Regulidae—goldcrests and kinglets

Family Elachuridae—spotted elachura or spotted wren-babbler

Family Hyliotidae—hyliotas

Family Troglodytidae—wrens

Family Polioptilidae—gnatcatchers

Family Sittidae—nuthatches

Family Tichodromidae—wallcreepers

Family Certhiidae—treecreepers

Family Mimidae—mockingbirds and thrashers

Family Sturnidae—starlings, mynas, and stripe-headed rhabdornis

Family Buphagidae—oxpeckers

Family Turdidae—thrushes

Family Muscicapidae—chats and Old World flycatchers

Family Cinclidae—dippers

Family Chloropseidae—leafbirds

Family Dicaeidae—flowerpeckers

Family Nectariniidae—sunbirds

Family Passeridae—Old World sparrows and snowfinches

Family Ploceidae—weavers and widowbirds

Family Estrildidae—waxbills, munias, and allies

Family Viduidae—indigobirds and whydahs

Family Peucedramidae—olive warblers

Family Prunellidae—accentors

Family Motacillidae—wagtails and pipits

Family Urocynchramidae—Przevalski's finches

Family Fringillidae—finches and euphonias

Family Calcariidae—longspurs and snow buntings

Family Rhodinocichlidae—thrush-tanagers

Family Emberizidae—buntings

Family Passerellidae—New World sparrows

Family Calyptophilidae—chat-tanagers

Family Phaenicophilidae—Hispaniolan tanagers

Family Neospingidae—Puerto Rican tanagers

Family Spindalidae—spindalises

Family Zeledoniidae—wrenthrushes

Family Teretistridae—Cuban warblers

Family Icteriidae—yellow-breasted chats

Family Parulidae—New World warblers

Family Icteridae—oropendolas, orioles, and blackbirds

Family Coerebidae—bananaquits

Family Mitrospingidae—mitrospingid tanagers

Family Cardinalidae—cardinals, grosbeaks, and (tanager) allies

Family Thraupidae—tanagers and allies

MAMMALS

The following mammalian taxonomy is based on the preliminary classification of Reeder and Helgen for the 4th edition of Mammal Species of the World: A Taxonomic and Geographic Reference *(in press).*

Subphylum Craniata

Class Mammalia (Synapsida)

Subclass Prototheria

Order Monotremata (5 species)

Family Ornithorhynchidae—duck-billed platypuses

Family Tachyglossidae—echidnas

Subclass Theria

Infraclass Metatheria

Order Didelphimorphia (91 species)

Family Didelphidae—American opossums

Family Glironiidae—bushy-tailed opossums

Family Caluromyidae—woolly opossums

Order Paucituberculata (6 species)

    - Family Caenolestidae—shrew or rat opossums
- Order Microbiotheria (1 species)
    - Family Microbiotheriidae—monito del montes
- Order Dasyuromorphia (71 species)
    - Family Myrmecobiidae—numbats
    - Family Dasyuridae—marsupial mice and Tasmanian devils
    - Family Thylacinidae (recently extinct)—thylacines
- Order Peramelemorphia (21 species)
    - Family Peramelidae—bandicoots and echymiperas
    - Family Thylacomyidae—bilbies
    - Family Chaeropodidae (recently extinct)—pig-footed bandicoots
- Order Diprotodontia (145 species)
    - Family Phascolarctidae—koalas
    - Family Vombatidae—wombats
    - Family Burramyidae—pygmy possums
    - Family Phalangeridae—brushtail possums and cuscuses
    - Family Acrobatidae—feathertail gliders and feathertail possums
    - Family Tarsipedidae—honey possums
    - Family Petauridae—striped and gliding possums
    - Family Pseudocheiridae—ringtail possums
    - Family Hypsiprymnodontidae—musky rat-kangaroos
    - Family Potoroidae—potoroos and bettongs
    - Family Macropodidae—wallabies, kangaroos, and pademelons
- Order Notoryctemorphia (2 species)
    - Family Notoryctidae—marsupial moles

Infraclass Metatheria

- Order Tenrecoidea—(51 species)
  - Family Tenrecidae—tenrecs
  - Family Potomogalidae—otter shrews
  - Family Chrysochloridae—golden moles
- Order Macroscelidea (19 species)
  - Family Macroscelididae—elephant shrews
- Order Tubulidentata (1 species)
  - Family Orycteropodidae—aardvarks
- Order Hyracoidea (4 or 5 species)
  - Family Procaviidae—hyraxes
- Order Proboscidea (3 species)
  - Family Elephantidae—elephants
- Order Sirenia (4 species)
  - Family Dugongidae—dugongs
  - Family Trichechidae—manatees
- Order Cingulata (21 species)
  - Family Dasypodidae—armadillos
- Order Pilosa (10 species)
  - Family Bradypodidae—three-toed sloths
  - Family Megalonychidae—two-toed tree sloths
  - Family Myrmecophagidae—true anteaters
  - Family Cyclopedidae—silky anteaters
- Order Scandentia (19 species)
  - Family Ptilocercidae—pen-tailed treeshrews
  - Family Tupaiidae—treeshrews
- Order Dermoptera (2 species)
  - Family Cynocephalidae—colugos
- Order Primates (450 species)

- Family Cheirogaleidae—dwarf lemurs and mouse lemurs
- Family Lemuridae—lemurs
- Family Lepilemuridae—sportive lemurs
- Family Indriidae—indriid lemurs and sifakas
- Family Daubentoniidae—aye-ayes
- Family Lorisidae—lorises and pottos
- Family Galagidae—bushbabies and galagos
- Family Tarsiidae—tarsiers
- Family Cebidae—New World monkeys, marmosets, and tamarins
- Family Pitheciidae—tiki and sati monkeys
- Family Atelidae—howler monkeys
- Family Cercopithecidae—Old World monkeys
- Family Hylobatidae—gibbons and siamangs
- Family Hominidae—gorillas, chimpanzees, orangutans, and humans

Order Lagomorpha (65 species)

- Family Ochotonidae—pikas
- Family Leporidae—rabbits and hares

Order Rodentia (approx. 2,291 species—approximately 42 percent of living mammalian species are rodents)

- Suborder Castorimorpha
  - Family Castoridae—beavers
  - Family Geomyidae—pocket gophers
  - Family Heteromyidae—kangaroo rats and kangaroo mice
- Suborder Myomorpha
  - Family Dipodidae—jerboas
  - Family Zapodidae—jumping mice
  - Family Sicistidae—birch mice

Family Platacanthomyidae—spiny mice and soft-furred tree mice

Family Spalacidae—zokors, bamboo rats, and blind mole rats

Family Calomyscidae—mouse-like hamsters

Family Nesomyidae—Madagascar rats and mice

Family Cricetidae—voles and mice

Family Muridae—Old World rats and mice

Suborder Anomaluromorpha

Family Anomaluridae—scaly-tailed squirrels

Family Pedetidae—springhares

Suborder Hystricomorpha

Family Ctenodactylidae—gundis

Family Diatomyidae—Laotian rock rats

Family Bathyergidae—mole rats

Family Hystricidae—Old World porcupines

Family Petromuridae—dassie rats

Family Thryonomyidae—cane rats

Family Erethizontidae—New World porcupines

Family Chinchillidae—viscachas and chinchillas

Family Dinomyidae—pacaranas

Family Caviidae—cavies, Patagonian “hares,” guinea pigs, and capybaras

Family Dasyproctidae—agoutis and acouchis

Family Cuniculidae—pacas

Family Ctenomyidae—tuco-tucos

Family Octodontidae—viscacha rats and coruros

Family Abrocomidae—chinchilla rats

Family Echimyidae—spiny rats

Family Capromyidae—hutias

Family Heptaxodontidae (recently extinct)—giant hutias

Family Myocastoridae—nutrias

Suborder Sciuromorpha

Family Aplodontidae—mountain beavers

Family Sciuridae—squirrels

Family Gliridae—dormice

Order Solenodonta

Family Solenodontidae—solenodons (2 species)

Family Nesophontidae (recently extinct)—*Nesophontes* (6–9 species)

Order Soricomorpha (415 species)

Family Soricidae—shrews

Family Talpidae—moles, shrew-moles, and desmans

Order Erinaceomorpha (31 species)

Family Erinaceidae—hedgehogs and gymnures

Family Galericidae—moonrats

Order Carnivora (286 species)

Suborder Feliformia

Family Felidae—cats

Family Herpestidae—mongooses

Family Hyaenidae—hyenas and aardwolves

Family Viverridae—civets and genets

Family Nandiniidae—African palm civets

Family Prionodontidae—linsangs

Family Eupleridae—Madagascar mongooses

Suborder Caniformia

Family Canidae—dogs, wolves, and foxes

  - Family Ursidae—bears
  - Family Mustelidae—weasels, otters, and badgers
  - Family Mephitidae—skunks
  - Family Odobenidae—walruses
  - Family Otariidae—eared seals
  - Family Phocidae—earless seals
  - Family Procyonidae—raccoons and coatis
  - Family Ailuridae—red pandas
- Order Pholidota (8 species)
  - Family Manidae—scaly anteaters (pangolins)
- Order Perissodactyla (16 to 18 species)
  - Family Equidae—horses, asses, and zebras
  - Family Tapiridae—tapirs
  - Family Rhinocerotidae—rhinoceroses
- Order Artiodactyla (377 to 380 species)
  - Family Suidae—pigs and warthogs
  - Family Tayassuidae—peccaries
  - Family Camelidae—camels and llamas
  - Family Tragulidae—chevrotains
  - Family Giraffidae—giraffes and okapis
  - Family Moschidae—musk deer
  - Family Cervidae—deer
  - Family Antilocapridae—pronghorn antelope
  - Family Bovidae—antelope, sheep, goats, bison, and cattle
  - Family Hippopotamidae—hippopotamuses
- Infraorder Cetacea
  - Parvorder Mysticeti (13 species)
    - Family Balaenidae—bowhead whales and right whales

    - Family Balaenopteridae—rorquals
    - Family Eschrichtiidae—gray whales
    - Family Neobalaenidae—pygmy right whales
  - Parvorder Odontoceti (74 species)
    - Family Delphinidae—dolphins
    - Family Monodontidae—narwhals and belugas
    - Family Phocoenidae—porpoises
    - Family Physeteridae—sperm whales
    - Family Kogiidae—pygmy whales and dwarf sperm whales
    - Family Platanistidae—Ganges River dolphin and Indus River dolphin
    - Family Iniidae—baijis and Amazon River dolphins
    - Family Pontoporiidae—franciscanas
    - Family Ziphiidae—beaked whales
- Order Chiroptera (1,200 species)
  - Suborder Yinpterochiroptera
    - Family Pteropodidae—Old World fruit bats
    - Family Hipposideridae—trident bats and leaf-nosed bats
    - Family Rhinolophidae—horseshoe bats
    - Family Rhinopomatidae—mouse-tailed bats
    - Family Craseonycteridae—Kitti’s hog-nosed bats
    - Family Megadermatidae—false vampire bats
  - Suborder Yangochiroptera
    - Family Emballonuridae—sac-winged, or sheath-tailed, bats
    - Family Nycteridae—slit-faced bats
    - Family Mystacinidae—short-tailed bats
    - Family Thyropteridae—disk-winged bats
    - Family Furipteridae—smoky bats

Family Noctilionidae—fishing bats

Family Mormoopidae—leaf-chinned bats

Family Phyllostomidae—New World leaf-nosed bats

Family Myzopodidae—sucker-footed bats

Family Natalidae—funnel-eared bats

Family Molossidae—free-tailed bats

Family Miniopteridae—long-fingered bats

Family Cistugidae—wing-gland bats

Family Vespertilionidae—common bats

APPENDIX B

Endangered Vertebrate Species in the United States and/or Trust Territories

The data are from the official website of the US Office of Endangered Species and are current as of September 4, 2018.

Mammals (66 records)

bat, Florida bonneted—*Eumops floridanus*

bat, gray—*Myotis grisescens*

bat, Hawaiian hoary—*Lasiurus cinereus semotus*

bat, Indiana—*Myotis sodalis*

bat, little Marianas fruit—*Pteropus tokudae*

bat, Mexican long-nosed—*Leptonycteris nivalis*

bat, Ozark big-eared—*Corynorhinus (= Plecotus) townsendii ingens*

bat, Pacific sheath-tailed—*Emballonura semicaudata rotensis*

bat, Pacific sheath-tailed—*Emballonura semicaudata semicaudata*

bat, Virginia big-eared—*Corynorhinus (= Plecotus) townsendii virginianus*

caribou, woodland—*Rangifer tarandus caribou*

deer, key—*Odocoileus virginianus clavium*

ferret, black-footed—*Mustela nigripes*

fox, San Joaquin kit—*Vulpes macrotis mutica*

jaguar—*Panthera onca*

jaguarundi, Gulf Coast—*Herpailurus (= Felis) yagouaroundi cacomitli*

jaguarundi, Sinaloan—*Herpailurus (= Felis) yagouaroundi tolteca*

kangaroo rat, Fresno—*Dipodomys nitratoides exilis*

kangaroo rat, giant—*Dipodomys ingens*

kangaroo rat, Morro Bay—*Dipodomys heermanni morroensis*

kangaroo rat, San Bernardino Merriam's—*Dipodomys merriami parvus*

kangaroo rat, Stephens'—*Dipodomys stephensi* (incl. *D. cascus*)

kangaroo rat, Tipton—*Dipodomys nitratoides nitratoides*

margay—*Leopardus (= Felis) wiedii*

mountain beaver, Point Arena—*Aplodontia rufa nigra*

mouse, Alabama beach—*Peromyscus polionotus ammobates*

mouse, Anastasia Island beach—*Peromyscus polionotus phasma*

mouse, Choctawhatchee beach—*Peromyscus polionotus allophrys*

mouse, Key Largo cotton—*Peromyscus gossypinus allapaticola*

mouse, New Mexico meadow jumping—*Zapus hudsonius luteus*

mouse, Pacific pocket—*Perognathus longimembris pacificus*

mouse, Perdido Key beach—*Peromyscus polionotus trissyllepsis*
mouse, salt marsh harvest—*Reithrodontomys raviventris*
mouse, St. Andrew beach—*Peromyscus polionotus peninsularis*
ocelot—*Leopardus (= Felis) pardalis*
panther, Florida—*Puma (= Felis) concolor coryi*
pronghorn, Sonoran—*Antilocapra americana sonoriensis*
rabbit, Columbia Basin Pygmy—*Brachylagus idahoensis*
rabbit, Lower Keys marsh—*Sylvilagus palustris hefneri*
rabbit, riparian brush—*Sylvilagus bachmani riparius*
rice rat—*Oryzomys palustris natator*
seal, Hawaiian monk—*Monachus schauinslandi*
seal, ringed—*Phoca (= Pusa) hispida ladogensis*
sea lion, Steller—*Eumetopias jubatus*
sheep, Peninsular bighorn—*Ovis canadensis nelsoni*
sheep, Sierra Nevada bighorn—*Ovis canadensis sierrae*
shrew, Buena Vista Lake ornate—*Sorex ornatus relictus*
squirrel, Carolina northern flying—*Glaucomys sabrinus coloratus*
squirrel, Mount Graham red—*Tamiasciurus hudsonicus grahamensis*
vole, Amargosa—*Microtus californicus scirpensis*
vole, Florida salt marsh—*Microtus pennsylvanicus dukecampbelli*
whale, beluga—*Delphinapterus leucas*
whale, blue—*Balaenoptera musculus*
whale, bowhead—*Balaena mysticetus*
whale, false killer—*Pseudorca crassidens*
whale, finback—*Balaenoptera physalus*
whale, killer—*Orcinus orca*
whale, North American right—*Eubalaena glacialis*
whale, North Pacific right—*Eubalaena japonica*

whale, sei—*Balaenoptera borealis*

whale, sperm—*Physeter catodon (= macrocephalus)*

wolf, gray—*Canis lupus*

wolf, Mexican—*Canis lupus baileyi*

wolf, red—*Canis rufus*

woodrat, Key Largo—*Neotoma floridana smalli*

woodrat, riparian (San Joaquin Valley)—*Neotoma fuscipes riparia*

Birds (80 records)

akekee—*Loxops caeruleirostris*

akepa, Hawaii—*Loxops coccineus*

akepa, Maui—*Loxops ochraceus*

akialoa, Kauai (honeycreeper)—*Akialoa stejnegeri*

akiapolaau (honeycreeper)—*Hemignathus wilsoni*

akikiki—*Oreomystis bairdi*

albatross, short-tailed—*Phoebastria (= Diomedea) albatrus*

blackbird, yellow-shouldered—*Agelaius xanthomus*

bobwhite, masked (quail)—*Colinus virginianus ridgwayi*

chicken, Attwater's greater prairie—*Tympanuchus cupido attwateri*

condor, California—*Gymnogyps californianus*

coot, Hawaiian—*Fulica americana alai*

crane, Mississippi sandhill—*Grus canadensis pulla*

crane, whooping—*Grus americana*

creeper, Hawaii—*Oreomystis mana*

creeper, Molokai—*Paroreomyza flammea*

creeper, Oahu—*Paroreomyza maculata*

crow, Hawaiian (= ‘alala)—*Corvus hawaiiensis*

crow, Mariana (= aga)—*Corvus kubaryi*

crow, white-necked—*Corvus leucognaphalus*

curlew, Eskimo—*Numenius borealis*
duck, Hawaiian (= koloa)—*Anas wyvilliana*
duck, Laysan—*Anas laysanensis*
elepaio, Oahu—*Chasiempis ibidis*
falcon, northern aplomada—*Falco femoralis septentrionalis*
finch, Laysan (honeycreeper)—*Telespyza cantans*
finch, Nihoa (honeycreeper)—*Telespyza ultima*
flycatcher, southwestern willow—*Empidonax traillii extimus*
gallinule, Hawaiian common—*Gallinula galeata sandvicensis*
goose, Hawaiian—*Branta (= Nesochen) sandvicensis*
ground-dove, friendly—*Gallicolumba stairi*
hawk, Hawaiian (= ‘lo)—*Butea solitarius*
hawk, Puerto Rican broad-winged—*Buteo platypterus brunnescens*
hawk, Puerto Rican sharp-shinned—*Accipiter striatus venator*
honeycreeper, crested (Akohekohe)—*Palmeria dolei*
‘I‘iwi (scarlet honeycreeper)—*Drepanis coccinea*
kingfisher, Guam Micronesian—*Halcyon cinnamomina cinnamomina*
kite, Everglade snail—*Rostrhamus sociabilis plumbeus*
mao (= ma’oma’o) (Samoan honeyeater)—*Gymnomyza samoensis*
megapode, Micronesian—*Megapodius laperouse*
millerbird, Nihoa (Old World warbler)—*Acrocephalus familiaris kingi*
moorhen, Mariana common—*Gallinula chloropus guami*
nightjar, Puerto Rican—*Caprimulgus noctitherus*
nukupuu, Kauai—*Hemignathus Hanapepe*
nukupuu, Maui—*Hemignathus affinis*
‘ō‘ō, Kauai (honeyeater)—*Moho braccatus*
‘ō‘ū (honeycreeper)—*Psittirostra psittacea*
palila (honeycreeper)—*Loxioides bailleui*

parrot, Puerto Rican—*Amazona vittata*
parrot, thick-billed—*Rhynchopsitta pachyrhyncha*
parrotbill, Maui (kiwikiu)—*Pseudonestor xanthophrys*
petrel, band-rumped storm—*Oceanodroma castro*
petrel, Bermuda—*Pterodroma cahow*
petrel, Hawaiian—*Pterodroma sandwichensis*
pigeon, Puerto Rican plain—*Columba inornata wetmorei*
plover, piping—*Charadrius melodus*
po'ouli (honeycreeper)—*Melamprosops phaeosoma*
rail, California clapper—*Rallus longirostris obsoletus*
rail, Guam—*Rallus owstoni*
rail, light-footed clapper—*Rallus longirostris levipes*
rail, Yuma clapper—*Rallus longirostris yumanensis*
shrike, San Clemente loggerhead—*Lanius ludovicianus mearnsi*
sparrow, Cape Sable seaside—*Ammodramus maritimus mirabilis*
sparrow, Florida grasshopper—*Ammodramus savannarum floridanus*
stilt, Hawaiian—*Himantopus mexicanus knudseni*
swiftlet, Mariana gray—*Aerodramus vanikorensis bartschi*
tern, California least—*Sterna antillarum browni*
tern, least—*Sterna antillarum*
tern, roseate—*Sterna dougallii dougallii*
thrush, large Kauai (= kamao)—*Myadestes myadestinus*
thrush, Molokai—*Myadestes lanaiensis rutha*
thrush, small Kauai (puaiohi)—*Myadestes palmeri*
vireo, least Bell's—*Vireo bellii pusillus*
warbler, Kirtland's—*Setophaga kirtlandii (= Dendroica kirtlandii)*
warbler, nightingale reed (Old World warbler)—*Acrocephalus luscinia*
warbler, Bachman's (= wood)—*Vermivora bachmanii*

warbler, golden-cheeked (= wood)—*Dendroica chrysoparia*

white-eye, bridled—*Zosterops conspicillatus conspicillatus*

white-eye, Rota bridled—*Zosterops rotensis*

woodpecker, ivory-billed—*Campephilus principalis*

woodpecker, red-cockaded—*Picoides borealis*

Reptiles (17 records)

anole, Culebra Island giant—*Anolis roosevelti*

boa, Puerto Rican—*Epicrates inornatus*

boa, Virgin Islands tree—*Epicrates monensis granti*

gecko, Monito—*Sphaerodactylus micropithecus*

lizard, blunt-nosed leopard—*Gambelia silus*

lizard, St. Croix ground—*Ameiva polops*

sea turtle, green—*Chelonia mydas*

sea turtle, hawksbill—*Eretmochelys imbricata*

sea turtle, Kemp's ridley—*Lepidochelys kempii*

sea turtle, leatherback—*Dermochelys coriacea*

sea turtle, loggerhead—*Caretta caretta*

skink, Slevin's—*Emoia slevini*

snake, narrow-headed garter—*Thamnophis rufipunctatus*

snake, San Francisco garter—*Thamnophis sirtalis tetrataenia*

turtle, Alabama red-bellied—*Pseudemys alabamensis*

turtle, Plymouth red-bellied—*Pseudemys rubriventris bangsi*

turtle, Sonoyta mud—*Kinosternon sonoriense longifemorale*

Amphibians (19 records)

coqui, Llanero—*Eleutherodactylus juanariveroi*

frog, dusky gopher—*Rana capito*

frog, mountain yellow-legged—*Rana muscosa*

frog, Sierra Nevada yellow-legged—*Rana sierra* hellbender, Ozark—*Cryptobranchus alleganiensis bishop*

salamander, Austin blind—*Eurycea waterlooensis*

salamander, Barton Springs—*Eurycea sosorum*

salamander, California tiger—*Ambystoma californiense*

salamander, desert slender—*Batrachoseps aridus*

salamander, Jemez Mountains—*Plethodon neomexicanus*

salamander, reticulated flatwoods—*Ambystoma bishopi*

salamander, Santa Cruz long-toed—*Ambystoma macrodactylum croceum*

salamander, Shenandoah—*Plethodon shenandoah*

salamander, Sonora tiger—*Ambystoma tigrinum stebbinsi*

salamander, Texas blind—*Typhlomolge rathbuni*

toad, arroyo (= arroyo southwestern)—*Anaxyrus californicus*

toad, Houston—*Bufo houstonensis*

toad, Wyoming—*Bufo hemiophrys baxteri*

waterdog, black warrior (= Sipsey Fork)—*Necturus alabamensis*

Fishes (87 records)

bocaccio—*Sebastes paucispinis*

cavefish, Alabama—*Speoplatyrhinus poulsoni*

chub, bonytail—*Gila elegans*

chub, Borax Lake—*Gila boraxobius*

chub, Gila—*Gila intermedia*

chub, humpback—*Gila cypha*

chub, Mohave tui—*Gila bicolor* ssp. *mohavensis*

chub, Owens tui—*Gila bicolor* ssp. *snyderi*

chub, Pahranagat roundtail—*Gila robusta jordani*

chub, Virgin River—*Gila seminuda (= robusta)*

chub, Yaqui—*Gila purpurea*

cui-ui—*Chasmistes cujus*

dace, Ash Meadows speckled— *Rhinichthys osculus nevadensis*

dace, Clover Valley speckled—*Rhinichthys osculus oligoporus*

dace, Independence Valley speckled—*Rhinichthys osculus lethoporus*

dace, Kendall Warm Springs—*Rhinichthys osculus thermalis*

dace, laurel—*Chrosomus saylori*

dace, moapa—*Moapa coriacea*

darter, amber—*Percina antesella*

darter, bluemask—*Etheostoma akatulo*

darter, boulder—*Etheostoma wapiti*

darter, Cumberland—*Etheostoma susanae*

darter, diamond—*Crystallaria cincotta*

darter, duskytail—*Etheostoma percnurum*

darter, Etowah—*Etheostoma etowahae*

darter, fountain—*Etheostoma fonticola*

darter, Maryland—*Etheostoma sellare*

darter, relict—*Etheostoma chienense*

darter, rush—*Etheostoma phytophilum*

darter, vermilion—*Etheostoma chermocki*

darter, watercress—*Etheostoma nuchale*

darter, yellowcheek—*Etheostoma moorei*

gambusia, Big Bend—*Gambusia gaigei*

gambusia, Clear Creek—*Gambusia heterochir*

gambusia, Pecos—*Gambusia nobilis*

gambusia, San Marcos—*Gambusia georgei*

goby, tidewater—*Eucyclogobius newberryi*

logperch, Conasauga—*Percina jenkinsi*

logperch, Roanoke—*Percina rex*

madtom, chucky—*Noturus crypticus*

madtom, pygmy—*Noturus stanauli*
madtom, Scioto—*Noturus trautmani*
madtom, smoky—*Noturus baileyi*
minnow, loach—*Tiaroga cobitis*
minnow, Rio Grande silvery—*Hybognathus amarus*
pikeminnow, Colorado (= squawfish)—*Ptychocheilus lucius*
poolfish, Pahrump—*Empetrichthys latos*
pupfish, Ash Meadows Amargosa—*Cyprinodon nevadensis mionectes*
pupfish, Comanche Springs—*Cyprinodon elegans*
pupfish, desert—*Cyprinodon macularius*
pupfish, Devils Hole—*Cyprinodon diabolis*
pupfish, Leon Springs—*Cyprinodon bovinus*
pupfish, Owens—*Cypinodon radiosus*
pupfish, Warm Springs—*Cyprinodon nevadensis pectoralis*
salmon, Atlantic—*Salmo salar*
salmon, Chinook—*Oncorhynchus (= Salmo) tshawytscha*
salmon, coho—*Oncorhynchus (= Salmo) kisutch*
salmon, sockeye—*Oncorhynchus (= Salmo) nerka*
sawfish, dwarf—*Pristis clavata*
sawfish, largetooth—*Pristis pristis*
sawfish, narrow—*Anoxypristis cuspidata*
sawfish, Smalltooth—*Pristis pectinata*
sculpin, grotto—*Cottus specus*
shark, scalloped hammerhead—*Sphyrna lewini*
shiner, Cahaba—*Notropis cahabae*
shiner, Cape Fear—*Notropis mekistocholas*
shiner, palezone—*Notropis albizonatus*
shiner, sharpnose—*Notropis oxyrhynchus*

shiner, smalleye—*Notropis buccula*

shiner, Topeka—*Notropis topeka (= tristis)*

spinedace, White River—*Lepidomeda albivallis*

springfish, Hiko White River—*Crenichthys baileyi grandis*

springfish, White River—*Crenichthys baileyi baileyi*

steelhead—*Oncorhynchus (= Salmo) mykiss*

stickleback, unarmored threespine—*Gasterosteus aculeatus williamsoni*

sturgeon, Alabama—*Scaphirhynchus suttkusi*

sturgeon, Atlantic—*Acipenser oxyrinchus oxyrinchus*

sturgeon, pallid—*Scaphirhynchus albus*

sturgeon, shortnose—*Acipenser brevirostrum*

sturgeon, white—*Acipenser transmontanus*

sucker, June—*Chasmistes liorus*

sucker, Lost River—*Deltistes luxatus*

sucker, razorback—*Xyrauchen texanus*

sucker, shortnose—*Chasmistes brevirostris*

sucker, Zuni bluehead—*Catostomus discobolus yarrowi*

topminnow, Gila (incl. Yaqui)—*Poeciliopsis occidentalis*

woundfin—*Plagopterus argentissimus*

APPENDIX C

Common Names for the Sexes, Young, and Groups of Select Animals

Excerpted from Lipton, 1968; Burns, 1972; and Mark and Menning, 1984.

Animal	Male	Female	Young	Group
antelope	buck	doe	kid	herd
bear	boar	sow	cub	sloth
beaver	boar	sow	pup	colony
bison	bull	cow	calf	herd
bobcat	tom	lioness/queen	kitten	litter
cat	tomcat (tom)	pussy/queen	kitten	clowder
cattle	bull	cow/heifer	calf	herd/drove
chicken	rooster	hen/pullet	chick	flock/peep
deer	buck/stag	doe	fawn	herd
dog	dog	bitch	pup	kennel
duck	drake	duck	duckling	flock
eagle	cock	hen	eaglet	convocation
elephant	bull	cow	calf	herd
fishes	cock	hen	fry	school
fox	reynard	vixen	cub/pup	earth/skulk
giraffe	bull	cow	calf	herd
goat	billy/buck	nanny	kid	trip
goose	gander	goose/dame	gosling	gaggle
hog	boar	sow/gilt	piglet/shoat	herd/drove
horse	stallion/colt	mare/filly	foal	stable/herd
kangaroo	buck	doe	joey	troop/herd
leopard	leopard	leopardess	cub	leap
lion	lion	lioness	cub	pride
otter	dog	bitch	cub	—
owl	owl	jenny	owlet	parliament
peafowl	peacock	peahen	—	flock
pheasant	cock	hen	—	nye/bouquet
pigeon	cock	hen	squab	flock
polecat	hob	jill	kitten	—
rabbit	buck	doe	kitten	colony
rat	buck	doe	—	colony
seal	bull	cow	pup	herd/harem/rookery
sheep	ram	ewe	lamb	flock/hurtle
swan	cob	pen	cygnet	flock
tiger	tiger	tigress	cub	—
turkey	tom	hen	poult	flock/rafter
walrus	bull	cow	cub	herd
whale	bull	cow	calf	herd/pod
wolf	he-wolf	she-wolf	pup	pack/rout
zebra	stallion	mare	colt	herd

Additional Group Terms:

Animal	**Group**	**Animal**	**Group**
apes	shrewdness	moles	labor
birds (small)	dissimulation	monkeys	troupe
camels	flock/herd	mules	barren
coots	covert	nightingales	watch
crows	murder	oxen	team/yoke/drove/herd
doves	flight	parrots	flock
ducks in flight	team	porpoises	school/gam/herd
ducks on water	paddling	quails	bevy
ducks (two)	brace	ravens	unkindness
eels	swarm	redwings	crowd
elk	gang	rhinoceroses	crash
ferrets	business	snakes (young)	bed
finches	charm	sparrows	host/tribe
frogs	army	squirrels	dray
geese (in flight)	flock	starlings	chattering/murmuration
geese (on water)	gaggle	storks	mustering
grouse	covey	swallows	flight
herons	siege	toads	knot
jays	band	turtledoves	pitying
larks	exaltation	turtles	bale
magpies	tidings	woodpeckers	descent
mallards	flush/puddling	wrens	herd

GLOSSARY

abomasum. Fourth and last chamber of the ruminant stomach.

abyssopelagic zone. Region of the oceanic zone from approximately 4,000 to 6,000 m (2.5–3.7 mi.); almost constant physical environment; continually dark, cold (4°C or 39 °F), and virtually unchanging in chemical composition.

accidental parthenogenesis. Development of a new individual from an unfertilized egg due to the physical or chemical stimulation of the egg.

acid rain. Precipitation with a pH value less than 5.6.

acinar. Cells in the pancreas that produce and secrete digestive enzymes.

acoelous. Describes a vertebra having the anterior and posterior articular surfaces of the centrum (body) flattened.

acrodont. Type of tooth attachment in which there are no sockets; teeth are attached to the summit of the jaw.

adaptive radiation. The diversification of a group of organisms into forms filling different ecological niches; see also *radiation*.

adipose fin. Fleshy fin, without rays, located behind the dorsal fin.

adpressed limbs. In salamanders, the situation in which the forelimbs are pushed backward and the hindlimbs are pushed forward along the sides of the body.

adrenal. Endocrine gland near or on the kidney; secretes epinephrine, norepinephrine, aldosterone, cortisone, and gonadocorticoids.

adrenocorticotropic hormone (ACTH). Hormone produced by the anterior pituitary gland that stimulates the secretion of hormones by the adrenal cortex.

adult. Mature individual; capable of producing sex cells (eggs, sperm).

aerial locomotion. Self-generated movements of an animal through the air; flying (bats).

afferent. Conducting or conducted inward or toward something (for nerves, the central nervous system; for blood vessels, the organ supplied.)

Agnatha. Taxon of vertebrates, comprising those without jaws.

aldosterone. Mineralocorticoid hormone produced by the adrenal cortex that induces sodium and water reabsorption and potassium excretion.

allantois. Extraembryonic saclike extension of the hindgut of amniotes, aiding in excretion and respiration.

Allen's Rule. Ecological principle describing a general trend among homeotherms for limbs to become longer and extremities (like ears) to become less compact in warmer climates than in colder ones; best applied within those species having wide north-south geographic ranges.

allopatric. Occupying different geographic regions.

altitudinal migration. Vertical migration; generally seasonal, as is seen in elk and some birds.

altricial. Young bird or mammal hatched or born in a helpless condition and requiring extensive parental care in order to survive.

alveolus. Respiratory pocket in the lungs; site of gas exchange (diffusion of oxygen and carbon dioxide across an alveolar-capillary membrane).

ambulatory locomotion. Walking.

ammocoetes. Larval form of the lamprey; occurs in streams with sandy bottoms.

amnion. Fluid-filled innermost extraembryonic sac surrounding the embryo of reptiles, birds, and mammals.

amniote. Vertebrate whose embryo possesses an amnion, chorion, and allantois (reptiles, birds, mammals).

amphicoelous. Describes a vertebra having concave anterior and posterior articular surfaces of the centrum (body).

amphistylic. Type of jaw suspension found in some sharks where the jaws and hyoid arch are braced directly against the cranium.

amplexus. Sexual embrace of frogs in which the male mounts the female so that he is dorsal to her; the male's forelimbs may grasp the female around the waist (inguinal) or around the pectoral region (axillary).

ampulla. Dilation at the end of each semicircular canal containing sensory epithelium; low-frequency electroreceptor in certain fishes (e.g., ampulla of Lorenzini).

anadromous. Fish that typically inhabit seas or lakes but ascend freshwater streams to spawn (e.g., salmon).

anal fin. Median unpaired fin situated posterior to the anus (vent) and in front of the caudal peduncle.

analogy. Features of two or more organisms that perform a similar function; similarity of function but not of embryonic (evolutionary) origin (e.g., a butterfly wing and a bat wing).

anamniote. Vertebrate that lacks an amnion, allantois, and chorion during development (agnathans, fishes, amphibians).

anapsid. Amniotes in which the skull lacks temporal openings; turtles are the only living representatives.

angular. Dermal bone that ensheathes part of Meckel's cartilage.

antler. Deciduous, usually branched, bony outgrowth on the head of various members of the deer family (Cervidae).

anuran. Tailless amphibian from the order Anura; a frog or toad.

aphotic. Without light; that portion of a body of water lying at a depth beyond the penetration of sunlight.

aplacental viviparity. See *ovoviviparous*.

aposematic coloration. Adaptation of some species' bright colors that serves as a warning to potential predators (e.g., skunks, poison dart frogs, coral snakes).

appendix. Saclike structure attached to the caecum in mammals; may contain bacteria in some herbivores; vestigial in some species, including humans.

apterium (pl. **apteria**). Area of skin in birds devoid of feathers located between the pterylae.

aquatic locomotion. Movement through the water; swimming.

arachnoid layer. Middle of the three meninges surrounding the brain and spinal cord in birds and mammals.

arboreal. Living in trees.

Archaeopteryx. Earliest known birdlike vertebrate; from the Jurassic.

archinephros (or **holonephros**). Ancestral vertebrate kidney, existing today only in hagfish embryos; extends the length of the coelomic cavity; composed of segmentally arranged tubules, each opening into the coelom via a nephrostome.

arciferous. Nonrigid type of pectoral girdle in anurans in which the two epicoracoids overlap; as opposed to firmisternal.

arginine vasotocin. See *oxytocin*.

arrector pili (pl. **arrectores pilorum**). Smooth muscle attached to a hair follicle; contraction pulls hair into a more vertical position; cause of “goose bumps” in humans.

arrector plumari. Smooth muscles attached to every feather follicle; permits “fluffing” of feathers.

artery. Blood vessel conducting blood away from the heart.

articular. Ossified posterior tip of Meckel’s cartilage; becomes the malleus in the middle ear of mammals.

Artiodactyla. Order of the ungulate or hooved mammals having an even number of toes (either two or four).

atlas. First cervical vertebra; articulates with the skull.

auditory tube. See *Eustachian tube*.

auricle. Earlike lobe of an atrium of the heart; also, the external ear (pinna).

autostylic. Type of jaw suspension in which the jaws articulate directly with the cranium.

autotomy. The breaking off of a part of the body as a defensive escape maneuver by the organism itself (e.g., the tail of glass lizards).

baculum (pl. **bacula**). Penis bone (os penis) present in some mammals.

baleen. Horny plates of epidermal origin in the upper jaws of certain whales; serve to filter plankton from seawater.

barb. Branch from the shaft of a feather; together, the barbs of a feather form the vane.

barbule. Projection that fringes the barbs of a typical feather.

barrier. Impediment restricting the distribution of one or more species; may be physical (land, water, elevation, topography), climatic (temperature, humidity, rainfall, sunlight), or biological (lack of food, presence of predators, or effective competitors).

bathypelagic zone. Region of the oceanic zone from 1,000 to 4,000 m (3,280–13,120 ft.); cold, quiet water; characterized by permanent darkness and great pressure.

benthic. Pertaining to the bottoms of oceans, seas, and lakes.

Bergmann's Rule. Ecological principle stating that populations of homeotherms living in cooler climates tend to have a larger body size and a smaller surface area–volume ratio than conspecific populations living in warmer climates.

bicornuate. Describes a uterus having two horns or extensions; the lower two-thirds of the uterus is fused while the upper third remains separate; found in many ungulates.

biodiversity. All living organisms (microorganisms, fungi, plants, and animals) in the biosphere or in a specified area.

biogeographic region. One of six worldwide areas proposed by Wallace (1876) in an attempt to divide the land masses into a classification reflecting the affinities of the terrestrial flora and fauna; the six areas are called the Palearctic, Nearctic, Oriental, Neotropical, Ethiopian, and Australian regions.

biological amplification. Process by which pesticides, toxic metals, and other substances become more concentrated in each successive trophic level of a food web.

biome. Major regional ecological community of plants and animals.

biotic potential. See *reproductive potential*.

biotic province. Geographic area used in classifying North American plant and animal communities and their distribution; proposed by Dice (1943).

bipartite. Describes a uterus in which paired uteri are separate for most of their length, but join to form a single cervix; found in most carnivores and some ruminants.

boreal forest. Needle-leaved evergreen, or coniferous, forest bordering subpolar regions; also called *taiga*.

Bowman's capsule (or **glomerular capsule**). Spherical structure of each nephron of the kidney enclosing the glomerulus.

brachiation. Arboreal form of locomotion with grasping hands and arm swings; body suspended below tree branches.

brackish. Water that has a salt concentration greater than fresh water and less than seawater.

branchial. Pertaining to gills.

branchiomeric. Muscles modified by pharyngeal system anterior (superior) to pectoral girdle.

bridge (or **lateral bridge**). In turtles, the narrow connection between the plastron and carapace on each side of the body.

bristle. Modified, usually vaneless, feather consisting of only a shaft.

buccopharyngeal mucosa. Highly vascularized epithelium in the pharynx of some amphibians; utilized in respiration.

bulb. Enlarged, layered base of a hair follicle.

Bya. Billion years ago.

caecum (pl. **caeca**). Blind sac arising from the digestive tract; in fishes, the pyloric caeca are slender, finger-like structures arising from the junction between the stomach and intestines; in tetrapods, there are usually one or two colic caeca at the junction of the small and large intestines.

calamus. Hollow, cylindrical basal portion of a feather shaft.

calcitonin. Hormone secreted by the thyroid gland; lowers calcium and phosphate levels in the blood by inhibiting bone breakdown and accelerating calcium absorption by the bones.

canine. Member of the dog family (Canidae); also the long, stout, cone-shaped pointed tooth just behind the incisors in mammals.

carapace. Dorsal shell of a turtle.

carina. Longitudinal ridge or plate of bone on the ventral side of the sternum in birds; also called the *keel*.

carinate. Term referring to all birds that possess a keeled sternum; all birds exclusive of the ratites.

carnassial. Modified premolar or molar tooth in the jaw of carnivores; possesses a sharp, bladelike cutting edge; used for cracking bones and shearing tendons.

carnivore. Animal that feeds on animal tissue; taxonomically, a member of the order Carnivora (Mammalia).

carotenoid. Group of fat-soluble pigments (yellows, browns, reds, oranges).

carpometacarpus. Bone formed by the fusion of carpal and metacarpal bones in a bird.

carpus. The wrist.

carrying capacity (K). Maximum number of individual organisms that the resources of a given area can support for an extended period of time; the most unfavorable period of the year is the most critical to the reproductive success and survival of a species.

catadromous. Fish that live in fresh water but migrate down a river or stream to the ocean to spawn.

caudal. Pertaining to the tail or rear.

caudal fin. Most posterior unpaired fin of fishes and some amphibians.

caudal peduncle. Slender portion of a fish behind the anal fin and bearing the caudal fin.

centrum (pl. **centra**). Thick, disk-shaped ventral (anterior) portion of a vertebra that is the weight-bearing part; also known as the body.

ceratotrichia. Fin rays in cartilaginous fishes.

cerebellum. Portion of the brain lying posterior to the medulla oblongata and pons; concerned with muscular control and coordination of movements.

cerebral hemisphere. One of a pair of dorsal portions of the forebrain.

cerebrospinal fluid. Fluid secreted in the ventricles of the brain; serves as a transport medium; circulates within the ventricles and spinal cord, also around the brain and spinal cord.

cerebrum. Part of the forebrain; consists of two hemispheres; composed of areas that receive sensory impulses (sensory areas), areas that control muscular movement (motor areas), and areas that deal with complex integrative functions like memory, emotions, reasoning, and intelligence (association areas).

cervical. Pertaining to the neck.

cervix. Lower portion of the mammalian uterus that projects into the vagina.

chaparral. Dense, shrubby, fire-resistant scrubland in regions of the world where most of the rain falls in the cool winter and summers are hot and dry; shrubs have small, thick, evergreen leaves and thick underground stems; found in California and in parts of Africa, Australia, Chile, and Europe.

chief cell. Cell in the stomach that secretes pepsinogen, a precursor of pepsin.

choana (pl. **choanae**). Internal naris; the opening of the nasal passage into the pharynx.

chondrocranium. Cartilaginous region of the skull surrounding the brain and special sense organs in Chondrichthyes.

Chordata. Phylum of animals with a notochord, dorsal, hollow nerve cord, and pharyngeal slits at some time during their development.

chorion. Outer of the double membrane that surrounds the embryos of reptiles, birds, and mammals; contributes to the placenta in mammals.

chromatophore. Pigment-containing cell.

clade. Taxon or other group consisting of an ancestral species and all of its descendants, forming a distinct branch on a phylogenetic tree.

cladistics. A method of classification of animal and plants according to the proportion of measurable characteristics that they have in common.

cladogram. Branching diagram representing the hypothesized relationships of a group of taxa; developed through cladistic analysis.

claspers. Paired intromittent organs in elasmobranchs and chimaeras; assist in the transfer of sperm into the female reproductive tract.

claw. Sharp, curved, laterally compressed nail at the end of a digit; present as a talon in some birds.

cleithrum. Bone of the pectoral girdle.

climax. Stable end of succession; a community that is capable of self-perpetuation under prevailing environmental conditions.

cline. Gradual change in a biological character along a geographic gradient.

clitoris. Female homologue of the male penis in mammals.

cloaca. Common chamber that receives the products of the digestive and urogenital ducts in monotremes, birds, reptiles, amphibians, and some fishes.

cochlea. Tubular auditory organ in the inner ear of crocodiles, birds, and mammals; spirally coiled in mammals. See also *spiral organ*.

coevolution. Joint evolution of two or more species that have a close ecological relationship; the evolution of one species in the relationship is partially directed or controlled by the evolution of the other.

colon. Portion of the large intestine; in mammals, divided into ascending, transverse, descending, and sigmoid portions.

columella. Slender bone connecting the tympanum with the internal ear in amphibians, reptiles, and birds; homologous with the hyomandibular bone of fishes and the stapes of mammals.

commensalism. Symbiotic relationship between species that is beneficial to one species but is neither beneficial nor harmful to the other.

comparative zoogeography. Study of the distribution of related groups of animals according to their external features.

competition. Interaction among individuals that are competing for the same space or resources.

competitive exclusion principle. Ecological rule stating that when there is competition for a niche between two or more species, only one species will be successful; to avoid competition, character displacement may occur among one or both species, or one species will be excluded from the habitat; see also *Gause's Rule*.

concertina locomotion. Type of locomotion in snakes; consists of alternate curving and straightening of the body; adaptive to living in burrows and tunnels.

concha (pl. **conchae**). Bone shaped like a scroll; found in the nasal cavity.

cone. Photoreceptor cell in the retina specialized for sharpness of vision and color.

contour feathers. Outermost body and flight feathers that form the contour or outline of a bird.

convergent evolution. Independent development of similar characteristics in unrelated species due to similar selective pressures caused by living under similar environmental conditions.

coprodeum. Most anterior region of former cloaca; receives the large intestine.

cornea. Nonvascular, transparent fibrous coat over the anterior portion of the eye through which the iris can be seen; continuous with the sclera.

corpora cavernosa. Paired columns of erectile tissue in the penis.

corpus callosum. Broad, transverse sheet of nerve fibers connecting the cerebral hemispheres.

corpus luteum. A hormone-secreting structure that develops in an ovary after an ovum has been discharged but degenerates after a few days unless pregnancy has begun.

corpus spongiosum. Single column of erectile tissue in the penis.

cortex. Outer layer of an organ (e.g., adrenal cortex); also, the convoluted layer of gray matter covering each cerebral hemisphere.

corticosterone. See *glucocorticoids*.

cortisol. See *glucocorticoids*.

cortisone. See *glucocorticoids*.

cosmoid scale. Small, thick fish scale composed of cosmine and covered by a thin layer of enamel; found today only on the coelacanth (*Latimeria*).

costal fold. Area between two costal grooves.

costal groove. Vertical groove in the sides of salamanders.

countercurrent exchange (or **counterflow**). Exchange of heat and/or oxygen between two fluids moving past each other in opposite directions.

crista (pl. **cristae**). Patches of sensory cells in the ampulla of a semicircular canal; functions in dynamic equilibrium.

crop. Membranous sac in the lower portion of the esophagus in some birds; used for the temporary storage of food.

crossopterygian. Primitive lobe-finned bony fishes (order Sarcopterygii) ancestral to the amphibians; the only living representative is the coelacanth (*Latimeria*).

ctenoid scale. Thin, overlapping dermal scale of fish; posterior margin with fine, toothlike spines.

cursorial locomotion. Running.

cutaneous. Pertaining to the skin.

cuticle. Outermost layer of a hair.

cycloid scale. Thin, overlapping dermal scale of fish; posterior margin smooth.

cytology. Study of cells and their internal structure and physiology.

deciduous. Shed seasonally, periodically, or at a certain life stage,

delayed fertilization. Fertilization following an extended storage of sperm within the female's body.

delayed implantation. Following fertilization, the mammalian embryo (blastocyst) ceases development and floats freely in the uterus for several months; occurs in some bats, armadillos, carnivores, pinnipeds, and artiodactyls.

deme. Local population of closely related animals.

dens (or **odontoid process**). Process on the anterior (superior) end of the second cervical vertebra (axis); articulates with the first cervical vertebra (atlas).

density-dependent. Mortality that varies directly with population density.

density-independent. Mortality that is unaffected by population density.

dentary. One of a pair of dermal bones making up part of the lower jaw; in mammals, the only bones making up the lower jaw.

derived. Referring to a trait that evolved later than an ancestral trait.

dermatocranium. Collectively the superficial bones of the skull that develop in the dermis without cartilaginous precursors.

dermis. Layer of skin beneath the epidermis.

determinate growth. Steady increase in size until maturity, after which growth slows and essentially ceases for the remainder of life; characteristic of birds and mammals.

dewlap. Extensible reddish throat fan in some male lizards.

diadromous. Migrating either from fresh water to seawater to spawn (catadromous) or from seawater to fresh water to spawn (anadromous).

diaphragm. Muscular partition between the abdominal and thoracic cavities in mammals.

diapsid. Amniote in which the skull has two pairs of temporal fossae; extant reptiles (except turtles) and birds.

diastema. Space separating the premolars from the incisor teeth in mammals that lack canines, like rabbits and rodents.

dichromatism. Having two or more color phases.

diencephalon. Part of the brain consisting primarily of the thalamus and the hypothalamus; posterior region of the prosencephalon.

digit. A finger or toe.

digitigrade. Condition in which the animal walks on the ends of its metacarpals and metatarsals; only the toes contact the ground in walking.

dimorphism. A species having two different structural forms or two color phases in a population.

dioecious. Having male and female sex organs in separate individuals (i.e., having separate sexes).

diphycercal. Tail that tapers to a point as in lungfishes; vertebral column extends to its tip without upturning.

diphyletic. A group whose members are derived from more than one ancestor; not of monophyletic origin.

direct development. In some anurans, the elimination of a free-living feeding tadpole stage; all development occurs inside the egg; hatchlings are fully formed, four-legged froglets.

disjunct. Species consisting of two or more isolated populations.

dispersal. Generalized movement of individuals within a population away from their original home range; nondirected movement in general.

DNA (deoxyribonucleic acid). An essential component of all living matter and a basic material in the chromosomes of the cell's nucleus; it contains the genetic code and transmits the hereditary pattern.

dormancy. State of inactivity; torpidity; see also *hibernation* and *estivation*.

dorsal fin. Median unpaired fin on the back; may be supported by spines and/or rays.

down feather. Small, fluffy feather lying beneath and between the contour feathers; principal function is insulation.

ductus deferens. See *vas deferens*.

duplex uterus. A uterus in which the uteri are completely separate, but joined to a single vagina; found in rabbits and rodents.

ecdysis. Shedding of the skin, as in a snake.

echolocation. Radar-like system used by some birds and some mammals (especially bats and cetaceans) for maneuvering and locating food.

ecological zoogeography. Study of the analogies between animal communities occupying similar habitats.

ecology. Science of the relationships between organisms and their environments.

ecotone. Transition zone between two adjacent ecosystems.

ecotourism. Travel that aims to increase the understanding of ecological (or natural) systems; ideally results in creation of jobs, increased economies, and preservation of habitat.

efferent. Conducted or conducting outward or away from something (for nerves, the central nervous system, for blood vessels, the organ supplied).

embryo. Developing organism, especially in the early stages; generally still contained within the egg or uterus.

emigration. Movement of an individual or part of a population permanently out of an area; a one-way movement.

endangered species. Species in imminent danger of extinction throughout all or a significant portion of its range.

endotherm. Vertebrate that maintains a relatively high body temperature primarily by internal heat production.

environmental resistance. Environmental factors that limit the number of young produced by a population; includes intraspecific aggression, available den sites, predation, disease, parasites, and climatic factors like rainfall, flooding, drought, and temperature; divided into two categories—density-dependent and density-independent.

epaxial. Muscle mass dorsal to the horizontal skeletogenous septum in fishes and amphibians.

epibranchial. Upper gill cartilage located between the pharyngobranchial and ceratobranchial cartilages; also, muscles above the gills in fishes.

epidermis. Outer epithelial portion of the skin.

epididymis. Part of the sperm duct that is coiled and lying adjacent to the testis; serves as a storage area for sperm.

epiglottis. Large, leaf-shaped cartilage lying on top of the larynx in mammals; covers the glottis during swallowing.

epinephrine. Hormone secreted by the adrenal medulla that prepares the body for stressful or emergency situations; also called adrenaline.

epipelagic zone. Region of the oceanic zone that receives abundant sunlight; phytoplankton and zooplankton are abundant.

epipubic bone. One of a pair of small bones in marsupials that articulate with the pubic bone and extend forward in the abdominal wall to provide additional support for the abdominal pouch.

equilibrium. State of balance.

erythrophore. Cell containing red pigment.

estivation. State of dormancy due to external stress resulting from long-term periods of heat.

estuary. Partially enclosed embayment where fresh water and seawater meet and mix.

ethology. Scientific study of animal behavior.

eustachian tube (or **auditory tube**). Passageway from the middle ear to the pharynx; serves to equalize pressure on both sides of the tympanum.

evolution. In biology, the change in the characteristics of a species over several generations; relies on the process of natural selection.

extinction. Total disappearance of a species or a higher taxon from the face of the Earth.

extirpation. Total disappearance of a taxon from a geographic area but not from its entire range.

extrinsic. In anatomy, originating on the appendages (e.g., extrinsic musculature).

facultative parthenogenesis. Development of a new individual from an unfertilized egg as an adaptation to changing conditions (only when this mode of reproduction is necessary as a last resort to produce off spring).

faunal zoogeography. Faunal lists of animal populations for specific areas.

feather. Epidermal derivative; a modified reptilian scale; the most distinctive characteristic of a bird.

femoral pores. Integumental glands that appear as openings in the scales on the undersurface of the thigh of most lizards.

femur. Proximal bone of the pelvic appendage; articulates with the pelvic girdle.

fenestra (pl. **fenestrae**). An opening within the bony braincase.

fibula. Lateral and smaller of the two distal bones of the lower hind leg.

filoplume. Very specialized, hairlike or bristle-like feather.

fin rays. Slender, flexible rods that stiffen the fins of fishes distal to the skeletal components; may be composed of cartilage, keratin, elastoidin fibers, or bone.

firmisternal. Type of pectoral girdle in amphibians that lacks epicoracoid horns; sternum fused to pectoral arch; found in ranids, microhylids, and dendrobatids.

fluke. The dorsoventrally compressed tail of a cetacean.

follicle. Small secretory sac or cavity; also invaginated portion of epidermis that gives rise to feathers and hairs.

follicle-stimulating hormone (FSH). Hormone secreted by the anterior pituitary gland that initiates development of ova and stimulates the ovaries to secrete estrogens; also initiates sperm production in males.

food chain. Sequence of organisms through which energy and nutrients move from one trophic (feeding) level of organisms to another in a series that normally begins with plants and ends with carnivores, detritus feeders, and decomposers.

food web. Interlocking pattern formed by a series of interconnecting food chains.

fossorial. Adapted for digging or burrowing through the soil.

founder effect (or **founder event or principle**). Principle that populations on oceanic islands and other isolated places may be established by a very small sample from a continent or another island. Such a sample may include only limited variability. Due to its small size, the genetic structure of the new population may be dramatically different from that of its ancestral population. Phenotypic characteristics that were stable in the ancestral population often reveal wide variation in the new population. As natural selection acts on the newly expressed variation, large changes in phenotype and reproductive properties occur, hastening the evolution of reproductive barriers between the ancestral and newly founded populations.

fragmentation. Divided habitat or one that is decreased in size; may no longer be large enough to meet the needs of all the species that formerly occupied it.

furculum. Fused clavicles, or wishbone, of a bird.

gamete. A mature haploid male or female germ cell which is able to unite with another of the opposite sex in sexual reproduction to form a zygote.

ganoid scale. Type of fish scale covered with an enamel-like substance known as ganoin; seldom overlapping; occurs in gars (Lepisosteidae).

Gartner's duct. In birds, a short, blind vessel embedded in the mesentery of the oviducts; vestige of mesonephric duct.

gastric juice. Digestive juice consisting of the combined secretions of chief cells, mucous cells, and parietal cells of the stomach.

gastrosteges. Ventral scales anterior to the anal plate; found in snakes.

Gause's Rule. Ecological principle stating that when there is competition for a niche between two or more species, only one species will be successful and the others will be excluded from the habitat; see *competitive exclusion principle*.

genome. The complete set of genes or genetic material present in a cell or organism.

genus (pl. **genera**). Taxon in which all species sharing certain characteristics are grouped; taxonomic level above species and below family and subfamily.

geographic race. Same as *subspecies*.

geographic range. Specific land or water area where a species normally occurs.

geologic range. Past and present distribution of a taxon over time.

gestation. Period during which an embryo is developing in the reproductive tract of the mother.

gill. Specialized structure covered by a thin, vascular epithelium that functions in the aquatic exchange of respiratory gases; may be internal or external; mainly confined to the pharyngeal region.

gill raker. Projection from the anterior surface of a gill arch; aids in filtering food from water.

gill slit. Paired opening from the pharynx through the body wall to the exterior.

girdle. Skeletal elements joining limbs to the body; pectoral girdle is associated with the forelimbs, pelvic girdle with the hindlimbs.

gizzard. Muscular portion of the stomach in birds; serves as a grinding chamber in crocodilians, some dinosaurs, and some birds.

glacial lake. Steep-sided lake gouged out of previously existing valley by advancing glacier; for example, Finger Lakes in central New York.

glans penis. Slightly enlarged region at the distal end of the penis.

glenoid fossa. Depression serving as a point of articulation for the pectoral appendage with the scapula.

glomerular capsule. See *Bowman's capsule*.

glomerulus (pl. **glomeruli**). Tuft of capillaries at the beginning of each nephron; enclosed by glomerular (Bowman's) capsule.

glottis. Anterior (superior) opening between the pharynx and the trachea.

glucagon. Hormone produced by the pancreas; increases blood sugar level.

glucocorticoids. Hormones secreted by the adrenal cortex, especially corticosterone, cortisol, and cortisone, which influence glucose metabolism.

gonad. Gland that produces gametes and hormones; the ovary in the female and the testis in the male.

gonopodium. Intromittent organ found in some teleost fishes.

gravid. Pregnant, carrying eggs or young.

graviportal locomotion. Walking by movement of column-like limbs used to support massive weight (elephants).

greenhouse gases. Certain gases (including carbon dioxide, methane, nitrous oxide, halons, and chlorofluorocarbons) produced on Earth by burning of fossil fuels and other processes; they allow the sun's rays to pass through but absorb and re-radiate heat back to Earth, causing the Earth to warm.

growth hormone (GH). Hormone produced by the anterior pituitary gland that causes body cells to grow; also stimulates protein synthesis and inhibits protein breakdown; promotes tissue repair; stimulates the breakdown of triglycerides into fatty acids and glycerol and the elevation of blood glucose concentration.

guanophore. See *iridophore*.

guard hair. Outer, coarser, and usually longer hairs making up the pelage of a mammal.

gubernaculum. Ligament in male mammals connecting the caudal pole of each embryonic testis to the labioscrotal pouch; assists in descent of testes into scrotum in some mammals.

gustatory. Related to the sense of taste.

habenula. Structure in the diencephalon; assists in coordinating the olfactory reflexes.

habitat. Place where an animal normally lives or where individuals of a population live.

hadopelagic zone. Region of the oceanic zone below 6,000 m (19,700 ft.); areas of ocean trenches.

hallux. First digit of the posterior limb; usually directed backward in birds.

hamulate. Having a small hook (hamulus).

hamulus (pl. **hamuli**). Hooked barbule of a feather.

hemal arch. Arch formed by paired transverse projections ventral to the centra of the caudal vertebrae and enclosing the caudal blood vessels.

hemal spine. Ventral projection from the ventral bony arch (hemal arch) of a caudal vertebra.

hemipenis (pl. **hemipenes**). Male copulatory organ in lizards and snakes.

hepatic. Relating to the liver.

herbivore. Organism that feeds on plant tissue.

hermaphrodite. Organism with both male and female functional reproductive organs.

heterocercal. Type of tail characteristic of sharks in which the dorsal lobe is larger than the ventral lobe and has caudal vertebrae extending into it.

heterocoelous. Describes a vertebra having the anterior and posterior articulating surfaces of the centrum (body) shaped like a saddle.

heterodont. Having teeth differentiated for various functions; tooth types include incisors, canines, premolars, and molars.

hibernation. Winter dormancy; condition of passing the winter in a torpid state during which the body temperature drops to near freezing (or below) and metabolic activities are drastically reduced.

historical zoogeography. Study of historical animal distribution; establishment of present-day distributions over geologic time.

holonephros. See *archinephros*.

home. Place of refuge within a home range; nest site.

homeostasis. Condition of physiological equilibrium with regard to temperature, fluid content, pressure, and the like.

homeotherm. Endothermic animal with a fairly constant body temperature.

home range. Area over which an animal moves during its normal daily activities.

homing. Ability to find the way home; returning home.

homocercal. Type of tail characteristic of most modern bony fishes in which the upper and lower lobes are about the same size.

homodont. Having teeth similar in form to one another; teeth may differ in size.

homology. Organs or structural features in different species of animals with common embryonic and evolutionary origins, but perhaps with different functions (e.g., a bat's wing and a human arm).

hoof. Horny sheath encasing the ends of the digit or foot in ungulate mammals.

horizontal undulatory. Type of locomotion used by snakes; the body glides along in a series of waves, with each part of the body passing along the same track; serpentine.

hormone. Chemical substance formed in one organ or body part and carried in the blood to another organ or body part, which it stimulates to functional activity.

host. Animal that harbors another as a parasite.

humerus. Proximal bone of the pectoral appendage; articulates with the glenoid fossa of the scapula.

hyoid. Second visceral arch; serves to support the tongue.

hyomandibula. Uppermost segment of the hyoid arch.

hyostylic. Type of jaw suspension wherein the hyomandibula is inserted between the jaws and cranium.

hypaxial. Muscle mass ventral to the horizontal skeletogenous septum in fishes and amphibians.

hypobranchial. Describes muscles below the gill region.

hypophysis. See *pituitary*.

hypothalamus. Portion of the diencephalon lying beneath the thalamus and forming the floor and part of the wall of the third ventricle of the brain.

imprinting. Period of rapid and usually stable learning during a critical period of early development of a member of a social species (usually involving recognition of its own species); may involve attraction to the first moving object seen.

incisor. Chisel-like cutting tooth at the front of the jaw.

incus. Middle ear bone of mammals, derived evolutionarily from the quadrate.

indeterminate growth. Pattern of growth that continues indefinitely in an animal or a structure; common in many fishes, amphibians, and reptiles.

index. Count of some object (tracks, leaf nests, etc.) that is related to the numerical population size of the animal being studied; can be used to estimate the population.

infrasound. Sound below the range of human hearing; below 20 Hz.

inguinal canal. Passageway in the abdominal wall for the spermatic cord in male mammals and for the round ligament in females.

innominate. Bone forming one-half of the mammalian pelvic girdle.

insectivorous. Insect-eating.

insulin. Hormone secreted by the pancreas that lowers blood glucose level.

integument. External covering or enveloping layer of the body; the skin.

intercalary. Cartilage between the ultimate and penultimate phalanges in hylid anurans.

intercostal. Between the ribs (e.g., intercostal muscles).

interfemoral membrane. Flight membrane of bats located between the hindlimbs and often involving the tail.

interstitial cell-stimulating hormone. See *luteinizing hormone*.

intrinsic. In anatomy, originating on the body (e.g., intrinsic musculature).

iridophore (or **guanophore**). Cell containing crystals that reflect and disperse light.

isolating mechanism. Structural, behavioral, or physiological mechanism that blocks or inhibits gene exchange between two populations.

jugular. Pertaining to the throat; in fishes, situated in front of the pectoral fins.

juvenal. Plumage or pelage acquired following the postnatal molt.

juvenile. Immature stage of development.

keel. See *carina*.

keratin. Relatively insoluble protein found in hair, feathers, nails, and other keratinized tissues of the epidermis; replaces cytoplasm in epidermal cells as they become cornified.

keratinocyte. Most numerous of the specialized epidermal cells; produces keratin.

labyrinthodont. A primitive amphibian; one of the first land vertebrates; with complex, “folded” teeth.

lagena. Auditory receptor of fishes, amphibians, and reptiles; homologous with cochlea of birds and mammals.

lamella (pl. **lamellae**). Thin, layered structure.

larva (pl. **larvae**). Immature stage of life between the embryo and the adult; often sharply different in form from the adult.

larynx. Modified upper portion of the respiratory tract of air-breathing vertebrates; bounded by the glottis above and the trachea below; voice box.

lateral bridge. See *bridge.*

lateral line. Part of the sensory system of fishes and amphibians; series of tubes in the lateral scales (variously developed or absent in fishes; present in larval amphibians) that sense water movements.

lentic system. Freshwater system consisting of flowing water.

life zone. Region of the ecological classification scheme proposed by C. Hart Merriam (1890); zone boundaries are determined by mean annual temperatures.

limnetic zone. Upper portion of the deeper open water of a lake where sunlight is sufficient to support photosynthesis.

lipophore. Pigment-bearing cell containing carotenoids responsible for yellow, orange, and red colors; pigment granules are soluble in lipids.

littoral zone. That portion of the seafloor between high and low tides—intertidal; in lakes, the shallow part from the shore to the lakeward limit of rooted aquatic plants.

longitudinal fissure. Deep median groove separating the cerebrum into two cerebral hemispheres.

loreal pit. See *pit organ.*

lotic system. Freshwater system consisting of still water.

luteinizing hormone (LH). Hormone secreted by the anterior pituitary gland that stimulates ovulation and progesterone secretion by the corpus luteum; stimulates production of "pigeon milk" in some birds; prepares mammary glands for milk secretion in female mammals; stimulates testosterone secretion by the testes in males; also called *interstitial cell-stimulating hormone* in males.

lymph. Fluid circulating in the lymphatic system.

macrogeographic migration. Long-distance migration (e.g., ducks, geese, many passerines, and humpback whales).

macula (pl. **maculae**). Patches of sensory cells in the utricle and saccule; functions in the maintenance of static equilibrium.

malleus. One of the three middle ear bones in mammals; evolutionarily derived from the articular.

mammillary body. Small, rounded body in the diencephalon posterior to the hypophysis; involved in reflexes related to the sense of smell.

mandible. Lower jaw.

mandibular arch. First pair of visceral arches in Chondrichthyes.

manus. Hand.

marginal. One of the lateral rows of scales in the carapace of turtles.

marsh. Shallow wetland dominated by grassy vegetation like cattails and sedges.

marsupium. Pouch of female marsupials.

masseter. Mammalian jaw muscle that moves the lower jaw forward and upward.

mass extinction. Catastrophic, worldwide event in which a large number of taxa disappear within an interval of just a few million years.

maxilla. Bone of the upper jaw lying above or behind and parallel to the premaxilla; the upper bill of birds.

Meckel’s cartilage. Ventral portion of the mandibular arch in Chondrichthyes; becomes encased by dermal bones in higher vertebrates.

medulla. Inner layer of either an organ (e.g., adrenal medulla) or a structure like a hair.

melanin. Brown-black pigment produced by skin melanocytes.

melanocyte-stimulating hormone (MSH). Hormone secreted by the anterior pituitary gland that stimulates the dispersion of melanin granules in melanocytes in amphibians, increasing skin pigmentation.

melanophore. Chromatophore containing the pigment melanin.

melatonin. Hormone produced by the pineal gland; thought to control adrenocortical function and cyclic activities like sleeping and eating.

meninges. Protective membranes enclosing the central nervous system; in mammals, these are the dura mater, arachnoid, and pia mater.

mental. Pertaining to the chin.

meristic. Divided into segments or serial parts; see also *metamerism*.

mesaxonic. Type of foot in which the axis passes through the middle digit, which is larger than the others; characteristic of perissodactyls (horses, zebras, asses, tapirs, and rhinoceroses).

mesencephalon. Middle of the three embryonic divisions of the brain.

mesonephros. Kidney formed of nephric tubules arising in the middle of the nephric ridge; usually a transient embryonic stage that replaces the pronephros, and is itself replaced by the metanephros.

mesopelagic zone. Region of the oceanic zone between 200 and 1,000 m (650 and 3,300 ft.); semidark; also known as the twilight zone.

metacarpal. Referring to that region of the hand or forelimb lying between the digits and the wrist; also, a bone of this region.

metamerism. Serial segmentation; made up of serially repeated parts.

metamorphosis. Transformation of an immature animal into an adult (e.g., tadpole to frog); change in the body form and way of life that ends the larval stage; also called transformation.

metanephros. Embryonic renal organs arising posterior to the mesonephros; the functional kidney of reptiles, birds, and mammals; drained by a ureter.

metatarsal. Referring to that region of the foot or hindlimb lying between the digits and the ankle; also, a bone of this region.

metatarsal tubercle. Small protuberance on the sole of the hind foot in amphibians; typically there are two—a large inner tubercle and a smaller outer tubercle; sometimes modified for digging.

microgeographic migration. Short-distance migration (e.g., salamanders, anurans, and others).

migration. Intentional, directional, usually seasonal movement of animals between two regions or habitats; a round-trip directional movement.

mitochondrion. An organelle found in large numbers in most cells in which the biochemical processes of respiration and energy production occur.

molar. Grinding tooth in the posterior region of the jaw.

monophyletic. A group of organisms descended from a common evolutionary ancestor or ancestral group, especially one not shared with any other group.

monophyodont. Having a single set of teeth without replacement during the animal's lifetime.

monotypic. Describes a species without a subspecies.

morphology. Study of the form and structure of living organisms.

mtDNA (mitochondrial DNA). See mitochondrion.

mucus. A viscid, slippery substance, typically not miscible with water, secreted by mucous membranes and glands for lubrication, protection, and so forth.

mutualism. Symbiotic relationship between two species in which both benefit from the association.

Mya. Million years ago.

myelin. Fatty sheath insulating a nerve fiber.

myomere. Muscle segment of the successive segmental trunk musculature.

myoseptum (pl. **myosepta**). Membrane separating adjacent myomeres.

naris (pl. **nares**). Opening of the nasal cavity; may be external or internal.

nasolabial groove. Groove from the nostril to the upper lip in plethodontid salamanders.

natural extinction. Normal disappearance of species over time.

natural selection. The process whereby organisms better adapted to their environment tend to survive and produce more offspring.

Nearctic. North America, Greenland, and Iceland.

nekton. Aquatic organisms that move actively through the water, rather than drifting or floating passively like plankton; all of the larger, aquatic, free-swimming animals (fishes, whales, etc.) in lakes, seas, and ponds; movement is largely independent of currents and waves.

Neornithes. Subclass of extinct and living birds with well-developed sternums and reduced tails, and with metacarpals and some carpals fused together.

neoteny. Retention of one or more juvenile characteristics into adulthood.

Neotropical. Pertaining to Central and South America.

nephron. Basic functional unit of the vertebrate kidney.

nephrostome. Ciliated, funnel-shaped opening of primitive glomeruli.

neritic. Portion of the sea overlying the continental shelf, specifically from the subtidal zone to a depth of 200 m 650 (ft.).

neural spine. Dorsal projection from the dorsal bony arch of a vertebra.

neurocranium. Part of the skull enclosing the brain.

neuromast. Mechanoreceptor cells on or near the surface of a fish or amphibian that are sensitive to vibrations in the water.

niche. Functional role and position of an organism in the ecosystem; how it lives and its relation to other species in a food chain or web.

nictitating membrane. More or less transparent eyelid located medial to the eye; cleanses and lubricates the cornea; “third” eyelid.

norepinephrine (or **noradrenalin**). Hormone secreted by the adrenal medulla that prepares the body for stressful or emergency situations.

notochord. Longitudinal dorsal rod of tissue that gives support to the bodies of lampreys, some adult fishes, and the embryos of chordates.

nuchal. Pertaining to the back of the neck; in turtles, the median anterior shield of the carapace; in lizards, the enlarged scales immediately posterior to the head.

nuptial plumage. Breeding plumage.

nuptial tubercle. Hardened process on the skin of the head of a fish, usually a breeding male; used to assist the male in maintaining contact with the female during breeding and to stimulate the female.

oblique septum. Tendinous, transverse partition separating the pleural cavities from the coelom in crocodilians and in some snakes and lizards.

oceanic zone. Portion of the sea beyond the continental shelf.

odontoid process. See *dens*.

olfactory. Relating to the sense of smell.

omasum. Third chamber of the ruminant stomach.

omnivore. Animal that feeds on both plant and animal matter.

oogenesis. Egg cell production in females.

operculum. Covering flap, as the gill cover of fishes and larval amphibians.

opisthocoelous. Type of vertebra with a convex anterior (superior) end of the centra and a concave posterior (inferior) end.

opisthoglyph. Rear-fanged snake.

opisthonephros. Adult kidney formed from the mesonephros and additional tubules from the posterior region of the nephric ridge; found in most adult fishes and amphibians.

organ of Corti. See *spiral organ*.

origin. In fish, the most anterior end of the dorsal fin or anal fin base; in muscle terminology, the site of attachment that usually remains fixed when the muscle contracts.

otolith. Calcified body in the sacculus of the inner ear.

outgroup. In cladistics, a species or group of species closely related to, but not included within, a taxon whose phylogeny is being studied; used as a reference for determining whether characters in other groups are ancestral or derived.

ovary. Female reproductive glands producing the ova and associated hormones.

oviducal glands (or **shell glands**). Glands that secrete albumin and shell materials around an egg.

oviduct. Tube serving to transport the eggs from the ovary to the cloaca or uterus and/or to house the eggs and embryos.

oviparous. Egg-laying; fertilized eggs develop outside the mother.

ovipositor. Papilla-like terminal portion of the oviduct in some teleost fishes.

ovisac. Enlarged caudal portion of the oviduct in some amphibians; provides for the temporary storage of eggs prior to oviposition.

ovoviviparous. Eggs retained and develop within the body of the female, but without placental attachment; also known as *aplacental viviparity*.

oxytocin. Hormone secreted by the posterior pituitary gland; stimulates smooth muscle contraction.

paedogenesis. See *paedomorphosis*.

paedomorphosis. Condition whereby a larva becomes sexually mature without transforming into the adult body form.

palatoquadrate (or **pterygoquadrate**). Cartilage forming the upper jaw of primitive fishes and Chondrichthyes; portions ossify and contribute to the palate, jaw articulation, and middle ear of other vertebrates.

Palearctic. Asia and Europe north of the Sahara Desert.

pancreas. Abdominal digestive (secretes pancreatic juice) and endocrine (secretes insulin and glucagon) gland.

pancreatic islets. Cells in the pancreas that produce the hormones insulin and glucagon.

Pangaea. Supercontinent comprising entire land mass of Earth approximately 250 Mya.

panniculus carnosus. Integumentary muscle derived from the hypaxial musculature.

papilla (pl. **papillae**). Small, pimple-like protuberance.

paraphyletic. A group of organisms descended from a common evolutionary ancestor or ancestral group, but not including all the descendant groups.

parasitism. Symbiotic relationship between two species in which one (the parasite) benefits while the other (the host) is harmed.

parathyroid. Endocrine gland adjacent to, or embedded in, the thyroid; secretes parathyroid hormone (parathormone) to raise the calcium level in the blood.

paraxonic. Type of foot in which the axis passes between the third and fourth digits, which are almost equally developed.

parotoid gland. Glandular swelling behind the eye of some anurans and salamanders; exudes a poisonous secretion.

parthenogenesis. Development of a new individual from an unfertilized egg.

patagium. Thin, often furry flight membrane found in gliding and flying mammals.

patella. Kneecap.

pectoral. Pertaining to the chest; in turtles, one of a pair of shields of the plastron.

pectoral fin. Usually the most anterior of the paired fins in fishes.

pectoral girdle. Bones that attach the forelimb to the axial skeleton.

pelagic. Pertaining to the open ocean waters; oceanic.

pelvic fin. One of a pair of fins in a ventral position well posterior to the pectoral fins (abdominal position) or ventral to the pectoral fins (thoracic position).

pelvis. Ring formed by the pelvic girdle around the caudal ends of the digestive and urogenital systems.

penis. Male organ used for intromission and sperm transfer in turtles, crocodilians, some birds, and mammals.

pentadactyl. Five-toed.

penultimate. Next to the last.

pericardium. Area around the heart; membrane around the heart.

peripheral. Term used for endangered species or subspecies at the edge of its range (threatened with extinction at the edge of its range, although not in its range as a whole).

Perissodactyla. Order of odd-toed ungulates; includes horses, zebras, asses, tapirs, and rhinoceroses.

peritoneum. Epithelial lining of the body cavity.

permafrost. Permanently frozen soil.

phalanx (pl. **phalanges**). One of the bones of a digit.

pharyngeal. Pertaining to the pharynx; a toothed bone of the throat region of fishes.

pharynx. The membrane-lined cavity behind the nose and mouth connecting them to the esophagus.

pheneticist. A person who makes taxonomic classifications according to phenetic data (grouping species on the basis of overall similarity).

phenogram. Diagram used by pheneticists for grouping species on the basis of overall similarity; dendrogram.

phenotype. The set of observable characteristics of an individual resulting from the interaction of its genotype with the environment.

pheromone. Chemical substance released by an animal that controls or alters the behavior of others of the same species.

photic. Relating to light; underwater region penetrated by sunlight.

photophore. Light-emitting organ in some fishes.

phylogenetic. Relating to the evolutionary development and diversification of a species or group of organisms, or of a particular feature of an organism.

physoclistic. In bony fishes, not having a connection between the pharynx and the swim bladder.

physiology. Science that deals with the functions of an organism and its organs, tissues, and cells.

physostomous. In bony fishes, having a connection between the pharynx and the swim bladder.

phytoplankton. Microscopic photosynthetic life in aquatic ecosystems; may be on or below the surface of the water.

pia mater. Innermost layer of the meninges surrounding the brain and spinal cord.

pineal eye. Median, light-sensitive structure (retina, lens, and cornea may be developed) found in agnathans, primitive fishes, and amphibians; an analogous organ, the parapineal or parietal eye, is found in *Sphenodon* and many lizards; in lampreys, both parapineal and pineal organs form eyelike structures.

pineal gland. Endocrine gland that produces the hormone melatonin.

pinna. External ear exclusive of the ear canal.

pit organ (or **loreal pit**). Specialized heat receptor between the eye and the nostril in crotalid snakes (Viperidae) and in boas and their relatives.

pituitary (or **hypophysis**). Endocrine gland at the base of the brain; composed of two lobes: the anterior lobe (adenohypophysis) produces and secretes growth hormone, thyroid-stimulating hormone, adrenocorticotropic hormone, follicle-stimulating hormone, luteinizing hormone, prolactin, and melanocyte-stimulating hormone; the posterior lobe (neurohypophysis) secretes antidiuretic hormone and oxytocin.

placenta. Structure composed of tissues through which an embryo receives nourishment and respiratory gases from the mother and has its wastes removed; typical of viviparous vertebrates.

placoid scale. Type of scale found in cartilaginous fishes; consists of basal plate of dentin embedded in the skin and a posteriorly pointing spine tipped with enamel.

plankton. Microscopic or weakly swimming plants and animals in aquatic ecosystems.

plantigrade. Type of locomotion in which the entire sole of the foot contacts the ground.

plastron. Ventral shell of a turtle.

plate tectonics. Arrangement and movements of rigid, slablike plates making up the Earth’s crust.

pleural. Pertaining to the lung.

pleurodont. Teeth attached to the side of the jaw.

pleuroperitoneal cavity. Body cavity of lower vertebrates containing the lungs and viscera.

plicae vocalis. Vocal organ of Pacific giant salamander (*Dicamptodon*).

poikilotherm. Organism that does not maintain a constant body temperature; an organism whose body temperature fluctuates with ambient thermal conditions.

pollex. Thumb or inner digit of the hand.

polyandry. Mating of one female with several males within a breeding season.

polygyny. Mating of one male with several females within a breeding season.

polyphyletic. Taxon having a number of evolutionary origins; members of a taxon that do not share a common ancestor.

polyphyodont. Ability to continually replace teeth throughout the animal's lifetime; examples are found in fishes, amphibians, and reptiles.

polytypic. Describes a species with two or more subspecies.

postjuvenal molt. Partial molt in birds in which the juvenal plumage, except for the flight feathers, is replaced by the first winter plumage.

postnatal molt. First molt in a bird or mammal; replaces the natal down or fur with the juvenal plumage or pelage.

powder down. Modified down feathers that grow continuously, disintegrating at the tips; keratin is given off as a fine powder of minute scalelike particles; used in preening plumage; may protect feathers from moisture; may affect the color of the bird.

prairie. A level or rolling tract of treeless land covered with coarse grass and rich soil.

precocial. Pertaining to birds and mammals born with their eyes and ears open, covered by down or fur, and able to run about shortly after hatching or birth.

predation. Act of one living organism killing and consuming another living organism.

predator. Animal that kills and eats other animals.

prehallux. Small bone on the medial side of the hind foot of some anurans; may have a sharp-edged tubercle for digging.

prehensile. Capable of grasping, as with the prehensile tail of an opossum or a New World monkey.

premaxilla (pl. **premaxillae**). Most anterior bone of the upper jaw; paired dermal bones.

premolar. Grinding tooth anterior to the molars; may be modified into a cutting tooth (carnassial) in carnivores.

prepuce. Loose-fitting skin covering the glans of the penis and the clitoris of mammals.

prey. Animal consumed by another as food.

primary feather. One of the flight feathers attached to the hand (manus).

procoelous. Pertaining to the centrum (body) of a vertebra with a concave anterior (articular) surface and a convex posterior surface.

proctodeum. Terminal portion of the rectum formed in the embryo by an ectodermal invagination.

profundal zone. Deep zone in aquatic ecosystems below the limnetic zone; in deep lakes, the region below the depth of light penetration.

prolactin. Hormone from the anterior pituitary gland; regulates a wide range of parental behavior patterns, including nest-building, the incubation of eggs, and the protection of young; promotes the secretion of "pigeon milk" in certain birds and milk in mammals.

pronephros. Most anterior portion of the archinephros (holonephros); functional only in adult hagfishes and larval fishes and amphibians; vestigial in amniote embryos.

prosencephalon. Most anterior of the three embryonic divisions of the brain.

proteroglyph. Venomous snake with rigid fangs; includes coral and sea snakes (Elapidae).

proventriculus. Glandular portion of the stomach of a bird; between the esophagus and the muscular portion (gizzard) of the stomach.

pseudobranch. Vestigial gill in the spiracle of elasmobranchs.

pterygiophore. Segment of cartilaginous skeleton supporting paired fins in cartilaginous fishes.

pterygoquadrate (or **palatoquadrate**). Dorsal portion of the mandibular arch in Chondrichthyes; cartilaginous.

pteryla (pl. **pterylae**). Area of skin in birds from which a group of feathers grows; a feather tract.

puboischiac plate. Ventral portion of the pelvic girdle of salamanders.

purine. Crystalline substance in chromatophores that reflects light.

pygostyle. Fused terminal caudal vertebrae of birds; supports the tail feathers.

pylorus. Posterior portion of the stomach that leads into the small intestine.

quadrate. Skull bone that articulates with the lower jaw in bony fishes, amphibians, reptiles, and birds; in mammals, it has become an ear ossicle, the incus.

rachis. Vane-bearing shaft of a feather.

radiation. Divergence out from a central point, in particular evolution from an ancestral animal group into a variety of new forms; see also *adaptive radiation*.

radius. Forearm bone on the lateral (thumb) side of the arm.

raptor. Bird of prey; includes hawks, owls, eagles, and condors.

rare. Of infrequent occurrence; formerly a category of classification along with endangered and status undetermined; later combined with endangered.

ratite. Flightless bird with a flat (unkeeled) sternum; includes the ostrich, rhea, and kiwi.

rectilinear locomotion. Type of locomotion used by snakes; the axis of the body is essentially straight and movement is effected by alternate movements of the ventral scutes and the body itself; the snake moves along a straight path without any lateral motion.

rectrix (pl. **rectrices**). Tail feather.

renal. Pertaining to the kidney.

reproductive potential. Maximum number of individuals a population can produce; also called *biotic potential*.

rete mirabile. Mass of intertwined capillaries specialized for heat and/or gas exchange between blood flowing in opposite directions.

reticulum. Second in the series of four chambers of the ruminant stomach.

retina. Light-sensitive layer at the back of the eye.

rhombencephalon. Posterior of the three embryonic brain divisions.

rift lake. Long, narrow lake formed by a fissure in the Earth's crust or by the sinking of a narrow strip of land.

RNA. Ribonucleic acid, a nucleic acid present in all living cells. Its principal role is to act as a messenger carrying instructions from DNA for controlling the synthesis of proteins.

rod. Photoreceptor cell in the retina specialized for light reception in dim light.

root. The basal portion of a hair.

rostrum. Preorbital part of the skull.

rugae. Internal folds of the stomach.

rumen. First and largest chamber of the four-chambered ruminant stomach; food here is subjected to bacterial action.

sacculus. Smaller of the two sacs (sacculus, utriculus) in the inner ear; contains maculae; functions in static equilibrium.

sacral. Pertaining to vertebrae modified for articulation with the pelvic girdle.

sacrum. Structure formed by the fusion of the sacral vertebrae; articulates with the pelvic girdle.

saltatorial. Adapted for jumping.

sampling estimate. Estimate derived from counts made on sample plots; has variability but permits a statistical measurement of the total population.

savanna. Large area of tropical or subtropical grassland, covered in part with trees and spiny shrubs.

scansorial locomotion. Limbs adapted for climbing (gray squirrels).

scapula. Bone of the pectoral girdle.

scent gland. Modified sudoriferous or sebaceous gland; used to mark an individual's territory, to attract members of the opposite sex, or to serve in defense.

sclera. Outer hardened layer of the eyeball.

sclerotic ring. Series of 10 to 18 overlapping platelike bones found in the lateral (or anterior) part of the sclera of the eyeball in birds; ringlike in most birds, but conelike in a few (hawks, owls).

scutes. Scales, especially the broad belly scales of snakes; also, scales on turtles.

sebaceous gland. Epidermal exocrine gland located in the dermis of mammals; almost always associated with a hair follicle; secretes sebum; also called an oil gland.

sebum. Secretion of sebaceous (oil) gland.

secondary feather. Flight feather attached to the ulna.

sectorial. Modified teeth (canine and premolar) in some primates; cutting edges present on upper canine and lower premolar in each half of the jaw.

semidormant hibernator. Species that enters a sleeplike state during cold weather but does not experience the drastic physiological changes that occur in a true hibernator.

semiplume. Loose-webbed contour feather.

septum. Wall between two cavities; also, a sheet of tissue dividing groups of muscles (e.g., horizontal skeletogenous septum).

shaft. Long, tapering central portion of a feather that consists of a hollow basal portion (calamus) and a solid, angular portion (rachis); the superficial portion of a hair that projects from the surface of the skin; also, the diaphysis portion of a bone.

shell glands. See *oviducal glands*.

sidewinder locomotion. Type of locomotion used by certain desert snakes; series of lateral, looping movements in which only a vertical force is applied and no more than two parts of the body contact the ground at any one time; resulting tracks are a series of parallel, diagonal, *J*-shaped marks.

simplex. Type of uterus in which the uterine horns are fused into a single structure; oviducts empty directly into the body of the uterus; found in some bats, the armadillo, and primates.

sinus. Cavity or space in tissues or in bone.

sister group. Relationship between two taxa that are each other's closest phylogenetic relatives.

solenoglyph. Venomous snake with hinged fangs; includes vipers and pit vipers.

speciation. Evolution of populations of a species into reproductively isolated groups and, ultimately, new species.

species. A group of living organisms consisting of similar individuals capable of exchanging genes or interbreeding. The species is the principal natural taxonomic unit, ranking below a genus.

spectacle. Transparent, permanently fused upper and lower eyelids in snakes, some lizards, and a few turtles.

speculum. Distinctively colored area on the secondary feathers of ducks.

spermatheca. Storage receptacle for sperm in the roof of the cloaca of some salamanders.

spermatogenesis. Formation of spermatozoa.

spermatophore. Packet enclosing spermatozoa; found in certain salamanders.

spermatozoa. Male sex cells; sperm.

sphincter. Constrictor muscle that serves to close an opening.

spiracle. Modified first gill opening of a shark; also, excurrent channel for a tadpole's gills.

spiral organ (or **organ of Corti**). Sensory epithelium within the cochlea.

spiral valve. Helical membrane in the intestine of sharks and primitive fishes that increases the absorptive surface area; also, a membrane that separates oxygenated from deoxygenated blood in the conus arteriosus of an amphibian heart.

splanchnocranium. Cartilage that forms jaws and visceral arches in fishes and gill-breathing amphibians.

spleen. Large abdominal gland belonging to the circulatory and lymphatic systems; serves as a blood reservoir and the site for the formation of some white blood cells.

squamosal. Dermal bone forming part of the posterior skull wall; in mammals, the site of articulation with the lower jaw.

stapes. Smallest of the three middle ear bones in mammals; evolutionarily derived from the columella (hyomandibula).

status undetermined. Category containing species that may be threatened or endangered with extinction, but about which there is not enough information to determine their status.

sternebra (pl. **sternebrae**). Bony segment of a mammalian sternum.

sternum. Breastbone.

subspecies. Genetically distinct geographic subunit of a species.

sudoriferous gland. Epidermal exocrine gland in the dermis or subcutaneous layer of a mammal that produces perspiration; also called a sweat gland.

swim bladder. Membranous gas-filled sac present in the dorsal portion of the abdominal cavity of some fishes; assists in regulating buoyancy.

symbiosis. Intimate relationship between members of different species; includes commensalism, mutualism, and parasitism.

sympatric. Describes two or more species living in the same general area.

symplesiomorphy. Sharing of ancestral characteristics among species.

synapomorphy. In cladistics, a homologous trait that is assumed to be uniquely derived because it occurs in two or more groups being classified, but not in the outgroups.

synapsid. Amniote in which the skull has a single pair of temporal openings bordered above by the postorbital and squamosal bones in mammal-like reptiles; variously modified in mammals.

synsacrum. Unique structure in birds in which the posterior thoracic vertebrae together with the lumbar, sacral, and anterior caudal vertebrae fuse with the pelvic girdle.

syrinx. Vocal organ of birds; located near the junction of the trachea and bronchi.

systematics. Science of classification and reconstruction of phylogeny.

taiga. Coniferous forest bordering the northern subpolar regions; also called *boreal forest*.

tapetum lucidum. Light-reflecting layer in the eyes of animals that returns light to the photoreceptor cells; best developed in nocturnal forms.

tarsometatarsus. Bone formed by the fusion of the distal tarsal elements with the metatarsals; found in birds and some dinosaurs.

tarsus. Ankle.

taxon (pl. **taxa**). Category like phylum, order, and so on, in which organisms are placed according to shared similarities and homologies.

taxonomy. Study of the principles of classification of organisms.

tectonic lake. Lake created by movement of the Earth's crust.

telencephalon. Anterior division of the forebrain.

terrestrial. Inhabiting land; opposite to aquatic.

territory. Defended area within an animal's home range.

testis (pl. **testes**). Male reproductive gland that produces sperm and the male sex hormone testosterone.

tetrapod. Vertebrate with four legs.

thalamus. Large oval structure located superior to the midbrain; part of the diencephalon; principal relay station for sensory impulses that reach the cerebral cortex from the spinal cord.

thecodont. Teeth set in bony sockets in the jaw.

thoracic. Relating to the thorax or chest.

threatened species. Species that are likely to become endangered within the foreseeable future throughout all or a significant portion of their range.

thymosin. Hormone produced by the thymus gland; stimulates the lymph glands to produce lymphocytes.

thymus. Endocrine gland in the neck that secretes thymosin.

thyroid. Endocrine gland in the neck region that secretes thyroxine, triiodothyronine, and calcitonin.

thyroid-stimulating hormone (TSH). Hormone secreted by the anterior pituitary gland that stimulates the synthesis and secretion of thyroxine and triiodothyronine by the thyroid gland.

thyroxine. Hormone secreted by the thyroid gland; assists in regulating metabolic activities.

tibia. Bone on the medial (big toe) side of the distal portion of the hindlimb.

tibiofibula. Bone in the hindlimb of anurans formed by the fusion of the tibia and fibula.

tibiotarsus. Bone formed by the fusion of the tibia and the proximal tarsal elements in birds and some dinosaurs.

trachea. Air tube extending from the pharynx to the bronchi of the lungs.

tragus. Fleshy projection inside the pinna of bats; arises from the inner base of the ear; function is unknown.

triiodothyronine. Hormone secreted by the thyroid gland; assists in regulating metabolic activities.

tropical rain forest. Tropical forest that receives almost daily rainfall; contains the highest species diversity of any biome.

tropical seasonal deciduous forest. Tropical forest with one or two dry seasons each year, during which time the leaves are dropped.

tropic hormone. Hormone whose target is another endocrine gland.

true census. Count of all individuals present in a given area.

tundra. Area in Arctic and alpine regions characterized by bare ground and absence of trees; dominated by mosses, lichens, sedges, forbs, and low shrubs; permafrost.

tympanum (or **tympanic membrane**). Eardrum.

ulna. The bone on the medial (little-finger) side of the forearm.

ultimobranchial bodies. Endocrine glands that develop from the last pair of pharyngeal pouches; may produce the hormone calcitonin.

ultrasound. Sound above the range of human hearing; above 20 Hz.

uncinate process. A posteriorly projecting process of the vertebral ribs of birds and certain reptiles.

underfur. Inner, finer, and usually shorter hairs making up the pelage of a mammal.

ungulate. Collective term used to designate hooved mammals.

unguligrade. Type of locomotion in which only the tips of the digits contact the ground.

ureter. Tube through which urine is conducted from the kidney to the cloaca or urinary bladder.

urethra. Tube through which urine is voided from the body of a mammal.

urodeum. Ventral portion of the cloaca in some vertebrates; receives the urogenital duct.

urogenital. Pertaining to the organs, ducts, and structures of the urinary and reproductive systems.

uropygial gland. Oil gland on the dorsal surface of the body at the base of the tail of a bird.

urosteges. Ventral scales posterior to the anal plate; found in snakes.

urostyle. Rodlike bone, representing a number of fused vertebrae, making up the posterior part of the vertebral column in anurans.

uterus. Hollow, muscular organ in which the fertilized ovum develops.

utriculus. Larger of the two sacs (sacculus, utriculus) in the inner ear; contains maculae; functions in static equilibrium.

vagina. Muscular, tubular organ that leads from the uterus to the vestibule of female mammals; situated between the urethra and the rectum.

vane. The flat part on either side of the shaft of a feather.

vasa efferentia. Modified mesonephric tubules in some male fishes that carry sperm from the testis to the mesonephric duct.

vas deferens (or **ductus deferens**). Sperm duct; tube through which sperm are ejaculated.

vasopressin. Hormone produced by the hypothalamus that stimulates water reabsorption from kidney cells into the blood as well as vasoconstriction of arterioles; also called antidiuretic hormone (ADH); released from the posterior pituitary gland.

vein. Blood vessel conducting blood toward the heart.

velvet. Vascularized skin covering the antlers during their development.

vent. External opening of the cloaca; used especially in reference to amphibians and reptiles.

ventricle. Cavity in the brain; also, a chamber of the heart.

ventricular trabecula (pl. **ventricular trabeculae**). Ridge in the ventricular wall of an amphibian heart that separates oxygenated from deoxygenated blood.

vermiform. Having a wormlike shape.

vertebra (pl. **vertebrae**). Segment of the vertebral, or spinal, column.

vertebrate. An animal distinguished by the possession of a backbone or spinal column. Includes fishes, amphibians, reptiles, birds, and mammals.

vestibule. Shallow space into which the vagina and urethra open in some female rodents and primates; also part of the inner ear.

viviparous. Giving birth to nonshelled young.

vocal sacs. Paired or unpaired resonating chambers in most male anurans.

volant locomotion. Capable of gliding (flying squirrels).

volcanic lake. Circular lake formed in the crater of an extinct volcano.

Weberian ossicles. Modified anterior vertebrae joining the ear with the swim bladder in suckers, minnows, catfishes, and characins.

xanthophore. Cell containing yellow pigments.

xeric. Characterized by dry environmental conditions.

yolk sac. Membrane enclosing the yolk in developing vertebrates.

ypsiloid cartilage. Cartilage extending forward from the pelvic girdle in the ventral body wall of certain salamanders.

zoogeography. Study of the geographic distribution of animals.

zooplankton. Microscopic animals in aquatic ecosystems.

zygodactyl. Condition in some birds in which two of the toes are oriented forward and two are oriented backward; found in woodpeckers, cuckoos, and some other birds.

zygomatic. Relating to the cheekbone.

zygote. Fertilized ovum; first cell of the next generation.

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About the Author

Dr. Donald W. Linzey, a native of Baltimore, Maryland, is a biologist living and working in southwestern Virginia. He received degrees from Western Maryland College (now McDaniel College) in Westminster, Maryland (BA, 1961), and Cornell University in Ithaca, New York (MS, 1963; PhD, 1966). He has taught general biology, comparative anatomy and physiology, herpetology, mammalogy, and a variety of ecological and natural science courses at Cornell University, the University of South Alabama, Wytheville Community College, and Virginia Tech. Since the early 1960s, he has studied mammals and other vertebrates in the eastern United States. In the mid-1960s, he worked as a park ranger and naturalist in the Great Smoky Mountains National Park and has continued conducting research in the park for the past 56 years. In 1999, he became chair of the Mammal Taxonomic Working Group and coordinated mammal investigations for the All-Taxa Biodiversity Inventory in the Park. In addition to authoring 12 texts and more than 200 articles for regional, national, and international scientific journals and other publications, Dr. Linzey is the Associate Editor for Vertebrates for McGraw-Hill's Encyclopedia of Science and Technology. He organized Virginia's first symposium on endangered and threatened plants and animals in 1978 and served as editor of the proceedings (1979).

From 1990 to 1998, Dr. Linzey directed a long-term multidisciplinary study of the decline of amphibians in Bermuda. He served as director of the Blue Ridge Highlands Regional Science Fair for 19 years and completed a three-year term on the Science Service Advisory Board, which oversees the annual Intel International Science and Engineering Fair. He has served on the boards of directors of the Virginia Museum of Natural History, Discover Life in America, and the Humane Society of Montgomery County. Dr. Linzey's awards include the Outstanding Faculty Award from the Virginia State Council of Higher Education (1996), the NISOD Award for Excellence in Teaching (1996, 1998, 2001), the Distinguished Service Award from Wytheville Community College (1998), the Chancellor's Professorship Award from the Virginia Community College System (1998), the 1999 and 2000 Virginia Professor of the Year Awards from the Carnegie Foundation for the Advancement of Teaching, the Distinguished Alumni Awards for Professional Achievement (2003) and Community Service (2010) from McDaniel College, and the Thomas Jefferson Medal for Outstanding Contributions to Natural Science Education by the Virginia Museum of Natural History (2013).

Dr. Linzey resides in Blacksburg, Virginia, with his wife, Juanita, and their 18-year-old rescue dog, Brandi. They have four sons.