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KELLEY M. STEWART

MAMMALOGY

ADAPTATION
DIVERSITY
ECOLOGY

FIFTH
EDITION

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Fifth Edition

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About the Authors

George A. Feldhamer is Professor Emeritus of Zoology and former Director of the Environmental Studies Program at Southern Illinois University. His research focused exclusively on mammalian populations, ecology, and management; biology of introduced deer; and threatened and endangered species of rodents and bats. He is a former associate editor for the *Journal of Forest Research* and the *Wildlife Society Bulletin*. He is the senior editor of *Wild Mammals of North America: Biology, Management, and Conservation* (2003) and an author of *Mammals of the National Parks* (2005) and *Deer: The Animal Answer Guide* (2012), all published by Johns Hopkins University Press. He was co-editor of *Ecology, Behavior, and Conservation of the Golden Mouse: A Model Species for Research* (2007), and an author of *Bats of Illinois*. Dr. Feldhamer has had 36 years of experience teaching an upper-division mammalogy course. In 2011, he received the Joseph Grinnell Award from the American Society of Mammalogists "to honor individuals who have made outstanding and sustained contributions to education in mammalogy."

Joseph F. Merritt was senior mammalogist with the Illinois Natural History Survey, University of Illinois. He is the former Director of Powdermill Biological Station of the Carnegie Museum of Natural History and served as Distinguished Visiting Professor at the US Air Force Academy in Colorado Springs, Colorado, during the academic year of 2004–2005. Dr. Merritt is a physiological ecologist and functional morphologist specializing in adaptations of mammals to cold. He is the author of *Guide to the Mammals of Pennsylvania*, published by the University of Pittsburgh Press, and editor of several technical monographs on specific taxa of mammals. His book *Biology of Small Mammals* was published by Johns Hopkins University Press in 2010. He is the recipient of the American Society of Mammalogist's 2015 Hartley H. T. Jackson Award and has served on the publications committee of the American Society of Mammalogists (ASM) since 1990. He is the former Editor-in-Chief of the *Journal of Mammalogy*. Dr. Merritt has instructed mammalogy for 43 years and currently teaches mammalogy at the University of Colorado Mountain Research Station.

Carey Krajewski is Professor of Zoology at Southern Illinois University. His research in mammalogy has involved molecular studies of marsupial phylogeny, particularly the systematics of dasyuromorphians, as well as the evolution of gruoid birds. He was an associate editor for the *Journal of Mammalogy* and *Molecular Phylogenetics and Evolution* and is currently associate editor of the *Journal of Mammalian Evolution*. From 1993 to 2010 Dr. Krajewski was an honorary research fellow in the Genetics Department at La Trobe University, Australia. He was named 2004 Outstanding Scholar in the College of Science at SIU and was Chair of the Zoology Department from 2011 to 2018.

Janet L. Rachlow is Professor of Wildlife Ecology in the Department of Fish and Wildlife Sciences at the University of Idaho. Her research focuses on behavioral ecology, conservation, and relationships between mammals and their environments, and her work has spanned mammalian taxa from ground squirrels to grizzly bears. In 2015, she received the Outstanding Researcher Award in the College of Natural Resources at the University of Idaho. Dr. Rachlow is a member of the IUCN Lagomorph Specialist Group and Vice President of the World Lagomorph Society, and she currently serves on the board of directors for the American Society of Mammalogists.

Kelley M. Stewart is an Associate Professor of large mammal ecology in the Department of Natural Resources and Environmental Science at the University of Nevada, Reno. Her research focuses on effects of density dependence, reproduction, and nutritional condition of large mammals on movement patterns, resource selection, population dynamics, and community structure. Dr. Stewart teaches courses in wildlife ecology at both the graduate and undergraduate levels. She was named the Teacher of the Year in 2012 by the College of Agriculture, Biotechnology, and Natural Resources at UNR. She has been primary advisor for 16 graduate students working on various aspects of ungulate ecology, 3 undergraduate Honors Students, and 2 postdoctoral research associates.

Brief Contents

Contents

Research on all aspects of mammals continues at a rapid pace, as it has for many decades. Considerable molecular and morphological work of the past 15 years has resulted in a substantial increase in the number of recognized extant mammalian families (167), genera (1,314), and species (6,399) (Burgin et al. 2018). It continues to be an exciting challenge to produce a textbook for a one-semester upper-level undergraduate or graduate mammalogy course, which balances both breadth and depth of coverage. In this edition, we have reduced the amount of text from the fourth edition while endeavoring to maintain and enhance relevant, up-to-date content.

The volume is divided into five parts. Part 1 includes the introductory and historical remarks in Chapter 1, as well as discussion of several topics that will be crucial for understanding the rest of the book. Chapter 2 gives an overview of the diverse methods that mammalogists employ in research and continues the story of natural history and taxonomic study up to the present. Chapter 3 reviews phylogenetic relationships among mammalian orders and gives a brief history of this contentious topic. Chapter 4 describes the evolution of synapsids based on the fossil record and provides a brief tutorial on the morphology of mammal teeth, arguably the most informative character set in mammalian paleontology. Chapter 5 introduces the conceptual foundations of biogeography and some of the modern analytical techniques used to understand the distribution of mammals.

Part 2 integrates mammalian characteristics including support and movement (Chapter 6), feeding and nutrition (Chapter 7), physiological and environmental adaptations (Chapter 8), and reproduction (Chapter 9). Part 3 (Chapters 10 through 21) is a survey of the mammalian orders and families, which describes key morphological, physiological, and behavioral traits, as well as fossil history. Part 4 (Chapters 22 through 26) examines sexual selection, mating systems, behavioral, population, and community ecology of mammals. In Part 5 we provide a brief overview of mammalian zoonotic **diseases** and parasites (Chapter 27), and finally current issues and initiatives in mammalian **conservation** (Chapter 28).

As in previous editions, all literature citations are collected at the end of the text to avoid redundancy. Technical terms throughout each chapter are in boldfaced type when they are first introduced, and those terms are defined in both the text and the glossary. Although there is continuity between sections and chapters of the text, instructors can select certain chapters based on individual interest, emphasis, or time constraints without sacrificing clarity and understanding.

The five authors bring a combined total of about 160 years of field and laboratory research experience working with mammals in a variety of settings—as well as many decades of teaching—to the collaborative endeavor of this book. Each of us has also benefited from years of suggestions, ideas, discussions, and constructive criticism from many teachers, colleagues, students, and friends.

With this edition of the textbook, we welcome two new coauthors and bid goodbye to two of the original coauthors, Lee C. Drickamer and Stephen H. Vessey. When the book was being conceived, Steve had taught **mammalogy** for many years, and Lee had taught ornithology. They helped envision a mammalogy textbook that differed from most previous books in this field by combining functional approach to the subject with the more traditional mammalogy textbook pattern of concentrating on a taxonomic framework as the basis for covering the subject. With George Feldhamer and Joseph Merritt, they helped put together a useful textbook that is now used in many mammalogy courses. We thank both Lee and Steve for their contributions to earlier editions of this book and to the field of mammalogy, as we welcome Janet Rachlow and Kelley Stewart as new coauthors.

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Their valued input continues to be reflected in this fifth edition.

PART 1

Introduction

The Science of Mammalogy

Mammals

Mammalogy is the study of **mammals**, organisms belonging to the taxonomic group Mammalia. One way of defining Mammalia is "the most recent common ancestor of monotremes (platypus and echidnas) and therians (marsupials and placental mammals) and all its descendants" (Rowe 1988; Figure 1.1). As in this example, modern biologists define all taxonomic groups by their evolutionary ancestry, not by their traits. Taxonomic groups such as Mammalia do indeed have diagnostic, distinguishing, characteristic, or common traits, but it is ancestry, not traits, that makes an organism a mammal. Thus, for instance, members of all living mammal species have **hair** and **mammary glands**, but a completely hairless mutant mouse would still be a mammal. This way of understanding taxonomic diversity is relatively new and confusing to many students, but it is one of the major conceptual advances of 20th-century biology. (See Chapter 4 for more information on the taxa shown in Figure 1.1.)

Still, what *is* a mammal? How would you know one when you saw it, given that organisms do not have their ancestry pinned to their sleeves? We can trace that ancestry by characterizing the familiar groups to which mammals belong in terms of **key adaptations**—traits that enhance an organism's evolutionary fitness and exert a major influence on the biology of a major taxonomic group. In order from more to less inclusive, mammals are the following: *eukaryotes* (organisms with cells containing a nucleus, membrane-bound organelles, and a cytoskeleton); *animals* (eukaryotes that are mobile, multicellular, and heterotrophic); *chordates* (animals with a notochord, dorsal hollow nerve chord, postanal tail, and pharyngeal slits); *vertebrates* (chordates with **vertebrae** and a **cranium**); *tetrapods* (vertebrates with four limbs); *amniotes* (tetrapods with three unique extraembryonic membranes—amnion, chorion, and allantois); and *synapsids* (members of **Synapsida**, amniotes with a single temporal opening on each side of the skull). Among living vertebrates, tetrapods are ancestrally terrestrial animals derived from one group of fishes; they include amphibians (frogs, salamanders, and
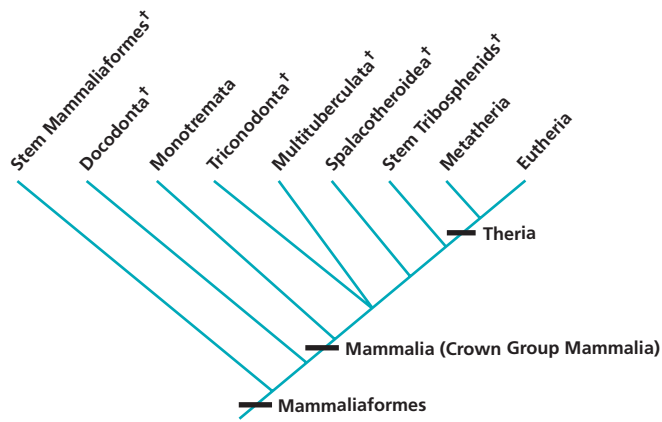
Figure 1.1 What is a mammal? The phylogenetic definition of Mammalia is all descendants from the last common ancestor of living mammals. This is the "Crown Group Mammalia" of many authors (Benton 2015), who consider Mammalia equivalent to Mammaliaformes as shown here (synapsids with a dentary-squamosal jaw joint; see below and Chapter 4). There is still debate about the branching order for some of these lineages. Daggers indicate extinct groups. *Based on Pough et al. (2013).*

caecilians) and amniotes. Amniotes comprise sauropsids (including reptiles and birds) and synapsids. Mammals are the only living synapsids, but there were many nonmammalian synapsids (please don't call them "mammal-like reptiles"—reptiles are sauropsids) that lived during the past 300 million years. Mammals (or the Mammaliaformes, as some authors term them) are distinguished from their extinct synapsid relatives by the structure of their jaw joint, which forms between the **dentary bone** of the mandible (in extant mammals, the dentary and mandible are synonymous; this was not the case in cynodonts) and the squamosal bone of the skull. Thus, the classification of Mammalia looks like this:

> Eukarya
>> Animalia
>>> Chordata
>>>> Vertebrata
>>>>> Tetrapoda
>>>>>> Amniota
>>>>>>> Synapsida
>>>>>>>> Mammalia

But still, what *is* a mammal? From the information above, you could (in principle) identify one if you could examine its entire anatomy, both macroscopically and microscopically. But ancestry and diagnostic traits are not the whole story of mammalian evolution. That story is very long indeed (see Chapter 4 and many of the chapters that follow), but a few aspects are worth mentioning at the outset. Again these are key adaptations. For example, mammals are like birds in that they are endotherms—that is, they maintain a relatively high body temperature by maintaining a correspondingly high **metabolic rate. Endothermy** has allowed mammals to thrive in a wide range of

thermal habitats, but also requires them to obtain much more energy from food than do comparably sized ectotherms. Indeed, one apt characterization of a mammal relative to other vertebrates is "an eating machine." Many of the traits we associate with mammals ultimately serve this purpose and form a correlated suite of adaptations that vary tremendously among major groups. Complex teeth and chewing actions, foraging strategies, locomotor specializations, and a wide range of body sizes—all have something to do with the voracious appetites of these high-energy animals. Mammals have big brains (themselves a major energy sink), which evolved from an early emphasis on olfaction to include the elaboration of neocortical layers that process diverse sensory information and coordinate more or less "intelligent" responses (Kas 2013), mostly for the purpose of eating. Hair (or **fur**), a trait mammals inherited from their more recent synapsid ancestors, is also correlated with endothermy: Acting as insulation, hair (or fur) traps body heat produced at great cost and keeps it from dissipating with every gentle breeze that passes over the skin.

A second adaptation that exerts heavy influence on mammalian biology is the energy invested in offspring (see Chapter 9). Mammals are either **oviparous** (i.e., lay eggs, as in the case of monotremes) or **viviparous** (i.e., give birth to live young, as marsupials and placentals do), but all provide their young with nutritious **milk** produced in the mammary glands of mothers, the trait for which mammals are named. As with endothermy, making milk requires energy from food. For monotremes and marsupials, milk production (**lactation**) constitutes the major maternal investment in offspring survival; but for placental mammals, suckling is preceded by a lengthy period of **gestation** (development in utero) during which the mother is supplying all offspring needs. In no species of mammal do mothers simply leave their offspring to fend for themselves (a common strategy in other vertebrates such as turtles). In many species a prolonged postnatal association between offspring and mothers (and sometimes fathers or more distant relatives) lies at the heart of complex social systems so familiar to humans. So, what are mammals? They are smart, mobile eating machines that exhibit great maternal care (Figure 1.2).

Why Study Mammals?

Why are mammals important ("to us" is implied)? The first answer modern biologists give is that mammals are significant components of functioning ecosystems, and functioning ecosystems are what give Earth a biosphere rather than a "dead-o-sphere." The anthropocentric corollary is that humans depend (more completely than most of us realize) on a biosphere that will support our swelling population (Crist et al. 2017). Mammals form critical links in terrestrial and aquatic food webs, transferring energy and nutrients that power biotic processes for maintaining

Figure 1.2 **Traits of mammals.** Mammals, such as this narbalek or little rock-wallaby (*Petrogale concinna*), are endothermic vertebrates with hair and mammary glands; they invest a relatively large amount of energy in raising relatively few offspring.

diverse life forms including, but certainly not limited to, our own. Many are keystone species, ecosystem engineers, or mutualists that impact biotic communities to a much greater extent than predicted by their numbers. If we want to understand the processes upon which our existence depends, we need to study mammals. Because mammals *are* important to us, we study them—both out of curiosity and self-interest. We want to know what kinds of mammals occur in the world, how they got there, and how they function in ecosystems, both as organisms and as collections of cells. Mammals are part of nature—they and the biotic processes in which they participate are natural phenomena. When we ask questions about the diversity and causes of natural phenomena, look for explanations in terms of other natural phenomena, and base our conclusions on rational interpretation of evidence, we are doing science. Mammalogy is the *scientific* study of mammals. Mammals are also valuable to humans as natural resources. We cultivate them for meat, dairy products, and materials (e.g., leather); we nurture them as pets, hunt them for sport, and use them as surrogates for ourselves in medical science. The US beef industry, built on just one species (the cow, *Bos taurus*), has a retail value around $100 billion (USDA 2017). Mammal husbandry on farms and ranches around the world has been a part of human cultures for thousands of years (Zeder 2012), and research into the processes by which mammals were **domesticated** is yielding new insights (Blaustein 2015). Mammals are by far our favorite nonhuman companions: in 2015, Americans spent over $60 billion on their pets—a sum that is part of an upward trend likely to continue (JAVMA News 2015). Veterinary medicine is an advanced science centered mostly on mammals and practiced with increasing effectiveness by trained professionals worldwide. The house mouse (*Mus musculus*) is one of the most

important *model organisms* (species used for scientific studies because they are easy to work with) in biomedical research and is valued for its small size, **fecundity**, short generation time, and relatively simple husbandry. There are now numerous "mouse models" of human diseases—lab strains created by controlled breeding with genotypes matching those of human diabetes, heart disease, obesity, and other afflictions. Cats, rats, dogs, and several other mammal species are also widely used in medical research.

Some mammals are important because they pose a threat to humans, especially when they act as disease **reservoirs** or **vectors** (see Chapter 27). Rodents are particularly common reservoirs for human pathogens (i.e., they host the pathogenic organisms, but do not get sick themselves). Han et al. (2015) found that 217 of 2,277 rodent species examined (about 10%) are reservoirs for **zoonoses** (diseases transmitted from animals to humans) caused by bacteria, fungi, flatworms, or protists. The authors attribute this to the high fecundity and short generation times of reservoir rodents. A particularly well-documented case of rodent-borne zoonosis is the 1993 outbreak of hantavirus pulmonary syndrome (HPS) in the southwestern United States, in which deer mice (*Peromyscus maniculatus*) were the reservoir, shedding virus in their urine, feces, and saliva (CDC 2012). This outbreak involved 24 diagnosed cases of human HPS, 12 of them fatal. Mammal species may also be pests when they are translocated outside their historical ranges and introduced into novel areas where they thrive at the expense of native species. The European rabbit (*Oryctolagus cuniculus*) is one such **invasive species** on the Iberian Peninsula, where it is outside its natural range. Rabbits spread in large numbers over the southern two-thirds of Australia following their introduction in the mid-1800s, and rabbit foraging has degraded arid-land vegetation to the detriment of native vertebrates (Australian Government 2011). In the 21st century, the most urgent mammalian science is conservation, the study of how human-induced changes to the biosphere are driving mammal (and many other) species toward **extinction** (Johnson et al. 2017). Since the 16th century, 82 mammal species have gone extinct, 2 have become extinct in the wild, and 1,194 have come to be threatened with extinction (IUCN 2018). Given that there are close to 6,500 recognized species of modern mammals (Burgin et al. 2018), it is sobering to realize that about 20% of them are gone or in serious decline. The greatest threat to mammals is habitat loss, driven by humanity's relentless conversion of natural areas into croplands, rangelands, mines, and developed real estate. Individual species may suffer from overexploitation by humans for food, sport, and animal products. Some regional mammal faunas have been decimated by invasive predators (often other mammals); for example, cats, rats, and foxes introduced into Australia have been responsible for the staggering death toll of its marsupials (Woinarski et al. 2015; Figure 1.3). All threats to mammals are aggravated by climate change. While mammalogists study the biological causes and consequences of the decline of mammals, conservation solutions go beyond biology to include integrated resource management, public

Figure 1.3 **Invasive species.** Camera trap documentation of a **feral** cat in southwestern Australia killing a native marsupial, the brush-tailed phascogale (*Phascogale tapoatafa*), whose current conservation status is "near threatened." *IUCN 2018.*

policy, sociology, psychology, economics, and ethics. These issues are discussed further in Chapter 28.

And of course, we humans are mammals. A single species within the Order Primates and most closely related to chimpanzees, humans originated from a hominin ancestor in Africa about 200,000 years ago (see Chapter 15). We share all the general adaptations of mammals and the specific ones of primates, but we are unique in possessing the evolutionary novelty of a hypertrophied brain and its associated intelligence, along with highly developed capacities for language, tool use, and sociality. Our biological heritage is both a blessing and a curse, allowing us to dominate the Earth for our benefit, even as we push it beyond its capacity to sustain us. Mammalogy places our species—the greatest but sloppiest ecosystem engineer of all time—into an evolutionary-ecological **context** that helps us understand the transformative events taking place in the world around us.

History of Mammalogy

ANTIQUITY

From times when most humans were hunters and gatherers through the beginnings of agriculture 9,000 to 12,000 years ago, a body of knowledge about mammals and other organisms was gleaned from experience and passed from generation to generation. With the advent of written language about 3,500 years ago, some of this knowledge was recorded in glyphs, augmenting artistic depictions and oral **traditions**. Particularly important in these early times was knowing enough about local mammals to exploit them

as food, avoid being harmed by them, and keep them as pets or work animals. Such mammalian lore formed the basis of later, more scholarly, bodies of written information in civilization centers around the world. Most of the history of mammalogy traces to the origins of Western science in classical Greece around 600 BCE.

Mayr (1982) credits three contributions of classical Greek culture to the development of modern biology: (1) an interest in natural history (observable facts about wild plants and animals); (2) philosophy, especially the commitment to explain natural phenomena with natural causes (i.e., science, or an early form of it); and (3) an interest in medicine, disease, anatomy, and physiology exemplified by the works of Hippocrates (460–377 BCE). Aristotle (384–322 BCE) is a towering figure among the Greeks in both natural history and philosophy. Works such as *Historia Animalium*, *De Partibus Animalium*, *De Motu Animalium*, and *De Generatione Animalium* reveal Aristotle's years of careful observation and reflection on the structure and life processes of organisms then known around the Mediterranean. From his familiarity with natural history and traditionally recognized groups (e.g., birds), along with philosophical principles that attached significance of purpose to certain characteristics (e.g., blood, reproduction), Aristotle developed a working classification (Singer 1959) that divided animals into vertebrates (*enaima*, with red blood) and invertebrates (*anaima*, without red blood). Vertebrates were partitioned into viviparous (live-bearing) and oviparous (egg-laying) types. Mammals were among the former (monotremes would not be known to Western science until 1798), but with distinct groups for humans, whales, and other mammals ("viviparous quadrupeds"). Superimposed on these groups was Aristotle's *scala naturae* ("ladder of nature"), a ranking from lower to higher based on traits revealing the increasing development of vegetative, animal, and rational souls (*psyche*). Mammals sit atop the ladder, just above other vertebrates, with humans above everything. This view of relationships persisted for centuries in one form or another; it was finally discredited in biology during the 19th century (especially in light of Darwinian theory), but vestiges persist even today in our thoughtless and inappropriate use of "higher" and "lower" to describe taxonomic groups (e.g., "higher primates" that resemble us versus "lower primates" that do not).

Works of natural historians later in antiquity contrast sharply with Aristotle's careful, often first-hand observations of animals. Prominent among the later natural historians is Pliny the Elder (23–79 CE), whose uncritical compilation of fabulous animal tales may be of cultural significance, but has little scientific value. Contrast the following passages from Aristotle and Pliny on the subject of elephants:

The elephant has four teeth on either side, by which it munches its food, grinding it like so much barley-meal, and, quite apart from these, it has its great teeth, or tusks, two in number. In the male these tusks are comparatively large and curved upwards; in the female, they are comparatively small and point in the opposite

direction; that is, they look downwards towards the ground. The elephant is furnished with teeth at birth, but the tusks are not then visible. (Aristotle, Historia Animalium *book II, part 5)*

This is known for certain, that upon a time there was one elephant among the rest, not so good of capacity, to take out his lessons, and learn that which was taught him: and being beaten and beaten again for that blockish and dull head of his, was found studying and conning those feats in the night, which he had been learning in the day time. But one of the greatest wonders of them was this, that they could mount up and climb against a rope; but more wonderful, that they should slide down again with their heads forward. (Pliny, Natural History, *book VIII; Philemon Holland translation)*

As noted by Mayr (1982), the study of animal natural history was unprogressive between Aristotle and the 1500s, except in the Muslim world, where Al-Jāhiz's (776–868) *Kitāb al-Hayawan* (Book of Animals) continued and expanded the Aristotelian tradition. During that interval, there were nonetheless some advances in anatomy and physiology, especially the works of the Roman physician Galen (CE 130–201). Galen dissected specimens from several species of mammals and wrote influential treatises on anatomy and physiology. His description of the musculoskeletal system of Barbary macaques (*Macaca sylvanus*) was treated as definitive for human anatomy prior to 16th-century work on human cadavers (Singer 1959). The Persian philosopher Avicenna (980–1037) authored seminal works on medical science (e.g., *The Book of Healing, The Canon of Medicine*). Scientific study of animals revived somewhat near the end of the Renaissance with work by Vesalius (1514–1564) on human anatomy, Belon (1517–1564) on natural history, and Harvey (1578–1657) on blood circulation and embryonic development, among others.

DISCOVERING BIOLOGICAL DIVERSITY IN THE 17TH AND 18TH CENTURIES

By the 1600s, European explorers were traveling to many parts of the world. The specimens they discovered, described, and brought back from distant lands stimulated interest in biological diversity. Although none of these early naturalists was strictly a mammalogist, their broad interests included mammals. One was Mark Catesby (1683–1749), an Englishman who made two expeditions to North America with financing from wealthy patrons. In 1754, he published a two-volume treatise, *The Natural History of Carolina, Florida, and the Bahama Islands*, which included original descriptions and color illustrations of native mammals (Figure 1.4). This was perhaps the earliest monograph on North American plants and animals. In it, Catesby continued the tradition—stretching back to Leonardo da Vinci (1452–1519)—of combining artistic skill and scientific observation to communicate biological information through paintings. That tradition has continued with such artist-naturalists as Georges Buffon (1707–1788), John

Figure 1.4 **Illustration from Mark Catesby.** Based on observations made during visits to southeastern North America in the early 1700s, Catesby (1754) painted and described a number of mammals, including this eastern chipmunk (*Tamias striatus*).

James Audubon (1785–1851), Alexander Wilson (1766–1813), John Gould (1804–1881), Ernst Haeckel (1834–1919), Louis Agassiz Fuertes (1874–1927), Roger Tory Peterson (1908–1996), Richard P. Grossenheider (1911–1975), Frank Knight (1941–), and others.

This period of exploration and discovery stimulated the development of modern taxonomy. English naturalist John Ray (1627–1705) suggested that a species is a group of organisms that can interbreed, an insight that would be the core of Mayr's (1942) influential **biological species concept** (see Chapter 2). As more types of organisms were discovered, the need became apparent for a coherent system of **taxonomy**, or rules to govern the naming and classifying of species. Several schemes were proposed after 1500, but that of Swedish botanist Carl von Linné (1707–1778), better known as Linnaeus (Figure 1.5), became universally adopted. Linnaeus's *Systema Naturae* (1758) is generally cited as the basis for modern animal taxonomy. Linnaeus considered species to be fixed, discrete, individually created entities, naturally organized into a set of hierarchical
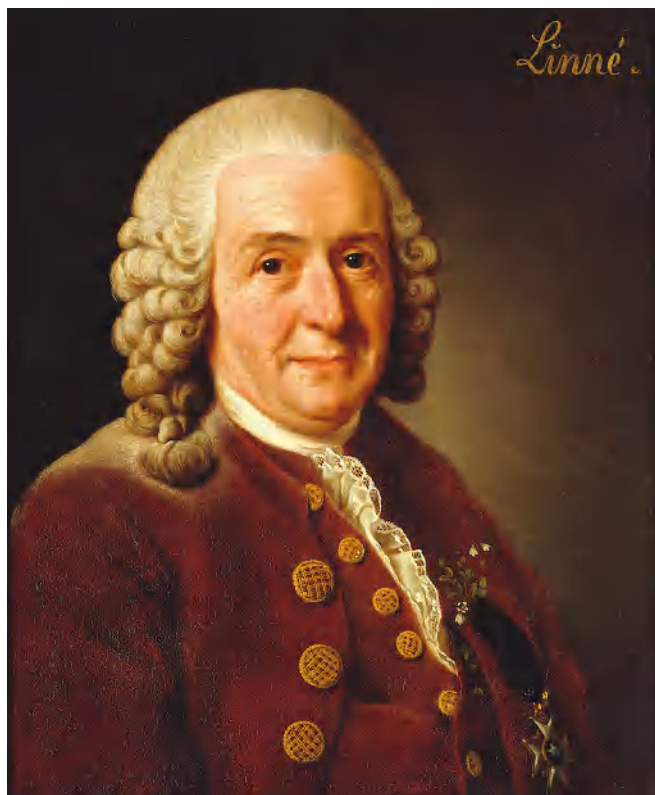
Figure 1.5 **Carolus Linnaeus.** Linnaeus is considered the founder of modern taxonomy. He formalized a system of binomial nomenclature in which each species is given a unique, two-word name. He also established a hierarchical scheme for classifying species into more inclusive groups.

(smaller within larger) groups recognized at specific **taxonomic ranks**. Thus, each species (e.g., the lion, *Panthera leo*) belongs to a genus (*Panthera*), which belongs to a family (Felidae), which belongs to an order (Carnivora), which belongs to a class (Mammalia). Membership in groups is determined by the physical characteristics of the organisms, beginning with descriptions of individual species. Each species is given a unique two-word name consisting of its genus name (a noun) and a specific epithet (an adjective), which are both in Latin or Latinized. This is the familiar **binomial nomenclature** we still use today.

Catesby, Ray, and Linnaeus are only three of many naturalists active in the 1600s and 1700s. This period also saw the rise of live-animal menageries (later known as zoological parks, or zoos) and natural history museums housing preserved specimens from around the world. Perhaps most remarkable among the latter was the extensive private collection of English biologist John Hunter (1728–1793). Derived from his lifelong passion for acquiring biological materials and performing comparative studies, it was the first to use displays of carefully prepared specimens to educate observers about the structure and diversity of organisms (Singer 1959). The Hunterian Museum in London, operated by the Royal College of Physicians and Surgeons, is still open to the public. Descriptions of organisms

and their parts made with microscopes were first published during the 17th century, including works by the great European microscopists Marcello Malphigi, Nehemia Grew, Jan Swammerdam, Antonie van Leewuenhoek, and Robert Hooke. Microscopic study of mammals helped establish the discipline of *histology*, the study of body tissues. By the dawn of the 19th century, a proliferation of collections, classifications, and monographs describing the great diversity of organisms was challenging traditional explanations of that diversity. The history of life on Earth was ripe for scientific explanation, and the coming century would provide it.

EXPLAINING BIOLOGICAL DIVERSITY IN THE 19TH CENTURY

In science, potentially correct explanations that are tested against their predictions are called *hypotheses*. As we now understand the growth of scientific knowledge, hypotheses can be (and usually are) rejected, but never absolutely proved, because there are too many possible hypotheses explaining a particular phenomenon for us to test them all. The good ones, then, are the ones that fail to be rejected. False hypotheses may be abandoned or modified and retested. A hypothesis that passes one test is subjected to another (perhaps based on a different prediction than the first), and another after that, and so on until it has passed numerous (or at least several critical) tests. Such hypotheses tend to explain many observations. In the tortuous history of science, some hypotheses survive tweaking and testing to explain so many observations that they become part of our worldview and engender new questions of their own. We often call these *theories*; they are part of scientific knowledge. In biology, there are many such theories: Schleiden and Schwann's cell theory, Mendel's theory of heredity, Pasteur's germ theory of disease, Bernard and Cannon's homeostasis theory, MacArthur and Wilson's theory of island biogeography, and others. But the theory of theories is Charles Darwin's theory of evolution. Darwin's first thesis, that species are related by genealogical ancestry and that they change, diversify, or go extinct over time, was established in the latter half of the 19th century (largely by Darwin himself); the second thesis, that natural selection is the process that produces adaptations, took most of the 20th century to formalize and test with rigor.

The 1800s began with a fascinating digression by a number of different naturalists and philosophers seeking to explain the anatomical similarities among members of major taxonomic groups (e.g., vertebrates). German poet-philosopher J. W. von Goethe (1749–1832) was impressed by the blueprint-like similarity of body structures among groups, such as the bone-for-bone correspondence of human and bird skeletons (Figure 1.6A–B) documented by Belon (1555). This led Goethe and German naturalist Lorenz Oken (1779–1851) to propound a theory of organic form in which members of a high-level taxonomic group show structural variations on a simple common
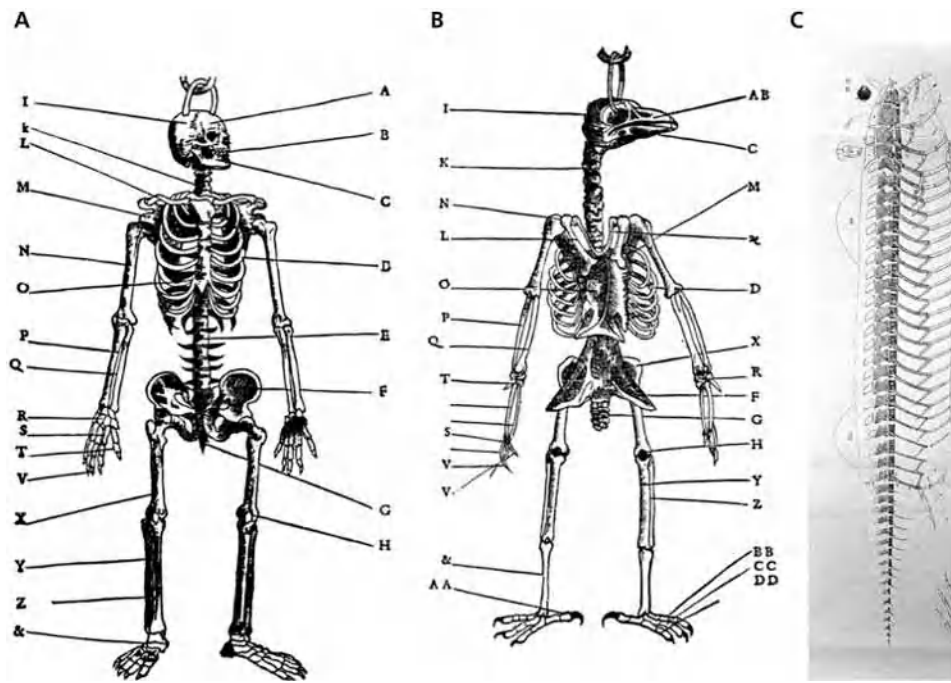
Figure 1.6 **Skeletons and archetypes.** (**A–B**) Belon's (1555) comparison of human and bird skeletons; (**C**) Owen's (1848) vertebrate archetype.

form, a metaphysical abstract that British paleontologist Richard Owen (1848) called an *archetype*. For example, the vertebrate skeletal archetype consisted of a longitudinally repeated series of vertebra- and rib-like elements that supposedly were modified in different ways to produce the actual skeleton of a vertebrate species. A provocative application of this idea was the "vertebral theory of the skull," in which the vertebrate cranium corresponds to modifications of the anterior-most archetypal elements. This school of thought—called Naturphilosophie, idealistic morphology, or transcendental anatomy—posited that the archetype was an eternal essence or idea that might be inferred through study of **morphology** (the study of form, a term Goethe coined), but was not a historical actuality. Although idealistic morphology was abandoned, it led Owen to the concept of **homology**, according to which structures in different species derived from the same archetypal elements, regardless of their current form or function. This concept, when reinterpreted by Darwin, illuminated a critical body of evidence supporting evolution.

Before Darwin, the first widely read arguments in favor of evolutionary change among species were those of French naturalist Jean-Baptiste Lamarck (1744–1829; Figure 1.7), whose mechanism of evolution included spontaneous generation, an inherent drive toward perfection, and inheritance of acquired characteristics—all subsequently rejected. Lamarck's greatest contemporary critic was his countryman and colleague at the Jardin des Plantes (botanical garden) in Paris, Georges Cuvier (1769–1832). Cuvier was the most important natural historian since Lin-

naeus, if not Aristotle. His monumental accomplishments, all achieved through careful study of physical evidence (mostly comparative anatomy) include the following: (1) establishing that fossils are remains of past organisms and document the reality of extinction, which he attributed to catastrophes in Earth history; (2) inspiring the development of functional morphology with his "principle of correlation of parts," the idea that the form of individual anatomical elements is determined by their mechanical relation to other elements in the performance of organismal functions; and (3) providing a new and influential classification of animals. This new scheme, published in Cuvier's *Le Règne animal* (1817), recognized four major groups (*embranchements*) of equal stature (not ranked from lower to higher) and unconnected by evolutionary or other historical relationships.

Classification of mammals varied among naturalists from Linneaus to Cuvier, depending on the significance they attached to particular traits, but all recognized mammals as a natural **taxon**. Linneaus's (1758) Class Mammalia comprised 8 orders: Primates = primates, colugos, and bats; Bruta = elephants, manatees, sloths, anteaters, pangolins; Ferae = carnivorans; Bestia = pigs, armadillos, insectivorans, opossums; Glires = rhinos, rabbits, rodents; Pecora = most even-toed ungulates; Belluae = horses, hippos; Cete = cetaceans. Oken (1802), convinced that there must be 5 classes of animals to match the 5 human senses, recognized mammals as Ophthalmozoa, exemplifying vision. Vertebrata (including mammals) was one of Cuvier's (1817) four *embranchements*; his Class Mammalia comprised 8 orders: Bimanes (humans), Quadrumanes (other primates), Carni-

Figure 1.7 **Jean-Baptiste Lamarck.** The early 19th-century French naturalist put forward a coherent (though incorrect) theory of evolution based on detailed knowledge of natural history.

vores, Rodents, Edentates, Pachyderms, Ruminants, and Cetaceans. Lamarck (1809) recognized 14 classes of animals, the first 10 of which were invertebrates and the last four vertebrates, including Mammals (Class XIV). Lamarck's groups were arranged according to his own *scala naturae*, tracing six stages of organization through which life evolves on its way to perfection. Fishes and reptiles represent the fifth stage, with "nerves terminating in a spinal cord and a brain which does not fill up the cavity of the cranium; heart with one ventricle and cold blood" (Lamarck 1809:156). Birds and mammals are at the sixth stage, showing "nerves terminating in a spinal cord, and in a brain which fills up the cavity of the cranium; heart with two ventricles and warm blood" (163). Lamarck noted that the egg-laying monotremes are "intermediate between birds and mammals . . . they are neither mammals, birds nor reptiles" (166). He recognized four orders of mammals: exungulates (cetaceans); amphibian mammals (pinnipeds and sirenians); unguiculates (edentates, rodents, marsupials, insectivores, terrestrial carnivorans, bats, and primates). Humans form an unnumbered class Bimana—"mammals with differentiated unguiculate [having nails or claws, not hooves] limbs; with three kinds of teeth and opposable thumbs" (169). Following his description of Bimana, Lamarck proposed the possibility of a "quadrumanus race" being "transformed into bimanous" by means of goal-directed behavior producing acquired traits (e.g.,

standing upright to "command a large and distant view"), which are then passed on to offspring.

The work of these naturalist-taxonomists demonstrates the scientific tradition from which evolutionary theory emerged—the primary quest to understand relationships among species ("the species problem" as it was called) and the necessity that such an understanding explain what was known about species' characteristics. Aristotle, Linnaeus, Oken, and Cuvier brought different background knowledge and assumptions to the problem, but all forged their answers in terms of static classifications: their way of understanding relationships among species was to discover traits that *define* natural groups. They could argue over whether particular characters delimited the groups that nature intended, but they agreed (as did virtually all of humanity) that defining traits would reveal natural groups. These thinkers were what Mayr (1982 and elsewhere) called *essentialists*—that is, they were convinced that groups such as Mammalia are unchanging and have essential (defining) characters, with the trick being to identify those characters, because nature so often covers its tracks. Lamarck was different. His stages of organization are more like floors in a tall building with multiple wings through which groups of organisms—spontaneously generated as "infusorians" (e.g., protists) in the basement—are constantly striving upward, generation after generation, through a series of linked stairwells toward the penthouse of perfection in each wing, with some lucky enough to reach the Bimana skydeck. Those that are now mammals belong to lineages whose ancestors were once reptiles; living primates had ancestors that were seals. Lamarck's view of *how* evolution happens is incorrect, but his view that *evolution happens* and his argument for it based on detailed information about biology (a term he coined) created a turning point in the history of science. And because the corpus of knowledge about mammals was more extensive than that for most other living groups, it is fair to say that mammalogy probably contributed as much or more to the early development of evolutionary thinking than other "ologies."

The history of Darwinism has been described in detail by many authors: Irvine's (1955) is an engaging description of events in Darwin's lifetime; Bowler's (2009) is a more comprehensive narrative. The outlines of a theory of evolution by natural selection first appeared in 1858 in a five-page paper by English naturalists Charles Darwin (1809–1882) and Alfred Russel Wallace (1823–1913) (Darwin and Wallace 1858). The two men had independently distilled the idea of natural selection by contemplating the species problem in light of their first-hand knowledge of natural history and familiarity with the writings of their predecessors (those discussed above and many others). Darwin's (1859) *On the Origin of Species* had been in preparation for nearly 20 years while he gathered information from a tremendous array of sources. Its chapters include the oft-recapitulated evidence for change through time and common ancestry—data from geology suggesting a great age of the Earth; the reality of species loss through extinction;

documentation of transitional forms that link recent and ancient species; similar species living in geographic proximity; reinterpretation of homology as ancestral similarity—as well as a carefully reasoned argument for natural selection, with support from an extensive body of knowledge on artificial selection. The scientific community accepted the historical fact of evolution relatively quickly after *On the Origin of Species*, but natural selection required a mechanism of heredity that was not available until the rediscovery of Gregor Mendel's (1866) laws of inheritance around 1900 (see below).

Mammals played a significant role in the *Origin of Species*; Darwin mentions at least 50 different mammal species or groups in developing his arguments. They appear most frequently in his chapter on "Mutual Affinities of Organic Beings," in which Darwin relates the basis of classification to his theory, demonstrating how evolution explains nested patterns of phenotypic variation within taxonomic groups, as well as **vestigial** traits (horses, giraffes, dogs, sirenians, lions, marsupials, and shrews are his main examples). His chapter on "Laws of Variation" also includes many mammal examples (equids, cetaceans, rodents, edentates, mustelids) as Darwin explores the causes of character variation among members of the same species. Darwin was not an expert on mammals (except domesticated ones), but the vast and growing literature on mammal biology in the mid-1800s could not fail to have had a major impact on the most important science book ever written.

While this revolution in biological thought was occurring, the study of mammalian natural history went on apace. A worldwide survey would be too lengthy, but highlights from North America illustrate a region where naturalists were particularly active in the 19th century. Thomas Bewick's *A General History of Quadrupeds* (1804) is the first truly American book on mammalogy. *The Viviparous Quadrupeds of North America* by John James Audubon and John Bachman (1790–1847) appeared in thirty parts between 1846 and 1854, with original paintings by the former and his son John Woodhouse Audubon; it was one of the last publications by the great American naturalist. Sir John Richardson's (1829–1837) *Fauna Boreali Americana* was a multivolume set with the revealing subtitle "The zoology of the northern parts of British America: containing descriptions of the objects of natural history collected on the late northern land expeditions, under command of Captain Sir John Franklin, R.N.,/by John Richardson, surgeon and naturalist to the expeditions"; the series included a volume on mammals.

Several books dealing specifically with mammalogy appeared during the second half of the 19th century. In the United States, most provided descriptions of mammals from eastern North America that had been known for centuries, to which were added new forms discovered during expeditions to the West. Many follow a typical format. For instance, the first 75 pages of Flower and Lydekker's *An Introduction to the Study of Mammals Living and Extinct* (1891) describe the structure and function of mammals, with emphasis on skeletal and dental traits. The remainder is devoted to accounts of individual mammalian orders. In addition to such general works, some treatises dealt with smaller groups or single species. An example of the former is Coues and Allen's *Monographs of North American Rodentia* (1877). Elliott Coues (1842–1899) later became the first curator of mammals at the US National Museum in Washington, DC. An example of the more specialist works is Morgan's *The American Beaver and His Works* (1868). John Gould's three-volume *Mammals of Australia* was completed in 1863.

Volumes like these raised the level of scientific literacy about mammals, which fed into the great theoretical treatises of the 19th century, including *The Origin of Species*. As the 20th century opened, biology was developing a new identity with a more complicated internal structure, but mammals continued to stimulate scientific questions and hypotheses in the young disciplines of evolution, genetics, ethology, molecular biology, and ecology.

INTEGRATING KNOWLEDGE OF BIOLOGICAL DIVERSITY IN THE 20TH CENTURY

In 1900, Carl Correns (1864–1933), Hugo de Vries (1848–1935), and Erich von Tschermak (1871–1962) derived rules of inheritance very similar to Mendel's and, in the process, brought Mendel's all-but-forgotten paper of 34 years earlier to scientific prominence. These rules would develop into the Mendelian theory of heredity as we understand it today, but were controversial for several decades while they were tested against alternative hypotheses (Provine 1971). Interestingly, the validation of natural selection and Mendelian heredity were closely intertwined during the birth of genetics, a term coined by English biologist William Bateson (1861–1926). As noted above, Darwin's model of selection required a mechanism for transmitting character variation from one generation to the next, while allowing the frequencies of different characters to change as a result of differential reproduction among parents with variable fitness. However, the leading hypothesis of heredity in 1900—*blending inheritance*—posited that deviations from average trait values in a population would tend to be reduced by each generation of mating (they would "regress toward the mean"), making natural selection a weak force at best. As we know today, the genetic bases of phenotypic traits are often more complex than imagined by Mendel, and it took many years for researchers to understand conflicting experimental results from breeding experiments. However, as support for Mendelism solidified, theoreticians such as Ronald Fisher (1890–1962), J. B. S. Haldane (1892–1964), and Sewall Wright (1889–1988) forged mathematical models of natural selection and other evolutionary forces to establish the discipline of *population genetics*, usually dated from Fisher's *The Genetical Theory of Natural Selection* (1930).

During the middle decades of the 20th century, naturalists linked the new genetics to the "species problem" that Darwin had tried to solve. These architects of this

"Modern Synthesis" came from a variety of backgrounds, but common themes in their work were (1) documenting that real species and populations contain much phenotypic (and presumably genetic) variation, and (2) demonstrating that evolutionary forces can explain the patterns of variation observed in nature. Among the most influential were Theodosius Dobzhansky (1900–1975), Ernst Mayr (1904–2005), and George Gaylord Simpson (1902–1984). Dobzhansky (1937) connected the abstract principles of mathematical population genetics to empirical studies of genetic variation, particularly chromosome variation in populations of fruit flies (*Drosophila*). Mayr was an ornithologist who addressed the species problem directly, arguing that species are reproductively isolated populations and showing that patterns of phenotypic variation in wild populations reveal the causes and processes of speciation (Mayr 1942). This emphasis on variation annihilated the essentialism of earlier taxonomists and replaced it with "population thinking." Simpson, a mammalian paleontologist, showed that the theory of natural selection was consistent with long-term patterns ("macroevolution") in the fossil record (Simpson 1944). Mayr (1969) and Simpson (1961) also founded the school of *evolutionary taxonomy*, advancing the principle that Linnaean classification should be based on evolutionary relationships (common ancestry) and **adaptive** divergence of species. We discuss further developments in animal taxonomy in Chapter 2.

The Modern Synthesis was more than an integration of natural history with population genetics; it also gave new life to several disciplines whose questions predated Darwin, but whose content was mostly descriptive prior to the 1900s. One of these was **biogeography**, which went back at least to the work of Prussian naturalist Alexander von Humboldt (1769–1859) on the worldwide distribution of plants. Dobzhansky and Mayr both emphasized the spatial distribution of variation within and between species for understanding evolutionary processes and explaining the geography of life. We take up this topic as it relates to mammals in Chapter 5. The science of embryology was also transformed by evolution. In the early 1800s, Estonian naturalist and *naturphilosoph* Karl Ernst von Baer (1792–1876) discovered the animal blastula and embryonic germ layers, the vertebrate notochord, and the mammalian ovum; he proposed the generalization that vertebrate embryos are more similar at early stages of development than at later stages ("von Baer's Law"). This observation became the focus of much evolutionary theorizing after the *Origin of Species*, including German biologist Ernst Haeckel's (1834–1919) too-restrictive *recapitulation theory* (that embryonic stages of descendant species correspond to adult stages of their ancestors; Gould 1977). The enigma of development persisted through the birth of experimental embryology in the late 1800s until the molecular biology revolution of the mid-20th century led to its modern incarnation as **developmental biology**. The insight of Jacob (1977) that organismal adaptations have the character of evolutionary "tinkering" with developmental programs, which was followed closely

by the discovery of homeotic regulatory genes, inspired the new discipline of evolutionary developmental biology ("evo-devo"; Arthur 2002; Carroll et al. 2005). **Ethology**, the study of animal behavior, arose in the mid-20th century when naturalists such as Austrian zoologist Konrad Lorenz (1903–1986) focused on explaining the adaptive nature of behavior (especially instinctive behavior) in nonhuman animals and how it reflects evolutionary relationships among species (Lorenz 1958). In Chapters 22–24 we explore key topics in mammalian behavior.

The roots of **molecular biology** extend back to microscopic studies of cell structure and the role of chromosomes in inheritance exemplified by the work of T. H. Morgan (1866–1945) on *Drosophila*. Bridges (1916), a student in the Morgan lab, validated the chromosomal theory of inheritance—that is, that genes reside on chromosomes. Subsequent milestones include Beadle and Tatum's (1941) "one gene-one enzyme" principle based on mutational studies of yeast biosynthetic pathways; Avery et al.'s (1944) and Hershey and Chase's (1952) experiments with bacteria and viruses suggesting that DNA is the genetic material; Watson and Crick's (1953) model of DNA structure; the mechanism of DNA replication (see Kornberg 1980); details of the transcription and translation machinery in the late 1950s and early 1960s, which were facilitated by new technology (electrophoresis, ultracentrifugation, electron microscopy); and working out of the genetic code following Nirenberg and Matthaei's (1961) experiments with polyuracil (Moore 1993). These momentous developments (many of which won Nobel prizes) took place outside of mainstream mammalogy, but the parallel development of biotechnology tools such as gel electrophoresis, histochemical staining, restriction analysis, and **DNA sequencing** revolutionized the study of mammal evolution. We describe molecular population genetics and systematics in Chapter 2.

Pre-Linnaean naturalists were well aware that organisms respond to, and shape, their environment in various ways while maintaining stable associations of species in local areas. This was conceptualized as the economy, harmony, or balance of nature, which Linnaeus integrated into his "natural theology" view of a static world divinely engineered for the service of humans (Bowler 1992). Work by Humboldt in the early 1800s prompted widespread interest in the effects of abiotic factors on geographic distributions and local adaptations of species, a theme taken up by Darwin. The discipline of **ecology**—a term coined by Haeckel (1866) to encapsulate his view of species' interdependence in nature's economy—emerged from attempts by field biologists to establish a rigorous approach to studying species-environment interactions. Botanists laid much of ecology's early foundation, including the ideas of an ecological *community* formed by locally interacting species (Warming 1909) and an *ecosystem* comprising a community and the abiotic factors that affect it (Tansley 1935). These plant ecologists explored causal processes underlying communities and ecosystems, as reflected in the debate between advocates of a "super-organism" model in which interspecific

interactions lead to a predictable *climax community* (Clements 1916) and those favoring a random-assembly process restricted by local abiotic factors and preexisting species (Gleason 1917). Elton's (1927) *Animal Ecology* articulated the main ecological questions being pursued by zoologists at the time, including the idea of a species' *niche* as first conceived by Joseph Grinnell (1917). Grinnell (1877–1939) was a distinguished early mammalogist, the first director of the University of California Berkeley's Museum of Vertebrate Zoology, and a graduate advisor to three architects of American mammalogy: William H. Burt (1903–1987), who helped develop the concepts of **home range** and territory; Lee R. Dice (1887–1977), who contributed to knowledge about interspecific **competition** and community structure; and E. Raymond Hall (1902–1986), who conducted extensive research on the taxonomy and distribution of mammals. Along with Cornell University's W. J. Hamilton Jr. (1902–1990), who studied life history traits, this cadre of researchers (Figure 1.8) gave the emerging discipline of mammalogy a firm and lasting connection to ecology.

Meanwhile, from its initial concern with community function, ecology expanded to lower and higher hierarchical levels. Work by A. J. Lotka (1880–1949), V. Volterra (1860–1940), and G. F. Gause (1910–1986) led to models of population growth and regulation, including the roles of density-independent and **density-dependent** factors (e.g., competition, predation). G. E. Hutchinson (1903–1991), E. P. Odum (1913–2002), and H. T. Odum (1924–2002) emphasized the relevance of biogeochemical cycles and energy flow as the engines of ecosystem function. In later decades of the 20th century, the interfaces between ecology, evolution, and genetics became productive areas of research, with progress summarized in landmark works such as Ford's *Ecological Genetics* (1964), MacArthur's *Geographical Ecology* (1972), and Pianka's *Evolutionary Ecology* (1974). At the turn of the millennium, ecology was still a relatively young science, but one with tremendous social relevance in the face of worldwide environmental degradation. Mammalian ecology is the subject of Chapters 24–26.

Modern Mammalogy as an Interdisciplinary Science

Mammalogists study mammals, but what kinds of research questions do they pursue? While mammalogy is firmly rooted in natural history (which, again, is the accumulation of knowledge by observation of organisms in the wild), the discipline has diversified in parallel with the history of biology. Many mammalogists still conduct natural history research, particularly on species in hard-to-reach places about which little is known. This literature includes works on distributions and regional diversity (e.g., Van Dyck and Strahan 2008), biology of major groups (e.g., Dickman and Woodford Ganf 2008), and in-depth analyses of single species (e.g., Coppinger and Coppinger 2016). Although mammals are one of the most thoroughly studied groups, taxonomy continues to be a major theme in mammalogy—including the discovery of new species (e.g., the Madidi titi monkey, *Callicebus aureipalati*; Wallace et al. 2006), revisions of existing genera (e.g., Helgen et al. 2009; D'Elia et al. 2016), and phylogenetic analyses (e.g., Westerman et al. 2016). Often in conjunction with those analyses, mammalogists continue to improve our knowledge of historical biogeography (e.g., Do Amaral et al. 2016) and are at the forefront of the emerging discipline of spatial ecology (e.g., Gonzalez-Borrajo et al. 2016). Mammalogists are active in anatomy (e.g., Cozzi et al. 2016), paleontology (e.g., Berta and Sumich 2017), foraging and nutritional ecology (e.g., Watts and Newsome 2017), endocrine physiology (e.g., Haase et al. 2016), reproductive biology (e.g., Hayssen and Orr 2017), social behavior (e.g., Ortega 2016), habitat selection (e.g., Long et al. 2016), life history studies (e.g., West and Capellini 2016), predator-prey interactions (e.g., Clements et al. 2016), disease biology (e.g., Han et al. 2016), and conservation (e.g., Voigt and Kingston 2016). Indeed, the contents of this book are—we hope—a fair reflection of what modern mammalogists do.

Mammalogy in the 21st century has a character that is distinct from that of previous generations, as is also true
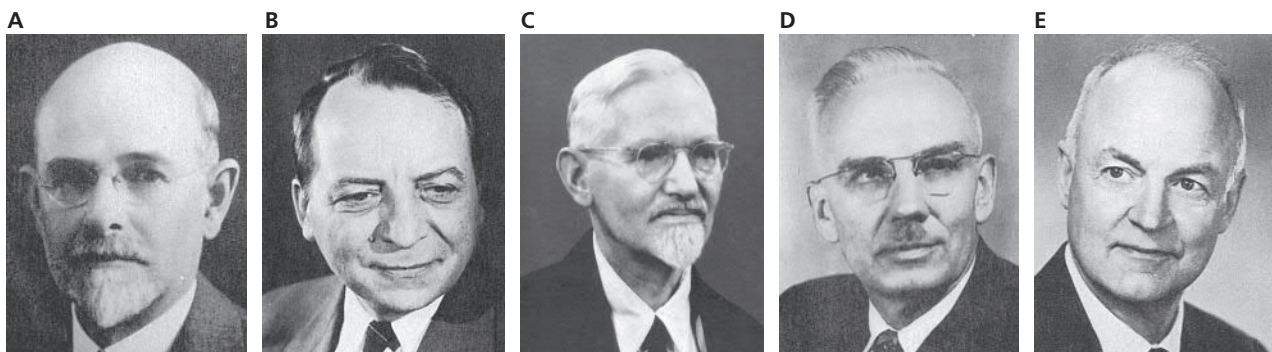

Figure 1.8 **Distinguished mammalogists.** The five men shown here were among a number of professionals who played key roles in establishing mammalogy as a discipline in North America during the 20th century. (**A**) Joseph Grinnell; (**B**) William C. Burt; (**C**) Lee R. Dice; (**D**) E. Raymond Hall; (**E**) William J. Hamilton, Jr.

for other taxon-focused disciplines such as ornithology, herpetology, and ichthyology. Although mammals are mammals, birds are birds, and so on, the interests and training of scientists that study them now go well beyond taxon-specific knowledge. Most mammalogists now have expertise in several of the following subjects: bioinformatics, biomechanics, biotechnology, chemistry, computer science, geography, geology, mathematics, mathematical modeling, physiology, statistics, and wildlife management. Mammalogy today is not so much a discipline in itself, but the intersection of ecology, evolution, genetics, morphology, and systematics with that large branch on the tree of life occupied by amniotes with fur and mammary glands.

Resources for Mammalogists

INFORMATION

We have tried to make this book worthy of the effort required to read it—effort that should be repaid with a foundation of scientific knowledge about mammals appropriate for advanced biology students. But that is not our only goal. Like most areas of science, mammalogy is experiencing a tremendous burst of research activity in the 21st century, resulting in a rapidly changing landscape of questions and answers. That information is found in the primary literature of peer-reviewed research, and we have taken great pains to link this text to it. When you read a statement such as "Competition between gray wolves (*Canis lupus*) and coyotes (*C. latrans*) produced significant **trophic cascade** in a north-central US forest (Flagel et al. 2017)," it is easy to ignore the citation at the end. But we urge you not to do so, at least not always. Wolf management is a significant public policy issue in the United States, such that understanding how wolves affect community dynamics has implications for both science and society. The kernel of knowledge expressed in the quoted sentence represents the result of a multiyear study by five researchers at one university and two state agencies, which was published in the *Journal of Mammalogy* after being critiqued by several other experts in the discipline who were unaffiliated with the work. Science—including mammalogy—is as much about *how* we acquire knowledge as it is about what we think we know. The latter changes frequently, but the former (critical evaluation of evidence) will always be the essence of how we learn about the natural world. To become familiar with it, you must read the primary literature. The peer-reviewed journals cited in the Suggested Readings and References sections of this text are the main outlets for research about mammals. Explore them!

Reading the primary literature is essential, but it is often more work than fun due to the telegraphic style in which research papers are usually written. Fortunately, mammalo-gists are like most scholars in that they like to write books, many of which are comprehensive summaries of knowledge on specific topics written in a narrative style that is much easier to read than a journal paper. If, for example, you want to know more about whales, manatees, or seals, you could consult Berta et al.'s *Marine Mammals: Evolutionary Biology*, 3rd edition (2015). To explore the biology of mammals weighing less than 5 kg, have a look at Merritt's *The Biology of Small Mammals* (2010). Such *secondary literature* sources are a boon to students (including very advanced ones) because their authors have done the hard work of synthesizing the primary literature. You will find many such volumes cited in this text, and there are hundreds more by reputable authors and editors accessible by an online search or visit to the library. If mammalogy is one of your passions, professional reference books are a resource for lifelong learning.

Of course, we live in the internet age, with information of all sorts available with just a few clicks. On the positive side, a careful search can return reliable sources on just about any topic. A gold mine of good information about mammalian (and many other) taxa can be found at the University of Michigan's Animal Diversity Web (ADW) site, animaldiversity.org, the Mammal Diversity Database (mammaldiversity.org), the multi-institutional *Encyclopedia of Life* at eol.org, and many others. On the negative side, there is much more misinformation on the internet than in journals or books. Indeed, you must evaluate web sites critically before trusting their content; Cornell University provides a useful guide at http://guides.library.cornell.edu/evaluating_Web_pages.

EXPERIENCE

The scientific literature provides access to all the knowledge that humanity has accumulated about the physical world, but most of us find that only partially satisfying. Science is an active process, and a good education in science—formal or informal—requires *doing* it. For students from kindergarten to graduate school, the pure experience of science is research—asking a question about nature and pursuing the answer by gathering and critically analyzing data. This is best done under the guidance of a mentor who can help with the sometimes formidable logistical and intellectual challenges. Researchers in mammalogy must be especially careful; because populations of so many species are declining, physical contact with wild mammals is governed by conservation laws in many parts of the world. Many countries also have legal safeguards for the humane treatment of mammals. Sikes et al. (2011) provide guidelines to which many mammal researchers adhere; educational and research institutions often have an institutional animal care and use committee (IACUC) that must approve mammal-handling protocols. This protection, which is prudent, enables students to participate meaningfully in responsible research on mammals. And that experience is priceless, so get some.

But science—especially biology—is not all about disciplined research investigations (though it would not be science

without them). A big part of what we do is *discovery*; this is true for science as a whole, but especially so for individual scientists. When Helgen et al. (2013) announced their discovery of the olinguito (*Bassaricyon neblina*) living in forests of the northern Andes Mountains, it was the first newly recognized species of Carnivora in several decades. That was exciting for all mammalogists, especially Helgen and his colleagues. Indeed, the personal experience of discovery can be deeply meaningful. Pulling dozens of white-footed mice (*Peromyscus leucopus*) out of traps during college produced no discovery new to science, but was a significant learning experience for most of this book's authors. Most mammalogists have similar stories. Nor must personal discoveries be made in a research setting—coming face to face (unexpectedly) with an elk (*Cervus canadensis*) in Yellowstone National Park, seeing a live okapi (*Okapia johnstoni*) for the first time at a zoo, catching a common brushtail possum (*Trichosurus vulpecula*) in a carport in suburban Melbourne, and holding a fossil tooth from the oldest monotreme (*Steropodon*) at the Australian Museum have all been transformative educational moments. Mammals can be observed in wild and not-so-wild places, found with considerable effort or no

effort at all, and appreciated with or without a scientific agenda. Visit wildlife preserves, Association of Zoos and Aquariums–accredited zoos and aquaria, and natural history museums whenever you can, and learn about the mammals you find there.

Finally, mammalogy is a community of scholars. Mammalogists around the world have formed professional societies to support one another and foster growth of their discipline, especially the training of students. The American Society of Mammalogists (ASM; www.mammalogy.org), the Society for Marine Mammalogy (www.marinemammalscience.org), and the Australian Mammal Society (australianmammals.org) are just a few of many examples. There are mammal societies in 12 Central and South American countries, and many others in Europe, Russia, and Asia. Websites for these can be found at www.mammalogy.org/committees/international-relations/mammal-societies. These societies usually meet annually, publish journals, maintain websites, distribute grant funds, contribute to public policy discussions, and play other roles in promoting the study and conservation of mammals. Most have relatively modest membership dues—so join and participate.

SUMMARY

- Mammals are a taxon (Class Mammalia) that can be defined as all descendants from the most recent common ancestor of monotremes, marsupials, and placental mammals. Among living vertebrates, they are unique in having hair, mammary glands, and several other traits (see Chapter 4). They are part of a larger group of amniotes known as synapsids, the nonmammalian members of which are extinct.

- Many key adaptations shared by all mammals are related to endothermy and the relatively large amount of energy invested in offspring.

- Mammals are important components of functioning ecosystems. They are valuable to humans as sources of food, natural products, labor, and companionship, as well as model organisms for biomedical research. Some pose threats as reservoirs for zoonoses or as invasive species.

- Some 20% of recognized mammals species are threatened with extinction due to anthropogenic activities.

- Mammalogy is the scientific study of mammals. Its roots are in the natural history tradition dating back to Aristotle and subsequent authors who observed and recorded information about mammals in the wild. It expanded with European exploration of the world during and after the 16th century, which, among other things, stimulated the development Linnaean taxonomy in the mid-1700s.

- Knowledge of mammalian natural history contributed significantly to the development of evolutionary theory in the

19th century. Prior to this, biologists were essentialists, defining taxa in terms of static characters. Lamarck introduced the first evolutionary theory with a biological basis, though its mechanisms were incorrect. Darwin's *On the Origin of Species* demonstrated the reality of common ancestry and biological change through time, but his proposed mechanism (natural selection) could not be validated until a correct theory of heredity was established in the 1900s.

- Evolutionary biologists in the mid-1900s showed that natural populations included tremendous phenotypic variation that could be explained by the action of evolutionary forces, including natural selection. Such "population thinking" replaced the essentialism of previous centuries: species and higher taxa are defined by their ancestry, not their characteristics.

- The 20th century also saw expansion of other biological disciplines stimulated by evolutionary theory. Of special relevance to mammalogy were biogeography, developmental biology, ethology, molecular biology, and ecology.

- Ecology initially developed with minimal influence from evolution as field biologists transformed the concept of "Nature's economy" into a coherent hierarchical theory of organism-environment interaction at individual, population, community, and ecosystem levels.

- Modern mammalogy is predominantly influenced by evolutionary biology and ecology, but with a growing interdisciplinary emphasis that integrates knowledge and methods

from mathematics, statistics, chemistry, computer science, geography, and management.

• The intellectual development of a mammalogist requires meaningful experience as well as a knowledge base. Research experience is the most professionally relevant, but personal

discovery is also important and can be facilitated by observing mammals in museums, zoos, preserves, and natural settings.

• The science of mammalogy is carried out by a worldwide community of scholars who support one another and the discipline through professional societies.

SUGGESTED READINGS

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DISCUSSION QUESTIONS

1. In the opening paragraph of this chapter, we assert that a mutant offspring of two mouse parents born without hair is a mammal. How does this relate to a popular definition of mammals as "extant amniotes with hair and mammary glands"? A similar question, illuminating for this one, comes from geometry, in which a square is defined as a plane figure with four equal straight sides and four right angles. Suppose you draw a square on a piece of paper, then erase two of the sides and connect the other two with a straight line, making a plane figure with three straight sides and three angles. This new figure looks like—and fits the definition of—a triangle, but it "came from" a square. Is it a square or a triangle? What's the difference between defining mammals and defining geometric shapes?

2. Gray wolves (*Canis lupus*) were part of the natural ecosystem in Yellowstone National Park, but were deliberately exterminated there (and throughout most of the contiguous 48 states) in the 1920s. How would you expect this extermination to affect ecosystem functions? Quite a lot about this case is known, especially from studies following the re-introduction of Yellowstone wolves in 1995. A simple internet search will yield useful information.

3. Natural history is often maligned as "old fashioned" compared to modern experimental biology, and this reputation has affected the value many people attach to expensive institutions such as natural history

museums and the specimen collections they maintain. Do natural history studies still have an important place in science? If you think so, what percentage of the national investment in basic research does natural history deserve? Explain your reasoning.

4. This chapter describes Aristotle, Linnaeus, Cuvier, and Lamarck as great biologists, yet many of their explanations of biological diversity are incorrect according to current understanding. How can individuals who were wrong about so much be great biologists?

5. Taxonomists before Linnaeus and continuing to the present day have tried to identify natural taxa, but with different understandings of what "natural" means in this context. What are some possible ways to define a natural taxon? Again, an internet search will provide access to a large literature on this question.

6. Theodosius Dobzhansky (1973) said, "Nothing in biology makes sense except in the light of evolution." Barry Commoner's (1971:29) "first law of ecology" is that "everything is connected to everything else." Francis Crick (1988) asserted, "Almost all aspects of life are engineered at the molecular level, and without understanding molecules we can only have a very sketchy understanding of life itself." These are powerful statements about the way biologists view the world. How do you see them impacting mammalogy in the past, present, and future?

Methods for Studying Mammals

Like most fields of biology, mammalogy relies on a diverse array of research methods that cross disciplinary boundaries. No single chapter could describe them all, so we present a selection of techniques that are widely used by researchers in different branches of mammalogy. For convenience, we divide this chapter into three major sections: field methods, laboratory and museum methods, and systematic methods. These categories are not disciplinary—a single research project might employ methods from each. For example, a phylogenetic study of a particular group of mammals might begin with field work in which specimens are collected, proceed to museum work in which those specimens are prepared and examined, and culminate with a reconstructed phylogeny, proposed classification, and estimated divergence times for major groups.

An overview such as we provide here will inevitably omit many important topics and lack detail on those that are discussed. Indeed, some of the techniques we describe are complex and scarcely amenable to cursory treatment. Our goal is to present these methods in the context of the research questions they were developed to address. We include extensive references to more thorough and advanced descriptions of each. Of course, no textbook treatment can replace hands-on experience and we strongly encourage mammalogy students to take advantage of any field, laboratory, or data-analysis opportunities associated with their course.

We cannot overemphasize the importance of mathematics and statistics in modern biology. Any student aspiring to a career in mammalogy *must* obtain sufficient training in modeling, probability theory, statistical inference, experimental design, and computing. These topics are too extensive for us to cover here, but readers may consult any number of helpful texts at introductory or advanced levels (e.g., Quinn and Keogh 2002; Morisson et al. 2008; Motulsky 2014; Zar 2010; Gotelli and Ellison 2013; Hector 2015).

Field Methods

Mammalogists often ask such questions as: How many squirrels live in a particular forest or woodlot? What are the sizes and shapes of their home ranges? Does their socio-spatial system include dominance hierarchies or territories? When are the squirrels most active? Answering questions like these usually entails identifying and monitoring individual animals in the field. But most mammals are difficult to observe directly in the wild because they spend at least part of their time in inaccessible places, are active at night, or are simply too small to see easily in their natural habitat. For these reasons, researchers have developed a set of indirect methods for studying mammals in the field.

TRAPPING AND MARKING

Trapping

Methods for capturing wild mammals include a variety of trapping and netting techniques (Wilson et al. 1996; Christman 2010; Hoffman et al. 2010). Whether mammals are live-trapped or killed depends on the nature of the study and the reason for their capture. Although many studies now employ livetrapping, kill-trapping is often necessary and justified. For instance, museum collections maintain reference specimens for taxonomic studies and biotic surveys, but the skin, skeleton, or tissue materials required for such analyses cannot be obtained from live animals. If trapped animals are to be used for a museum collection, it is necessary to ensure that the specimen is not damaged by the capture procedure. Trapping to remove animals, such as pest species, from an area can best be accomplished with kill traps, guns, or poison. Mammal trapping of any sort usually requires permits issued by government conservation authorities and procedures approved by an institutional animal care and use committee (IACUC). Mammalogists must follow standard, legally mandated practices for safe and humane handling of trapped animals, such as those published by the American Society of Mammalogists (Sikes et al. 2011).

Live traps come in several types and sizes (Powell and Proulx 2003). For small rodents, the most widely used are sophisticated Longworth traps, simpler Sherman or Elliott traps made of sheet metal, wire-mesh Tomahawk traps, and newer plastic BioEcoSS TubeTraps (Lambert et al. 2005). For species of intermediate size, such as raccoons (*Procyon lotor*), larger Tomahawk or Havahart traps with wire mesh sides are available (Baldwin et al. 2004). Box traps (Figure 2.1) are constructed for capturing large mammals such as ungulates or carnivorans (Grassman et al. 2005). The dimensions and operations of such traps are adapted to the subject species. Box traps can also be used to capture groups of smaller animals. Rood (1975) used large box traps to capture banded mongoose (*Mungos mungo*) groups

in East Africa, and enclosures have been used to trap groups of ungulates (Kichenside 1998) and primates (Rawlins et al. 1984). Pitfall traps, consisting of a can or bucket buried in the ground, are used to capture very small mammals, such as mice and shrews (Umetsu et al. 2006; Santos-Filho et al. 2015). Pitfall traps are most frequently employed as kill traps, but may function as live traps if checked frequently. Padded leghold traps can be used for medium-large species (Luengos Vidal et al. 2016). Mist nets are often the method of choice to catch bats, particularly when the bats follow a regular flight path to and from their roost (Trevelin et al. 2017). Larger nets, fired by guns, have been used to capture ungulates such as bighorn sheep (*Ovis canadensis*; DeCesare and Pletscher 2006). Kill ("snap") traps used with small mammals include Museum Special, Victor, and McGill types (Stanley et al. 2014). Traps for capturing burrowing mammals include the "harpoon mole," cinch, and Macabee-type gopher traps. Descriptions of these and other special-purpose traps and trapping methods are provided by Martin and colleagues (2001).

Guns that fire tranquilizer darts are often used to immobilize larger mammals (Kreeger 2012). This technique is helpful when animals are held for only a brief period, after which they may be given an antagonist drug to reverse the anesthetic. For example, Lowe and Alderman (2014) anesthetized female moose (*Alces alces*) with darts shot from a helicopter to study the effects of population monitoring on fecundity and recruitment. Auer and coworkers (2010) immobilized red deer (*Cervus elaphus*) with shots from a dart gun to study the effects of different anesthetics during surgery. Dart guns can also be used to catch animals for translocation or captive study (Jessup et al. 2014).

The care of animals captured in the wild and held in captivity has been important since the advent of zoological parks and the use of mammals as laboratory subjects.

Figure 2.1 **Stephenson box trap.** Large box traps of the type shown here are used to capture larger mammals, such as white-tailed deer (*Odocoileus virginianus*). Animals captured in this manner can be measured, tagged, dyed for individual identification, or fitted with collars for tracking by radiotelemetry.

In a landmark volume, Crandall (1964) spelled out many of the procedures to be followed in caring for captive mammals. This topic has become increasingly significant as zoos and wildlife parks expand their mission to include conservation as well as exhibition. Working with captive mammals has enabled us to get a better understanding of their physiology and behavior, information that is critical for management of captive populations (Flacke et al. 2016). Kleiman and colleagues (2010) provide an updated compendium of procedures to care for captive mammals.

Marking

Appropriate marking techniques vary with the species being studied and whether individuals are free-ranging, held in zoos, or are laboratory stocks (Silvy et al. 2012). For techniques used with zoo and laboratory animals, see Kalk and Rice (2010) and Lane-Petter (1978), respectively. Here we are concerned only with free-ranging mammals and those maintained in semi-natural conditions.

In some instances, physical features of individual mammals can be used for identification. Individuals of large-bodied species (e.g., ungulates, primates) can be identified by a profile of observable characteristics such as size, coloration, scars or other marks of injury, and behavior patterns. **Vibrissae** spot patterns have been used to identify individual polar bears (Anderson et al. 2010). This approach is well-developed in studies of cetaceans, many of which show natural color or shape variations on their tail flukes and dorsal fins (Elwen et al. 2014). Such markings can be photographed and the images archived for a permanently accessible record of individual identification (Mizroch et al. 2004). Photographic identification has been enhanced by computerized matching techniques (Torres et al. 2017). Cunningham (2009) used a computer matching system to estimate the size of a harbor seal (*Phoca vitulina*) population.

In species with more cryptic habits and appearances, artificial marking devices are used to identify individuals that have been captured and released. The most common devices are coded metal or plastic ear tags (Tettamanti et al. 2015) or dyes (Michener 2004). Researchers engaged in long-term field studies may give animals permanent brands or tattoos. McGregor and Jones (2016) argued that use of electronic tattoo pens is a minimally invasive technique for marking medium-sized Australian marsupials. Freeze-branding with liquid nitrogen results in permanent white hairs or unpigmented skin where the liquid was applied; this is a common technique for large mammals such as cattle or horses (Turner et al. 2007). Clipping fur patterns and using depilatories to remove patches of hair have been used as marking techniques in several species (Glennon et al. 2002), as have toe clips (Borremans et al. 2015) and ear notching (Ngene et al. 2011). The latter marks may be visible from a distance in larger mammals, particularly with the use of binoculars.

MONITORING

Methods for monitoring the movements of wild mammals may be divided into those that involve tracking physical signs of animals and those that involve radio tagging. Both are widely used, and the choice of method is dictated by the nature of the species studied, the research question, and the cost of conducting the research. Researchers must also ensure that the monitoring procedure does not alter the behavior or survivorship of the animals being studied.

Powder tracking (Lemen and Freeman 1985) involves coating a small mammal with a fluorescent dust; its movements after release can then be traced at night with an ultraviolet light. This technique has been used to study space use (Kraft and Stapp 2013), habitat selection (Long et al. 2013), food hoarding (White and Geluso 2012), and dispersal (Kuykendall and Keller 2011). Bait marking can also be used to assess spatial relations. When small plastic pellets are ingested with bait food, the locations of feces containing pellets mark areas visited by individuals (Kilshaw et al. 2009). Fecal pellet surveys have been used to monitor wild populations of ungulates (McShea et al. 2001), snowshoe hares (Lewis et al. 2011), and rodents (Whisson et al. 2015), while tracking tubes (or tunnels) have been used with smaller mammals (Wilkinson et al. 2012; Stolen et al. 2014). Activity patterns and habitat use in species with low population density, secretive habits, or **nocturnal** activity may be monitored with camera traps (Franco et al. 2011; O'Connor et al. 2017). Aquatic species pose special problems for field monitoring; Churchfield and colleagues (2000) used baited tubes to survey water shrews (*Neomys fodiens*). Field monitoring of wild populations has been revolutionized by DNA markers (see "Genetics and Molecular Techniques" later in this chapter) associated with scat, hair, or other biological residues (Ma et al. 2016).

The use of **passive integrated transponder (PIT)** tags began as a means of identifying individuals in the field (Neubaum et al. 2005), but has developed into an effective monitoring technique for mammals and other vertebrates (Smyth and Nebel 2013). PIT tags are small (1 cm), glass-encased, electronic devices implanted beneath the skin. Each PIT tag contains an integrated circuit with a digital identification code and an antenna that transmits the code when it is activated by the electric field of a transceiver. If an animal is close enough to a transceiver for its PIT to be activated, the tag transmits its code to a data-logging system that identifies the individual. PIT tags are inexpensive and long-lasting; they require no internal battery and can persist safely after implantation for many years. O'Shea and coworkers (2010) fitted nearly 3,000 big brown bats (*Eptesicus fuscus*) with PIT tags for a study of population recruitment patterns in Colorado. Soanes and colleagues (2015) used PIT tags and cameras to monitor the use of road-crossing structures by arboreal marsupials in Australia.

Radiotelemetry has been used extensively in wildlife tracking since the 1950s (Bensen 2010). A radiotelemetry system includes a battery-powered radio transmitter at-

Figure 2.2 **Animal marking.** The Asian elephant (*Elephas maximus*) shown here has a neck collar.

Figure 2.3 **Radio collars.** A variety of radio collars have been developed to use with mammals of different sizes. The collar, battery, and transmitter should not exceed about 10% of the weight of the animal. Thus, with constraints on collar size in smaller mammals, there are often limitations on the size of the battery and, consequently, on both the length of time the transmitter will be functional and the distance over which the signal can be detected.

tached to an individual mammal, the signal of which is detected by an antenna connected to a receiver (Kenward 2000; Millspaugh et al. 2012a). Transmitters can be placed in collars (Figures 2.2, 2.3) or implanted; receiver antennae may be handheld, mounted (on ground vehicles, aircraft, or towers), or on satellites. The receiver translates the signal into audible sound or stores it digitally for analysis. The position of an animal is determined by triangulation using two or more bearings taken with one antenna moved to different locations or multiple fixed antennae at different locations (Millspaugh et al. 2012b).

In addition to pinpointing the locations of specific animals, radiotelemetry can be used to assess ecological traits in the field, including dispersal and home range (Fey et al. 2016; Figure 2.4), habitat use (Aarts et al. 2008), **homing** behavior (Lawes et al. 2012), and survival (Wittmer et al. 2016). For example, Hauver and colleagues (2013) used radio collars and genetic assays to study the role of space use in the mating systems of raccoons (*Procyon lotor*). Radiotelemetry allowed Hardman and coworkers (2016) to monitor survival of two species of reintroduced hare-wallabies

(*Lagorchestes*) in Western Australia and demonstrate that feral cats were responsible for all mortality of monitored individuals. Physiological measurements such as body-core temperature and heart rate can also be relayed by transmitters (Zervanos and Salsbury 2003; Dechmann et al. 2011) to assess activity levels and energy expenditures.

A **geographic information system (GIS)** is computer software used to store, manipulate, and analyze spatial data (Demers 2009; O'Neil et al. 2012; Wegman et al. 2016). First developed in the 1970s (Tomlinson et al. 1976), GIS implementation involves taking data from maps, aerial photographs, satellite images, ground surveys, and other sources and converting them to digital format. Geographic data include spatial coordinates, topography, environmental variables, locations of discrete objects, or virtually anything that can be displayed on a map. The data are integrated, analyzed, and visualized with software, and GIS databases are now available for much of the world. The **global positioning system (GPS)**, derived from navigation satellites developed by the US Department of Defense in the 1970s, uses satellite radio signals to pinpoint
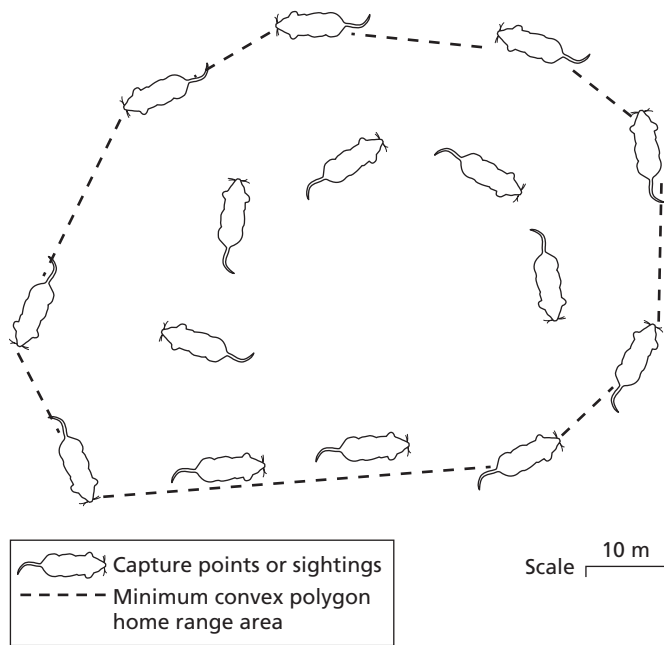
Figure 2.4 **Home range.** The home range of a mammal can be plotted from a series of radiotransmitter locations. Home-range area can vary with the age, sex, season, population density, and reproductive condition of the animal.

the latitude, longitude, and elevation of a receiver on the ground (Levitan and Harte 2016). GPS information can be stored for subsequent analysis, frequently in conjunction with GIS data.

Remote sensing technologies, including GIS and GPS, have developed rapidly during the past 40 years, and their application in mammalogy has expanded (Franklin 2009). They are often used to study home range (Ramanankira-hina et al. 2016), population density (O'Kane et al. 2014), movement patterns (Porter and Garber 2013), predation (Sand et al. 2005), and habitat use (Reisland and Lambert 2016). De Souza and colleagues (2015) recorded roadkill mammals along a highway through Brazil's Pantanal wetland, importing GPS coordinates of carcasses into a GIS system and discovering a tenfold increase in vehicle-wildlife collisions between 2002 and 2012, particularly in lowland areas during high-water periods. Although radiotelemetry and GPS are powerful technologies, the equipment is somewhat costly. As a result, GPS researchers may be forced to monitor fewer individuals than are typical of physical tracking studies; development of low-cost systems is an active area of research (Zucco and Mourao 2009).

Methodological and statistical problems can complicate the collection and analysis of radiotelemetry data. As noted above, the transmitter should not interfere with an animal's normal activity, nor should the animal's behavior be affected by the capture, handling, and attachment procedures (Golabek et al. 2008). Rasiulis and colleagues (2014) found that heavy transmitter collars reduced annual sur-

vival by 18% in a population of migrating caribou (*Rangifer tarandus*). Electrical lines or environmental obstacles (e.g., hills, trees) between the antenna and the transmitter may cause inaccurate triangulation. **Autocorrelation** occurs when locations ("fixes") are obtained too close together in time, such that each location is strongly dependent on the previous one. Such lack of independence among data points causes home-range size to be underestimated. The appropriate interval between locations depends on the behavior pattern of the species studied, which in turn may be affected by environmental variables. Planella and coworkers (2016) showed that increasing the interval between GPS recordings (10, 20, 40, and 60 minutes) causes a corresponding reduction in detection rates of wolves in northeastern Spain.

Data obtained from trapping, marking, and monitoring are especially important for studying habitat use and biotic diversity (Buckland et al. 2001; Goad et al. 2014). One of the most common approaches is a **mark-recapture study** in which individuals from a population are captured, marked, released, and recaptured later (Krebs 2013). Recapture rates can be used to estimate demographic parameters, reproductive patterns, and home-range size (Dracup et al. 2016). Population size can be estimated from such data with several methods—Lincoln-Petersen (Lincoln 1930; Peterson 1896), Schnabel (1938), Chapman (1954), Jolly-Seber (Seber 1982), and others—which differ in their assumptions and statistical properties (McCrea and Morgan 2014). Analysis of mark-recapture data may be complicated by the assumption that all members of a population are equally catchable. This assumption is violated if, for instance, animals of different sexes or ages have different capture probabilities. In addition, some individuals become more catchable after repeated captures ("trap happy") or avoid traps after initial capture ("trap shy"). The impacts of "catchability" and other parameters on estimates of population parameters have been incorporated into statistical models of the trapping process (Hammond and Anthony 2006) and implemented by analytical computer programs such as CAPTURE (Otis et al. 1978) and MARK (White and Burnham 1999). Grimm and colleagues (2014) explored the performance of several such models in estimating the size of a well-studied population.

OBSERVATIONAL METHODS

Many mammals can be observed directly in the wild, particularly those that are large and live in open habitats. **Diurnal** species are easiest to observe, but nocturnal mammals can be viewed with night-vision scopes (Rancourt et al. 2005) or infrared imaging (Betke et al. 2008). Watching mammals provides data on life history characteristics such as movements, habitat use, foraging, territoriality, reproduction, and interspecific interactions. Behavior, both

individual and social, is most commonly recorded using observational methods.

Basic methods for making observational records have been summarized by Altmann (1974), Crockett and Ha (2012), and Dawkins (2007). The choice of observational sampling technique should be based on what information is needed and what behavioral activities can be seen and recorded. Behavior can be variable in the same individual over time and among individuals. Thus, a well-formulated hypothesis and appropriate experimental design are important considerations in selecting an observational method. Observations can be made with the unaided eye, through binoculars or telescopes, with still photographs, or with video recording. The latter has proven especially valuable because it allows multiple observers to study one observational sequence repeatedly and in slow motion.

Some observational sampling techniques record only behavioral *states* (general categories of behavior) such as "grooming" or "feeding", while other methods note *events* (specific brief actions) such as a "yawn" or "tail flick"; some methods record both. The two most common methods of observational sampling are focal animal and scan sampling. **Focal animal sampling** is the recording of specified behavior states or events by a given individual (or group) in bouts of prescribed length (Figure 2.5), sometimes with video technology. Kolowski and colleagues (2007) observed Kenyan spotted hyenas (*Crocuta crocuta*) in 2- or 15-hour bouts to determine daily activity patterns, movements, and den use. They found that females whose territories included areas with livestock grazing were less active and showed less den use than those in undisturbed territories.

Figure 2.5 **Social interaction among Barbary macaques on Gibraltar.** Focal animal sampling can be used to examine interactions among members of a group. Watching a single individual for a prescribed time period provides an accurate picture of its activities. In the case shown here, two individuals are engaged in grooming behavior.

Scan sampling involves recording the behavioral state (e.g., resting, grooming, moving) of each animal in a small group at predetermined intervals (such as every 15 seconds) or over a predetermined block of time (such as 30 minutes). Bearzi (2006) used scan-sampling to study feeding associations between groups of dolphins and California sea lions (*Zalophus californianus*) in Santa Monica Bay, California. Data were recorded on the behavior of all individuals in dolphin groups during observation periods of >25 min. Together with observations on the proximity and behavior of nearby sea lions, Bearzi (2006) concluded that sea lions follow and exploit the superior food-finding ability of dolphin groups. This study also employed video recording, GPS monitoring, and GIS analysis. Scan sampling and focal animal sampling are often used together. In a study of how ungulates use natural licks in British Columbia, Ayotte and coworkers (2008) used scan sampling every 15 minutes during 6-hour bouts to count the numbers of individuals of 4 species present at specific licks and focal animal observation to record behaviors of single individuals. Hirschler and coworkers (2016) found that focal-animal and scan sampling produced significantly different estimates of vigilance behavior in a population of prairie dogs (*Cynomys gunnisoni*).

Other observational methods include instantaneous sampling (sequentially recording the behavioral state of an animal at the end of each observation interval), all-occurrences sampling (recording all occurrences of a particular event in a group of animals), and *ad-libitum* sampling (recording all the states or events of all organisms in a group). Such methods are described in more detail by Altmann (1974) and Dawkins (2007). In addition to passive observation, researchers may use sound playback to test hypotheses that involve vocalizations. In this method, calls that have been recorded are played to animals in particular situations, and the animals' reactions are monitored. For example, Demartsev and colleagues (2016) used playback of the "snort" component of male rock hyrax (*Procavia capensis*) songs to demonstrate that this harsh sound produced distinct vocal responses from **conspecifics.**

A key issue that arises in observational studies, regardless of sampling method, is the **observability** of animals under study. "Observability" has two meanings in behavioral research. In the first sense, it refers to whether the habitat permits regular, direct observation of an animal. Topography and vegetation can interfere with an investigator's ability to observe terrestrial or arboreal mammals, and observability issues are especially challenging for marine species (Nowacek et al. 2016). A second meaning of "observability" is that some individuals may be more conspicuous than others, perhaps depending on their age, sex, dominance status, or physiological state. For example, observability of white-tailed deer (*Odocoileus virginianus*) in Oklahoma declined with increasing predation risk from human hunters, suggesting that early season hunting will maximize harvest rates of this common game species (Little et al. 2014).

Laboratory and Museum Methods

PHYSIOLOGICAL MEASURES

Physiology is the study of how tissues and organs function. The scope of this discipline, even if restricted to mammals, is extremely broad, as is the range of experimental methods that physiologists employ. Modern animal physiology encompasses molecular, cellular, and biochemical processes in addition to the more traditional whole-organism approaches of previous decades (Hill et al. 2016). Mammalogists have focused on a smaller, but still diverse, set of topics including nutrition, energy metabolism, reproduction, behavior, sensory mechanisms, growth, locomotion, disease, stress, and water balance. An overview of methods employed in the first three of these areas illustrates how mammalogists approach the study of physiology.

Nutrition

Nutrients are substances that an animal must obtain from its diet to serve as raw materials for energy production, growth, and other metabolic functions. Nutrients include water, proteins, lipids, carbohydrates, nucleic acids, fiber, salts, vitamins, and trace elements. **Nutritional requirements**, both the quantity and kinds of nutrients, may vary significantly among species and individuals in different physiological states. For this reason, it is difficult to determine the precise nutritional requirements of a species, though it is usually possible to identify major dietary components. Dietary preferences of wild mammals are usually determined by direct observation or examination of scats and stomach contents. Stomach content analysis provides a more complete assessment of diet if a sufficient number of individuals can be examined, but field mammalogists more often analyze scats to estimate dietary preferences (Wiens et al. 2006) because it is nondestructive and non-invasive. Although only partially digested food items can be identified by visual inspection, DNA typing can also be used to identify prey in fecal samples (Casper et al. 2007). Traditional dietary classification is based on the primary trophic level occupied by a species (i.e., herbivore, carnivore, omnivore). However, these categories conceal considerable variation in food types that significantly affect a species' functional role in an ecosystem. Pineda-Munoz and Alroy (2014) proposed a more fine-grained classification of mammal diets based on volumetric analyses of stomach contents from 139 terrestrial species in 13 therian orders (Table 2.1). This scheme, based on primary (>50% of gut contents) and secondary (20%–50% of gut contents) food types, recognizes dietary generalists (<50% gut contents of any single food type) and 22 categories of specialists. For example, a species that consumes 60% invertebrate and 40% vertebrate food is an "insectivore-carnivore." The distribution of species among categories demonstrates that although most terrestrial mammals are specialists, most also have mixed diets. The authors argue that the traditional category of omnivore, in particular, is too vague to be useful in research on terrestrial food webs.

Researchers are frequently interested in assessing the **nutritional condition** of wild mammals (Sinclair et al. 2006) as a means of understanding how food limitation influences population dynamics. Nutritional condition is a composite of several variables that reflect how well an animal has assimilated the raw materials for metabolism, and it can be indexed by external body measurements, urine chemistry, assays of electrical conductivity, or direct chemical analyses. Cook and colleagues (2004) assessed the nutritional condition of female elk in Yellowstone National Park using three measured variables: body fat, body mass, and thickness of the *longissimus dorsi* muscle. The body fat index was a function of a "rump body condition score" and "subcutaneous rump fat thickness," the latter measured with **ultrasound** imaging. Ultrasonography was also used to measure thickness of the *longissiumus*, an index of protein catabolism. Body mass was a function of chest girth circumference, body fat percentage, age, and pregnancy status. Cook and coworkers (2004) found that nutritional

Table 2.1	Dietary classification of terrestrial mammals based on analysis of gut contents	
Food Type	**Primary Diet (>50% of food)**	**Secondary Diets (20–50% of food)***
Vertebrates	Carnivore	—, frugivore
Invertebrates	Insectivore	—, carnivore, granivore, herbivore, frugivore
Green plants	Herbivore	—, mixer, frugivore, granivore, insectivore
Seeds	Granivore	—, herbivore, insectivore
Fruit	Frugivore	—, herbivore, gumnivore, insectivore
Fungus	Fungivore	—, herbivore
Flowers-gum	Gumnivore	—
Multiple food types	Generalist	<50% of any single food type

Based on Pineda-Munoz and Alroy (2014).

*"—" indicates specialist in a single food type.

condition was independent of age in Yellowstone elk, but strongly related to lactational status and pregnancy. They suggested that nutritional limitation during severe winters is a major density-dependent factor limiting elk populations. Researchers have also developed methods that use electrical conductivity to estimate fat reserves in live animals, including bioelectric impedance analysis (Pitt et al. 2006) and total body electrical conductivity (Wirsing et al. 2002). Franco and colleagues (2017) correlated blood levels of the hormone leptin with body fat in the monito del monte (*Dromiciops gliroides*), showing that the nutritional condition of this South American marsupial is at a minimum during the energetically demanding stage of sexual maturation in the austral summer. Lipid and protein contents can also be assayed by direct chemical analysis of dried carcasses if **destructive sampling** is feasible.

Metabolism

Metabolism is the sum total of all chemical reactions taking place in an organism. The rate of these reactions is affected by body temperature, body mass, muscle activity, and other energetic demands of life. Thus, the metabolic rate—the amount of heat energy released per unit time, usually expressed as kilojoules per day (kJ/d)—of a mammal is a fundamental consideration in studies of thermoregulation, hibernation, torpor, locomotor performance, foraging, and reproductive behavior. Mammalogists are concerned with two measures of metabolism: **basal metabolic rate (BMR)** is the rate of energy conversion in a resting animal, with no food in its intestine, at an ambient temperature that causes no thermal stress; **field metabolic rate (FMR)** is the rate of energy use in an animal engaging in normal activities under natural conditions (Hill et al. 2016). FMR is typically higher, more variable, and more difficult to measure than BMR.

BMR is commonly determined in the laboratory with a respirometer, a device that measures the rate of oxygen and carbon dioxide exchange during normal breathing (Lighton 2008). This approach exploits the direct relationship between oxygen consumption and energy production by aerobic respiration. A test animal is confined to an air-filled chamber for a specified period during which the amount of oxygen in the chamber is monitored. In a closed chamber, aerobic respiration causes a decrease in O_2 concentration and an increase in CO_2 from their initial (atmospheric) values. The difference between initial and final concentrations of O_2 (oxygen consumption), standardized to one hour of respiration, measures BMR in units of ml O_2 per hour. Open chamber respirometers are also widely used, but the estimation of BMR is slightly more complicated. Because body mass and BMR are correlated, oxygen flux is typically standardized by the organism's weight; *mass-specific* BMR is expressed as ml $O_2/(g/h)$. The relationship between body mass and BMR has fascinated vertebrate physiologists for over a century, after it was shown

that the two variables are related by an **allometric** power law, BMR $= a M^b$. In this equation, *a* is a scaling constant, M is body mass, and *b* has been estimated as the slope of a log-log regression line of BMR on M (Capellini et al. 2010). The predictive value of the allometric equation, and the key to understanding its biological meaning, lies in the value of *b*. Since the work of Kleiber (1932), who regressed BMRs from a sample of mammal species onto corresponding values of body mass, $b = 0.75$ has been widely cited. However, such studies assume that species are independent data points, an assumption violated by phylogenetic relationships (Felsenstein 1985b). Statistical methods can now account for this nonindependence by performing correlation analyses on a phylogeny. White and coworkers (2009) and Capellini and coworkers (2010) performed such phylogenetically informed regression on mammalian BMR data and found that the value of the scaling exponent varies significantly ($b = 0.48$ to 0.82) among major lineages (Figure 2.6); this suggests that no single value applies to all mammals. Thus, the allometric relationship between BMR and body mass has evolved. We explore the biological interpretation of metabolic scaling in Chapter 8.

The most popular method for measuring mammal FMRs involves use of "doubly labeled water" (DLW; Speakman 1997), often in combination with studies of physiological water flux. Water molecules with radioisotopes of oxygen (^{18}O) and hydrogen (deuterium or tritium) are injected into an animal, and repeated blood samples are taken at intervals of hours or days. Loss of isotopic oxygen in blood over time is related to rate of CO_2 loss (L/d), which in turn is proportional to metabolic rate (kJ/d). Williams and colleagues (1997) used this technique to measure seasonal variation in metabolic rates of South African aardwolves. During summer, the average aardwolf produced 112.5 L of CO_2 per day, or 2891.2 kJ/d of energy; in winter the corresponding values were 71.8 L/d and 1844.8 kJ/d. These are significantly lower than values predicted for other eutherians of comparable size, but mirror the reduced FMRs characteristic of most myrmecophagus (ant- or termite-eating) mammals (McNab 1984), including the marsupial numbat (Hume 2003). Munn and colleagues (2016) used DLW to show that FMRs of western grey kangaroos (*Macropus fuliginosus*) were less than half that of comparably sized merino sheep (*Ovis aries*). Given that the two species compete for food when they co-occur, this suggests that native kangaroos exert lower grazing pressure than do introduced sheep.

Reproduction

Because production of progeny is a basic measure of individual fitness and important to understanding population dynamics, much attention has been given to mammalian reproductive biology. Data on the number of females producing young, litter size, and juvenile survivorship provide the basic information for studies of population growth.
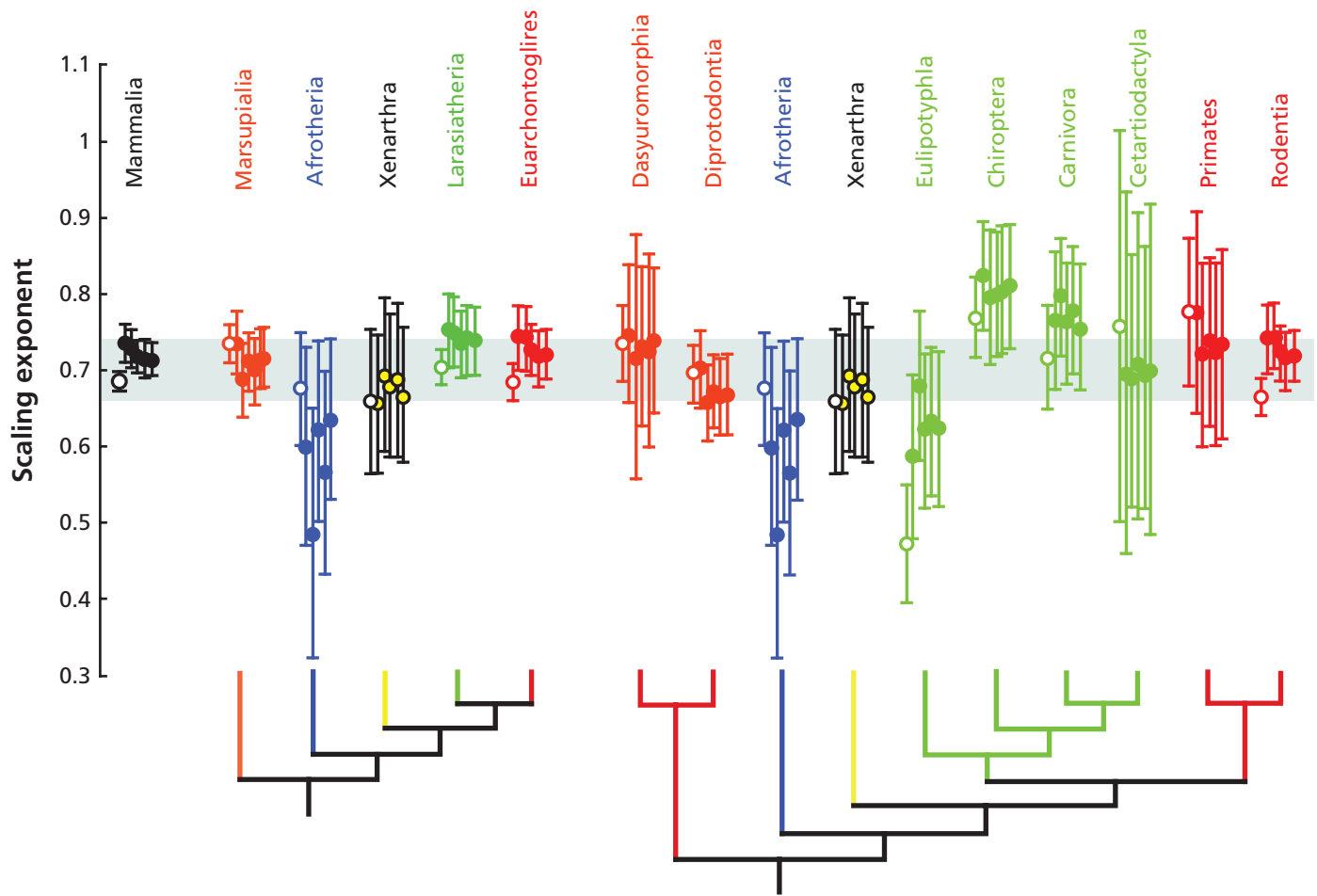
Figure 2.6 Lineage-specific variation of basal metabolic rate scaling exponents. The horizontal dimension accommodates an estimated phylogeny of mammalian orders; the vertical dimension shows values of the exponent b in $BMR = aM^b$ estimated with phylogenetically informed regression for individual groups on the tree. Shaded region indicates the range of b (0.67–0.75) usually reported from nonphylogenetic analyses. *Adapted from White et al. (2009).*

Numerous techniques have been developed for assessing the reproductive condition of males and females.

For many male mammals, the testes are only scrotal just prior to and during the breeding season; thus, determining whether the testes of an individual are scrotal ("descended") or abdominal provides an important clue to its reproductive status. In male marsupials, reproductive maturity is marked by spermatorrhoea, the discharge of sperm into the urine (McAllan 2003). The weights of testes and accessory sex glands are also useful indices of reproductive activity (Morrow et al. 2016; Murphy et al. 2005). Sperm count and sperm morphology, assessed by microscopic examination of ejaculates, provide data on numbers of spermatozoa and the proportion of defective or abnormal sperm (Tannenbaum and Beasley 2016). Levels of reproductive **hormones** also reveal male reproductive status and can be measured by **radioimmunoassay** (**RIA**), a technique that uses radioactively labeled antibodies to bind and quantify amounts of specific proteins (e.g., androgens) from samples of body fluids (de Souza Ameral et al. 2009). Testosterone levels vary seasonally but also exhibit changes due to stress,

aggression, dominance status, sexual stimulation, and overall health.

Most female mammals also breed seasonally. A first step in assessing female reproduction is detection of estrus, the period during which a female is behaviorally and physiologically receptive to mating attempts. Estrus is the result of hormonal changes associated with the maturation of ovarian follicles and subsequent release of ova. During estrus, females tolerate mating solicitation by males; they may adopt a lordosis posture with the head and hindquarters elevated, and back depressed to permit intromission. One consequence of the increase in circulating estrogens during estrus is cornification of cells that line the vaginal walls. Vaginal epithelial cells obtained with a moist swab can be examined under a microscope, with appropriate histological staining, to provide an indication of whether the animal is, or has recently been, in estrus (Akinloye and Oke 2014).

Ovulation rate, the number of ova released at the onset of estrus, can be determined in live animals by flushing the reproductive tract immediately after ovulation. If the animal is sacrificed, ovaries can be examined histologically to assess
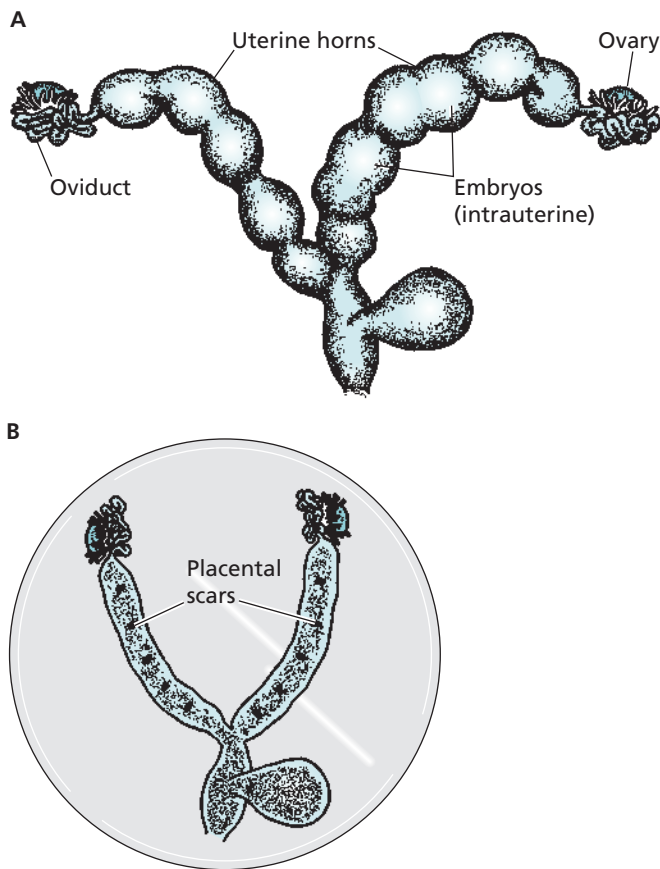
A

B

Figure 2.7 **Indications of pregnancy.** (**A**) The swellings in two uterine horns are from a pregnant white-footed mouse; each swelling represents a fetus and associated placenta. (**B**) The uterine horns, dissected from the abdominal cavity, are compressed between the bottom and inverted top of a Petri dish, revealing the placental scars along both horns. This information can be used to determine the number of embryos that implanted in the uterus.

follicular development and check for the corpora lutea ("yellow bodies"), the remnants of ruptured follicles (de Bruin et al. 2012). Counting placental scars (Figure 2.7) in the uterus indicates the number of fetuses that implanted during the most recent pregnancy (Fournier-Chambrillon et al. 2010).

In living female mammals that must be examined repeatedly, several other procedures can be employed to assess reproduction. **Laparotomy** is a surgical examination of the reproductive tract to determine the condition of the ovaries and uterus (Green et al. 2002). With the invention of fiber-optic techniques, laparotomy can be replaced by **laparascopy** (Schulman et al. 2015). For larger mammals, ultrasonography can be used to examine the morphology of the reproductive tract and check for the presence and condition of developing fetuses (Domingues et al. 2007; McNay et al. 2006).

We can use RIA or enzyme-linked immunosorbent assay (ELISA; Nelson and Kriegsfeld 2016) on blood samples to determine circulating levels of female reproductive hormones such as estrogens, progesterone, and prolactin (Norris and Lopez 2010). It is also possible to assay hormones in urine and feces (Asa et al. 2007; Bourke et al. 2011; DeMatteo et al. 2006). This noninvasive technique has been applied to both males and females, and it allows investigators to obtain hormone measurements on free-ranging mammals.

STABLE ISOTOPE ANALYSIS

Mammalogists, archaeologists, paleontologists, and ecologists now exploit technology that allows study of isotope ratios for key elements in biological tissues. Much of this research has focused on animal diets, habitat properties and preferences, dispersal, and migration (Ben-David and Flaherty 2012), though applications in other areas are numerous and diverse. Isotopes are atoms of a particular element that differ in their numbers of neutrons and, hence, atomic masses. The nuclei of radioisotopes are unstable and emit gamma rays or subatomic particles ("radiation") when they decay. In contrast and as their name implies, **stable isotopes** are long-lived and do not emit radiation. Radioisotopes have a long history of use in biotechnology and medicine (e.g., X-rays), but study of stable isotopes has expanded dramatically in recent decades. Most ecological studies involve isotopes of carbon, nitrogen, oxygen, hydrogen, sulfur, and a few other elements that play major roles in tissue structure or metabolism.

Although isotopes of the same element participate in the same kinds of chemical reactions, their behavior in those reactions varies as a function of their differing atomic masses. For example, water molecules with hydrogen (^1H) evaporate more readily than those with deuterium (^2H) because hydrogen bonds between water molecules are weaker than deuterium bonds. The distinctive behavior of isotopes extends to physiological reactions, including those mediated by enzymes. Typically the lightest isotope of a particular atom is most abundant in nature, but the actual ratio of heavy to light isotopes in a particular specimen depends on the physical and chemical processes by which the specimen formed. The change in isotopic ratios as reactants are metabolically converted to products, known as "fractionation" or "discrimination," is why ratios in a product (e.g., animal tissue) can be used to infer the source of reactants (e.g., food types) or the processes by which the product formed (Sulzman 2007).

Consider two isotopes of carbon, ^{12}C and ^{13}C, and the ratio (R) between them in a particular tissue sample: $R_{sample} = {^{13}C}/{^{12}C}$. To establish a common currency of isotopic ratios, values for an actual sample are compared to those of an international standard or proxy thereof. For example, the standard ratio (R_{std}) for carbon is that recorded from the Vienna Peedee Belemnite rock formation (Ben-David and Flaherty 2012). The isotopic value of a particular sample is calculated as a fractional deviation (δ) of the sample ratio from that of the standard, expressed in parts per thousand (‰):

$$\delta^{13}C = (R_{sample} - R_{std})/R_{std} \times 1000.$$

Samples for which ratios exceed standard values are said to be enriched in the heavier isotope; those with ratios below standard values are depleted (and have negative δs). Isotope ratios of tissue samples are measured with mass spectrometry.

To illustrate the application of stable isotope analysis in mammalogy, we focus on estimating the components of an individual animal's diet. Suppose our focal animal is a carnivore (e.g., a wolf) and its prey are two species of herbivores (e.g., moose and elk). A seemingly straightforward question is, "What percentage of the wolf's diet consists of moose versus elk?" One approach is to watch the wolf feeding, but this would require many hours of observation to obtain meaningful percentages. Alternatively, we could examine stomach contents or excreta, but these data would require either sacrificing the wolf or collecting and analyzing many scats; in both approaches, it may difficult to distinguish accurately between moose and elk tissues. Stable isotope analysis exploits the different isotopic values (e.g., $\delta^{13}C$) of prey that have distinctive diets—in this example, moose and elk might differ in the proportions of C_3 and C_4 plants they consume. Because the wolf's only source of dietary carbon is its food, its isotopic ratio ($\delta^{13}C_{wolf}$) is a function of the fractional contributions from each prey type:

$$\delta^{13}C_{wolf} = f_{moose}\delta^{13}C_{moose} + f_{elk}\delta^{13}C_{elk}.$$

Here f_{moose} and f_{elk} are the dietary fractions of moose and elk, respectively, and sum to 1. The equation above represents a mixing model that can be solved for f-values given experimentally determined $\delta^{13}C$s (Phillips 2012). In practice, estimating dietary fractions usually involves multiple isotopes (e.g., $\delta^{13}C$ and $\delta^{15}N$), accounting for isotopic enrichment by trophic level, and quantifying sources of uncertainty to provide confidence intervals on estimates.

An instructive example of this method is Yeakel and colleagues' (2009) study of the famous man-eating lions of Tsavo, Kenya—subject of the 1996 Hollywood film *The Ghost and the Darkness*. These two male lions were responsible for killing a considerable number of railroad workers in the Tsavo region in 1898, a period of drought and rinderpest epidemic that depressed native herbivore populations (Patterson 2004). Both lions were eventually shot and their remains transferred to the Field Museum of Natural History in Chicago, Illinois. Popular accounts of their history placed the number of human victims between 28 and 135, but examination of historical documents and the museum specimens led Peterhans and colleagues (2001) to endorse the lower end of this range. Yeakel and coworkers (2009) used $\delta^{13}C$ and $\delta^{15}N$ from the man-eater specimens, modern lions, 8 potential ungulate prey species, and late 19th-century human remains from the Tsavo region to reconstruct the man-eaters' dietary proportions; $\delta^{13}C$ and $\delta^{15}N$ values were obtained from collagen in bone, a tissue that is replaced relatively slowly and therefore records dietary contributions over many years. Isotope values in man-eaters were also obtained from keratin in hair, a rap-

idly replaced tissue that recorded dietary intake during the final 3 months of life (the end of the period during which the lions took human prey). Using a statistical mixing model, Yeakel and coworkers (2009) estimated that both lions preyed primarily on grazing ungulates throughout most of their lives, but hair keratin ratios reflected intake of human tissue during the final three months. Interestingly, just one of the lions was responsible for most human victims. Given basic assumptions about lion feeding habits, Yeakel and coworkers (2009) estimated that this individual took 24.2 human victims, with the other accounting for 10.5. These estimates support the lower values of human death toll from historical accounts and illuminate the extent to which individual carnivores adjust their diets in times of food scarcity.

GENETICS AND MOLECULAR TECHNIQUES

For most of its history, mammalian biology focused on studying whole animals or their preserved remains. As understanding of the biochemical basis of heredity progressed throughout the 20th century, however, sophisticated laboratory methods were developed to assay variation in chromosomes, proteins, and nucleic acids. Mammals have been a central group in such research since its inception (Wahrman and Zahavi 1955; Harris 1966; Avise et al. 1979), and the use of "molecular markers" has allowed mammalogists to develop new and powerful approaches to the study of population genetics, speciation, and phylogeny.

Chromosomes

The study of mammalian cytology involves visualization of chromosomes obtained from cells in the metaphase portion of mitotic division (Hsu 1979). At this stage, the chromosomes are condensed (i.e., DNA is tightly wound around nucleosomes within sister chromatids) and appear as rod-shaped structures when viewed under a light microscope. Typically, photomicrographs of mitotic spreads are edited for publication such that chromosomes from an individual cell are arranged in order of size. Such an image is termed the **karyotype** of a cell. The karyotype is usually the same for all cells of an individual (unless mutations have occurred), but sometimes shows variation (polymorphism) among individuals from the same species. Karyotypes often vary considerably among species, and such variation may provide insights into chromosome evolution (Kawada et al. 2008).

Karyotypes contain two major types of information: the diploid (2N) number of chromosomes within a cell and the morphology of each chromosome. A chromosome's morphology is described by its size, pattern of secondary constrictions, and position of its centromere—metacentric if
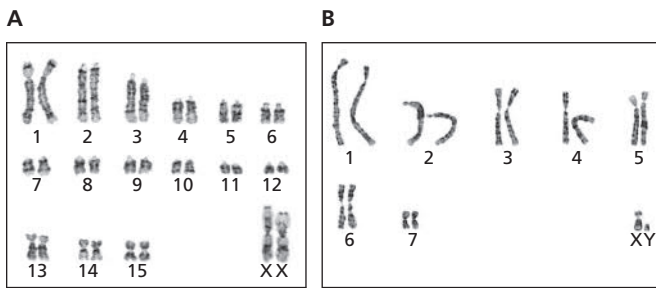
Figure 2.8 **G-banded karyotypes of marsupials.**
(**A**) Rufous bettong (*Aepyprymnus rufescens*); (**B**) tammar
wallaby (*Macropus eugenii*). The chromosomes are arranged in
homologous pairs and numbered sequentially from largest to
smallest.

the centromere is at the center of the chromosome, acrocentric if the centromere is closer to one end (Hartwell et al. 2011). More detailed information about the chromosomes can be revealed by differential staining. One procedure, named after the chemical dye Giemsa, produces "G-bands" on chromosomes; the dark-staining bands correspond to DNA regions that are low in guanine (G) and cytosine (C) nucleotides, and usually contain few genes. The G-banding pattern of each pair of homologous chromosomes in a cell is unique (Figure 2.8). Similarly, "C-banding" reveals areas of repetitive DNA sequences associated with centromeres (Krebs et al. 2013).

Diploid numbers of mammals range from 2N = 6 in the Indian muntjac deer (*Muntiacus muntjak*) (Graphodatsky et al. 2011) to 2N = 102 in the plains viscacha rat (*Tympanoctomys barrerae*) (Contreras et al. 1990). Within groups, karyotypes may be highly conserved (e.g., dasyurid marsupials, felids) or highly variable (e.g., **diprotodontian** marsupials, canids, gibbons). Where karyotypes of closely related species differ, they can usually be related to one another by simple rearrangements such as fusions, fissions, inversions, and translocations. Indeed, careful comparison of morphology and banding patterns may reveal the evolutionary history of rearrangements within a group (Dobigny et al. 2017).

During the past three decades, **molecular cytogenetics** has exploited the **in situ hybridization** technique to map the locations of specific DNA sequences on chromosomes (Fan 2010). In this method, a single-stranded DNA fragment of known sequence (the probe) is "labeled" with a radioisotope or biotin molecule that will allow it to be visualized. A solution containing the probe is then applied to a chromosome preparation that has been denatured (i.e., the DNA has been made single-stranded). During subsequent incubation, the probe binds specifically to its homolog(s) on the chromosome(s) by virtue of their complementary sequences. Upon visualization, the probe appears as a dark-staining or fluorescent region on the chromosome spread, revealing the physical location of its homologous sequence. Although early studies em-

ployed repetitive DNA probes, such as ribosomal RNA genes, a wide variety of probes is currently in use, including single-copy genes. Most recent studies use biotin-labeled probes that are visualized with fluorescently labeled antibodies (fluorescence in situ hybridization, or "FISH"). Digital imaging of FISH preparations involving multiple probes is referred to as "chromosome painting" and can yield precise physical maps for several genes on a single spread (Van Stedum and King 2010). Such studies have been extremely useful for establishing patterns of **synteny**, the localization of homologous genes on the same chromosome in different species, often among distantly related taxa (Kemkemer et al. 2009).

Protein Electrophoresis

Evolutionary geneticists have employed several methods for studying variation at the protein level, including comparative immunology (Maxson and Maxson 1990) and direct amino acid sequencing (Goodman 1978). By far the most widely used approach, however, has been **protein** (allozyme) **electrophoresis** (Wilkesman and Kurz 2017). Allozymes are alleles of enzymes, and electrophoresis is a method used to separate macromolecules based on their charge and mobility through a porous medium (e.g., starch). Distinct protein alleles have, by definition, different amino acid sequences, and these in turn may result in different chemical properties (e.g., charge, size, shape). When placed in a slab of starch or cellulose acetate immersed in aqueous buffer and subjected to an electric current, allozyme molecules will move through the medium at rates determined by their physical properties. After the gel is run for a specified period, different allozymes will be physically separated, occurring at different locations within the gel. Enzymes catalyze specific biochemical reactions, and these can be coupled to specific staining reactions to reveal the precise location of allozymes on a gel. Such histochemical staining allows different alleles at a particular enzyme locus to be identified by their mobility (Figure 2.9), and the organism from which those alleles came to be characterized as a homozygote (two copies of the same allele) or a heterozygote (two alleles).

Prior to the development of DNA assays, allozyme electrophoresis was the method of choice for a wide range of genetic problems in mammalogy—from parentage-dispersal studies (Patton and Feder 1981) to phylogenetic reconstruction (Baverstock et al. 1982). In most of these areas, allozymes have now been abandoned in favor of DNA markers. This derives in large part from the increased information content of DNA data, especially the ability to quantify differences among alleles and the generally higher level of variation among organisms at the DNA level. However, allozyme electrophoresis continues to be a valuable tool in molecular ecology (Wennerstrom et al. 2016).
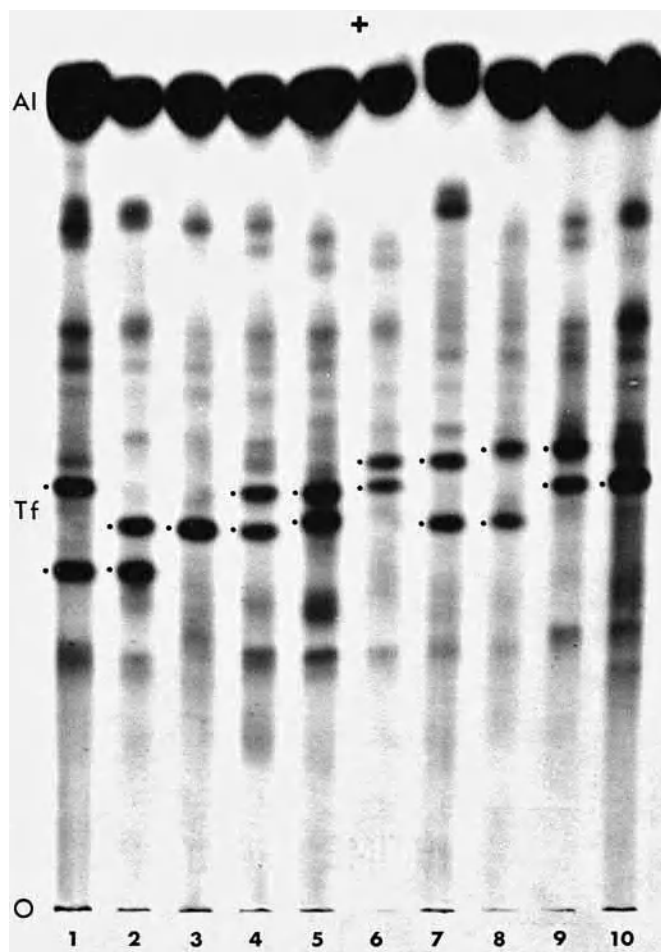
Figure 2.9 **Protein electrophoresis.** Allozyme electrophoresis of albumin (Al) and transferrin (Tf) alleles in white-footed mice. These are two of the most common proteins in mammalian blood. Note the variation in Tf alleles among individuals 1–10. Individuals 3 and 10 are homozygotes; the others are heterozygotes.

DNA Sequences

Two indirect measures of DNA sequence variation led to major advances in mammalian systematics and population biology during the 1980s and 1990s, but, like allozymes, have given way to direct sequencing methods. Whole-genome DNA hybridization (Springer and Krajewski 1989) was used primarily for phylogeny reconstruction in marsupials (Kirsch et al. 1997), rodents (Catzeflis et al. 1993), bats (Kirsch et al. 1995), and primates (Caccone and Powell 1989). Restriction-site analysis led to the development of **DNA fingerprinting** and intraspecific phylogeography and has been applied widely in studies of parentage, **kinship**, speciation, hybridization, conservation genetics, and phylogeny (Avise 2004). These methods helped lay the foundation for many hypotheses about mammalian evolution that have since been investigated with DNA sequence and microsatellite data; some of these are described in later chapters.

Development of the **polymerase chain reaction** (**PCR**; Mullis and Faloona 1987) brought DNA sequence and fragment analysis within the technological reach of most evolutionary geneticists. Prior to this, in vivo cloning procedures were required to isolate particular DNA fragments and manufacture sufficient copies of them for visualization or sequencing. In PCR, target sequences are amplified in vitro with a thermostable DNA polymerase that extends short, oligonucleotide primers that have annealed to their homologs at sites flanking a target region (hence, primers are used in pairs, with each member corresponding to one of the two complementary DNA strands of the target sequence). Initial PCR mixtures contain a small amount of genomic DNA, many copies of each primer, free nucleotides, and DNA polymerase in an aqueous solution with appropriate pH and Mg^{+2} concentration. Typically, PCR targets a specific gene or region for amplification; thus, primer design requires that the sequence of short regions ("primer sites") flanking the target be known in advance. Primers are usually 15–25 nucleotides in length, just long enough to ensure specific and stable annealing to the primer sites. PCR proceeds through multiple cycles of primer annealing, extension, and denaturation carried out in an automated thermocycler. During each cycle, the polymerase adds nucleotides to the free sugar (3') ends of the primers using the complementary strand of target DNA as a template (Figure 2.10). At the completion of a cycle, the region of DNA between primers has been copied and is available to serve as a template in the next cycle. By repeating this process, the number of copies of the target sequence increases geometrically; 30 cycles is sufficient to produce a billion copies of a single template molecule. This vast excess of amplified DNA fragments can be separated from the original genomic DNA, visualized by gel electrophoresis, and purified for subsequent sequencing or other analysis (McPherson and Møller 2006). The sensitivity of PCR has made it possible to recover and analyze DNA sequences from the remains of long-dead, or even extinct, mammals (de Bruyn et al. 2011; Lorenzen et al. 2011).

Most DNA studies in mammalogy focus on either **microsatellite markers** or DNA sequences. The former are derived from genomic loci showing tandem (back-to-back) repeats of 2–4 basepair (bp) motifs spanning less than about 150 bp (Goodwin et al. 2010). Because these loci are highly prone to slip-strand mispairing during DNA replication (Graur 2016), they have a high mutation rate that generates considerable variation in allele size (i.e., number of repeat units) among individuals. Microsatellite markers tend to be most useful for population-level problems such as genetic subdivision (Eldridge et al. 2017). DNA sequences, on the other hand, have been used at all levels of the taxonomic hierarchy, though they have been most widely applied to phylogeographic and phylogenetic questions.

In principle, assays of microsatellites are straightforward. Given primers that amplify a locus of interest, the assay consists simply of high-resolution gel electrophoresis to determine the allele size(s) found in a particular in-
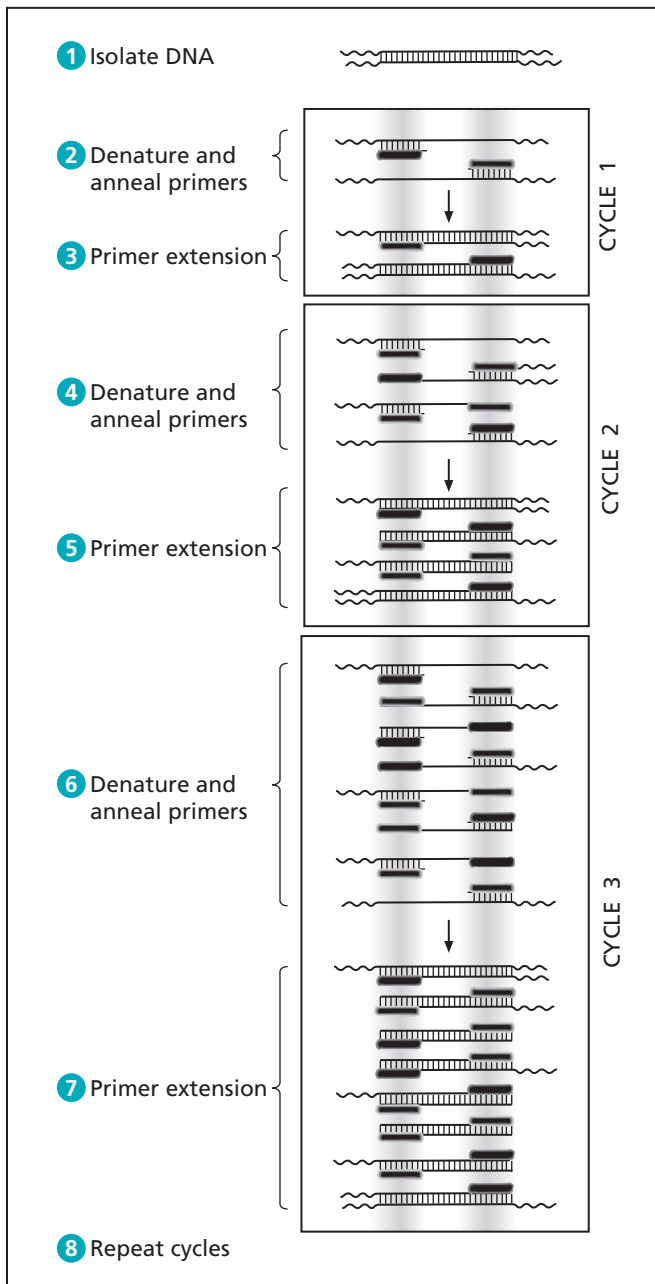
Figure 2.10 Polymerase chain reaction. PCR involves multiple cycles of denaturation, primer annealing, and primer extension, resulting in a geometric increase in the number of copies of a target sequence.

dividual. This is accomplished by comparing the mobility of amplified fragments with DNA sequences of known length ("size ladders"), on the principle that the rate at which DNA molecules migrate through an electrophoretic gel is inversely proportional to their length (Figure 2.11). Once the genotypes of all individuals in a sample have been scored, the size and frequency distributions of alleles lead directly into analyses of parentage, gene flow, or population history. In practice, however, there are some technical hurdles. For one thing, microsatellite loci that are

highly variable in one species may be much less so in other, closely related species ("ascertainment bias"). This means that useful loci, and the primers that amplify them, may need to be identified *de novo* for different species, a process that requires preparation and screening of genomic libraries. PCR amplification of microsatellite loci also entails idiosyncrasies that can affect interpretation of data. For example, PCR is inefficient for alleles with very large or very small repeat numbers; when such alleles fail to appear on scoring gels, heterozygotes may be mistaken for homozygotes ("allelic dropout"). Alternatively, the PCR itself may be subject to strand slippage and produce amplification products containing more or fewer repeat units than the template, which appear as multiple "stutter" bands on a scoring gel. Investigators regularly monitor their data for such phenomena, and the value of microsatellites as highly variable markers has far outweighed these complications.

Until recently, the most commonly used DNA sequencing method was the "chain-termination" technique developed by Sanger and colleagues (1977). In this approach, an oligonucleotide primer is annealed to purified, denatured template DNA (e.g., obtained from a PCR reaction) and incubated in a solution with DNA polymerase, free nucleotides (dNTPs), and fluorescently labeled "dideoxy" nucleotides (ddNTPs). As in PCR, the polymerase extends the primer at its 3' end by incorporating free nucleotides and forming a sequence complementary to that of the template (Hillis et al. 1996). However, when a ddNTP is added to a growing chain, elongation is terminated because the ddNTP lacks the 3' hydroxyl necessary for addition of another nucleotide. By adjusting the relative amounts of dNTPs and ddNTPs, sequencing reactions produce an array of DNA fragments such that every nucleotide position in the template sequence is represented by a fragment that terminates at that position. Thus, for example, sequencing a 100-basepair template would produce fragments of length 1, 2, . . . 100 (ignoring the primer length). When electrophoresed through a high-resolution gel, these fragments separate in 1-base increments, and the series of terminal ddNTPs in the fragments corresponds to the sequence of the template. Because each ddNTP carries a different fluorescent label, the position of each fragment in the gel and the identity of its terminal base can be detected by fluorescence imaging.

Technological advances greatly improved the efficiency of Sanger sequencing. For example, **cycle sequencing** combines PCR with dideoxy chain-termination chemistry to allow sequencing templates in very small amounts. In this approach, a thermostable DNA polymerase is used to incorporate dNTPs and ddNTPs into growing chains, but the reaction is repeated many times in a thermocycler to produce a linear amplification of DNA fragments, which can then be separated by electrophoresis. Many studies have employed automated cycle sequencing with capillary electrophoresis, in which separation, visualization, and electronic documentation of sequencing products takes place within a single, compact instrument (Figure 2.12).
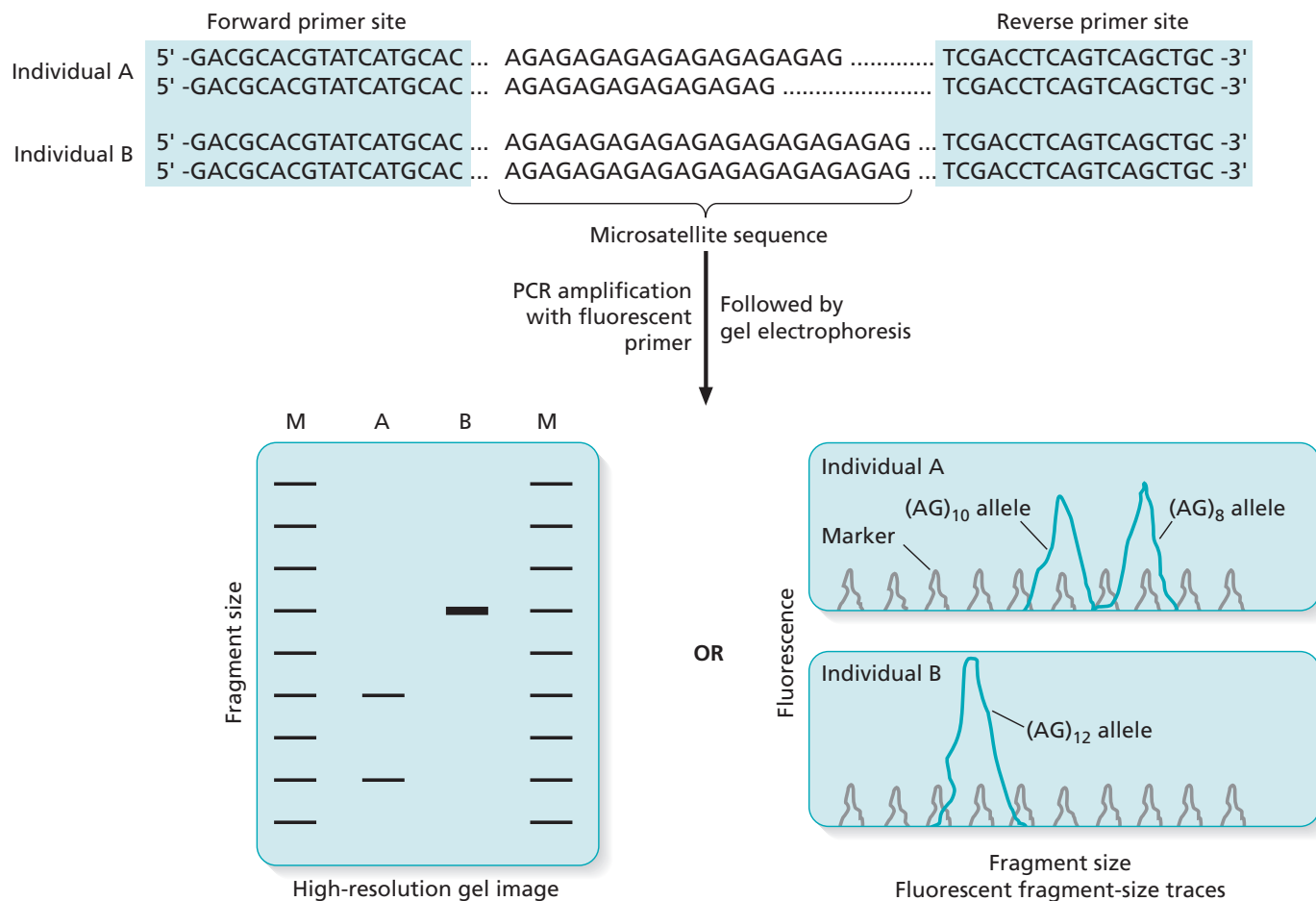
Figure 2.11 Microsatellite analysis. Individuals A and B have different microsatellite alleles as shown at the top. A is hetero-zygous with an $(AG)_{10}$ and an $(AG)_8$ allele; B is homozygous with two $(AG)_{12}$ alleles. Dots indicate DNA sequence between PCR primer sites and the microsatellite locus. After amplification, the genotypes of A and B can be visualized as lanes in an electropherogram or as separate fluorescent traces from an automated fragment analyzer. "M" indicates a series of DNA size standards in 1-base increments.

Tubes containing extension fragments from cycle-sequencing reactions are placed in a robotic device that successively loads each sample into one end of a capillary tube filled with a separation polymer. Electrophoresis takes place in the capillary; as fragments pass a fixed point, their fluorescent labels are excited by a laser, and the distinct color emitted by each ddNTP is detected by a charge-coupled camera and stored as a digital record. Computer software integrates these records and produces a "trace" of each reaction, from which a base-calling algorithm reconstructs the sequence of nucleotides in the original template.

In recent years, several forms of **next-generation sequencing** methods that rely on parallel determination of (typically) millions of short (50–750 bases) sequence fragments simultaneously (Shendure and Ji 2008) have been developed. These fragmentary reads are then assembled into longer, continuous sequences by linking together their regions of overlap. The assembly procedure is carried out by high-speed computational methods and is a central task in the rapidly growing discipline of **bioinformatics**. Next-generation sequencing has greatly facilitated the study of **genomes** from a variety of mammal groups. A significant

issue in genomic analysis of a particular taxon is whether a reference sequence from a closely related species is available. Ideally, a reference sequence is a complete genome that has been fully assembled and annotated such that the physical location of individual sequences, the boundaries of coding regions, and the identity of genes at particular loci are known. Having such a reference makes analysis of new genomic data sets much easier and more robust than the alternative *de novo* assembly (da Fonseca et al. 2016). To this end, a consortium of geneticists proposed the *Genome 10K* project to develop a reference set of 10,000 complete genomes distributed across Vertebrata (Genome 10K Community of Scientists 2009); a recent progress report (Koepfli et al. 2015) described 277 reference genomes at or near completion by the consortium.

The most widely studied sequence in mammalogy is the **mitochondrial DNA (mtDNA)** molecule. Mitochondria, organelles in which the reactions of cellular respiration take place, are the result of an ancient **symbiosis** between an aerobic prokaryote and the evolving eukaryotic cell (Krebs et al. 2013). Each mitochondrion includes one or more copies of a circular DNA molecule, a remnant of the ancestral
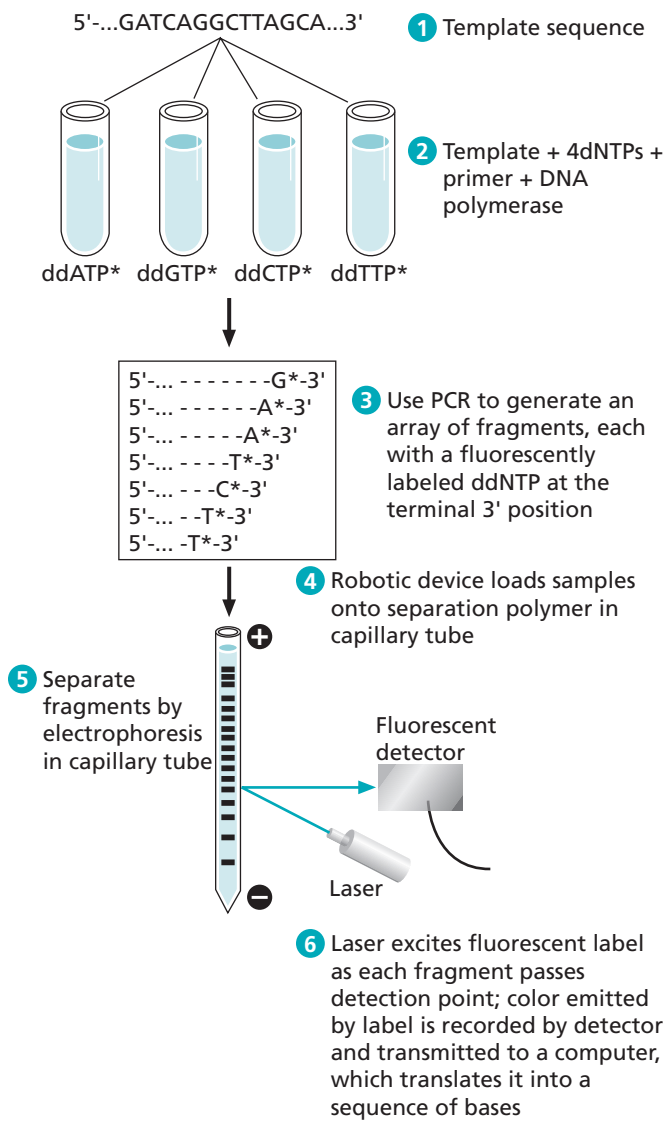
Figure 2.12 Automated DNA sequencing. An amplified template sequence is subjected to cycle-sequencing reactions that include free nucleotides (dNTPs), one primer, DNA polymerase, and one of four chain-terminating dideoxy nucleotides (ddNTP). Each ddNTP has a different fluorescent label (asterisks). Resulting DNA fragments are separated by size with capillary electrophoresis. The series of fluorescent signals emitted by each fragment as it passes the detector is assembled into a DNA sequence by the computer. *Adapted from Atherly et al. (1999) and Hartwell et al. (2011).*

Figure 2.13 The mouse mitochondrial genome. The mouse mtDNA molecule is just over 16,000 bases long. Protein-coding, ribosomal RNA (rRNA), and noncoding (CR) regions are labeled inside the circle; transfer RNA (tRNA) genes are indicated outside the circle by the one-letter abbreviations of their corresponding amino acids. *Adapted from Bibb et al. (1981).*

symbiont's chromosome, consisting of approximately 16,000 bases. The gene content of this molecule is highly conserved among mammals (Figure 2.13); it consists of 22 transfer RNA, 2 ribosomal RNA, and 13 protein-coding genes, as well as a noncoding "control" region. With minor exceptions, the arrangement of these loci on the mtDNA molecule is also conserved. Several properties of mammalian mtDNA make it attractive to evolutionary geneticists. First, it is a haploid, homoplasmic, nonrecombining marker—that is, the vast majority of mtDNA molecules within an organism have identical sequences (Eleftherios

and Rand 2000). Second, it has a higher average rate of sequence evolution than nuclear DNA, probably due to lack of a DNA repair mechanism. Even so, mtDNA shows a considerable range of rate variation among its loci, from very rapidly evolving portions of the control region to more conserved protein-coding genes (e.g., cytochrome oxidase subunit II). Third, it is transmitted to offspring through the egg cytoplasm (maternal inheritance), making it a marker that tracks the history of maternal lineages. Collectively, these properties make mtDNA relatively easy to isolate experimentally and ensure that variations among mtDNA sequences (**haplotypes**) can be used to address genetic problems at levels from intraspecific phylogeography to intraordinal phylogeny (Avise 2004).

Although mtDNA sequences have had a major impact in studies of mammal evolution, they are not suitable for all research questions. In particular, molecular systematists concerned with relationships among major mammalian groups (e.g., orders), for which common ancestors existed in the Cretaceous or Early Tertiary, have turned to more slowly evolving genes in the nucleus. In part as a result of their lower average rates of change, nuclear coding sequences are less prone than mtDNA to multiple substitutions at the same sites over long periods of evolutionary time (Springer et al. 2001a). As such, they preserve a phylogenetic "signal" that can be used to relate very divergent groups of mammals. In addition, the nuclear genome

(about 3 billion bases in a haploid human cell) is vastly more diverse in structure and properties than mtDNA. It contains sequences that evolve very rapidly (e.g., introns, pseudogenes, intergenic regions), at intermediate rates (e.g., most exons), or very slowly (e.g., conserved exons, small subunit ribosomal RNAs) and thereby provides markers with levels of variation appropriate for specific evolutionary questions. It is now common for nuclear and mitochondrial DNA markers to be used together in studies of mammal phylogeny (Westerman et al. 2016) and population genetics (Moska et al. 2016).

Perhaps the most exciting recent development in mammalian genetics is the ability to study DNA variation across the entire genome, largely as a result of next-generation sequencing technology. As of 2017, complete genome sequences from approximately 137 mammal species have been published, and many more are in progress (National Center for Biotechnology Information, www.ncbi.nlm.nih .gov/genomes). Equally significant for evolutionary and ecological studies, cost- and labor-efficient methods have been developed to compare sequences of many loci (e.g., thousands) from across the genomes of multiple individuals and species. For example, restriction-site associated DNA sequencing (RADSeq; Davey and Blaxter 2010) uses PCR and next-generation sequencing to assay variation at 100- to 400-base genomic fragments that are adjacent to (within ca. 400 bases of) cut sites for a particular restriction enzyme. The RADseq approach can provide data on thousands of genetic markers for many individuals and thus facilitate population-genetic studies of closely related species (Lanier et al. 2015), particularly when no reference genome exists. When a reference sequence is available, researchers can use it to perform targeted sequencing of genomic markers with appropriate variation (e.g., introns) or assay polymorphisms in the transcriptome (i.e., genes). Carneiro and coworkers (2014) targeted intron and transcriptome variation to study gene flow between subspecies of European rabbit (*Oryctolagus cuniculus*). At the other end of the spectrum, McCormack and colleagues (2012) used targeted capture of ultraconserved elements (i.e., slowly evolving DNA sequences) to study phylogenetic relationships among orders of placental mammals. These and other approaches have given rise to the discipline of phylogenomics (DeSalle and Rosenfeld 2012).

ANALYSES OF MUSEUM SPECIMENS

Systematic Collections

In 1994, a group of systematists organized by three professional societies produced a report entitled *Systematics Agenda 2000* (1994), a declaration of priorities for dealing with the worldwide loss of biodiversity (see Daly et al. 2012 for an updated "Systematics Agenda 2020"). Among the major components of their action plan was enhancing systematic collections, justified as follows (p. 16): "Collections contain the primary evidence for the existence of species, document their presence at particular sites, and serve as the ultimate standards for comparisons and identifications of species." The central role of carefully prepared specimens, representing the preserved remains of organisms in well-organized collections, has been characteristic of biological taxonomy for centuries and remains a critical part of mammalogy (McLean et al. 2016).

The phrase "museum specimen" refers not only to specimens housed in institutions called "museums," but also to those in university departments, government agencies, and private holdings. In mammalogy, such specimens are of several major types (Hall 1962). A **study skin** is the preserved integument (pelage, epidermis, and superficial dermis) of a mammal, from which muscles, internal organs, and most bones have been removed (Figure 2.14). For small mammals, study skins are usually stuffed with cotton after chemical treatment, then dried in a flattened, linear pose. Larger skins may be dessicated or tanned, then stored as hides. Skulls and skeletons are dried bones recovered from an animal that has been skinned and defleshed. **Spirit** (fluid) **specimens** are carcasses, or portions thereof, preserved in alcohol. Many spirit specimens are initially fixed in formalin, a chemical that induces cross-linking of proteins and thereby immobilizes the cell contents of tissues. Fossils are the remains of dead organisms, usually preserved in rock. Tissue samples are pieces of flesh, aliquots of blood, or hairs that are frozen or immersed in a solution that prevents degradation of protein and DNA molecules. For several decades, mammalogists have also extracted, purified, and preserved (usually frozen) DNA samples from animal tissues (Camacho-Sanchez et al. 2013). However, a tissue or DNA sample is of limited utility unless it is accompanied by a **voucher specimen**—a skin, skull, or other whole-organism remnant that serves to identify the source of the sample.

Curation is the task of maintaining a collection of museum specimens, including their initial preparation, safe

Figure 2.14 Study skins. This series of study skins from white-footed mice could be used to examine differences in pelage characteristics, which might vary with habitat or locality.

storage, organization, and accessibility to researchers. The value of museum specimens comes not only from the anatomical structures and taxonomic history that they preserve, but also from the documentation they provide that a particular species occurred in a particular place at a particular time. Thus, one of the most important jobs of a curator is to maintain an accurate, complete, and accessible specimen database. Typically, each specimen is labeled with a unique alphanumeric code that ties it to a record that includes the name of the collector, date of collection, collection locality (often with habitat information), and perhaps other data such as field measurements or behavioral observations. Modern collections make efficient use of computer database technology, in many cases making complete lists of specimens and associated information available on the internet. Cook and colleagues (2014) argue that digital collection data are a largely untapped resource for educating college students about biodiversity; perhaps your instructor will tap it on your behalf.

Specimen-Based Studies

Museum collections represent the archived results of field collections. Mammals taken from the wild and preserved as museum specimens are the primary documentation of mammalian biodiversity in specific areas of the world. Regional surveys of mammal diversity are based on information derived primarily from these collections, either through an author's original observations or previously published records. Flannery (1995), for example, documented the occurrence of nearly 190 living mammal species indigenous to New Guinea. The record of museum specimens allowed Flannery to describe key aspects of the biology of each species, including its distribution, altitudinal range, habitat association, taxonomic history, and measurements indicative of body size. Faunal surveys of this sort comprise a major goal of *Systematics Agenda 2020* (Daly et al., 2012).

Museum specimens are a primary source of information on the morphology of mammals, and they have been particularly valuable for systematic studies involving comparative anatomy. Descriptions of new mammal species typically rely on painstaking comparison of all skins and skulls from a particular taxon available in museum collections, and may include the postcranial skeleton and soft tissues as well. Craniodental characters scored from skulls have been used extensively for phylogenetic analysis of living and fossil mammals, the latter frequently represented *only* by their teeth (see Chapter 4). Skins and spirit specimens can be examined for parasites, pathogens, environmental pollutants, or other trace chemicals.

Skins, skulls, and skeletons are also the basis of **morphometric** studies, which analyze the shape of anatomical structures (Lestrel 2000; Cardini and Loy 2013). Morphometrics has been an invaluable tool in research on mammalian developmental and functional anatomy (Shapiro

et al. 2005; Marquez et al. 2017), shape evolution (Hendges et al. 2016), and sexual dimorphism (Gomes and Valente 2016). One of the most widespread applications of morphometrics in mammalogy is in the study of intraspecific variation (see Intraspecific Variation below), particularly that associated with subspecies designations. For example, Bezerra and de Oliveira (2012) used multivariate statistical analysis of 25 craniodental measurements from 78 South American spiny rats (*Clyomys*) housed in 6 different collections to evaluate the distinctness of recognized species. Their findings led them to recommend that one of the species (*C. bishopi*) be merged with the other (*C. laticeps*), but also identified a morphometrically distinct group of specimens from the western portion of the genus range, which may represent an unrecognized species.

Museum collections have become the largest repository of tissue and DNA samples for molecular analyses of mammals, including systematics, ecology, conservation genetics, and forensics. These samples, tied to voucher specimens and preserved over long periods of time, will become increasingly significant as more populations of wild mammals decline and access to them becomes restricted by conservation management. Moreover, it is now common practice to recover DNA from bits of study skins, dried flesh adhering to bones, or even the bones themselves (Hofreiter 2012). In some cases, DNA has been extracted from spirit specimens fixed in formalin (Bibi et al. 2015). Thus, specimens prepared long before the development of modern biotechnology represent an immense archive of genetic data. Because recovering DNA from such specimens may entail the permanent loss of some preserved tissue, however, most museums have explicit policies for destructive sampling, which weigh this loss against the potential gain of information from genetic analysis.

Systematic Methods

INTRASPECIFIC VARIATION

Taxonomists and evolutionary biologists share a preoccupation with the variation (**polymorphism**) found in natural populations. Indeed, a major component of the 20th-century "Modern Synthesis" in evolutionary biology was documentation that patterns of phenotypic variation in natural populations are consistent with the predictions of evolutionary theory (Dobzhansky 1937; Mayr 1942, 1963). Evolutionary interpretation of such variation in turn provided a conceptual basis for modern taxonomy (Mayr 1969; Simpson 1961). Methods for measuring genetic variation became available in the 1960s (Harris 1966), and the data they provided immediately reinvigorated discussion about the roles of mutation, natural selection, and genetic drift in determining levels of polymorphism (Kimura 1983;

Lewontin 1974). Moreover, the development of molecular population genetics provided new technological and analytical tools with which to study phenomena such as inbreeding, migration, population subdivision, and effective population size. Thus, interpreting patterns of intraspecific variation is a central theme in modern mammalogy.

The study of phenotypic variation in mammals emphasizes interindividual, temporal, and spatial dimensions. An especially significant form of interindividual variation is **sexual dimorphism**, the possession of different phenotypic characteristics by males and females of the same species. The most frequently studied morphological features include body size and ornamental, secondary sex characteristics. "Rensch's rule" (see Rensch 1959) is the observation that in species with males that are larger than females, sexual size dimorphism (SSD) increases with increasing average body size; the inverse is true in groups with females that are larger than males. This generalization has been supported for some mammals (Lindenfors et al. 2007), but not others (Astúa 2010), especially when the correlation is tested in a phylogenetic framework (Bidau and Martinez 2016). The relationship of SSD and body size may depend on ecological (Noonan et al. 2016) or other factors (Martinez and Bidau 2016) that differ among species or larger taxonomic groups. Differentiation between the sexes is thought to result from sexual selection, adaptation to different parental roles, or intersexual competition for food (Derocher et al. 2005). Although most studies have focused on **dimorphic** traits of the phenotype, some researchers have begun to explore the underlying genetic bases for anatomical, physiological, and behavioral differences between the sexes (Rinn and Snyder 2005; Willmore et al. 2009). Research on temporal variation is dominated by studies of growth, particularly as it relates to postnatal development and age-specific selection pressures (Wellbergen 2010).

Analyses of spatial variation in mammals focus on the extent to which geographically separated populations are taxonomically, genetically, or adaptationally distinct. It is common for mammals of the same species to show different characteristics in different portions of their range. When geographically disjunct populations display different traits, they are often recognized taxonomically as **subspecies**. Subspecies differentiation may involve discrete morphological (Sutton and Patterson 2000), morphometric (Turvey et al. 2015), behavioral (Latour and Ganem 2017), or genetic (Meredith et al. 2007) differences, or (most often in recent years) a combination of these (Hafner and Smith 2010). Formal recognition of subspecies as units of biodiversity continues to play an important role in conservation biology (Laguardia et al. 2017), though this taxonomic category is not applied consistently across mammal groups (Gippoliti and Amori 2007). In other cases, one or more traits may show continuous variation along some geographic axis, thus forming a **cline**. Clines may be the result of secondary contact between populations that diverged in isolation, primary contact with a gradient of selection pres-

sures among populations along a transect, selection against hybrid individuals from partially isolated populations, or mixing ("diffusion") of individuals from two currently isolated populations. Genetic markers have greatly facilitated the study of clines in mammals (Sutter et al. 2013).

The genetic distinctness of populations may provide insights into current or historical levels of gene flow among them. Allozymes, mtDNA, and microsatellite loci have been extensively applied to such problems. Because it is often difficult to measure migration directly (e.g., by tagging individuals), geneticists use the frequencies and divergence of alleles to quantify levels of population subdivision, and from these make inferences about gene flow. Commonly used measures of population subdivision are Wright's (1951) F statistics, correlation coefficients that partition allele-frequency variation among three levels (total population, subdivisions, and individuals within subdivisions) in a hierarchically structured population. One of these, F_{ST}, is interpreted as the genetic differentiation of subpopulations, with $F_{ST} = 0$ indicating panmixia and $F_{ST} = 1$ indicating complete isolation (Hamilton 2009). In practice, values of F_{ST} are usually intermediate. Estimates of effective population size or effective number of migrants are obtained by relating an observed F_{ST} to its expectation under specific models of population structure, such as Wright's (1940) "island model." Conceptually similar approaches have been formulated for use with DNA sequences (Lynch and Crease 1990) and microsatellites (Feldman et al. 1999). In addition to allele frequencies, these data types include measures of sequence or repeat-length differences between pairs of alleles. Partitioning sequence and microsatellite variation among levels of a hierarchically sampled geographic region has been termed "analysis of molecular variance," or AMOVA (Excoffier et al. 1992), and is widely used in mammalogy to assess whether populations are genetically distinct (Ojeda 2010). Other statistical methods, including those in Pritchard and colleagues' (2000) STRUCTURE software, also estimate the number of distinct populations represented by allelic data from individuals (see application to walrus populations by Sonsthagen et al. 2012). Moreover, a plot of the frequency of haplotype pairs showing increasing numbers of sequence differences—a mismatch distribution (Rogers and Harpending 1992)—can be used to infer whether individual populations have undergone expansions or bottlenecks in the recent past (Wisely et al. 2008). Integration of molecular population genetics with landscape ecology to address questions about how environmental factors influence patterns of genetic variation has given rise to the emerging discipline of landscape genetics (Montgelard et al. 2014). Howell and coworkers (2017) used this approach to document the influence of agricultural landscape features on population structures of two species of mice (*Peromyscus*).

Evolutionary geneticists now frequently incorporate **coalescent theory** (Wakely 2006) into models of population divergence, allowing more robust estimates of parameters such as historical gene flow, effective population size, and

divergence time (Hey 2010). Coalescent theory is a probabilistic model framework for understanding how evolutionary and demographic forces (e.g., genetic drift, gene flow, recombination, selection) affect the genealogy of homologous DNA sequences (e.g., gene copies) in a population. By comparing observed relationships among alleles to their expectations under a coalescent model, researchers can make inferences about the evolutionary history of the population(s) in which the alleles are evolving. Coalescent theory is also having a significant impact on phylogeography and phylogenetic inference (see sections below and Chapter 3).

INTRASPECIFIC PHYLOGEOGRAPHY

Avise and colleagues (1987) coined the phrase intraspecific **phylogeography** to denote study of the geographical distribution of genealogical lineages within species. Most animal phylogeography studies have employed mtDNA because its unique properties are ideal for identifying genealogical lineages. Specifically, animal mtDNA is maternally inherited, nonrecombining, and rapidly evolving; thus, the mutation history of mtDNA haplotypes corresponds to the genealogical relationship of the maternal lineages within the species through which those haplotypes are transmitted. Methods of phylogenetic inference (discussed in another section below) can be applied to haplotypes associated with animals from specific localities, and the **gene tree** obtained can be related back to the geographic origin of the animals. For example, Andersen and Light (2012) obtained sequences of three mitochondrial genes from 63 specimens of hispid pocket mouse (*Chaetodipus hispidus*) sampled from across the range of the four recognized subspecies in the central United States and Mexico (Figure 2.15A). Phylogenetic analysis of these sequences revealed that haplotypes formed four clusters corresponding to populations separated by topographical dispersal barriers (Southern Coahuila filter-barrier, Deming Plains, and Balcones Escarpment in Figure 2.15B). Interestingly, the phylogeographic groups do not correspond to morphologically defined subspecies. Although mtDNA is still the most widely used marker for studies of mammalian phylogeography, many recent investigations also utilize nuclear DNA, including targeted autosomal (Bryja et al. 2016) and sex-linked (Barbosa et al. 2016) sequences, single nucleotide polymorphisms (SNPs) from across the genome assayed by RADseq (Puckett et al. 2016), and microsatellite loci (Vonhof et al. 2016).

SPECIES BOUNDARIES

Recognition and naming of species has been a cornerstone of taxonomy for centuries. Species are the units of biodiversity, the outer limits of population genetics, the constituents of higher taxa, and the entities related by phylogeny.

The processes by which new species arise from preexisting species (**speciation**) has been the subject of intense theoretical and empirical research since the time of Darwin (Seehausen et al. 2014). Ironically, even as our understanding of speciation mechanisms increases, biologists remain divided on the question of what constitutes a species. The dispute centers on the value of different criteria for defining the biological term "species" versus those used for recognizing species in nature. The extremes of this argument were apparent in two early alternative species concepts. Simpson (1951:289) defined an evolutionary species as a "lineage (ancestral-descendant sequence of interbreeding populations) evolving independently of others, with its own unitary evolutionary role and tendencies." This definition is theoretically well motivated, but entirely nonoperational. In contrast, the traditional morphospecies as described by Cain (1954) is operational, in that species are delimited by diagnostic morphological traits, but it has no connection with evolutionary theory. Species concepts currently in use have more common ground with theory and practice, but often conflict when applied to populations at intermediate stages of speciation. The impossibility of predicting the outcome of incipient speciation led O'Hara (1993) to suggest that no solution to this "species problem" would be forthcoming. Nevertheless, the science of recognizing species continues and is an integral part of systematic mammalogy.

The **biological species concept** (**BSC**) of Mayr (1942) has long been popular in mammalogy. In this concept, populations are considered distinct species when they are reproductively isolated from one another. The BSC is easiest to apply when two or more populations occur in the same area but do not hybridize. It is more problematic when limited hybridization takes place, and entirely nonoperational when populations are geographically isolated. In applying the BSC, few studies directly assess the extent of reproductive isolation. Rather, the maintenance of diagnostic phenotypes in different populations is taken as evidence of a barrier to gene flow (i.e., a species boundary). Given the difficulties inherent in applying the BSC, many taxonomists have recently advocated the **phylogenetic species concept** (**PSC**): "a species is the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent" (Cracraft 1983:170). The PSC emphasizes diagnosability and common ancestry as criteria for establishing a species boundary; the former has been standard practice in systematics for centuries, but the latter relies on a phylogenetic interpretation of character variation. De Queiroz (2007) proposed a unified view that treats species as evolving lineages and recognizes the multiplicity of evidence that may be brought to bear on their delimitation. This general lineage concept has been widely embraced by researchers seeking to integrate genetic data with other aspects of species recognition. Indeed, some taxonomists (e.g., Tautz et al. 2003)
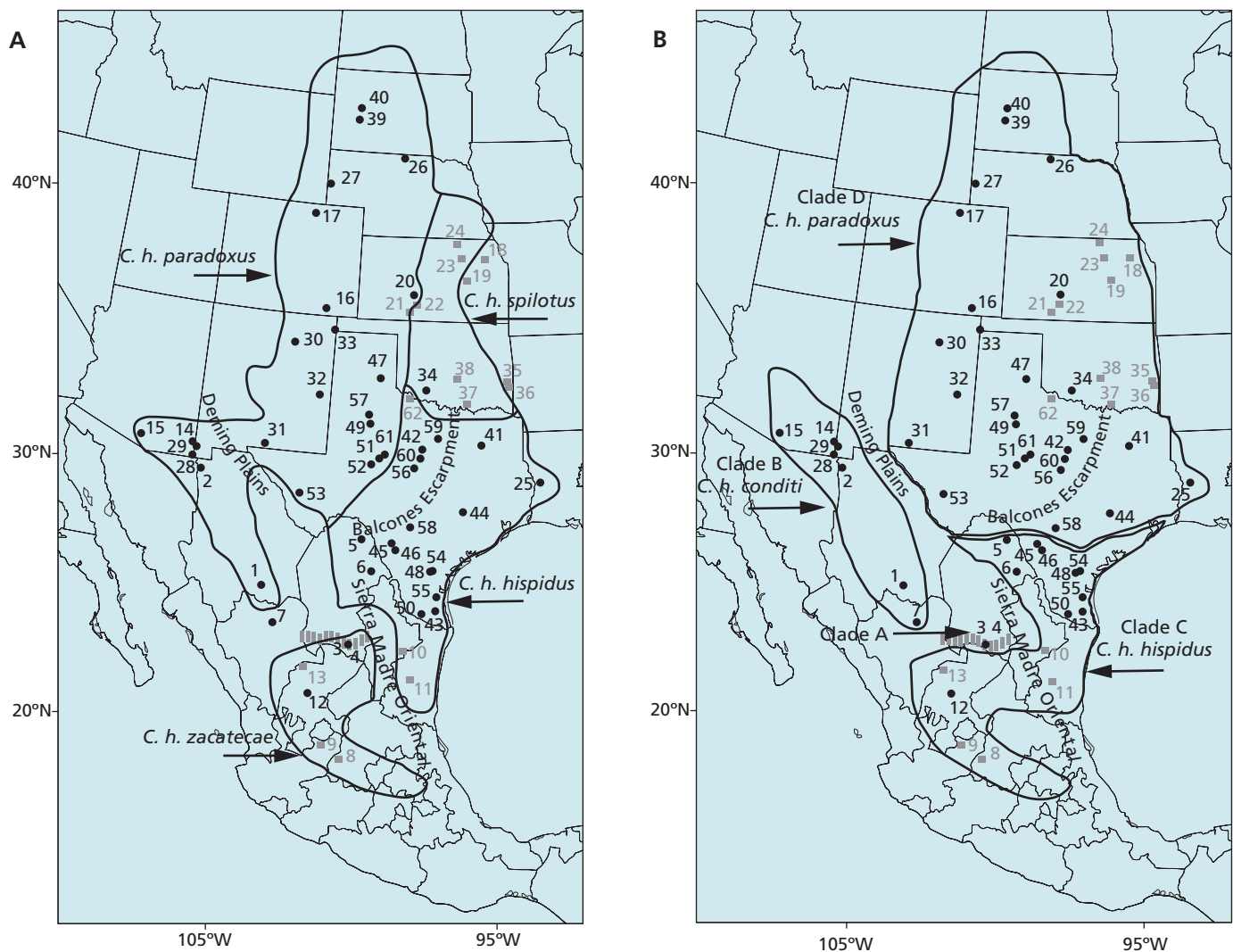
Figure 2.15 **Intraspecific phylogeography.** (**A**) Map of the central United States and Mexico showing the distribution of morphologically defined subspecies of hispid pocket mouse (*Chaetodipus hispidus*). Numbers indicate collecting localities of genetic samples. (**B**) Distribution of haplogroups identified by phylogenetic analysis of mtDNA sequences. Note that the boundaries of haplogroups coincide more closely with topographic barriers to dispersal. *Adapted from figures 1 and 5 of Andersen and Light (2012).*

have argued that molecular markers are critical for thorough documentation of species boundaries.

The widespread application of molecular methods in mammalian systematics has had a profound effect on the study of species boundaries during the past few decades. Molecular markers can be used to assess directly the level of gene flow among populations—information that is crucial to application of the BSC. Phylogeographic analysis of haplotypes from specific loci may reveal the extent to which members of different populations are genealogically distinct, thus providing critical insight for use of the PSC. Indeed, it is common to find morphological species descriptions accompanied by phylogeographic analyses confirming the **reciprocal monophyly** of haplotypes from species in the study group (i.e., all haplotypes recovered from one species are more closely related to one another than to those from any other species), although this is not

a necessary criterion (Knowles and Carstens 2007). The past ten years have seen a proliferation of statistical "species delimitation methods" that operate primarily on molecular sequence data (Carstens et al. 2013). These methods compare observed patterns of variation and inferred relationships among haplotypes to expectations from models that include both inter- and intrapopulation divergence. To give just one example, Liu and colleagues (2017) applied the generalized mixed Yule coalescent (GMYC) model of Pons and coworkers (2006) and the genealogical sorting index (*gsi*) of Cummings and colleagues (2008) in an mtDNA study of Chinese voles (Arvicolini). GMYC estimates the most likely point on a haplotype tree scaled to time where branching rate switches from that predicted by a speciation (Yule) model to that predicted by the coalescent model; haplotype clusters more recent than this time point represent potential species. The *gsi* measures the ex-

tent to which haplotypes assigned to predefined groups form exclusive clusters on an inferred tree, relative to a null model formed by randomly assigning haplotypes to groups. Using these methods in conjunction with morphological data, Liu and colleagues (2017) described two new species of *Neodon* voles from southwestern China. Recently, Freudenstein and coworkers (2017) found the general lineage concept and exclusive use of molecular species delimitation methods to be theoretically and practically inadequate and argued instead for the centrality of phenotypic traits that influence niche dimensions for defining species as meaningful units of biodiversity.

Whichever concept is employed—and there are many others (Hausdorf 2011)—the standard for describing new species of mammals has been, and continues to be, diagnosis. Can we identify characteristics of individual organisms that will allow us, with a high degree of confidence, to assign those organisms to one group or another? Mammalogists adhere to the practice of designating **type specimens** as described by the International Commission on Zoological Nomenclature (1999). Most type specimens are preserved carcasses, skins, skulls, skeletons, or other anatomical remains in a museum collection. Under the rules of nomenclature, the type is the "name bearing" specimen and functions as a historical reference for the Latin binomial used to denote a particular species. The type concept has engendered a distinct format for species description (Winston 1999) that is widely followed by mammalogists. Descriptions of new species are frequently embedded in a **taxonomic revision** of some larger group, such as a genus. In conducting a traditional revision, taxonomists examine as many specimens as possible from the group under review and identify features that diagnose each putative species. In addition, descriptive information is provided that will assist in the identification of future specimens. Thus, for example, when Woolley (2005) identified a new species of three-striped dasyure (*Myoictis leucura*), the formal description included a summary of the type material (i.e., relevant museum voucher-specimens), geographic distribution of the new species, diagnostic traits, description of other anatomical features, and a comparison of the new species to the three other recognized species of *Myoictis*. Such thorough and careful description helps ensure that species-level classification is as objective and stable as possible.

PHYLOGENETIC INFERENCE

A **phylogeny** is a speciation history for some group of species. Phylogenies are usually depicted as trees, on which current species form terminal branches, ancestral species are internal branches, speciation events are nodes, and the common ancestor of all species under study is the root

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Description of a new species of dasyurid marsupial, *Myoictis leucura*, by Woolley (2005)

In the original publication, the text below follows similar descriptions of three recognized species in the same genus and is accompanied by photographs of study skins, skull, and teeth from each species. Eleven key characters serve to differentiate the four species.

Myoictis leucura n. sp.

- **Type material.** Holotype AM 17122. Skin and skull of adult male. Collected in 1985 by K. Aplin at Agofia, Mt. Sisa (Haliago), Papua New Guinea, 16°17′S 142°45′E, 650 m. The tip of the tail has been damaged in preparation of the skin (white portion reduced in length from 9 mm, when the specimen was first examined in spirit, to 5 mm on the prepared skin). Paratype AM 18091, adult female in alcohol, skull extracted, collected in 1985 by K. Aplin at Namosado, Mt. Sisa (Haliago), 06°142′S 142°47′E, 750–1,000 m.

- **Distribution.** Southern side of the central mountain ranges in Papua New Guinea from Mt. Bosavi in the west to Mt. Victoria/Vanapa R. in the east. Altitude records range from 650 to 1,600 m.

- **Diagnosis.** *Myoictis leucura* differs from other species of *Myoictis* in having a white-tipped tail with long hairs on the top and sides of the tail, the hairs decreasing in length towards the tip.

- **Description.** The external appearance of the holotype is similar to the specimen shown in Fig. 3c [of the original publication] except that the portion of the tail that is white is shorter. The general coat colour is dark reddish brown above, with brighter, reddish hairs between the black dorsal stripes, and lighter below. The dorsal stripes extend from behind the ears to the rump, and the median stripe extends forward on the head. Red auricular patches are absent. The ears and feet are dark. The first interdigital and thenar footpads are generally not fused. Body dimensions can be found in Table 2 [of original]. The posterior palatal foramina are large, and P_3 is single rooted. Females have four nipples.

- **Comparison with other species.** Differences between *Myoictis leucura* and other species are summarized in Table 2 [of the original publication]. *Myoictis leucura* can be distinguished from *M. wallacei*, *M. wavicus*, and *M. melas* by the form of the tail. *Myoictis leucura* is larger than *M. wavicus* but similar in size to *M. wallacei* and *M. melas* with respect to mass, head-body length, foot length, basicranial length and length of the lower molar tooth row. The females of *M. leucura* (and *M. wavicus*) differ from *M. wallacei* and *M. melas* in having four rather than six nipples. *Myoictis leucura* can be distinguished from *M. melas* by the larger size of the posterior palatal foramina and by the presence of the third premolar tooth. *Myoictis leucura* can be distinguished from both *M. wallacei* and *M. melas* by the upper premolar tooth row gradient, and from *M. wallacei* in having a single rooted, as opposed to a double rooted, lower third premolar tooth. Differences in coat colour between the species are described earlier.
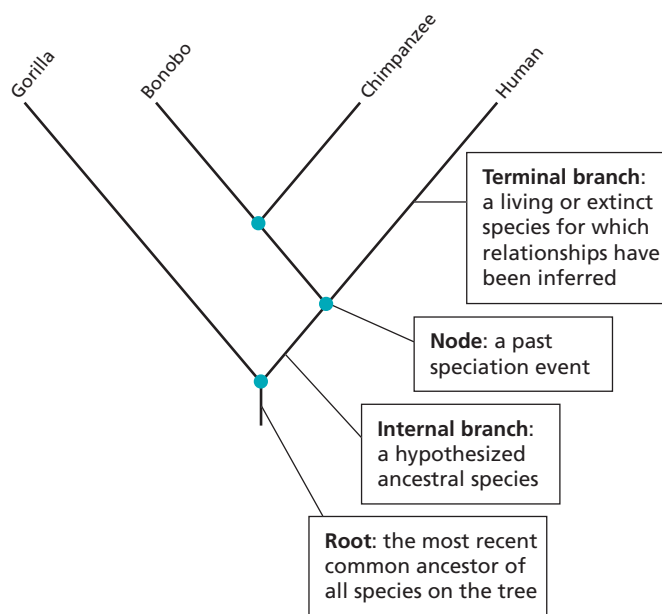
Figure 2.16 **The parts of a phylogenetic tree.** Relationships among four species of hominoid primates are depicted as a tree, with the time dimension moving from bottom to top. The degree of phylogenetic relationship among any set of species is given by the relative age of their most recent common ancestor. Monophyletic groups include an ancestral species, all of its descendants, and nothing else. On this tree, (bonobo + chimpanzee) and (bonobo + chimpanzee + human) are examples of monophyletic groups.

(Figure 2.16). Every phylogeny implies a time dimension in which the tips of terminal branches are closest to the present and the root is farthest in the past. Understood in this way, a phylogenetic tree illustrates that the measure of evolutionary relationship for any two species is the time elapsed since their most recent common ancestor: if species A and B are more closely related to each other than either is to C, this means precisely that A and B diverged from a common ancestor more recently than did A and C or B and C. A group of species that includes a common ancestor, all of its descendants, and nothing else is a **monophyletic group**, or **clade**. Two monophyletic groups that are each other's closest relatives are **sister groups**. Phylogenetics is the research program that seeks to reconstruct the "Tree of Life" (i.e., the phylogeny of all species), though individual phylogenetic studies are much smaller in scope. Mammalian phylogenetics has been contentious for most of its history (see Chapter 3).

Phylogenetics became widely acknowledged as a distinct branch of systematics following the publication of Hennig (1966), though phylogenetic inference methods had begun to be developed even before Hennig's work (e.g., Edwards and Cavalli-Sforza 1963). To estimate a phylogeny, systematists rely on evidence presented by the species whose relationships are in question. This evidence consists of **characters**—heritable features of organisms that vary

among species and, if interpreted in light of reasonable assumptions about evolution, reveal patterns of common ancestry. Most methodological progress in phylogenetics has involved the development of analytical tools to estimate relationships from patterns of character variation. This is now a vast and complex literature, of which we will discuss only the most fundamental aspects.

Characters come in many forms, but the most frequently studied are anatomical and molecular. An anatomical character may be any feature of the body of an organism that is heritable, and descriptions of such characters are correspondingly diverse. Molecular characters are ultimately protein or DNA sequences, but variation in those sequences has been assayed in many ways: presence of particular allozymes or restriction sites, relative strength of antibody affinities for albumin proteins, thermal stability of artificially hybridized DNA strands from different species, or (most commonly now) direct comparison of amino acid or nucleotide sequences. It is significant that characters are *selected* for phylogenetic analysis by investigators, usually because they have desirable properties (e.g., heritability, variation) for the phylogenetic problem at hand; not all characters are equally useful. Variation is captured by descriptions of the *states* of a character in different species. For example, Wroe and coworkers (2000) found two states for the character "shape of upper incisors" in dasyuromorphian marsupials: "peg-shaped" and "spatulate." Typically, each species possesses a single state of each character, but sometimes researchers include polymorphic characters (i.e., those that show more than one state in some species).

Perhaps the most critical consideration in selecting a character for phylogenetic analysis is that it be **homologous** among the species studied. A homologous character is one that species share by inheritance from a common ancestor that also possessed it. For example, "wings" are homologous among bats because bats are descended from a common ancestor that had wings. "Tusks" are not homologous between elephants and walruses: elephant tusks are incisors, walrus tusks are canines, and the most recent common ancestor of elephants and walruses had neither. Variation in the form of wings among bats might reveal something about their phylogeny, but the form of tusks in elephants and walruses has no bearing on their relationship to one another. Homology of molecular characters must be considered at two levels, the locus and the site. For example, mammalogists have made extensive use of cytochrome *b* gene sequences, but always on the assumption that species share cytochrome *b* genes because their common ancestor had one. This is reasonable for loci that have not been *duplicated* in the genome. Thus, sequences of myoglobin (an oxygen-binding protein in muscle cells) should not be compared with sequences of hemoglobin (oxygen-binding proteins in blood cells) for reconstructing phylogeny: myoglobin and hemoglobin are related by a gene duplication that predates the diversification of mammals (Hardison 2005). Even when comparing homologous loci,

the homology of individual sites is a crucial consideration. Is position 1143 in the cytochrome *b* gene of the Virginia opossum (*Didelphis virginiana*) homologous to position 1143 in the Norway rat (*Rattus norvegicus*)? When sequences differ in length due to insertions or deletions in their evolutionary history, site homology may be difficult to assess. Making this assessment is the goal of sequence **alignment** (DeSalle and Rosenfeld 2013).

Unfortunately, it is often impossible to know that a particular character is homologous across all species in a group unless one already knows something about phylogeny. For example, Pettigrew (1986) argued that megachiropteran bats are more closely related to primates than to microchiropterans. If this hypothesis were true, wings would not be homologous across the two bat clades and would instead have arisen by **convergent evolution** from separate ancestors. Thus, assumptions about character homology are really hypotheses that may be, to some extent, tested by phylogenetic analysis. Hennig (1966:206) insightfully referred to the relationship between hypotheses of homology and phylogeny as "reciprocal illumination." A mistaken hypothesis of homology, in which similar derived states are shared by species due to convergent evolution, is called **homoplasy**.

A second critical feature of characters selected for phylogenetic analysis is that they be independent of one another, such that patterns of covariation among species can legitimately be attributed to co-ancestry rather than other causes. Characters may be correlated for several reasons. For example, "3rd premolar = present or absent" and "3rd premolar size = large or small" are *logically* correlated characters: premolars are necessarily present if they are also small. Some characters may be *functionally* correlated: gliding locomotion occurs in mammals such as colugos and flying squirrels that have a patagium (a flap of skin that stretches from wrists to ankles). Characters may be *structurally* correlated. Ribosomal RNA sequences maintain their secondary structure by complementary base-pairing of nucleotides in stem regions: an "A" at one stem position necessitates a "T" at the complementary position elsewhere in the sequence (Knies et al. 2008). Characters may be *developmentally* correlated: levels of the cell signaling protein ectodysplasin during embryonic development affect the number and shape of cusps on mouse molars (Kangas et al. 2004). Although character correlation is seldom an all-or-nothing relationship, systematists try to select characters that are not tightly correlated.

In addition to the problem of selecting characters, systematists must usually choose which species to include in a phylogenetic study, a consideration called **taxon sampling**. Suppose we wish to study relationships among five species in a genus that is known to be monophyletic. In this situation, exhaustive sampling is probably feasible—that is, we can include all species in our study. Exhaustive sampling may be infeasible for more diverse groups, particularly in molecular studies for which fresh tissue is required, and in

these cases investigators employ **exemplars**—species that represent known or suspected clades within a larger taxon of interest. For example, a study of interordinal relationships among marsupials might use one or more species from each of the seven living, monophyletic orders. As with any sampling scheme, phylogenetic accuracy increases with denser taxon sampling; the use of exemplars represents a trade-off between feasibility and thoroughness. A further consideration in taxon sampling is choice of **outgroups**, species that are clearly not part of the group under study (the "ingroup") but are closely related enough that their position on an estimated phylogeny serves to locate the ingroup root or helps to infer the primitive states of ingroup characters (Smith 1994).

Once appropriate sets of taxa and characters have been identified and all states determined, the results are assembled into a **data matrix** in which species define rows, characters define columns, and states are the cell values. For molecular sequences, the data matrix is an alignment. From this point, phylogenetic analysis can take several different directions. The most fundamental distinction among methods currently in use is model-based versus model-free approaches. Model-based procedures are explicitly statistical and include additive-distance, maximum-likelihood, Bayesian, and species-tree methods (Yang 2014). Each relies on a probabilistic model of evolution that specifies relative rates of change among the states of characters, and perhaps sets other constraints on character evolution. Model-based methods are most often applied to molecular sequences because alignments represent relatively large numbers of characters with regularities in their substitution patterns. For just one example, transition substitutions (A-G and C-T) occur at measurably higher rates than transversion substitutions (all other pairs) in animal mtDNA (Moritz et al. 1987); this pattern can be incorporated into a model that informs our choice of a phylogeny. Molecular systematists expend considerable effort identifying models that accurately and economically apply to particular data sets (Posada 2009). The computational requirements of model-based analyses are considerable, but are facilitated by software packages such as PAUP* (Swofford 2002), MEGA (Tamura et al. 2013), RAxML (Stamatakis 2014), MRBAYES (Ronquist et al. 2012), and STAR (Liu et al. 2009).

The most widely used model-free approach to phylogenetic inference is **parsimony**, the principle that the best estimate of phylogeny from a particular data matrix is that which requires the fewest character-state changes. Although its methodological underpinnings have been intensely debated (Farris 1983; Felsenstein 2004; Sober 1988), parsimony is the dominant analytical framework for morphological characters and is employed with molecular data as well. Parsimony analysis of anatomical traits is sometimes combined with character analysis of the sort championed by Hennig (1966). Typically, uninformative characters—those that require the same number of state changes on all possible trees—are excluded from a data

matrix. Investigators may use fossil, outgroup, or developmental data to decide which state of a character is phylogenetically primitive (ancestral) for the ingroup (i.e., they may polarize the states). In some cases, a stepwise series of evolutionary transformations between states can be inferred and the states ordered for phylogenetic analysis. Researchers may decide that some characters are less prone to homoplasy than others, and therefore apply differential weights across columns of the data matrix. Polarization, ordering, and weighting use a priori hypotheses about character evolution to constrain the search for a minimum-length tree. However, character hypotheses are often difficult to defend and many investigators perform unpolarized, unordered, and uniformly weighted parsimony analyses. This is especially true, if not universally appropriate, for parsimony analyses of molecular sequence data (Cracraft and Helm-Bychowski 1991).

Obtaining an optimal phylogeny for a particular data matrix under any of the above criteria is not the end of phylogenetic inference. Investigators want to know how much better the best tree is than other trees, or how much *support* the data provide for specific groups on the optimal tree. There are several ways to make a statistical assessment of whether the difference in optimality scores between alternative trees is significant (Felsenstein 2004). Such tree-comparison tests allow researchers to decide whether an a priori hypothesis of phylogeny is consistent with a particular data matrix, even if it does not match the optimal tree for that matrix. The most widely used method of assessing support for individual branches on an optimal tree is **bootstrapping** (Felsenstein 1985a). Characters are resampled with replacement from the original data matrix to create many pseudoreplicate matrices and an optimal tree is obtained for each. This process mimics the sampling of new characters that have the same properties as the ones actually sampled and thus approximates the level of character-sampling error inherent in the original data. The frequency with which a particular clade on the optimal tree appears among pseudoreplicates is a measure of that clade's support by the original data. Trees estimated with Bayesian methods include "posterior probability" values for each clade, which reflect the frequency with which those clades were recovered as optimal during the tree-sampling process (Yang and Ranala 2012). Groups that appear on an estimated tree, but are poorly resolved, must be viewed with caution.

CLASSIFICATION

Since the time of Linneaus, biologists have grouped species into progressively more inclusive categories to produce hierarchical classifications. Thus, Mammalia is one of several groups within Chordata, Rodentia is one of several groups within Mammalia, Cricetidae is one of several groups within Rodentia, *Cricetus* is one of several

groups within Cricetidae, and *Cricetus cricetus* (the common hamster) is one of several species within *Cricetus*. Although the concept of hierarchical classification is almost universally accepted by systematists, the criteria used to place groups within groups have been extremely controversial. Perhaps the strongest argument in Hennig's (1966) foundational work is that **biological classifications** should exclusively reflect phylogeny. In other words, *only monophyletic groups should be recognized* (i.e., named). For most of the history of biological taxonomy, such a tenet was impractical because detailed phylogenies were unknown. "Evolutionary" classifications (Simpson 1961), developed after Darwin, emphasized groups delineated by shared anatomical adaptations, whether those adaptations involved primitive or derived characters (but to the exclusion of convergent ones). However, after robust methods of phylogenetic inference began to be developed in the 1960s, Hennig's call for a **phylogenetic classification** gained many adherents and is currently advocated by most practicing taxonomists.

Unfortunately, most major taxonomic groups (including those of mammals) were named long before Hennig, and many such names have attained the status of tradition. Moreover, the difficulty in applying monophyly as a criterion for classification is that our understanding of phylogeny, though far more advanced than it was a century ago, is still undergoing revision. Sometimes traditional and phylogenetic groups coincide, as in the case of bats (Chiroptera), primates (Primates), or rabbits (Lagomorpha). In other cases, relationships have become sufficiently established that phylogenetic groups have supplanted or restricted traditional ones. Thus, mammalogists no longer use "Insectivora" to denote a group that includes tree shrews. The latter are recognized as a major clade (Scandentia) more closely related to primates than to ordinary shrews. When phylogenetic results conflict, classificatory issues become contentious. Such was the case for whales and dolphins versus even-toed ungulates: morphological evidence (Novacek 1992) favored treating these as sister groups (Cetacea and Artiodactyla, respectively), whereas molecular data (Zhou et al. 2011) support inclusion of the former within the latter (giving a single group, Cetartiodactyla—see Chapters 19 and 20). In any event, the stability of classification is now tied to progress in phylogenetic reconstruction: as the tree of life takes on a more definite shape, so too will the names applied to its branches.

ESTIMATING DIVERGENCE TIMES

Systematists have long been interested in knowing the absolute ages of evolutionary events. For example, how long ago did metatherian mammals (marsupials and their fossil relatives) branch off from the lineage leading to eutherians (placental mammals and their fossil relatives)? For
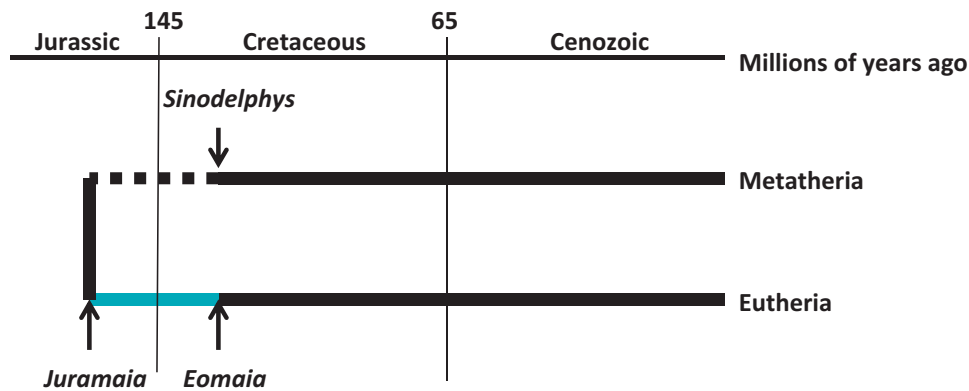
Figure 2.17 **Fossil first occurrences and divergence dates of sister groups Metatheria and Eutheria.** From 2003 to 2011, the oldest metatherian and eutherian fossils known were *Sinodelphys* and *Eomaia* from the Early Cretaceous, which suggested that the two lineages diverged at least 125 mya. In 2011, discovery of *Juramaia*, a fossil eutherian from the Late Jurassic, extended the minimum divergence date of both lineages to 165 mya. The tan line indicates extension of the eutherian fossil record; the dashed line shows the interval during which metatherians form a ghost lineage.

much of the history of mammalogy, answering such questions has been the province of paleontology. Fossils provide direct evidence that members of specific groups existed at specific times in the past. Two considerations are critical for interpreting fossil evidence of divergence time: (1) the cladogenic event must be defined by phylogenetic analysis; and (2) the age of the oldest fossils represent a *minimum* estimate of divergence time—that is, the lineages may have diverged earlier, but left no fossils or only fossils that have yet to be discovered. For nearly a decade, the oldest known metatherian and eutherian fossils—*Sinodelphys* (Luo et al. 2003) and *Eomaia* (Ji et al. 2002), respectively—were contemporaries from the Early Cretaceous Yixian Formation in Liaoning Province, China, approximately 125 million years old. But this date would tell us little about the divergence time of metatherians and eutherians if we did not consider them sister groups, or if we could not place *Sinodephys* within Metatheria and *Eomaia* within Eutheria. The latter assignment has in fact been questioned by O'Leary and colleagues (2013), though it remains widely accepted (see Meng 2014). But note how phylogenetic uncertainty limits the relevance of a fossil age for estimating divergence time. In any case, assuming the two lineages were distinct by the Early Cretaceous, their actual divergence must be somewhat older.

This picture changed when Luo and coworkers (2011) described the eutherian *Juramaia* from Late Jurassic deposits in Liaoning, thereby extending the age of eutherians to some 160 mya (Figure 2.17). Again, phylogeny gives the framework for interpreting first-occurrence fossils. Given that metatherians and eutherians are sister-groups, both lineages existed (by definition) after their separation from a common ancestor. Thus, the oldest fossils representing *either* lineage provide a minimum divergence date for both. Although fossil metatherians do not appear until the Early Cretaceous, the metatherian lineage must have been present at least since the Late Jurassic; from the Late Jurassic
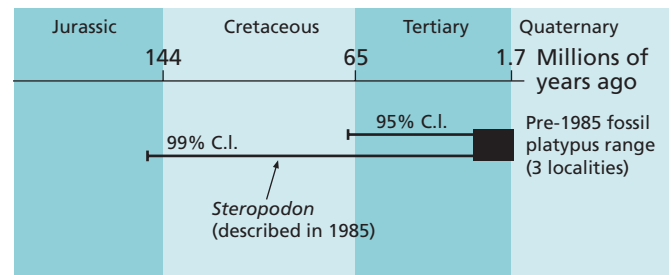
Figure 2.18 **The fossil record of platypuses.** Confidence intervals are shown for the pre-1985 stratigraphic range of platypus fossils. The arrow shows the stratigraphic level of *Steropodon*, an Australian platypus fossil described in 1985. *Adapted from Marshall (1990).*

to the Early Cretaceous, metatherians are a **ghost lineage** (an evolutionary lineage inferred to exist but which has no fossil record; Norrell 1992).

Fossil first-occurrences provide point estimates of divergence times that are likely to be underestimates due to the existence of lineages prior to their oldest fossils. Paleontologists have attempted to obtain more meaningful interval estimates by modeling the fossil record as the outcome of a stochastic process such that the times (or stratigraphic levels) at which fossils occur are randomly distributed (Marshall 1990). This approach allows one to calculate a confidence interval for the stratigraphic range of a lineage. Depending on the model employed and the distribution of actual fossil horizons, a 95% or 99% confidence interval on a lineage's duration may indicate that the lineage could be much older than its oldest fossils. Prior to 1985, the monotreme fossil record consisted of three localities from the Pleistocene and Middle Miocene, but Marshall (1990) noted that an estimated 99% confidence interval on this range extended back to the Late Jurassic (Figure 2.18). *Steropodon*, a fossil platypus from the

Cretaceous of Australia discovered by Archer and colleagues (1985), fell squarely within this interval and extended the minimum age of monotremes by over 80 million years. The examples of *Juramaia* and *Steropodon* illustrate the pitfalls of a too-literal reading of the fossil record in estimating divergence times.

The advent of molecular data in phylogenetics brought with it the possibility of estimating temporal divergence from sequence divergence. Zuckerkandl and Pauling (1965) first proposed the existence of a **molecular clock**, such that the rate of sequence evolution is roughly the same for any given protein in all lineages. Many studies have evaluated the molecular clock for different kinds of molecular data, different loci, different groups of organisms, and different models of evolution (Lanfear et al. 2010). The almost universal realization has been that there is considerable variation in the rate of sequence evolution among loci and lineages, although there are examples of local clocks, or loci that show roughly uniform rates of change within a particular group of closely related species. In these cases, researchers have applied molecular-clock dating to obtain estimates of divergence times.

If a local clock can be documented, we can calculate divergence times if we know the divergence rate. For example, if sequences diverge at 2% of their sites per million years (my), sequences that are 10% different must have separated from a common ancestor 10% / (2%/my) = 5 mya. Of course, the divergence rate is never known and must be estimated, usually by calibration of observed sequence differences against some independently estimated divergence date. Calibration points are most often obtained from the fossil record or past geographic events (e.g., continental separations) that can be stratigraphically or radiometrically dated. This simple logic has been justly criticized on numerous methodological grounds (e.g., Graur and Martin 2004), but has nonetheless produced many reasonable (if approximate) timescales for phylogenies of closely related species (e.g., Krajewski et al. 2000; Mercer and Roth 2003).

At deeper phylogenetic levels, the compound sources of error in molecular-clock estimates become much more problematic. For a given locus, rates of change usually are not uniform *among* branches of the phylogenetic tree and sometimes are not constant over time *within* branches of the tree. Moreover, the fossil record may be so poor that few reliable calibration points can be obtained. In the face of such complications, modern analytical methods for sequence data allow divergence times to be estimated, along with confidence intervals (Kumar and Hedges 2016). Such relaxed clock methods include the penalized likelihood approach of Sanderson (2002) and the Bayesian approaches of Thorne and Kishino (2002), Drummond and colleagues (2006), and Yang and Rannala (2006). The latter employ probabilistic models of changing evolutionary rates over a phylogeny (rather than assuming a uniform constant rate) and use fossil or other constraints on specific divergence times (rather than as fixed calibration points). Tamura and colleagues (2012) proposed a conceptually distinct and computationally efficient method for statistical estimation of divergence times on molecular phylogenies without using a model of lineage-specific rate variation. We will discuss the application of some of these methods to the diversification of mammal orders in Chapter 3.

SUMMARY

- Research in mammalogy relies on many specific techniques for studying mammals in the field or laboratory, assembling and studying preserved specimens, and analyzing data obtained to address hypotheses about evolution and ecology. A background in statistics and experimental design is essential for modern mammalogists.

- Mammals are captured in the field using techniques adapted for the size of the mammal and the purpose of collection. Small and intermediate-sized terrestrial species are taken in live traps or kill traps placed on the ground and checked regularly. Large terrestrial mammals may be anesthetized with dart guns, trapped with nets, or herded into enclosures. Bats are most frequently captured with mist nets. Mammalogists follow standard procedures for the safe and humane treatment of wild animals in the field and in captive settings.

- Individuals of large, active species may be identified in the field by characteristics such as size, coloration, or behavior patterns. Smaller, more cryptic mammals are identified with tags, collars, dyes, fur shavings, toe clips, ear notches, and radioisotopes.

- The movements of mammals in the field can be monitored by physical tracking procedures or with radio signals. Passive integrated transponder (PIT) tags, which are small devices usually implanted beneath the skin, transmit a unique code when excited by the electronic field of a reader. Radiotelemetry uses radio transmitters attached to animals, the signals of which are detected with antennae connected to receivers; the animal's location is determined by triangulation after taking fixes from two or more locations. The Global Positioning System (GPS) allows

animals fitted with GPS collars to be located by satellite. Analyses of animal movement and habitat use have been greatly facilitated by the development of computer geographic information systems (GIS). Geographic data can be integrated with mark-recapture studies to estimate population size, home-range size, and other life-history traits. Such analyses are enhanced by statistical modeling of the trapping process.

- The behavior of wild mammals is most often studied by direct observation or video recording. Given a hypothesis about behavior, researchers perform observational sampling by noting the occurrence of behavioral states or events in the animals under appropriate conditions. The most general observational sampling techniques are focal animal and scan sampling.

- In mammalogy, physiology research focuses on whole-organism analyses of nutrition, metabolism, reproduction, and other aspects of organ and tissue function. Nutritional requirements vary among species and are usually assessed by dietary preferences, which in turn are assessed by direct observation of feeding, stomach content analysis, or scat analysis. The nutritional condition of mammals reflects the extent to which their nutritional requirements are being met. Basal (resting) metabolic rate (BMR) is negatively correlated with body size. Field metabolic rates (FMRs), characteristic of mammals engaging in normal activities, are measured with doubly labeled water and show more variation than BMRs. Depending on the species, the reproductive condition of males can be determined by descended testes, spermatorrhea, or sperm counts. Female estrus is indicated by behavioral changes, cornified vaginal epithelium cells, or surgical examination. Levels of reproductive hormones in both sexes can be monitored with immunological assays.

- Stable isotope analysis can be used to study the diets, habitat preferences, and movements of wild mammals. This method exploits the different isotopic ratios of carbon, nitrogen, phosphorus and other common atoms in mammal tissue that result from varying environmental sources and fractionation processes.

- Molecular markers have become important tools for studying mammalian evolution and ecology. The number and morphology of chromosomes within a mammalian cell is its karyotype. Protein electrophoresis allows researchers to determine the genotype of many individuals at many enzyme loci with relative ease, thereby providing insight on levels of genetic variation in populations. The polymerase chain reaction (PCR) enables researchers to assay DNA sequence variation without in vivo cloning, and DNA markers are currently the most widely employed tool in mammalian evolutionary genetics. Microsatellites are regions of DNA in which short sequences (1–4 bases) occur as tandem repeats. Their high mutation rate generates variation in repeat number among individuals, making them extremely useful for population genetics. Technological advances have made it possible to obtain DNA sequences from a wide range of sources quickly and easily. Mitochondrial DNA (mtDNA) is the most frequently studied sequence in mammalogy, principally due to its haploid, nonrecombining, and maternally transmitted mode of inheritance. However, mtDNA is most informative for closely related taxa, and mammalogists have turned to the nuclear genome to address a broader range of evolutionary questions.

- Systematic collections of museum specimens are central to the study of mammalian diversity. Museum specimens include study skins, skulls, skeletons, spirit-preserved carcasses, fossils, tissue specimens, and DNA samples. Curation of such collections includes maintaining an accurate and accessible database as well as the specimens themselves. Museum specimens form the basis of regional biotic surveys and research in comparative anatomy, systematics, morphometrics, and evolutionary genetics.

- The study of intraspecific variation in mammals includes sexual dimorphism, growth, and population subdivision. In the latter, molecular markers play important roles in assessing gene flow, effective population size, and geographic structuring of genetic variation. Intraspecific phylogeography is the study of genealogical and geographical relationships among lineages within a species, often with a view to understanding the history of population subdivision.

- Like other biologists, mammalogists have struggled to formulate a coherent and operational definition of species. While several definitions are current, all of them emphasize the ability to diagnose species by heritable characteristics. Mammalogists adhere to the practice of designating type specimens and follow the rules of the International Code of Zoological Nomenclature in giving formal names to species and higher taxa. Species descriptions and analyses of species boundaries are specimen-based undertakings that, in mammalogy, have come to rely heavily on the use of molecular information.

- The goal of phylogenetics is to reconstruct precise evolutionary relationships among species using the evidence provided by characters. Characters are selected for phylogenetic analysis on the basis of homology, levels of variation, and independence. Modern phylogenetic inference methods are model-based (e.g., maximum likelihood, Bayesian analysis) or model-free (e.g., parsimony) and include some measure of support for individual clades. Phylogeny is the primary basis for supraspecific classification, though uncertainty about some mammalian relationships has produced disagreement about the composition of taxonomic groups. Statistical analyses of the fossil record and molecular sequence divergence can provide reasonable estimates of divergence times on a phylogeny, though confidence intervals on these estimates may be quite large.

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DISCUSSION QUESTIONS

1. Suppose you must determine which species of mammals occur in a 10-hectare plot, along with estimates of the relative abundance of each species. The plot includes a variety of habitat types such as forest, brush, and open grassy areas. Outline a proposal for this research project, noting which methods described in this chapter would be most helpful. How would published works or reference collections facilitate your study?

2. As a result of the survey you performed in the previous question, you discover some mice that you cannot identify and you suspect they represent a new species (i.e., one that has not yet been formally described). What steps would you take to determine whether this is true?

3. Suppose the mice you discovered in Question 2 do represent a new species, which you describe and include in a genus that contains nine other species, all of which are relatively common but have disjunct ranges scattered across your continent. No phylogeny of this genus has ever been suggested, and your university invites you to prepare a proposal to obtain such a phylogeny. What are the major activities that this project will entail? What logistic and financial considerations are relevant?

4. Many species of mammals are currently endangered, facing the very real possibility of extinction, often due to destruction of their habitat by human activities. What, if any, special considerations should be given to studying endangered species with the methods described in this chapter? Make a series of general policy recommendations.

5. You are asked to develop a general activity time budget for pronghorn antelope (*Antilocapra americana*) living at several sites in northern Colorado. Describe the methods you might use to conduct such a study. What problems might be encountered? What measures could you adopt to resolve those difficulties?

CHAPTER 3

Phylogeny and Diversification of Mammals

Relationships and Classification of Living Mammalian Orders

SIMPSON'S CLASSIFICATION OF MAMMALS

The comprehensive classification of mammals put forward by Simpson (1945) is a landmark in the history of mammalogy. Critically synthesizing and building upon generations of taxonomic work by previous authors—some pre-evolutionary or speculative, some grounded in evidence and careful reasoning—Simpson's scheme (Table 3.1) exerts a strong influence on our thinking about mammalian diversity to this day. Although much of mammalian classification has changed as a result of subsequent research, many of Simpson's groups and the names he assigned them remain integral to the vocabulary of vertebrate systematics. Here we focus on the identity and groupings of living mammalian orders (information on intraordinal classification is provided in Chapters 10–21). Understanding the historical development of mammal ordinal classification from Simpson to the present day (Table 10.1) illustrates the ineluctable connection between taxonomy and phylogeny, the transforming influence of phylogenetic methodology, the illuminating power of fossil discoveries, and the breakthroughs of molecular systematics.

George Gaylord Simpson (1902–1984) was an American paleontologist and among the most influential evolutionary biologists of the 20th century. Along with Ernst Mayr, Theodosius Dobzhansky, G. Ledyard Stebbins, and others, he was an architect of the "New Synthesis" in evolutionary biology— the integration of population genetics theory with natural history data to form a comprehensive, explanatory model of the evolutionary process. His classification of mammals was only one of many significant works. In addition to classic evolutionary writings, he provided a textbook of systematic zoology (Simpson 1961) that formalized many of the principles underlying his classification of mammals. Along with Mayr and others (e.g., Mayr et al. 1953), Simpson was a champion of what came to be known as "evolutionary taxonomy,"

Table 3.1 Simpson's (1945) classification of living mammalian orders

Class Mammalia

Subclass Prototheria
    Order Monotremata (platypus, echidna)
Subclass Theria
  Infraclass Metatheria
    Order Marsupialia (marsupials)
  Infraclass Eutheria
   Cohort Unguiculata
    Order Insectivora (hedgehogs, shrews, moles, tenrecs,
      golden moles, solenodons, elphant shrews, tree shrews)
    Order Dermoptera (flying lemurs)
    Order Primates (prosimians, monkeys, apes)
    Order Chiroptera (bats)
    Order Edentata (sloths, anteaters, armadillos)
    Order Pholidota (pangolins)
   Cohort Glires
    Order Rodentia (rodents)
    Order Lagomorpha (rabbits, hares, pikas)
   Cohort Mutica
    Order Cetacea (whales, dolphins, porpoises)
   Cohort Ferungulata
   Superorder Ferae
    Order Carnivora (dogs, cats, pinnipeds)
   Superorder Protoungulata
    Order Tubulidentata (aardvarks)
   Superorder Paenungulata
    Order Proboscidea (elephants)
    Order Hyracoidea (hyraxes)
    Order Sirenia (manatees, dugongs)
   Superorder Mesaxonia
    Order Perissodactyla (horses, tapirs, rhinoceroses)
   Superorder Paraxonia
    Order Artiodactyla (cattle, deer, camels, hippos, pigs,
      pecarries, tragulids, giraffes, pronghorns)

a systematic philosophy holding that classification should reflect phylogeny and shared adaptations (Ridley 1986). This is distinct from the dictum of phylogenetic systematists (Chapter 2) that classification should reflect phylogeny alone. Although modern systematics embraces the latter position, Simpson's classification of mammals is very much a work of evolutionary taxonomy. Specifically, the classification admits the possibility that some groups are paraphyletic (i.e., constituted by some but not all descendants of a single common ancestor, often characterized by shared primitive characters). Admittedly paraphyletic orders, such as "Insectivora," were certain to be reclassified by phylogenetic systematists as knowledge of evolutionary relationships improved. Others that seemed monophyletic, such as Artiodactyla, have been seriously challenged by molecular or other data. Most of Simpson's orders, as we will see, have survived decades of subsequent research and are now recognized as monophyletic groups (Table 10.1). The same cannot be said of his supraordinal groups.

In the sections that follow, we explore the basis for current departures from Simpson's classification, as well as some provocative challenges to it that ultimately failed.

Such a review, constrained to just a few pages, is possible largely because Simpson's (1945) monograph so thoroughly summarized the character evidence and arguments of previous taxonomists (Szalay 1999).

MONOTREMES AND PROTOTHERIA

Species of platypus and echidna are highly distinct from other mammals. Their egg-laying reproductive mode and other unusual characteristics (Chapter 10) are a mixture of primitive and specialized conditions (Hand 2006), though derived features of their nasal and frontal bones have been considered indicative of monophyly (Augee 1983). More problematic has been the "Subclass Prototheria" and the relationships of monotremes to other living mammals. Although Simpson (1945) restricted Prototheria to monotremes, the larger taxon has been thought by others to include fossil groups such as triconodonts, docodonts, and multituberculates (Rose 2006). Evidence for this view was discredited by Kemp (1983), and subsequent paleontologists have struggled to place monotremes reliably among extinct mammal clades. Luo and coworkers (2001) suggested that monotremes form an ancient clade (Australosphenida) with two Cretaceous genera from the Southern Hemisphere, deeply divergent from therian mammals and implying parallel origins of tribosphenic molars (see Chapter 4). Thus it is not clear at present which nonmonotreme taxa, if any, should be considered prototherians.

This situation was complicated by Janke and colleagues (1996 and subsequent papers), who recovered a phylogenetic tree from mitochondrial genomes, which suggested that monotremes and marsupials are sister groups apart from eutherians. This relationship was first posited by Gregory (1947), whose "palimpsest theory" united monotremes and marsupials in a clade he called "Marsupionta." If correct, the theory would imply that the many derived traits shared by therian mammals (marsupials and placentals) are convergent rather than homologous. The ensuing controversy prompted Kirsch and Mayer (1998), whose DNA hybridization study also favored Marsupionta, to review the anatomical evidence for mammalian subclasses and conclude that the case for therian monophyly was in fact equivocal. They argued, for example, that the reproductive systems of marsupials and placentals are so distinct that "live birth" in the two groups cannot be considered a homologous character. This uncomfortable situation persisted even as contradictory (but inconclusive) molecular evidence mounted, until van Rheede and colleagues (2006), Kullberg and coworkers (2008), and Hutley (2009) presented large DNA-sequence data sets from nuclear protein-coding genes, which strongly rejected Marsupionta in favor of Theria. Whether the initial mitochondrial and DNA hybridization results were idiosyncratic or based on insufficient data for such ancient divergences, the molecular Marsupionta episode seems to have resolved itself in support of Simpson's (1945) arrangement. Even so, it encouraged a

valuable reassessment of traditional phenotypic characters that has enriched our understanding of early mammalian evolution.

MARSUPIALS

There has been little debate in recent decades that living marsupials constitute a monophyletic group. However, taxonomists after Ride (1964) have rejected Simpson's (1945) "lumping" of all marsupials into a single order. The seven living orders recognized today are those of Aplin and Archer (1987) and include several groups that were referred by Simpson to lower ranks—e.g., the current Order Peramelemorphia (bandicoots) corresponds to Simpson's Superfamily Perameloidea. Much more significant is our improved understanding of how these orders are related.

Marsupial evolution has long been considered a biogeographic puzzle involving dispersal or vicariance among southern continents (Chapter 10), but the exact phylogenetic relationship of American and Australiasian taxa was unclear. Are either or both of these groups monophyletic? A breakthrough on this question came when Szalay (1982) showed that the American order Microbiotheria (today represented by one species of *Dromiciops*; Súarez-Villota et al. 2018) shares derived features of its ankle joint with Australasian marsupials. This stimulated a reappraisal of other anatomical and cytological evidence such that Aplin and Archer (1987) recognized Szalay's cohorts Ameridelphia (didelphimorphs and paucituberculates) and Australidelphia (microbiotheres and Australasian orders) as monophyletic sister groups. Subsequent molecular studies consistently supported the monophyly of Australidelphia, though placement of microbiotheres within that clade proved elusive until Amrine-Madsen and coworkers (2003). Using sequences of five nuclear genes, these authors resolved *Dromiciops* as sister to a clade of all living Australasian orders, a result that has persisted through the most recent molecular analyses of marsupials (Meredith et al. 2008; Mitchell et al. 2014). Support for Ameridelphia, on the other hand, has waned. Aplin and Archer (1987) cited a single key character—epididymal sperm-pairing—as linking didelphimorphs and paucituberculates. Molecular studies, however, generally fail to unite the two orders, and instead place the root of Marsupialia between them (e.g., Meredith et al. 2008; Mitchell et al. 2014). Moreover, sperm-pairing appears to be different in the two groups—side by side in didelphimorphs and head to head in paucituberculates (Temple-Smith 1987). The most comprehensive analysis of mammalian ordinal relationships (Meredith et al. 2011) places paucituberculates as the earliest branch among living marsupials (Figure 3.1), but location of the marsupial root is best considered unresolved.

Within Australidelphia, it has become clear that the carnivorous orders Dasyuromorphia, Peramelemorphia, and Notoryctemorphia form a clade apart from the herbivorous Diprotodontia (Figure 3.1). This arrangement allows us to interpret the long-standing conflict over dental and pedal similarities among marsupials. Dasyuromorphs, bandicoots, and didelphimorphs are **polyprotodont** ("many first teeth") in that they possess multiple lower incisors per quadrant, whereas diprotodonts and paucituberculates have a single pair of lower incisors. However, bandicoots and diprotodonts are **syndactylous**—the second and third digits of their hind feet are enclosed in a single sheath of soft tissue—in contrast to the typical **didactylous** (separate toes) condition of dasyuromorphs. The molecular tree implies that both sets of traits have evolved convergently among marsupials and neither is indicative of phylogenetic relationships. This tree also yields the first confident placement of the enigmatic marsupial moles (notoryctemorphs), whose highly specialized skeleton has precluded a clear resolution of relationships based on morphology.

INSECTIVORES

Simpson (1945:175) considered his Order Insectivora as "something of a scrap basket for small animals of generally primitive character that are not clearly referable to some more distinctive order." Within Insectivora, however, he noted that "four fairly well-defined groups have long been recognized"—(1) tenrecs and golden moles, (2) hedgehogs, (3) shrews and moles, and (4) elephant shrews and tree shrews—although he did not propose subordinal divisions for them. Modern taxonomy (Table 10.1) recognizes the first three as distinct orders (Afrosoricida, Erinaceomorpha, and Soricomorpha, respectively), but splits the last into separate groups (Macroscelidea and Scandentia). Simpson (1945) felt that tree shrews were closer to primates than to other insectivores; this highlighted the explicitly paraphyletic nature of his Insectivora. If these groups do not form a single clade, to what other mammals is each of them related?

Morphologists debated a number of possible arrangements (summarized by Novacek 1992), but no hypothesis was consistently supported until a series of molecular studies beginning in the mid-1990s converged on our present understanding of insectivoran affinities. Using nuclear and mitochondrial gene sequences, Stanhope and colleagues (1996, 1998a, 1998b), Madsen and coworkers (1997), and Springer and colleagues (1997, 1999) documented that afrosoricidans and macroscelideans are part of a larger clade that includes Simpson's (1945) paenungulates (elephants, sirenians, and hyraxes) and the aardvark (Figure 3.1). This clade, named "Afrotheria" by Stanhope and colleagues (1998b) because of its members' distributions and fossil origins, is discussed further in its own section below. Stanhope and coworkers (1998b) and later authors also found that hedgehogs and soricomorphs are sister groups, a clade that Waddell and colleagues (1999) called "Eulipotyphla." Tree shrews (Scandentia) have been much harder to place, with both morphological and molecular data persistently suggesting, but not resolving, an association with dermop-
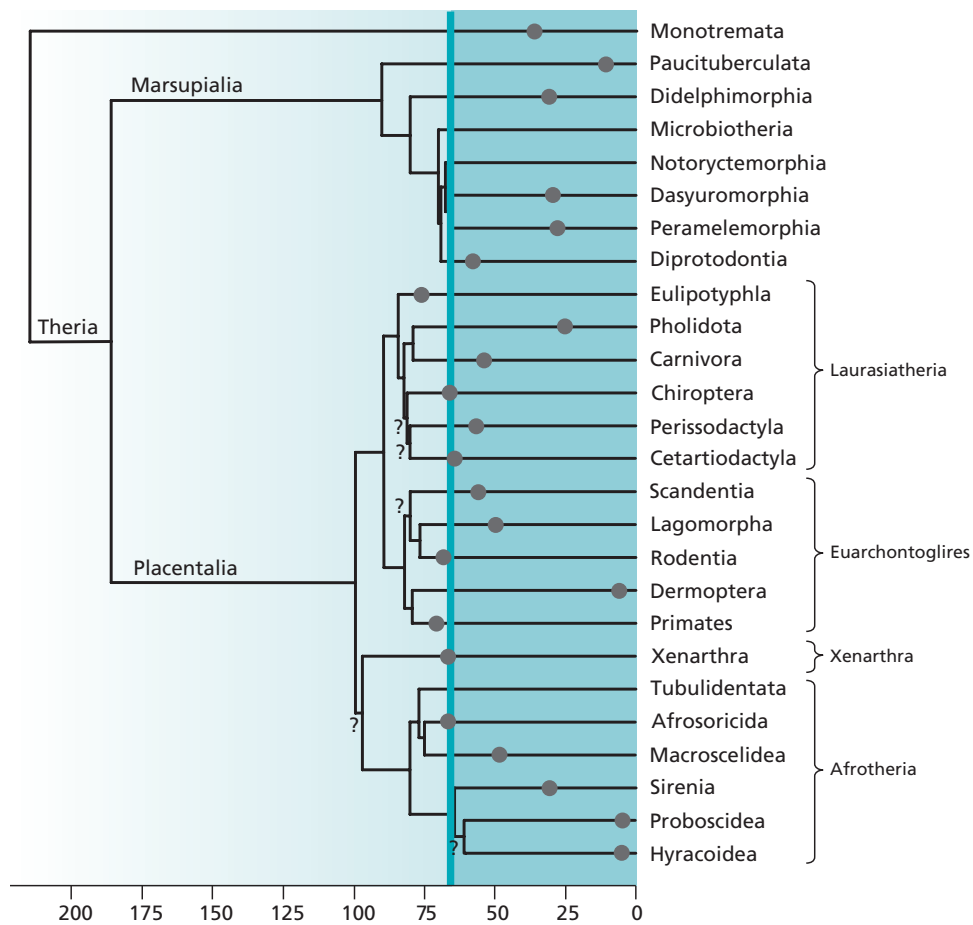
Figure 3.1 Phylogenetic time tree of mammalian orders. Branching order is based on likelihood analysis of amino acid sequences of 26 gene fragments (11,010 aligned amino acids) from 164 mammal species (representing 97%–99% of extant families) and 5 nonmammalian vertebrate outgroups. Divergence times were estimated with a relaxed clock method using autocorrelated rates and hard-bounded constraints. Nodes with question marks (?) were considered poorly supported by the authors. The time scale at bottom is in mya, and the Cretaceous-Paleogene (KPg) boundary at 66 mya is indicated by the tan, vertical line. Dots on each ordinal branch show the point estimate of the time of earliest diversification of extant lineages within each order. *Adapted from Meredith et al. (2011).*

terans (colugos) and primates (Novacek 1992; Murphy et al. 2001a, 2001b; Song et al. 2012), in keeping with Simpson's (1945) opinion noted above. Murphy and colleagues (2001a) and Meredith and coworkers (2011) placed tree shrews, dermopterans, and primates in the large clade Euarchontoglires (see next section), but the sister group of scandentians is still unclear. Song and colleagues (2012) resolved primates as the sister of scandentians, but O'Leary and coworkers (2013) placed dermopterans in this position. What is clear, however, is that "insectivorans" are a phylogenetically diverse group of lineages scattered across the eutherian tree.

EUARCHONTOGLIRES

Gregory (1910) proposed Superorder Archonta to include bats (Chiroptera), colugos (Dermoptera), primates, and

scandentians. Some members of these orders share a derived ankle morphology (the sustentacular facet of the astragalus) and a pendant penis. Although Simpson (1945) rejected Archonta, subsequent morphocladistic studies including larger sets of characters found support for it (Novacek 1992). DNA sequence data, beginning with Adkins and Honeycutt (1991), separated bats from the other archontan groups (the latter named "Euarchonta" by Waddell et al. 1999). Divorcing bats and colugos was a particularly jarring result from the standpoint of morphology in that many derived characters shared by the two groups (Simmons and Geisler 1998) must be interpreted as convergent, probably correlated adaptations for flying or gliding (Springer et al. 2007). Miyamoto (1996) and subsequent authors found support in sequence data for placing euarchontans in a clade with rodents and lagomorphs (Simpson's Glires); Murphy and coworkers (2001a) named this taxon "Euarchontoglires" (Figure 3.1), and it is now recognized

as one of four major clades of living eutherians (Meredith et al. 2011; Song et al. 2012). The extent to which this DNA-based grouping of orders (as well as that for Afrotheria and Laurasiatheria, discussed below) impugns the ability of morphological studies to resolve deep branches of placental mammals gave rise to a spirited debate (Springer et al. 2007, 2008; Asher et al. 2008).

Within Euarchontoglires, there are two historical controversies about ordinal monophyly—one (regarding bats) initiated by morphology and the other (regarding rodents) by molecular data—which were both ultimately resolved in favor of the taxonomic status quo. Reviewing them provides a useful perspective on the conflict between molecules and morphology and the evaluation of hypotheses in systematic biology.

Chiroptera is traditionally divided into two suborders, Megachiroptera (fruit bats, or "megabats") and Microchiroptera (all other bats, or "microbats") (Chapter 21). Pettigrew (1986) found that the neural pathway that transmits visual information from eyes to midbrain has a derived anatomical structure in megabats that is otherwise found only in primates and dermopterans. For example, in these groups, the retinotectal pathway (characteristic of almost all other mammals, including microbats) is greatly reduced in favor of an alternative connection, the geniculostriate pathway (Pettigrew and Jamieson 1987). Based on this and several other characters, Pettigrew (1991) concluded that megabats, dermopterans, and primates form a clade apart from microbats and, therefore, that powered **flight** evolved separately in micro- and megachiropterans. Pettigrew argued that the likelihood of convergent evolution in visual pathways is smaller than that of **convergence** in flight characters, the latter constituting in his view the only strong evidence at the time for bat monophyly. This position was disputed by Baker and colleagues (1991), who reaffirmed the wing homologies of mega- and microbats, cited several derived traits not associated with flight shared by all bats, and challenged Pettigrew's **cladistic** analyses of neuroanatomical traits. In their early molecular study of Archonta, Adkins and Honeycutt (1991) reported mtDNA sequence data in favor of bat monophyly. This was followed by several other sequence (e.g., Stanhope et al. 1992) and DNA hybridization (Kirsch et al. 1995) analyses that reached a similar conclusion; Simmons (1994) summarized the corroborating morphological evidence. Currently, most mammalian systematists consider that Chiroptera is monophyletic. Ironically, several of the molecular data sets mustered to address this problem have suggested that Microchiroptera is **diphyletic**—that is, some microbats (rhinolophoids) are closer to megabats than they are to other microbats (Springer et al. 2001b, Teeling et al. 2005; see also Feijoo and Parada 2017). Morphocladistic analyses (Gunnell and Simmons 2005) and some combined molecular-morphological analyses (O'Leary et al. 2013) continue to support the traditional suborders (Gunnell and Simmons 2005) and the conflict remains unresolved—although see the suborder terminology we use in Chapter 21.

In the title of their paper in the journal *Nature*, Graur and coworkers (1991) posed the question, "Is the guinea pig a rodent?" Based on their phylogenetic analyses of protein sequences, the answer seemed to be no. Instead the guinea pig appeared as an early placental lineage comparable to other recognized orders, implying that neither Rodentia nor Glires is monophyletic. D'Echeria and colleagues (1996) were more confident; based on analyses of complete mitochondrial genomes, their *Nature* paper declared, "The guinea pig is not a rodent." Given the apparently strong craniodental evidence for rodent monophyly (Luckett and Hartenberger 1993), controversy was bound to ensue. Early molecular studies included few taxa and simple phylogenetic analyses, both features that immediately called their results into question (Thomas 1994). Philippe (1997) recovered a monophyletic Rodentia from the complete mtDNA sequences of D'Echeria and coworkers (1996) by including three additional nonrodent species, though the rodent clade was not strongly supported. Sullivan and Swofford (1997) reanalyzed the data under more realistic models of sequence evolution (allowing for variation in substitution rates among sites) and found that rodent monophyly could not be rejected by mitochondrial protein-coding sequences. Subsequent molecular studies tried to address both shortcomings, some supporting rodent monophyly (e.g., Adkins et al. 2001) and others rejecting it (e.g., Reyes et al. 1998). Not until the benchmark paper by Murphy and colleagues (2001b) were sufficient taxon-sampling (64 species representing all placental orders, including 16 rodents), sequence-sampling (ca. 10 kb from 18 genes), and analytical rigor brought to bear on this issue, with the result that all rodent exemplars were recovered as part of a monophyletic group sister to Lagomorpha (rabbits and hares) in the traditional cohort Glires. This finding was replicated by Murphy and coworkers (2001a), the more rodent-focused study of Huchon and coworkers (2002), and subsequent work such that rodent monophyly is now considered settled. Although in some ways a false start, this episode heightened awareness among molecular systematists about the importance of using appropriate phylogenetic estimation methods, sampling enough taxa, and choosing loci with appropriate evolutionary rates for resolving deep divergences among mammals (Springer et al. 2004).

XENARTHRA

On the nomenclature of edentates, Simpson (1945:191) noted, "'Edentata' has always meant 'Xenarthra [armadillos, sloths, and anteaters] plus' whatever other forms were supposed to belong here." In Simpson's view, the latter included only the early Tertiary palaeanodonts. "Edentata" and "Xenarthra" have both been used to name the order that includes living armadillos, sloths, and anteaters, but current classification (Table 10.1) recognizes two orders, Cingulata (armadillos) and Pilosa (sloths and anteaters). Molecular data (e.g., Murphy et al. 2001a) are consistent

with this arrangement and provide strong support for cingulatans and pilosans as sister groups, such that Xenarthra is typically recognized as a supraordinal taxon. The difficulty has been in determining where xenarthrans fit on the mammalian tree. Morphologists have variously placed them in a group with pangolins (Pholidota), as sister to all other placentals ("Epitheria"), or even as a clade ("Paratheria") separate from marsupials and other placentals (Gaudin et al. 1996). Such inconsistency reflects the highly derived anatomy of xenarthrans (for which the term "bizarre" is often employed by professional anatomists; see Chapter 13). Initial DNA-sequence studies consistently placed Xenarthra near the root of Placentalia, but without much support for any particular resolution (Murphy et al. 2004). The latter difficulty is to be expected when lineages are produced by a relatively rapid series of speciation events, as seems to be the case for mammalian orders. Frustrated by the lack of resolution in sequence data, Murphy and colleagues (2007) scanned the published complete genomes of human, armadillo, elephant, opossum, and 13 other vertebrate taxa, along with unpublished genomes of several additional mammals for insertion-deletion events ("indels") within coding sequences. Such indels, which appear as distinct gaps in a multispecies sequence alignment, are examples of rare genomic changes (RGCs) (Springer et al. 2004). They are rare because of the low probability that a random insertion or deletion in a functional gene sequence will survive in the face of purifying selection. Because they are rare, they may be less likely to have evolved convergently in species that share them. Murphy and coworkers (2007) screened over 180,000 distinct exons and found four with indels that could be validated as homologous; all four supported a sister pairing of xenarthrans and afrotherians ("Atlantogenata"). Although Meredith and colleagues (2011) considered the placement of xenarthrans unsettled by molecular data, further support for Atlantogenata came from analyses of large sequence data sets (Prasad et al. 2008, Song et al. 2012). Based on combined molecular and morphological data, however, O'Leary and coworkers (2013) favored the Epitheria hypothesis. Whatever their sister-group, xenarthrans are one of the four deep lineages of eutherian mammals (Asher et al. 2009).

CETARTIODACTYLA

Simpson (1945:213) opined that cetaceans "are on the whole the most peculiar and aberrant of mammals. Their place in the sequence of cohorts and orders is indeed quite impossible to determine." Van Valen (1966) suggested that cetaceans are related to a Paleogene group of carnivorous ungulates, the mesonychians. This hypothesis gained further support when Gingerich and colleagues (1990) described the distinctly paraxonic vestigial hind foot of the Eocene whale *Basilosaurus*. Paraxonic feet are characteristic of mesonychians and modern artiodactyls ("even-toed ungulates") in that the body weight is borne on parallel axes running through robust digits III and IV (see Chapter 19). This feature suggested a common ancestry for the three groups (Novacek 1992), which was subsequently supported by additional cetacean fossils, morphological characters, and early molecular analyses. However, Graur and Higgins's (1994) protein and mtDNA sequence investigation showed that cetaceans are nested *within* Artiodactyla. This study included only four taxa, and its implication that artiodactyls are not monophyletic received little credence at the time. However, an analysis of mitochondrial cytochrome *b* genes by Irwin and Arnason (1994) had better taxonomic sampling and suggested that the closest living relatives of cetaceans are in fact hippopotamuses (members of the artiodactyl family Hippopotamidae). In what was perhaps the most unanticipated series of congruences in mammalian molecular systematics, numerous subsequent studies with more taxa and a greater variety of molecular markers confirmed the whale-hippo clade within the larger set of artiodactyl lineages (reviewed by Gatesy and O'Leary 2001). The same result occurs in the foundational work on placental interordinal relationships by Madsen and coworkers (2001) and Murphy and colleagues (2001a, 2001b), more recent molecular analyses by Meredith and coworkers (2011) and Hassanin and colleagues (2012), and combined DNA-morphology studies by Gatesy and coworkers (2013) and O'Leary and colleagues (2013). The clade comprising cetaceans and artiodactyls was named "Cetartiodactyla" by Montgelard and colleagues (1997); that comprising cetaceans and hippos was called "Whippomorpha"—a whimsical combination of *wh*ale and *hippo*—by Wadell and coworkers (1999). Documentation by Gingerich and colleagues (2001) of a "double-pulley" astragalus in the Eocene whale *Rhodocetus* solidified the case for Cetartiodactyla (this derived trait was formerly thought to occur only in artiodactyls), but morphological data alone have so far provided little support for Whippomorpha (O'Leary and Gatesy 2008). The closest relative of cetaceans among artiodactyls remains controversial.

AFROTHERIA

Simpson (1945) traced the **alliance** of proboscideans, sirenians, and hyraxes in his Superorder Paenungulata to Gill (1870). The morphological traits upon which this grouping is based are described in Chapter 12, and it has received fairly consistent support from molecular studies (e.g., Kuntner et al. 2010). Although Simpson placed paeunuglates together with aardvarks (Tubulidentata), carnivorans, perissodactyls, and artiodactyls in a cohort Ferungulata, molecular data have redistributed these taxa into the major clades Afrotheria and Laurasiatheria (Figure 3.1). Stanhope and colleagues (1996) and Madsen and coworkers (1997) reported nuclear DNA sequences linking elephant shrews (Macroscelida) to aardvarks and paenungulates apart from other "ferungulates." Springer and colleagues (1997) and Stanhope and coworkers

(1998a) added golden moles (Afrosoricida) to this clade, and Stanhope and colleagues (1998b) named it "Afrotheria." Confirmatory results were provided by Springer and coworkers (1999), Madsen and colleagues (2001), Murphy and coworkers (2001a, 2001b), Arnason and colleagues (2002), Song and coworkers (2012), and O'Leary and colleagues (2013). Sánchez-Villagra and coworkers (2007) argued that an increase in the number of thoracolumbar vertebrae in afrotherians (from the primitive mammalian state of 19 to 20 or more) is a derived homology for the group, and some support from other morphological analyses has also been adduced (see Tabuce et al. 2008). Thus, Afrotheria brings together six orders that have common ancestries in Africa (as indicated by the fossil record), whereas morphological studies have consistently placed these lineages in diverse positions scattered across the placental tree.

LAURASIATHERIA

Molecular data have united the remainder of Simpson's (1945) ferungulates (Carnivora and Perissodactyla) with cetartiodactyls, bats (Chiroptera), pangolins (Pholidota), and eulipotyphlans in a superordinal clade named "Laurasiatheria," reflecting the predominantly "laurasian" (Eurasia + North America) distributions or presumed origins of its members. Strong molecular evidence for this group was first presented by Madsen and colleagues (2001), who drew attention to a pattern of parallel evolution between laurasiatherians and afrotherians: aquatic (cetacean and sirenian), ungulate (perissodactyl-artiodactyl and hyracoid), ant-eating (pholidote and tubulidentate) and insectivore (eulipotyphlan and afrosoricidan) forms occur in both groups. These parallel radiations resemble those between marsupials and placentals recognized much earlier by (among others) Simpson (1949). Many subsequent molecular studies provided support for Laurasiatheria (e.g., Scally et al. 2001; Murphy et al. 2001a, 2001b; Waddell and Shelley 2003; Mathee et al. 2007; Song et al. 2012), and O'Leary and coworkers (2013) gave several potential morphological **synapomorphies** from their analyses of combined molecular and morphological characters.

BOREOEUTHERIA

Although evident (if poorly resolved) in early studies such as those of Stanhope and colleagues (1996), the sister relationship of Laurasiatheria and Euarchontoglires was convincingly recovered by the multilocus DNA-sequence analyses of Eizirik and coworkers (2001), Scally and colleagues (2001), and Murphy and coworkers (2001a, 2001b). Springer and de Jong (2001) named this clade "Boreoeutheria" ("northern eutherians"), reflecting the first fossil occurrences of most of its constituent orders

on northern continents (Figure 3.1). All four sets of authors drew attention to the biogeographic implications of this arrangement. If the sister group of Boreoeutheria is Xenarthra, Afrotheria, or a clade composed of both, occurrence of the oldest fossils of most xenarthran and afrotherian lineages on southern continents suggests that the ancestor of living placental mammals probably lived on the southern supercontinent of Gondwana (see below for a discussion of divergence times, and Chapter 5 for a discussion of historical biogeography). Perhaps, moreover, the great radiation of boreoeutherians can be traced to a single dispersal event from Gondwana to the northern supercontinent Laurasia (Scally et al. 2001). Although specific scenarios such as this depend on placement of the placental root, the cladogenic events that produced major groups of living placentals do seem to have been influenced by continental break-ups in the later Mesozoic (Springer et al. 2011).

THE ROOT OF PLACENTALIA

As noted above, Meredith and coworkers (2011) suggested that the earliest divergence of living eutherian clades separated either Xenarthra + Afrotheria (Atlantogenata) from Boreoeutheria (amino acid analyses, Figure 3.1) or Xenarthra + Boreoeutheria (Exafroplacentalia) from Afrotheria (DNA analyses). The former result was also obtained by Prasad and colleagues (2008), Wildman and coworkers (2007), Hallström and colleagues (2007), and Song and coworkers (2012) on the basis of large DNA sequence data sets. However, Kriegs and colleagues (2006) found that the distribution of homologous retroposon indels across the mammalian genome favored placing the root between Xenarthra and Afrotheria + Boreoeutheria ("Epitheria"); O'Leary and coworkers (2013) obtained the same result with combined morphological and molecular data. Waddell and Shelley (2005) questioned the adequacy of current phylogenetic inference methods with available molecular data for robustly discriminating basal eutherian divergences. Hallström and Janke (2008) concluded that the root is inherently difficult to resolve because of rapid diversification and complex speciation processes that characterized early eutherian lineages (see also Foley et al. 2016). Nishihara and colleagues (2009) analyzed retroposons and found approximately equal support for all three possible roots of the placental tree (i.e., xenarthrans, afrotherians, or boreoeutherians as sister to the rest) and suggested that the three lineages arose almost simultaneously. In contrast, Tarver and coworkers (2016) argued that use of appropriate evolutionary models for DNA sequence characters allows the placental root to be placed with confidence between Atlantogenata and Boreoeutheria (see also Feijoo and Parada 2017).

Dr. Mark Springer—Genes, Trees, and the Evolution of Mammals

"The stream of heredity makes phylogeny," wrote Simpson (1945:5), "in a sense, it is phylogeny." He went on to lament that genetic data were so scarce in the mid-20th century, that they were "not in themselves adequate for the reconstruction of more than a very few, sharply isolated, and quite minor parts of the general phylogeny of animals." Perhaps no other mammalogist has risen to the challenge of Simpson's lament more than Mark Springer, Professor of Biology at the University of California–Riverside (UCR). An author of over 130 research papers, Springer's work with students and collaborators has revolutionized our understanding of mammalian relationships. A hallmark of these papers is their interdisciplinary basis, spanning phylogenetics, paleontology, genomics, and molecular biology. A native, and still resident, of Claremont, California, Springer traces his breadth of interest to the diverse undergraduate science courses he took at Citrus College and Cal Poly Pomona—including a final quarter of 33 credits while working two jobs. He said that while exploring journals at the library of Claremont College after graduation, "I realized that what I really enjoy is deep time." In the PhD program at UC-Riverside, he worked under paleontologist Michael Woodburne on a phylogenetic study of diprotodontian marsupials. Woodburne encouraged him to add a molecular component, and an NSF Dissertation Improvement Grant allowed him to work in the DNA hybridization lab of John Kirsch at the University of Wisconsin–Madison. After completing his PhD in biology in 1988 (and an MS in geology in 1989), Springer started a postdoctoral fellowship on genome evolution with Roy Britten at the California Institute of Technology. The postdoc allowed him to develop expertise with a range of molecular techniques, including Polymerase Chain Reaction (PCR).

Hired as a tenure-track geneticist at UCR in 1991, Springer embarked on his quest to clarify the phylogeny of mammals and the evolution of their genomes. It took many years to assemble tissue samples, and early studies of mitochondrial DNA led to intriguing but inconclusive results about mammalian affinities. However, later collaboration with Michael Stanhope (now at Cornell University) on nuclear gene trees led to the discovery of Afrotheria and other supraordinal mammal clades. Springer has also contributed significantly to intraordinal systematics, especially for marsupials and bats. Intrigued by inactivating mutations in visual system genes of the blind marsupial mole (Notoryctes), he has published many analyses of pseudogene ("genomic fossil") evolution, including visual, dental, and olfactory loci. When a 2012 paper challenged aspects of the molecular phylogeny of mammals on methodological grounds, Springer and colleague John Gatesy (now at the American Museum of Natural History) entered the debate over "coalescent" versus "concatenation" methods in molecular phylogenetics. This literature has now clarified many issues about methods of inferring species trees from gene trees. Reflecting on this body of work, Springer emphasizes the importance of collaborators such as Stanhope, Gatesy, the late Wilfried de Jong, William Murphy (Texas A&M University), and Emma Teeling (University College Dublin). Looking to the future, Springer's interests include using mammals with regressive phenotypes (e.g., loss of cones in the retinas of some cetaceans) as model systems for studying comparable human disease conditions. Research, he notes, often leads in unanticipated directions: "One never knows."

Timing of the Mammalian Radiations

DIVERGENCE OF MONOTREMES, MARSUPIALS, AND EUTHERIANS

Mammals belong to a larger monophyletic group of amniotes known as Synapsida, the oldest fossils of which come from the Late Paleozoic, more than 320 mya (see Chapter 4). Systematists refer to the clade including all descendants from the most recent common ancestor of living lineages in a taxon as the "crown group" for that taxon. Thus, the crown group for Mammalia is all descendants from the common ancestor of monotremes and therians; extinct lineages that diverged prior to this ancestor are known as "stem groups." The recognition of crown groups is essential in molecular analyses of divergence times, because inferences drawn from the DNA of living organisms cannot be applied directly to stem-group lineages.

How long ago did the ancestor of crown-group mammals live? As of this writing, the oldest fossils of its three surviving descendant lineages are as follows: *Steropodon* (monotreme, Lower Cretaceous of Australia, ca. 110 mya, Archer et al. 1985); *Sinodelphys* (metatherian, Lower Cretaceous of China, ca. 125 mya, Luo et al. 2003); *Juramaia* (eutherian, Upper Jurassic, ca. 160 mya, Luo et al. 2011).

Given that the common ancestor of these lineages must be at least as old as the oldest of its descendants, crown-group mammals have been around since the Jurassic or longer. However, the relative scarcity of mammal fossils throughout most of the Mesozoic means that monotremes, marsupials, and placentals did not occur in the age of dinosaurs at anything like their current diversity. When did the great adaptive radiations of mammals take place? There are two primary sources of evidence—the fossil record and molecular clocks—and they have often produced very different answers.

Fossil monotremes are almost as scarce as the living species, with the Cretaceous specimens followed by others from the Paleocene and later Tertiary, all rather like the extant platypus and echidnas (Hand 2006). Messer and colleagues (1998) calibrated genetic distances for the α-lactalbumin gene to estimate a separation of monotremes from therians in the Jurassic, some 163–186 mya, but later molecular dates ranged from 204 to 237 Mya (reviewed by Madsen 2009). Meredith and coworkers (2011) gave a mean date of 218 mya with a confidence interval (203–238 mya) lying entirely in the Triassic (Figure 3.1). Thus, the difference between the best DNA-based estimate of divergence between monotremes and therians is some 58 my older than the oldest fossil that records the existence of either lineage (but see Woodburne et al. 2003). The probability that lineages originate before their oldest fossils has long been appreciated (e.g., Simpson 1944), but 58 million years represents nearly 27% of the history of crown-group mammals if they originated in the Late Triassic. Such a long period of missing fossils made the molecular estimates of divergence difficult for paleontologists and others to accept.

In one of the first attempts to date deep divergences with sequences from a large number of loci, Kumar and Hedges (1998) independently calibrated rates of change in 658 nuclear genes from 207 vertebrates and estimated a date of 173 mya for the marsupial-placental split. Penny and coworkers (1999) obtained a similar date (176 mya) from analyses of protein sequences. These estimates were based on simple, or "strict," molecular clock assumptions (see Chapter 2). When Woodburne and colleagues (2003) applied a relaxed clock method to two protein sequences, they obtained estimates of 182–190 mya for the therian ancestor. Bininda-Emonds and coworkers (2007) used a supertree method (Sanderson et al. 1998) encompassing nearly all extant mammals along with divergence times estimated from strict clocks of 66 genes to suggest a somewhat later date (147 mya). However, the supertree method was criticized by Meredith and colleagues (2011), whose sequence-concatenation, or "supermatrix," approach (de Quiroz and Gatesy 2007) yielded an even older date of 190 mya (Figure 3.1). The methods used by Meredith and coworkers (2011) are described more fully in the discussion of placental radiations below. Recent phylogenomic analyses by dos Reis and colleagues (2012) placed the marsupial-placental separation at 168–178 mya, which is similar to the date (169 mya) obtained by Foley and coworkers (2016) from reanal-

ysis of an expanded version of the Meredith and colleagues (2011) dataset and to the range (157–170 mya) obtained by Tarver and coworkers (2016) from a genomic data set. Despite the discrepancies among date estimates, there seems to be broad agreement (even with the fossil record) that the evolutionary separation of marsupials and placentals took place sometime in the Jurassic period.

THE ORIGIN OF CROWN-GROUP MARSUPIALS

If marsupials arose as early as 168–178 mya and *Sinodelphys* is a stem marsupial at 125 mya, how old was the common ancestor of crown-group lineages? The oldest crown-group fossils are from the Late Cretaceous (65–79 mya; Case et al. 2005). Kirsch and coworkers (1997) proposed a 72-mya date for this ancestor based on calibrated DNA hybridization distances, and Springer (1997) estimated 65 mya based on distances from 12S rRNA gene sequences. Nilsson and colleagues (2003, 2004) used relaxed clock analyses of complete mitochondrial genomes to place the split at 64–69 mya. Thus, several different sources of molecular information suggested an origin of crown-group marsupials near the Cretaceous-Paleogene ("KPg") boundary.

For most studies above, the choice of fossils and associated dates used in calibration of molecular clocks was somewhat haphazard. In a landmark paper, Benton and Donoghue (2007) developed a more rigorous methodology for fossil calibrations. The exercise is predicated on reliable phylogenetic placement of fossils, an accurate phylogeny of the clades being dated, and robust minimum ages for rock layers containing the fossils. If such information is available, a particular fossil places a "hard bound" on the minimum age of a clade—that is, the clade *must* be at least as old as the oldest fossil belonging to it. If such information is not available, calibrations for minimum ages may be treated as "soft bounds" in divergence analyses. Bounds can also be placed on the maximum age of a clade as, for example, when rich fossiliferous strata show no trace of a particular group that would likely be represented if it were present. In all cases, however, fossil calibration dates should be thoroughly vetted and hard- versus soft-bound ages distinguished.

Meredith and coworkers (2008) applied the methods of Benton and Donoghue (2007) to place fossil constraints on marsupial divergence times estimated with relaxed molecular clocks. Bayesian analysis of 5 concatenated (i.e., merged into a single data matrix) nuclear gene sequences produced a tree for marsupial exemplars representing all orders and most families, as well as several placental outgroups. On this tree, only 3 interordinal nodes among marsupials were poorly supported; the other, well-supported nodes are consistent with those in Figure 3.1. Meredith and colleagues (2008) then used the paleontological literature to place hard bounds on minimum and maximum ages for 13 nodes of the tree. With these constraints in place, relaxed clock estimates from the 5 gene sequences dated the

base of Marsupialia to 74–89 mya in the Late Cretaceous, with interordinal divergences occurring between 56 and 86 mya. The later study by Meredith and coworkers (2011) used similar dating methods with more loci (26) to estimate the origin of marsupials at 81 mya (Figure 3.1), while genomic analyses by dos Reis and colleagues (2012) suggested 64–84 mya. Expanded analyses by Mitchell and coworkers (2014) and Foley and colleagues (2016) yielded similar estimates of 87 and 85 mya, respectively. These recent estimates imply that crown-group marsupials arose near the time of their oldest fossils, before the KPg boundary.

PLACENTAL MAMMAL DIVERSIFICATION

The strict molecular clock analyses of Kumar and Hedges (1998) suggested that most placental orders diverged in the Cretaceous, as early as 129 mya for xenarthrans. This finding ran strongly counter to the prevailing notion that placental diversification took place just after the KPg boundary and its associated mass extinction (Hedges et al. 1996). The post-KPg model of placental origins is derived from the fossil record of living orders, most of which are truncated in the earliest Tertiary. Subsequent paleontological studies used quantitative analyses of fossil data (Alroy 1999) or models of origination, extinction, and preservation (Foote et al. 1999) to conclude that the origins of placental orders are unlikely to be much older than what the fossil record documents.

From a strictly paleontological perspective, distinguishing among the models may be viewed as a problem in evaluating the fossil record's *adequacy*—its ability to record dates of lineage originations as a function of cladogenic rates, as well as probabilities of fossil preservation and sampling. Archibald and Deutschman (2001) used simulations of all three processes to determine whether the observed

Archibald and Deutschman (2001) framed much of the subsequent debate on placental diversification by describing three alternative models of the historical process (Figure 3.2). These models make a crucial distinction between the times of *origin* of an order (ordinal origination) and radiation of lineages *within* the order (intraordinal diversification). The first must be at least as old as the second, and the interval between them is analogous to a "fuse." In the Explosive Model, the fuse interval is exceedingly brief—both ordinal originations and intraordinal diversifications occurred within about 10 my after the KPg boundary. In the Long-Fuse Model, most intraordinal diversification happened just after the KPg boundary, but the orders themselves arose in the Cretaceous. In the Short-Fuse Model, orders originated and diversified in the Cretaceous prior to the KPg extinctions. The traditional view from paleontology (e.g., Foote et al. 1999) is consistent with the Explosive or (for a few orders) Long-Fuse models; the molecular results of Kumar and Hedges (1998) correspond to the Short-Fuse Model.

Figure 3.2 Alternative models for diversification of placental mammals. Light branches indicate intraordinal diversification; dark branches indicate ordinal origination. The timescale below each tree indicates the position of the KPg boundary. *Redrawn from Springer et al. (2003).*

temporal distribution of placental crown-group fossils could be due to chance alone. They concluded that it cannot and that the placental fossil record is inconsistent with a Short-Fuse Model.

In an early attempt to address this paleontological-molecular discrepancy, Springer and coworkers (2003) used

a taxon sample that included all living placental orders, a gene sample of 21 loci, minimum fossil ages for 13 robust branch points, and a relaxed clock method for estimating divergence times. Their results supported a Long-Fuse Model in which all but 3 living placental orders arose some 77–107 mya in the Late Cretaceous, with intraordinal diversifications occurring 50–77 mya on both sides of the KPg boundary. Wible and colleagues (2007) reevaluated the fossil record and phylogeny of early placentals in their description of the Cretaceous cimolestid *Maelestes*. They concluded that there are no Cretaceous fossils assignable to crown-group Placentalia and that the placental radiation followed the Explosive Model near the KPg boundary.

The supertree analysis of Bininda-Emonds and coworkers (2007) was a major, if controversial, benchmark in the study of eutherian diversification. As noted previously, these authors assembled a supertree for nearly all living mammal species from over 2,500 published phylogenies and linked it to an alignment of 66 gene sequences (>50,000 bases). Divergence times were estimated from local molecular clocks (i.e., rates of sequence evolution were assumed to be similar within specific clades but allowed to vary among them) and calibrated by 30 reliable fossil dates or by interpolation from a "pure birth" model of lineage origination for unresolved (polytomous) nodes. Results indicated that most placental ordinal origination took place 85–100 mya, which is roughly consistent with the dates of Springer and colleagues (2003). However, the analysis also suggested a short fuse for the more diverse placental orders, which appeared to radiate into basal lineages about 14 my after their origin and 10 my before the KPg boundary. Orders with few lineages (e.g., Xenarthra) had longer fuses, with extant forms arising in the Tertiary. Moreover, lineage-through-time plots suggested that, after their initial radiation in the Cretaceous, the large orders experienced very little cladogenesis until the Eocene or later, when most of their modern diversity was established. Bininda-Emonds and coworkers (2007) interpreted their findings as evidence for "the delayed rise of present-day mammals" and their dated phylogeny has been used in several macroevolutionary studies (e.g., Davies et al. 2008, Stadler 2011).

Meredith and colleagues (2011:521) argued that the Bininda-Emonds and coworkers (2007) supertree results were "compromised by including numerous source phylogenies with overlapping data . . . inferred from a topology that contained numerous polytomies and . . . dated with a combination of local molecular clocks and pure birth interpolation." The first criticism bears on the supertree estimate of phylogeny in that using multiple source trees inferred from the same data set (e.g., a particular locus) effectively biases the supertree toward branching patterns implied by the overrepresented data. The second criticism bears on the estimated dates and is essentially the argument made in the molecular-dating literature that estimates drawn from strict, calibrated, local clocks are less reliable than those obtained from properly constrained relaxed

clocks. Both problems are exacerbated when unresolved nodes are resolved for dating by a random model.

To overcome these problems, Meredith and colleagues (2011) undertook a supermatrix analysis of 164 mammal species representing 97%–99% of extant families and DNA sequences from 26 protein-coding loci (35,603 bases). Maximum-likelihood and Bayesian analyses of these data yielded the tree shown in Figure 3.1. Approximately 30% of the nodes on this tree were not resolved by Bininda-Emonds and coworkers (2007), but 90% of them have high bootstrap support and Bayesian posterior probabilities. As discussed above, this tree recovers most of what is currently accepted about the supraordinal phylogeny of mammals. To obtain divergence time estimates, Meredith and colleagues (2011) placed minimum and maximum age constraints on 82 nodes using fossil dates vetted as described by Benton and coworkers (2009) and applied a range of relaxed clock analyses. The results show a distinct Long-Fuse pattern, with all superordinal clades and most orders originating in the Late Cretaceous (80–101 mya) but not diversifying into modern lineages until near the KPg boundary or in the Cenozoic. The latter range of dates brings molecular divergence estimates more closely into line with the fossil record. Based on genomic datasets, dos Reis and colleagues (2012) estimated ordinal originations at 80–90 mya and most intraordinal diversifications at 45–65 mya. Meredith and coworkers (2011) linked ordinal origination to the Cretaceous Terrestrial Revolution initiated by the radiation of angiosperms 80–125 mya (Lloyd et al. 2008, Benton 2010), and intraordinal diversification to the KPg mass extinction. Both were global phenomena that dramatically increased the "ecospace diversity" available to evolving mammals.

O'Leary and colleagues (2013) revisited the problem of placental divergence times in their analysis of 86 living and 40 fossil species (representing all living orders and several key extinct lineages) with a combination of 4,541 morphological characters and sequences from 27 nuclear genes. The tree obtained from this analysis was broadly similar to that of Meredith and coworkers (2011), but differed in the placement of several orders within superordinal groups. Minimum divergence dates were obtained by fixing the ages of 82 fossils assigned to specific tree branches and applying ghost lineage analysis (see Chapter 2). The results support an Explosive Model of placental evolution, with both interordinal divergence and ordinal diversification occurring shortly after the KPg boundary. However, as noted by the authors and explained by Yoder (2013), ghost lineage analysis necessarily generates *minimum* divergence dates consistent with a phylogenetically literal reading of the fossil record. This is in marked contrast to the probabilistic methods used by molecular workers to convert branch lengths into time estimates. Foley and colleagues (2016) further note that the O'Leary and coworkers (2013) timetree entails unrealistically high estimates of molecular evolution rates in early Paleogene lineages leading to crown placentals; these rates are comparable to those ob-

served among modern viruses. Their analysis of an expanded data set from Meredith and colleagues (2011) yielded ordinal originations in the range 66–99 mya and intraordinal diversifications in the Paleogene, thus reaffirming the Long-Fuse Model. Bayesian molecular clock analysis of a genomic data set by Tarver and colleagues (2016) yielded divergence estimates of 86–100 mya among crown Placentalia lineages. Ronquist and coworkers (2016) dated the initial split within Placentalia at ca. 85 mya with the relatively new "total evidence dating" method.

Phillips (2016) argued that divergence dates obtained by Meredith and colleagues (2011) were inflated by calibration errors, due in part to the influence of slowly evolving sequences in taxa with large body size and long lifespan. When such calibrations were removed or more tightly constrained, placental divergences conformed to a "soft explosive" model in which the deepest branches reach to the Cretaceous, but the post-KPg ordinal radiation predicted by the fossil record is recovered. Springer and coworkers (2017) strongly criticized Phillips's (2016) results, pointing out that they include many instances of counterfactual "zombie lineages" (i.e., crown groups with molecular divergence estimates *younger* than their oldest fossils) and thereby indicated an overall bias toward underestimation of divergence times. Springer and colleagues (2017) applied a less extreme correction for rate inflation by removing only the largest and longest-lived clades from the data set; their reanalysis again yielded placental divergences in the Cretaceous—though slightly younger than those of Meredith and coworkers (2011)—consistent with a Long-Fuse Model.

In summary, there is an emerging consensus of support for the traditional notion that most intraordinal diversifications of placental mammals took place either shortly before or after the KPg boundary some 66 mya. Views on ordinal origination, however, remain deeply divided between proponents of the Long-Fuse Model with orders forming in the Cretaceous and those favoring an Explosive Model with orders originating just before their diversification in the Tertiary. Resolution of this issue will have a major influence on our understanding of the evolutionary forces that brought about the spectacular diversity of modern mammals.

SUMMARY

- Phylogenetics is the study of the history, diversification, and relationships among taxa.
  - Phylogenies are based on evidence from fossils, morphology, and molecular characters.
  - There is often conflict, however, between morphological and molecular evidence.

- George Gaylord Simpson was an early leader in the study of mammalian phylogeny.
  - Much of his classification from 1945 remains relevant today.
  - A current view of mammalian ordinal relationships is given in Figure 3.1.

- Extant monotremes contain only the platypus and echidnas (spiny anteaters).
  - They are clearly monophyletic.
  - Relationships among the living monotremes and extinct lineages that may fall within the Subclass Prototheria are not clear, however.

- Marsupials also are a monophyletic group.
  - Seven living orders are recognized today (see Chapter 10) in two cohorts.
  - The cohort Australidelphia includes the four orders found in Australia and the monotypic Order Microbiotheria in South America.

- The cohort Ameridelphia, with the New World Orders Paucituberulata and Didelphimorphia, is based on morphological characters; it has little support from molecular studies, however.
  - Characteristics of dentition (polyprotodont versus diprotodont) and digits (syndactylous versus didactylous), once used to differentiate marsupial orders, currently are believed to represent convergence.

- Among eutherians, "insectivores" traditionally represented a "waste basket" order of numerous taxa of unknown affinities.
  - Molecular studies increased understanding of the relationships of these taxa.
  - Today, seven orders are recognized, although they are very diverse phylogenetically.

- Bats (Chapter 21) are a monophyletic group, as are rodents, which form a sister group to lagomorphs (rabbits and hares; see Chapter 16).

- Xenarthrans are one of the four deep lineages of eutherians.
  - Currently, two orders are recognized as sister groups: Cingulata (armadillos) and Pilosa (sloths and anteaters; see Chapter 13).

- It has been known for over 50 years that cetaceans (whales) are related to artiodactyls (even-toed ungulates).

- Recent molecular work has shown that cetaceans are actually nested within the artiodactyls (even-toed ungulates).
  - Within artiodactyls, whales are most closely related to the hippopotamuses (see Chapters 19 and 20).

- Afrotheria (Figure 3.1) includes six orders with common African ancestry.
  - This group is based on molecular, not morphological, data.

- Likewise, Laurasiatheria brings together six orders on the basis of molecular rather than morphological relationships.

- The "crown group" for a taxon refers to a clade of all descendants from the most recent common ancestor of living lineages in the group.
  - A "stem group" is a set of extinct lineages that diverged prior to the crown-group ancestor.
  - The age of the oldest known fossils for the three crown-group lineages of mammals are: monotremes about 110 my; marsupials about 125 my; and eutherians about 160 my.

- Divergence time estimates based on fossils versus molecular clocks differ greatly, however.
  - Regardless, it is clear that marsupials and placentals diverged during the Jurassic Period.

- There are three alternative models for the relationship between the times of ordinal origination and intraordinal diversification of placental mammals (see Figure 3.2).
  - The interval between these two events can be thought of as a "fuse."
  - The three models are: Explosive (very short interval); Long-Fuse (origin in Cretaceous with diversification after KPg boundary); and Short-Fuse (both events prior to KPg boundary).
  - Again, fossil and molecular evidence favor different models.
  - Origin of orders likely was linked to the increase in angio-sperms and intraordinal diversification to extinction of dinosaurs.
  - Most intraordinal diversifications of placentals probably took place slightly before or after 66 mya.

SUGGESTED READINGS

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Meredith, R.W., J. E. Janečka, J. Gatesy, et al. 2011. Impacts of the Cretaceous terrestrial revolution on mammal diversification. Science 334:521–524.

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Yang, Z., and P. C. J. Donoghue. 2016. Dating species divergences using rocks and clocks. Phil. Trans. R. Soc. B 371:20150126.

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DISCUSSION QUESTIONS

1. The formerly recognized orders "Cetacea" (whales and dolphins) and "Artiodactyla" (even-toed ungulates) have been part of mammalian taxonomy for many decades, and their recent merger into Cetartiodactyla is jarring to many mammalogists. G. G. Simpson might have argued that, phylogeny notwithstanding, cetaceans and artiodactyls should be recognized as separate orders because they represent different "adaptive zones" (i.e., integrated sets of adaptations to specific lifestyles). Phylogenetic systematists, on the other hand, maintain that classifications lose their integrity and predictive value if they include non-monophyletic groups. What are the pros and cons of these two positions on biological classification, especially with respect to Cetartiodactyla?

2. The mammalian fossil record includes few representatives of modern orders from the Cretaceous (most have their first occurrence in later Tertiary deposits), but many analyses of DNA sequence data suggest that ordinal originations took place in the Late Cretaceous. What are some possible explanations for this discrepancy and what kind of information would be required to evaluate them?

3. It has been extremely difficult to resolve the branching order of the earliest splits among living eutherian superordinal lineages (the "placental root"), even with large molecular data sets. What factors could be responsible for this phenomenon? What strategies are molecular and morphological systematists likely to pursue in order to address it?

Evolution and Dental Characteristics

Mammals evolved from a lineage of tetrapods during the 100-my period from the Late Paleozoic to the Early Mesozoic. The distribution, adaptive radiation, and resulting diversity seen in today's mammalian fauna are products of the evolutionary process operating throughout hundreds of millions of years—a process that continues today. In this chapter, we describe evolutionary morphological changes from amniotes to mammalian structural organization, including the development of mammalian traits and the emergence of early mammals. We continue tracking changes in mammals throughout the Mesozoic era and the explosive adaptive radiation of mammals beginning in the Early Cenozoic. We also describe dental characteristics of early mammals and how these teeth developed into the dentition seen in modern mammals.

Synapsid Lineage

The Amniota are a monophyletic group that arose from amphibian-like tetrapods in the early Carboniferous period of the Paleozoic (Table 4.1). This group showed a key morphological change adaptive for reproduction on land, namely, development of the **cleidoic**, or shelled, egg. The amniotes represent the common ancestor of all reptiles and mammals. By the late Carboniferous period, the amniotes had diverged into three lineages: the synapsids, anapsids, and diapsids (Figure 4.1). These groups were distinguished by the number, size, and position of lateral temporal openings (fossa) in the skull, which were used to facilitate attachment of jaw muscles. Mammals arose from the phylogenetic lineage or clade called the **Synapsida** (Prothero 1998; Hickman et al. 2004; Kielan-Jaworowska et al 2004; Benton 2005; Kemp 2005; Pough et al. 2005). The synapsids were the first group of amniotes to radiate widely in terrestrial habitats. They first appeared in the Late Paleozoic, about 320 mya in North America (see Table 4.1). They were the dominant land animals for 70 my, but had passed their

Table 4.1   Geologic time divisions

Era	Period	Epoch	Myr BP (approx.)	Biological Events
Cenozoic	Quaternary	Recent	0.01	
		Pleistocene	1.8	
	Neogene	Pliocene	5	
		Miocene	24	Most mammalian families in evidence
	Tertiary	Oligocene	37	
	Paleogene	Eocene	54	Origin of most mammalian orders
		Paleocene	65	Mammalian radiation, Dinosaurs extinct
Mesozoic	Cretaceous		144	Dinosaurs abundant
	Jurassic		213	
	Triassic		248	First mammals
Paleozoic	Permian			
	Carboniferous	Pennsylvanian	320	Synapsids
		Mississippian	360	
	Devonian		408	Devonian tetrapods
	Silurian		438	First jawed fishes
	Ordovician		505	First vertebrates and land plants
	Cambrian		590	Invertebrates

evolutionary peak by the time of the emergence of the dinosaurs. Early synapsids diverged into diverse herbivorous and carnivorous forms: the pelycosaurs and therapsids. The **Pelycosauria** was the most primitive of the two groups and is known from fossil remains in North America and South Africa (Dilkes and Reisz 1996). The **Therapsida**, the more advanced group, were the top carnivores in the food web. They are known from fossil remains in Russia, South Africa (Carroll 1988), and China (Rubidge 1994; Jinling et al. 1996).

Therapsids have traditionally been referred to as "mammal-like reptiles" (Romer 1966; Kemp 1982). In recent years, however, new phylogenetic techniques have overturned much of what we thought about mammalian evolution. Current research in cladistic zoology focuses on the hierarchical arrangement of monophyletic groups. Reptiles are not a monophyletic group; rather they are paraphyletic (not all members are descendants of a single common ancestor). As a result, the Class Reptilia is no longer recognized as a valid taxon by cladists; reptiles are referred to as "amniotes"—neither birds nor mammals. Mammals and our transitional "mammal-like reptiles" did not evolve from reptiles, as was customarily thought; in-stead, reptiles and mammals shared a common ancestor (the Amniota) from which each group evolved in divergent ways (Hickman et al. 2004; Pough et al. 2005).

PELYCOSAURS AND THERAPSIDS

Pelycosaurs, like all synapsids, were distinguished by a single lateral temporal opening, with the postorbital and squamosal bones meeting above. They were common by the end of the Pennsylvanian epoch (Figure 4.2). By that time, they had radiated into three suborders. The Ophiacodontia, with several known families, were the most primitive. They were semiaquatic and ate fish. The Edaphosauria were terrestrial herbivores and were probably preyed on by the third group—the carnivorous Sphenacodontia (Kermack and Kermack 1984). The sphenacodonts, such as Genus *Dimetrodon* (Figures 4.3A and 4.4A), were the dominant carnivores throughout the early Permian period. All sphenacodonts shared a unique feature: a reflected lamina of the angular bone in the lower jaw. This feature was to become part of the development of the middle ear in later synapsids and mammals. The sphenacodonts eventually

A

Synapsid

B

Anapsid

C

Diapsid
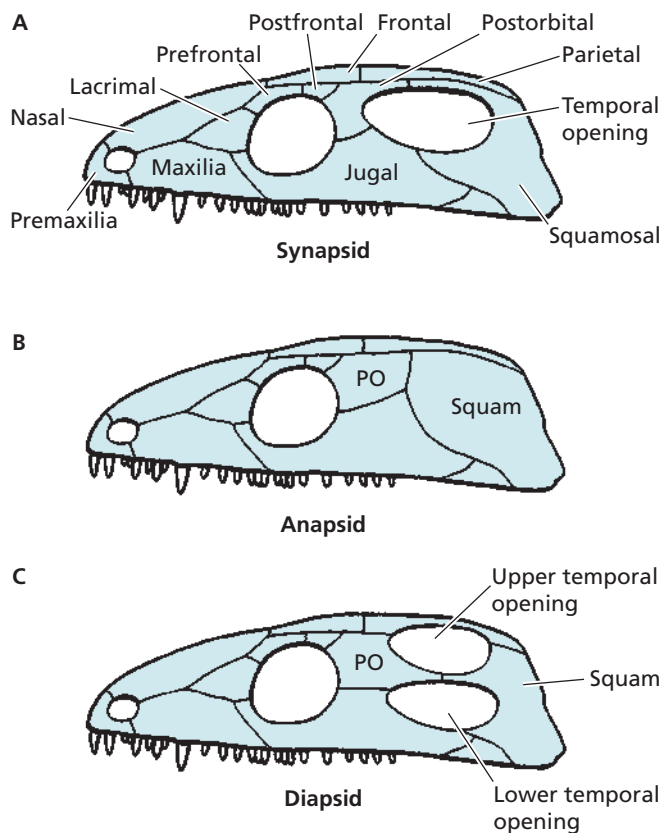
Figure 4.1 **Temporal openings of skulls in three groups of amniotes.** (**A**) Synapsida, the group from which mammals arose. Note the articulation of the postorbital (PO) and squamosal (Squam) bones above the single temporal opening. (**B**) Anapsida, with no temporal opening. This group led to turtles. (**C**) Diapsida, named for the two temporal openings on each side of the skull. Lizards and snakes arose from the diapsids. *Adapted from Kermack and Kermack (1984).*

gave rise to the Therapsida. The therapsids are thought to be monophyletic (Benton 2005). By the middle to late Permian period, all pelycosaurs were replaced by the more advanced therapsids (Figure 4.3B) (Rowe 1993; Wible et al. 1995; Benton 1997).

The oldest known therapsids date from the Late Permian. Therapsids may be divided into two suborders: **Anomodontia** and **Theriodontia** (see Figure 4.2). The anomodonts included two lineages, the Dinocephalia and the Eotitanosuchia, neither of which left Triassic descendants. The largest and most successful group of anomodonts was the Dicynodontia. They enjoyed a worldwide distribution (although the continents were not in their current positions) and were the dominant terrestrial herbivores for 60 my from the Mid-Permian until the Late Triassic, when the last of the various lines of anomodonts became extinct.

The other suborder of therapsids was the Theriodontia. They were primarily carnivorous and much more diverse and successful than the herbivorous anomodonts. Several different theriodont lines are recognized in the fossil record (see Figure 4.2). The gorgonopsians were the prevalent

theriodonts throughout the Late Permian, but they did not survive into the Triassic period. The therocephalians were a much more advanced and diverse group. They paralleled the other advanced theriodont group, the **Cynodontia**, in some of their mammal-like characteristics, including a secondary palate and complex **cheekteeth** (postcanine teeth; the premolars and molars). Therocephalians did not show changes in position of the jaw muscles, however, as did cynodonts. The therocephalians were extinct by the Early Triassic, and only the cynodonts possessed the specialized cranial and skeletal features that eventually led to the evolution of the mammals.

CYNODONTIA

Cynodonts existed for 70 my, throughout the Triassic to the Middle Jurassic. During this time, the several recognized families of cynodonts developed many of the transitional anatomical features leading from synapsids to the earliest mammals (Hotton et al. 1986). Later cynodonts included diverse herbivores (gomphodonts and tritylodonts) as well as carnivores (cynognathids and tritheledonts). Several cynodont characteristics approached mammalian grade—that is, a level of organization similar to mammals. These characteristics included changes in dentition to tricuspid (**cusps** are the projections, or "bumps," on the **occlusal** [chewing] surface of a tooth) and double-rooted cheekteeth; jaw structure and masseter muscles (increased dentary size with reduction in postdentary bones and development of a glenoid fossa on the squamosal bone); hearing; postcranial skeleton (differentiated vertebrae, including modification of the first two vertebrae, the atlas/axis complex, modified pectoral and pelvic girdles, and thoracic ribs); and their phalangeal formula (Crompton and Jenkins 1979; Dawson and Krishtalka 1984). Several of these changes are discussed in more detail later in this chapter. Changes in cynodonts and early Mesozoic mammals also included more erect posture and efficient movement as well as increased adaptability in feeding. For example, development of the masseter muscles was associated with changes in the jaw, especially enlargement of the dentary bone and reduction in the number and size of postdentary bones (see Figure 4.4), and development of the zygomatic arch, temporal openings of the skull, and the eventual development of the lateral wall of the braincase. These developments reduced stress on the jaw joint, increased the force of the bite, and protected the brain.

The evolution of synapsids to mammals was a continuum, with a "mammal" necessarily (if somewhat arbitrarily) defined by the articulation of the squamosal and dentary bones (Brocklehurst and Froebisch 2014). As noted previously, synapsids had several bones in the lower jaw in addition to the dentary (see Figures 4.4 and 4.5A). The joint between the lower jaw and the cranium was formed by the **quadrate** and **articular bones**. In transitional forms, as cynodonts became more mammal-like, postdentary bones
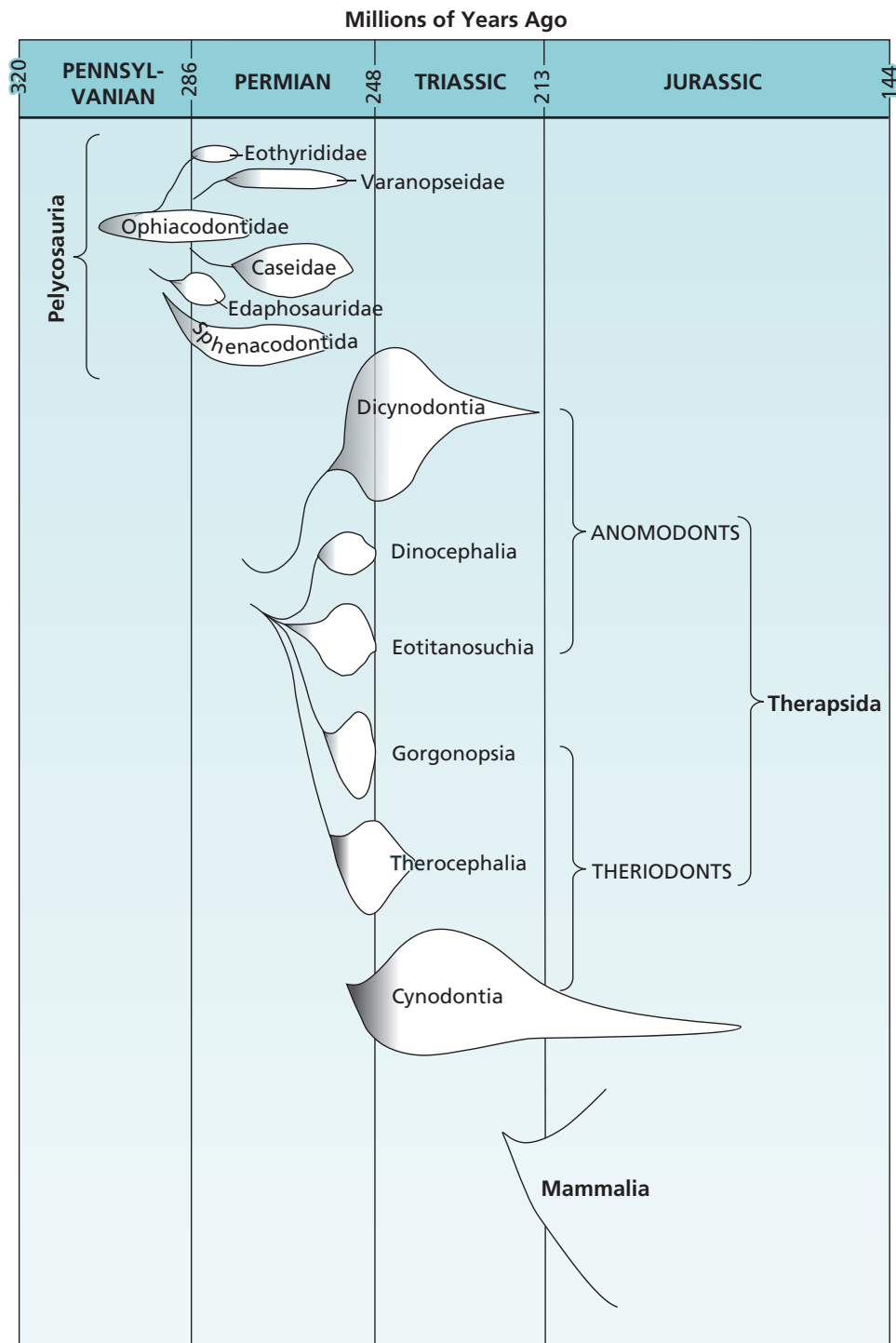
Figure 4.2 **The major groups of synapsids.** The Pelycosauria were early synapsids. The more advanced Therapsida arose from the carnivorous group of pelycosaurs called "sphenacodonts." Therapsids included lineages of both herbivores (the anomodonts) and carnivores (the theriodonts). It was from a branch of the theriodonts, specifically the cynodonts, that mammals arose over 200 mya. Widths of each lineage suggest relative abundance. *Adapted from Carroll (1988).*

continued to decrease in size. The primitive quadrate-articular joint remained, and an additional joint formed between the cranial squamosal and the surangular bones of the jaw. This occurred because of the progressive enlargement of the dentary bone and concurrent reduction in size of the postdentary bones. Certain lineages of cyn-

odonts had a double-hinged jaw joint; the dentary bone articulated with the squamosal laterally, and the quadrate and articular bones also formed a medial jaw articulation (Crompton 1972).

This later joint served not only as a hinge but also to transmit sound to the tympanic membrane. This membrane

A

Reflected
lamina

B
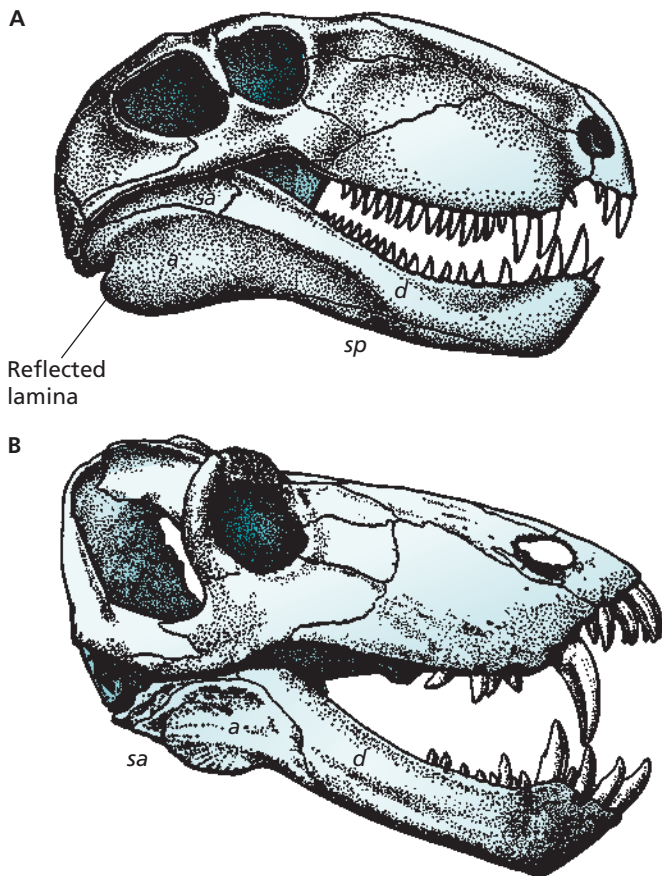
Figure 4.3 **Contrast between pelycosaurs and therapsids.**
(**A**) Skull of *Dimetrodon*, a common carnivorous sphenacodont
Pelycosaur. Relatively primitive features include the small
temporal opening and large angular bone (*a*). Other postden-
tary (*d*) bones include the surangular (*sa*) and the splenial (*sp*).
These bones are larger than those in (**B**) *Titanophoneus*, a more
advanced therapsid, with a large temporal opening and smaller
postdentary bones. *Note*: Not to the same scale. *Adapted from
Romer (1966).*

A

B

C

D

E

Figure 4.4 content:

Key
1 dentary
2 angular
3 prearticular
4 coronoid
5 splenial
6 surangular
7 articular

Figure 4.4 **Medial view of lower jaw.** The progressive
enlargement of the dentary bone (shaded) and reduction in
postdentary bones is evident when comparing jaws of primitive
mammal-like reptiles: (**A**) *Dimetrodon*, an early Permian
pelycosaur; (**B**) *Cynarioides*, a late Permian therapsid;
(**C**) *Cynognathus*, an early Triassic cynodont; (**D**) *Ictidosaur*, a
late Triassic-early Jurassic cynodont. The dentary is the sole
bone in the jaw of mammals (**E**). *Adapted from Savage and
Long (1986).*

was supported by the reflected lamina of the angular bone
(Figure 4.6). Only one relatively large middle ear bone,
the **stapes**, conducted sound from the tympanic mem-
brane to the inner ear in stem mammals. Eventually,
sound transmission became the only function of the quad-
rate and articular bones as the dentary became the only
bone in the lower jaw. The articulation between the den-
tary and squamosal bones is the characteristic used to de-
fine a mammal. The position and reduction in size of the
quadrate-articular joint was associated with the transfor-
mation of these bones into **ossicles** in the mammalian
middle ear (see Figure 4.5B). The long attachment arm of
the **malleus** to the tympanic membrane in modern mam-
mals is called the **manubrium** and is derived from the for-
mer retroarticular process of the articular bone. In con-
junction with the large tympanic membrane and the much
smaller fenestra ovalis, this lever system (enhanced by the
long "lever" arm of the manubrium) not only transmits

sound waves but also amplifies them. Low-pressure sound
waves carried by air are increased to the higher pressure
necessary for conduction through the fluid of the inner
ear—the cochlear endolymph. This results in increased au-
ditory acuity. As with many other changes from reptilian
to mammalian organization, these two features are inter-
related. That is, the reduction in size of the postdentary jaw
bones increased not only auditory acuity, especially of
high-frequency sound, but also the efficiency of chewing.

By the time the cynodonts became extinct in the Mid-
Jurassic period, several well-defined groups of mammals
already existed. Thus, from synapsids that existed 320 mya
to the emergence of the earliest identifiable mammals about
70 my later, evidence in the fossil record indicates several
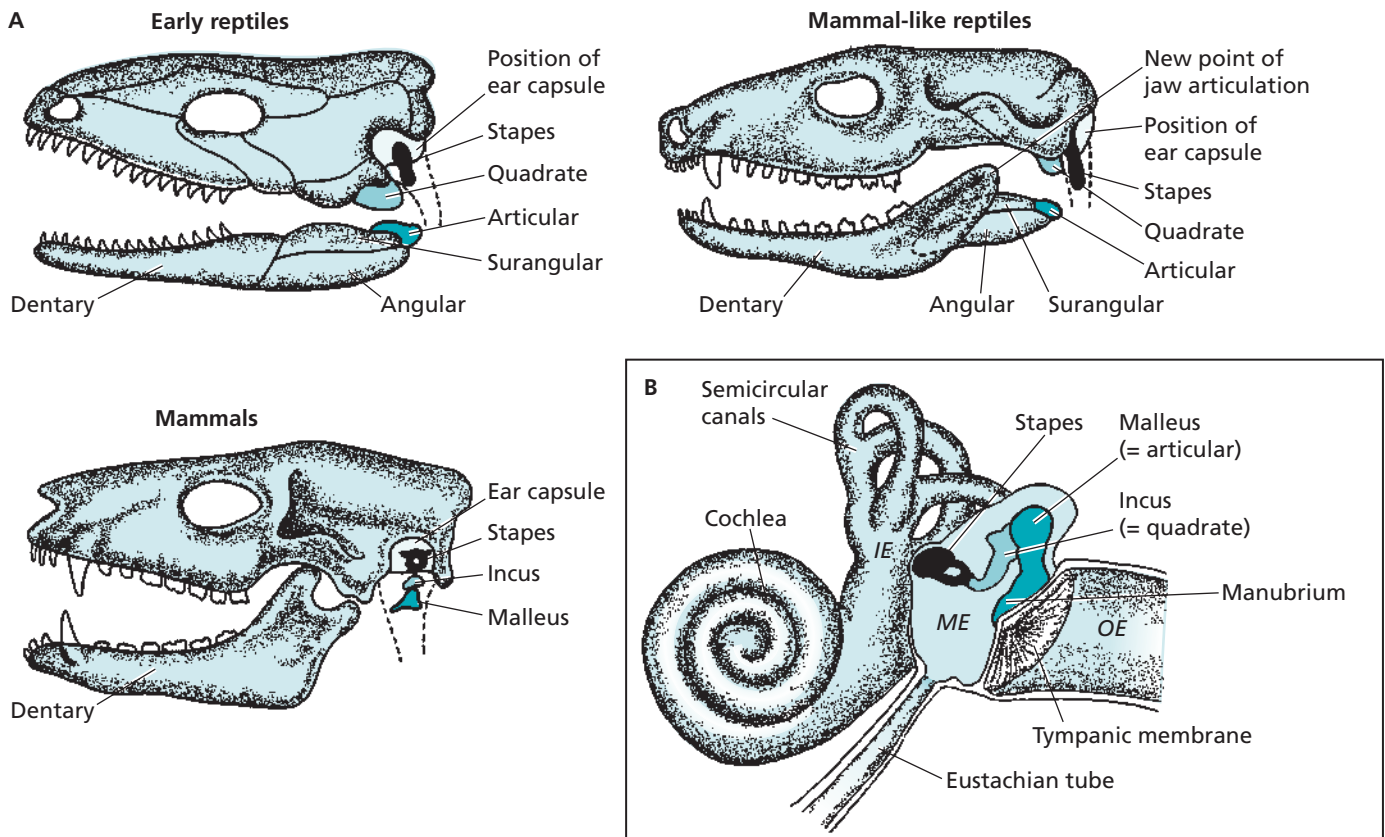
Figure 4.5 **Transition of the jaw and history of the ear ossicles.** Please note that we use traditional terminology in the following caption as pertains to Early Reptiles (= amniotes), and Mammal-like reptiles (= synapsids). (**A**) Simplified transition of the jaw structure from reptiles through mammal-like reptiles to mammals, showing the increase in size of the dentary bone and decrease in postdentary bones. The quadrate and articular bones of mammal-like reptiles eventually changed from their dual role of jaw joint and sound transmission to solely sound transmission in mammals. (**B**) Outer ear (*OE*), middle ear (*ME*), and inner ear (*IE*) of modern mammals. The tympanic membrane is now supported by the tympanic bone, derived from the former reflected lamina of the angular bone (see Figure 4.6). The articular bone has become the first of the three small bones (ossicles) in the middle ear, specifically, the malleus. The second ossicle, the **incus**, is derived from the quadrate bone. The mammalian stapes, much reduced in size from the reptilian stapes, connects the incus to the inner ear through the fenestra ovalis (the "oval window"). Thus, in mammals, the stapes is not connected directly to the tympanic membrane as in reptiles, but instead is connected through a lever system of two small bones—the malleus (former articular bone) and the incus (former quadrate bone)—the familiar "hammer, anvil, and stirrup." *Adapted from Simpson and Beck (1965).*

anatomical trends in organization that resulted in a mammalian grade (see the next section). Paleontologists have isolated many important osteological characters defining the mammalian grade of evolution. Some studies have focused on early amniotes (Hopson 1991; Laurin and Reisz 1995), whereas others delineate characters and relationships during the nonmammal-to-mammal transition period (Wible 1991; Crompton and Luo 1993; Luo and Crompton 1994; Wible et al. 1995; Kielan-Jaworowska 1997). Associated changes must also have occurred in the soft anatomy, physiology, metabolism, and related features of synapsids, which are not evident from fossil remains. These features were interrelated in terms of increased efficiency of metabolism needed for endothermy, better food gathering and processing methods, increased auditory acuity, and other adaptations to maintain internal homeostasis and enhance survival.

Origin of Mammals: Monophyletic or Polyphyletic?

During the Early Jurassic, one of two events happened. Either a single lineage of therapsids gave rise to early mammals, or two or more therapsid lines independently achieved the mammalian grade of organization (Figure 4.7) (Rowe and Gauthier 1992). In the first case, early mammals subsequently split into two divergent lines, the prototherians (which today include the monotremes—see Chapter 10), and another line, which after many adaptive radiations, gave rise to therians (the metatherians and eutherians, or "placental," mammals). This scenario posits a monophyletic origin for mammals (Rowe and Gauthier 1992). In the second case, the characteristics of the three major mammalian groups (infraclasses) are seen as strictly convergent, with
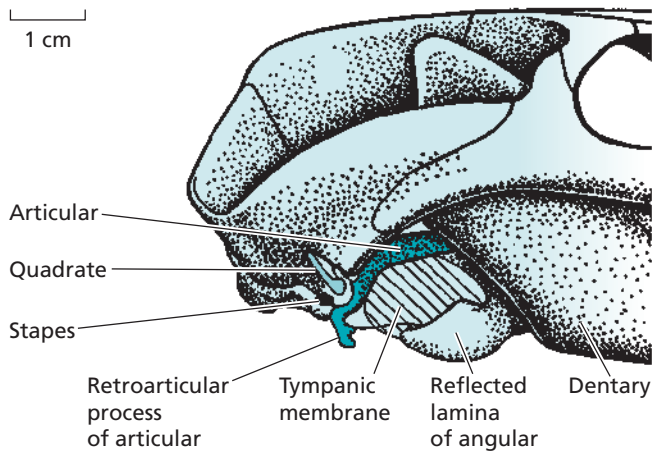
Figure 4.6 Tympanic membrane in a mammal-like reptile (= synapsids). Posterior part of the cranium in an advanced mammal-like reptile, *Thrinaxodon liorhinus*. Note the jaw joint, the location of the tympanic membrane, and its relationship to the postdentary bones. The quadrate and articular bones form the jaw joint as well as transmit sound from the tympanic membrane to the stapes. *Adapted from Lillegraven et al. (1979).*

Figure 4.7 Diagram of alternative hypotheses of the origin of mammals. In the monophyletic scheme, the major groups of mammals alive today diverged from a common ancestral line of amniotes. Conversely, the three major groups may have converged from at least two distinct, separate lines of amniotes. Most authorities suggest mammals had a monophyletic origin.

mammals having a polyphyletic origin (Cifelli 2001). The question of monophyly persists because different interpretations can be drawn from a fragmentary and incomplete fossil record. If the mammal node is supported by characteristics that evolved at different times in different lineages, such as three bones in the middle ear that were derived from the jaw joint, then by definition, mammals are polyphyletic. Most monophyletic groups are supported by multiple characters, and they are presumed to be independent. It is their separate derivation in independent groups that makes these characters indicate polyphyly. As noted, however, most authorities consider mammals to be the taxa sharing the single dentary bone with a squamosal-dentary articulation (Rowe 1996) and their common ancestor. This definition, based on common ancestry, makes mammals monophyletic (Rowe and Gauthier 1992; Benton 1997).

The First Mammals

EARLY MESOZOIC MAMMALS

As we have seen, therapsids achieved many mammalian features; however, only mammals had the primary jaw joint composed of the dentary and squamosal bones. Also, they had **diphyodont** dentition (only two sets of teeth during an individual's lifetime) with complex occlusion. However, the mammalian fauna in the Mesozoic era and for the first 100 my of the existence of mammals was strikingly different

from what we see today (Prothero 1998). Until the Early Cenozoic, mammals were a relatively rare and insignificant part of the fauna compared with the larger, widespread, specialized, and well-adapted lineages of reptiles. Mammals were small (mouse-sized), relatively uncommon, and probably nocturnal. Because the majority of the terrestrial reptiles were diurnal, mammals could better avoid predation by being nocturnal. Throughout this era, mammals appeared to be a narrowly restricted offshoot, confined to a few phyletic lines. It is interesting that the fossil record shows little overlap in size between the smallest dinosaurs and the largest mammals for the 140 my when these two groups shared the terrestrial environment. In general, the smallest dinosaurs were many times larger than the largest mammals. Mammals did not attain large body sizes until after the extinction of the dinosaurs (Lillegraven 1979).

Mammalian phylogeny can be depicted as in Figure 4.8. The great evolutionary "bush" of diverse Mesozoic mammalian clades is the dominating feature in their taxic evolutionary pattern (Cifelli 2001; Luo et al. 2001; Ji et al. 2002; Luo 2007; O'Leary 2013; Newham et al. 2014). The almost fully resolved **cladogram** (Figure 4.8) of all Mesozoic mammal groups, together with their improved records of temporal distribution of fossils, suggest that mammalian diversification occurred episodically during the entire span of Mesozoic mammalian history. Five episodes of diversifications occurred (see Figure 4.8). The earliest diversifications of stem eutherians and stem metatherians, as documented by the currently available fossil record, predate the likely time window estimated by molecular studies, which indicates that some superordinal clades of placental mammals may have extended back into the Cretaceous (e.g., split off the earliest placental superordinal clades around 108 ± 6 mya; Murphy et al. 2001a, 2001b; Cifelli et al. 2014).
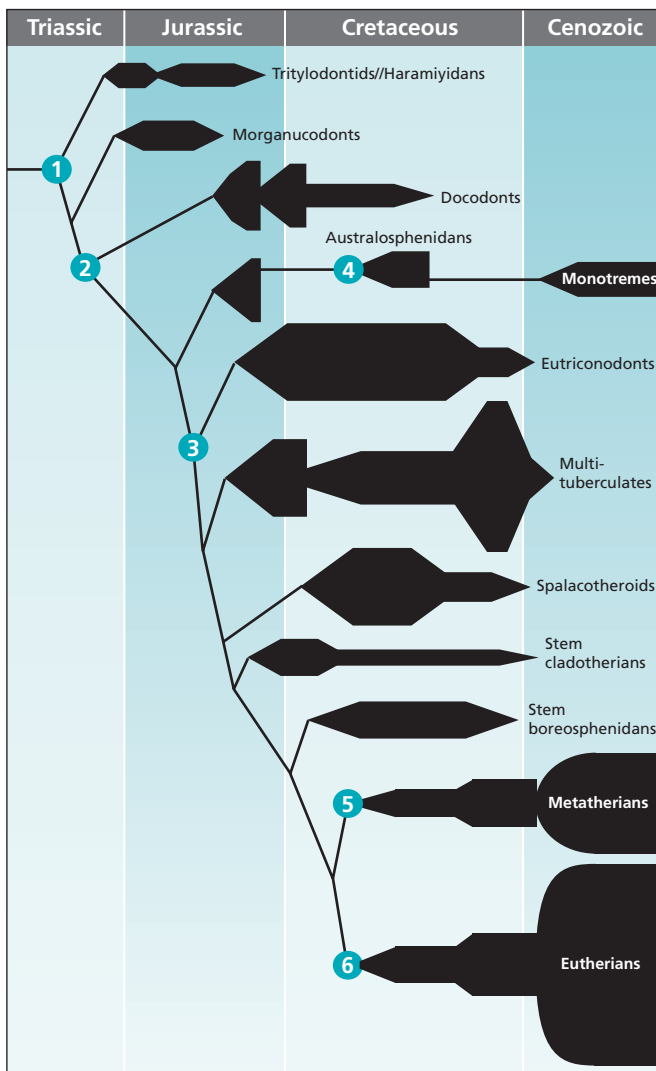
Figure 4.8 **Mesozoic mammal clades.** Overview of the temporal distribution and phylogeny of clades of Mesozoic and major extant groups of mammals.

Six episodes (nodes) of diversification occurred, most typified by phylogenetic dead-end branches without ancestor-descendant relationship. Six episodes (*nodes*) of diversification are as follows:

1. The earliest-known episode of diversification occurred in the **Late Triassic-Early Jurassic** on a global scale, when haramiyidans, morganucodontans, kuehneotheriids, and docodontans appeared (*Node 1*, blue branches and dots);

2. The next episode occurred globally with peak density in the **Middle Jurassic**, with diversification of docodonts and splits of several extinct groups of mammals (*Node 2*, green and yellow);

3. The **Late Jurassic** diversification occurred primarily in Laurasia among eutriconodonts, spalacotheriids, dryolestoids, and peramurans (*Node 3*);

4. The **Early Cretaceous** episode saw diversification on the Gondwanan continents within the australosphenidans and character-based monotremes and basal splits of eutherians and metatherians and diversification of tricondontids on the Laurasian contenents (*Node 4*);

5. **Late Cretaceous** diversification occurred in stem-based metatherians (including marsupials) (*Node 5*);

6. **Late Cretaceous** diversification occurred in stem-based eutherians (including placentals), within cimolodontan multituberculates on the northern continents, and within gondwanatherians on the southern continents (*Node 6*).

The shape of branches corresponds to changes in biodiversity in each lineage through time; wider areas reflect greater diversity. The phylogeny is based on Luo and Wible (2005), Luo et al. (2007), Bonaparte et al. (2005), and Meng et al. (2006). *Adapted from Luo et al. (2002), Ji et al. (2002), and Luo (2007).*

EARLY PROTOTHERIANS

Members of the Family Morganucodontidae are among the most primitive known mammals, with Genus *Morganucodon* abundant in the fossil history (see Figure 4.8). Members of this family from the Late Triassic of Europe represent the earliest known mammals (Mammaliaformes). Morganucodontids may have been the ancestors of later major groups, including the unknown ancestors of **monotremes**. Relationships among lines of Mesozoic mammals are unclear, however, and affinities of the morganucodontids to later groups remain uncertain. They may be considered "prototherian" only in that they did not form the ancestry of the marsupials and placental mammals. Although monotremes today are numerically an insignificant part of the mammalian fauna, prototherian mammals during the Mesozoic era were numerous and diverse.

Several distinct mammalian structural features are present in morganucodontidae and evolved among several different lineages (Crompton and Jenkins 1979; Carroll 1988). These features included dentary-squamosal articulation, although involvement of the quadrate and articular bones remained. Besides incisors and canines, the cheekteeth were differentiated into premolars and molars. The occlusal surfaces (the portion of the crowns that contact each other when an animal chews) of the upper and lower molars were clearly mammalian. The cochlear region was large relative to skull size. The first two vertebrae were similar to those seen in later mammals, and two occipital condyles were present. Thoracic and lumbar vertebrae and the pelvic region were distinct from the reptilian pattern. Morganucodontids had a mammalian posture, with the legs beneath the body, not splayed out as in reptiles. Also, the vertebrae allowed flexion and extension of the spine during locomotion. Thus, many interrelated features of the skull and postcranial skeleton that define mammals were evident in morganucodontids (as well as in late cynodonts). These features continued to be refined in later groups of Late Jurassic and Early Cretaceous lineages of mammals. The most prominent of these lines were the triconodonts, amphilestids, docodonts, and multituberculates—groups defined on the basis of tooth structure and associated adaptive feeding types.

The **Triconodonta** were a successful lineage that extended 120 my from the Late Triassic to the Late Cretaceous (Cifelli and Madsen 1998). They included the early Morganucodontidae. The triconodonts were small, carnivorous mammals named for their molars, which had three cusps arranged in a row (Figure 4.9A). The **amphilestids** occurred from the Mid-Jurassic to the Early Cretaceous. They had a linear row of cusps much like morganucodontids. The amphilestid Genus *Gobiconodon*, from the Early Cretaceous, is noteworthy because it had deciduous molars (Carroll 1988). The **Docodonta** are known only from the Late Jurassic and may have arisen from the triconodonts (Luo et al. 2015). Based only on teeth and jaws from which they have been described, they appear to have been omnivores. The lower molars were rectangular with prominent cusps. These are the most complex teeth seen in fossils from the Jurassic period (Meng et al. 2015) and achieve the same complexity as later Cretaceous therians (Figure 4.9B). The advanced teeth of docodonts were in contrast to the retention of reptilian jaw articulation in this group. This demonstrates an important point. The suite of characteristics seen in mammals evolved at different rates within and among a number of lineages, and often in association with retained primitive reptilian characters.

A third order, the **Multituberculata**, was another successful mammalian line that extended about 120 my from the Late Jurassic to the Late Eocene, concurrent with the emergence and radiation of flowering plants (Cifelli et al. 2013). Multituberculates were primarily herbivorous and had a single pair of large, procumbent lower incisors, as do modern rodents (Wall and Krause 1992; Kielan-Jaworowska 1997; Xi et al. 2015). However, they also had as many as three pairs of upper incisors. The order is named for the molariform teeth, which had up to eight large, conical cusps (Figure 4.9C). These cusps were arranged in triangles in anterior molars but in longitudinal rows in the posterior teeth. The posterior lower premolar often was very large and was used for shearing (Figure 4.9D). Multituberculates and eutherian mammals coexisted for more than 70 my. The decline of multituberculates began in the Late Paleocene. The last multituberculates appeared in the Late Eocene of North America (Van Valen and Sloan 1966). Multituberculates probably were replaced by true rodents, primates, and other eutherian herbivores. The Triconodonta, Haramiyoidea, Docodonta, and Multituberculata have unclear phylogenetic placement (Jenkins et al. 1997).

EARLY THERIANS

Remains of the earliest therians (formerly known as pantotheres) occur in rock strata that also contain the prototherian morganucodontids. Two orders are known only from teeth and jaw fragments: the **Symmetrodonta** and the **Eupantotheria**. The earliest known symmetrodonts, within the Family Kuehnoetheriidae, are the Genera *Kue-*
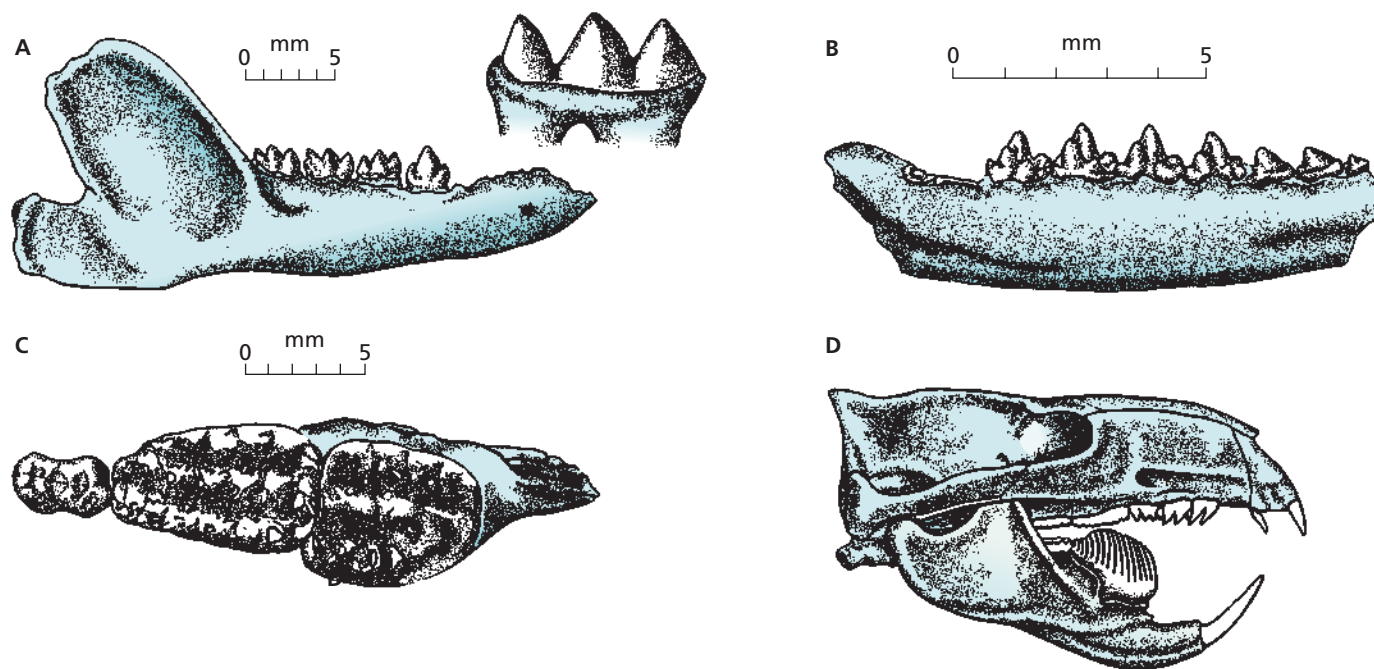
Figure 4.9 **Representative dentition from the "prototherian" line of early mammals.** (**A**) Lateral view of the right jaw and medial view of a lower molar from Genus *Triconodon*, a triconodont; (**B**) lingual view of the left mandible from the docodont *Borealestes serendipitus*; (**C**) occlusal view of the upper premolar and molars of the multituberculate *Meniscoessus robustus*; (**D**) lateral view of the skull of Genus *Ptilodus*, showing the enlarged shearing posterior lower premolar. Note the completely formed braincase for muscle attachment and the large dentary with coronoid process. The actual length of the skull is approximately 8 cm. *Adapted from Lillegraven et al. (1979).*

hneotherium and *Kuhneon*—very small carnivores or insectivores from the Late Triassic (Hu et al. 1997). Later Jurassic pantotheres radiated into numerous different lines and adaptive feeding niches during the Cretaceous period. A significant feature of pantotheres was their molars, which had three principal cusps in triangular arrangement. This tribosphenic tooth pattern (the basic pattern for later mammals; see the next section) allowed for both shearing and grinding food. The most diverse family of eupantotheres, the **Dryolestidae**, may have been omnivorous and survived into the Early Cretaceous. Based on derived dental characteristics, advanced therians, that is, distinguishable **metatherians** and **eutherians**, probably originated within the eupantothere Family **Peramuridae** by the Middle to Late Cretaceous, if not before. Peramurids are known only from the Late Jurassic Genus *Peramus*. Genetic evidence (timed by the molecular clock) indicates that the marsupial lineage split from a therian ancestor about 173 mya, much earlier than estimated by fossil evidence (Kumar and Hedges 1998). The earliest known marsupial, *Kokopellia*, is known from the Middle Cretaceous of North America (Utah; Cifelli 1993; Cifelli and Muizon 1997). The earliest known eutherian mammal, *Eomaia scansoria*, was recently discovered from the Lower Cretaceous Yixian Formation of northeastern China (Ji et al. 2002). We estimate *Eomaia* to be about 125 my; this extends the oldest eutherian records with skull and skeleton by about 40–50 my. In contrast to terrestrial locomotor features of other Cretaceous eutherians, *E. scansoria*, possessed fore- and hindfeet morphology adaptive for **scansorial** locomotion. Such locomotor morphology may offer clues to the evolution of scansorial abilities of early eutherians (Ji et al. 2002).

TRIBOSPHENIC MOLARS

As noted previously, early mammals had tooth cusps arranged longitudinally (see Figure 4.9A and C). Metatherians and eutherians, and their immediate ancestors in the Cretaceous period (referred to generally as "theria of metatherian-eutherian grade"), had more advanced **tribosphenic** (or tritubercular) molars (Butler 1992; Smith and Tchernov 1992; Muizon and Lange-Badre 1997; Luo et al. 2001; Cifelli and Davis 2015). These are named for the three large cusps arranged in a triangular pattern. A tribosphenic upper molar (Figure 4.10) consists of a **trigon** with three cusps, a **protocone** that is lingual (the apex of the triangle points inward toward the tongue), and an anterior, labial (outward toward the cheek) **paracone** and posterior **metacone**. A lower molar, or **trigonid** (an -*id* suffix always denotes mandibular dentition), consists of these three cusps and a "heel," or talonid basin. In lower molars, the protoconid is labial (not lingual, as in the upper molars), whereas the paraconid and metaconid are lingual. The **talonid** of the lower molars also has smaller accessory cusps. These often include a labial **hypoconid**, a posterior **hypoconulid**, and a lingual **entoconid** (see Figure 4.10).
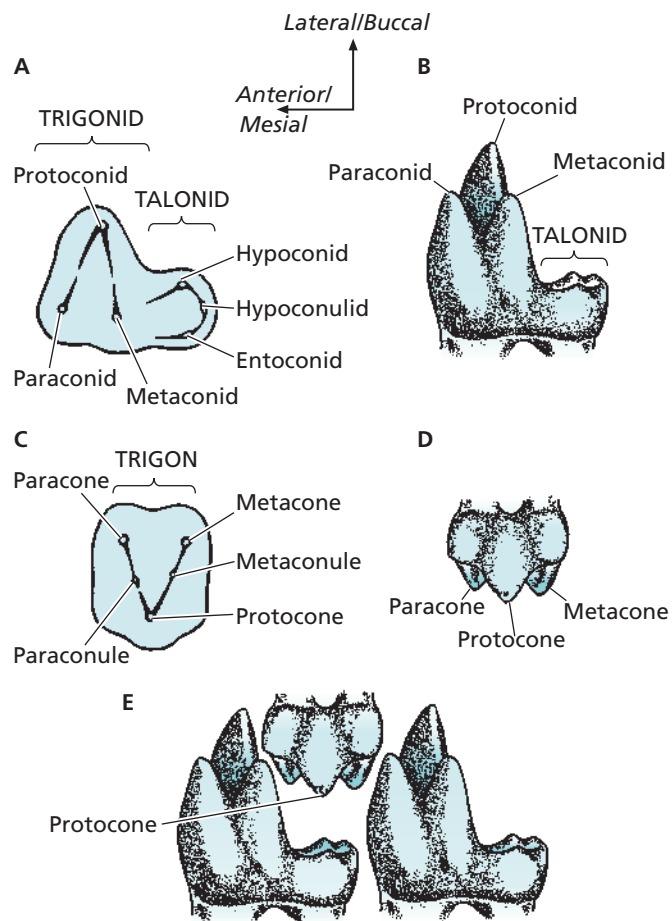
Figure 4.10 Nomenclature of the cusps of tribosphenic dentition. A lower molar in (**A**) occlusal view and (**B**) lingual view, and an upper molar in (**C**) occlusal and (**D**) lingual views. The upper and lower dentition is shown in occlusion in (**E**). The addition of a fourth cusp, the hypocone, forms a quadrituberculate upper molar. *Adapted from Kermack and Kermack (1984).*

Thus, the occlusal view of the trigon(id) of tribosphenic molars is a somewhat asymmetrical, three-cusped triangle (see Figure 4.10A,C). The apex of the triangle points lingually (inward toward the tongue) in upper molars and labially (outward toward the cheek) in lower molars. During occlusion, a crushing or grinding action occurs as the protocone of an upper molar contacts the talonid basin of the opposite lower molar. Food is not only crushed but also sheared. Shearing results from several facets of the upper and lower molars coming together (see Crompton and Hiiemae 1969; Bown and Kraus 1979)—for example, the anterior face of a paracone and the posterior face of a protoconid and metaconid.

The basic pattern of the tribosphenic molar in early mammals was very important because it is believed to be the ancestor of modern therian mammals (Hopson 1994). It is seen today in lineages such as marsupials and insectivores and has been modified in other modern mammals. For example, molars have become square (**euthemorphic**) with the addition of another main cusp (the **hypocone**)

posterior to the protocone. Such four-cusped (**quadritu-bercular**) molars occur in many species of modern mammals, including humans. Cusps are often connected by a series of crests or ridges, as in many "insectivores" (see Figure 17.1). Hershkovitz (1971) provided an exhaustive treatment of cusp patterns, homologies, and associated terminology.

Cenozoic Mammals and Mammalian Radiation

The different mammalian lineages seen today began with diversification of mammals during the Early Cenozoic. This radiation resulted from two major events that occurred worldwide. The first was the extinction of the dominant terrestrial vertebrate fauna, the dinosaurs, at the end of the Cretaceous period. There are several hypotheses as to why dinosaurs died out so quickly. Nobody knows

for sure, although strong evidence suggests that extinction of the dinosaurs was caused by a large asteroid that struck the earth, resulting in major climate and vegetation changes. Whatever the reason, disappearance of the dominant Mesozoic reptiles opened new adaptive opportunities and resulted in a worldwide mammalian radiation (O'Leary et al. 2013; Liu et al 2017). Rapid expansion and divergence of the mammals was also facilitated by the breakup of the large continental land mass (**Pangaea**) that had been in place during much of the time of the dinosaurs (Fooden 1972). Continental drift throughout the Early Cenozoic (Figure 4.11) allowed major genetic differentiation of the various phyletic lines to proceed in relative isolation. These two factors, in addition to ever-expanding faunal and floral diversity worldwide, allowed mammals to occupy increasingly specialized ecological roles. As a result, for most modern mammals, ordinal differentiation was underway by the Early Cenozoic, and for many groups probably since the Late Mesozoic. Most extant orders are recognized in the fossil record by the beginning of the Eocene epoch, and most families date from before the Miocene. Mammals
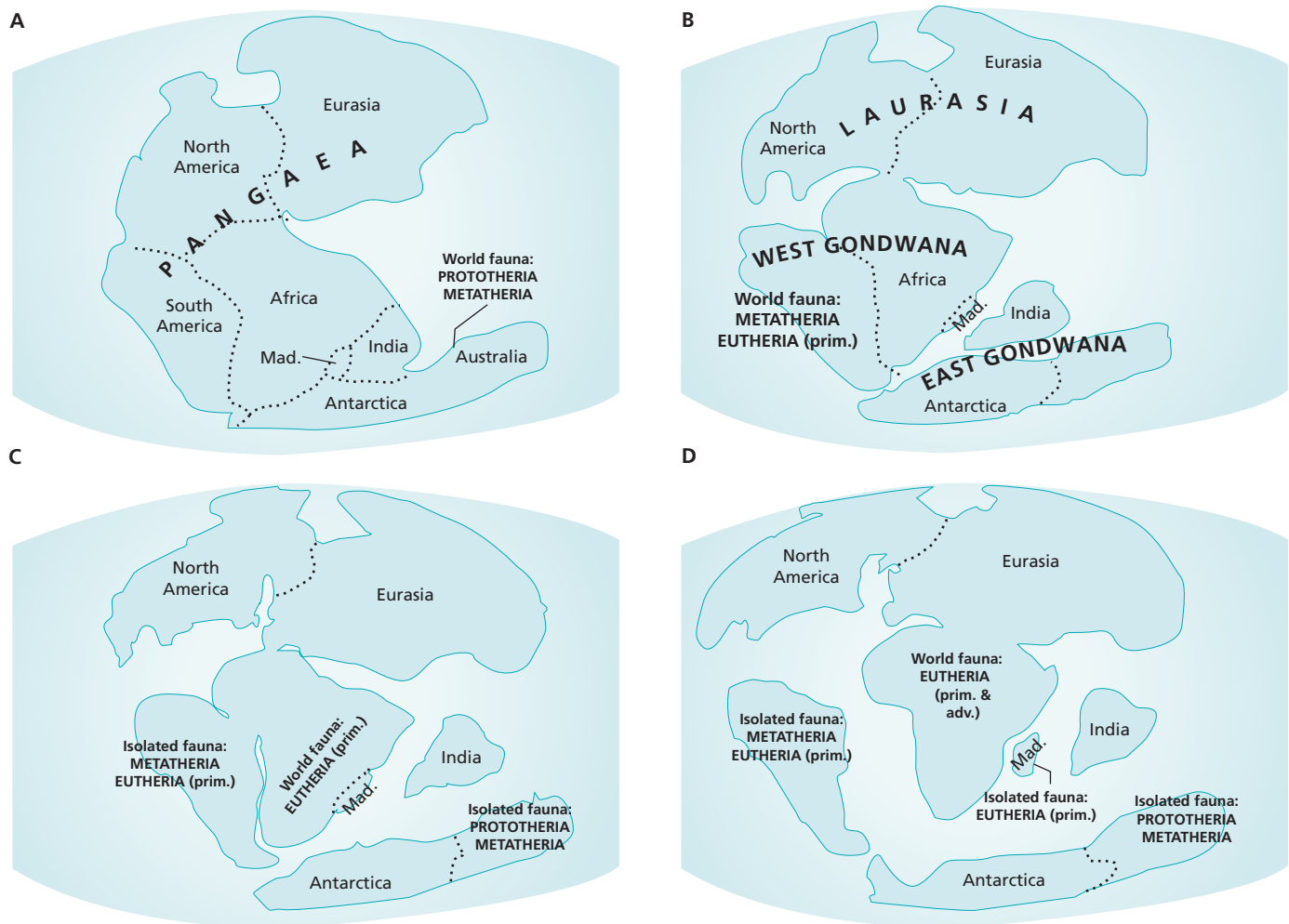
Figure 4.11 Early continental land masses. The breakup of the single large land mass (Pangaea) beginning about 200 mya and eventual isolation of the continents that promoted differentiation of the various mammalian phyletic lines following the Cretaceous period. (**A**) 2.00×10^8 years ago; (**B**) 1.8×10^8 years ago; (**C**) 1.35×10^8 years ago; (**D**) 6.5×10^7 years ago. *Data from Fooden (1972).*

have been the dominant terrestrial vertebrates ever since—for the last 65 my.

Interrelationship of Characteristics and Increased Metabolism

The changes in skeletal features noted in the following section occurred in association with metabolism, physiology, and reproduction—all of which were related to and developed concurrently with maintenance of endothermy (Grigg et al. 2004; Kemp 2006; McNab 2012). Features of the soft anatomy related to endothermy are not visible in the fossil record because these organ systems do not fossilize; however, many of these features can be inferred. Evolutionary changes from reptiles to mammals can be related to increased metabolic demands of mammals. Mammals need approximately ten times the amount of food and oxygen that reptiles of similar size need to maintain their high body temperature. Endothermy demands an efficient supply of oxygen to the lungs for aerobic metabolism, a widespread and constant food supply, and the ability to obtain and process that food quickly and efficiently (McNab 2002, 2012; Kemp 2005, 2006). Thus, from reptilian to mammalian organization, most of the trends summarized in the following section relate directly to efficient homeostasis. All these trends are no doubt interrelated in a much more complicated and sophisticated manner than can be appreciated from a simple reconstruction from fossil history. The adaptive significance and interrelationship in post-dentary bones and increase in the size of the dentary bone offer an excellent example of this. These interrelated changes in anatomy not only increased efficiency of chewing and digestion but also directly enhanced auditory acuity through greater efficiency of vibrations from the tympanic membrane. Enhanced hearing can help an individual avoid predators or capture prey more efficiently.
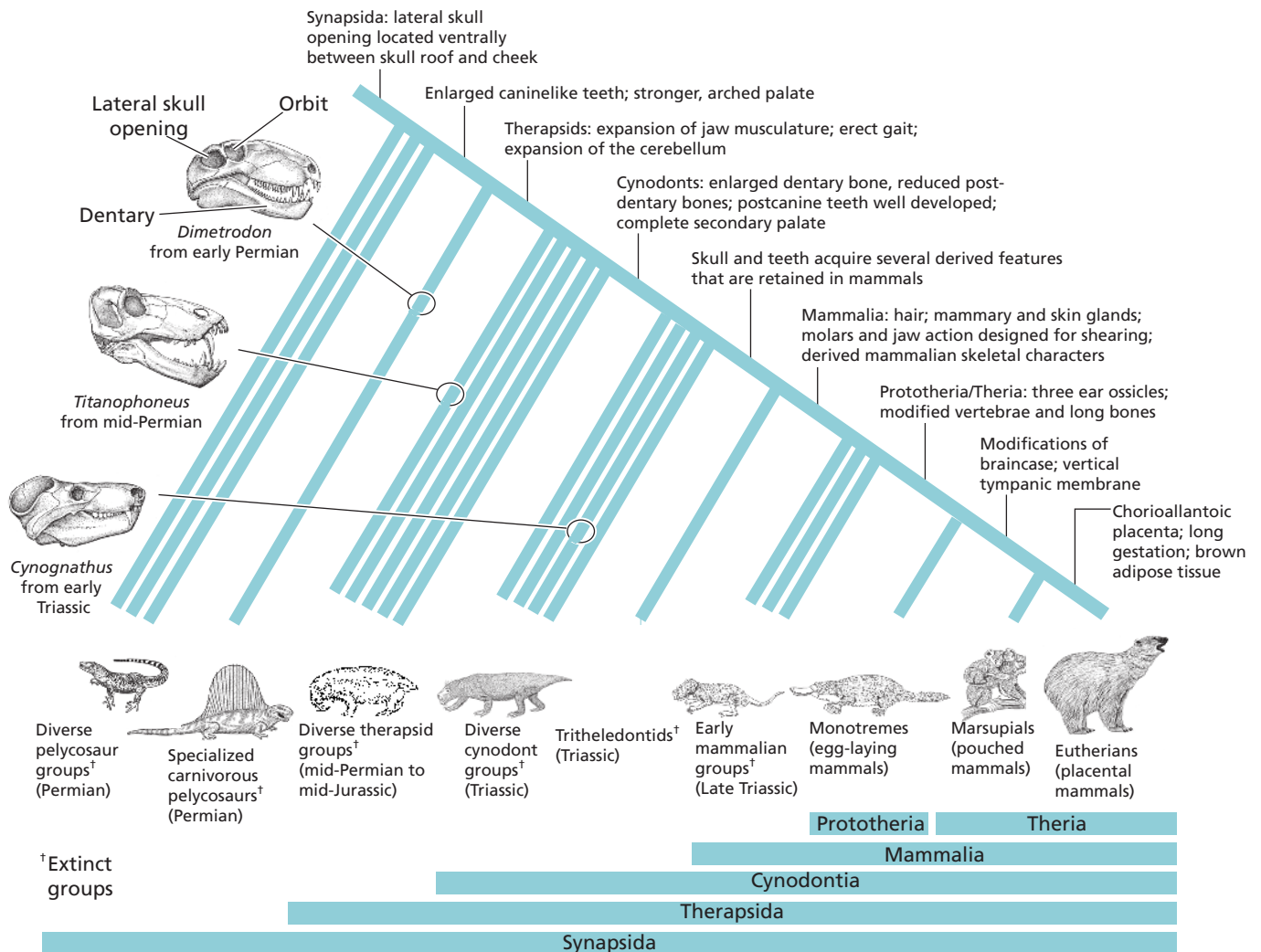
Figure 4.12 **Mammalian evolutionary trends.** General summary of mammalian evolutionary trends from ancestral synapsids to modern mammals.

Summary of Anatomical Trends in Organization from Mammal-Like Amniotes to Mammals

Several morphological trends were evident in the evolution of mammals from their mammal-like reptilian ancestors (see Figure 4.12). Many of these trends have been noted, as have some of the interrelationships among them. Also, remember that different characters appeared at different times and in different phyletic lines. The process of change from reptile to mammal certainly did not proceed in orderly, progressive, or easily defined steps. The following trends are evident, however, in the evolution of mammals from reptiles:

1. The temporal opening of the skull of therapsids was enlarged (see Figure 4.13). This was associated with eventual movement of the origin of the jaw muscles from the inner surface of the temporal region in mammal-like reptiles to the outer surface of the brain case and newly developed zygomatic arch in mammals (Figure 4.13).
2. These changes paralleled development of a larger, heavier dentary bone for processing the food necessary for higher metabolic activity and maintenance of homeostasis. Thus, the dentary bone became progressively larger as the postdentary bones were reduced in size (see Figure 4.4). As noted earlier, the articular and quadrate bones diminished in size and became part of the middle ear. Remember, however, that several other bones in the lower jaw were retained for a long time, even after the emergence of the dentary-squamosal articulation.
3. The **maxillary** and palatine bones extended posteriorly and medially, forming a secondary palate (Figure 4.14). This resulted in more efficient airflow, allowing a constant supply of oxygen to the lungs while permitting chewing and thus enhancing metabolism. It may also have affected suckling in neonates (Maier et al. 1996).
4. Dentition changed from **homodont** (uniform, peg-like tooth structure with little occlusion) to

Figure 4.14 **Formation of the secondary palate.** Ventral views of the cranium of (**A**) Genus *Dimetrodon*, a pelycosaur, and (**B**) Genus *Cynognathus*, a more advanced cynodont. Note that the internal nares (*n*) open immediately to the front of the mouth in the primitive form, but in the cynodont, the air enters the back of the mouth because of the medial extension of the maxillary (*m*) and palatine (*p*) bones that form a secondary palate. Also notice the one occipital condyle in *Dimetrodon* and the development of two occipital condyles in *Cynognathus*. *Adapted from Romer (1966).*

Figure 4.13 **Muscle attachment and the temporal opening.** Lateral view and cross section of the skulls of (**A**) an early synapsid and (**B**) a mammal showing movement of the origin of the muscle attachment to the lower jaw from inside the cranium to outside the cranium. Muscle attachment was around the edge of the temporal openings in mammal-like reptiles. Muscle attachment moved to the outside of the cranium with complete ossification of the braincase and formation of the zygomatic arch in mammals. *Radinsky (1987).*

Figure 4.15 **Conformation of limbs.** A reptile adopts a sprawling gait with the limbs emerging horizontally from the body. A mammal adopts an upright stance with the limbs placed directly beneath the body; this is mechanically much more efficient. *Adapted from Savage and Long (1986).*
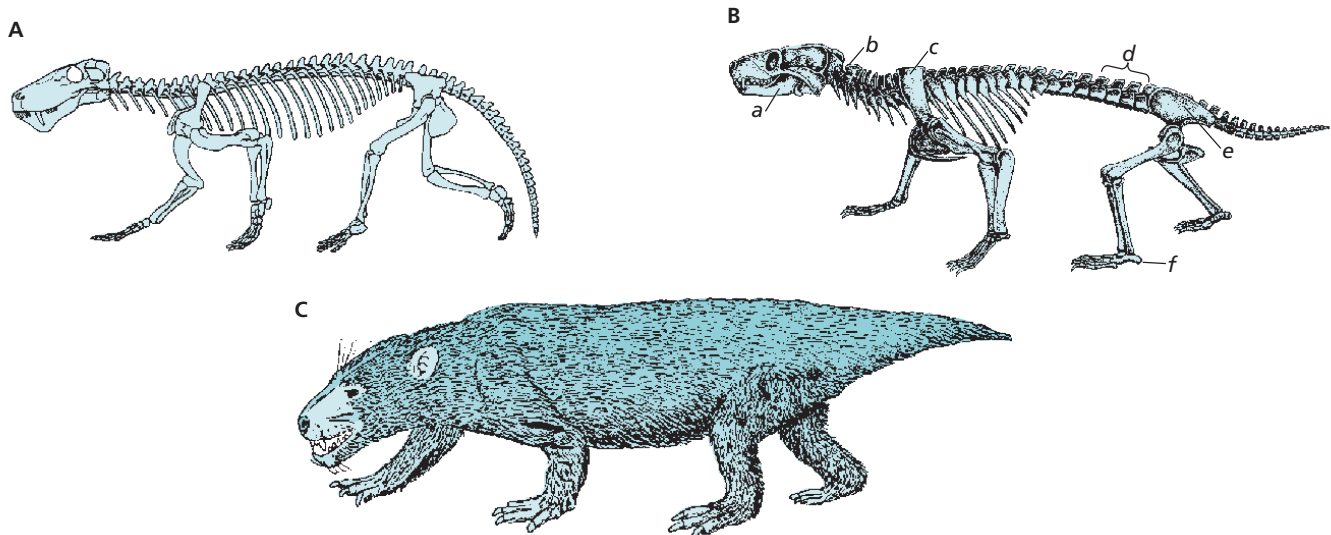
Figure 4.16 **Evolutionary trends in therapsids toward the development of mammals.** (**A**) Genus *Lycaenops*, an early theriodont from the late Permian period; (**B**) an early Triassic cynodont, Genus *Thrinaxodon*, showing formation of distinct mammalian characteristics, including enlargement of the dentary bone, with the coronoid process extending above the zygomatic arch (*a*); the second cervical vertebra (axis) with a spine (*b*); enlargement of the scapula (*c*); formation of distinct lumbar vertebrae and associated reduction in the number of ribs (*d*); enlargement of the pelvic bones (*e*); and formation of a heel bone (*tuber calcanei*) and distinct plantigrade feet (*f*); (**C**) lifelike reconstruction (hair is hypothetical) of *Thrinaxodon*, which was about the size of a weasel. *Adapted from Hotton et al. (1986).*

strongly **heterodont** (teeth differentiated on the basis of form and function) in association with obtaining and processing foods more efficiently. Chewing efficiency also was enhanced by the development of tribosphenic molars (Luo et al. 2001).

5. A change occurred from one occipital condyle in amniotes to two in advanced synapsids and mammals (see Figure 4.14). This reduced tension on the spinal cord when the head was moved up and down and allowed finer control of head movements, but decreased lateral movement.

6. Limbs rotated 90° from the "splayed" reptilian stance (i.e., horizontal from the body and parallel to the ground) to directly beneath the body (perpendicular to the ground; Figure 4.15). Additional changes resulted in the pectoral and pelvic girdles, including loss of the coracoid, precoracoid, and interclavicle bones in the pectoral girdle, although monotremes still retain them. In the pelvic girdle, the separate bones found in reptiles fused in mammals and moved to a more anteriodorsal orientation. Mammals can therefore move with less energy expenditure than reptiles.

7. Cervical and lumbar ribs were lost completely, and the number and size of thoracic ribs were reduced. In association with changes in the vertebrae and scapula (Figure 4.16), as well as others, this again allowed for more flexibility in movement, especially dorsoventral flexion of the spine.

8. The number of carpal and tarsal bones was reduced, and the phalangeal formula was reduced from the

reptilian 2-3-4-5-3 (forefeet) and 2-3-4-5-4 (hind feet) to the typical 2-3-3-3-3 found in most mammals (Hopson 1995).

Many of these skeletal transformations, as well as differences in the soft anatomy, are evident in reptiles and mammals today (see Table 4.2). The generally accepted feature used in the recognition of early mammals is a jaw joint with squamosal-dentary articulation. This is first seen in the Mesozoic era about 220 mya and was the result of a 100-my process of change. Any single criterion separating mammal-like reptiles and early mammals becomes more arbitrary, however, as fossil history becomes more complete.

Characteristics of Modern Mammals

We noted several characteristic skeletal trends associated with the evolution of mammals (Hickman et al. 2004; Benton, 2005; Kemp 2005) (Table 4.2). The single dentary bone and three ossicles of the middle ear are unique to mammals. Two occipital condyles, epiphyses on many long bones (which result in determinant growth, unlike reptiles), and a tympanic bone are other mammalian skeletal characteristics. Among the vertebrates, several aspects of the soft anatomy of mammals are also unique.

Probably the most obvious mammalian feature is hair, or fur. These terms are synonymous—structurally,

Table 4.2 Different characteristics of reptiles and mammals

Reptiles	Mammals
More than one bone in mandible; with quadrate-articular articulation of jaw joint	Single bone in mandible; with squamosal-dentary articulation
One occipital condyle	Two occipital condyles
Long bones without epiphyses (indeterminate growth)	Long bones with epiphyses (determinant growth)
Unfused pelvic bones	Fused pelvic bones
Secondary palate usually absent	Secondary palate present
Middle ear with one ossicle (stapes-columella)	Middle ear with three ossicles (malleus, incus, and stapes)
Phalangeal formula 2-3-4-5-3 (4)	Phalangeal formula usually 2-3-3-3-3
Dentition homodont and polyphyodont	Dentition often heterodont and diphyodont
Epidermis with scales	Epidermis with hair
Oviparous or ovoviviparous	Viviparous (except for the monotremes)
Three-chambered heart in most	Four-chambered heart with left aortic arch
Ectothermic with low metabolic rate	Endothermic with high metabolic rate
Nonmuscular diaphragm	Muscular diaphragm
No mammary glands	Mammary glands present
Relatively small, simple brain	Relatively large, complex brain

From Bourliére (1964). Reprinted by permission.

no difference exists between hair and fur. There are several types of hair, and one or more types make up the **pelage** (coat) of mammals. Mammals have a four-chambered heart, with a functional left aortic arch. Birds also have a four-chambered heart but with a functional right aortic arch. The biconcave **erythrocytes** (red blood cells) of mammals are **enucleate** (without a nucleus). Not having a nucleus enhances the oxygen-carrying capacity of these cells. Female mammals have milk-producing **mammary glands** (**mammae**). This character is, of course, the basis for the name of the Class Mammalia. Finally, mammals have a muscular **diaphragm** separating the thoracic and abdominal cavities. Other aspects of the soft anatomy can be used to characterize mammals. These either are not unique to mammals or are not found in all mammals. For example, the **corpus callosum**, a bundle of nerve fibers that integrates the two cerebral hemispheres of the brain in eutherians, does not occur in monotremes and marsupials. Likewise, a true vascular chorioallantoic **placenta** occurs only in eutherians (except for marsupial bandicoots—see Chapter 10). Aspects of mammalian dentition are discussed in the following sections. Other general mammalian characteristics, including **locomotion** (movement), feeding, hair, and reproduction, are examined in greater detail in Part 2.

Dentition

Teeth are one of the most important aspects of living mammals. Also, many fossil lineages are described only on the basis of their teeth. Although all mammals begin life on a diet of milk, they eventually enter into one of a variety of adaptive feeding modes. An individual's teeth reflect its trophic level and feeding specialization. A number of different feeding niches are available, and as a result, mammalian dentition shows a number of different modifications. These modifications are derived in large part from the basic tribosphenic pattern, which allowed much more efficient processing of food necessary for endothermy and is retained in more primitive groups, such as "insectivores", tree shrews, elephant shrews (Chapter 11), and some marsupials (Chapter 10). Besides their role in feeding, teeth can also function secondarily in burrowing, grooming, and defending. Whereas mammals show little skeletal variation, except in their limbs, a great deal of variation occurs in their dental patterns.

Teeth may occur in three bones in mammals: the premaxilla and maxilla of the cranium and the mandible (dentary bones). Most species have teeth in all three of these bones; others have a much reduced dentition in only one or two of these bones. Still other species are **edentate**, that is, they have no permanent teeth at all.

TOOTH STRUCTURE

The portion of the tooth above the gum line is the **crown**, and the **roots** are below the gum line (Figure 4.17). In most species, **enamel** overlays **dentine** in the crown of the tooth. Enamel is harder, heavier, and more resistant to friction than any other vertebrate tissue. It is acellular, cannot regenerate, and is made up of crystallized calcium phosphate (hydroxyapatite). Enamel is ectodermal in origin, whereas dentine is of dermal origin and makes up most of the tooth.
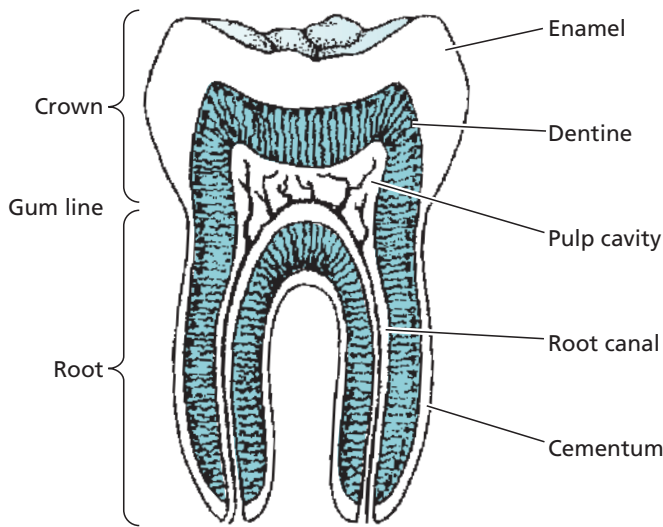
Figure 4.17 Longitudinal section of a mammalian molar. The tooth is seated in an alveolus (socket). With increased age, the enamel wears away, and progressively more dentine is exposed in most species. Also, an additional layer of cementum is often deposited each year. *Adapted from DeBlase and Martin (1981).*

In some species, such as the aardvark, Order Tubulidentata (Chapter 11), and Order Cingulata (Chapter 13), the teeth have no enamel. Rodent incisors have enamel only on the anterior surface, which causes differential wear and continuous sharpening of the incisors for gnawing. Within the dentine is the **pulp cavity**, in which blood vessels and nerves maintain the dentine. In **open-rooted** teeth, growth is continual, and such teeth are termed "ever-growing." Incisors of rodents are a prime example of ever-growing, open-rooted teeth (see Figure 16.3). Alternatively, teeth stop growing and begin to wear down with age when the opening to the pulp cavity closes. Wear on teeth that are **closed-rooted** may be used to estimate an individual's age. Just as the crown of a tooth usually is covered with enamel, the root is covered with **cementum**. This is a modified bony material deposited throughout an individual's life. Cementum annuli are often deposited much like the rings of a tree, and as with tree rings, the annuli can sometimes be used to determine an individual's age. A socket in a bone containing the tooth roots is an **alveolus**. Connective tissue between the cementum and the alveolar bone holds the tooth in place.

One of the anatomical trends noted previously was the change from homodont dentition of synapsids to heterodont dentition in mammals. Certain modern mammalian lines have homodont dentition, for example, the toothed whales (odontocetes) and armadillos (Order Cingulata: Dasypodidae). Still other groups, such as the platypus and spiny echidnas (monotremes), are edentate. So are several unrelated mammalian lineages that feed on ants and termites, for example, true anteaters (Order Pilosa: Myr-

mecophagidae) and pangolins, or scaly anteaters (Order Pholidota: Manidae). A special case of edentate mammals is the mysticete whale, in which teeth have been replaced with **baleen** in the upper jaw (see chapter 20). The edentate condition is secondarily derived; that is, teeth develop and sometimes emerge in embryos but are resorbed or lost prior to parturition.

Most mammals have heterodont dentition, with well-defined incisors, canines, premolars, and molars. **Incisors** are the anterior-most teeth, with the upper incisors rooted in the premaxilla. All lower teeth are rooted in the dentary bones. The incisors often function to cut or gnaw, as in rodents and lagomorphs. Incisors are usually structurally simple with a single root. Sometimes, though, they are highly modified and serve a variety of purposes. In shrews (Order Soricomorpha: Soricidae), the first pair of incisors is long and curved (Hutterer 2005c). They appear to function as forceps in seizing insect prey. Vampire bats have blade-like upper incisors for making incisions. Incisors are sometimes modified as tusks, as in elephants and male narwhals (*Monodon monoceros*). Some groups, such as deer, have lost the upper incisors but have retained the lower ones. They clip vegetation by cutting against a tough, pad-like tissue in place of the upper incisors.

Canines are posterior to the incisors. There is never more than one pair of upper and lower canines in modern mammals. These teeth generally are **unicuspid** (i.e., they have one cusp) with a single root. In carnivores and some other groups, canines are often enlarged and elongated for piercing and tearing prey. They may even form tusks in certain species, such as the walrus (*Odobenus rosmarus*) and pigs (Order Artiodactyla: Suidae). In species of deer without antlers, musk deer (Genus *Moschus*) and the Chinese water deer (*Hydropotes inermis*), males have elongated, tusk-like upper canines.

Premolars are posterior to the canines and anterior to the molars. Generally, teeth in the posterior part of a dental arcade are structurally more complex than anterior teeth. Premolars are generally smaller than molars and have two roots, whereas molars usually have three. Premolars may be unicuspid, or they may look the same as molars, but premolars have deciduous counterparts ("milk teeth"). **Molars** have multicusps and no deciduous counterparts; that is, they are not replaced. The premolars and molars are often considered together as "cheekteeth" or "postcanine" or "molariform" teeth, especially in species in which they are difficult to differentiate. Molariform dentition is used for grinding food. As such, these teeth usually have the greatest degree of specialization in cusp patterns and ridges associated with a particular feeding niche. The height of the crown varies among species. Teeth with low crowns are termed **brachyodont** and often are found among omnivores. Herbivores consume forage that is often highly abrasive and contains large amounts of silica. This wears teeth down more rapidly than does a carnivorous diet, and it is therefore adaptive for an herbivore to
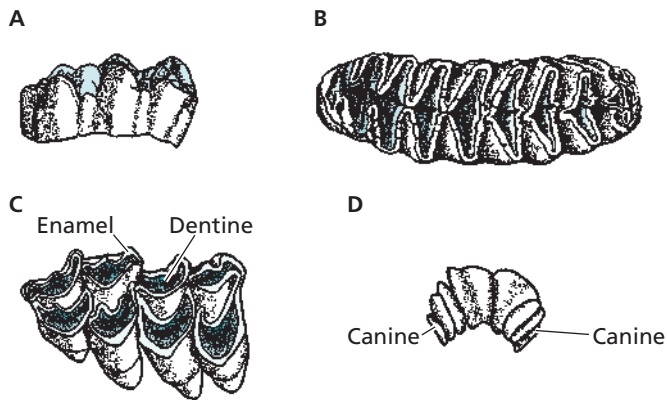
Figure 4.18 Occlusal surfaces. Teeth showing general types of occlusal surfaces: (**A**) a pig, with a bunodont surface; (**B**) the lophodont dentition of an African elephant, with cusps in the form of transverse ridges; (**C**) a deer, with selenodont teeth forming crescent-shaped ridges. The enamel appears lighter than the dentine. (**D**) Dorsal view of the lower incisors of a white-tailed deer, showing the lateral "incisiform" canines. *Note*: The teeth are not to the same scale.

Figure 4.19 Mandibular condyle and muscle groups. The position of the mandibular condyle (*arrow*) relative to the plane of the teeth differs between (**A**) carnivores and (**B**) herbivores. Thus, the temporalis muscles (*1*) are the primary group of chewing muscles in carnivores, whereas the masseters (*2*) are the primary group in herbivores. *Adapted from Radinsky (1987).*

have high-crowned, or **hypsodont**, cheekteeth (Martin et al. 2001).

In addition to differences in crown height, occlusal surfaces are quite variable. Specifically, the cusp patterns are often highly modified (Figure 4.18A–C). Brachyodont cheekteeth are often **bunodont**, with rounded cusps for crushing and grinding, as in most monkeys and pigs. Alternatively, the cusps may form continuous ridges, or **lophs**, such as occur in elephants, in a pattern termed **lophodont**. Sometimes the lophs are isolated and crescent-shaped, as in deer, in which case they are called **selenodont**. Loph patterns may become so complex that it is difficult to discern the original cusp pattern. A great deal of diversity in cusp patterns is evident among individual families or within an order such as the rodents (e.g., see Figure 16.4). Another example of specialization is found in many modern carnivores, which have **carnassial** or **sectorial** teeth for shearing. Carnassial teeth in modern carnivores are always the last upper premolar and the first lower molar. These teeth are particularly well developed in the cat (Family Felidae) and the dog (Family Canidae). They still occur but are less evident in more omnivorous groups, including many of the ursids (see Figure 18.4). When carnassials are used on one side of the mouth, they are not aligned on the other side and cannot be used. Likewise, in most species, when the anterior dentition (incisors or canines) is used, cheekteeth do not occlude, and when the animal chews with the cheekteeth, incisors do not come together.

Many species have lost teeth through evolutionary time so that a gap, or **diastema**, occurs in the toothrow. All rodents and lagomorphs have lost their canines and have a diastema between their incisors and the anteriormost cheekteeth (see Figure 16.3). Deer (Family Cervidae) also have a diastema between the lower incisiform teeth and the

cheekteeth. Moreover, deer can be used to illustrate that teeth in a given position may resemble the teeth next to them. What appears to be the last lower "incisor" in a deer jaw is actually a canine. Because it functions as an incisor, however, its form has changed through time to accommodate its function. It has become "incisiform," that is, indistinguishable from the three true incisors on each side of the midline (see Figure 4.18D).

The structure of the lower jaw and primary use of different muscle groups differ between herbivores and carnivores. In herbivores, the mandibular condyle and its articulation with the fossa of the cranium is elevated above the mandibular dentition. This gives maximum advantage to the masseter muscles in closing the jaw. In carnivores, the temporal muscles are the primary muscle group closing the jaw, and the mandibular articulation is level with the dentition (Figure 4.19). Also, carnivore jaws close in a shearing manner, similar to scissors. Conversely, when the jaw of an herbivore closes, all the opposing teeth occlude together.

TOOTH REPLACEMENT

Generally, mammals have two sets of teeth during their lifetime; that is, they are diphyodont. The deciduous, or "milk" teeth, are replaced by permanent dentition later in life. In many species, the pattern of tooth replacement is used to estimate the age of individuals. In eutherian mammals, all the teeth except the molars have deciduous counterparts. It is unclear, however, whether molars are permanent teeth without preceding milk teeth or "late" milk teeth without succeeding permanent teeth. In metatherians, only the last premolar is deciduous; the remaining postcanine teeth are not replaced. Deciduous incisors and canines do not erupt, and only the permanent anterior dentition is seen (Luckett and Woolley 1996). Certain eutherians, such as shrews, appear to have only permanent teeth because the deciduous teeth are resorbed during fetal development. With few exceptions, replacement of deciduous teeth by their permanent counterparts is vertical, with the permanent tooth erupting from below and pushing out the worn-down deciduous tooth. In elephants (Order Proboscidea) and manatees (Order Sirenia: Trichechidae), however, tooth replacement is horizontal. Teeth in the posterior part of the mandible slowly move forward and replace anterior cheekteeth as they wear down and fall out (see Figure 12.6).

DENTAL FORMULAE

A dental formula provides a useful shorthand description of the total number and position of teeth in a given species. Dental formulae are always given in the following order: incisors, canines, premolars, and molars. Thus, the dental formula for the brown hyena (*Parahyaena brunnea*) is 3/3, 1/1, 4/3, 1/1. This means there are 3 upper (numbers above the line) and 3 lower incisors (numbers below the line), 1 upper and lower canine, 4 upper and 3 lower premolars, and 1 upper and 1 lower molar. Because dentition is bilaterally symmetrical, dental formulae are given for one side of the mouth only and may be multiplied by 2 to arrive at the total number of teeth in the mouth. The hyena has 17 teeth on each side of the mouth (9 upper and 8 lower), for a total of 34. Many species have lost teeth in a particular position through evolutionary time. For example, white-tailed deer (*Odocoileus virginianus*) have lost the upper incisors and canines. Thus, their dental formula is 0/3, 0/1, 3/3, 3/3 = 32 (Figure 4.20). Again, because the tooth order given in a dental formula is always the same, words or abbreviations for incisors, canines, premolars, and molars are not necessary. If there are no teeth in a position, as in the white-tailed deer, a zero is shown, but the position is not deleted. Thus rodents, which have no upper or lower canines, have a canine formula of 0/0.

Abbreviations are often used when describing particular teeth. Superscripts and subscripts may be used with ab-
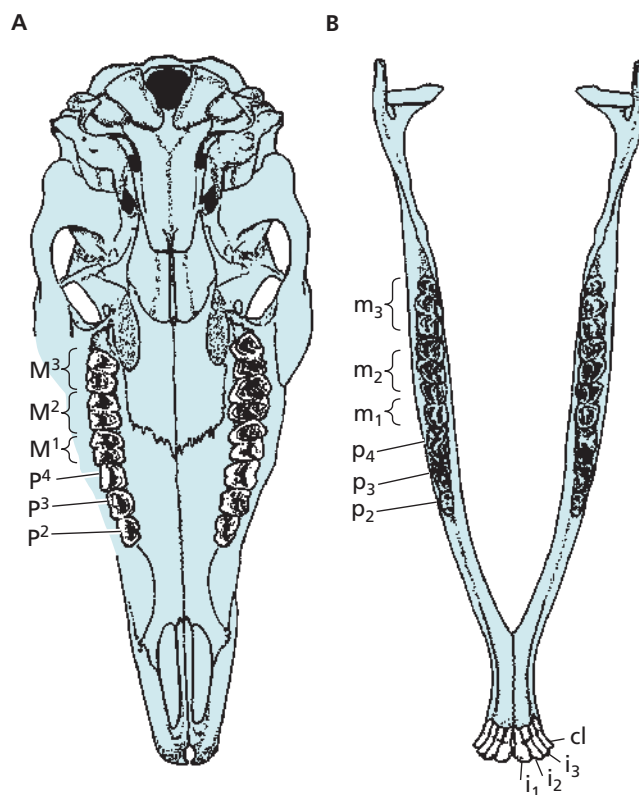
Figure 4.20 Tooth position and structure. (A) Ventral view of the upper dentition; (**B**) dorsal view of the lower dentition of the white-tailed deer, showing the number and structure of teeth in each position. For further discussion of the abbreviations, see text.

breviations for tooth type. For example, P^2 refers to the second upper premolar, whereas P_2 means the second lower premolar. Alternatively, you may see capital letters used to refer to upper teeth (e.g., P2), and lowercase letters for lower teeth (p2). Care must be taken to avoid confusion when referring to particular teeth.

PRIMITIVE DENTAL FORMULAE

For most species of extant mammals, there is a maximum number of each type of tooth. Presumably, these maxima represent the ancestral condition. Thus, although species tend to lose teeth (see the next section), very few exceed the primitive number of incisors, canines, premolars, and molars. In eutherians, the primitive dental formula is 3/3, 1/1, 4/4, 3/3 = 44. This means ancestral eutherian mammals had 44 teeth. Thus, most modern eutherians will not have more than 3 upper or lower incisors per quadrant, more than 1 upper and lower canine, and so forth. For metatherians, the primitive dental formula is 5/4, 1/1, 3/3, 4/4 = 50. Although very few species exceed the primitive number, the toothed whales often have more than 44 teeth; some species actually have over 200. Among terrestrial

species, only the giant armadillo (*Priodontes giganteus*), bat-eared fox (*Otocyon megalotis*), and marsupial numbat (*Myrmecobius fasciatus*) exceed the primitive numbers of teeth.

The evolutionary trend is toward reduction from the primitive dental formula. In the white-tailed deer noted earlier, three upper and lower premolars occur in each quadrant (side of the mouth). One premolar (the first position) has been lost over evolutionary time. The most anterior upper and lower premolars are actually P^2 and P_2, although they may be described as the "first" premolars in the arcade (row). Similar examples could be cited for most other species.

DENTAL ANOMALIES

Occasionally, an individual's dental complement is different from that normally seen in the species. Such congenital anomalies or abnormalities may involve **supernumerary** dentition (extra teeth in a position) or, conversely, **agenesis** (reduced number of teeth in a position). Anomalies may be unilateral, occurring on one side of the jaw, or bilateral, occurring on both sides. Although they are rare, dental anomalies have been reported in representative species from most orders of mammals (Miles and Grigson 1990; Koyasu et al. 2005).

SUMMARY

- The evolution of mammals from therapsids occurred during a 70-my period from the Late Paleozoic to the Early Mesozoic, with mammals appearing about 220 mya. During this time, numerous changes occurred in the skull, dentition, and skeleton from the synapsid to the mammalian form. These skeletal changes, along with concurrent changes in soft anatomy, adapted mammals for improved ability to maintain homeostasis. Mammals became more efficient at gathering and processing food than synapsids and developed a much higher metabolic rate (although some dinosaurs may also have had high metabolic rates).

- Such evolutionary conditions set the stage for the explosive adaptive radiation of mammals during the 70-my period after their initial appearance. The radiation of numerous phylogenetic lines of mammals, from shrews to elephants and rodents to whales, occurred after the extinction of the dominant terrestrial vertebrates—the dinosaurs. Mammalian radiation was further enhanced by genetic isolation of phylogenetic lines resulting from continental drift and the separation of the continental land masses as well as increased diversity of flowering plants throughout the world. Most mammalian orders today are recognized from the Eocene epoch, whereas most families are evident by the Miocene.

- Diversity of form and function is manifested in the highly interrelated characteristics of modern mammals. The broad diversity of modern mammals in terms of their dentition, locomotion, pelage, feeding, and reproduction enables them to adapt to the wide range of biomes and habitats. Many of the general characteristics noted in this chapter are discussed in detail in Part 2. The extent of mammalian diversity is seen in Part 3, where the orders and families of extant mammals are examined.

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DISCUSSION QUESTIONS

1. What reasons can you give for mammals being so much smaller than even the smallest dinosaurs for the 140 my they were on earth together? What might have been the adaptive advantages to mammals of having been so small?

2. Because they were so small, what morphological and physiological characteristics were necessary for early mammals to survive?

3. Why does heterodont dentition of an early mammal allow an individual a much broader range of feeding possibilities than the homodont dentition of synapsids?

4. Before you read Chapter 7, list as many different mammalian feeding adaptations as you can think of.

5. How did the concurrent rise in the diversity of other fauna and flora early in the Cenozoic era affect the potential for early mammals to radiate into different lineages?

CHAPTER 5

Biogeography

How do scientists explain the abundance of marsupials in Australia and South America, along with their scarcity on northern continents? Why are there members of Camelidae in central Asia, North Africa, and South America? What factors led to the present distribution of primates, extending from Japan to Africa and including South, but not North, America? **Biogeography** is the study of the distribution of organisms, both living and extinct, on the Earth (Lomolino et al. 2017).

We have already encountered geographic considerations in our discussion of home ranges (the "distributions" of individual organisms), faunal surveys, and phylogeographic analyses of species boundaries (Chapter 2), as well as the influence of continental drift on mammalian radiations (Chapter 3). The most basic datum in biogeography is the **species range**—the complete area of the Earth over which individuals of a particular species occur. Species ranges are usually inferred from museum-specimen records, but observational data and ecological modeling are also important for mammals. Ranges are dynamic, changing over time because of abiotic and biotic factors. For example, lions were once widespread throughout Africa and southwestern Asia; today, they are restricted to several isolated populations scattered throughout Africa and one small population in northwest India (Figure 5.1). A fundamental question posed by biogeography is, what factors determine the range of a species? The same question, but from a slightly different perspective, is also important: why does a particular region harbor the particular set of species we observe there? The answers invariably have to do with two kinds of causal factors, history and ecology, that define major research traditions within biogeography.

Historical biogeography emphasizes the study of changes in species ranges that have taken place over evolutionary time. It encompasses evolutionary and earth history, and brings information from both to bear on biogeographic problems. One of the distribution patterns most intriguing to historical biogeographers is **endemism**, the restriction of a species' range to a circumscribed area. Why, for example, are long-beaked echidnas (*Zaglossus bruijni*) found only in New Guinea? Even more striking are patterns of endemism that
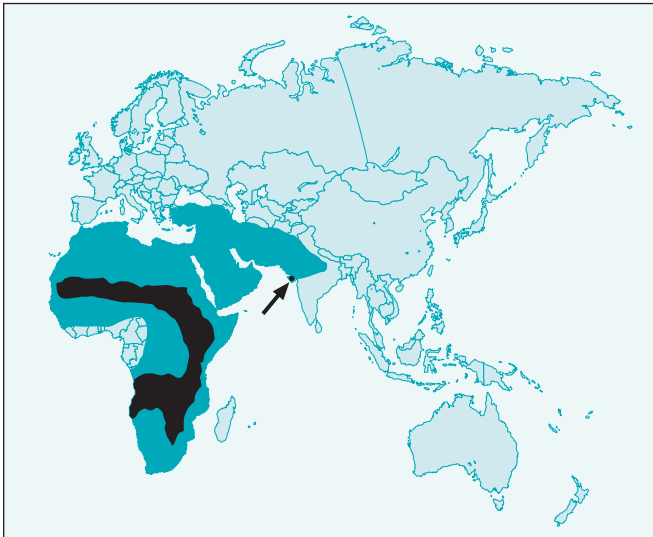
Figure 5.1 **Changes in species range.** The lion (*Panthera leo*) was once distributed throughout much of Africa and southwestern Asia, including the Arabian Peninsula (*dark blue shading*). Today, lions still inhabit many areas of Africa (*black shading*), but their range in Asia has been reduced to a small remnant population in the Gir Forest of India (*black dot with arrow*). Redrawn from Burton and Pearson (1987).

characterize areas—why are *so many* mammal species found only in New Guinea (Flannery 1995)? A second pattern of interest is the **disjunct distribution**—a gap in the range of related species or clades. Marsupials are now found in Australasia and South America. How does this distribution relate to the evolutionary history of marsupials? Do the species on each continent represent separate monophyletic groups that are each other's closest relatives? How did these groups, which clearly have a single common ancestor, become separated by two oceans? It is often the case that several groups show the same disjunctions: monotremes, though currently endemic to Australasia, also have fossil representatives in South America (Pascual et al. 1992).

    Ecological biogeography focuses on the current distributions of species and seeks to explain those distributions in terms of community-level interactions among organisms and their environment. One common line of inquiry has to do with **species richness**: why do some regions of the Earth (e.g., the tropics) harbor vastly more species than other regions (e.g., Antarctica)? What determines the number and identity of species on an island? Because answers to such questions involve evolutionary adaptations, ecological biogeography frequently entails studying the patterns of morphological, physiological, or life-history variation among organisms in different places. Until recently, historical and ecological biogeography were largely separate disciplines (Posadas et al. 2006), but practitioners now realize that both perspectives are necessary to arrive at complete explanations of geographic patterns (Morrone 2009).

Global Provincialism of Mammal Distributions

BIOGEOGRAPHIC REGIONALIZATION

If one were to tabulate the numbers of species in major clades of virtually any group of animals or plants that occur in different continental regions of the Earth, two patterns would be readily apparent. First, different regions harbor distinct taxonomic assemblages—that is to say, there is endemism on a worldwide scale. Second, there are dramatic differences in species richness among continental regions: some regions constitute **centers of diversity** and others do not. These observations, together with knowledge of phylogenetic relationships, demonstrate the **provincialism** of life on Earth, a pattern evident in the tetrapod fossil record since the Early Mesozoic (Sidor et al. 2013). Provincialism in terrestrial animal distributions led Wallace (1876) to divide the world into 6 faunal regions, each with a distinct assemblage of species: Palearctic, Nearctic, Neotropical, Ethiopian, Oriental, and Australian (Figure 5.2). This was one of the first attempts at biogeographic **regionalization**, the estimation of boundaries between areas of endemism/centers of diversity. Darlington (1957) and Simpson (1965) provided important syntheses of descriptive information on vertebrate distributions, generally endorsing the regions recognized by Wallace. Recently, Holt and colleagues (2013) refined the boundaries of world **zoogeographic** regions based on distributional data and phylogenetic relationships for 21,037 species of amphibians, birds, and mammals. They identified 11 major realms comparable to Wallace's faunal regions, but recognized distinct realms for some of Wallace's transition zones. For example, Holt and colleagues (2013) distinguished a Panamanian realm comprising the Central American component of Wallace's Neotropics, a Saharo-Arabian realm across northern Africa to the western edge of the Indian subcontinent, and a Sino-Japanese realm from the Tibetan Plateau to the China coast. They also assigned New Guinea to Oceania and Madagascar to its own realm. The extent to which this new regionalization will replace Wallace's original remains to be seen (Kreft and Jetz 2013), but the work highlights the increasing interdependence of biogeography and phylogenetics (Knapp 2013).

    As reflected in Holt and colleagues (2013), biogeographers are intrigued by transition zones between regions, as well as what species compositions in these zones can tell us about the historical-ecological determinants of biodiversity. Perhaps the most famous transition zone is that between Wallace's Oriental and Australian regions, where the position of Wallace's Line (Figure 5.2) has stimulated over a century of studies on the mixture of faunal elements in the Malay Archipelago (van Oosterzee 2006, Esselstyn et al. 2010). Although Wallace and subsequent authors noted a sharp break in faunal compositions between the islands of

Figure 5.2 Faunal regions. The land surfaces of the world can be divided into six major faunal regions based on geographic barriers, geological history, and the distribution of vertebrate species. Oceanic islands and the open ocean can be considered an additional region. Considerable differences are evident in mammalian family diversity and the number of endemic families among these regions. The boundary between Oriental and Australian regions is Wallace's Line.

Bali and Lombok and extending north along the Makassar Strait, Holt and colleagues (2013) placed the break east of Sulawesi (except for birds). Biogeographers have also undertaken regionalizations on smaller scales. The Interim Biogeographic Regionalisation for Australia (IBRA, Ebach 2012), managed by Australia's Department of Environment and Energy, identifies 89 bioregions across the continent based on fauna, flora, geomorphology, and climate. The IRBA serves as a framework for understanding species distributions and a basis for conservation planning.

FAUNAL REGIONS

Here we summarize the extent, ecosystem characteristics, and assemblage of mammals for each of Wallace's (1876) faunal regions. Continental ecosystems are classified as **biomes**, each with a specific type of plant community determined by climate and soil characteristics. The major terrestrial biomes are tropical rainforest, tropical deciduous forest, savanna, desert, chaparral, grasslands, temperate deciduous forests, temperate rainforests, taiga, and tundra. Of course, mammals also occur in freshwater and marine ecosystems. Freshwater species are usually considered part of the terrestrial biomes in which their lakes, rivers, etc. occur. Marine species may be associated with coastal waters or the open ocean; for convenience, we will discuss the ocean as if it were a single faunal region. Ceballos and Ehrlich (2006) provide a more detailed summary of mammalian distributions in biogeographic regions.

Palearctic

The Palearctic, largest of the faunal regions, consists of the northern Old World, including Europe, Russia, central

Asia, and northern China. It is separated from the Ethiopian region by deserts, from the Oriental region by mountains, and from the Nearctic by the Bering Strait. An east-west band of taiga centered on 60°N latitude dominates the Palearctic, with tundra to the north. The southwestern Palearctic includes the Mongolian steppes, while temperate deciduous forest and chaparral occur in Europe. There are no endemic mammal families in the Palearctic, and only one endemic subfamily (Spalacinae, the blind mole-rats). Species diversity is concentrated in the warm, wet areas of the southeast and southwest. The Palearctic mammal fauna represents a mixture of Nearctic, Ethiopian, and Oriental elements. Many Paleactic families also occur in the Nearctic, primarily because these regions were connected for extended periods by the Bering land bridge between Siberia and Alaska. Species of cervids, bovids, and ursids occur in all three regions; suids, hyaenids, and viverrids are shared with Oriental and Ethiopian regions; glirids, dipodids, and procaviids also occur in the Ethiopian region. The Palearctic includes widespread, continuously distributed species from the rodent families Muridae and Sciuridae, as well as from the carnivoran families Mustelidae, Canidae, and Felidae.

Nearctic

This region extends from the Arctic in northern Canada to the central Mexican plateau, and includes Greenland. It is separated from the Palearctic by the Bering Strait and from the Neotropics by the Mexican-Central American transition zone. Like the Palearctic, the northern Nearctic consists of tundra and taiga, with temperate deciduous forest in the southeast, grassland in the south central, and desert-chaparral in the southwest. Relatively few mammalian families occur in the Nearctic, and only two (Antilocapridae and Aplodontidae) are endemic. Species diversity is highest in the west and south due to topographic variation and mild climate, respectively. The biotic similarity of Nearctic and Palearctic regions is such that they are often grouped together as the Holarctic, and two mammal families (Ochotonidae and Castoridae) have Holarctic distributions. The current Nearctic-Neotropical land connection formed relatively recently and became the dispersal route for the Great American Biotic Interchange (discussed later in this chapter). As a result, several families (e.g., Didelphidae, Erethizontidae, Tayasuidae, Heteromyidae, Dasypodidae) now occur in both regions.

Neotropical

The Neotropics extend from central Mexico to South America. This region is mostly isolated by oceans, but its northern boundary roughly coincides with a transition from xeric subtropical desert to moister tropical forests. Tropical wet forests of Amazonia dominate the central

Neotropics, with grasslands and desert to the south, and alpine habitats associated with the Andes along the western margin. The Neotropics have a large number of mammal families, and many of them are endemic. Most of the species diversity is concentrated at low latitudes in Amazonian rainforests and flanking savannas or scrub forests (González-Maya et al. 2017). Several families of hystricognath rodents, pilosans, primates, marsupials, and soricomorphans are endemic to the Neotropics. The Caribbean Islands and Patagonia are considered parts of the Neotropics, but the biotas of these areas are quite distinct. Indeed, the Caribbean bat fauna is more similar to that of North and Central America than to that of South America (Procheş 2005).

Ethiopian

This region includes Madagascar and sub-Saharan Africa. The Sahara and Middle East form a transition zone between Ethiopian and southern Palearctic regions. Sub-Saharan Africa includes a band of tropical rainforest centered on the equator and extending along the Gulf of Guinea and north to the Senegal River. The rainforest is flanked by broad savannas covering mid-latitude regions, and southwestern Africa is mostly desert. Madagascar has rainforest along its eastern coast and savanna in the west, with both habitats running in north-south bands parallel to the central highlands. The Ethiopian region shares much of its mammal fauna with the Oriental and Palearctic regions. Its great diversity of mammals has been attributed in part to restriction of Plio-Pleistocene extinctions to very large (>1000 kg) species coupled with diversification of moderately large (200–1,000 kg) forms (Nieto et al. 2005). Among endemics, lemuroid primates and sucker-footed bats (Myzopodidae) are restricted to Madagascar. The remaining Ethiopian endemics are families of rodents, lorisoid primates, terrestrial cetartiodactyls, tenrecs (Tenrecidae), golden moles (Chrysochloridae), elephant shrews (Macroscelididae), and the aardvark (Orycteropodidae).

Oriental

The Oriental region consists of the Indian subcontinent, Southeast Asia, and the Malay Archipelago north and west of Wallace's Line. It is isolated from the Palearctic by deserts and mountains, and from the Australian region by a transition zone known as "Wallacea" (extending east from Wallace's Line to encompass the Lesser Sunda Islands, Sulawesi, and the Moluccas). Much of the Oriental region is tropical forest. Most of its mammal families are shared with the Ethiopian region, and many are shared with the Palearctic. Mammal diversity is high in the Orient, but only five families are endemic: colugos (Cynocephalidae), tree shrews (Tupaiidae), hog-nosed

bats (Craseonycteridae), gibbons (Hylobatidae), and tarsiers (Tarsiidae). The Orient's position as a tropical crossroads between Palearctic, Ethiopian, and Australian regions may explain its high diversity, but low endemicity, of mammal families.

Australian

This region includes Australia and New Guinea. It is bounded to the northwest by Wallacea and on all other fronts by ocean. Most of Australia is desert, but coastal areas show a diverse set of biomes—tropical forests in the north (and in New Guinea), temperate deciduous forest in the southeast, chaparral in the south, and temperate rainforest in eastern Tasmania. Australia is the most isolated faunal region, sharing few of its mammal families with other areas. The endemics are monotremes (Ornithorhynchidae, Tachyglossidae) and marsupials from the orders Dasyuromorphia, Notoryctemorphia, Peramelemorphia, and Diprotodontia. The only recent route of exchange for Australian mammals is via Wallacea, and two eutherian groups—bats and murid rodents—have invaded by this route. Indeed, based on bat distributions, Procheş (2005) found that New Guinea is more closely allied with the Oriental than the Australian region. Areas adjacent to Australia are also distinct. New Zealand has only three native nonhuman mammals, all bats, and two of these represent the endemic Family Mystacinidae (Flannery 1984). Melanesia also harbors a distinctive bat fauna (Procheş 2005).

Oceanic

Oceanic mammals include those that live on islands remote from continents and those that are fully marine. The mammal faunas of Micronesia and Polynesia illustrate several general patterns for oceanic islands: there are few native mammals, those that do occur are mostly bats or small rodents, and human movements across the ocean have facilitated dispersal (Darlington 1957). Among marine groups, Sirenians (manatees and dugongs; Chapter 12) occur along tropical coasts and associated deep river areas. Pinnipeds (seals and sea lions; Chapter 18) breed on pack ice, nearshore rocks, or coastal areas, but some forage at considerable distances from land. Most cetaceans (whales and dolphins; Chapter 20) are denizens of the open ocean. Larger whale species show extensive migrations between high-latitude feeding and low-latitude breeding areas, whereas smaller toothed whales occur within latitudinal zones. The distributions of **marine mammals** seem to be tied to their food sources; thus, large cetaceans move across multiple oceanic provinces whereas smaller species have more circumscribed ranges. Spalding and coworkers (2007) reviewed the challenges involved in developing a global regionalization scheme for ocean biogeography.

Historical Biogeography

ABIOTIC PROCESSES

Plate Tectonics and Continental Drift

The suggestion that landmasses of the Earth move over geological time (**continental drift**) was formalized by Wegener (1915) but not accepted until the 1960s because no geological mechanism was known that could account for such movement. **Plate tectonics** (Dietz 1961; Hess 1962) provided the mechanism. The Earth's crust, including continents and ocean floors, is made of rocky plates that float on denser, partially melted mantle rock. There are some ten major plates and many minor ones, separated from one another by ridges, trenches, or faults (Figure 5.3). As heat from Earth's core radiates outward, it creates convection cells in viscous mantle rock. Midocean ridges are sites where molten basalt from the mantle spews onto the surface and pushes the crust laterally ("seafloor spreading"), driving the movement of plates. When continental plates collide, they may form mountains (e.g., the Himalayas). Dense oceanic rock plunging below lighter continental plates produces subduction zones (trenches) associated with earthquakes and volcanic eruptions. The mountainous, volcanic islands of Japan mark a zone of subduction between Pacific and Eurasian plates.

As a result of tectonic processes, continents have collided, merged, and fragmented during Earth history. In doing so, they have carried their biotas along with them and profoundly influenced the distribution of organisms. Continental fragmentation is a principal mechanism of **vicariance**, the geographic isolation of populations of a once-widespread species by development of a physical barrier (e.g., an ocean) within the ancestral species range (Rosen 1978). Geographic isolation initiates speciation, and subsequent evolution within descendant lineages may produce diverse clades on different continents. Continental drift is only one of many ways to erect or destroy such a barrier, but it is a major historical determinant of provincialism among faunal regions. Vicariance on a smaller scale has influenced biogeographic patterns within regions.

Past movements and positions of continents can be inferred from paleomagnetic, petrological, stratigraphic, and structural information. When the first synapsids appeared in the Carboniferous, the landmasses of North America, Greenland, Western Europe, and Siberia had moved close to the equator and eventually merged to form a supercontinent, Laurasia. South America, Antarctica, Africa, India, and Australia were similarly merged near the South Pole to form the supercontinent Gondwana. By the Permian, Laurasia and Gondwana had coalesced to a single landmass, Pangaea, which would persist for some 160 my (Figure 5.4). In the Jurassic, when the world's synapsid fauna contained therapsids, cynodonts, and early mammals, Pangea began to split apart. Separation of Laurasia and Gondwana opened
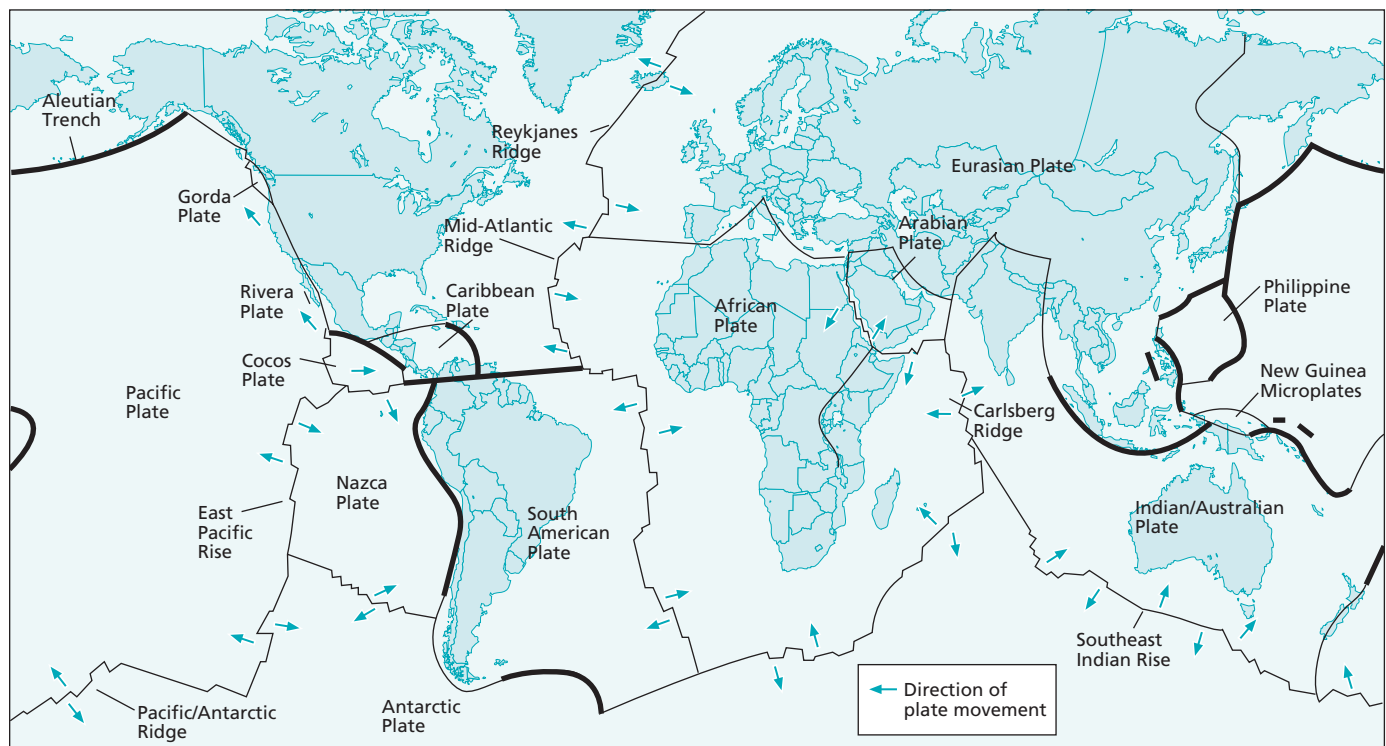
Figure 5.3 **Tectonic plates.** This map shows the boundaries of the major tectonic plates of the Earth's crust and the direction of their current movement (*indicated by arrows*). Oceanic trenches are shown as thickened lines.

Figure 5.4 The supercontinent of Pangea. A reconstruction of Pangea in the Permian. Northern regions comprising Laurasia are in light blue; southern regions comprising Gondwana are in dark blue.

a circumtropical waterway, the Tethys Sea, which moderated climate throughout the later Mesozoic when elevated sea levels resulted in extensive epicontinental seas. In the Cenozoic, the continents fragmented, rotated, and drifted to their present locations; at the same time, mammals evolved, diversified, and spread over the globe.

Climate Change

The climate, or long-term weather pattern, of a particular area on Earth results from interactions among sunlight, the atmosphere, land, and water. A portion of the sun's infrared radiation that reaches the earth is reflected, trapped by CO_2 and other greenhouse gases, and warms the atmosphere. Because the Earth tilts on its axis, the amount of sunlight reaching the surface varies with latitude. At the equator, sunlight meets the Earth at nearly a right angle and the amount of solar energy per unit area is high, making the tropics warm. At higher latitudes, the incident angle is more oblique and temperatures are lower. Moreover, as the Earth's tilt changes throughout the year, warm and cold temperatures alternate seasonally between northern and southern hemispheres. As equatorial air rises, it cools and loses moisture, which falls as tropical rain. The same air masses sink at approximately 30° north and south latitude, but they are dry and absorb surface moisture; Earth's great deserts occur at these latitudes. Earth's rotation interacts with moving air masses to produce easterly or westerly winds, depending on latitude. Prevailing winds blowing over mountains drop moisture on the windward sides, but create dry, rain-shadow conditions on the leeward. These same factors move seawater in clockwise or counterclockwise gyres around ocean basins and, by distributing warm water from the equator to coastal areas, provide a moder-

ating influence on the climate of continental margins. To the extent that this interplay of variables creates a stable climate in a particular area, it also determines the abiotic selection regime to which resident organisms must adapt.

However, climates are not stable over evolutionary time. Continental positions affect air and ocean circulation and profoundly influence regional climates. Moreover, variations in Earth's orbit affect how much sunlight reaches different parts of the world and trigger climate changes by "orbital forcing"; variation in the energy output of the sun ("solar forcing") can have the same effect. The influence of climate forcing is mediated by conditions in the atmosphere (e.g., levels of greenhouse gases, tropospheric aerosols that influence cloud formation) and acts through the global carbon cycle (Pälike et al. 2006). Because of variation in, and interaction among, these factors, Earth history is characterized by alternating periods of "icehouse" and "hothouse" conditions. Extreme icehouse conditions produced ice ages, extended periods during which global mean temperature was low and glaciers expanded across continents. It was in the context of such climate variation that synapsids and their mammalian descendants originated and diversified.

Ice Ages

At several times in Earth history, levels of greenhouse gases fell, continents occupied positions blocking the flow of equatorial ocean water to the poles, and orbital variations affected Earth's solar heat budget. In the Early Carboniferous, much of Gondwana was near the South Pole, while closure of the Tethys Sea blocked circumtropical currents and disrupted warm-water flow to the Antarctic. This caused cooler summers, the accumulation of winter snow in highland areas, and growth of alpine glaciers. At the same time, atmospheric CO_2 levels dropped, possibly due to elevated oxygen produced by land plants in the world's extensive equatorial swamps (Berner 1997). As Earth became colder, glaciers spread from the highlands and covered much of southern Gondwana, initiating the Karoo Ice Age. In tropical Laurasia, far from the Karoo ice fields, we find the oldest fossil synapsids—pelycosaurs such as *Archaeothryis* and *Eothryis*. By the time the Karoo glaciers receded at the end of the Permian, all major lineages of pelycosaurs and noncynodont therapsids had appeared, many with representatives in Gondwana (Benton 2014). Ironically, few of them would survive into the Triassic.

After a period of cooling in the Late Cretaceous, hothouse conditions prevailed again until the Eocene. In the Oligocene, atmospheric CO_2 levels began to drop and fragmenting continents allowed cold polar water to move toward the equator. Glacial ice occurred in Antarctica and, by the Pliocene, covered the North Pole as well. From the mid-Miocene on, the world became cooler and drier until, roughly 2 mya, it plunged into the Pleistocene ice age. Glaciation during this period was most dramatic in the Nearctic, where ice covered most of modern Canada and the

northern United States, shifting tundra and taiga habitats southward. In the Palearctic, ice covered northern Europe but a unique steppe-tundra habitat developed in Siberia and Beringia. Between about 1.7 million and 10,000 years ago, continental glaciers advanced and retreated 4 times, giving rise to a cycle of glacial and interglacial periods that culminated in the Recent. The distributions of many modern mammals are still responding to the last glacial retreat.

Refugia

Refugia are circumscribed areas within a larger biome that preserve biodiversity during periods of environmental change (Lomolino et al 2017). **Nunataks**, refugia within the continental ice sheets of glacial periods, were ice-free pockets of variable size. In them, remnants of the preglacial biotas survived until the ice retreated. Nunataks such as the "driftless area" in southwestern Wisconsin, northwestern Illinois, and eastern Iowa, served as sources of new populations for surrounding areas once the glaciers receded (Figure 5.5). The least weasel (*Mustela nivalis*) and Franklin's ground squirrel (*Poliocitellus franklinii*) likely survived in the driftless area during the last glaciation. Mountaintops can also be refugia for taxa with narrow altitudinal distributions: as communities shift their distribution to higher or lower elevations during periods of climate change, their constituent taxa are alternately isolated from and merged with those from nearby mountains.

Tropical rainforests around the world contain enormous species diversity. When Pleistocene glaciers covered much of the landscape in northern latitudes, rainforests became

Figure 5.5 **Driftless area.** An area in northwestern Illinois, east central Iowa, and southwestern Wisconsin, known as the "driftless area," remained free of ice sheets during the Pleistocene glaciations and served as a refugium. Several species of plants and animals, including mammals, spread outward from the driftless area as the glaciers receded.

fragmented—in effect, islands of forest in large areas of open grassland—due to the cooler, drier conditions at tropical latitudes. During interglacial periods, forest refugia expanded and became connected. Haffer (1969, 1997) suggested that cycles of rainforest fragmentation are a major cause of vertebrate diversity in the Amazon. According to this hypothesis, vicariant isolation led to differentiation among populations of the same species in different refugia. When forests became contiguous again during interglacials, isolated populations had become reproductively isolated. This is just one of several competing hypotheses that may explain Amazonia's extreme biodiversity (Nores 1999). Turchetto-Zolet and coworkers (2013) and Garzón-Orduña and coworkers (2015) give modern perspectives on this complex topic.

Oceanic islands have also been refugia, particularly islands close to larger landmasses that experienced environmental change, as was the case for Madagascar (Eisenberg 1981). Malagasy endemic tenrecids and lemuriforms have their earliest fossil representatives from the African Miocene and Eocene, respectively (Asher and Hofreiter 2006; Seiffert 2012); this suggests origins for both groups in continental areas where they are now rare or extinct. Within Madagascar, however, they underwent extensive radiations and now occupy a variety of niches. Madagascar may have served as a refuge where, isolated from mainland competitors, tenrecs and lemuriforms survived and diversified.

BIOTIC PROCESSES

Dispersal

The term "dispersal" has two closely related meanings in biology. Individuals or small groups may leave their natal area to breed elsewhere; such movement occurs within the lifetime of an organism and constitutes **ecological dispersal**. "Dispersal" is also used in a biogeographic sense, referring to the extension of a species range—that is, **species dispersal**. These processes are related in that individual movements are the basis for changing species ranges. Two mechanisms of species dispersal are usually recognized. **Passive dispersal**, such as rafting or human transport, involves movements in which the dispersing organisms have no active role. **Active dispersal** involves an accumulation of ecological dispersal events in which individuals move by their own locomotion.

Active dispersal occurs via several pathways (Simpson 1940). A **corridor route** provides minimal resistance to the passage of animals between two areas. The present connection between Europe and Asia is a corridor that allows extensive interchange of terrestrial animals. Many mammalian taxa, down to the level of genera and species, are distributed throughout Eurasia because of this corridor. A **filter route** allows only certain species to pass from one area to another. A good example is the Bering land bridge that connected Siberia and Alaska at times of lowered sea levels in the later Cenozoic. Only mammals such as voles

(*Microtus, Myodes*), which were adapted to the cold climate of Beringia, could successfully cross between North America and Asia. Another example is the Panamanian land bridge that formed between North and South America over 3 mya. Extreme habitats such as deserts or mountains can also act as filter routes that separate faunal regions and subregions. Dispersal can also take place via **sweepstakes routes**, in which some unusual occurrence carries an organism or group of organisms beyond the limits of their former range and lands them in a habitat where they can survive and reproduce. The most common examples involve mammals moving across water barriers by rafting (terrestrial species) or wind-assisted flight (bats). The mystacinid bats of New Zealand have Oligo-Miocene fossil representatives in Australia, which suggests that they crossed the Tasman Sea by an aerial sweepstakes route sometime in the later Tertiary (Hand et al. 1998).

Extinction and Diversification

Paleobiologists generally recognize two kinds of extinction. **Background extinction** refers to the incidental loss of species due to local factors such as habitat change, interspecific competition, predation, and so on. **Mass extinction** involves the simultaneous, catastrophic, and worldwide loss of species from many taxonomic groups. There have been several mass extinctions in the history of life, and synapsids have experienced at least four of them. The Permo-Triassic extinction, perhaps the result of a runaway greenhouse effect initiated by massive volcanism, eliminated the last pelycosaurs, most therapsid lineages, and a few early cynodont groups (Pough et al. 2013). The mid-Triassic extinction of herbivorous synapsids (e.g., dicynodonts, diademodontids) may have facilitated the early diversification of dinosaurs (Benton 2014). Several therapsid and cynodont lineages survived the end-Triassic extinction that wiped out many tetrapod families. The Cretaceous-Tertiary extinction (likely triggered by an asteroid impact) eliminated dinosaurs but cleared the way for subsequent diversification of therian mammals.

In the context of historical biogeography, extinction (especially background extinction) is often invoked to explain the *absence* of species from areas where, based on some biogeographic hypothesis, they are expected to occur. For example, monotremes are one of several mammalian groups currently restricted to southern continents, and it is likely that this reflects a Gondwanan distribution of their most recent ancestors (Weisbecker and Beck 2015). Although living monotremes are restricted to Australasia, the Paleocene fossil platypus *Monotrematum* from Argentina documents a broader Gondwanan distribution for the group (Pascual et al. 1992). It is often the case, however, that fossils have not yet confirmed extinctions postulated by biogeographic hypotheses.

Just as extinction reduces the species richness of a clade, evolutionary diversification increases it. Diversification in

this sense is nothing more than speciation followed by genotypic and phenotypic divergence, but the most noteworthy cases took place rapidly, produced many descendants, and were geographically restricted. We often refer to them as **adaptive radiations**, and several of the most spectacular have already been mentioned—namely, the lemuriform primates of Madagascar (over 100 living species), the New World monkeys (ca. 100 species), and the Australasian marsupials (ca. 240 species). In these and other cases, the ancestors of a lineage dispersed into a new region or became vicariantly isolated in a remote portion of their ancestral range. These progenitors may have encountered little competition in their new ranges if ecologically similar species were lacking or if they themselves out-competed resident species or were preadapted to subsequent environmental changes that drove their competitors extinct. Interestingly, the result of diversification is not always divergence. A striking regularity in mammal phylogeny is the number of times ecologically similar species have arisen in different areas and from different ancestors because of **convergent evolution**. For example, myrmecophagy (ant- or termite-eating) and its specialized cranial morphology have evolved in six orders (Figure 5.6): anteaters (Pilosa), pangolins (Pholidota),
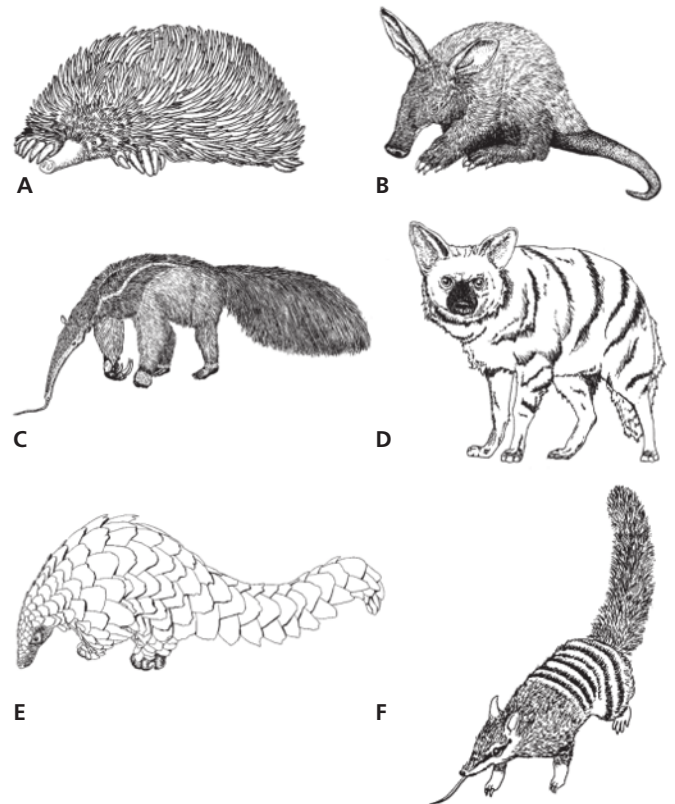
Figure 5.6 **Convergence.** Convergence is evident in these unrelated lineages of ant-eating mammals. All have a long rostrum and a sticky, extensible tongue. (**A**) Echidna (Monotremata); (**B**) aardvark (Tubulidentata); (**C**) giant anteater (Pilosa); (**D**) aardwolf (Carnivora); (**E**) pangolin (Pholidota); (**F**) numbat (Dasyuromorphia). *Note*: not to scale.

aardwolves (Carnivora), aardvarks (Tubulidentata), numbats (Dasyuromorphia), and echidnas (Monotremata).

BIOGEOGRAPHIC INFERENCE

Distributional Patterns and Historical Hypotheses

Research in historical biogeography seeks to explain current species distributions in light of phylogeny and earth history. The former emphasizes the evolutionary past of the species under study, and the latter the evolutionary past of the regions those species occupy. Thus, like most areas of comparative biology, historical biogeography requires a phylogenetic framework. The distributional patterns we have discussed so far, provincialism and endemism, are predicated on phylogenetic hypotheses for major mammalian groups, such as monophyly of Monotremata, Marsupialia, Lemuriformes. Not all biogeographic problems are so straightforward. The most frequently studied distribution pattern is **disjunction**, the geographic isolation of sister groups, which can be observed at the level of species or larger clades. For example, the western quoll (*Dasyurus geoffroii*) and the bronze quoll (*D. spartacus*) are sister species of dasyurid marsupials (Krajewski et al. 2004); the western quoll is restricted to southwestern Australia and the bronze quoll is endemic to New Guinea. At the other extreme, Australasian marsupials are a monophyletic group whose sister is the South American Microbiotheria (Meredith et al. 2008; Nilsson et al. 2010; Duchêne et al. 2018).

Prior to the acceptance of continental drift and awareness of past climate change, biogeographers assumed that dispersal and extinction were the major causes of disjunction. In a tectonically and climatically static world, the simplest way to establish a disjunction is for an ancestral species that occurs in one area to send propagules into a second area, isolated from the first, which then give rise to a new species. Alternatively, an ancestral species may expand its range into a new area, but later experience range contraction or extinction of intermediate populations, leaving an isolated colony that undergoes speciation (Darlington 1957). This dispersalist framework led early biogeographers to focus on "centers of origin" for particular taxa—that is, the ranges of ancestral species. Unfortunately, the criteria used to infer such centers were not robust and many dispersalist scenarios were speculative. For example, Mathew (1915) argued that major mammalian groups arose in northern continents, with the more recently evolved and competitively superior forms displacing older, less well-adapted groups southward. Such scenarios relied on the types of dispersal routes described above or posited ephemeral land bridges and lost continents (Archer 1984a). Analytical methods for inferring ancestral areas have been developed (Bremer 1992; Ronquist 1994; Hausdorf 1998), but most modern studies of historical biogeography use these in the context of studying the evolution of geographic ranges on a phylogeny.

Vicariance and Dispersal

The nearly simultaneous development of phylogenetic systematics and plate tectonics theory in the 1960s gave a new conceptual framework to historical biogeography. It became reasonable to postulate that current species distributions reflect past fragmentation or connection of the continents on which ancestral species lived. Indeed, changing connections among Caribbean landmasses were the driving force in Rosen's (1975) classic study of vicariance. Biogeographers realized that the causal links between geographic isolation, speciation, diversification, and extinction have the potential to explain the origin of current distribution patterns. Out of this realization emerged vicariance biogeography, a research program committed to explaining distributions as resulting from the interplay between phylogeny and "area relationships." The logic of vicariance biogeography is straightforward (Figure 5.7). Suppose species *A* occurs throughout an ancestral area that is split in two by a dispersal barrier. In one part of the range (area I), species *A* or its descendants persist; in the other part, a new species (*B*) arises by allopatric speciation. Now suppose that the area occupied by *B* or its descendants is subdivided into areas II and III, resulting in a second isolation that produces species *C* in area III. In this scenario, the sequence of speciation events results in a phylogeny on which *B* and *C* are sisters apart from *A*; the sequence of range divisions results in area relationships in which II and III were more recently connected than either was with I. Because range fragmentation and speciation events occurred in parallel, area and phylogenetic relationships coincide.

Vicariance and dispersal hypotheses were once viewed as mutually exclusive. However, they differ only in the *timing* of dispersal: vicariant models posit dispersal of an ancestral species throughout an ancestral area prior to the development of barriers; dispersal models assume that the barriers came first (Kirsch 1984b). Given the phylogeny and current distribution of species in the example above, a dispersal scenario might posit that the three already distinct areas were simply colonized in the order I→II→III or I→III→II, with a speciation event corresponding to each colonization (Figure 5.7). If both vicariance and dispersal scenarios are plausible, how do we choose between them? Vicariance biogeographers argued that, because a sequence of area fragmentations affects *all* species that occur in those areas, a vicariance hypothesis predicts that the phylogenies of multiple, independent groups will be *congruent*—that is, taxa from areas II and III will be sisters apart from their relatives in area I, and this will be true for many groups that inhabit the areas.

Several problems arose as biogeographers tried to implement vicariance reasoning. First, area relationships are usually difficult to work out, especially when the areas do not correspond to discrete landmasses. Such areas may even be difficult to define. Continental biogeographers frequently attempt to do so from species distributions them-
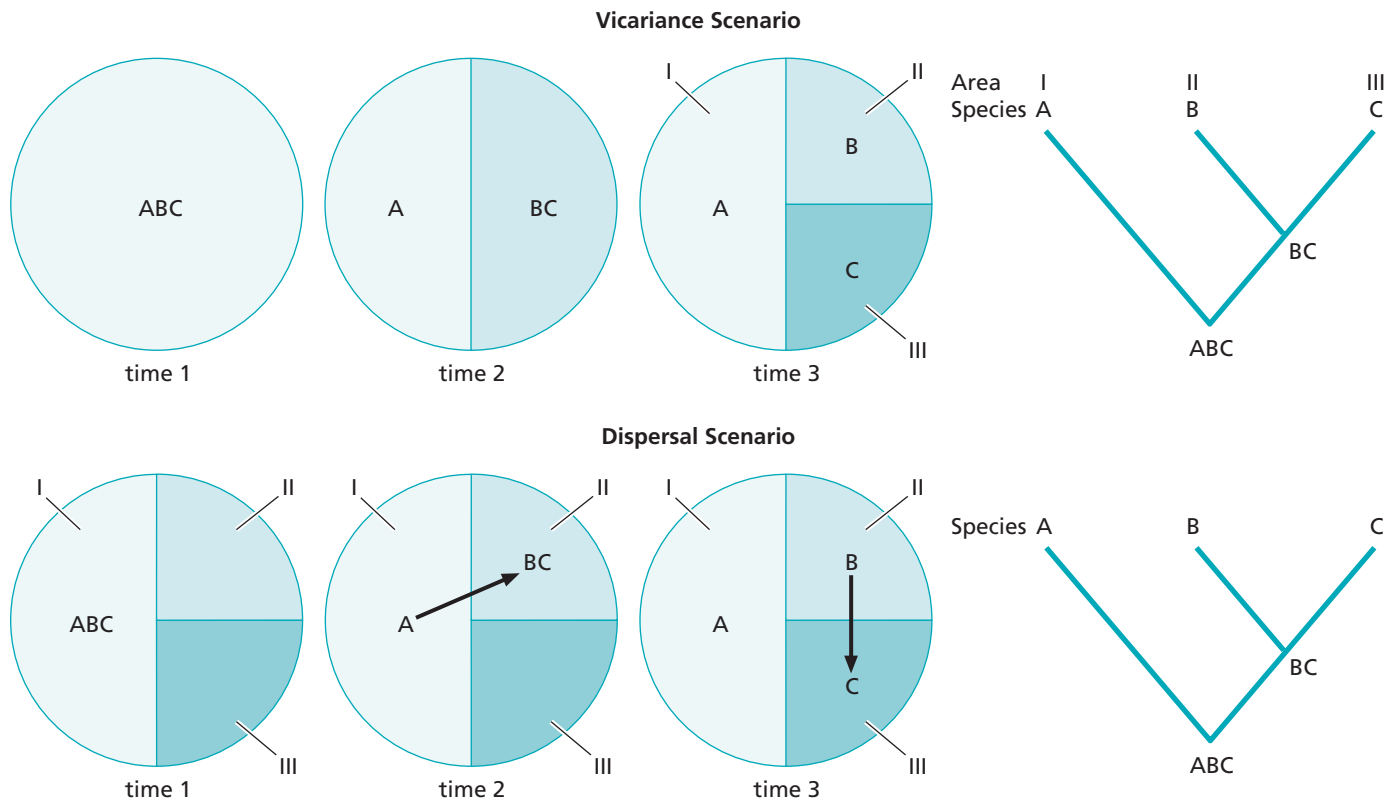
Figure 5.7 **Vicariance and dispersal.** Species *A*, *B*, and *C* evolve in areas I, II, and III. In the vicariance model, the ancestral species (*ABC*) is widespread, and the areas are contiguous at time 1. At time 2, a barrier isolates species *A* and the ancestor of *B* and C (*BC*). At time 3, a second barrier results in species *B* and C. The phylogeny of species and the area cladogram are identical. In the dispersal model, the three areas are distinct at time 1. At time 2, a dispersal event (*arrow*) isolates ancestor *BC* in area II. At time 3, a second dispersal event isolates species *C* in area III. The phylogeny of species is consistent with both scenarios. *Redrawn from Brown and Gibson (1983).*

selves, identifying areas of endemism within faunal regions (Hausdorf 2002). However, attempts at fine-scale regionalization often yield areas for some groups that are not congruent with those for other groups. Even if such areas can be identified, their history is often obscure. Therefore, vicariance biogeographers have relied on congruent phylogenies to reveal area relationships (Nelson and Platnick 1981). Of course, estimated phylogenies also have degrees of uncertainty that complicate the assessment of congruence among them. Moreover, it has become obvious that few species distributions were formed by vicariance alone—dispersal, change in community compositions over time, and evolving climatic conditions make inferring the geographic history of organisms a complicated endeavor. In response to these challenges, researchers have developed a variety of analytical techniques to extract historical information from current distributions and phylogenies.

Analytical Biogeography

Techniques of biogeographic and phylogenetic analysis developed in parallel, and the two disciplines share many methodological approaches. One of these has been the ap-

plication of **parsimony**, the principle that the best estimate of relationships is the one that minimizes the number of events required to explain the observed data. In phylogeny reconstruction, the data are characters and the events are state-changes (Chapter 2); in biogeography, the data are species distributions and the events are vicariance, dispersal, speciation, and extinction. In recent years, biogeographic inference has come to rely on more mathematical and statistical techniques in attempting to cope with the complexity of evolutionary history. The literature on these techniques is quite large, and we provide only a brief summary of major methods. Our discussion is guided by the overview of historical biogeographic methods in Lomolino and colleagues (2017). These authors make a distinction between "area biogeography" (attempts to reconstruct the history of areas from the distributions and phylogenies of species inhabiting them) and "taxon biogeography" (analyses focused on the history of a single lineage with species occurring in distinct areas).

Phylogenetic biogeography (Brundin 1966, 1988) emphasized the predictive value of phylogeny for reconstructing biogeographic history: within a single clade, disjunct sister groups provide evidence of vicariance, and sympatric sisters suggest dispersal. Congruence among the

phylogenies of independent, codistributed clades supports a common vicariant history. Phylogenetic biogeography was tightly linked, however, to the "peripheral isolation" model of speciation, in which new species originate only at the margin of their ancestor's range and possess derived characters (Hennig 1966). This model implies that the spatial distribution of species runs parallel to the primitive-derived sequence of their characters, and its practitioners emphasized dispersal and **center-of-origin** aspects of biogeographic history (Morrone and Crisci 1995). In contrast, Croizat's (1964) **panbiogeography** assumed a strong causal link between Earth history and vicariance. Croizat plotted the disjunct distributions of species within a clade on a map and connected occupied areas by lines to depict an individual track. Congruence among individual tracks for multiple, independent groups produced a generalized track corresponding to an ancestral biota, the distribution of which was assumed to have been fragmented by past geological events. Although Page (1987) and Craw (1988) refined panbiogeographic analysis, it has largely been abandoned because it makes limited use of phylogenetic information (Platnick and Nelson 1988).

Rosen (1978) initiated the development of **cladistic biogeography**, the primary goal of which was to infer area relationships. In this approach, the distribution and phylogeny of taxa are taken as evidence from which the vicariant history of areas is reconstructed. Rosen (1978) introduced the concept of an "area cladogram," a depiction of area relationships implied by the phylogeny of species in a single clade. To form an area cladogram, replace the species names at the tips of a phylogeny with the areas in which those species occur. Area relationships can be inferred when multiple taxa show congruent area cladograms. Frequently, however, area cladograms contain unique or incongruent elements. Rosen suggested that such elements be deleted to produce a reduced area cladogram that shows vicariance relationships for some of the original areas (Figure 5.8). Instances of incongruence are explained by dispersal in one or more of the taxa.

Nelson and Platnick (1981) developed the logic of this approach into a procedure for constructing general area cladograms, amenable to the inclusion of many independent taxa and implementation by computer algorithms. Cladistic biogeography regularly encounters three major complications (Figure 5.9): widespread species (those present in multiple areas); missing areas (those absent in one or more area cladograms); and redundant distributions (areas with more than one species of a particular clade). These problems are addressed in the construction of general area cladograms by one of three approaches (dubbed "assumptions 0, 1, and 2"), which differ in how they interpret distribution patterns as evidence for vicariance, dispersal, or extinction. Area cladograms can be constructed by several methods, perhaps the most common being Brooks parsimony analysis, or BPA (Wiley 1987). In this method, each branch of a primary area cladogram is represented as a single binary character, with the 1-state designating the occurrence of a taxon or clade in an area.
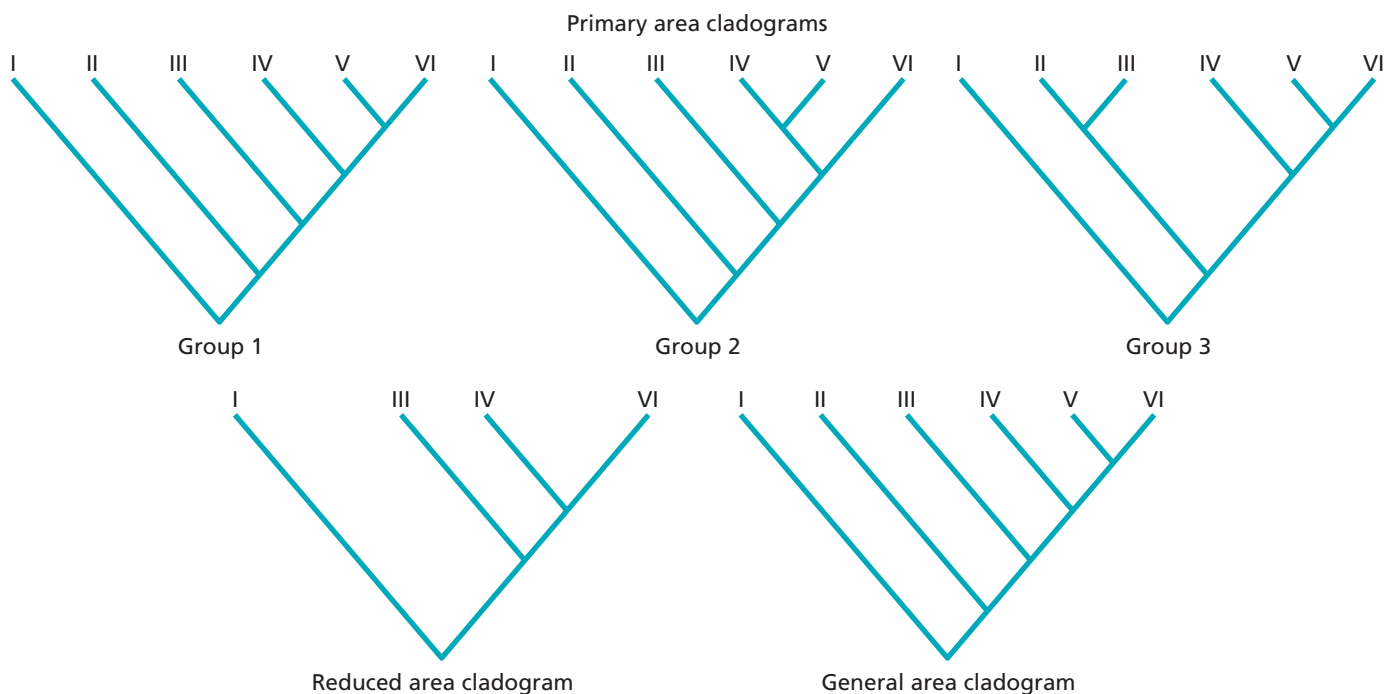
Figure 5.8 **Area cladograms.** Primary area cladograms (*top*) are the phylogenies of codistributed groups (Groups 1, 2, and 3) on which species names have been replaced by the areas (I–VI) in which the species occur. The primary area cladograms disagree on the relationships of areas II and VI. The reduced area cladogram (*bottom left*) is formed by deleting incongruent taxa. One possible general area cladogram, constructed using the cladistic biogeography approach, is shown at the bottom right. This tree minimizes the number of dispersal events required to explain the incongruent relationships of areas II and VI in the primary area cladograms.

| Areas | I | I, II | III | IV | I | II | IV | I | I | II | III | IV |
| Species | A | B | C | D | E | F | G | H | I | J | K | L |

Widespread species **Missing area** **Redundant distribution**
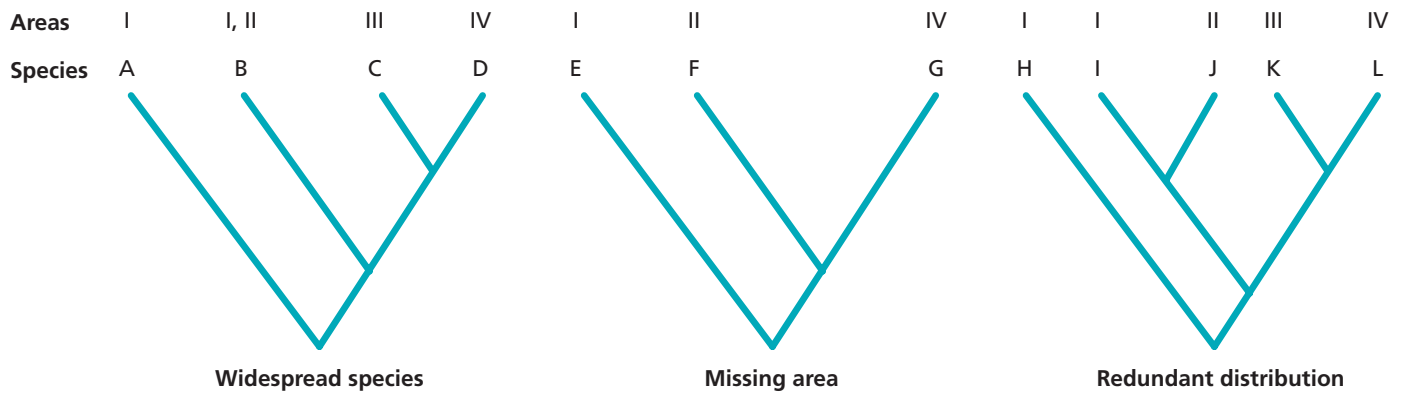
Figure 5.9 Problems for cladistic biogeography. In the cladogram on the left, B is a widespread species because it occurs in two areas (I and II). In the center, III is a missing area because no species in the clade occurs there. On the right, species H and I occur in area I resulting in a redundant distribution. Such distributions cannot be explained by vicariance alone; they require some dispersal, extinction, or failure to speciate.

Characters for all primary cladograms are assembled in a data matrix along with a hypothetical outgroup showing all 0-states. Parsimony analysis of this matrix produces a general area cladogram. Extensions of this approach (Brooks et al. 2001; Wiley and Lieberman 2011) allow instances of widespread species, missing areas, and redundant distributions to be inferred. Page (1990) pointed out that area relationships estimated from congruent phylogenies also assume temporal congruence of the branch points, an idea that was often ignored in early cladistic biogeography studies (Donoghue and Moore 2003).

Ronquist and Nylin (1990) were the first to apply an explicitly statistical approach to reconstructing histories of cospeciation, ushering in a suite of "**event-based methods**" in historical biogeography (Crisci et al. 2003). Ronquist (1997) noted that areas seldom have a unique history that can be recovered from species phylogenies because different groups respond differently to dispersal barriers. His dispersal-vicariance analysis (DIVA) refocused attention on the distributional history of species within a single clade (taxon biogeography) rather than area relationships. DIVA begins with an estimated phylogeny and the ranges of taxa at its tips; it assumes a model in which speciation takes place primarily by vicariance, and distributional events are assigned different costs (e.g., vicariance or sympatric speciation = 0, dispersal or extinction = 1). DIVA uses parsimony to estimate ranges at ancestral nodes. Assuming that ancestral ranges must contain at least one area occupied by daughter nodes facilitates the search for an optimal reconstruction. DIVA has been widely used since its introduction, but the original algorithm assumes the starting phylogeny is known with certainty (rarely a safe assumption in comparative biology) and often produces multiple, equally parsimonious estimates of ancestral areas. Yu and colleagues (2010) developed Statistical-DIVA (S-DIVA) to address both issues by analyzing a set of plausible trees for some group of species and calculating the frequencies of alternative area reconstructions at each node. Ree and colleagues (2005) and Ree and Smith (2008) developed a like-lihood method to infer geographic range evolution within specific clades based on probabilistic modeling of dispersal, extinction, and cladogenesis (DEC) events. Unlike DIVA, DEC considers the information provided by branch lengths on estimated phylogenies when evaluating ancestral area reconstructions, including the possibility of using external (e.g., geological) information to constrain dispersal and extinction rates in different time intervals. DEC is computationally intensive when there are many (e.g., >20) areas; Landis and colleagues' (2013) BayArea program extends the model-based approach to larger phylogenies. Yu and coworkers (2015) developed a user-friendly software package (RASP) that implements DIVA, S-DIVA, DEC, and BayArea methods. Matzke's (2013) BioGeo-BEARS program allows researchers to statistically test the biogeographic models assumed by DIVA, DEC, and BayArea for a given phylogeny with species distributions.

Comparative Phylogeography

In Chapter 3 we described intraspecific phylogeography, the study of how lineages of conspecific organisms, identified by molecular markers, are spatially distributed and the processes that led to those distributions. Phylogeography is thus a way to study historical biogeography, but its emphasis on intraspecific patterns has made it most illuminating for recent divergences (i.e., within the last 20 my). Phylogeographic inferences, like those drawn from analytical biogeography, are most robust when based on patterns observed in multiple, independent, codistributed species (Cracraft 1989). Zink (1996) coined the phrase **comparative phylogeography** to describe this research program, but its roots go back to the concept of "genealogical concordance" articulated by Avise and Ball (1990). Avise (1996, 2000) defined four aspects of genealogical concordance that are the foundations of comparative phylogeography (Figure 5.10): (1) concordance across sequence characters within a gene (lineages defined by individual gene trees are
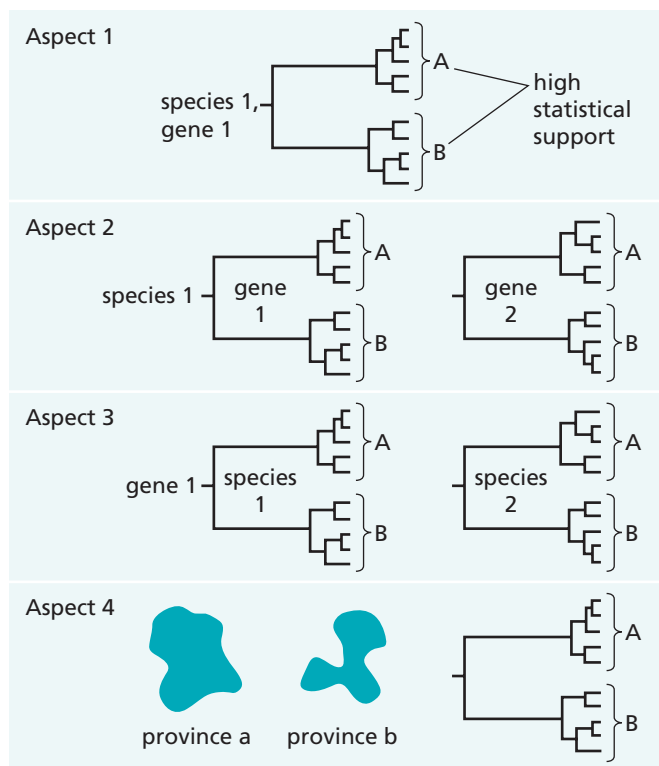
Figure 5.10 **Genealogical concordance.** These four aspects of genealogical concordance form the basis of comparative phylogeography. Together, they provide strong evidence that a common set of historical factors, such as vicariance, has shaped the biogeographic histories of codistributed taxa. *Redrawn from Avise (2000).*

well-supported); (2) concordance in significant genealogical partitions across multiple genes within a species (the same well-supported lineages are recovered by several molecular markers); (3) concordance in the geography of gene-tree partitions across multiple codistributed species (well-supported lineages within several species have congruent distributions); and (4) concordance of gene-tree partitions with spatial boundaries between biogeographic provinces (the distribution of well-supported lineages within several species corresponds to areas of endemism). When such concordance applies, phylogeographers infer that a common set of historical factors (e.g., vicariant events) has shaped the distributions of species in a region.

Cracraft (1988) suggested that the study of biogeography *within* faunal regions (e.g., continents) would be complicated by their long history of successive vicariance and dispersal episodes, ranging from the very old ("deep history") to the more recent ("shallow history"). Such layering of events produces incongruent distribution patterns when groups with deep and shallow histories are compared, thus confounding evaluation of genealogical concordance. For phylogeographers, the transition between deep and shallow history is roughly the Tertiary-Quaternary boundary, some 2 mya (Riddle 1996). Lineage divergences can be dated with respect to this boundary by molecular

population-genetic techniques (see Chapter 2), providing an assessment of whether phylogeographic patterns are temporally, as well as spatially, congruent (Edwards and Beerli 2000).

Comparative phylogeography has been most successful in reconstructing events in the shallow part of deep history. Within the last 5–10 my, many instances of cryptic divergence have taken place in mammals and other taxa, characterized by deeply divergent lineages within species that are not marked by phenotypic differences. When cryptic lineages occupy different areas of endemism, detecting them with molecular markers reveals a disjunction within the range of what had been considered a single widespread species (Arbogast and Kenagy 2001). Such studies have been crucial in identifying areas of endemism within continents and determining the geographic history of those areas (Riddle et al. 2000; Sullivan et al. 2000; Costa 2006). Phylogeographic analyses of shallow time are strengthened by analyses that incorporate statistical principles from population genetics, such as coalescent theory (Knowles 2009), and by inclusion of ecological data (Hickerson et al. 2010).

The widespread availability of GIS data has led to a suite of methods called ecological niche models (ENMs), which provide a novel approach to the study of biogeography (Alvarano-Serrano and Knowles 2014). Given a validated species distribution derived from museum records or field surveys, records of occurrence at specific localities are coded as map coordinates (records of absence at other localities may also be informative). Abiotic environmental variables (e.g., temperature, precipitation) for these localities are then retrieved from a GIS database and correlations established with species occurrences. Several sophisticated algorithms are available for converting these correlations into a model of suitable habitats for the species, which can then be used to predict past, current, or future distributions, provided adequate environmental data are available. ENMs are often used in phylogeographic studies to help assess the nature of barriers or connections among genetically distinct populations, as well as in conservation research to predict biodiversity patterns in areas that have been poorly sampled by collectors. A recent special issue of *Hystrix, The Italian Journal of Mammalogy* includes ten papers illustrating the application of ENMs in mammal ecology (see Russo et al. 2016).

EXAMPLES

Dispersal, Vicariance, and the Early History of Marsupials

Patterson (1981) used traditional ideas about marsupial phylogeny to produce an area cladogram showing close historical affinities between Australia and New Guinea on the one hand and South America, North America, and Eurasia on the other. More or less congruent results were obtained for osteoglossine fishes, chelid turtles, galliform

birds, ratite birds, and hylid frogs, thus implying a general area cladogram with the same structure. This reflects the then-current notion of a fundamental evolutionary split between Australasian and New World marsupials resulting from the Late-Mesozoic breakup of Gondwana. However, knowledge of marsupial evolution expanded considerably after 1981 and challenged this simple picture.

The oldest fossil non-marsupial metherians are from the Cretaceous of Asia and North America, including such forms as *Sinodelphis*, *Holoclemensia*, *Deltatheridium*, *Asiatherium*, *Kokopelia*, pediomyids, glasbiids, stagodontids, and alphadontids (Luo et al. 2003; but note that Bi et al. [2018] challenge the metatherian affinities of *Sinodelphis*). Horovitz and coworkers (2009) argued that the North American herpetotheriids, with putative fossils dating to the Late Cretaceous, are sister to crown-group marsupials, which appear in the Paleocene of North America (peradectids). The oldest South American marsupials are from Paleocene deposits in Argentina and include polydolopidomorphians, peradectids, didelphimorphians, sparassodonts, and microbiotherians (Goin et al. 2006). The oldest Australian fossils are from the Eocene Tingamarra Local Fauna (55 mya) of Queensland and including *Thylacotinga*, *Chulpasia*, and *Djarthia* of uncertain ordinal affiliations (Sigé et al. 2009). Is the history of these groups consistent with Patterson's (1981) area cladogram? To find out, we must consider marsupial phylogeny and Gondwanan geology.

Building on earlier studies, Wilson and colleagues (2016) performed an extensive phylogenetic analysis of metatherian fossil taxa, while Meredith and coworkers (2008) and Duchêne and coworkers (2018) supplied the most complete molecular phylogeny of living marsupial orders to date. Integrating these results gives a modern perspective on marsupial phylogeny (Figure 5.11). The prevalence of North American lineages among marsupial sister groups,

along with peradictids and herpteotheriids near the base of the marsupial tree, suggested to Wilson and colleagues (2016) that marsupials arose in North American and subsequently dispersed to South America. Among modern South American forms, Microbiotheria is sister to a monophyletic group of Australasian orders. These results reject part of Patterson's (1981) area cladogram—some South American taxa are more closely related to Australasian than to North American ones. However, a close relationship between Australia and New Guinea is supported in that three of the four living australidelphian orders have representatives in both areas.

Based on this evidence, researchers generally agree that marsupials arose in what is now the Holarctic, then dispersed from North to South America (Case et al. 2005). The dates for this dispersal are bracketed by the Cretaceous Los Alamitos Local Fauna (73–83 mya) of Patagonia and the Paleocene Argentinian fossils (ca. 62 mya): the former includes many mammals but no marsupials, whereas the latter includes the oldest South American marsupials (Goin et al. 2006). The nature of the north-to-south dispersal path is unclear; by the Late Cretaceous, Laurasia and Gondwana were well separated, and the existence of a corridor route is unlikely. Patterson and Pascual (1968) speculated that marsupials (and placental condylarths) moved via filter or sweepstakes routes over the water barrier between North and South America at this time and that further separation of the continents produced vicariant isolation of the two faunas. Marsupials underwent a spectacular radiation in South America during the Tertiary, producing at least five major clades and numerous species that filled insectivore, omnivore, and carnivore niches. But how and when did they get to Australia?

Even when Pangea was at its most extensive, South America and Australia were not contiguous—between
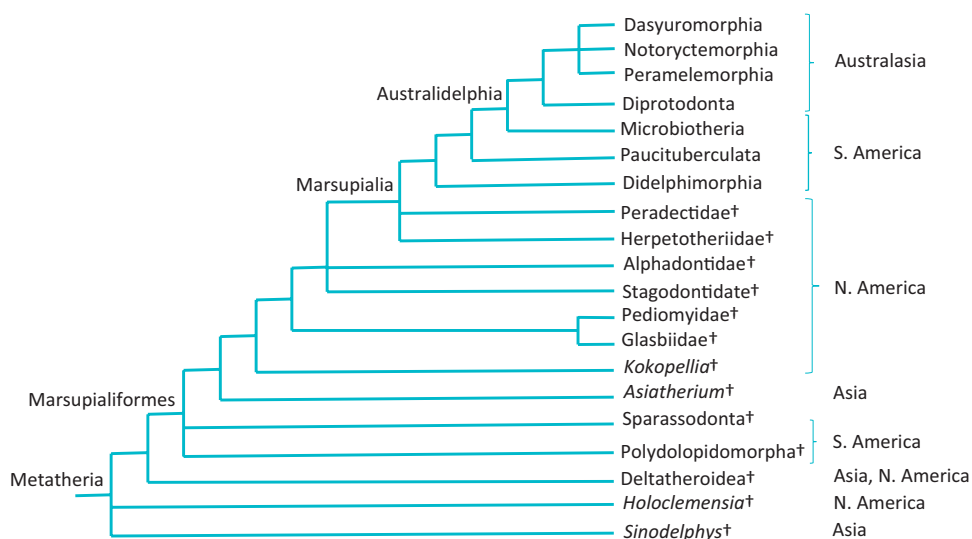
Figure 5.11 **Metatherian phylogeny.** Estimated phylogeny of key metatherian groups based on Duchêne et al. (2018), Horovitz et al. (2009), Meredith et al. (2008), and Wilson et al. (2016). Geographic occurrence of each group is shown to the right. Daggers indicate extinct taxa.

Figure 5.12 **Gondwana in the early Eocene.** Movement of marsupials from South America to Antarctica, and from Antarctica to Australia, likely took place just prior to this date. Dark shading indicates continental shelves less than 2000 m deep. *Redrawn from Woodburne and Case (1996).*

them lay Antarctica, and it was via this landmass that marsupials must have dispersed to Australia (Figure 5.12). Geologic evidence suggests that southern South America and the Antarctic peninsula were contiguous from the Cretaceous until the Late Eocene (36 mya) opening of the Drake Passage. Polydolopoids, didelphimorphians, and perhaps microbiotheres have been recovered from the Late Eocene (37–41 mya) of Seymour Island, adjacent to the Antarctic peninsula. The anatomy of these animals, particularly the microbiotheres, suggests that they are too specialized to be direct ancestors of Australian marsupials. Their closest relatives are South American forms from deposits from 51–54 mya, though the two faunas share no genera. Based on this evidence, Woodburne and Case (1996) concluded that the ancestors of Australian marsupials dispersed across Antarctica no later than the Early Eocene, and perhaps much earlier.

To reach Australia, marsupials must have moved from the Antarctic peninsula across East Antarctica and into southeastern Australia via the South Tasman Rise. Geologic and climatic data suggest that the latter connection was submerged by the Early Paleocene (64 mya) and that glacial ice was present in Antarctica by the Late Eocene (35 Mya). During this interval, overland dispersal became increasingly unlikely as the corridor evolved into a filter route. Woodburne and Case (1996) and Goin and colleagues (1999) argued for dispersal and subsequent isolation of Australian marsupials prior to the Early Paleocene (64 mya). In contrast, Wroe and Archer (2006) cited po-

tentially close relationships between the oldest Australian marsupials (*Thylacotinga* and *Djarthia*, 55 mya) and South American forms as evidence for a later, perhaps Eocene, vicariance. Modern Australian marsupial orders and many families first appear in Late Oligocene (26 mya), though Woodburne and Case (1996) suggested that the ordinal radiation had taken place by the Early Eocene (53 mya). Beck (2012) introduced considerable uncertainty into this discussion by describing a putative non-australidelphian metatherian from the Eocene Tingamarra fauna of Australia.

The Great American Biotic Interchange

After North and South America separated in the Late Mesozoic, they remained isolated by a marine barrier until the Pliocene (ca. 3.5 mya). During this interval, mammal evolution on the two continents proceeded more or less independently. The Tertiary fossil record of South America documents three phases of mammal evolution (Pough et al. 2013), beginning with the Paleocene remains of marsupials, xenarthrans, and archaic ungulates. Marsupials likely arrived by dispersal from North America, but edentates and archaic ungulates appear to have originated in South America. Throughout the Tertiary, these groups diversified to produce a spectacular array of forms including 5 orders of marsupials, 6 orders of archaic ungulates such as litopterns and notoungulates, and edentates such as glyptodonts and ground sloths (Patterson and Costa 2012). Marsupials filled the niches occupied by placental insectivores, carnivores, and rodents on northern continents, while placentals dominated herbivorous niches. The second phase began with the arrival of hystricognath ("caviomorph") rodents and ceboid monkeys via a sweepstakes route from West Africa in the Oligocene. Like the older mammal groups, these too underwent adaptive radiations during the Miocene—their living descendants comprise 11 and 4 neotropical families, respectively. The third phase began in the Late Miocene, when North and South America had drifted close enough to one another for limited mammalian dispersal across island chains. At this time, procyonids (raccoons) moved from north to south, and megalonychid ground sloths reached Florida. In the North American Tertiary, marsupials went extinct, while carnivorans, perissodactyls, artiodactyls, proboscideans, soricimorphs, lagomorphs, and sciuromorph rodents diversified.

In the Pliocene, some 3.5 mya, the land connection between North and South America was reestablished by emergence of the Isthmus of Panama, which initiated extensive dispersal of mammals between the two continents—an event widely referred to as the "Great American Biotic Interchange" (Marshall 1988b; note that Montes et al. [2015] suggest that the isthmus formed much earlier in the Middle Miocene). The isthmus was initially dominated by savannas similar to those in areas to the north and south, and thus constituted a corridor for southward-dispersing mammals such as horses and deer, as well as
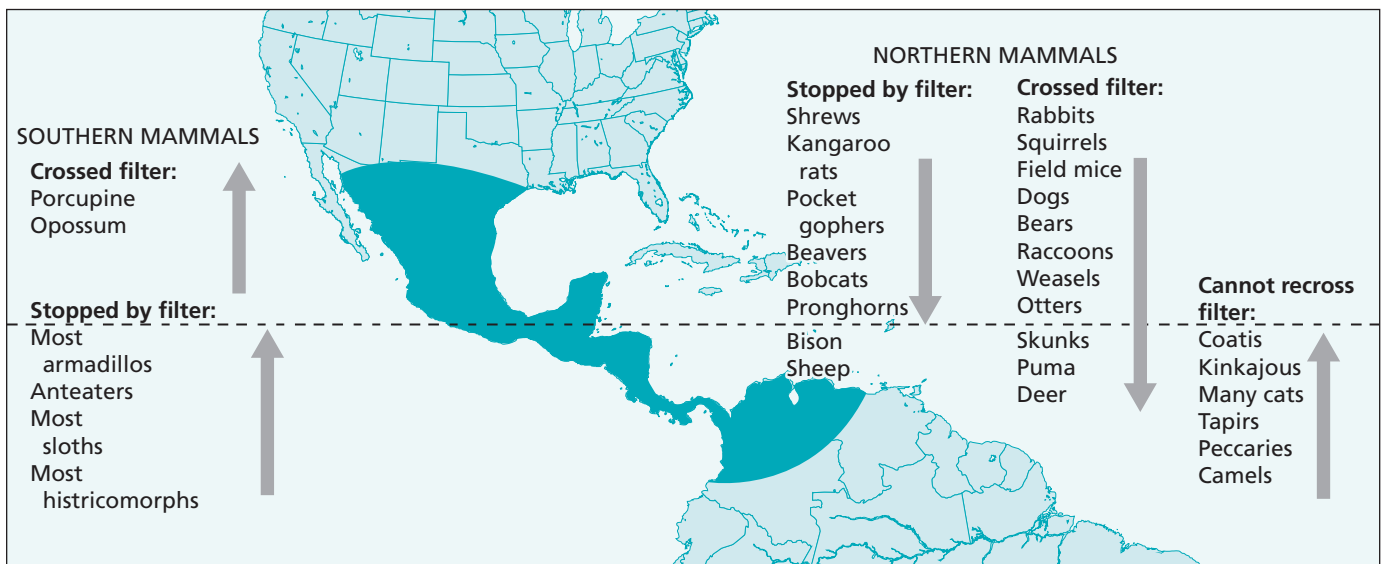
Figure 5.13 **The Great American Biotic Interchange.** During the Pleistocene, the tropical forests of Central America and the Panamanian isthmus were a filter route that permitted the dispersal of some mammals but created a dispersal barrier for others. *After Simpson (1950).*

Figure 5.14 **Virginia opossum.** The only living marsupial found in the United States, *Didelphis virginiana* crossed the Panamanian isthmus from South America during the Great American Biotic Interchange.

northbound glyptodonts, ground sloths, and notoungulates (Pough et al. 2013). However, development of tropical forests in Panama during the Early Pleistocene converted the isthmus into a filter route through which weasels, bears, cats, dogs, tapirs, llamas, peccaries, gomphotheres, shrews, rabbits, and voles invaded the south, while opossums, anteaters, armadillos, capybaras, and porcupines moved north (Figure 5.13). In the Pliocene, these mixed faunas seemed to coexist on both continents, but Pleistocene extinctions took

a heavier toll on South American forms: glyptodonts, ground sloths, and notoungulates disappeared, as did many of the Pliocene invaders from the north (e.g., horses, gomphotheres). Today, Virginia opossums (*Didelphis virginiana*), porcupines (*Erethizon dorsatum*), and 9-banded armadillos (*Dasypus novemcinctus*) are the only South American mammals that have established ranges north of the Rio Grande (Figure 5.14). In contrast, roughly 50% of modern South American genera are derived from North American immigrants.

Historical Biogeography of Eutherian Orders

As discussed in Chapter 3, the living eutherian orders represent 4 major clades—Xenarthra, Afrotheria, Laurasiatheria, and Euarchontoglires. Springer and coworkers (2011) used a molecular phylogeny of eutherians similar to that in Figure 3.1 as a framework for reconstructing ancestral areas using several analytical approaches. In particular, the branch points on the phylogeny were dated using relaxed clock methods with multiple fossil calibrations and minimum/maximum constraints (see Chapter 2, "Estimating Divergence Times"). The resulting trees with estimates of ancestral areas constitute "ancestral area chronograms" that can be related to past geological events and elucidate the paleogeography of early eutherian evolution. Springer and colleagues considered 4 continental areas (Africa, Eurasia, North America, and South America) and a tree of 43 terrestrial placentals representing all orders except Chiroptera. Areas were assigned to these taxa based on either their current geographic ranges or the continental location of the oldest fossil representing each lineage. Ancestral areas were then estimated with 9 different techniques, including the DIVA and DEC methods described above. Springer

and coworkers (2011) also developed minimum area change (MAC) parsimony, a method similar to DIVA, except that it assigns non-zero costs to gains or losses of an area and uses differential costs of area changes reconstructed on cladograms scaled to time ("area chronograms"). The result from MAC parsimony analysis using extant ranges is shown in Figure 5.15.

Given that all terrestrial Afrotherian orders are restricted to—and have their first fossil occurrences in—Africa, it is not surprising that parsimony returns Africa as the ancestral area for this clade. Moreover, the timing of interordinal diversification (Late Cretaceous-Paleocene) corresponds to a period during which Africa was isolated from both South America and Eurasia (Springer et al. 1997). Similarly, living and fossil xenarthrans are known almost exclusively from South America, which is unambiguously reconstructed as their ancestral area. Sloths, anteaters, and armadillos represent one of several South American lineages that evolved in "splendid isolation" (Simpson 1980) during the Early Cenozoic.

Despite the greater geographic dispersion of Laurasiatheria and Euarchontoglires, the ancestral area of both clades (and their common ancestor) is inferred as Eurasia, with many of the deep divergences within each group also taking place there. This is consistent with the scarcity of fossil eutherians in North America until the latest Cretaceous (Cifelli and Davis 2003). Areas for deeper nodes uniting the four clades are highly ambiguous, as are the phylogenetic relationships among them (Chapter 3). However, the overall pattern of divergence dates and ancestral areas is consistent with the suggestion of Murphy and colleagues (2001a) that early placental cladogenesis was induced by vicariant separation of Cretaceous lineages in Africa and South America.

Comparative Phylogeography of Savanna Ungulates in Africa

The savanna, or tropical grassland, biome of Africa extends along the southern margin of the Sahara from the Atlantic to the Indian Oceans and along the eastern continental margin from Ethiopia-Somalia to South Africa. Bounded
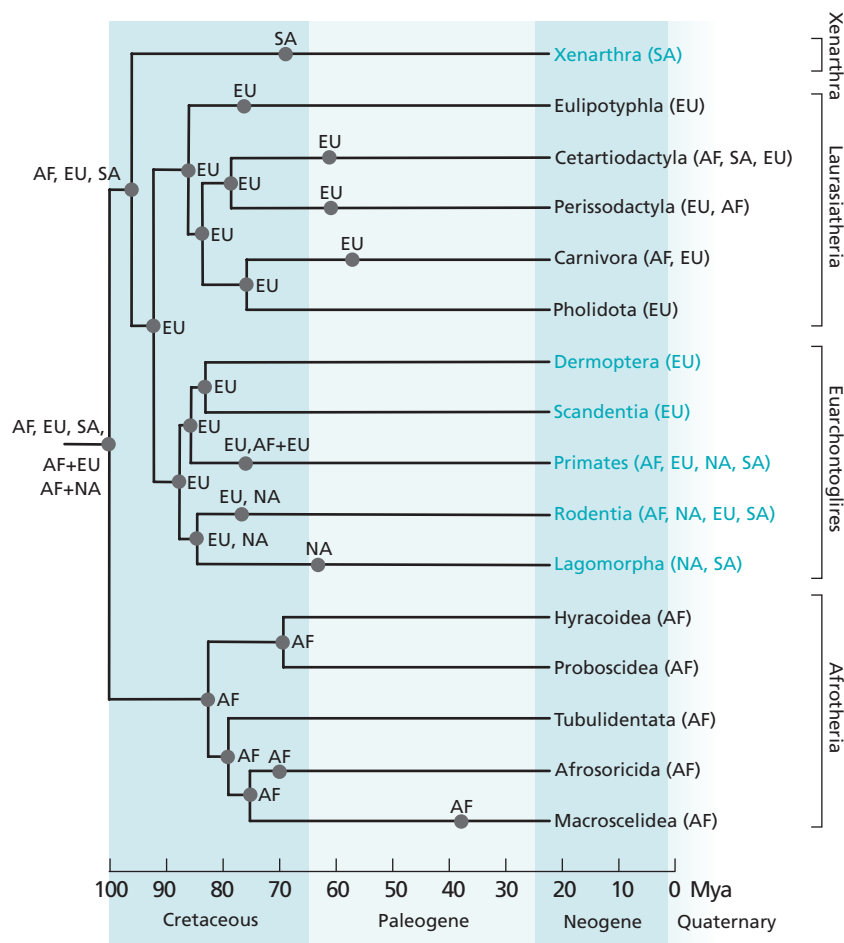
Figure 5.15 Ancestral area chronogram. Phylogeny and divergence times of placental mammal orders with ancestral areas reconstructed with minimum area change parsimony. Current areas for extant species included in the original analysis are shown in parentheses after ordinal names. Dots on terminal branches show the estimated basal divergence dates of individual orders. Multiple ancestral areas listed for internal branches indicate equally parsimonious reconstructions. Area abbreviations: AF = Africa, EU = Eurasia, NA = North America, SA = South America. *Based on Springer et al. (2011).*

to the south and west by the tropical forests of central Africa, the savanna experiences seasonal rainfall but is warm (24–29°C) throughout the year. The habitat is dominated by grasses, forbs, and scattered trees, and is home to a tremendous variety of mammalian herbivores, most of them ungulates belonging to the cetartiodactyl Family Bovidae (e.g. wildebeest). Lorenzen and colleagues (2012) synthesized the results of numerous phylogeographic studies using mitochondrial and microsatellite DNA conducted on these species and found a striking consistency in the patterns they revealed.

Figure 5.16 shows that genetically distinct populations of 14 bovid and 5 non-bovid ungulates segregate into 1 or more of 5 regions within the African savanna. The deepest phylogeographic split separates populations in northern and southern areas (e.g., common warthog), while more recent divergences distinguish west-east populations in the northern region (e.g., kob) and northeast-southwest populations in the southern region (e.g., greater kudu). Lorenzen and colleagues (2012) suggest that these areas of genetic endemism represent savanna refugia that were isolated to varying degrees by Pleistocene climate fluctuations during the past 2.8 my. While much of the northern hemisphere experienced advances and retreats of continental glaciers during the Pleistocene, the "ice age" of Africa was characterized by alternating periods of warm-wet (pluvial) with cool-dry (interpluvial) conditions. Pollen records show that savannas contracted and forests expanded during pluvial periods, while the reverse changes occurred during interpluvials. Isolation of savanna ungulates in pluvial refugia would produce genetic divergence within species, which would remain evident (at least for a time) after savannas expanded during interpluvials. This is, in effect, Haffer's (1969) Pleistocene refugia theory applied to African—rather than Amazonian—animals.

Lorenzen and colleagues (2012) argued that the prominent north-south phylogeographic split in savanna ungulates is due to repeated isolation of these broad areas by expanded tropical forests of central Africa during pluvial periods. When isolated populations reestablished contact during interpluvials, they did so in east Africa, a region that now constitutes a "suture zone" in which secondary contact is manifest by a wide range of genetic patterns including admixture, one-way gene flow, limited hybridization, and reproductive isolation within and among resident species. In addition, genetic analyses reveal that some eastern populations originated by dispersal (colonization) from southern areas (e.g., wildebeest), whereas some southern populations were established by colonists from the east (e.g., giraffe). Such dispersal histories are indicated when one genetic lineage (the colonist) arises within another (the ancestor). Lorenzen and colleagues (2012) suggest that the genetic distinctness of eastern populations reflects high spatial variation in food and temporal variation in temperature, rather than extensive dispersal barriers, within this region. Thus, while northwestern and southern areas represent savanna refugia of the Pleistocene, the diverse un-gulates of eastern Africa derive from a more complex set of historical and ecological processes.

Ecological Biogeography

Major topics in ecological biogeography include community assembly, island biogeography, and macroecology. Because these subjects are so deeply rooted in community ecology, we defer discussion of them to Chapter 26. Here we summarize several key geographic phenomena that have been observed in mammals and explained by ecological determinants.

ECOGEOGRAPHIC PATTERNS OBSERVED IN MAMMALS

Since the 19th century, a number of regularities have been noted in the ways that organismal characteristics of mammals vary with geography. Many of these patterns have been codified as "ecogeographic rules," and for the sake of convenience, we use this terminology here. However, none of the patterns is invariant, some are of questionable generality, and all are the result of complex interactions among multiple historical and environmental factors. Thus they are "rules" only in the loosest sense. Lomolino and coworkers (2017) provide a critical discussion of ecogeographic rules, including their applicability to nonmammalian groups, and conclude that there is as much to be learned about the causes of geographic variation from studying the exceptions to the rules as from the rules themselves.

The Island Rule

Small mammals on islands tend to have larger body sizes than their close relatives or ancestors on the mainland (insular gigantism). Large mammals show the opposite trend, with island species usually smaller than their mainland counterparts (insular dwarfism). Foster (1964) drew attention to the generality of these patterns, and Van Valen (1973) reified them as the **island rule** (Figure 5.17A). Their generality has been both supported (Faurby and Svenning 2016; Lomolino et al. 2017) and challenged (Lokatis and Jeschke 2018) by modern quantitative analyses. Gigantism has most frequently been described in rodents (Michaux et al. 2002; Nolfo-Clements et al. 2017), though the pattern is not universal (Millien 2004). Dwarfism has been documented in many groups, including proboscideans (Herridge and Lister 2012), terrestrial cetartiodactyls (Peterson et al. 2011), primates (Welch 2009; Montgomery 2013), and xenarthrans (Anderson and Handley 2002). Application of the island rule in carnivores has been difficult to interpret (Meiri et al. 2009). To take just one example,
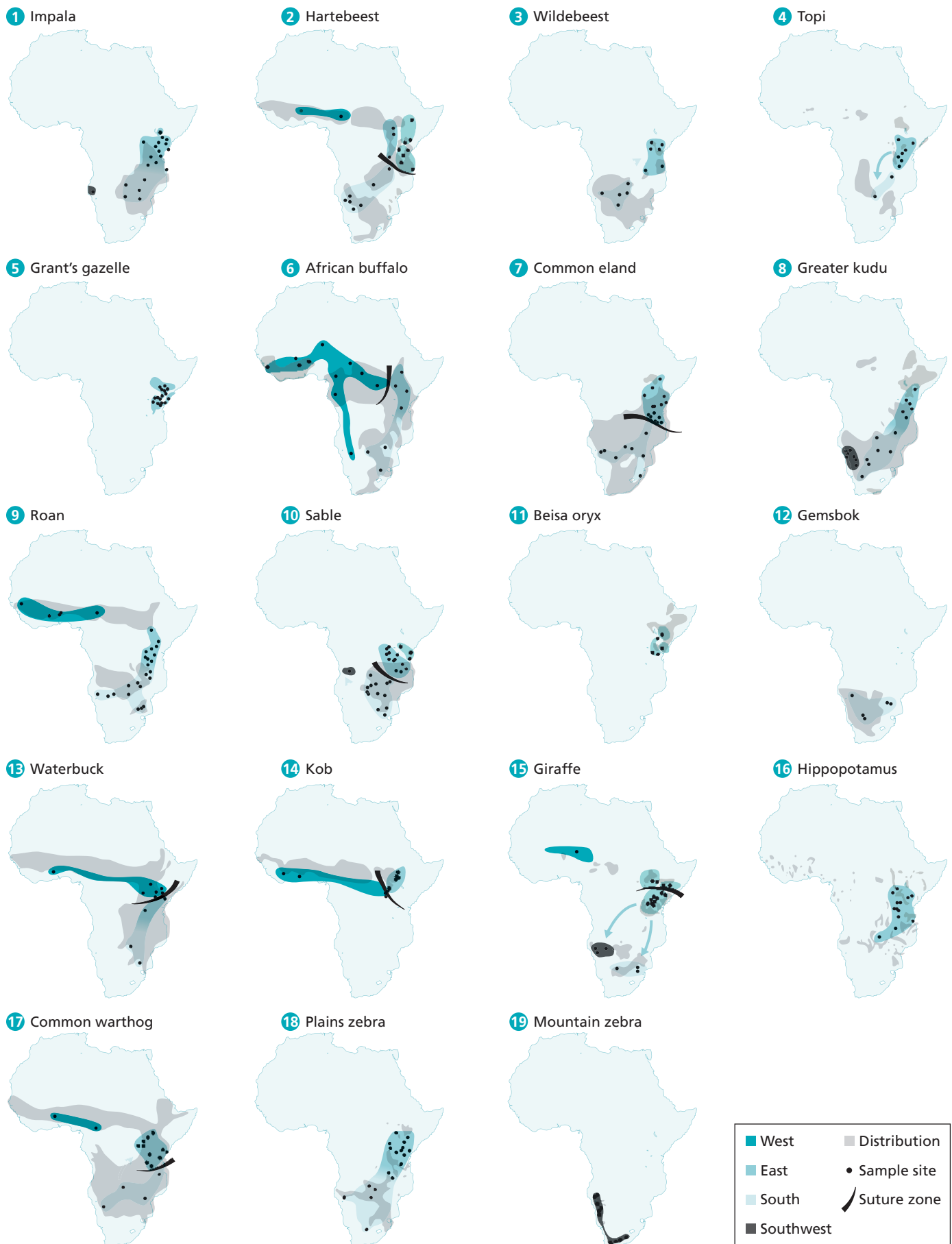
Figure 5.16 Comparative phylogeography of African savanna ungulates. Distributions of 19 ungulate taxa (*gray areas*), genetic sampling localities (*dots*), and phylogeographic regions (*shades of blue and black*). West, east, south, and southwest areas harbor genetically distinct populations of the species indicated and likely represent Pleistocene refugia. Arrows indicate inferred colonization events, and thick black lines mark the suture zone in East Africa. *Redrawn from Lorenzen (2012).*

A

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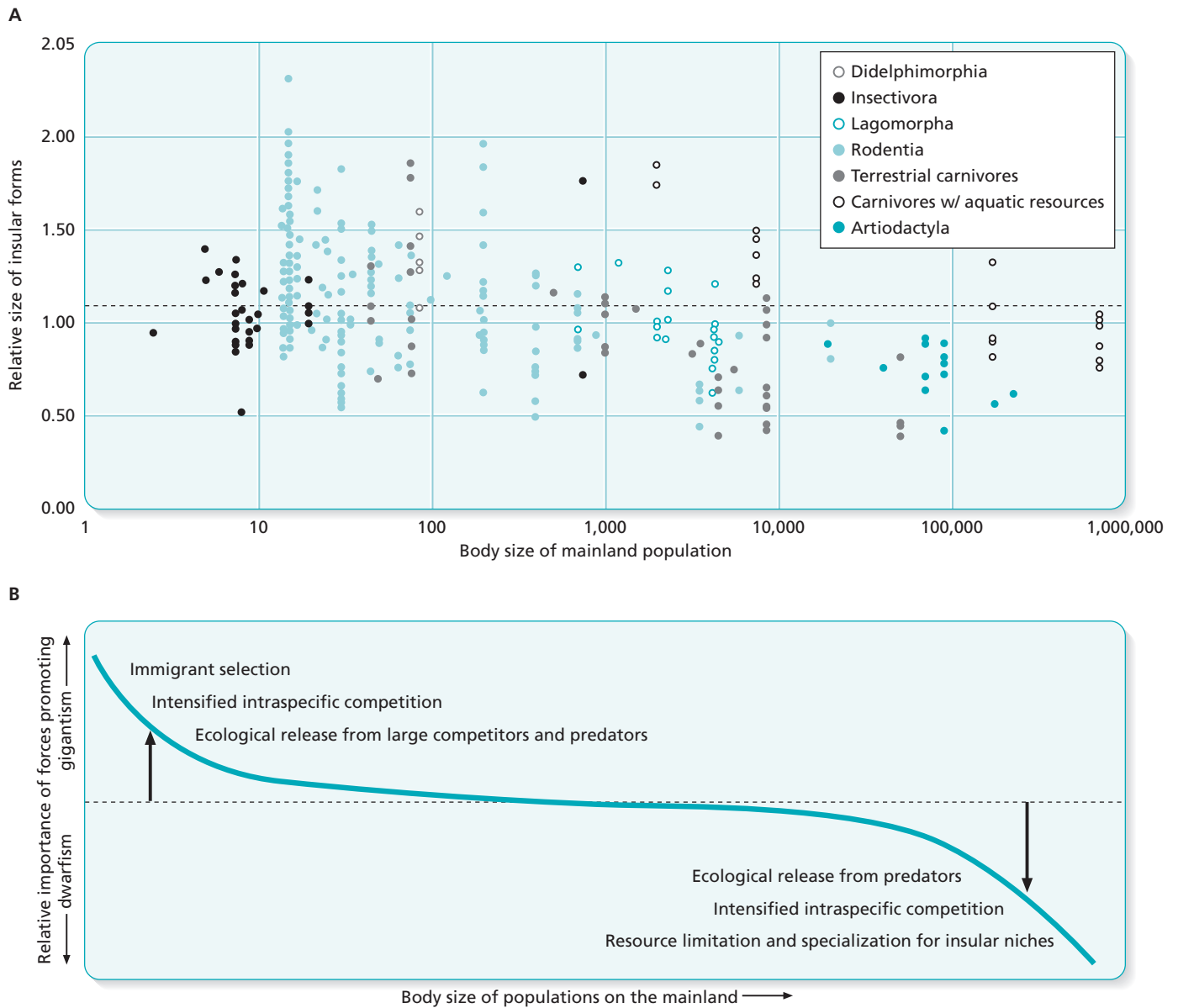
Figure 5.17 The island rule. (**A**) Relative body size of island mammals (proportion of body mass of mainland relatives) plotted as a function of body mass of mainland relatives. (**B**) The effects of selective forces on the size of island mammals vary as a function of the ancestral (mainland) body size. *Redrawn from Lomolino (2005).*

McFadden and Meiri (2012) compared the dwarf raccoon *Procyon pygmaeus* of Cozumel Island with its closest relative (*P. lotor*) on the Central American mainland and other islands. They found that dwarf raccoons evolved a 17.8% size reduction in approximately 3,000 years of isolation on Cozumel Island, significantly more than that shown by several island populations of *P. lotor*. Interestingly, the extreme morphological divergence of *P. pygmaeus* was not reflected in its genetic divergence from mainland *P. lotor*, which was small and similar to insular *P. lotor* populations.

A considerable literature exists on the evolutionary causes of insular gigantism and dwarfism (Lomolino et al. 2017). Heaney (1978) found a correlation between body and island sizes in insular tri-colored squirrels (*Callosciurus pre-*

vostii) of Southeast Asia. Because larger islands tend to have more resident species than smaller islands, Heaney argued that insular mammals experience variable levels of food limitation, predation, and competition depending on the size of the island they occupy. For large mammals, resource limitation on small islands should be the most intense selection pressure and favor reduced body size (but see Meiri et al. 2005); for smaller mammals, reduced interspecific competition ("ecological release") should favor larger size. Lomolino (1985) noted that the latter trend could be reinforced by immigrant selection—that is, larger individuals (especially in smaller species) have a better chance of colonizing islands in the first place. Moreover, the species composition of islands will be affected by their

area and distance from mainland source populations. Lomolino (2005) argued that the island rule is a general pattern emerging from this array of selective forces (Figure 5.18), and Lomolino and coworkers (2011) articulated a general model of body size evolution in which insular species evolve toward an optimal size determined by their basic body plans and ecological interactions (see also Palombo 2009).

Bergmann's Rule

One of the earliest ecogeographic rules was that of Bergmann (1847), who observed that the body sizes of mammals and birds tend to increase with increasing latitude. Originally framed to describe trends among species, **Bergmann's rule** was interpreted primarily as a pattern of intraspecific variation by Mayr (1956), though current research encompasses both levels. The trend seemed to hold statistically for mammals in general (Ashton et al. 2000), though Gohli and Voje's (2016) survey of 22 mammal families revealed a significant Bergmann pattern in only one (Canidae). Clauss and colleagues (2013) found a strong correlation between latitude and body size for closely (but not distantly) related mammal species; Joaquin Torres-Romero and coworkers (2016) found strong correlations among body size, latitude, and sea surface temperatures in marine mammals. Rodriquez and colleagues (2008) found that Bergmann's rule applied to Western Hemisphere mammals in cold (northern Nearctic), but not warm (southern Nearctic and Neotropical) macroclimates; the latter showing a strong influence of local and regional abiotic factors on body size. Moreover, variation in some small-bodied mammals, such as tuco-tucos (*Ctenomys*; Medina et al. 2007), appears to contradict Bergmann's rule in that body size decreases with increasing latitude. Faurby and Araujo (2017) argued that anthropogenic global warming effects on the distribution of extant mammals leads to systematic underestimation of the strength of Bergmann's rule.

Bergmann's (1847) original explanation for a latitudinal size gradient was based on the superior heat-conserving capacity of large-bodied endotherms. A typical large mammal has a lower surface-to-volume ratio than a small mammal, and hence a smaller surface area across which to lose body heat at cold temperatures. Indeed, Blackburn and Hawkins (2004; see also Teplitsky and Millien [2014]; Joaquin Torres-Romero et al. [2016]) found that average annual temperature is the strongest predictor, among six variables evaluated, of average body mass in North American mammals (Figure 5.18). Thermoregulatory constraints also appear to be causally related to latitudinal variation in the size of grey mouse lemurs (*Microcebus murinus*) in Madagascar (Lahann et al. 2006). However, McNab (1971) rejected Bergmann's hypothesis as a general explanation, noting that large mammals living in extreme environments at high latitudes face a greater challenge in meeting their energy requirements than do small mammals in the same habitats. Thus, McNab (1971) suggested that large body
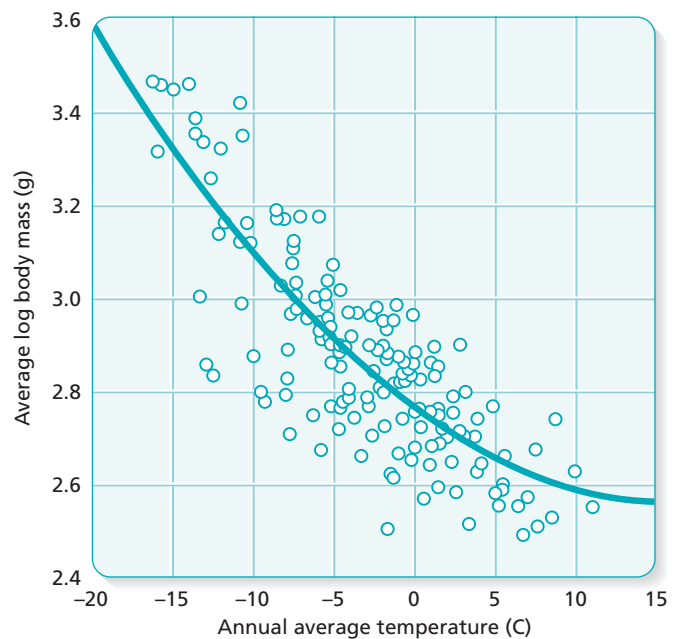
Figure 5.18 Bergmann's rule and temperature. The mean values of log (body mass in grams) as a function of average annual temperature experienced by species of northern North American mammals. The curve is a best-fit polynomial regression. *Redrawn from Blackburn and Hawkins (2004).*

size might be the evolutionary result of reduced interspecific competition in species-poor communities at high latitudes— the same kind of "ecological release" on body size that has been suggested to explain the island rule. McNab (2002) also emphasized the greater ability of large mammals to survive prolonged periods of energy deprivation or thermal stress by virtue of their lower critical temperatures and increased capacity to store food and water. Brown and colleagues (2017) suggest a more complex foraging model in which the fitness trade-off between search and handling efficiencies explain both Bergmann's rule and the inverse correlation between body size and food quality in herbivores. Other recent attempts to explain Bergmann's rule have focused on integrating abiotic factors that vary at regional scales (Rodriquez et al. 2008) with biotic factors such as range size (Meiri et al. 2007) and food availability (Wolverton et al. 2009; Zhang et al. 2012; Sepulveda et al. 2013), as well as accounting for phylogenetic correlation between body size and latitude (Kamilar et al. 2012). Lomolino and coworkers (2017) advocated applying such integrative analyses to all determinants of body size, not just those related to latitude. Orcutt and Hopkins (2013) suggested that these determinants are likely to be complex, taxon-specific, and strongly influenced by past climate changes.

Allen's Rule, Gloger's Rule, and Rapoport's Rule

Extending Bergmann's reasoning about thermoregulatory adaptations in endotherms, Allen (1877) observed that

mammals and birds living in cold climates have shorter appendages than do their close relatives in warm climates. Long limbs, tails, ears, or other appendages increase the surface area for heat dissipation in mammals, which might be adaptive as a cooling mechanism in hot, dry environments (Schmidt-Nielsen 1979). The traditional example of **Allen's rule** is correlation of ear length with air temperature in foxes (Canidae) and hares (*Lepus*; Hesse 1937; Griffling 1974), but few other mammalian examples have been discovered. Stevenson (1986) confirmed the correlation for size-specific ear and tail lengths in *Lepus*, but rejected it for cottontail rabbits (*Sylvilagus*), as well as showing that hind foot length in both groups was *negatively* correlated with temperature. The latter pattern was also found for tail length in tuco-tucos (*Ctenomys*; Bidau et al. 2011). Lindsay (1987) interpreted the results of a multivariate analysis of craniometric characters in Rocky Mountain red squirrels (*Tamiasciurus hudsonicus*) as consistent with Allen's rule. Whereas Tilkens and colleagues (2007) confirmed the physiological correlation between heat dissipation and appendage length in hominin primates, Serrat and coworkers (2008) suggested that enhanced growth of appendages in warm climates might be due to the direct influence of temperature on cartilage production rather than selection on developmental genes.

Gloger (1883) noticed an apparent correlation between the plumage colors of closely related birds and the humidity levels of their habitats, with darker forms more frequently found in humid environments and lighter forms in dry areas. In mammals, the rule would apply to pelage color—for example, white polar bears (*Ursus maritinus*) inhabiting the dry Arctic contrast with brown grizzly bears (*U. arctos*) in the somewhat more humid tundra and boreal forests of North America and Eurasia. **Gloger's rule** has been documented in primates (Kamilar and Bradley 2011), including human skin color (Chaplin 2004), but its generality appears limited. Lomolino and colleagues (2017) suggested that it may be a manifestation of selection for **cryptic coloration** in some mammals, and that clines in pelage color opposite to that predicted by Gloger (i.e., darker pelage in drier habitats) may reflect thermoregulatory adaptations. Several studies have documented an adaptive (predator-avoidance) correlation between dorsal pelage color and soil color in rodents, including deer mice (*Peromyscus maniculatus*; Dice 1947), pocket gophers (*Geomys bursarius*; Krupa and Geluso 2000), and pocket mice (*Chaetodipus intermedius*; Hoekstra et al. 2005).

Rapoport (1982) noted that the latitudinal breadth of species ranges in mammals tends to increase from the equator to the poles. Stevens (1989) called this pattern **Rapoport's rule**, documented it in other groups of organisms, and argued that it results from species' responses to a gradient of increasing climatic variability at higher latitudes. Species living at high latitudes are adapted to a relatively broad seasonal range of environmental conditions and are able to expand their geographic ranges accordingly. In contrast, tropical species are adapted to a more stable climate, have evolved toward ecological specialization, and have narrower distributions. Rapoport's rule has been supported (often with caveats) in quantitative studies of primates (Harcourt 2006), North American mammals (Arita et al. 2005), and New World bats and marsupials (Lyons and Willig 1997). However, Gaston and coworkers (1998) argued that the pattern is limited to high-latitude taxa in the Holarctic and that statistical flaws undermine alleged documentations of it. Indeed, Smith and colleagues (1994) argued that Rapoport's rule does not apply to Australian mammals. Colwell and Lees (2000) suggested that Rapoport's gradient is due to a statistical artifact, the "mid-domain effect," in which chance alone results in more species with narrower ranges nearer to the equator than to the poles. A significant mid-domain effect was shown by Luo and colleagues' (2011) study of terrestrial mammal ranges in China. Davies and coworkers (2011) suggested that the Rapoport pattern is more the result of long-term climate variations (e.g., Pleistocene glaciation) than current seasonality in temperate latitudes.

GRADIENTS IN SPECIES DIVERSITY

The Latitudinal Gradient

Perhaps the first global ecological pattern described by naturalists was that species diversity (i.e., the number of species per unit area) decreases from the equator toward the poles, a trend that holds for most groups of organisms (Hawkins 2001). It is apparent in Darlington's (1957) counts of tropical and temperate mammal species in eastern Asia (180 and 100, respectively). One of the earliest detailed demonstrations of this pattern for mammals was given by Simpson (1964), who tabulated the number of species occurring in 150 square-mile quadrats throughout North America (Figure 5.19). Simpson found that over 160 mammal species can occur within a single quadrat of Costa Rican tropical forest, with diversity dropping in an irregular but unmistakable trend to a low of about 20 species per quadrat in northern Canada and Alaska. Since Simpson's classic work, the general latitudinal gradient of species diversity has been confirmed for mammals in general (Schipper et al. 2008) and separately for terrestrial and marine forms (Lomolino et al. 2017 and references therein). The latitudinal trend is not a monotonic decline from the equator to the poles; rather it displays considerable local variation. For many groups, it is dominated by high but variable species diversity within the tropics and an abrupt drop between tropical and subtropical latitudes (Figure 5.19).

Despite the ubiquity of the latitudinal trend, it does not apply to all mammal groups or regions. For example, the diversity of soricomorphs (shrews and moles) is higher in temperate than in tropical areas (Cotgreave and Stockley 1994). Andrews and O'Brien (2000) suggested that different latitudinal gradients apply to large versus small African mammals, as well as to species with different feeding

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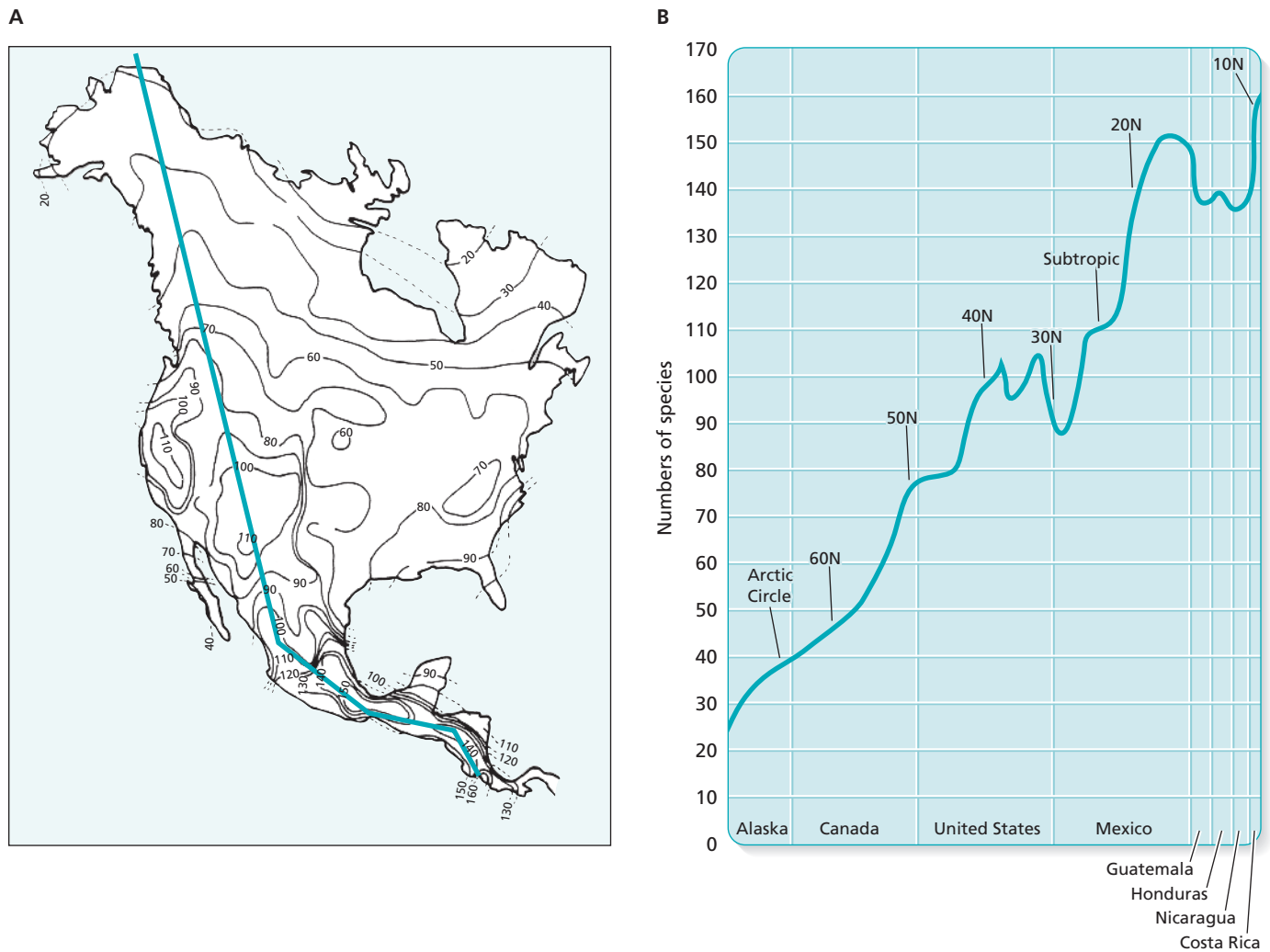
Figure 5.19 **Latitudinal gradient in species diversity.** (**A**) Contour map showing the number of species of mammals per 150-square-mile quadrat in North and Central America; (**B**) plot of diversity along the transect (*solid line*) shown in (**A**). *Redrawn from Simpson (1964).*

strategies. The steepness of the gradient may vary over time. Marcot and colleagues (2016) showed that the high current gradient for North American mammals developed within the past 4 my; for much of the Cenozoic, the gradient was much weaker.

Numerous explanations have been suggested for the latitudinal gradient in species diversity. Lomolino and colleagues (2017) list 24 such hypotheses in 3 categories that were published through 2014: null models such as the mid-domain effect (see above); ecological feedback models that emphasize habitat complexity and species interactions; and abiotic models based on environmental conditions, area, and age of land masses. These models attempt to evaluate the influence of latitudinally varying ecological conditions on evolutionary processes (speciation, extinction, and dispersal) that determine regional species richness. For example, the tropical niche conservatism model (Wiens and Donoghue 2004) posits that most clades originate in the tropics and rarely invade the temperate zone. The out-of-

the-tropics model (Jablonski et al. 2006) also assumes that most clades originate in the tropics and experience low extinction rates there, but asserts that colonization of temperate regions is common. The metabolic theory (Allen et al. 2006) argues that the higher primary productivity of tropical habitats results in higher speciation and lower extinction rates there than in temperate habitats. Recently, some of these hypotheses have been tested with phylogenetic methods. Jansson and coworkers (2013) analyzed 111 phylogenies of mammals, birds, insects, and angiosperms; their results supported the out-of-the-tropics model in that many tropical-to-temperate transitions were inferred. Weir and Schluter (2007) compared divergence times of avian and mammalian sister species at different latitudes and concluded that speciation rates are *lower* in the tropics than at higher latitudes, contrary to predictions of the metabolic theory but arguably consistent with the out-of-the-tropics model. Buckley and colleagues (2010) showed that the direction of diversity gradients in terrestrial mammals de-

pends on the ages and distributions of clades. Young clades or those with widespread temperate-zone distributions (e.g., **caniform** carnivorans) show more diversity at cooler temperatures, whereas clades with restricted distributions and tropical origins (e.g., **feliform** carnivorans) exhibit the usual decreasing gradient with latitude. These and many other recent studies highlight the significance that evolutionary ecologists attach to understanding this most striking biogeographic pattern.

Elevational and Peninsular Gradients

Ecologists have long been aware that elevation exerts a powerful influence on the composition of biological communities and the diversity of species within those communities (Whittaker 1975). Initial studies emphasized the species-poor nature of mountaintops relative to more diverse habitats in adjacent lowlands (e.g., Patterson et al. 1996). In a few cases, the elevational gradient of species diversity is a steady decrease from low to high elevations (Figure 5.20A; Kasangaki et al. 2003). Explanations for this pattern have emphasized the changing climatic characteristics along a mountainside (Hapold and Hapold 1989). At higher elevations, temperature and oxygen levels drop while moisture becomes tied up in frosts. These abiotic conditions result in lower primary productivity on mountaintops and a correspondingly less diverse community. However, most studies with thorough geographic sampling (e.g., Ferro and Barquez 2009, Krystufek et al. 2011) have suggested that species diversity peaks at middle, rather than low, elevations (Figure 5.20B). Lomolino and colleagues (2017) note that this pattern is expected if one considers how the relative isolation and areas of elevation zones interact with changing climatic conditions. The conical shape of most mountains ensures that high-elevation zones are smaller and more isolated from one another than lower zones, resulting in lower immigration and higher extinction rates. Isolation, however, also promotes speciation. The net effect of these countervailing factors is that species diversity should be relatively high at the base of mountains, highest at middle elevations, and lowest on mountaintops. Recent authors (Rowe 2009; Wu et al. 2013) also emphasize that, although elevational diversity gradients are common, their causes at particular localities may be species-specific and diverse rather than simple and uniform. Elevational effects are also responsible for the increased species diversity in areas with topographic variation (Simpson 1964), such as the western United States (Figure 5.19A).

   Simpson (1964) noted that the number of mammal species on North American peninsulas declines toward their terminal ends. This peninsular effect is evident in Simpson's map (Figure 5.19A) if one examines diversity contours in Baja California, Florida, and the Yucatan. The pattern in Baja California was demonstrated for heteromyid rodents by Taylor and Regal (1978), for small mammals on the Iberian Peninsula by Barbosa and Benzal (1996), for ro-
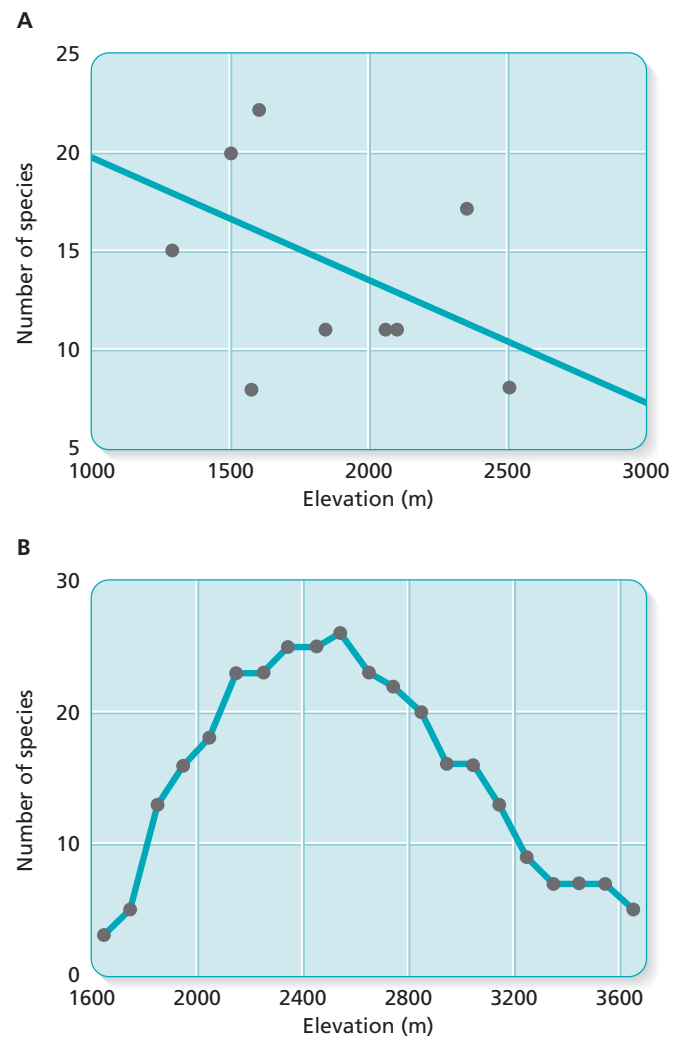
Figure 5.20 Elevational gradient in species diversity. (**A**) In Bwindi Impenetrable National Park, Uganda, the diversity of small rodents shows a steady decrease with altitude. Dots represent collecting localities, and the line is a linear regression. (**B**) In the Uinta Mountains of the southwestern United States, the diversity of small nonflying mammals peaks at intermediate altitudes. *Redrawn from Kasangaki et al. (2003) and Rowe (2005).*

dents in Italy by Contoli (2000), and for nonvolant mammals in Europe by Baquero and Telleria (2001). On the other hand, Lawlor (1983) argued that there is no peninsular effect in Baja for soricomorphs, lagomorphs, geomyid and murid rodents, carnivorans, or bats. Simpson (1964) attributed the gradient to declining immigration rates and increasing extinction rates as one moves closer to the terminus of a peninsula, both effects due to isolation from the mainland, reduced land area, and limited habitat diversity (Lomolino et al. 2017). Some authors (e.g., Lawlor 1983) have found this kind of explanation insufficient to account for the variation in peninsular diversity patterns among different groups and have argued instead that factors such as topographic complexity, ecological barriers, and the dispersal abilities of resident species determine whether a particular group will show the peninsular effect.

SUMMARY

- Biogeography is the study of how organisms are distributed on the Earth and of the causal processes that determine those distributions. The most fundamental datum for biogeography is the species range, the entire area over which individuals of a species occur.

- Historical biogeography is concerned with changes in species ranges over time, as well as how such changes result from evolutionary (e.g., speciation, extinction, dispersal) and geological (e.g., continental drift, climate change) processes. Ecological biogeography focuses on how species ranges are influenced by factors such as migration, community interactions, and physiological or morphological adaptations.

- Mammal distributions, like those of most organisms, show varying degrees of endemism or restriction to specific areas. On a worldwide scale, endemism results in provincialism—distinct faunal regions or provinces that harbor diverse groups of closely related species.

- Biogeographic regionalization is the scientific process of identifying areas of endemism at different spatial scales. The most common global regionalization applied to mammals recognizes six regions—Palearctic, Nearctic, Neotropical, Ethiopian, Oriental, and Australian. Mammals are also found on oceanic islands (mostly rodents and bats), in coastal waters (e.g., pinnipeds and sirenians), or in the open ocean (cetaceans).

- Scientific acceptance of continental drift and plate tectonics theory in the 1960s revolutionized our understanding of historical biogeography. Throughout the Phanerozoic eon, continents have moved, coalesced, and fragmented, carrying their biotas with them and producing the most significant historical influence on current provincialism.

- Scientists have also become aware that, because of continental drift and other factors, climate conditions have varied dramatically throughout Earth history, displaying alternating periods of "hothouse" and "icehouse" conditions. Extreme icehouse conditions produced ice ages, during which glaciers advanced across portions of continents and many species distributions were contracted into small refugia.

- Since their origin in the Late Mesozoic, synapsids have experienced both continental movements and climate changes, and have responded to them evolutionarily in a variety of ways. One response is dispersal, which involves extension of a species range into previously unoccupied areas. Corridor routes are dispersal pathways through which many species may move with little ecological resistance. Filter routes are accessible to some species but not others, depending on their ecological tolerances. Sweepstakes routes are the result of rare events that move individuals across a dispersal barrier into an area where they can successfully reproduce.

- Another possible response to environmental change is vicariance, in which the ancestral range of a species is fragmented by a dispersal barrier, which, in turn, induces speciation and subsequent diversification of lineages in isolated geographic areas. Vicariance followed by diversification is thought to be the primary mechanism by which patterns of endemism arise.

- Species may also respond to environmental changes by going extinct. Background extinction is the result of ecological processes that lead to the demise of individual species, whereas mass extinctions are worldwide events that result in the simultaneous loss of many species from different major groups.

- Historical biogeographic hypotheses are usually framed to explain patterns of disjunction, such as the geographic separation of sister groups. Early biogeographers emphasized dispersal and extinction as the primary processes that determine species distributions, but awareness of continental drift and climate change, coupled with the development of rigorous methods of phylogeny reconstruction, led to a stronger emphasis on the role of vicariance.

- Cladistic biogeographers focus on reconstructing the history of areas from the phylogenies and current distributions of species in those areas. The key to inferring area relationships is congruence among the phylogenies of multiple, codistributed species. However, cladistic biogeography is complicated by widespread and missing species, species with multiple representatives in the same area, and the temporal incongruence of biogeographic events that affected groups in a single region. Nevertheless, there are now powerful algorithmic approaches to biogeographic inference, including model-based methods that apply statistical principles.

- Molecular techniques have also been brought to bear on questions of historical biogeography. Comparative phylogeography uses principles of genealogical concordance to formulate and test hypotheses of recent vicariance and dispersal by examining the genetic structure of populations throughout the ranges of individual species.

- The early evolutionary history of marsupials illustrates the value of combining paleontological, geological, and phylogenetic information to understand the biogeographic history of a major mammalian group. Marsupials probably originated in North America during the Cretaceous and dispersed by a sweepstakes route to South America, where they diversified during the Cenozoic. Some of these taxa, including microbiotheres, made their way across the Antarctic peninsula, East Antarctica, the South Tasman Rise, and into Australia by the Paleocene or Eocene. Breakup of the Gondwanan continents isolated the common ancestor of Australian marsupials, which underwent a spectacular radiation throughout the later Tertiary Period as Australia drifted north to its current position.

- Fossils have also documented the biogeographic history of South America. Along with marsupials, the Paleocene

mammal fauna of South America contained archaic ungulates, diverse edentates, and condylarths. Hystricomorph rodents and ceboid primates arrived during the Oligocene; procyonids from North America invaded via island chains in the Miocene. In the Pliocene (or perhaps Miocene), the Panamanian land bridge emerged and formed the dispersal route for the Great American Biotic Interchange of mammals between the two continents. Pleistocene extinctions took a much heavier toll on South American forms, however, resulting in a relatively large proportion of current South American species being derived from northern ancestors.

- Analytical biogeography methods used in conjunction with area chronograms based on DNA sequences and fossil calibrations have illuminated the ancestral areas of eutherian orders. Afrotherians appear to have originated in Africa, xenarthrans in South America, and boreoeutherians in Eurasia—all during the Late Cretaceous and associated with continental separations.

- Comparative phylogeographic analyses of African savanna ungulates suggests that Pleistocene climate fluctuations created refugia north and south of the tropical forest in central Africa, as well as in eastern and western areas within the northern and southern zones. High ungulate diversity in East Africa appears related to the high spatial and temporal heterogeneity of environmental conditions within this region.

- Since the 19th century, ecological biogeographers have noted regularities in the geographical pattern of variation in morphological and life-history characters of mammals. These patterns have been codified as ecogeographic rules, although their generality is often quite limited.
  - The "island rule" is that island representatives of large-bodied mammal species are often smaller than their mainland relatives (insular dwarfism), whereas small-bodied species on islands tend to be larger than their counterparts on the mainland (insular gigantism).
  - Rapoport's rule is that the latitudinal breadth of species ranges tends to increase with increasing latitude.
  - The same trend in body size—larger individuals occur at higher latitudes—constitutes Bergmann's rule.
  - According to Allen's rule, individuals that live in cold climates have shorter appendages than do conspecifics in warmer areas. Gloger's rule suggests that species living in dry areas have darker pelage than their relatives in humid areas.

- Ecological biogeographers are also concerned with explaining large-scale patterns in species diversity. The first such pattern to be described is that the number of species per unit area tends to decrease with latitude, with tropical habitats harboring the greatest diversity. Similarly, species diversity changes with elevation in montane areas, peaking at mid-elevations and declining toward the summits. Species numbers also decline as one moves toward the terminus of a peninsula. Again, these trends are not universal, and the factors that produce them are complex.

- Models that integrate the effects of various ecological processes on rates of dispersal, extinction, and speciation have been formulated and are currently being tested, often with phylogenetic methods.

SUGGESTED READINGS

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McCarthy, D. 2009. Here be dragons: how the study of animal and plant distributions revolutionized our views of life and Earth. Oxford Univ. Press, Oxford, UK.

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DISCUSSION QUESTIONS

1. Using a field guide for mammals, select an order with numerous species in North America (or any other continent). Count the numbers of species in the order that occur at 5- or 10-degree increments of latitude. In light of the information in this chapter, what factors might explain differences in species richness at the different latitudes?

2. Some species of mammals, such as house mice (*Mus musculus*), have extremely broad distributions. Others, such as the Kangaroo Island dunnart (*Sminthopsis aitkeni*), occur only in very small areas (e.g., Kangaroo Island off the coast of South Australia). Most mammal species have range sizes between these two extremes. What factors do you think help to explain the variation in range size among species?

3. Select your favorite mammalian family and determine the distribution of each species within it using guidebooks or the internet. Based on your knowledge of geography and climate, along with information about the niches and phylogeny of these species, what can you say about the factors that produced the current distribution of the family?

4. How is biogeography related to conservation biology? What kinds of information could biogeographers supply that might assist in developing a conservation management plan for an individual species or a group of related species?

PART 2

Structure and Function

In Part 2, we examine the relationships between the anatomical parts of a mammal (its structure) and the way those parts work together to accomplish fundamental life processes (their function). Our goal is to understand how anatomy and physiology have been shaped by natural selection in response to varied environmental circumstances. We give special attention to the morphological adaptations of mammals in general, as well as to some of the specialized body structures associated with particular lifestyles. Later, in Parts 3 and 4, we describe the anatomical features characteristic of major mammalian groups and explore how morphology and physiology are related to mammal behavior.

Chapter 6 describes the outer covering of a mammal's body (the skin, or integument), the support system provided by the axial and appendicular skeletons, and the muscles that power movement. Chapter 6 concludes with an examination of locomotor adaptations among mammals. Chapter 7 covers the ways in which mammals obtain and process food, including a discussion of how variation in tooth structure relates to different modes of chewing. This chapter also explores how the digestive system extracts nutrients from food and how mammals store energy. In Chapter 8, we discuss the concept of homeostasis and how it is maintained. This includes a description of the circulatory, respiratory, and urinary systems and how they interact to accomplish respiration, osmoregulation, thermoregulation, and energy conservation. In Chapter 9, we explore the morphological structures and physiological processes by which mammals reproduce.

Integument, Support, and Movement

Imagine a cheetah (*Acinonyx jubatus*) slowly stalking a Thomson's gazelle (*Gazella thomsonii*) on the African savanna. The cheetah blends into the dappled shade under acacia trees and warily follows the gazelle at a distance. Suddenly, it sprints after the gazelle in an all-out dash to capture its prey (Figure 6.1). We are amazed by the cheetah's burst of speed and by the graceful, powerful movements of its legs as it races toward the gazelle. What body structures enable the cheetah to make such a swift attack? What body processes are at work to produce the smooth, forceful run of this predator?

The cheetah's body, like that of other mammals, is adapted for its way of life. Its fur protects and camouflages it. As it runs or walks, each stride involves intricately coordinated movements of muscles and bones throughout its body. To understand the dynamics of locomotion, we must first examine the arrangement of skin, bones, and muscles in a mammal's body. This chapter starts with the outside of a mammal—the integument—and then moves under the skin to explore the skeleton and the muscles that power movement. In the final section, we show how the integument and musculoskeletal system relate to modes of locomotion.

Integument

The skin, or **integument**, is the interface between a mammal and the external environment. Its primary role is to separate the internal, homeostatically regulated milieu of tissues and cells from the vagaries of outside conditions. The integument of mammals also has two more specific functions: water conservation and insulation. An impervious outer layer of skin is a trait shared by all amniotes and an adaptation for preventing evaporative loss of body water in the dry air of terrestrial habitats. As endotherms, mammals must also conserve body heat that is energetically expensive to produce. The outermost layer of their integument has evolved a relatively simple structure—hair—that traps a layer of air

next to the skin and prevents convective heat loss. Feathers perform the same function in birds, the other group of endothermic vertebrates. The integument serves other critical functions as well, including the ability to dissipate excess heat by evaporative cooling, communication via pelage color or patterns, sensory capabilities for obtaining information about the environment, and production of diverse secretions from specialized glands. Moreover, the skin has produced some uniquely mammalian structures such as the surfaces of horns, antlers, nails, and hoofs.

STRUCTURE AND FUNCTION

Skin

Vertebrate skin consists of an outer epidermis and inner dermis, below which is a hypodermis or subcutaneous region that overlies muscle (Figure 6.2; Kardong 2012). The **epidermis** of mammals consists of several layers: an inner *stratum basale* (or germinativum), intermediate strata showing stages of keratinization, and an outer *stratum corneum*. Stem cells in the *stratum basale* divide continually and some of the daughter cells migrate into the overlying strata where they manufacture large amounts of the protein keratin (i.e., they become keratinized or cornified), a process that causes them to die by the time they reach the *stratum corneum*. Keratin is water-insoluble and thus the keratinized *stratum corneum* prevents desiccation of the underlying skin. Cells of the *stratum corneum* are shed and replaced throughout the life of a mammal. The thickness of the *stratum corneum*

Figure 6.1 **Cheetah and gazelle.** This scene of a cheetah attempting to run down a gazelle shows the general body form of each animal, as well as their integuments and color patterns. Both species are cursorial, or running, mammals, but the structures of their limb bones are extremely different.
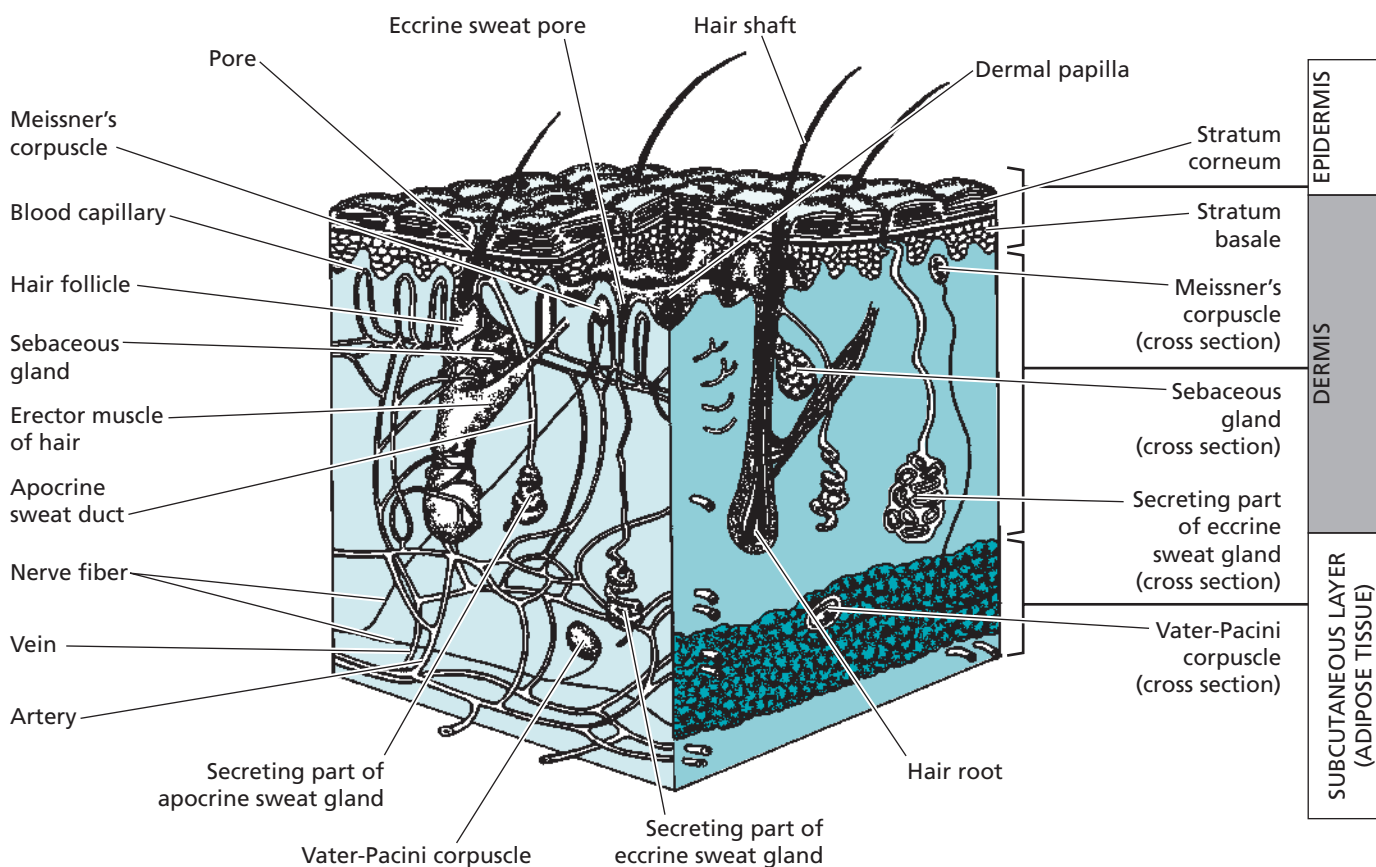
Figure 6.2 **Mammalian skin.** Three-dimensional section through the skin and subcutaneous region of a mammal. Glands and hair are epidermal structures that grow into the dermis during development.

varies among regions of the body and among species. It is very thick in the foot pads of most species. These surfaces experience regular abrasion against rough substrates during locomotion, and thickening of the *stratum corneum* provides protection against excess wear. Epidermal thickening may even result in a distinct cell layer—the *stratum lucidum*—just below the *stratum corneum*. Cells in the *stratum lucidum* are translucent due to large amounts of keratohyaline, a precursor of keratin.

At the boundary between the epidermis and dermis are melanophores, cells that contain **melanin**. This brown pigment absorbs ultraviolet radiation from the sun, which might otherwise damage the underlying dermal tissue. Melanin in the dark tongues of giraffes (*Giraffa camelopardalis*) protects the tissue from sunburn as the animals lift their heads into the branches of trees to forage for leaves. In humans, synthesis of melanin increases upon exposure to sunlight and produces tanning. Extensions of melanophores reach into the epidermis where they inject their pigments into developing hair cells (see next section). In a few cases, such as the bright ischial callosities of baboons, pigmented patches of skin are used as visual signals. The blue and red coloration on the scrotum and perineal region of male vervets (*Chlorocebus aethiops*) is used in dominance displays.

The thick mammalian **dermis** contains connective tissue, blood vessels, nerves, and slips of integumentary muscle. The epidermis has no blood supply of its own, so metabolic needs of cells in the *stratum basale* are met by diffusive exchange of nutrients and waste products with the highly vascularized dermis. Constriction and dilation of dermal arterioles helps regulate heat loss by directing blood toward or away from the surface of the skin. Encapsulated sensory nerve endings in the dermis terminate at tactile receptors such as Pacinian (Vater-Pacini) corpuscles or the Meissner's corpuscles of primates (Figure 6.2). Receptor stimulation results in firing of the associated nerve and transmission of an impulse to the central nervous system. A tiny **smooth muscle**, the *arrector pili*, inserts at the base of each hair within the dermis. When they contract, *arrectores pilorum* cause hairs to stand erect, a response that may conserve heat by thickening the dead-air layer above the skin, or act as a visual signal (e.g., when "hairs stand on end" on the neck of a snarling dog). Although hairs and integumentary glands are derived from epidermal cells, their bases grow down into the dermal layer as they develop (Figure 6.2).

Below the skin lies a **hypodermis** consisting of loose connective and adipose (fat) tissues. Connective tissue causes the skin to adhere to underlying muscle, whereas subcutaneous fat serves as insulation and an energy reserve. Some sensory receptors (e.g., Pacinian corpuscles) also occur in the hypodermis.

Hair

Hair is a unique characteristic of mammals, but its evolutionary origin is obscure. Derived from the *stratum cor-*

neum, the hairs of mammals occupy the same structural position and perform some of the same functions as the epidermal scales of nonavian reptiles and the feathers of birds. As noted previously, hair provides insulation for mammals, so perhaps its evolution was tied to the origin of endothermy. However, there is an inconsistency in this scenario: insulatory fur would be maladaptive for an ancestral ectotherm that relied on efficient heat exchange with the environment for thermoregulation, but some form of insulation appears to be necessary for endothermy to be energetically cost-effective (Pough et al. 2013). Indeed, evidence for endothermy (respiratory turbinate bones in the nasal cavity) can be found in Permian therapsids long before the earliest mammal (Ruben and Jones 2000; but see Kemp 2006). The Permian therocephalian *Estemmenosuchus* has an exceptionally well-preserved skin impression that lacks any trace of hair (Kardong 2012). In contrast, the oldest synapsid known to have had fur, the docodont *Castorocauda*, did not occur until the Middle Jurassic (Ji et al. 2006), though indirect evidence suggests that hair may have been present in the Late Triassic stem mammal *Morganucodon* (Pough et al. 2013). Given this long lapse between the apparent origin of endothermy and the origin of hair, it seems unlikely that hair evolved in response to selection for insulation. What, then, explains its origin?

Maderson (1972) suggested that hairs originated as tactile receptors between the scales of early synapsids and later were coopted as insulation after the evolution of endothermy. Stenn and colleagues (2008) and Dhouailly (2009) proposed that hairs evolved through modification of the developmental processes that produced skin glands in ancestral synapsids, a view supported by some experimental evidence (e.g., Alibardi 2012). These authors suggest that lepidosaur scales, avian feathers, and mammalian hairs—all derivatives of the *stratum corneum*—represent divergent evolutionary trends in development of the amniote epidermis. Each had distinct adaptive values, but all owe their origin to changes in a common set of morphogenetic signals between the epidermis and underlying dermis.

A hair follicle begins its development in the *stratum basale* (Butcher 1951) and grows down into the dermis, inducing the formation of a dermal papilla (Figure 6.3). The papilla becomes vascularized and serves as a conduit for nutrients and waste products with the developing hair. Where it reaches the base of the dermis, the follicle swells to form a bulb around the dermal papilla. Continual mitosis occurs within the bulb, where root cells synthesize keratin and grow outward to form a **shaft** of dead cells, which eventually emerges from the surface of the skin. As the hair is differentiating, so too are dermal cells that will form the *arrector pili* muscle and follicle cells that will form a sebaceous gland. The root of each hair becomes surrounded by sensory nerve endings that transmit tactile signals to the brain whenever the shaft is displaced (Figure 6.2).

A typical hair has three structural layers. The **medulla** occupies the center of the shaft and consists of sparse, irregular cells connected by keratin strands and surrounded
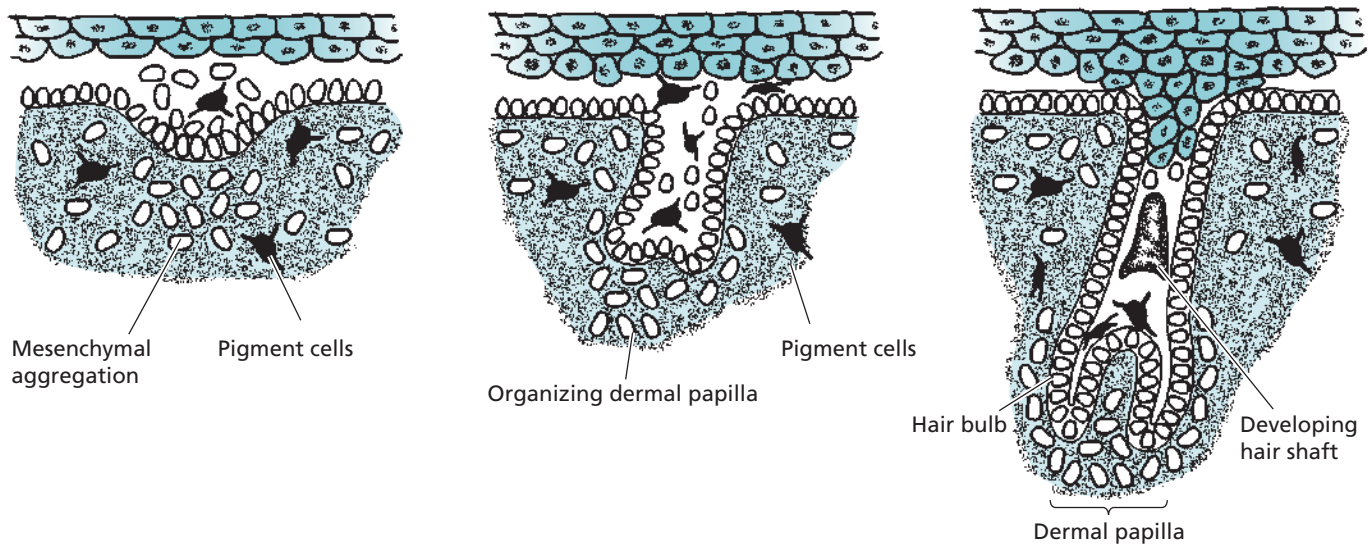
Figure 6.3 **Hair development.** At left, epidermis invades the dermis (*shaded*) at the site where an individual hair will form. At center, a dermal papilla organizes beneath the epidermal invagination, which is beginning to form a follicle. At right, a hair shaft begins to differentiate within the follicle, and a bulb of epidermal cells surrounds the dermal papilla. *Adapted from Searle (1968).*

by air space. The medullas of some species, including deer, lack cells altogether, and the hairs are hollow. The **cortex**, composed of tightly packed cells, surrounds the medulla and comprises most of the shaft. A thin, transparent **cuticle** forms a scale-like pattern on the surface of the hair. Cuticle patterns vary greatly among species (Figure 6.4) and have been used to identify closely related forms (Wooley and Valente 1992).

Hair can be classified in a variety of ways (Martin et al. 2011). One distinction recognizes different growth patterns. **Angora** hair grows continuously to produce long, flowing shafts that may or may not be shed (e.g., a horse's mane). **Definitive hairs** attain a fixed length before being shed and replaced (e.g., **body hairs** of a dog). The two main functional types of hairs are vibrissae and pelage (fur). Vibrissae are long, stiff hairs that function as tactile receptors and exhibit definitive growth. The most common are "whiskers" in the facial region of nocturnal species, but they are also found on the tails of some fossorial species or on the legs of others. Active vibrissae can be erected voluntarily, whereas passive ones cannot. **Pelage** consists of long, coarse **guard hairs** underlain by **underfur** that is short, dense, and fine. The most common type of guard hair is an **awn**, characterized by an expanded distal end, a weak base, and definitive growth. Awns usually lie in one direction, giving the pelage a distinct nap. **Spines** are the stiff, enlarged guard hairs that exhibit definitive growth and form the protective quills of porcupines, echidnas, and hedgehogs. **Bristles** are firm, generally long hairs that exhibit angora growth to form manes; they function as visual signals that augment facial expressions (e.g., lions) or body postures (e.g., horses). **Wool** is long, soft, and usually curly. **Velli** are the very short, fine hairs found on newborns (often referred to as "down" or "fuzz"). The "scales" of pan-

golins are agglutinated keratin fibers developmentally similar to hairs. Hair typically grows in tracts with a distinct orientation, or grain, relative to the body surface (Jones 1924).

Hair color is determined by the distribution and density of melanin granules within the shaft, as well as the proportion of two forms of melanin. **Pheomelanin** produces shades of red and yellow, whereas **eumelanin** is black or brown. "**Agouti**" hair results from a mixture or banding of these pigments. Gray or white hair results from the absence of melanin and an increase in the volume of air vacuoles within the medulla. White hair (along with pale skin and pink eyes) may be due to a genetic condition, **albinism**, in which melanin production is blocked. Although rare overall, albinism has reached high frequencies in some populations, such as the albino gray squirrels (*Sciurus carolinensis*) of Olney, Illinois. The opposite of albinism is **melanism**, in which the pelage is very dark due to high levels of melanin. Melanic forms of several mammal species have been described, including fox squirrels (*Sciurus niger*) and red foxes (*Vulpes vulpes*).

The pelage color of a species, or populations within a species, is an evolutionary response to several environmental pressures. One common factor seems to be the adaptive value of camouflage. As noted in Chapter 5, Gloger's rule predicts that mammals from arid regions will tend to be paler than those from more humid areas. This is probably an example of **crypsis**, in which the color of the animal matches that of the substrate (e.g., the desert floor is more lightly colored than that of forests or grasslands; Benson 1933). Mammals that display **countershading** have lighter-colored pelage on the ventral portion of the body than on the dorsal portion. This causes them to look white (like the sky) when viewed from below, but dark (like the
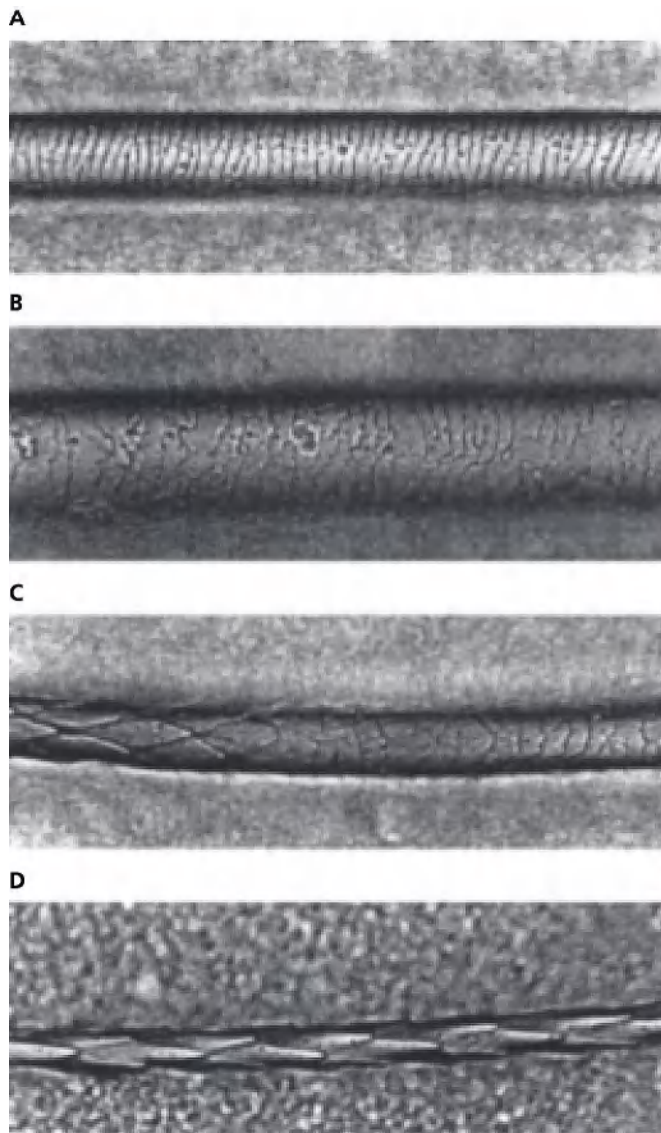
Figure 6.4 **Hair cuticles.** Scale patterns on the cuticles of primary guard hairs vary among species and even within regions of the same hair. These light micrographs show guard hairs of two dasyurid marsupials. (**A**) *Murexia melanurus*; (**B**) *Phascolosorex doriae* (distal portion); (**C**) *P. doriae* (transition region); (**D**) *P. doriae* (proximal region).

ground) when viewed from above, and therefore they appear less conspicuous from either angle. Many species show cryptic coloration in which the pelage blends in with the horizontal background against which an animal is viewed. White-tailed deer fauns (*Odocoileus virginianus*) have light-colored spots on their brown fur that conceal them in the dappled shade characteristic of temperate forests. Other species have **disruptive coloration** patterns that distort the outline of their bodies. For example, the black-and-white banding pattern of zebras (*Equus* spp.) causes them to appear larger than their actual size in the eyes of predators. Singaravelan and colleagues (2010) showed that cryptic coloration in spiny mice (*Acomys cahirinus*) from Israel is achieved by varying the ratio

of eumelanin (black) to pheomelanin among habitats within the same general area.

Many mammals periodically replace their fur by **molting**, which occurs in three principal patterns. Young mammals, particularly rodents, undergo a **postjuvenile molt** that starts after weaning (Figure 6.5). Molting patterns have been described for many small mammal species, such as red-backed voles (*Myodes gapperi*; Sare et al. 2005) and deer mice (*Peromyscus maniculatus*; Sinclair et al. 1998). Mammals living in temperate latitudes undergo a fairly rapid **annual molt** during which most hairs are replaced. This process is important for animals in cooler environments because daily activities wear down their hairs, resulting in less effective insulation during winter unless the hairs are replaced. Annual molts require considerable energy for the rapid growth of new hair and may be timed to avoid overlap with other energy-demanding activities such as late gestation and suckling, as in deer mice (Tabacaru et al. 2011), or to coordinate with migrations, as in hoary bats (*Lasiurus cinereus*; Cryan et al. 2004). Some mammals, such as Cape hares (*Lepus capensis*; Lu 2003), have a **seasonal molt** that replaces their pelage more than once a year. Some species have camouflage coloration that changes with season: ermine (*Mustela vison*) and arctic foxes (*Alopex lagopus*) have a white coat during the winter, matching the snow-covered landscape they inhabit, but molt into a darker coat for the summer (Figure 6.6). As evidence for the adaptive value of seasonal molts, Zimova and coworkers (2016) found that a climate-change induced mismatch between the timing of molt in snowshoe hares (*Lepus americanus*) and seasonal snow cover in Montana resulted in a significant increase in hare mortality. Animals in molt can be recognized by short or partially elongated hairs, which are dark at the base, growing among mature hairs that are light to the base. Fully developed molt lines can be seen in short-haired species such as moles, shrews, and pocket gophers. The skin of a molting mammal is dark or speckled due to presence of pigment-injecting melanophores just below the surface.

Integumentary Glands

Three types of glands are derived from the epidermis of mammalian skin—sebaceous, eccrine, and apocrine glands. More specialized structures, such as scent and mammary glands, are derived from these basic types. Like hairs, epidermal glands have their base in the dermis but are connected to the surface of the skin or hair by a duct. **Sebaceous glands** are generally associated with hair follicles (Figure 6.2) and secrete an oily product (sebum) that keeps the hair shaft moist and waterproof. These glands are situated such that contraction of integumentary muscles causes sebum to be squeezed onto the shaft. Sebaceous glands not associated with hairs occur on the lips, penis, labia minora, and nipples. Examples of specialized sebaceous glands include those that produce lanolin in sheep,
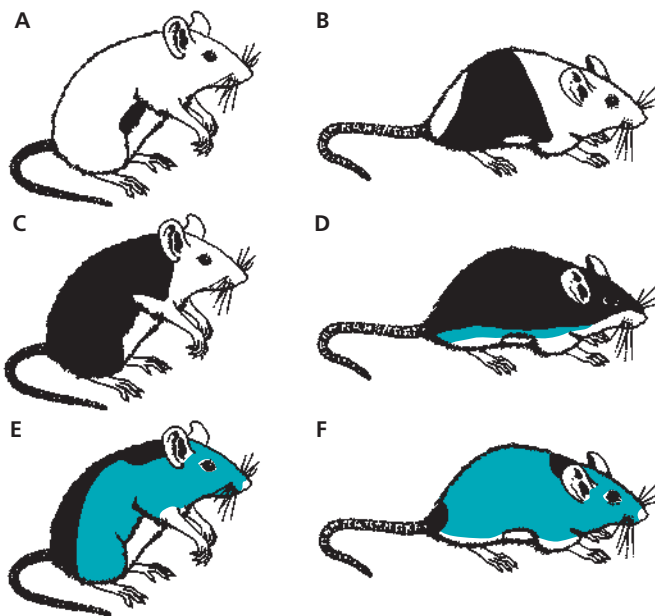
Figure 6.5 **Molting.** The postjuvenile molt of the golden mouse (*Ochrotomys nuttalli*) proceeds in a regular manner from the underside of the flanks dorsally to the back of the neck and base of the tail. Letters A–F refer to the chronological sequence of the molt. *Adapted from Linzey and Linzey (1967).*

Figure 6.6 **Seasonal changes of coat color.** Weasels (*Mustela*) may change their coat color seasonally. They molt to a mostly white pelage (*top*) for the winter, which camouflages them against the snowy background. The summer pelage (*bottom)* is brown on the dorsal surface and flanks and white on the ventral surface; this shading more closely resembles summer background colors.

ceruminous glands that secrete a waxy protective lubricant (cerumen) into the outer ear canal, and Meibomian glands in the eyelid that moisten the conjunctiva.

Eccrine glands produce a watery secretion (e.g., sweat), lie deep in the dermis, are not associated with hairs, and are connected to the skin surface by coiled ducts (Figure 6.2). They function immediately after birth. Evaporation of eccrine secretions from the skin results in evaporative cooling, an important thermoregulatory mechanism in some mammals. Eccrine glands are most common on surfaces (e.g., soles and palms) that come in regular contact with a substrate, where their secretions increase adhesion and tactile sensitivity. **Apocrine** (sudoriferous) glands produce viscous fluids that act as chemical signals, are located near hair follicles, and begin functioning at puberty. The distribution of eccrine and apocrine glands over the body varies, but they are most common in areas where fur is the least dense (e.g., the feet of cats, dogs, rodents, and primates; the lips of rabbits; the snout of platypuses). In humans and chimpanzees, eccrine glands are broadly distributed, but apocrine glands occur primarily in the axillae (armpits), anogenital region, naval areas, and nipples. Ciliary glands that drain onto the eyelashes of many mammals are apocrine glands; these are absent in pangolins, cetaceans, sirenians, and echidnas.

Scent glands may be either modified sebaceous or apocrine glands. The composition and function of the secretions they produce vary widely, but many act as **pheromone** (chemical signals that convey information between members of the same species). Scents may be used to deter predators, as in skunks, to mark territories, as in deer, to

mark sites for spatial orientation, as in weasels and badgers, or to mediate sexual and social interactions (Greenwood et al. 2005; Sharpe 2015). Scent glands can be found in almost any location on the body, including the anal area (rodents and mustelids), back (kangaroo rats), head (elephants, peccaries), forelimbs (lemurs, carnivorans), and hind limbs (ungulates). Some mammals spread scented glandular secretions onto their fur, possibly to enhance the effectiveness or persistence of the chemical signal. The yellowish color often seen on the fur of opossums is the result of such behavior.

The structures for which Mammalia is named, **mammary glands**, are specialized epidermal glands. They develop at one or more points along parallel ridges ("milk lines") of embryonic skin in the ventrolateral body wall, with epidermal cells growing deep into the hypodermis to form an extensive branching system of ducts that terminate in alveoli and are surrounded by milk-producing cells. At the surface, the ducts extend through an elevated nipple or teat to open at its apex (Figure 6.7). In many species, adipose tissue forms beneath the mammary gland to produce breasts. The number and location of glands vary among species: one axillary pair in dermopterans and marmosets; one thoracic pair in anthropoid primates; one inguinal pair in perissodactyls and cetaceans; one thoracic and one inguinal pair in soricomorphs and some lemurs; two pairs on the side in nutrias (*Myocastor coypus*); up to five pairs from the axillae to the inguinal regions in rodents, cats, dogs, pigs, and edentates; up to ten pairs in the pouches of some marsupials. The Virginia opossum (*Didelphis virginiana*) has 13 mammary glands—12 in a circle and 1 in the center. Monotreme mammary glands lack nipples, but the surface openings of milk ducts are marked by tufts of hair.

With few exceptions, mammary glands are functional only in females. Late in pregnancy, hormones such as prolactin stimulate the proliferation of alveoli, adipose tissue, and milk-producing cells. Milk is an aqueous mixture of protein, lipid, and carbohydrate that serves as nourishment

A Monotreme

B Human

C Ungulate

Alveoli

Cystern

Nipple

Teat

Hairs
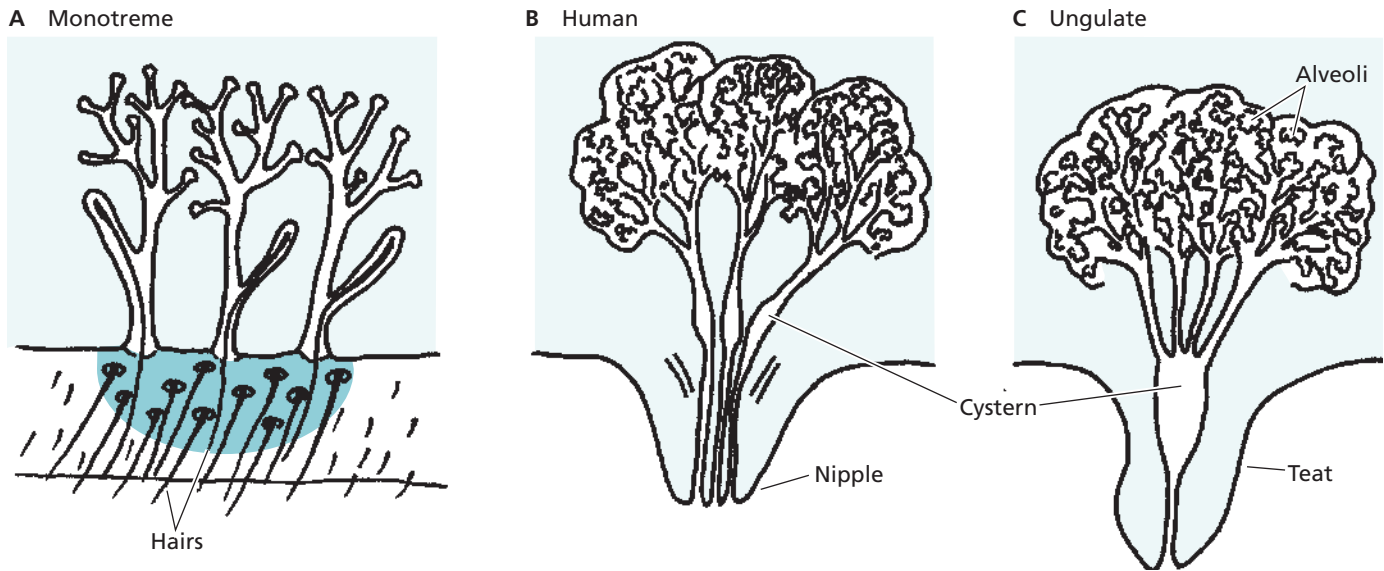
Figure 6.7 **Mammary glands.** Milk-producing cells surround the alveoli of mammary glands, which project into the hypodermal portion of the skin and may be surrounded by adipose tissue forming breasts. The arrangement of ducts varies among species. Monotremes lack nipples or teats. *Modified from Kent and Carr (2001).*

for young. The relative proportions of different nutrients in milk vary among species (Table 6.1). In general, young grow more quickly in species with higher proportions of protein in their milk (Bouliére 1964). Skibiel et al. (2013) performed an extensive phylogenetic comparative analysis of variation in milk composition among mammals and found a significant phylogenetic effect; after controlling for it, maternal diet and duration of milk production explained most of the variation in milk composition. The composition of milk also changes over the course of the suckling period (Abbondanza et al. 2013). When a female gives birth, mammary glands have produced a significant amount of milk that is stored in the alveoli. When suckling commences, nerve impulses travel from the nipple to the brain causing the hormone oxytocin to be released by the **hypothalamus**. Oxytocin stimulates contraction of muscle slips around the alveoli and forces milk into the ducts, a process known as "milk letdown." The flow of milk from mother to suckling is **lactation**.

The evolutionary origin of mammary glands is unclear. Although they are undoubtedly epidermal, their precise homology with sebaceous, eccrine, or apocrine glands is not obvious, nor is it absolutely certain that the mammary glands of monotremes are homologous with those of therians. Even more problematic is inferring the timing and initial adaptive value of lactation. Pond (1977) argued that suckling must have preceded the appearance of diphyodont dentition (see Chapter 4); the latter is a prerequisite for precise tooth occlusion and could not have evolved in neonates that used their teeth for chewing. If correct, this places the origin of lactation just prior to the emergence of diphyodont teeth with complex occlusal surfaces (probably during the evolutionary transition from cynodonts to true mammals; Pough et al. 2013). The origin of milk itself may relate to the early adaptive value of glandular secretions for eggs or hatchlings that were incubated by parents (Blackburn 1991). Modern milk contains proteins that are similar to lysozymes and act as antimicrobial agents (Vorbach et al. 2006). Such secretions may have protected the surface of eggs or young from infection in early mammals; if ingested by hatchlings, the same protection might have extended to the digestive tract. It is also possible that maternal antibodies could be transferred to young via an integumentary secretion, as they are in modern milk. Once ingestion of the secretion became established, evolution of the nutritional aspect of lactation and the associated anatomical features of mammary glands could proceed (Kardong 2012). Kawasaki and colleagues (2011) argued that the casein proteins characteristic of milk evolved by duplication and divergence of an ancestral gene expressed during the development of vertebrate teeth.

CLAWS, NAILS, AND HOOVES

Claws, nails, and hooves are keratinized structures that develop from the *stratum corneum* at the ends of digits (Hamrick 2002). **Claws** are the most primitive form, appearing early in amniote evolution and still common in nonavian reptiles, birds, and mammals. A claw consists of two parts: a heavily keratinized, convex, dorsal **unguis** and a softer, ventral **subunguis** that is continuous with the pad at the end of a digit (Figure 6.8A). Both layers are wrapped around the dorsolateral surface of the last phalanx (see Homberger et al. [2009] for a detailed anatomical description). Mammals use their claws for **climbing**, digging, fighting, and defending. In some groups, such as felids, the sharp claws are retractable, an arrangement that may be

Table 6.1 Milk composition*

	Water	Protein	Fat	Sugar	Ash
Marsupials					
Kangaroo (wallaroo)	3.5	9.7	8.1	3.1	1.5
Primates					
Rhesus monkey	88.4	2.2	2.7	6.4	0.2
Orangutan	88.5	1.4	3.5	6.0	0.2
Human	88.0	1.2	3.8	7.0	0.2
Xenarthrans					
Giant anteater	63.0	11.0	20.0	0.3	0.8
Lagomorphs					
Rabbit	71.3	12.3	13.1	1.9	2.3
Rodents					
Guinea pig	81.9	7.4	7.2	2.7	0.8
Rat	72.9	9.2	12.6	3.3	1.4
Carnivores					
Cat	81.6	10.1	6.3	4.4	0.7
Dog	76.3	9.3	9.5	3.0	1.2
European red fox	81.6	6.6	5.9	4.9	0.9
Pinnipeds					
California sea lion	47.3	13.5	35	0	0.6
Harp seal	43.8	11.9	42.8	0	0.9
Hooded seal	49.9	6.7	40.4	0	0.9
Cetaceans					
Bottle-nosed dolphin	44.9	10.6	34.9	0.9	0.5
Blue whale	47.2	12.8	38.1	?	1.4
Fin whale	54.1	13.1	30.6	?	1.4
Ungulates					
Indian elephant	0.7	3.6	17.6	5.6	0.6
Zebra	86.2	3.0	4.8	5.3	0.7
Black rhinoceros	?	1.5	0.3	6.5	0.3
Collared peccary	?	5.8	3.5	6.5	0.6
Hippopotamus	90.4	0.6	4.5	4.4	0.1
Camel	87.7	3.5	3.4	4.8	0.7
White-tailed deer	65.9	10.4	19.7	2.6	1.4
Reindeer	64.8	10.7	20.3	2.5	1.4
Giraffe	77.1	5.8	12.5	3.4	0.9
American bison	86.9	4.8	1.7	5.7	0.9
Cow	87.0	3.3	3.7	4.8	0.7

From Bourlière (1964). Reprinted by permission.

*The composition of milk in different mammal species varies in the pro-
portions of protein, fat, and sugar. Notice high fat content for pinnipeds,
cetaceans, and lagomorphs. In lagomorphs, the mother usually feeds her
young once per day.

Figure 6.8 Claws, nails, and hooves. Longitudinal
sections through the ends of digits. Unguis is solid black,
subunguis is white, and digital pad is blue. (**A**) Claws are the
most common cornified epidermal structure at the ends of
digits in mammals. The tough outer unguis wraps around the
surface and sides of the terminal phalanx; the softer subunguis is
continuous with the pad on the underside of the digit. (**B**) Nails
occur in primates. The unguis is flattened, the subunguis
reduced, and the digital pad highly innervated. (**C**) Hooves
occur in ungulates. A thick unguis surrounds the terminal
phalanx, and the subunguis overlies a thickened foot pad.

advantageous during peaceful interactions with conspecif-
ics and young (Figure 6.9). Felids are more adept at manip-
ulating objects with their forepaws than are canids, which
lack retractable claws. Russell and Bryant (2001) suggested
that reversion to less retractable claws in cheetahs (*Acinonyx
jubatus*) is associated with this species' unique hunting be-
havior, including a diminished use of the forepaws in
feeding. Claws, like nails and hooves, are ever-growing in
mammals and must be worn down by abrasion.

Nails cover only the dorsal surface of a phalanx, the un-
guis being broad and flat, and the subunguis reduced (Fig-
ure 6.8B). They are modified claws that evolved in primates
(Soligo and Muller 1999) to facilitate gripping and object
manipulation by the hands and feet. Along with the devel-
opment of nails, the number of sensory nerve endings in the
dermis at the ends of primate digits has greatly increased.

Hooves are characteristic of ungulates and also derived
from claws. They consist of a much-thickened, U- or V-
shaped unguis that completely surrounds the subunguis,
which in turn forms the sole of the foot (Figure 6.8C).
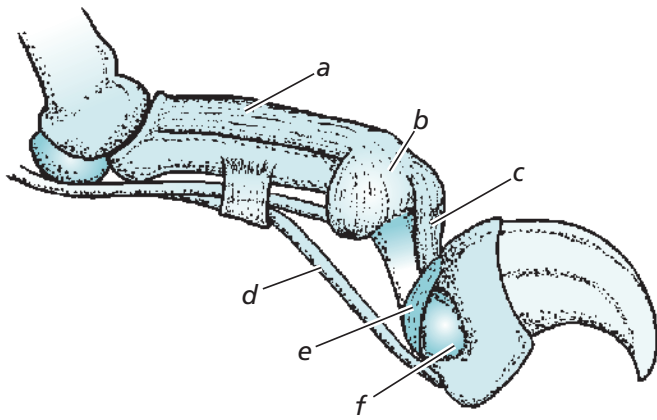
Figure 6.9 Retractable claw. The retractible claw mechanism of the mountain lion (*Puma concolor*) involves (**A**) an extensor muscle, (**B**) a middle interphalangeal joint, (**C**) a tendon of extensor muscle, (**D**) tendon of flexor muscle, (**E**) a lateral dorsal elastic ligament, and (**F**) a distal interphalangeal joint. *Adapted from Gonyea and Ashworth (1975).*

Hooves occur in conjunction with a reduction in the number of digits in ungulates, both features being adaptations for cursorial locomotion. A more primitive hoof structure appears in hyraxes (Hyracoidea).

HORNS AND ANTLERS

Among extant mammals, head ornamentation occurs only in cetartiodactyls and perissodactyls. "Horn" refers to a surface made of keratin. True **horns**, found only in bovids (cattle), have an inner core of dermal bone (derived from the frontal bone of the skull) covered by a keratinized sheath (derived from epidermis; see Figure 19.12E). Bovid horns usually grow continuously throughout the life of the animal, remain unbranched, are never shed, and occur in both sexes. They often function in intrasexual competition for mates, and their size may be correlated with individual health status (Ezenwa and Jolles 2008). Growth rings at the base of the horns may be used to determine the age of an individual. Barbosa et al. (2010) performed stable isotope analysis (see Chapter 2) on ibex horns to study the effects of changing atmospheric CO_2 levels on water-use efficiency in an alpine grassland. Pronghorn antelope (*Antilocapra americana*), endemic to the American West, are unique in having two-branched "horns," the keratinized sheath of which is shed and regrown each year (O'Gara and Matson 1975). Antilocaprids also display sexual dimorphism in horn size, with female horns being smaller and not forked, unlike those of males (see Figure 19.12D). The **hair horns** of rhinoceroses (Rhinocerotidae) are masses of agglutinated, keratinized epidermal cells that develop above the dorsal surface of the nasal bones in both sexes and are not shed (see Figure 19.12A).

Antlers are branched head ornaments made entirely of bone and found in cervids (deer; see Figure 19.12C). As they grow, antlers are covered by a layer of "velvet," highly vascularized skin that supplies the growing bone tissue with nutrients. When bone growth is complete, the blood supply to velvet is cut off and the dead skin is worn away. After the annual **rut**, or mating season, hormones induce a weakening of the bone just above the base of each antler, such that the distal portion of the antlers are shed. New antlers develop each year, and their growth is one of the fastest examples of organogenesis known among animals (Price et al. 2005). Antlers develop only in male cervids, except for caribou (*Rangifer tarandus*), in which they occur in both sexes. Giraffes and okapi (Giraffidae) have two bony projections (ossicones) that develop from separate ossification centers and then fuse to the skull near the suture of the frontal and parietal bones. They are permanently covered by skin and hair (see Figure 19.12B) and occur in both sexes. These structures are not homologous to bovid horns or cervid antlers.

Head ornaments can have a variety of functions, but they are often adapted for intraspecific competition among males (Kitchener 2000). This is especially evident in Rocky Mountain bighorns (*Ovis canadensis*), in that males compete during the rut by running toward each other and butting heads. Horns and antlers may be used defensively to ward off predators, as markers of social rank (Ciuti and Apollonio 2011), or as advertisements of male fertility (Malo et al. 2005). The size of antlers (like that of horns) seems to be an accurate indication of relative male quality in species subject to sexual selection (Ciuti and Apollonio 2011). The phylogenetic comparative analyses of Stankowich and Caro (2009) suggested that horns evolved as antipredator adaptations in large, conspicuous female bovids living in open habitats. Some of these functions are discussed more thoroughly in Part 4.

Basic Skeletal Patterns

A detailed description of the mammalian skeleton would require several volumes, because an understanding of skeletal anatomy has been central to mammalian systematics, paleontology, and biomechanics for many decades. Our goal here is to provide an overview of the skeleton, with an emphasis on the relationship between structure and function. More detailed information on the skeletal morphology of specific groups can be found in Part 3. The skeleton is the body's framework: it provides structural support against the force of gravity, a system of levers that function in locomotion, attachment points for the muscles that drive movement, and a protective casing for vital organs. Vertebrate skeletons consist of two subdivisions: the **axial skeleton** corresponds to the skull, vertebral column, ribs, and sternum; the **appendicular skeleton** comprises bones of the pectoral and pelvic girdles and their associated limbs.

SKULL

Comparative anatomists divide the skull into three portions, each with a distinct developmental origin: the neurocranium (or primary braincase), the dermatocranium (membrane bones that surround the neurocranium), and the splanchnocranium (jaws and other derivatives of the embryonic pharyngeal arches). The neurocranium consists of bones, few of which are visible on the surface of the skull, that ossify in the shape of a bowl to hold the brain. Many of the bones are perforated by openings (**foramina**) that allow passage of nerves and blood vessels (Figure 6.10). At the back of the skull, a ring of occipital bones (basioccipital, exoccipitals, supraoccipital) forms a **foramen magnum** through which the spinal cord passes and a pair of occipital condyles on either side that articulate with the vertebral column. Just anterior to these on both sides of the skull, a series of otic centers ossify around the inner ear and coalesce to form the petrosal bone of adults. Sphenoid bones form the anteromedial floor of the braincase (basisphenoid, presphenoids) and contribute to the wall of the orbit (orbitosphenoid). Ethmoid elements surround the nasal area, giving rise to scroll-like **turbinal bones** that support the olfactory and nasal epithelia, a perforated cribiform plate that fibers of the olfactory nerve pass through, and a mesethmoid bone forming the nasal septum.

Overlying the neurocranium, and in intimate association with it, are dermatocranial bones that form within the hypodermis of developing embryos. Paired roofing bones (nasals, frontals, parietals) occur on either side of the dorsal midline, forming a median **sagittal crest** that marks the dorsalmost origin of the temporalis jaw muscle. At the rear angle of the skull (the temporal region), a squamosal bone contributes to the jaw joint and the posterior portion of the

zygomatic arch. The arch, a point of origin for the masseter muscle, is completed anteriorly by a jugal bone. Lacrimal bones form in the anteromedial corners of each orbit. Remnants of embryonic cartilage in the upper jaw are invested by dermal bones to form paired, tooth-bearing premaxillae and maxillae; portions of the same embryonic cartilages ossify in the posterior walls of the orbits as alisphenoid bones. On the ventral portion of the cranium, bones of the primary palate (vomer, palatine, pterygoid) lie alongside neurocranial bones. The premaxillae, maxillae, and palatines develop wing-like processes that grow ventrally and medially to meet at the midline and form a complete secondary palate. The hollow tube between the primary and secondary palates is the nasal passageway for respiratory air from the external to internal nares.

The lower jaw, or **mandible**, consists of right and left tooth-bearing bones (dentaries) that meet anteriorly at the mandibular symphysis. Each dentary articulates with a squamosal bone of the cranium to form the characteristic dentary-squamosal jaw joint of mammals. The masseteric fossa, a depression on the lateral surface of the dentary, marks the insertion site of the masseter muscle; the temporalis muscle inserts dorsally on the coronoid process. The dentary bone develops by ensheathing the anterior portion of the embryonic lower-jaw cartilage. At its posterior end, however, remnants of this cartilage and that of the upper jaw ossify as small ossicles (malleus and incus, respectively) within the middle-ear cavity. These sound-transmitting ossicles are homologous to bones (articular and quadrate, respectively) that formed the jaw-joint of nonmammalian synapsids. A third ossicle, the stapes, is common to all tetrapods and is derived from the dorsalmost element of the second pharyngeal arch in fishes. A fourth lower-jaw bone of mammalian ancestors, the angular, is
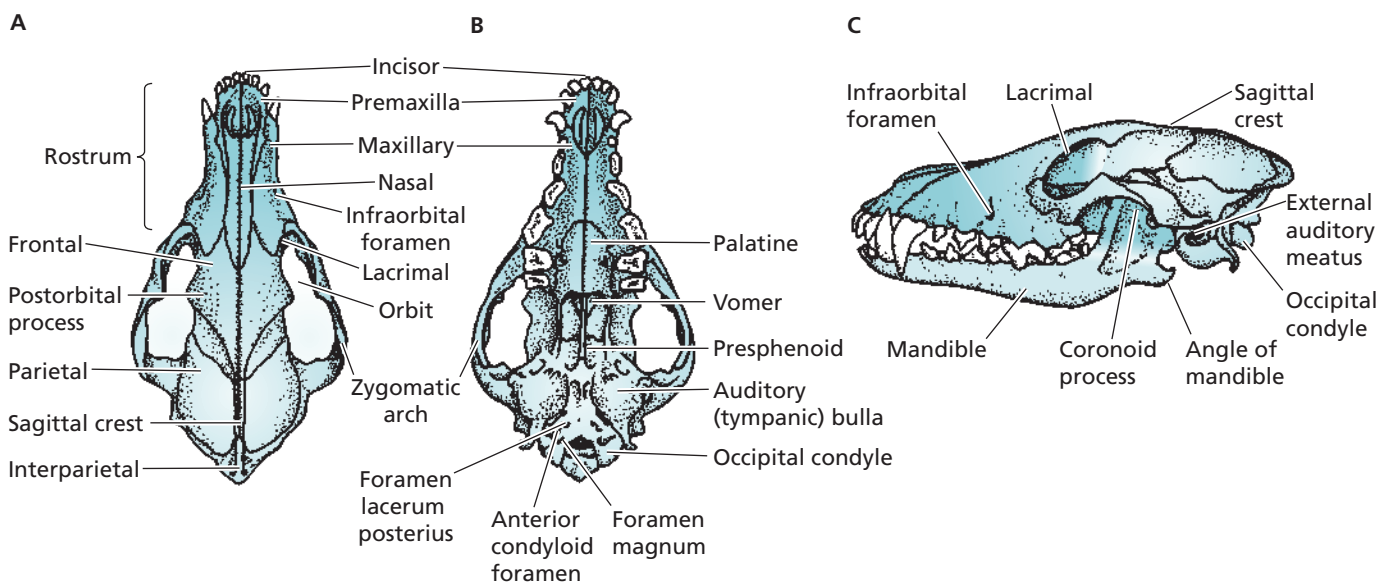
Figure 6.10 **Anatomy of the skull.** The skull of a coyote (*Canis latrans*). (**A**) Dorsal view of cranium; (**B**) ventral view of cranium; (**C**) lateral view of cranium and mandible. *Adapted from Gunderson and Beer (1975).*

homologous to the tympanic bone that frames the eardrum (**tympanum**) of mammals.

The **hyoid apparatus**, located in the throat region, consists of an H-shaped array of small bones that support the tongue and larynx (Figure 6.11). These are derived from the second through fifth pharyngeal arches of embryos, which are homologous to portions of the corresponding gill arches in fish.

VERTEBRAE, RIBS, AND STERNUM

The bodies of mammals that are permanently marine, like those of fish, can be supported by their buoyancy in water. For terrestrial mammals, the skeleton and muscles must support the body against the downward pull of gravity. The vertebral column ("backbone"), suspended above the ground by limbs, is the central element in this architecture (Figure 6.11). The column consists of a series of bony elements (**vertebrae**) separated from one another by cartilaginous intervertebral discs extending from the base of the skull to the tail. Within each disc is a pulpy nucleus, a gelatinous remnant of the embryonic notochord. The entire

column is sheathed in longitudinal bands of ligaments and axial muscles that determine its flexibility. Thomson (1942) likened the vertebral column to the deck and girders of a suspension bridge, with the limbs corresponding to the bridge's pillars. Indeed, many organs in the body cavity are attached to, or suspended from, the vertebral column.

An individual vertebra consists of a circular centrum on top of which are paired neural arches that form a canal for the spinal cord. Various articular surfaces (apophyses) occur at the margins of centra, marking sites where the vertebrae make contact with one another or (in the thoracic region) with ribs. Other vertebral processes mark the attachment points of axial muscles and ligaments. Various foramina occur within and between centra, the most significant being the intervertebral foramina through which spinal nerves emerge.

Tetrapod vertebral columns display regional specialization (i.e., vertebrae in different parts of the column have distinct morphologies and functions). In mammals there are five regions, each with a corresponding type of vertebra (Figure 6.11). All mammals except sloths and manatees have seven **cervical** vertebrae in the neck The first cervical vertebra, the **atlas**, articulates anteriorly with the oc-
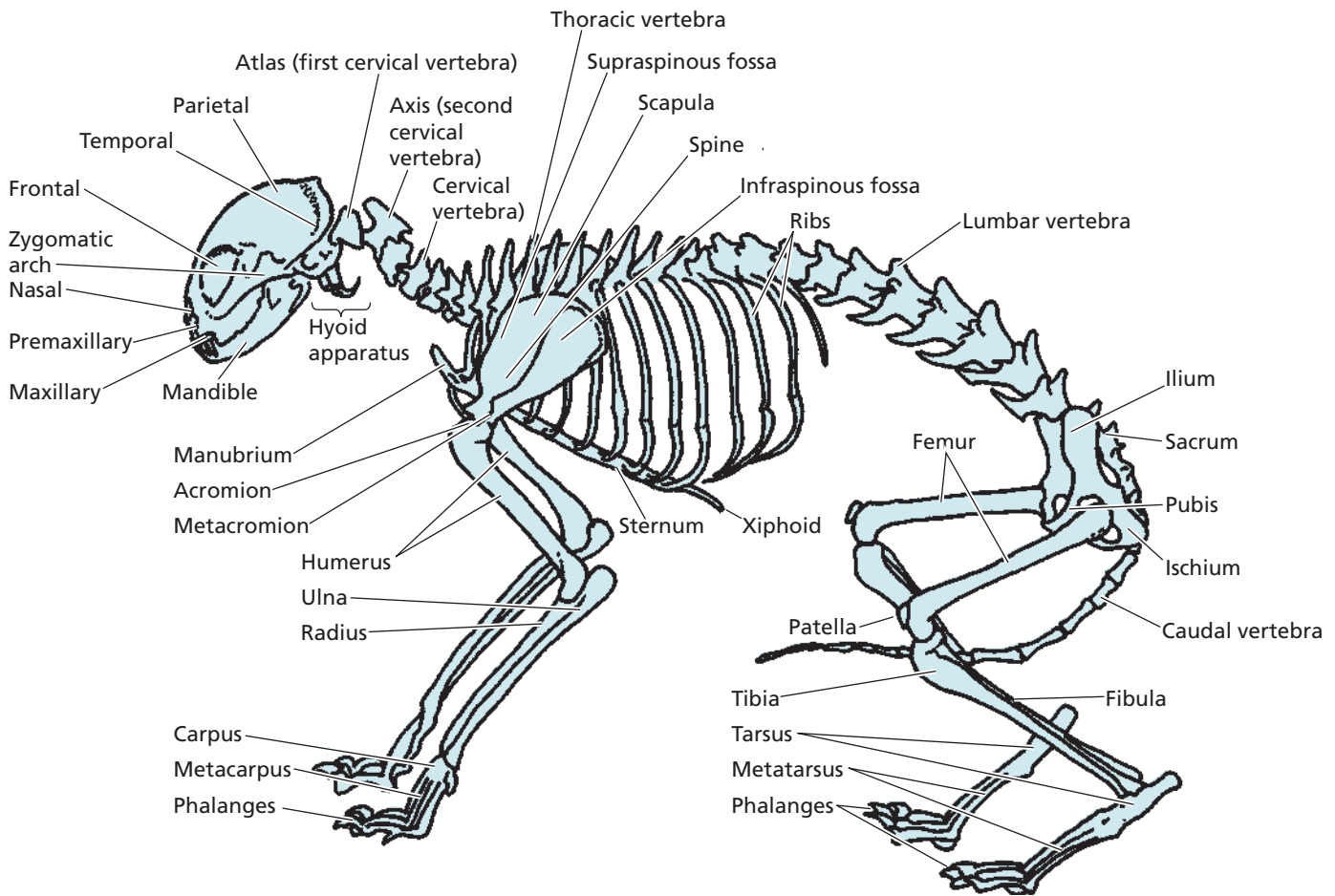
Figure 6.11 Cat skeleton. Lateral view of the skeleton of a domestic cat (*Felis catus*). Note the digitigrade foot posture and reduced **clavicle** (the small bone just anterior to the head of the humerus), which does not articulate with the rest of the skeleton. These are cursorial adaptations. *Adapted from Kistler et al. (1975).*

cipital condyles of the skull and posteriorly with the second cervical, or **axis**. The structure of this joint allows mammals to move their skulls both vertically and horizontally, independently of the body trunk, thereby improving their ability to position sensory receptors on the head for maximum sensitivity to external stimuli. Fish, amphibians, and most reptiles have much less flexibility. Posterior to the cervicals, 12–15 **thoracic** vertebrae occur in the chest region and articulate with ribs; the long, dorsocaudally oriented spinous process*s* of mammalian thoracics make these vertebrae readily identifiable. In the lower back region are 4–7 **lumbar** vertebrae, which may be partially or entirely fused to one another. In most mammals, the **sacral** vertebrae (usually 3–5, but as many as 13 in edentates) are fused to form a sacrum that articulates with the pelvic girdle. A variable number (3–50) of **caudal** vertebrae occur in the tail, usually diminishing in size and structural complexity toward the distal end. The 4–5 vestigial caudals of hominoid primates fuse to form a rigid coccyx ("tailbone") posterior to the sacrum.

The remainder of the axial skeleton consists of **ribs** attached to thoracic vertebrae at their dorsal ends and to a **sternum** via costal cartilages or a more anterior rib at their ventral ends. Most mammals have 12 pairs of ribs, but the number ranges from 9 (in whales) to 24 (in sloths). The posterior ribs usually fail to reach the sternum, terminating instead as "floating" ribs. Gorillas and chimpanzees have ribs on their first two lumbar vertebrae. The rib cage, or thoracic basket, surrounds and protects the heart and lungs. Ribs also provide attachment surfaces for muscles that expand or compress the thoracic cavity.

APPENDICULAR SKELETON

The **pectoral girdle** is the skeleton of the shoulder, forming a complex surface for muscle attachment and articulation of the forelimb. Primitively, the pectoral girdle consisted of an inner layer of replacement bones (precoracoid, coracoid, scapula) and an outer layer of dermal bones (clavicle, interclavicle). This arrangement occurred in therapsids and is still found in living monotremes. In therian mammals, however, the pectoral bones are typically reduced to just two—the clavicle ("collar bone") and the scapula ("shoulder blade"). In cursorial mammals (e.g., cats, ungulates) and cetaceans, the clavicle is reduced or lost, leaving the scapula as the only substantial bone of the girdle (Figure 6.11). Mammalian pectoral girdles do not make contact with the axial skeleton; they are suspended in a sling of appendicular muscles, which allows considerable flexibility in one or more planes of motion. In contrast, the **pelvic girdle** is firmly braced against the sacrum at a broad sacroiliac joint. The pelvis consists of three fused bones on each side—an anteroventral pubis, a posteroventral ischium, and a dorsally oriented ilium that articulates with the sacrum. These elements coalesce during development into a pair of innominate bones ("coxae") that meet ven-

trally at the ischiopubic symphysis and form a bony ring around the lower abdomen. The pelvic girdle is vestigial in cetaceans.

Forelimbs and hind limbs have a common architecture, consisting of a proximal propodium, an intermediate epipodium, and a distal autopodium. In the forelimb, the propodium consists of a single long bone, the humerus, which articulates proximally at the glenoid fossa of the scapula (Figure 6.11). Distally the humerus articulates with paired epipodial bones in the forearm, the medial radius and lateral ulna, forming the elbow joint. The ulna is sometimes reduced, as in bats. The proximal part of the autopodium consists primitively of three rows of small carpal (wrist) bones, but these are often reduced or fused in extant mammals. Beyond the wrist, there are primitively five metacarpals forming the palm, followed by two or more phalanges comprising each digit. Metacarpals and phalanges may be reduced or lost in some cursorial species that have fewer than five digits. In the hind limb, the propodial bone is the femur, articulating proximally at the acetabulum of the pelvis to form the ball-and-socket hip joint. Distally, the femur meets paired epipodial bones (the tibia and fibula) to form the knee joint. Tarsal bones form the ankle joint and were primitively arranged much like the carpals. In modern terrestrial mammals, the number of tarsals is usually reduced, but one of the proximal bones is expanded posteriorly to form a heel, the insertion site of the powerful shank muscles (via Achilles's tendon). Metatarsals (one per digit) form the sole, articulating distally with one or more phalanges in the digits. Hind limbs are absent in cetaceans and sirenians.

Muscles

As with the skeleton, our presentation of the basic musculature of mammals is much briefer than what might be justified by the enormous body of information available (Kardong 2012). Muscles may be classified in several ways, but we are here concerned with **somatic muscles**, those that orient the body in the external environment. Somatic muscles are **striated** (i.e., histological preparations show the presence of sarcomeres), skeletal (i.e., attached to bones by tendons), and voluntary (i.e., can be contracted at will). As such, they provide the force to move the skeleton's levers, resulting in general body movements and locomotion. Nonsomatic (i.e., visceral) muscles are smooth or cardiac types, nonskeletal, and involuntary.

The distribution of somatic muscles in mammals follows the architecture of the skeleton (Figure 6.12). Axial muscles are those having their origins and insertions on the axial skeleton, or on connective tissues associated with it. Dorsally, these muscles are disposed as longitudinal bands lying above the transverse processes and alongside the neural spines of vertebrae. In general, they serve to extend
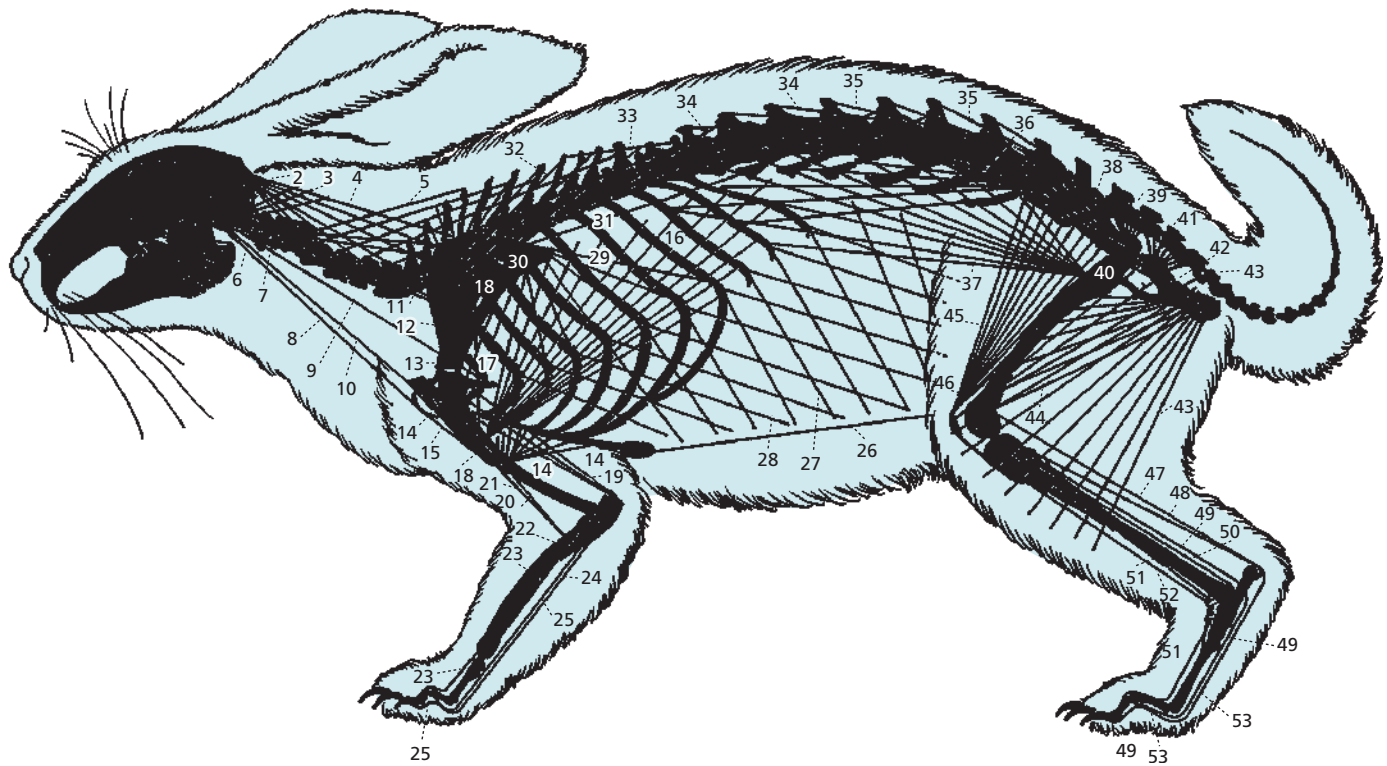
Figure 6.12 Muscle groups. Schematic representation of muscle groups in the European rabbit (*Oryctolagus cuniculus*). Axial muscles are indicated by numbered lines with both ends terminating on bones of the axial skeleton (skull, vertebral column, sternum); appendicular muscles indicated by lines with one or both ends terminating on bones of the appendicular skeleton (pectoral and pelvic girdles and limbs). Notice the groups of muscles that operate the limbs are positioned to work in opposition to one another.

(straighten) the spine. Ventrally, axial muscles below the transverse processes of vertebrae flex (arch) the spine; others form the multilayered body wall. Anteriorly, the diaphragm and thoracic muscles power ventilation of the lungs. Appendicular muscles are those that insert on the girdles or limbs; their contraction drives limb movements and locomotion. In most mammals, the appendicular musculature is extremely well developed and results in the unparalleled locomotor diversity of mammals compared to other vertebrates.

Modes of Locomotion

Many mammals use walking as their primary means of locomotion, and this appears to be the primitive pattern. Others are specialized for running. Kangaroos, some rodents, rabbits, and hares employ hopping, jumping, or leaping to get around. Climbing is a primary activity of arboreal species, such as many primates and sloths, and a secondary locomotor pattern for many other species that are mainly terrestrial. Some species are specialized for burrowing, including moles and many subterranean rodents. Dermopterans, some rodents, and some marsupials have

the ability to glide, and one group (bats) has evolved powered flight. Other mammals spend all or most of their time in water, and for them swimming is the dominant form of locomotion. This group includes marine mammals (cetaceans, sirenians, and pinnipeds) as well as freshwater species such as beavers and muskrats. We will examine each of these in turn. Note, however, that most mammals use more than one means of movement.

WALKING AND RUNNING

Most mammals are quadrupedal, though a few (including humans) have evolved some form of bipedal locomotion. Species that move predominantly by walking are called **ambulatory**, and those with adaptations for running are **cursorial**. The primitive, walking gait is associated with a **plantigrade** foot posture in which all or most of the palms and soles are in contact with the substrate. This means that the metatarsals and phalanges of the hind foot and the metacarpals and phalanges of the front foot are oriented parallel to the ground, as in humans. Cursorial mammals have one of two foot postures. **Digitigrade** species (e.g., cats, dogs) have elevated the metacarpals and metatarsals to an acute angle, leaving only the phalanges in contact with the substrate (see Figure 6.11). Most digitigrade spe-

cies have reduced one of their digits, leaving only four functional toes for locomotion. **Unguligrade** mammals (e.g., ungulates) have elevated the phalanges, as well as the metacarpals and metatarsals, such that only the tips of the phalanges are in contact with the ground (see Figure 19.26). Along with their foot posture, ungulates have further reduced the number of digits to three (e.g., tapirs), two (e.g., artiodactyls), or one (e.g., horses) (see Figure 19.1); they have also developed hooves and increased the length of the functional metacarpals, metatarsals, and phalanges.

Hildebrand (1985b) identified four functional requirements for animals that walk or run: (1) support and stability even though the feet make only intermittent contact with the substrate; (2) propulsion to move the body forward; (3) maneuverability; and (4) endurance (see also Hildebrand et al. [2001] and Liem et al. [2001]). The first challenge is partly postural. Large, heavy species such as elephants and hippopotamuses are **graviportal**: their legs are directly under the body, their propodial and epipodial bones are columnar, and their ankle and knee joints are nearly vertical. This arrangement allows the skeleton to bear most of the large body weight, taking the burden off postural muscles that would otherwise require large amounts of energy. Lighter mammals such as deer have their limbs positioned slightly outside the trunk axis and rely more on muscles for postural support and stability during locomotion.

Different approaches to propulsion result in distinct **gaits** (the oscillation patterns of the limbs during forward movement) for walking and running mammals. In ambulatory species, each foot is on the ground for at least half the duration of a single stride cycle; in cursorial species each foot is on the ground less than half the time. Walking, pacing, and trotting all involve equal spacing of the feet making contact with the substrate, with the footfalls evenly spaced in time (Hildebrand et al. 2001). These are symmetrical gaits (Figure 6.13). Walking is the most stable gait because of the prolonged contact of the feet with the ground (Figure 6.13D). This pattern reduces the possibility of the front and hind limbs interfering with one another. Pacing, often seen in long-legged carnivorans and camelids, involves the simultaneous movement of both legs on
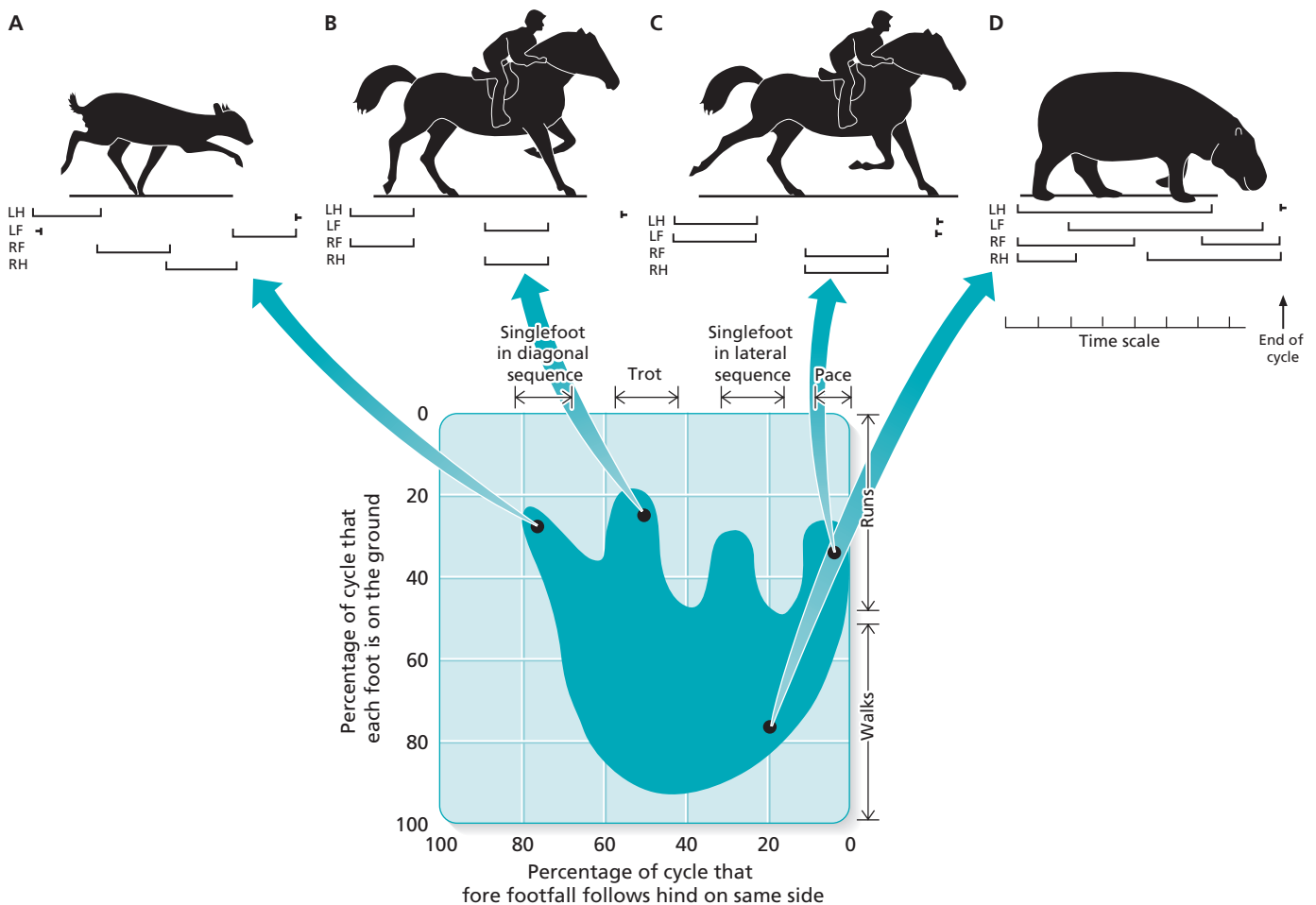
Figure 6.13 Symmetrical gaits for walking and running. The graph shows the percentage of time during a single stride cycle that each foot is in contact with the substrate (vertical axis) versus the percentage of the cycle during which the feet on the same side of the animal touch the ground consecutively. (**A**) Fast running in a small antelope; (**B**) fast running trot in a horse; (**C**) moderate running pace in a horse; (**D**) moderate walking in a hippopotamus. *Adapted from Hildebrand et al. (1985).*

the same side of the body (Figure 6.13C). Trotting involves synchronously moving the two legs that are diagonally opposite one another (Figure 6.13B) and provides somewhat more stability than pacing. Fast trotting (Figure 6.13A) is how many short-legged cursorial species run. Gaits such as galloping and bounding, in which the footfalls are unevenly spaced in time, are asymmetrical. At moderate to high velocities, these gaits entail having all four feet off the ground simultaneously for a portion of the stride cycle.

Models of animal movement (Hildebrand et al. 2001; Liem et al. 2001) are based on the idea that the legs swing below the body like a pendulum. Jointed limbs and their associated muscles, tendons, and ligaments work like levers. Several predictions from such models are supported by the comparative anatomy of mammals. Faster species have relatively longer limbs than slower species. Cursorial mammals tend to have limb joints that restrict movement to a single plane, forward and backward, parallel to the body. The insertion points of many muscles used for running have shifted so that they are nearer to, and in the same plane as, the lever joint they operate. Reducing weight in the distal portion of the limbs also increases running speed. This is accomplished by bone reduction and fusion in the lower legs (e.g. the cannon bone of horses) and by moving the appendicular muscles nearer to the body's center of mass, with long tendons stretching to the distal limb joints. Tendons and ligaments that cross joints can function like springs when the joints are flexed, storing energy that is released during subsequent extension (Alexander and Bennet-Clark 1977). Ungulates, for example, have a long "springing" ligament connecting their metacarpals or metatarsals with more distal phalanges.

Maneuverability, the capacity to change direction during locomotion, is required by both predators and prey. Most cursorial mammals can alter their gait momentarily, such that both legs on the same side (or both hind legs) strike the ground simultaneously, resulting in an angular shift in the direction of movement. Some mammals can turn their bodies (spinal flexion) while in the air, thereby altering their direction. Just as when we round a curve on a bicycle, mammals lean their weight in the direction of a turn to maintain balance and control. Running mammals that are large and heavy tend to be less maneuverable and agile than smaller, lighter ones.

Endurance results from integration of an animal's musculoskeletal and physiological adaptations. The musculoskeletal traits described here contribute to efficient motion of the limbs. Moreover, the appendicular muscles of cursorial mammals tend to be rich in "fast-twitch" fibers capable of rapid, powerful contractions (Goldspink 1981; Kardong 2012). The study of joint mechanics, models of ambulatory and cursorial movement, and research in bioenergetics have become quite sophisticated in recent years and incorporated principles from mechanical engineering and physics (Bejan and Marden 2006). Bertram (2016) provides a comprehensive treatment of the biomechanics of locomotion in terrestrial mammals.

Consider again the example of the cheetah and gazelle from the beginning of this chapter. Both the predator and the prey are cursorial species, with digitigrade and unguligrade foot postures, respectively. The faster speed of the cheetah might predict that the predator will invariably win the race, but the distance and length of time over which each species can maintain its top speed (i.e., its endurance) must also be considered. Cheetahs can move swiftly for relatively short distances, a few hundred meters at most, whereas the endurance of the gazelle is considerably greater. Thus, the cheetah needs to be close enough when it begins its dash so that it can overtake the gazelle quickly; if it fails, it will soon be outdistanced by its prey. Maneuverability is also an important factor; the greater the speed, the less the maneuverability.

JUMPING AND RICOCHETING

Jumping and ricocheting are forms of **saltatorial** locomotion. Jumping involves the use of all four feet, as in the case of rabbits. Ricocheting (or "bipedal hopping") involves propulsion with only the hind limbs, such as in kangaroos, kangaroo rats, and jumping mice (Figure 6.14). Mammals that employ ricochetal locomotion spend much of their time in a bipedal position, using the forepaws only occasionally for slow, short-distance movements. The forelimbs of such animals are shorter than the hind limbs and are often employed for manipulating objects such as food. Most mammals (indeed, most vertebrates) that use saltatorial locomotion are relatively small, with kangaroos (up to 90-kg body mass) being exceptions.

Because saltatorial movement has evolved in several different groups, the anatomical similarities shared by jumping or ricocheting species are the result of convergent evolution (Emerson 1985). The principal adaptation is lengthening

Figure 6.14 **Ricochetal locomotion.** Kangaroos, such as the red kangaroo (*Macropus rufus*) shown here, move by ricochetal (bipedal) hopping. Notice the robust hind legs and feet that are used to propel the animal forward with each bound.

one or more segments of the hind limbs, usually the tibia, and development of long, elastic tendons that stretch across the knee and ankle joints. Especially in large hoppers, energy stored in these tendons as the limbs recover from one jump (i.e., during landing) is released during the next propulsive leap forward. Small bouncing species store relatively less energy in tendons, but reduce the cost of propulsion by using a lower collision angle (e.g., a more nearly vertical hop) (Gutman et al. 2013). Other adaptations for saltatorial locomotion include: (1) a posterior shift in the center of body mass to avoid tumbling forward or backward when thrusting with the hind limbs; (2) an enlargement of muscles in the hip region, with lengthy tendons; (3) changes in the size and arrangement of bones in the pelvic girdle to accompany shifts in musculature and the center of body mass; (4) larger hind feet for takeoff and landing; and (5) a longer tail for balance.

Arboreal clinging and leaping become ricochetal locomotion in some lemurs (Figure 6.15), tarsiers, and the white-faced saki (*Pithecia pithecia*). These animals often cling to a tree trunk with all four limbs, drop down to the ground, land on their hind feet, then bound back up into another tree. Primates that leap and ricochet have longer femurs than do other primates, allowing them to make longer leaps by increasing the lever action of their hip muscles (Connour et al. 2000). Tarsiers, which leap great distances from branch to branch, also have elongated shank and tarsal bones such that their thighs, lower legs, and feet are of roughly equal length (Macdonald 1984).

CLIMBING

Climbing mammals use their limbs to move about in trees—that is, they employ **arboreal** locomotion and display a suite of corresponding adaptations (Cartmill 1985). In species that also spend a substantial portion of their time on the ground, climbing is accomplished primarily by use of claws. Small arboreal mammals, such as squirrels, gain a holdfast in tree bark with their sharp claws and are able to maneuver on trunks and branches with considerable agility. Larger species, such as bears (Figure 6.16), use their claws in a similar manner but are much less agile. These species possess footpads to provide friction that aids in gripping tree limbs securely, as well as increased numbers of sensory receptors on their palms, soles, and ventral surfaces of digits. Sloths employ their claws to hang underneath tree branches for extended periods. Arboreality in mammals with a plantigrade foot posture is facilitated by the flexible joint between metacarpals or metatarsals and phalanges, thus allowing the hands and feet to be used for grasping. Primate digits are even more flexible—mobile joints between phalanges in the hand allow them to wrap their fingers around branches or other objects. Such hands, and occasionally feet, are said to be **prehensile**. Old World monkeys and apes have evolved an opposable thumb that can be rotated toward the tips of the other digits. Their thumb has a saddle joint at the base of the proximal phalanx, is oriented at nearly a right angle to
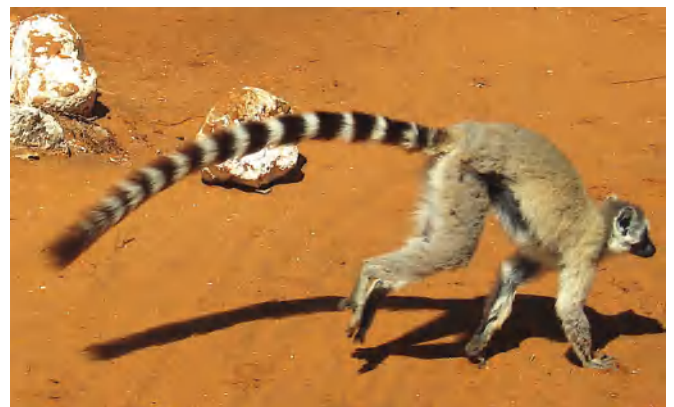
Figure 6.15 Saltatorial locomotion. Lemurs such as the ring-tailed lemur (*Lemur catta*) use a specialized form of saltatorial locomotion involving ricochetal movement from one tree (**A**) to the ground (**B**), and then back to another tree.
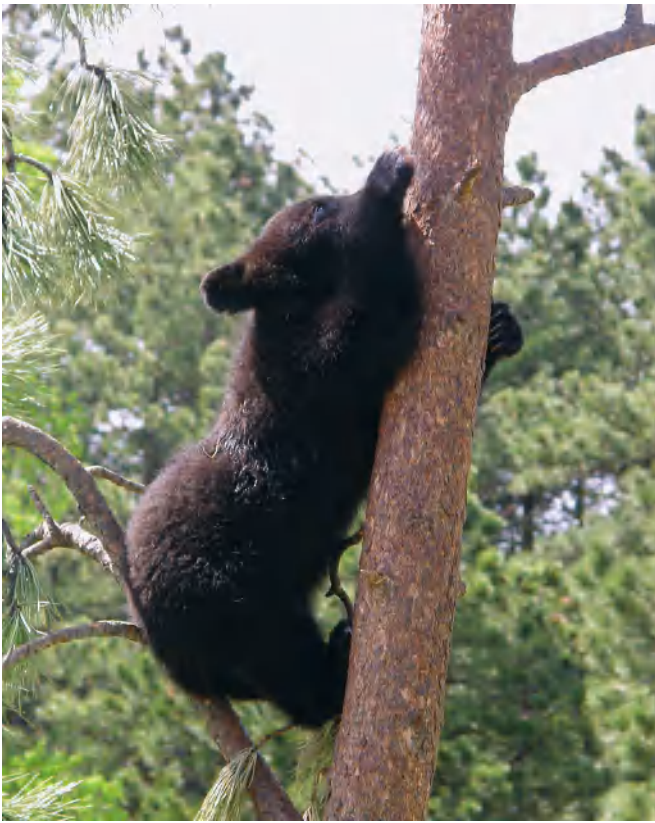
Figure 6.16 Tree climbing. When a black bear (*Ursus americanus*) climbs a tree, it grasps the trunk with its forepaws and hind feet, aided by lateral pressure from the arms and legs and by claws on the ends of its digits.

the first finger, and is attached to a powerful muscle (the *adductor pollicis*). Partial opposability is found in the thumbs and great toes of many primates. **Brachiation**, swinging from branch to branch using the forelimbs, is best developed in gibbons (Hylobatidae) but is also found in other primates. Brachiators have large clavicles anchored to the sternum, relatively long forelimbs, grasping hands, and opposable great toes. Their stout pectoral girdle stabilizes the shoulder joint, allowing the forelimb to bear the weight of the animal (Kardong 2012). Humans have this kind of pectoral girdle, a reflection of our arboreal ancestry.

Many arboreal mammals have long tails, which they use for balance (e.g., harvest mice of the genus *Reithrodontomys*). Some lemurs and Old World monkeys use their tails as a brace against tree trunks during climbing. In a few species of South American monkeys, the tail has become a prehensile appendage used to grasp branches. The distal portion of the tail in these species has developed friction pads and an increased number of tactile receptors similar to the gripping hands and feet of other climbing mammals.

DIGGING AND BURROWING

Mammals that dig in the soil to find food or create shelter are called **fossorial**. It is useful to distinguish the terms "fossorial" and **subterranean**: the former refers to animals with adaptations for digging, whereas the latter refers to species that live virtually their entire lives underground (Lacey et al. 2000). Among mammals, there are more fossorial than subterranean species. The limbs of digging species are short and powered by strong appendicular muscles. Digging is usually accomplished by scratching at the soil with forepaws to excavate a hole or tunnel large enough to accommodate the animal's body. A series of rapid alternate strokes of the forelimbs loosens soil in front of the digger, pushing excavated material posteriorly under the belly, after which the hind limbs kick it further back or compact it. Marsupial moles (Notoryctemorphia) and golden moles (Chrysochloridae) use fore and hind limbs to dig through sand but do not leave a permanent burrow. Golden moles use their heads and chests to open a gap in the sand that is then excavated with the forelimbs (Kardong 2012). Bateman (1959) described a golden mole (*Amblysomus hottentotus*) weighing less than 60 g that moved a 9 kg iron plate with its head in order to escape from a fishbowl filled with soil. In true moles (Talpidae), the short humerus is highly sculpted as a means of increasing surface area for muscle attachment, the distal bones of the forelimb are enlarged, and the wrist joint is rotated outward such that abduction and extension of the limb result in a lateral digging stroke; recovery is accomplished by rotating the limb downward (see Figure 17.8). Some tunnel-diggers will periodically clear the passage behind them by turning around and pushing the excavated soil back out to the surface.

Many fossorial rodents also use their teeth as digging tools, including spalacids (e.g., root rats, bamboo rats, blind mole-rats), geomyids (pocket gophers), and bathyergids (African mole-rats). These animals have large incisors external to the lips, allowing them to dig with their teeth while their mouths remain closed. Their skulls have a broad rostrum and stout zygomatic arches for attachment of powerful masseter (jaw-closing) muscles, as well as well-developed neck musculature for moving the head (Macdonald 1984).

Subterranean species show additional morphological specializations (Figure 6.17). Their eyes are small and probably sightless, as in bathyergids and talpids, or vestigial, as in marsupial moles and blind mole-rats. Tactile receptors in the snout are well developed, and vibrissae may occur on the tail, body wall, or legs. Senses of hearing and smell are usually well developed, with most species lacking external pinnae and some possessing **valvular** nostrils that can be closed during digging.

Many other mammals—including monotremes (platypus and echidnas), marsupials (e.g., wombats), and numerous placental species—excavate soil for nesting, food storage, hibernation, refuge from predators, or other functions (Reichman and Smith 1990). Burrows may be used continuously over months or years, or they may be used briefly and abandoned. Some species construct different kinds of burrows for different purposes. For example, hamsters (Cricetidae) make separate chambers for sleeping, food storage, and defecation. Woodchucks (*Marmota*) usually

Figure 6.17 Burrowing. Moles, such as this eastern mole (*Scalopus aquaticus*), live their entire lives underground. A key adaptation for this subterranean existence is the modification of the hands and feet for digging. Moles build extensive tunnel systems just below the surface, primarily as a means of finding food.

have a summer burrow in an open area and a winter burrow in more forested habitat.

GLIDING AND FLYING

Gliding has evolved independently in several groups of mammals—gliding possums (Petauridae, Pseudocheiridae, Acrobatidae), colugos (Dermoptera), and members of Rodentia such as "flying" squirrels. In each of these groups, gliding species are arboreal and use their gliding ability as a means of moving among tree branches. The principal morphological adaptation is a **patagium**, an extension of skin that stretches from the lateral neck and body wall to the wrists and ankles, as well as to the tips of the fingers, toes, and tail in colugos (see Figure 14.2). The animal leaps from a perch extending its limbs and tail such that the patagium acts as an airfoil. Aerodynamic control during gliding and landing is accomplished by adjusting the position of the limbs (Byrnes and Spence 2011; Jackson and Schouten 2012). The patagium may be used for protection or insulation when wrapped around the body like a cloak; colugos also use it as a pouch in which to hold neonates.

Among mammals, only bats (Chiroptera) have evolved true powered flight, or **volant** locomotion. With the exception of swimming, flying is the most energetically efficient means of moving a body of a given mass between two points (Norberg 1990). A bat's wing is also a patagium, but its skeletal support—principally the autopodial bones—is more highly modified than in gliding mammals (Figure 6.18; also see Figure 21.3). The broad and slightly keeled sternum serves as the point of origin for flight muscles. The shoulder includes a stout clavicle and a locking mechanism to keep the joint at an appropriate angle (locking devices may also occur in the elbow, wrist, and digits).

The radius is thin and elongated, but the ulna is reduced distal to the elbow, which prevents rotational movement of the forearm. At the wrist, central and distal carpals are lost, and the three proximal carpals fuse to form a single bone. The first digit is unmodified and bears a claw, but digits 2–5 have greatly elongated metacarpals followed by two or three phalanges that are oval in cross section (Hildebrand et al. 2001). The radius and bones of digit 2 support the leading edge of the wing, while digits 3–5 form struts extending to the trailing edge. Digit 1 (the thumb) may function in the awkward terrestrial-arboreal locomotion of bats or aerodynamically as a leading-edge flap for the wing. The patagium stretches from the body wall anterior to the forelimb to the short hind limbs and a portion of the tail. Bats, like birds, have a stiff, compact body trunk (including several fused vertebrae and proximally fused ribs in some species) for aerodynamic efficiency. We discuss the aerodynamics of bat flight in Chapter 21.

How did flight evolve in bats? Current authors agree that the common ancestor of all bats was a small, quadrupedal animal with generalized forelimb anatomy (Speakman 2001). Unfortunately, the bat fossil record shows no transitional forms—the oldest fossils (e.g., *Icaronycteris* from the Eocene) have wing-like forelimbs very similar to those of modern species. Sears and colleagues (2006) confirmed that the relative lengths of bones in digits 3–5 are the same in living and fossil bats. They also showed that embryonic digits in the hands of modern bats are initially similar to those of mice, but subsequently become elongated
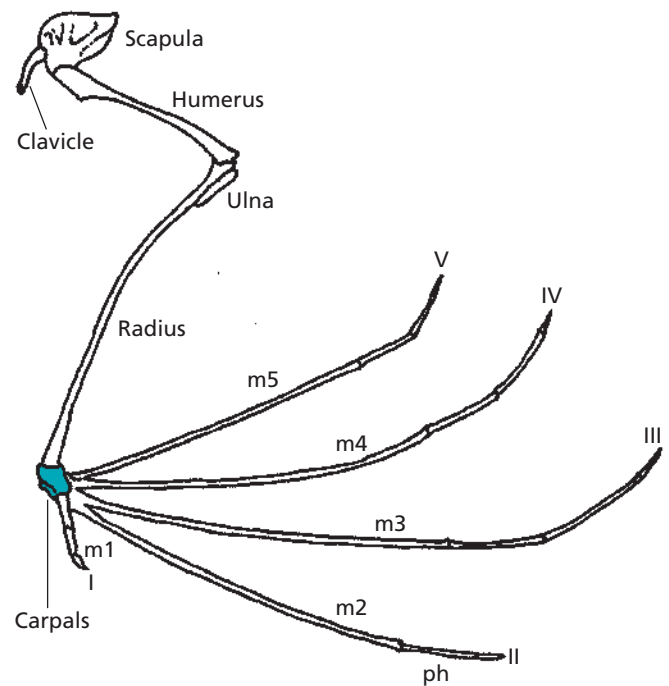
Figure 6.18 Bat wing skeleton. The pectoral girdle and right wing of a bat. Note the elongated radius and metacarpals (m2–m5) on digits II–V, the reduced ulna, and the fusion of carpals into a single wrist bone. *Redrawn from Kent and Carr (2001).*

due to locally increased expression of a bone morphogenetic protein gene. Causal hypotheses for the evolution of flight in bats have linked this trait to echolocation, a mechanism used by many bats for navigation (see Chapter 21). Giannini (2012; see also Teeling et al. [2012]) reviewed three scenarios. (1) Echolocation may have evolved before flight ("echolocation first") as an adaptation for navigation and/or foraging. The observation that some shrews also use sonar is consistent with this model; Carter and Adams (2016) suggest that nascent echolocation abilities in ancestral ("shrew-like") bats were elaborated during the subsequent evolution of flight. (2) Flight may have evolved before echolocation ("flight first"), as the end point of a trend that began with arboreal leaping and gliding. This scenario is supported by the anatomy of *Onychonycteris finneyi*, an Eocene fossil that may represent the sister group of all other bats; it shows evidence of powered flight but not echolocation (Simmons et al. 2008). (3) Echolocation and flight may have evolved together ("tandem evolution"). Ancestral bats may have leaped and glided while relying on enhanced visual perception, thereby establishing a selection pressure favoring both echolocation and powered flight. If echolocation and flight each originated only once among bats (Springer et al. 2001b), this scenario is plausible. However, much of the debate turns on explaining the absence of echolocation in pteropodids (fruit bats). Details of bat development and biomechanical modeling suggested to Adams and Shaw (2013) that flying bats evolved from strictly terrestrial ancestors without passing through arboreal or gliding stages.

SWIMMING

All mammals that spend a significant portion of their time in water evolved from terrestrial ancestors. Because water is generally cooler than average body temperatures and more thermally conductive than air, aquatic and marine mammals must conserve heat when they are in water. Most species have thick coats of fur or body fat that serve as insulation and provide buoyancy. **Amphibious** (semiaquatic) species occur in many groups (monotremes, marsupials, tenrecs, rodents, soricomorphs, carnivorans, and cetartiodactyls); most of these animals are equally at home in water or on land (Figure 6.19). Webbing between the toes in many species increases the surface area in contact with the water for propulsion, especially significant in that semiaquatic mammals swim by alternating strokes of the limbs (paraxial swimming), much as they walk on land (Webb and Blake 1985). Water shrews (*Sorex palustris*) have stiff hairs between the toes (**fimbriation**) that serve the same function as webbing. Muskrat tails are laterally flattened, and those of beavers are dorsoventrally flattened; both can be used for propulsion or like a rudder for directional control. Within the rodent Family Castoridae, fossil evidence suggests that

Figure 6.19 Swimming. Muskrats (*Ondatra zibethicus*) are amphibious mammals, spending a portion of their time in the water. They have a tail that is laterally flattened, which can be used as a propeller and a rudder (e.g., when the animal swims with its limbs).

swimming evolved only once in the Early Miocene lineage; this led to modern beavers (Rybczynski 2007).

Pinnipeds (seals, sea lions, walruses; see Chapter 18) are fully **aquatic mammals** that move onto land only to breed and give birth. The autopodia of pinnipeds have evolved into flippers, with all five digits encased in a single sheath of integument; tails are absent or rudimentary. In the water, wriggling (earless, or true) seals (Phocidae) generate propulsion with their hind limbs, which are caudally directed. This orientation is permanent, the tibial portion of both hind limbs being enclosed with the proximal tail in a common neck of integument. Phocids swim by lateral undulations of the posterior trunk and hind limbs, facilitated by flexion at the knee and ankle joints that produces a sculling motion. On land, however, the hind limbs are of no use and phocids are forced to pull themselves along the substrate with their front flippers and wriggle with their trunk. Walruses (Odobenidae) also swim by sculling, though much more weakly than phocids. Eared (or fur) seals and sea lions (Otariidae) employ a modified form of paraxial swimming, generating thrust by moving their forelimbs in synchrony while their back and caudally directed hind limbs undulate dorsoventrally. Unlike phocids, otariids are able to rotate their rear flippers forward when they are on land, allowing for an awkward but distinctly quadrupedal gait. This ability is especially well developed in pups and gives them much more agility on land than is possible for adults.

Anatomical specializations for a fully aquatic life reach their pinnacle among marine mammals—those that never come onto land. There are two such groups, Cetacea

(whales) and Sirenia (manatees and the dugong). The axial skeleton of these animals is simplified, with the cervical vertebrae partially fused and interlocking facets lost between trunk and tail vertebrae. Hind limbs and sacrum are absent, and the pelvic girdle is vestigial. The tails are modified into horizontal flukes that provide propulsion by dorsoventral undulation. Forelimbs are modified into flippers and frequently show an increase in the number of phalanges; they are used as stabilizers and have no role in propulsion. In cetaceans, the body trunk is fusiform, a friction-reducing adaptation for fast swimming. The buoyancy provided by water has removed some of the restrictions on body size that would accompany a terrestrial tetrapod, allowing some whales to reach gigantic body sizes. Other noteworthy adaptations of marine mammals are discussed in Chapters 18 and 20.

SUMMARY

- Study of the integument and musculoskeletal system tells us a great deal about the integration of form and function in the evolution of mammalian body forms. This is especially evident in the context of locomotion, where mammals are unparalleled among vertebrates in their morphological and functional diversity.

- The integument consists of an outer epidermis and an inner dermis. The epidermis contains a basal layer of dividing cells that become impregnated with keratin as they move superficially, ultimately forming a layer of dead tissue on the surface of the body, which prevents desiccation and damage to the underlying skin.

- Epidermal derivatives include many uniquely mammalian characteristics such as hair, sebaceous glands, **sweat glands**, mammary glands, nails, hooves, horns, and antlers.

- The dermis contains integumentary muscles that insert on hairs, general somatic receptors and associated sensory nerves, blood vessels, and connective tissue. Beneath the dermis, a layer of subcutaneous fat serves as insulation and an energy reservoir.

- The mammalian skeleton has axial and appendicular divisions.

- The skull, the anteriormost portion of the axial skeleton, consists of a cranium and mandible.

- The cranium includes bones of two different embryonic origins: the neurocranium (occipital, otic, sphenoid, and ethmoid bones) forms the primary braincase; the dermatocranium consists of roofing, upper jaw, temporal, and secondary palate bones.

- The mandible is formed by dentary bones that articulate with the squamosal bone of the cranium to form the characteristic mammalian jaw joint.

- The remainder of the axial skeleton consists of the hyoid apparatus, vertebral column, ribs, and sternum.

- Bones of the pectoral and pelvic girdles, along with their associated limbs, constitute the appendicular skeleton. Fore- and hind limbs have a common structural design, with a proximal propodium, intermediate epipodium, and distal autopodium.

- Like the skeleton, mammalian musculature has axial and appendicular divisions.

- Axial muscles are disposed as parallel bands along the vertebral column that flex or extend the spine, as a multilayered body wall in the trunk region, and as thoracic muscles associated with ventilation.

- Appendicular muscles insert on bones of the appendicular skeleton and power the limbs. Skeletal muscles are somatic (derived from mesodermal somites), striated (sarcomeres visible in histological preparations), and voluntary.

- Walking mammals have an ambulatory gait and plantigrade foot posture.

- Running mammals are cursorial; they display gaits and foot postures that vary with running speed and species. Some cursorial species, such as cats, have a digitigrade foot; others, such as ungulates, are unguligrade. Cursorial locomotion is frequently associated with reduction in the number of digits and lengthening of those digits that remain.

- Jumping and ricocheting mammals use saltatorial locomotion; they frequently have enlarged hind limbs and reduced forelimbs.

- Climbing mammals are arboreal, variously making use of claws, flexible autopodial joints, or prehensile tails for grasping branches. Brachiators have stout, weight-bearing shoulder joints and long forelimbs.

- Digging and burrowing species are fossorial, and those that spend nearly all of their time underground are subterranean. Most digging mammals scratch at the soil with their forelimbs, but several groups of fossorial rodents dig with their incisor teeth.

- Gliding mammals are arboreal species with a patagium that serves as an airfoil when extended during leaps between trees. Powered flight occurs in bats, the only volant mammals. Bat wings consist of a patagium, with skeletal support provided primarily by modified autopodial bones.

- Semiaquatic mammals are adapted for both swimming and terrestrial locomotion; most swim by alternating strokes of their limbs. Pinnipeds are marine carnivorans that leave the ocean to reproduce. Their limbs are modified as flippers. The hind limbs of true seals are permanently reoriented caudally to function in sculling. Sea lions swim by paddling with the forelimbs and can rotate their hind limbs forward for terrestrial locomotion. Cetaceans and sirenians are fully marine. They swim by dorsoventral undulation of their tail, which is modified to form a horizontal fluke. Their hind limbs are absent and their forelimbs are flippers.

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DISCUSSION QUESTIONS

1. Using the internet or other reference material, compare the skeleton of a generalized mammal such as the Virginia opossum (*Didelphis virginiana*) to that of a generalized reptile such as a tuatara (*Sphenodon* spp.). What differences are apparent in bones of the cranium and mandible? How does the arrangement of bones in the pectoral and pelvic girdles differ, and how does this relate to locomotor differences in the two species?

2. Mammalian skin contains all tissue types recognized by histologists (i.e., epithelium, connective tissue, muscle, and nerves). Consult a reference text and identify the tissue type of each integumentary structure described in this chapter. How are the functions of these structures related to their histological properties?

3. Bodybuilding programs for humans attempt to increase the strength and mass of specific muscle groups in both the axial and appendicular divisions. Consult a trainer's handbook or similar reference and relate specific exercises to the muscles they are designed to enhance. Which of these exercises would be possible for a nonprimate mammal to perform?

4. Bats and birds are both capable of powered flight, but this capacity evolved independently in the two groups. Find illustrations of the skeleton of a bird's wing and compare it to the bat wing shown in this chapter. What are the anatomical similarities and differences? How do the two types of wing function to produce lift and thrust?

5. Marine mammals (e.g., pinnipeds) and marine birds (e.g., penguins) share many adaptations for swimming and survival in cold ocean water. Compare the integument and skeletal anatomy of these groups and note the similarities and differences in their locomotor and thermoregulatory adaptations.

CHAPTER 7

Modes of Feeding

Mammals, like all organisms, require energy and nutrients for maintenance, growth, activity, and reproduction—that is, for survival. Maintaining a high body temperature, which is a key feature of Class Mammalia, requires regular acquisition of food. The food of mammals ranges from microscopic forms such as diatoms and crustaceans—a staple in the diet of the largest mammals, the baleen whales—to sedentary forms such as plants used by the most abundant mammals, the rodents. Mammals consume food of high-energy content (blood of vertebrates and insects) as well as of low-energy value (grasses and stems). The food of mammals may be highly specialized and restricted (nectar of localized plants) or rather general and readily available (grasses and herbs). To meet their high-energy needs, mammals have evolved a diverse array of trophic, or nutritional, specializations. The adaptive radiation in food-gathering morphologies is diverse and reflects the diversity of available food.

In this chapter, we detail the feeding apparatus of mammals, focusing on the capturing (teeth, tongue, and jaw musculature) and processing (alimentary canal) of food. Feeding integrates the sense organs and locomotor adaptations (see Chapter 6). Although different orders of mammals are sometimes grouped according to their modes of feeding (i.e., Carnivora), food habits cannot be employed as a systematic criterion because many members of an order may depart from these feeding generalizations. Thus, to enhance understanding of nutritional adaptations, we suggest consulting specific chapters to unite anatomical specializations of different groups with their dietary habits. At the end of the chapter, we will briefly examine some general principles regarding mammalian foraging strategies.

Foods and Feeding

We understand the **life-history traits** and food habits of extant mammals by examining their teeth. As discussed in Chapter 4, all mam-
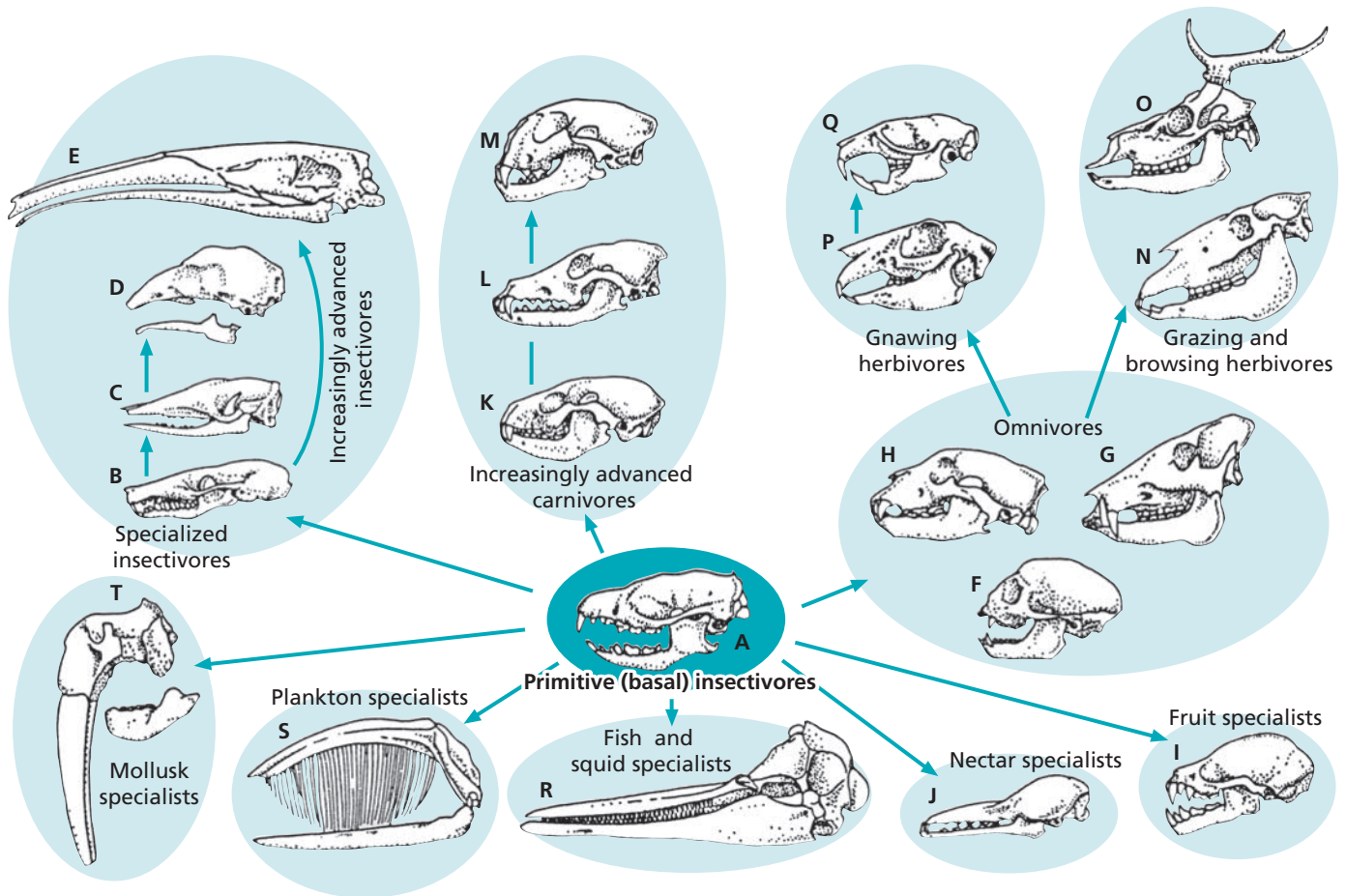
Figure 7.1 Skull and dentition specialization. Feeding specializations in the dentition and skulls of mammals relate to their dietary habits: (**A**) hedgehog; (**B**) mole; (**C**) armadillo; (**D**) anteater; (**E**) giant anteater; (**F**) marmoset; (**G**) peccary; (**H**) bear; (**I**) fruit-eating bat; (**J**) nectar-eating bat; (**K**) raccoon; (**L**) coyote; (**M**) mountain lion; (**N**) horse; (**O**) deer; (**P**) jackrabbit; (**Q**) woodrat; (**R**) porpoise; (**S**) right whale; (**T**) walrus. *Adapted from Rogers (1986).*

mals, except certain whales, monotremes, and anteaters, have teeth, and these structures are inextricably linked with food habits. As mammals evolved in the Mesozoic, major changes occurred in their dentition and jaw musculature; teeth became differentiated to perform specialized functions. Within extant species, several trophic groups can be recognized—namely, insectivorous, carnivorous, herbivorous, and omnivorous mammals. Other specialized modes of feeding have evolved from these four basic plans (Figure 7.1).

INSECTIVOROUS

Insectivory

Mammals that consume insects, other small arthropods, or worms are referred to as **insectivorous** (meaning "insect-eating"). We know from examination of Triassic mammals that the insectivorous feeding niche represented the primitive, or basal, condition of eutherian mammals.

Today, this feeding niche is exploited by members of nine orders of mammals: echidnas and the platypus (Order Monotremata); marsupial moles (Order Notoryctemorphia), solenodons, hedgehogs, shrews, moles, and desmans (Order Eulipotyphla); most bats (Order Chiroptera); anteaters and armadillos (Orders Cingulata and Pilosa); pangolins (Order Pholidota); aardvarks (Order Tubulidentata); and the aardwolf (Order Carnivora; see Figure 7.1). Many other orders of mammals also have members that exhibit insectivorous habits. The dentition of hedgehogs, shrews, moles, and most bats is typified by numerous sharp teeth with sharp cones and blades for piercing, shearing, and ultimately crushing the tough chitinous exoskeletons of insects. In many forms, the lower incisors are slightly **procumbent** (pointing forward and upward) to aid in grasping prey (see Figure 7.1). Because insectivorous mammals consume minimal amounts of fibrous vegetative material, prolonged fermentation is not required; their alimentary canals are short, and most insectivores and chiropterans lack a cecum (Figure 7.2).

A **Insectivore** **B** **Carnivore** **C** **Nonruminant herbivore** **D** **Ruminant herbivore**
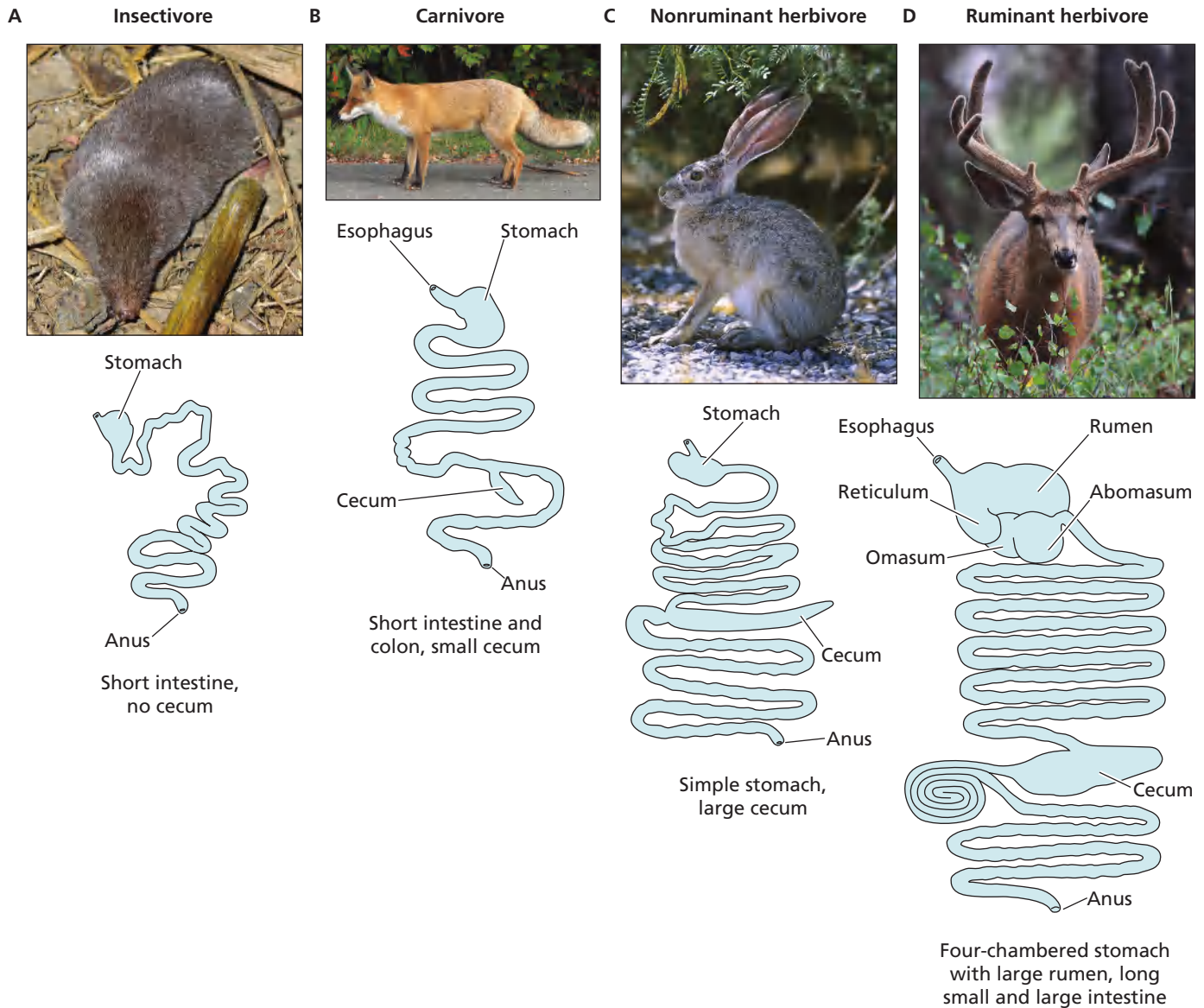
Figure 7.2 **Digestive system.** The digestive systems of mammals, illustrating the differences in morphology that correspond to different diets: (**A**) short-tailed shrew; (**B**) red fox; (**C**) black-tailed jackrabbit; (**D**) mule deer.

Aerial Insectivores

The most abundant foods are plants and insects; it is therefore not surprising that the most abundant mammals are rodents and bats. Chiropterans occupy ecological niches in almost all habitats of the world; the diversity of their diets is unparalleled among extant mammals. The majority (70%) of "microchiropterans" (see Chapter 21 for current terminology associated with this group) is insectivorous (Black 1974; Whitaker 1988; Whitaker et al. 1996; Neuweiler 2000; Patterson et al. 2003; Gonsalves et al. 2013; Nelson and Gillam 2017). All bats residing north of 38°N and south of 40°S latitude are insectivorous. Bats may consume 50% of their body mass in insects each night. For example, lactating female big brown bats (*Eptesicus fuscus*) nightly consume a quantity of insects that is equivalent to

more than their body mass (Kurta et al. 1990; Kurta 2017). Throughout their range, insectivorous bats feed on a diverse array of arthropods, ranging from scorpions, spiders, and crustaceans to soft-bodied and hard-bodied insects (Whitaker 1994b; Neuweiler 2000; Schulz 2000; McWilliams 2005; Dodd et al. 2012; Moosman et al. 2012; Coleman and Barclay 2013; McCraken et al. 2018). North American bats, namely, the little brown bat (*Myotis lucifugus*) and big brown bat, are major consumers of mosquitoes. Recent evidence derived from maternity roosts of *M. lucifugus* and *E. fuscus* in Wisconsin indicate that taxonomic richness of mosquitoes is higher than previously shown (Wray et al. 2018).

Insectivorous bats are voracious eaters: Mexican free-tailed bats (*Tadarida brasiliensis*) in central Texas, totaling

some 20 million individuals, may consume up to a quarter of a million pounds of insects nightly and fly as high as 10,000 feet (3,000 m) in search of their prey (Kunz et al. 1995; Whitaker et al. 1996; McCracken 2003; Han and Wilkins 2015). Sadly, many species of bats are experiencing declines in their population numbers. Using data derived from thermal imaging technology, Betke et al. (2008) found a major reduction in population estimates of colony size in *T. brasiliensis* from 54 million, obtained in 1957 prior to thermal imaging technology, to 4 million in 6 major cave colonies in the southwestern United States. Insects are either captured in the mouth or trapped by a wing tip or the uropatagium (see Figure 21.3). Foraging styles vary depending on the species. Within a given habitat, feeding assemblages of bats can be quite diverse and may be divided into different guilds, such as species that glean insects or those that forage within forest openings, over water, and in open-air zones above the forest canopy (Findley 1993; Nowak 1999; Lacki et. al 2007; Andreas et al. 2012).

The trophic niche of insectivorous bats may be assessed by determining echolocation calls plus morphological attributes of a species, including its wing, jaw, and tooth morphology, brain size, and external dimensions (Findley and Wilson 1982; Entwistle et al. 1996; Bogdanowicz et al. 1999). The size of prey varies in relation to the predator's jaw morphology, from very small midges and mosquitoes to large beetles. Freeman (1979, 1981, 1988) predicted food habits of molossids by assessing jaw structure and mechanics; beetle-eaters were characterized by more robust skulls and fewer but larger teeth, whereas moth-eaters had delicate skulls and numerous smaller teeth. Under field conditions, Freeman and Lemen (2010) quantified bite forces of 39 species of 6 families of New World bats with a variety of diets.

Most insectivorous bats are generalists and opportunistic feeders, but remarkable specialists do occur (Whitaker 1994b). Golden-tipped bats (*Kerivoula papuensis*) of southeastern Australia feed by gleaning, flying slowly in dense vegetation and hovering and plucking orb spiders from their webs (Richards 1990; Strahan 1995). Pallid bats (*Antrozous pallidus*) of the southwestern United States feed on beetles, Jerusalem crickets, sphinx moths, scorpions, and small vertebrates gleaned from the ground (Adams 2003; Lenhart et al. 2010).

Some species of phyllostomid bats show impressive plasticity in dietary habits and are known to supplement nectar diets with insects, pollen, and fruit (Schondube et al. 2001; Fleming et al. 2009; Sanchez and Dos Santos 2015). In contrast, very few insectivorous species (Vespertilionidae) supplement diets with nectar and fruit. Pallid bats are an exception. These bats reside in the Sonoran Desert of northwestern Mexico and typically hunt by listening and will glean large arthropods off the ground or plant surfaces; however, Frick and associates (Frick et al. 2009) noted that *A. pallidus* go a step farther. On the Baja peninsula in Mexico, pallid bats are regular visitors to cardon cactus flowers and feed by "plunging their faces into the corolla to lap pooled nectar" (Frick et al. 2009:1157). These same cactus flowers are visited by phyllostomid bats such as *Leptonycteris yerbabuenae*, the Mexican lesser-long nosed bat. Recent work by Frick and colleagues (Frick et al. 2014) shows that pallid bats seasonally rely on cactus nectar during spring months. It turns out that *A. pallidus* are better pollinators of the cardon cactus than the nectar-specialist *L. yerbabuenae* in that the former deliver more pollen grains per visit, which is surprising given they lack morphological adaptations for nectar-feeding (Frick et al. 2013).

Terrestrial Insectivores

The platypus is a semiaquatic insectivore that feeds on benthic worms, insects, mollusks, and small invertebrates—those creatures that live at the bottom of a body of water (see Chapter 10). Food obtained during a dive is stored in large cheek pouches that open to the rear of the bill. When the cheek pouches are full, the platypus rests on the surface of the water, and the food is transferred to the rear of the mouth and masticated by horny pads. As in other insectivores, the alimentary canal of platypuses is simple and lacks gastric glands. Cheek pouches are thought to replace the stomach as a food storage area (Harrop and Hume 1980).

The bill of a platypus is soft, pliable, and very sensitive, with nostrils at the tip—quite unlike that of a true duck. The bill is its main sensory organ for navigation and locating food; it is highly innervated both for tactile reception and to sense electric fields generated by the muscle contractions of prey (Scheich et al. 1986; Manger and Pettigrew 1995; Proske et al. 1998). In Chapter 10 we describe the fascinating arrangement of mechanoreceptors and electroreceptors of the platypus.

Four species of mammal produce a venomous saliva: the northern short-tailed shrew (*Blarina brevicauda*) of North America (Figure 7.3A), the European water shrew (*Neomys fodiens*; Figure 7.3B), the Mediterranean shrew (*Neomys anomalous*), and the Hispaniolan Solenodon (*Solenodon paradoxus*; Figure 7.3C). The toxin of *Blarina brevicauda* was purified and characterized as a lethal mammalian venom possessing a tissue kallikrein-like protease activity derived from the submaxillary and sublingual glands (Kita et al. 2004, 2005). Research by Tomasi (1978) and Martin (1981) demonstrated the importance of venom in the hoarding behavior of *Blarina*. In both *Blarina* and *Neomys*, the toxin is stored in submaxillary glands and is administered to the prey through a concave medial surface in the first lower incisors. Extracts of this toxin administered to mice affect the nervous, respiratory, and vascular systems, causing irregular respiration, paralysis, and convulsions, followed by death (Lawrence 1945; Kita et al. 2004, 2005; Merritt 2010; Kowalski and Rychlik 2018). *Blarina* bites its prey, immobilizing it, and caches it below ground in a comatose state. Caching sites are marked by defecation and urination and provide shrews with a source of fresh food for some time. The ability to cache unused prey ensures that a predictable

A

B

C
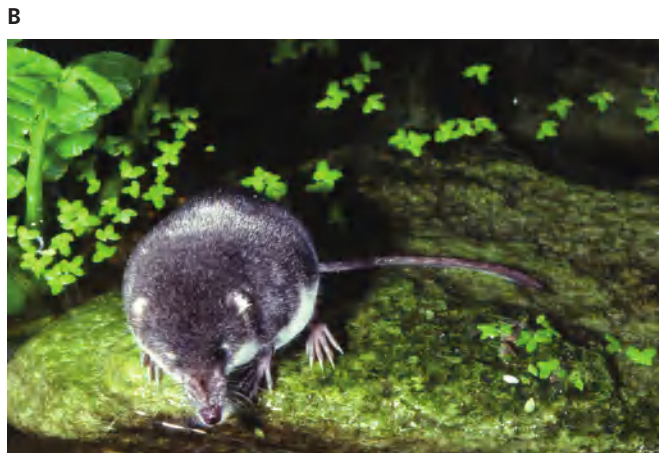
Figure 7.3 **Venomous mammals.** (**A**) Northern short-tailed shrew (*Blarina brevicauda*); (**B**) European water shrew (*Neomys fodiens*); (**C**) Hispaniolan solenodon (*Solenodon paradoxus*).

quick energy source is accessible and readily available if prey is scarce (Churchfield 1990).

Several groups of insectivorous mammals are **myrmecophagous** (meaning "ant-eaters"). Representatives include the armadillo (*Dasypus*), silky anteater (*Cyclopes*), giant anteater (*Myrmecophaga*), pangolin (*Manis*), aardvark (*Orycteropus afer*), and numbat (*Myrmecobius fasciatus*), which feed on colonial insects, such as ants and termites. Reduction of teeth is common among myrmecophagous mammals, and their dentition departs from the "insectivorous" design of the hedgehogs, shrews, and moles. They possess numerous peg-like teeth (armadillos) or no teeth at all (echidnas, anteaters, and pangolins). The marsupial numbat, the sole member of the Family Myrmecobiidae, possesses numerous small, delicate teeth—the total number may be as high as 52. The aardvark is a special case, characterized by columnar cheekteeth composed of vertical tubes of dentine within a matrix of pulp (see Figure 11.8). Mammals that consume colonial insects such as termites and ants possess long, extendible, worm-like tongues (Chan 1995; Reiss 1997). Elongated snouts and strong front feet used as digging tools enable anteaters and aardvarks to burrow rapidly into and tear apart termite hills. Their highly maneuverable, sticky tongues are effective in reaching the inner recesses of ant and termite nests. The tongue may be three times the length of the head; in several groups of anteaters, the tongue is anchored at the posterior end of the sternum rather than the throat (Hildebrand 1995; Figure 7.4). Greatly enlarged salivary glands situated in the neck produce a viscous, sticky secretion that coats the tongue and is important in the breakdown of chitin.

Echidnas consume ants, termites, and earthworms, but they do not have teeth or even horny grinding plates on the rear of their jaw, as does the platypus. Rather, a pad of horny spines on the back of the tongue grinds against similar spines on the palate to crush the exoskeletons of arthropods. The mouth of the echidna is positioned at the
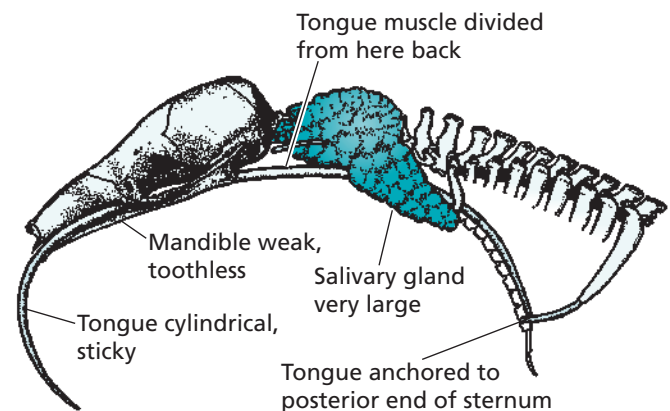
Figure 7.4 **Anteater tongue specialization.** The long, worm-like tongue of the collared anteater (*Tamandua*) is anchored to the posterior end of the sternum and can be protruded extensively to assist in capturing ants and termites. *Adapted from Hildebrand (1995).*

very tip of its elongated snout and can be opened only enough to permit passage of the long, sticky, protrusile tongue. Because there are no glands in the stomach of echidnas, digestive enzymes are not present. The amylase present in the saliva therefore assists in the breakdown of insect chitin within the stomach. Like the insectivores, the monotremes have a simple alimentary canal with a tiny, nonfunctional cecum (Harrop and Hume 1980; Sprent and Nicol 2016).

Insects represent a staple in the diets of many other mammals; for example, several species of harvester termites (Genus *Trinervitermes*) form the chief food of the aardwolf (*Proteles cristatus*) of southern Africa (Koehler and Richard-son 1990). A single aardwolf was estimated to consume about 105 million termites a year (Kruuk and Sands 1972). Slender-tailed meerkats (*Suricata suricatta*) are small gregarious mongooses residing in thorn and grassland savannah of the Kalahari Desert of southern Africa, where 78% of their diet consisted of larvae and adult Coleoptera supplemented by small reptiles (Doolan and Macdonald 1996). The bat-eared fox (*Otocyon megalotis*) of eastern and southern Africa consumes primarily termites and beetles; close to 70% of its diet consists of harvester termites (Genus *Hodotermes*) and dung beetles (Family Scarabaeidae). A combination of extremely long ears and small, numerous teeth enhances the bat-eared fox's ability to detect, capture, and consume its prey.

Rodents are notably omnivorous, but one, the grasshopper mouse (Genus *Onychomys*) of North America, is unique in having a diet composed almost entirely of grasshoppers, crickets, and ground-dwelling beetles (McCarty 1975, 1978; Williams 2009). Grasshopper mice have evolved specialized attack strategies to avoid the defensive secretions of insect prey such as beetles (Genera *Elodes* and *Chlaenius*). When attacking a whip-scorpion, *Onychomys* first immobilizes the tail and then attacks the head. A marsupial that is comparable to the grasshopper mouse, the mulgara (*Dasycercus cristicauda*), resides in the arid sandy regions of central Australia (Figure 7.5) About the size of eastern chipmunks (*Tamias striatus*), mulgaras specialize in consuming large insects, spiders, and rodents. They are reported to be relatively uncommon but their numbers will increase dramatically if prey such as house mice (*Mus musculus*) is abundant. Like *Onchomys*, mulgaras are nononsense predators—but they follow a certain etiquette. They are reported to fiercely attack a mouse and devour it methodically from head to tail, inverting the skin in neat, fastidious fashion as they dine (Chen et al. 1998; Dickman et al. 2001; Haythornthwaite and Dickman 2006).

Insectivorous mammals are broadly distributed and exhibit remarkable adaptations for locating food. Like the platypus, which relies on tactile receptors on their bill to locate food under water, certain moles employ a similar system underground (Manger and Pettigrew 1996; Grand et al. 1998). Talpids have poor vision but acute hearing and touch. The snouts of moles and desmans are equipped with several thousand sensitive tactile organs, known as **Eimer's**

Figure 7.5 Marsupial carnivore. The ecological equivalent to the North American grasshopper mouse (*Onychomys leucogaster*) is the mulgara (*Dasycercus cristicauda*), a marsupial carnivore that lives in the arid sandy deserts of Australia. Mulgaras are closely related to Tasmanian devils (Family Dasyuridae). *Adapted from Koertner 2008.*

organs, located on the nose (Quilliam 1966; Gorman and Stone 1990; Catania 1995a, 1995b, 1995c, 2000; Catania and Kaas 1996; Marasco et al. 2007; Sawyer and Catania 2016). In the star-nosed mole (*Condylura cristata*) of North America, touch receptors are distributed among 22 fleshy, tentacle-like appendages around the tip of the nose. Eimer's organs appear as "a mass of bulbous protuberances, reminiscent of a miniature cobbled street" (Gorman and Stone 1990:47). Each organ is surrounded at its base by a blood-filled sinus sitting on a network of sensory nerves. Nerve endings pass up from this network into a thick epidermal cap. When the mole touches an object, Eimer organs rock on their fluid foundation, transmitting the stimulus to the underlying nerve endings via sensory nerves to the central nervous system. There, stimuli are received and integrated from other organs that have been "altered," thus providing information about the characteristics of the stimulus (Gorman and Stone 1990) (Figure 7.6).

Several species of shrews have invaded the aquatic world and undertake frequent forays to pursue macro-invertebrate prey. As noted in Chapter 17, convergent evolution has occurred several times in the Family Soricidae. Adaptations enhancing a semiaquatic life have developed in four genera—*Sorex*, *Neomys*, *Nectogale*, and *Chimarrogale*—which inhabit two continents.

Water shrews are well adapted for diving and swimming in search of prey. Their snouts are used to probe into the underwater substrate; the dense array of whiskers around their nostrils aid in detection of prey by perceiving shape and texture. These small mammals possess a fringe of stiff hairs called "fibrillae" on the lateral edges of the hind feet and toes, as well as on the ventral surface of the tail. The hairs on the feet rise up during the down stroke to increase surface area of the foot, but fold down and out of the way during the upstroke. As a result, the surface area of the foot

is increased at the crucial moment to benefit propulsion. While underwater, a fimbriated tail is adaptive in preventing rolling and tends to stabilize body motion while swimming. Perhaps the water shrew best adapted for swimming is the Tibetan water shrew (*Nectogale elegans*), an inhabitant of montane streams in the Himalaya Mountains and southeastern Tibet. Their fimbriated fore- and hind feet

A

B
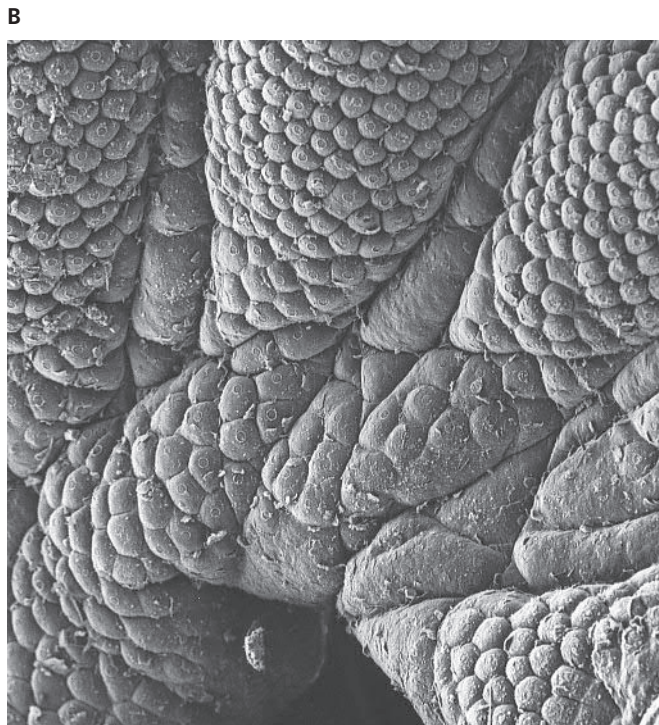
Figure 7.6 **Mole specializations.** (**A**) The star-nosed mole of North America is unique among mammals in possessing 22 fleshy, tentacle-like appendages surrounding the tip of its nose. (**B**) Eimer's organs on the nose of a star-nosed mole, as shown in a scanning electron micrograph.

are fully webbed, and disc-like pads on the base and small scales on the dorsal surface of their feet are helpful in traversing wet stones and perhaps in holding prey. Their nostrils are located behind the nose shield which may prevent water from entering.

In the New World, three species—the American water shrew (*Sorex palustris*), the marsh shrew (*S. bendirii*), and the Glacier Bay water shrew (*S. alaskanus*)—are dedicated swimmers. The most widespread species is the 10–15 g American water shrew, found throughout Alaska and Canada and down to the northern mountain regions of the United States. As with most shrews, their eyes are minute, and their ears are small and hidden under the bicolored coat that is jet black above and silver below. The species is rarely found far from water; its nests of dried moss tend to be within bankside burrows, under boulders, or along streamside tangles of roots. In eastern North America, for example, *S. palustrus* can be found in rocky-bottom streams surrounded by forests of hemlock, spruce, and rhododendron (Merritt 2010).

Like all other shrews, water shrews are active around the clock—about 12 1-hour foraging bouts in a 24-hour period. On a given day, these secretive insectivores forage excitedly for short periods and then suddenly drop off to sleep. Their diet consists primarily of small aquatic animals such as snails, worms, small fish and their eggs, and insects, including nymphs of caddis flies, stone flies, and mayflies. Terrestrial invertebrates are also consumed. Interestingly, the diet of water shrews may include large amounts of slugs, snails, and earthworms in addition to the fungus *Endogone* (Beneski and Stinson 1987).

They are active throughout the year, even foraging below the ice during winter. When swimming underwater or crawling on stream bottoms, water shrews appear to be a small silver submarine or a self-propelled bubble. In addition to being an adept underwater swimmer, *S. palustris* is reported to walk or glide on water. One study documented a water shrew running more than 1.5 m across the smooth surface of a pond (Jackson 1961). This impressive achievement is feasible because the fibrillae can hold small globules of air and act as a sort of hydrofoil.

Even though water shrews are excellent divers, reported to sustain forced dives of up to almost 48 seconds, remaining underwater is difficult (Calder 1969). This is due to their very dense, water-repellent fur, which does not allow water to penetrate, trapping air bubbles that enhance buoyancy. As a result, the shrew surfaces and floats like a cork whenever it stops paddling.

Perhaps the most spectacular adaptation of the American water shrew is its ability to detect prey underwater—using their sense of smell. Investigations have shown that water shrews can detect odorants while underwater. Recently, Kenneth Catania examined hunting behavior of water shrews in the laboratory using a high-speed video system and infrared lighting (Catania 2006, 2012; Catania et al. 2008). In addition to employing "underwater sniffing" to detect prey, water shrews like platypuses, star-nosed

Underwater Sniffing

Perhaps the most spectacular adaptation of the American water shrew (*Sorex palustris*) is its ability to detect prey underwater—using its sense of smell! Investigations have shown that water shrews can detect odorants while underwater.

Recently, Kenneth Catania and colleagues examined the hunting behavior of water shrews in the laboratory. Using high-speed video recordings and infrared lighting, they found that water shrews continuously emitted and reinhaled air from their nostrils while foraging underwater, which indicated that they could be "sniffing" odors while submerged (see figure). To test this idea, they trained water shrews to follow an underwater scent trail that was randomly laid on either of two paths leading to a food reward. The shrews performed the task with great accuracy. However, when the bubbles they exhaled during underwater sniffing were blocked by a fine steel grid placed over the scent trail, they were unable to follow the scent. Previous investigators likely overlooked the underwater sniffing ability of the shrews because it happens very quickly and requires high-speed, underwater photography to see. Interestingly, underwater sniffing is also known to occur in another semiaquatic mammal, the star-nosed mole (*Condylura cristata*).

Both water shrews and star-nosed moles seem to have adapted their olfactory systems for use underwater. While foraging underwater, they exhale air bubbles through their nostrils—often directly onto the objects or prey that they are investigating.

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A

B

(**A**) Foraging in the American water shrew (*Sorex palustris*); (**B**) laboratory study showing underwater sniffing by the American water shrew. The bubble is in contact with a wax object.
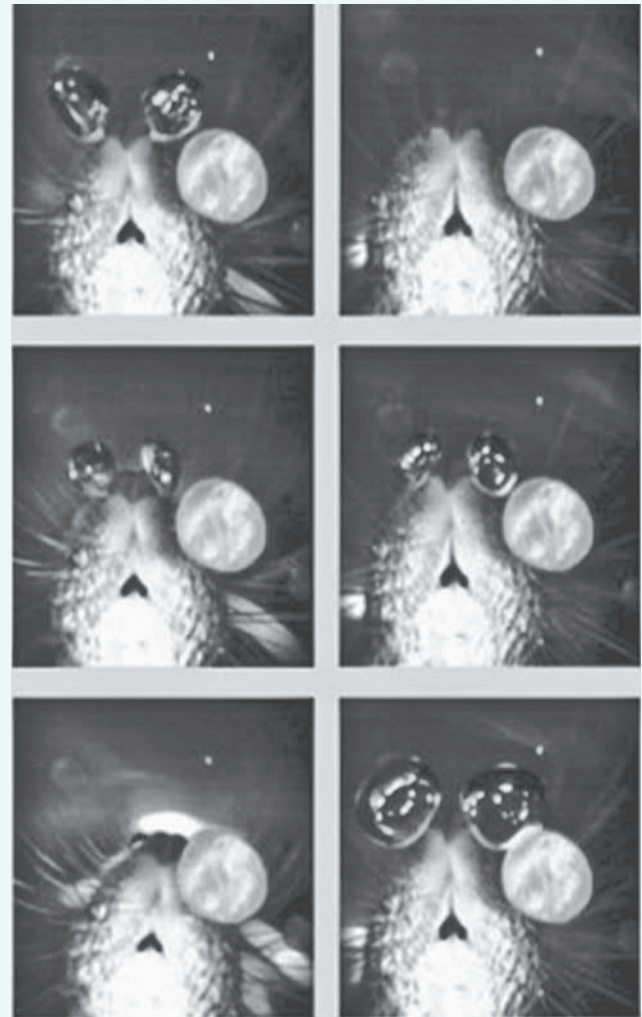
moles and desmans mentioned earlier and in chapter 17 (breakout box) have evolved mechanoreceptors to aid underwater hunting. Investigations of Catania and associates (Catania et al. 2013) have shown that water shrews possess a neocortex around their nose and mouth dominated by large whiskers. These specialized somatosensory cells called "barrelettes" are housed in the brainstem and crucial for locating prey underwater (Catania et al. 2013).

Like anteaters with their long protrusile tongues, some arboreal primates and marsupials employ elongated digits

A

B

Figure 7.7 Insect-eaters. (**A**) The aye-aye (*Daubentoria madagascariensis*) feeds primarily on the tree-burrowing larvae of beetles. (**B**) It bites into the bark with its powerful incisors and crushes and extracts insect larvae with its elongated third finger.

to secure well-hidden insect prey. The 3rd finger of the aye-aye (*Daubentonia madagascariensis*) of Madagascar and the 4th finger of two species of striped possums (*Dactylopsila*) from Australasia are uniquely adapted as probes for removing insects from the crevices of trees (Figure 7.7). Using its keen hearing, an aye-aye detects larval insects hidden under the bark of dead branches. It then exposes prey by gnawing off the overlying bark with its incisors, then inserting its 3rd finger to crush and extract larvae, which it transfers to its mouth (Oxnard 1981; Erickson

1991, 1994; Krakauer et al. 2002; Pellis and Pellis 2012; Sefczek et al. 2012, 2017). Aye-ayes may have filled this insect-eating niche on Madagascar, which elsewhere is occupied by woodpeckers (Macdonald 1984; Thompson et al. 2016). The higher elevations of forests in New Guinea are home to an example of how similar evolutionary pressures have acted on two different mammals that inhabit two distant islands, producing almost identical feeding specializations. It is a fascinating case of convergent evolution in feeding specializations of a Malagasy primate, the aye-aye, and a New Zealand marsupial, the long-fingered triok (*Dactylopsila palpator*). Like aye-ayes, trioks have a pronounced sense of hearing adaptive for locating insect grubs chewing deep within inner recesses of trees and rotting logs. Elongated tongues and sharp, powerful, chisel-like incisors assist in tearing through the bark—reportedly, entire trees can be scarified by teeth marks. Trioks then use their greatly elongated 4th finger (recall aye-ayes used their 3rd finger) equipped with a hooked nail to extract tunneling larvae. As with the North American pileated woodpecker (*Dryocopus pileatus*), feeding activities of trioks can be observed by the presence of woodchips at the base of the excavation. However, a rather pungent odor may also alert an observer to the presence of the triok. The body odor is reminiscent of that of a striped skunk (*Mephitis mephitis*). That, combined with bold black and white markings, makes a strong case of convergence of trioks with skunks.

Tarsiers (Genus *Tarsius*) from islands of Southeast Asia are primarily insectivorous. They are equipped with long legs (the name "tarsier" refers to the elongated tarsal, or ankle) and have exceedingly large eyes that face forward to permit stereoscopic vision. Acute directional hearing aids in locating and pinpointing prey and efficient sit-wait-and-ambush predatory tactics are a key to their success as a premier nocturnal predator. Tarsiers capture arthropods, such as ants, beetles, and cockroaches, in trees or on the ground by leaping and pinning the prey down with both hands and quickly dispatching the victim with several bites (Roberts and Kohn 1993; Grow et al. 2013).

CARNIVOROUS

Carnivory

Carnivorous (meaning "meat-eating") mammals feed primarily on animal material. Members of this group comprise the flesh- or meat-eating members of the Order Carnivora (see Chapter 18) and the marsupial dasyurids (see Chapter 10). The Carnivora include the canids, mustelids, felids, and allies. Order Carnivora is represented by a diverse array of feeding types and dental morphologies, ranging from obligatory meat-eaters with large carnassial teeth, such as felids and hyaenids, to members such as the giant pandas (*Ailuropoda melanoleuca*), which have crushing molars and feed exclusively on bamboo shoots (see Figure 7.1). During

their evolution, carnivores retained a versatile dentition, with different teeth adapted for cutting meat, crushing bone, and grinding insects and fruits (Van Valkenburgh 1989, 1991; Gittleman and Van Valkenburgh 1997). Animal material is mostly protein and is converted to energy more efficiently than plant material is. Thus, as in the insectivorous mammals, the alimentary canal of carnivorous mammals is short, and the cecum is small or absent (see Figure 7.2).

Most carnivores are predators typified by strong skulls, jaws, and sharp incisors and canine teeth designed to kill and dismember prey. Killing techniques of predators differ; felids and mustelids kill with a single, penetrating bite, whereas hyaenids and canids may kill with several shallower bites. Once the prey is subdued, carnivores rely on their large, strong, pointed canine teeth to tear and shear flesh into hunks, which are then swallowed without being finely divided in the mouth. Most carnivores also have a pair of carnassial teeth—a combination in which the last upper premolar and the first lower molar form a powerful shearing mechanism when the mouth is closed (Figure 7.8). The carnassials are most highly developed in the felids and canids and least developed in the more omnivorous families of ursids and procyonids (Figure 18.4). Carnivores bite by employing a chopping motion. Because they have large, crushing molars in addition to carnassials, dogs can crush bones, whereas cats cannot.

Terrestrial Carnivores

With the exception of otters (Mustelidae; Subfamily Lutrinae), which are efficient marine and aquatic carnivores, most mustelids hunt on land. Mustelids are active, fierce hunters, many with specialized methods of killing prey (King 1990; Powell 1993). For example, the long-tailed weasel (*Mustela frenata*) of North America kills its victim by inflicting a rapid bite to the base of the skull or by severing the jugular vein with its sharp teeth. It first consumes the brain, then the heart, lungs, and ultimately the entire body, including bones and fur.

Felids are highly adapted for capturing and consuming vertebrate prey. Their senses of smell and hearing are acute. Their eyes, larger than those of most carnivores, face forward, thus providing the binocular vision and depth perception vital to locating prey. Their long, stiff, highly sensitive vibrissae are especially useful for foraging at night. Long, sharp, usually retractile claws serve as effective meat hooks for capturing, slashing, and manipulating prey. Cats use their long, sharp canines for grasping prey and their well-developed carnassials for shearing food (Sanderson and Watson 2011; Rostro-Garcia et al. 2015). The tongue of felids is covered with many sharply pointed papillae, which are well suited for holding prey and scraping meat from a carcass (Van Dunstone and Gorman 1993; Pierce et al. 2000; Ross et al. 2010; Elbrock and Wittmer 2013; Donadio and Buskirk 2016; Miranda et al. 2018).

Canids are opportunistic hunters that rely on high intelligence, social organization, and superb behavioral adaptability (see Chapter 23). Small canids such as cape foxes (*Vulpes chama*), bat-eared foxes (*Otocyon megalotis*), and black-backed jackals (*Canis mesomelas*) occur in southern Africa and hunt singly or in pairs (Kamler et al., 2012, 2013), whereas larger canids, such as gray wolves (*Canis lupus*) and African hunting dogs (*Lycaon pictus*), hunt in packs of up to 30 members, seeking prey that are far larger than themselves (Paradiso and Nowak 1982; J. D. Gittleman 1989, 1996; Valkenburgh 1989, 1991; Fuller and Kat 1993; Fanshawe and Fitzgibbon 1993; Cozzi et al. 2012, 2013; Hayward et al. 2017; Hinton et al. 2017; Stanek et al. 2017). As noted above, gray wolves and coyotes (*Canis latrans*) hunt in packs and are well-known predators of ungulate species; coyotes tend to prey more on neonates since coyotes are smaller than wolves (Berger et al. 2008; Hinton et al. 2017). Most canids possess dental morphologies adaptive for omnivorous diets; however, four species possess specialized morphological and behavioral adaptations for an exclusively carnivorous diet, termed "hypercarnivory." Hypercarnivorous species of canids include wolves, African hunting dogs, dholes (*Cuon alpinus*), and bush dogs (*Speolthos venaticus*) (Van Valkenburgh 1991; Kamler et al. 2012; Smith et al. 2017).
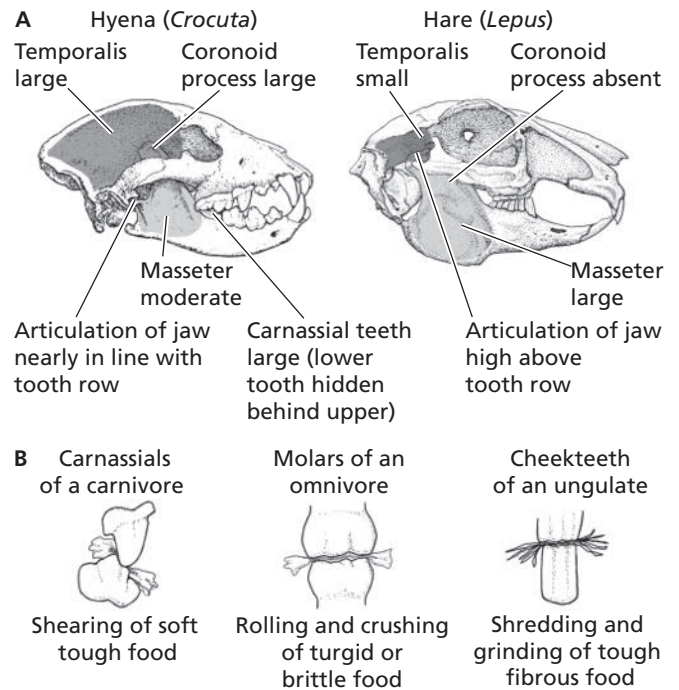
Figure 7.8 Kinds of teeth. (**A**) Comparison of the jaw mechanics of a carnivore (*left*) and an herbivore (*right*). Note that the carnivore possesses a large temporalis muscle and a moderate masseter muscle attached to a large coronoid process. Herbivores possess a large masseter muscle and a small temporalis, and the coronoid process is absent. (**B**) The occlusal surface of teeth are adapted for processing three principal kinds of food: (*left to right*) shearing of soft, tough food (e.g., the carnassials of a carnivore); rolling and crushing of brittle food (e.g., molars of an omnivore); and shredding and grinding of tough fibrous food (e.g., cheekteeth of an ungulate). *Adapted from Hildebrand (1995).*

In Africa, camera trapping was employed to assess competition strategies of coexisting guilds of small sympatric carnivores. Temporal and spatial partitioning occurred as a means of reducing ecological overlap of African wildcats (*Felis silvestris*), grey mongooses (*Galerella pulverulena*), small-spotted genets (*Genetta genetta*), striped polecats (*Ictonyx striatus*), and yellow mongooses (*Cynictis penicillata*) (de Satgé et al. 2017).

The jaw muscles of carnivorous mammals differ from those of herbivores (see Figure 7.8) in terms of the relative importance of the three major adductor muscles of the mandible: the **temporalis**, **masseter**, and **pterygoideus.** Carnivores must first seize and hold their prey with the canines, which requires a large force at the front of the jaws. The very large temporalis muscles function in holding the jaws closed and aid in the vertical chewing action. In carnivores, the masseter muscle is comparatively small and serves to stabilize the articulation of the jaw, and the pterygoideus muscle helps position the carnassials. In contrast, herbivores rely heavily on a large masseter muscle to maintain a horizontal movement of molars for grinding fibrous food.

Aerial Carnivores

Most chiropterans feed on insects taken on the wing (Whitaker 1988). Certain species of bats are quite specialized, however, in that they feed on small vertebrates such as rodents, birds, frogs, lizards, small fish, and even other bats. The "carnivorous" bats (or animalivorous; *sensu* Patterson et al. 2003) comprise six families: Megadermatidae, Hipposideridae, Nycteridae, Phyllostomidae, Noctilionidae, and Vespertilionidae (Norberg and Fenton 1988; Pavey and Burwell 1997; Dondini and Vergari 2000; Bonato et al. 2004; Thabah et al. 2007). As noted earlier, the shape of the skull and teeth in bats is a good indicator of diet. For example, the carnivorous false vampire bat (*Vampyrum spectrum*), the largest bat in the New World, has a massive skull equipped with strong, sharp canine teeth and shearing molars adapted for crushing bones and cutting flesh (Figure 7.9). Once thought to be a true vampire bat, *Vampyrum* does not consume blood. Its diet consists of birds, bats, rodents, and some insects and fruit (Gardner 1977). Asian false vampire bats (*Megaderma lyra*) prey on small vertebrates, such as mice, baby birds, and frogs, which are carried to the roost to be eaten. The frog-eating bat (*Trachops cirrhosus*), a phyllostomid, consumes primarily insects and small vertebrates such as frogs and lizards (Tuttle and Ryan 1981; Bruns et al. 1989; Halfwerk et al. 2014). Able to locate and distinguish between different species of frogs by listening for and analyzing their unique calls, *Trachops* can discriminate between poisonous and palatable species (Ryan and Tuttle 1983). Bird-eating has been reported primarily from gleaning tropical bats that occasionally capture resting birds (Norberg and Fenton 1988). Recently, researchers have found birds to be an important item in the diet of giant noctule bats (*Nyctalus lasiopterus*) from temperate regions of Spain and Italy (Dondini and Vergari 2000), great evening

Figure 7.9 *Vampyrum spectrum.* The carnivorous false vampire bat is the largest bat in the New World. It is equipped with strong, sharp canine teeth and shearing molars adapted for crushing bones and cutting flesh.

bats (*Ia io*) from India and China (Thabah et al. 2007), and bird-like noctule bats (*Nyctalus aviator*) from Japan (Fukui et al. 2013). It is noteworthy that giant noctule bats may capture migrating birds while flying at high elevations (Ibáñez et al. 2001; Popa-Lisseanu et al. 2007).

The morphology of teeth, alimentary canal, and limbs is strongly correlated with food habits, a fact that is well illustrated by the only **sanguinivorous** (meaning "blood-eating") mammals—the vampire bats. Three species consume blood, and all are phyllostomids confined to the New World from Mexico to northern Argentina. The common vampire bat (*Desmodus rotundus*) preys exclusively on mammals, but the white-winged vampire bat (*Diaemus youngi*) and the hairy-legged vampire bat (*Diphylla ecaudata*) prefer avian prey (Altenbach 1979; Greenhall et al. 1983, 1984; Hermanson et al. 1993; Greenhall and Schutt 1996; Schutt and Altenbach 1997; Ito et al. 2016). *Desmodus rotundus* is a medium-sized bat weighing between 25 g and 40 g (Figure 7.10) and preys primarily on medium-sized and large terrestrial mammals (Mayen 2003). When found near human settlements, these bats will ingest blood from cattle, horses, mules, goats, pigs, sheep, and humans and transmit pathogens such as the rabies virus (Mayen 2003; Messenger et al. 2003). Today, vampire bats occur in close proximity to livestock farming and show a high degree of preference for cattle (Voigt and Kelm 2006). Morphologically, *D. rotundus* are adapted for a diet of blood in the following ways:

1. The rostrum is reduced, supporting upper incisors and canines that are unusually large and knife-like, with the sharp points of the incisors fitting into pits in the lower jaw.
2. Cheekteeth are tiny (there is no need to chew blood).
3. The tongue possesses a pair of grooves at each border that function like drinking straws.
4. The stomach is long and tubular, highly distensible, and well vascularized to enhance the storage of blood and absorption of water.

A

B

C

Esophagus

Stomach

Intestine

Anus
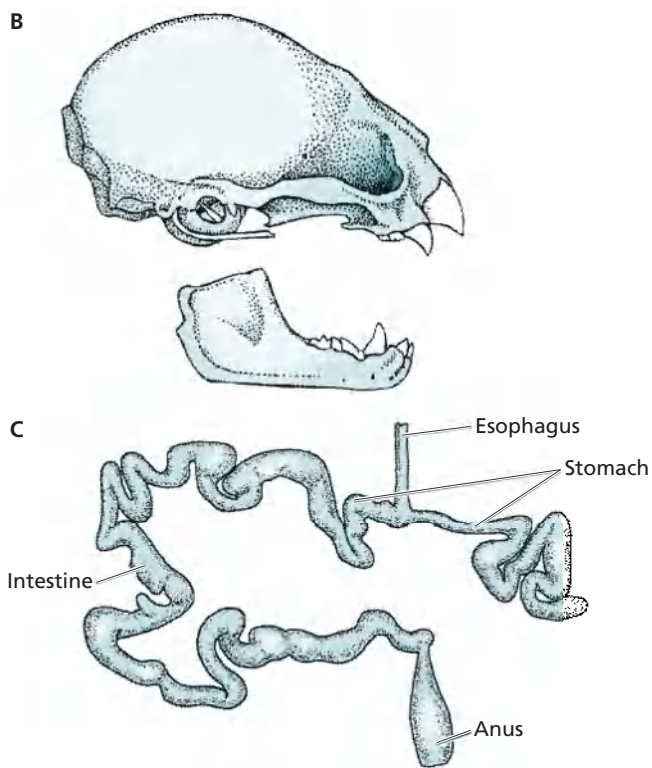
Figure 7.10 Vampire bats. (A) The vampire bat (*Desmodus rotundus*) occurs only in the New World, ranging from northern Mexico to southern South America. **(B)** The skull of the vampire bat showing the bladelike upper incisors and canines. The sharp points of the upper incisors fit into distinct pits in the lower jaw behind the incisors. **(C)** The alimentary canal of the vampire bat. The stomach serves to store large amounts of blood and absorb water rather than to digest protein, as with most mammals. *Adapted from H. Gunderson (1976).*

5. The small intestine is thin-walled and twice as long as the stomach.
6. The kidneys have a unique excretory ability linked with feeding and roosting behavior (McFarland and Wimsatt 1969).
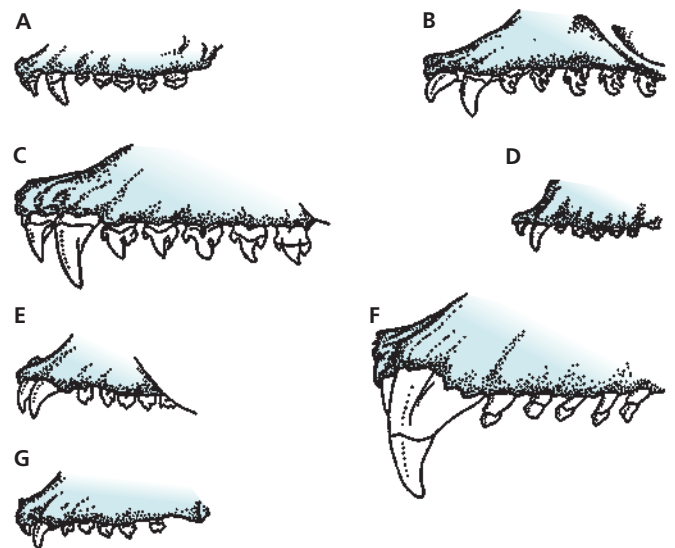
Figure 7.11 Pinniped dentition. Comparison of the dentition of seals: **(A)** harbor seal (*Phoca vitulina*); **(B)** crabeater seal (*Lobodon carcinophagus*); **(C)** leopard seal (*Hydrurga leptonyx*); **(D)** ringed seal (*P. hispida*); **(E)** Ross seal (*Ommatophoca rossii*); **(F)** elephant seal (Genus *Mirounga*); **(G)** bearded seal (*Erignathus barbatus*). The teeth of the upper and lower jaws of the crabeater seal **(B)** intermesh to form sieves adaptive for straining krill from the sea. *Adapted from Bonner (1990).*

Also, the humerus is strong and well developed. It supports a thumb that is unusually long and equipped with 3 pads that function like a sole. The forelimbs are unique and greatly aid terrestrial locomotion (Altenbach 1979). It detects vascular areas of its victims by use of specialized heat-sensitive pits surrounding its nose (Kurten and Schmidt 1982). Bats typically land on the ground near the leg of the host and climb or jump to a feeding site, usually the legs, shoulders, or neck. The upper incisors and canines are used to remove a small piece of skin from the victim or make an incision several millimeters deep. Movement of blood is facilitated by several anticoagulants in the bat's saliva. The flow of blood is maintained by peristaltic waves of the tongue as the bat rapidly licks and continuously abrades the wound. Up to 13 *Desmodus* at a time have been observed feeding on the neck of a cow, with a feeding time of 9–40 minutes. Within a 3-hour period, 7 bats may feed from the same wound, one after another.

The long and highly vascularized stomach of *Desmodus* does not function for protein digestion as in most mammals. Rather, it is important in the storage of blood and the absorption of water to concentrate the blood. Average consumption of blood in the wild is about 20 mL/day (Wimsatt and Guerriere 1962). Bats may consume up to 50% of their body mass in blood per night, which could impose serious constraints on their ability to fly. Vampire bats cope with this potential problem by employing a unique "two-phase" renal function: in the first phase, which occurs at the feeding site, water is excreted; during the second phase, which takes place at the roost, urine is concentrated. About an

hour after feeding, bats rapidly lose much of the water taken in with the blood meal—about 25% of the ingested blood is excreted as urine. This weight loss is essential to enabling the bats to fly back to the roost. At the roost, digestion of the partially dehydrated blood continues. Bats concentrate wastes and thus excrete highly concentrated urine. The kidney of vampire bats may surpass that of many desert mammals in its ability to concentrate urine and thus conserve water. In addition to relying on superb kidney function for water conservation, vampire bats practice blood-sharing at the roosting site by regurgitating blood into the mouth of another bat (Wilkinson 1985, 1987; Altringham 1996).

This food-sharing is a fascinating social behavior—and a rare example of **reciprocal altruism** (Carter and Wilkinson 2013a, 2015, 2016, 2017; Carter and Leffer 2015; Carter et al. 2017; Wilkinson et al. 2016). Interestingly, vampire bats may starve to death if they do not eat for about three days. In roosting colonies of females (males roost individually), a bat that has recently eaten will regurgitate blood to a roost-mate that is close to starvation. Food-sharing even occurs between unrelated individuals, but only between bats that have a close roosting association—that is, sharing occurs with those bats who can return the favor when necessary.

Aquatic Carnivores

Cetaceans that feed on small marine organisms show a second type of specialized dentition called "baleen." Baleen whales (the mysticetes) are filter, or suspension, feeders—that is, they strain small organisms, known collectively as "plankton," from the water by use of the baleen sieves in the front of their mouths (Pivorunds 1979; Voelker 1986; Lambertsen et al. 1995). The structure and function of baleen and feeding habits of the mysticetes are detailed in Chapter 20.

Although baleen whales are touted as the filter-feeders par excellence, they are equaled by one of the pinnipeds—namely, the crabeater seal (*Lobodon carcinophagus*), which is distributed along the leading edge of the Antarctic pack ice and is a major consumer of **krill**. The population consumes up to 160 million tons per year (Øritsland 1977; Bonner 1990; Croll and Tershy 2002; Heithaus and Dill 2002). The
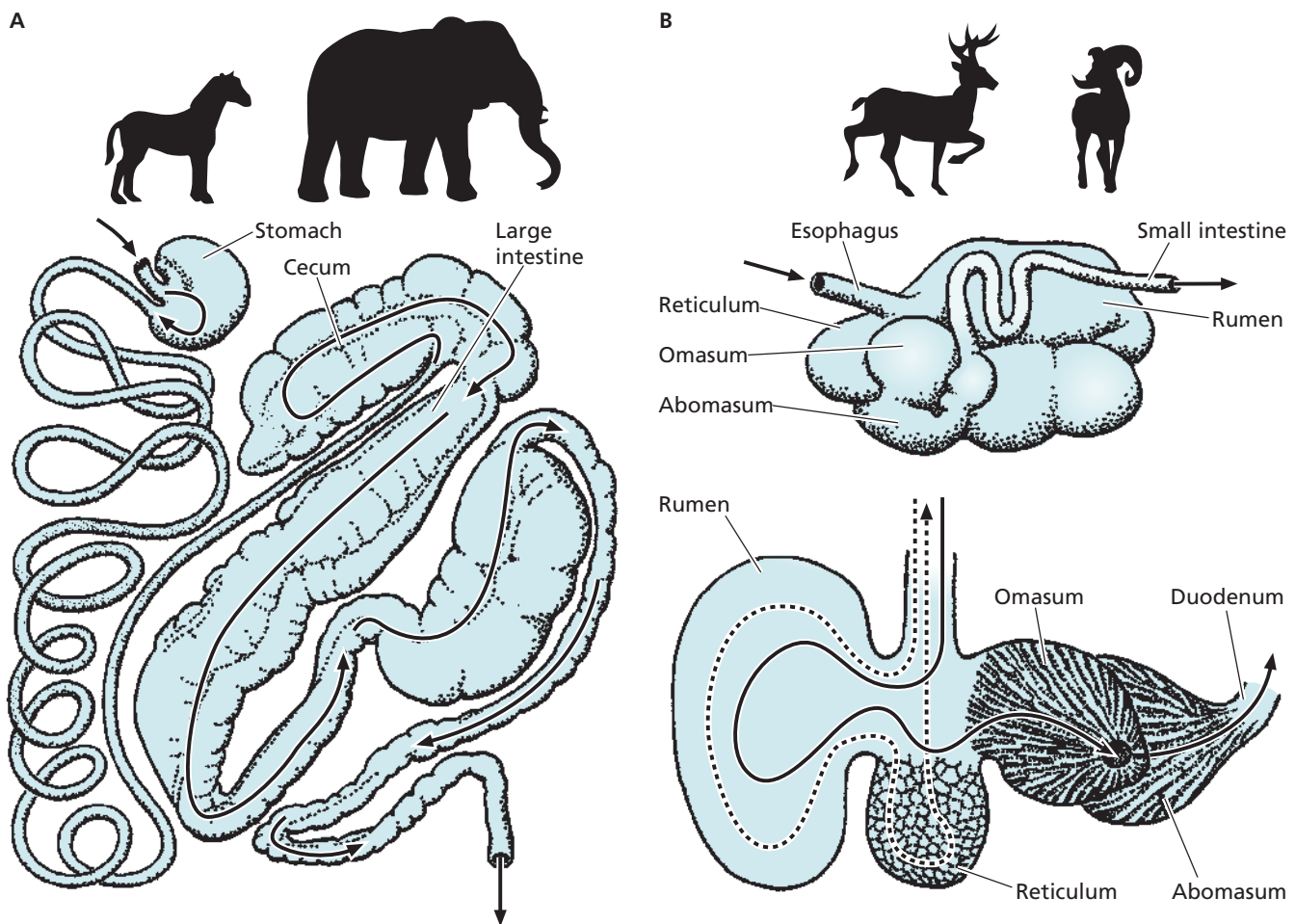
Figure 7.12 **Hindgut and foregut fermentation.** Two digestive systems of herbivorous mammals: (**A**) Hindgut fermentation (monogastric digestive system) is characteristic of perissodactyls, such as horses, zebras, asses, tapirs, and rhinoceroses, in addition to other herbivores such as elephants, lagomorphs, and rodents. (**B**) Foregut fermentation (digastric digestive system) is typified by artiodactyls, such as cervids and bovids, and by kangaroos and colobus monkeys. *Adapted from Pough et al. (2005).*

teeth of crabeater seals are well adapted for straining krill from the sea. Their cheekteeth possess elaborate cusps (Figure 7.11; see also Figure 18.31) such that when the jaws close, the cusps intermesh to form an effective sieve for separating krill from the water being forced out of the mouth. Unlike baleen whales, crabeater seals are selective feeders, and foraging is directed at individual prey rather than large masses. This eliminates the amount of water taken in, and thus a less extensive filtering system is required. Seals locate a swarm of krill and direct their snouts to the prey. By depressing the floor of their mouth, they effectively suck the prey into their mouth. Once it is inside, the jaws are closed, and the tongue is raised, expelling excess water and filtering the krill through the matrix formed by the interlocking lobulate cheekteeth. When a sufficient bolus of food is collected in the mouth, it is swallowed. The average meal of krill for a crabeater seal is about 8 kg (Øritsland 1977).

Predators that eat fish are **piscivorous** (meaning "fish-eating"). At least three species of bats are known to capture and eat fish: the greater bulldog bat (*Noctilio leporinus*), the fish-eating bat (*Myotis vivesi*), and the large-footed bat (*M. adversus*; Brooke 1994; Nowak 1994; Otalora-Ardila et al. 2013, 2017). Bulldog, or fisherman, bats are remarkable for their structural and behavioral modifications for capturing and consuming fish. Bulldog bats (the name stems from their large, jowl-like upper lip resembling that of a bulldog—see Figure 21.25) are characterized by unusually long hind limbs and large feet equipped with sharp, recurved, and laterally flattened claws. Bulldog bats employ echolocation to detect ripples caused by fish swimming near the surface of the water (Brown et al. 1983; Wenstrup and Suthers 1984; Altringham 1996). They skim low, dragging their feet through the water with limbs and hook-like claws rotated forward, which act as a gaff (fishing spear). Once gaffed, fish are quickly transferred to the mouth, where long, thin canines combine with large upper lips and elastic cheeks to form a sort of internal pouch to secure the slippery fish. Fish up to 8 cm long may be captured, and from 30 to 40 fish may be taken per night. The bulldog bat usually forages over small pools, slow-moving rivers, or sheltered lagoons (Bloedel 1955; Wenstrup and Suthers 1984; Altenbach 1989; Findley 1993; Brook 1994; Nowak 1994, 1999; Schnitzler et al. 1994).

Among mammals, piscivory is common in seals, sea lions, and dolphins. Toothed whales, porpoises, and dolphins (Odontocetes) are fish and squid specialists (see Table 20.1; Figures 20.3 and 20.6). They have numerous, small, simple teeth that are all alike (homodont). To optimize prey capture, the mouth of a porpoise or dolphin forms a fish trap similar to that used by other fish-eating vertebrates, such as gars, crocodiles, and mergansers. The adaptive value of this morphology is clear: fish are active and slippery and must be trapped and swallowed quickly to prevent their escape. Killer whales (*Orcinus orca*) are the largest predators that take other mammals. They are opportunistic feeders that consume fish, squid, baleen whales, and smaller cetaceans, pinnipeds, penguins, and other aquatic birds, and marine invertebrates. Foraging success is optimized by cooperation. Pods vary from 4 to 40 individuals, with adults and older juveniles cooperatively herding fish, aided by underwater vocalizations. Leopard seals (*Hydrurga leptonyx*) represent the top-level predators in the Antarctic ecosystem (Hiruki et al. 1999; Hall-Aspland and Rogers 2004), where they feed on krill, cephalopods, crustaceans, fish, seals, and penguins. The diet tends to vary with the age of the seals, with juveniles consuming primarily krill and adults shifting to penguins and seals. From January to March, penguins form the staple in the diet of leopard seals in the Antarctic (Siniff and Stone 1985). Sperm whales (Family Physeteridae) feed primarily on squid. When consumed, the beak of a squid may act as an irritant to stimulate the production of ambergris from the stomach and intestines of the whale (Macdonald 1984; Voelker 1986). **Ambergris,** once used as a fixative in the cosmetic industry, is a form of excrement from sperm whales. One lump taken from a sperm whale in the Antarctic weighed 421 kg (926 lb; Slijper 1979).

As in the odontocetes, the jaws and teeth of pinnipeds are adapted for grasping prey, not chewing it, and most prey are swallowed whole. Because meat requires only a short period for digestion compared with vegetable matter, one would expect pinnipeds to have a short alimentary canal (see Figure 7.2). This is not the case with some seals, however; an adult male southern elephant seal (*Mirounga leonina*) possessed a small intestine 202 m in length—42 times its body length. The reason for this long gut is unknown. Like other carnivorous mammals, seals have a relatively short cecum, colon, and rectum.

HERBIVOROUS

Herbivory

Herbivorous (meaning "plant-eating") mammals consume green plants and thus constitute the base of the consumer food web. Plant food is far more abundant than animal food, but its energy content is lower. Gaining access to the protein within leaves and stems is difficult due to the tough fibrous cell walls of plants. We can divide herbivores into two main groups: (1) browsers and grazers, such as the hoofed mammals—the Perissodactyla and Cetartiodactyla (see Chapter 19)—and (2) the gnawers—the Rodentia and Lagomorpha (Chapter 16). Other important herbivores are the kangaroos, wallabies, wombats, langurs, sloths, elephants, and hyraxes, as well as the aquatic grazers such as manatees and dugongs. It is noteworthy that over one half of the extant species of bats uses plants as food or for shelter (Fleming 1993; Kunz 1996; Kunz and Fenton 2003; Patterson et al. 2003). Herbivores feed on a great diversity of foods, including grasses, leaves, fruit, seeds, nectar, pollen, and even the sap, resins, or gums of plants. Herbivores share unifying characteristics in the design of the skull, teeth, and alimentary canal, which are adapted for feeding on cellulose-rich herbs and grasses for which mammals lack

digestive enzymes. In general, herbivorous mammals are typified by skulls in which canines are reduced or absent (see Figure 7.1) and broad molars are adapted for crushing, shredding, and grinding fibrous plant tissue (see Figure 7.8). Rodents are characterized by the presence of a single pair of ever-growing, chisel-like incisors on both the upper and lower jaws. Lagomorphs have an additional pair of "secondary" upper incisors that are located immediately behind the first pair. Because canine teeth are absent, a wide gap (diastema) occurs between the incisors and cheekteeth. Plant-eaters typically possess a long intestine with either a simple stomach (nonruminant herbivores) or one that has internal folds and is divided into several functionally different chambers (ruminant herbivores; see Figure 7.2).

Omnivorous mammals, such as primates, bears, pigs, and some rodents, possess teeth with low crowns (brachyodont), well-developed roots and root canals, and rounded cusps (bunodont) adaptive for a generalized diet (see Figure 7.8). These teeth are not very effective in shredding and grinding tough fibrous plant tissue, and several modifications of this basic design have evolved among herbivores. In response to dietary needs, elephants and some rodents have cheekteeth characterized by transverse ridges, or lophs, on their grinding surface (lophodont). In the ungulates, wear on the surfaces of the teeth from chewing on course plant tissue produces and maintains the transverse ridges. Because enamel, dentine, and cement have different degrees of hardness, continuous grinding maintains the rough surface. In horses, these teeth are hypsodont (high-crowned) with complex, folded ridges on the surface. In **ruminant cetartiodactyls**, such as goats, cows, and deer, the grinding surfaces of the teeth have longitudinal crescents, or "half-moons" (selenodont), adaptive for breaking down tough plant material.

The jaw muscles of herbivores differ from those of carnivores. The movement in mastication is from side to side (not up and down, as in carnivores), and the upper cheekteeth slide across the complementary surfaces of the lower teeth in a sweeping motion. For herbivores, the major muscles involved in mastication are the masseter and pterygoideus, and the temporalis muscle is smaller than that found in carnivores (see Figure 7.8). Nonruminant grazers such as horses use their large incisors to snip and cut tough, fibrous stems. They consume large quantities of fibrous food and have robust lower jaws supporting a large masseter muscle used primarily for closing the jaw. Because leaves require less mastication than grasses due to their lower fiber content, the lower jaw and masseter complex of deer and other browsers are not as pronounced as in horses. Moreover, unlike horses and other perissodactyls, ruminant cetartiodactyls have lost their upper incisors, and they crop foliage by use of the lower incisors biting against a callous pad on their upper gum, which acts as a sort of cutting board. Cows are well adapted for eating grasses, which they pull free by twisting them around their mobile tongue held against their lower incisors. After biting off the foliage, the cow holds it within the diastema before moving it back to the cheekteeth for grinding. A distance between the lower incisors and the

cheekteeth offers the advantage of allowing for a narrow snout that can penetrate into small spaces to crop food, as seen in smaller deer, antelopes, and rodents (see Figure 7.1).

Although the specialized teeth of herbivores effectively shred and grind the cell walls of plant tissue and release their contents, only certain enzymes can digest cellulose. Mammals, however, do not produce these **cellulolytic** (cellulose-splitting) enzymes, so they rely on symbiotic microorganisms residing in their alimentary canal. These microorganisms break down and metabolize the cellulose of plants and release fatty acids and sugars that can be absorbed and used by the mammal host. Rodents and lagomorphs become inoculated with the appropriate anaerobic protozoans and bacteria by eating maternal feces, whereas young ungulates commonly consume soil to acquire their microorganisms. Ungulates have evolved two different systems for breaking down cellulose: foregut fermentation (rumination) and hindgut fermentation (Putman 1988; Robbins 1993).

Foregut Fermentation

Rumination (requiring a **digastric digestive system**), also called **foregut fermentation**, is typified by cetartiodactyls such as camelids, giraffids, hippopotamuses antilocaprids, cervids, and bovids (see Chapter 19), as well as by kangaroos, koalas, sloths, lemurs, proboscis monkeys, and colobus monkeys (Freudenberger et al. 1989; Alexander, 1993b; Oates et al. 1994; Stevens and Hume 1996; Logan, 2003; Moquin et al. 2010; Macandza et al. 2012; Perrin 2013; Rivals et al. 2014; Matsuda et al. 2015). Foregut fermenters possess a complex, multichambered stomach with cellulose-digesting microorganisms. Colobus monkeys have mastered the art of rumination. For example, like other colobus monkeys, the mantled guereza (*Colobus guereza*) is able to digest leaves and other plant fibers by virtue of a large, multichambered stomach housing an impressive bacterial fauna adapted to breaking down course fibrous foods (Figure 7.13). After food is procured by cropping or grazing, it immediately passes to the first and largest chamber of the network, the **rumen** (see Figures 7.2 and 7.12). Here, the food is moistened and kneaded and thereby thoroughly mixed with microorganisms that ferment the food. Large particles of food float on top of the rumen fluid and pass to the second chamber, the **reticulum**—a blind-end sac with honeycomb partitions in its walls. The reticulum is where a softened mass called the "cud" is formed. Fermentation occurs in both the rumen and reticulum, and both absorb the main products of fermentation, which are short-chain fatty acids. When the animal is at rest, this softened mass is regurgitated, allowing the animal to "chew its cud," or "ruminate." At this time, the mass is further broken down by a potent enzyme, **salivary amylase**. The food is then swallowed a second time and enters the third chamber, the **omasum**, where muscular walls knead it further. The fourth, and final, chamber, the **abomasum**, is the true stomach. Here, digestive enzymes that kill any escaping microorganisms are secreted, and protein digestion is

completed. Digested material then passes into the small intestine, where the products of microbial digestion and acid digestion are absorbed. Some additional fermentation and absorption occur in the cecum.

Hindgut Fermentation

The **monogastric system**, which is needed for **hindgut fermentation**, is characteristic of horses, zebras, tapirs, rhinoceroses, howler monkeys, elephants, lagomorphs, hyraxes, rodents, and some arboreal marsupials (Prins and Kreulen 1990; Alexander 1993b; Macandza et al. 2012) (see Figures 7.2 and 7.12). Hindgut fermenters masticate food as they eat, initiating digestion with salivary enzymes. Digestion continues by enzymatic activity within the simple stomach, and food then moves rapidly into the small intestine as new food is eaten. Unlike ruminant cetartiodactyls, hindgut fermenters do not regurgitate their food. Nutrients are absorbed in the small intestine. Finely ground particles of food pass from the small intestine into the cecum, and larger food particles move through the large intestine and are passed as feces. Among the hindgut fermenters, the colon acts as the principal fermentation chamber for the larger species, while the cecum fulfills this function in the smaller species (Hume 1989).

The two kinds of fermentation processes that take place in herbivores have clear advantages and disadvantages (Montgomery 1978; Dawson 1995; see Figure 7.13). Foregut fermentation tends to be very efficient because microorganisms begin to break down the plant material before it reaches the small intestine, where it is absorbed. Furthermore, in foregut fermenters, microorganisms from the rumen are themselves broken down by acids in the true

Figure 7.13 **Mantled guereza.** The mantled guereza (*Colobus guereza*) possesses a multichambered stomach with cellulose-digesting microorganisms, which enable them to derive nutrients from highly fibrous foods. Foregut fermentation (also called "rumination") is typified by artiodacyls such as camelids, giraffids, hippopotamuses, antilocaprids, cervids and bovids, as well as kangaroos, sloths, and colobus monkeys.

stomach (abomasum). The resulting material, which contains the carbohydrates and protein synthesized by the microorganisms as well as the products of fermentation, moves into the small intestine and colon. Lastly, the microorganisms in the rumen can detoxify many harmful alkaloids in the plants that foregut fermenters consume.

In contrast, food passes rapidly into the small intestine in hindgut fermenters and is then mixed with microorganisms in the cecum. These animals do not digest the microorganisms present in the cecum and thus cannot exploit this potential source of nutrients. In addition, hindgut fermenters must absorb toxic plant chemicals into the bloodstream and transport them to the liver for detoxification or sequestration.

Efficiency may indeed be the trademark of foregut fermenters; however, hindgut fermenters are able to process material much more rapidly. For example, food moves through the gut of a horse in about 30–45 hours, whereas it may take a cow from 70–100 hours to process food. Hindgut fermenters efficiently digest food high in protein because large volumes of food can be processed rapidly. Furthermore, hindgut fermentation is effective when forage is dominated by indigestible materials, such as silica and resins, because these compounds move quickly through the alimentary canal by bypassing the cecum. In sum, due to their lowered efficiency, hindgut fermenters must eat large volumes of food in a short time. The foregut system is comparatively slow because food cannot pass out of the rumen until it has been ground into very fine particles. Thus, ruminants do poorly on forage containing high levels of resins and tannins because these compounds inhibit the function of microorganisms in the rumen. Furthermore, plants with high silica content break down slowly and thus impede movement of food out of the rumen.

The digestive physiology of herbivores influences their ecology and distribution in several ways. Ruminants benefit most from foods that require an optimally efficient digestive system, whereas the best forage for hindgut fermenters is that which facilitates speed of digestion. Each strategy has advantages for survival in particular ecological niches. Speed of digestion may not be important to ruminant cetartiodactyls. When food is available in the form of tender, short herbage with high protein content, ruminant digestive efficiency pays off. The process of rumination also permits animals to feed quickly and then move to safe cover to chew the cud at leisure. For environments such as the arctic tundra, where food is limited but of high quality, ruminants such as the muskox (*Ovibos moschatus*) and caribou (*Rangifer tarandus*) have an advantage. As we will learn in Chapter 8, some ruminants, such as elands and oryx, also survive well in the deserts of Africa. Although absorption of the products of protein digestion is similar in ruminants and hindgut fermenters, ruminants have the advantage of being able to recycle urea. This allows these mammals to survive with very little water, whereas perissodactyls residing in xeric areas must drink daily to balance the urea in their urine.
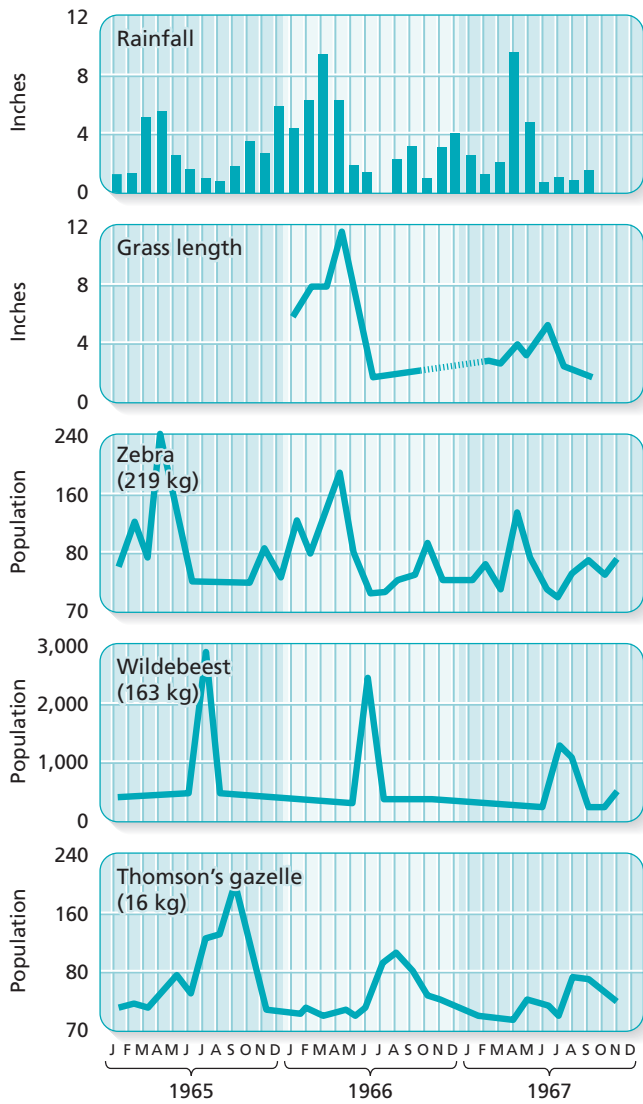
Figure 7.14 Ungulates of the Serengeti. Populations of migrating zebras, wildebeests, and Thomson's gazelles in relation to rainfall and length of grass on the Serengeti Plains of Africa. *Data from Bell (1971).*

When food is of low quality, with high fiber content, yet is not limited in quantity, a premium is placed on the ability to process large amounts quickly. Perissodactyls can survive in regions typified by seasonal drought and poor-quality food—places where ruminants could not process food fast enough to survive.

On the Serengeti Plains of East Africa, dense migrating herds of ungulates influence plant succession and finely partition available resources. They respond to growth of grasses in a predictable sequence (Figure 7.14; Gwynne and Bell 1968; Bell 1971). First, perissodactyls such as the plains zebra (*Equus* [*burchellii*] *quagga*) enter the long-grass communities of the plains and consume many of the longer stems of grasses. Next come large herds of wildebeests (*Connochaetes taurinus*), trampling and grazing the grasses to short heights. The last invasion of ungulates is that of
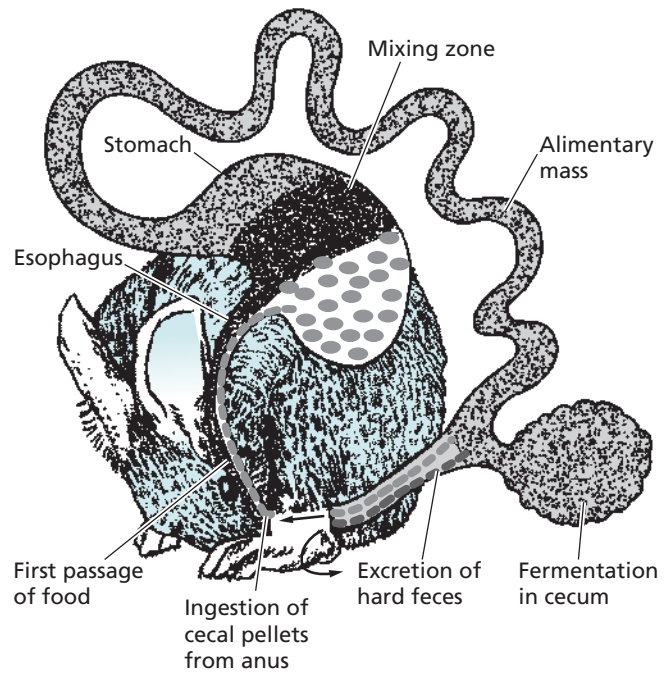
Figure 7.15 Coprophagy. Coprophagy occurs in shrews, rodents, and lagomorphs. The digestive tract of lagomorphs is highly modified for coping with large quantities of vegetation. The alimentary canal has a large cecum, which contains bacterial flora to aid in the digestion of cellulose. *Adapted from MacDonald (1984).*

Thomson's gazelles (*Gazella thomsonii*), which feed on short grass during the dry season. In addition to different spatial and temporal division of resources, these ungulates sort out available food according to different parts of plants. Zebras consume mostly stems and sheaths of grasses and almost no leaves. Wildebeests eat great numbers of sheaths and leaves, and gazelles eat grass sheaths and herbs not consumed by the other two species. Because grass stems and sheaths are low in protein and high in lignin, and leaves are high in protein and low in lignin, it appears that zebras fare poorly and gazelles do quite well. As we learned earlier, however, perissodactyls such as zebras process twice the volume of plant material that ruminant cetartiodactyls can and therefore compensate with quantity (volume) for what their forage lacks in quality. In addition, because zebras are larger than wildebeests and gazelles, they require less energy per unit mass than the smaller mammals.

There are more species of ruminant cetartiodactyls than perissodactyl hindgut fermenters among the ungulates. This may be due in part to the ability of ruminants to recycle nitrogen and digest protein-rich bacteria. As a result of this ability, they do not have to gain all of their amino acids in forage and can focus feeding on specific, preferred species of plants. This independence of forage selection permits ruminants the freedom to partition resources in finer fashion than most perissodactyls can.

Gnawing Mammals

One of the most successful groups of herbivores is the gnawing mammals—namely, the rodents and lagomorphs. Like the ungulates, rodents and lagomorphs cannot produce the enzyme cellulase, so they facilitate the fermentation of fibrous forage with the aid of bacteria and protozoa. As with the perissodactyls, rodents and lagomorphs do not ruminate, and hindgut fermentation occurs in the colon and cecum (see Figure 7.2). The only rodents that lack a cecum are dormice (Family Gliridae), which indicates that their diet possesses little cellulose. Compared with that of ruminants, the stomach of rodents is simple but possesses from one to three chambers (Carleton 1973, 1985; Hume 1994). The small intestine is comparatively short, and the hindgut (colon and cecum) is complex, with the cecum having many spiral folds, recesses, and sac-like expansions (Bjornhag 1994). Within Order Rodentia, variation in morphology of digestive systems is correlated with diet. For example, the sciurids (squirrels, chipmunks, and marmots), which feed on a variety of seeds, nuts, fruits, and herbs, have a much simpler digestive system than grass-eating arvicolines do (voles and lemmings; Batzli 1985; Batzli and Hume 1994). Variation in the morphology and function of the gastrointestinal tracts of voles correlates with diet and thermal stress. For example, high-fiber diets coupled with cold acclimation of arvicoline rodents such as prairie voles (*Microtus ochrogaster*) may result in higher rates of food intake and increases in the size of the hindgut (Hammond and Wunder 1991).

Rodent skulls are characterized by their large gnawing incisors (see Figure 16.3), but they also show features common to all herbivores. The incisors (see Figures 7.1 and 7.8) are used to gnaw through hard plant coverings to reach the tender material inside as well as for nibbling grasses and shrubs. The lips can be folded in behind the incisors to prevent chips of bark or soil from entering the mouth during gnawing. As in other herbivores, a diastema posterior to the incisors results from the absence of canine and premolar teeth. Most mouse-like rodents lack premolars, but jumping mice (Zapodidae) have one on both sides of the upper jaw, and squirrel- and cavy-like rodents have one or two premolars on either side of the jaw. Food can also be held in the diastema before it is passed back to the cheekteeth for processing—this is most obvious in grass-eating herbivores. Among rodents, members of at least 4 families (hamsters, pocket gophers, pocket mice, and squirrels) have either internal or external cheek pouches that open near the angle of the mouth. External cheek pouches can be everted for cleaning. Cheek pouches are well adapted for carrying food; an early biologist discovered a total of 32 beechnuts in the cheek pouches of an eastern chipmunk (*Tamias striatus*; Allen 1938). In herbivores, 3 main masticatory muscles—the masseter, pterygoideus, and digastricus—regulate how these animals shred and grind tough, fibrous food (see Figure 7.8). The arrangement and function of these muscles are responsible for the forward and backward jaw movements of rodents, in contrast to the lateral chewing movements of lagomorphs.

Coprophagy

Digestion of cellulose in hindgut fermenters, such as rodents, lagomorphs, and the marsupial common ringtail, occurs in the cecum. Because there is no regurgitation and the rate of passage of forage is rapid, these mammals process a minimal amount of the fiber when they first ingest plants. As a result, **coprophagy** (refection), the feeding on feces, has evolved in lagomorphs, rodents, shrews, and some marsupials (McBee 1971; Kenagy and Hoyt 1980; Macdonald 1984; Proctor-Grey 1984; Alexander 1993a; Stevens and Hume 1995; Hirakawa 2001; Langer 2002; Shichijo et al. 2013; Naumova et al. 2015). The cecum, located between the small and large intestines, houses bacteria that aid in digestion of cellulose (see Figure 7.15). Most products of digestion, except for certain nutrients such as essential B vitamins produced by microbial fermentation, pass through the gut into the bloodstream. Such minerals and vitamins would be lost if lagomorphs did not eat some of their feces and so pass them through the gut twice. To optimize the uptake of essential vitamins and minerals and enhance assimilation of energy, lagomorphs produce two kinds of feces. The first
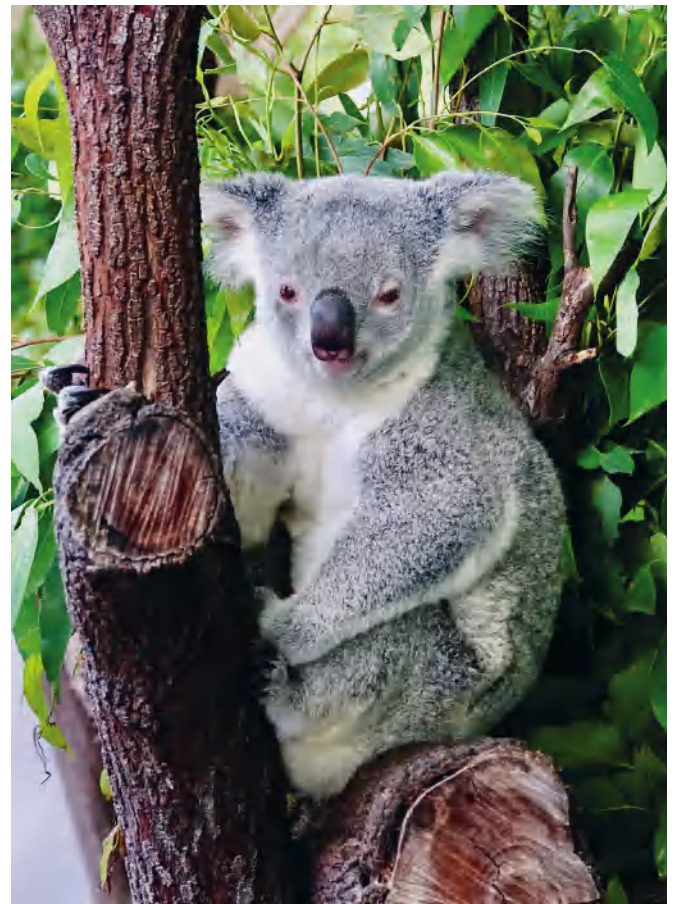
Figure 7.16 **Koala.** The koala (*Phascolarctos cinereus*) occurs in *Eucalyptus* forests and woodlands of Australia. It lives alone or in small groups and is well adapted for arboreal life. Climbing is enhanced by its strong limbs, sharp claws, and two opposable digits on its forepaw and the first toe of the foot.

are moist, mucus-coated, black cecal pellets excreted and promptly eaten directly from the anus. These are stored in the stomach and mixed with food derived from the alimentary mass. The second are hard, round feces that are passed normally. The frequency of coprophagy in rabbits is usually twice daily. Prevention of coprophagy in laboratory rats resulted in a 15% to 25% reduction in growth. Another coprophagous mammal is the mountain beaver (*Aplodontia rufa*), which extracts fecal pellets from its anus individually with its incisors. It caches these in underground fecal chambers to reingest them at a later time. Coprophagy has been documented in about nine species of shrews, including the northern short-tailed shrew (*Blarina brevicauda*) (Merritt and Vessey 2000). The adaptive significance of coprophagy for shrews is unknown, but it may represent a technique of reducing daily food intake and extracting certain essential nutrients and vitamins from available food.

Herbivory is not confined to ungulates, rodents, and lagomorphs. Orders such as Carnivora and Chiroptera have species with strong herbivorous habits. The Orders Rodentia and Chiroptera comprise the greatest number of species of mammals; their success is due in part to adaptive radiation in feeding techniques, including insectivory, granivory, folivory, frugivory, nectarivory, and gummivory (Eisenberg 1981).

Specializations in Herbivory

Granivory

Herbivorous mammals that consume primarily fruits, nuts, and seeds are referred to as **granivorous** (meaning "seed-eating"). Equipped with large, external, fur-lined cheek pouches and a keen sense of smell, heteromyid rodents represent the most specialized seed-eaters. Kangaroo rats (Genus *Dipodomys*), kangaroo mice (Genus *Microdipodops*), and pocket mice (Genera *Perognathus* and *Chaetidipus*) of North American deserts are primarily granivorous (Vander Wall 1995; Schooley et al. 2000; Duval et al. 2005; Murray et al. 2006; Beck and Vander Wall 2010; White and Geluso 2012). Seeds are also the mainstay for tropical and subtropical species of heteromyids (Genera *Heteromys* and *Liomys*), which harvest fruits, nuts, and seeds from shrubs and trees and cache these propagules in underground burrows (Fleming 1970, 1974; Sanchez-Cordero and Fleming 1993). The diversity and availability of seeds in desert ecosystems is a key to the evolutionary success of the heteromyids (Price and Mittler 2006). In terms of the biomass of seeds harvested, heteromyids are rivaled only by ants as important granivores inhabiting North American deserts (Brown and Davidson 1977). Rodents are reported to use over 75% of all seeds produced at certain Mohave and Chihuahuan Desert sites (Brown et al. 1979). In the Mohave Desert of California, Merriam's kangaroo rat (*Dipodomys merriami*) consumed over 95% of the seeds produced by the annual redstem filaree (*Erodium cicutarium*) (Soholt 1973). Maxi-

mum numbers of seeds produced in desert habitats of North America range from 80 to 1480 kg/ha (Tevis 1958; French et al. 1974; M'Closkey 1978). Minimum densities of seeds that remain in the soil years after the last seed crop are rarely below 1,000 seeds/m^2 (Nelson and Chew 1977; Reichman and Oberstein 1977).

As a result of the abundant seed resources and competition with ants, birds, and other rodents, heteromyids have evolved fascinating morphological and behavioral adaptations to optimize their foraging success. All heteromyids cache seeds. They collect large quantities of seeds and store them either in larders within their burrows or scatter hoard them in small, buried caches outside the burrow. They employ their large cheek pouches to collect many seeds in single foraging bouts (Brown et al. 1979). Seeds used by heteromyids are derived primarily from grasses and forbs and are quite small, usually less than 3 mm long and weighing less than 25 mg. Kangaroo rats collect most of their seeds directly from plants by clipping fruiting stalks and removing seeds from felled seed heads or by plucking seeds from fruit located close to the ground. Heteromyids may also collect seeds, primarily located in clumps, from the surface of the soil or strain them from the soil (Eisenberg 1963; Randall 1993; Reichman and Price 1993). Seeds are relocated by olfactory cues coupled with memory (Jacobs 1992; Rebar 1995; Vander Wall 1995). Merriam's kangaroo rat and the Arizona pocket mouse (*Perognathus amplus*) may locate seeds below the surface of the soil by detecting concentrated odor characteristics of buried seeds (Reichman 1981; Smith and Reichman 1984; Reichman and Rebar 1985). Although quite opportunistic in their quest for food, squirrels and chipmunks (Family Sciuridae) are principally granivorous (Smallwood et al. 2001; Steele and Koprowski 2001; Vander Wall et al. 2006). Several genera of Families Cricetidae and Muridae readily cache seeds, including, for example, *Peromyscus* (Vander Wall et al. 2006), *Apodemus* (Abe et al. 2006; Xiao and Zhang 2006), *Leopoldamys*, and *Rattus* (Cheng et al. 2005; Xiao and Zhang 2006).

Folivory

Animals that exhibit adaptations for consuming leaves, stems, buds, and other green portions of plants are referred to as **folivorous** (meaning "leaf-eater"). About 4% of mammals specialize in the consumption of leaves and stems (Eisenberg 1978). Like grazing and browsing mentioned earlier, consuming leaves and stems requires considerable morphological adjustment in dentition, jaw musculature, and gut morphology. In response to predation of leaves by herbivores, plants have evolved diverse chemical defenses (Freeland and Janzen 1974; Belovsky and Schmitz 1994; Foley and McArthur 1994; Dunham and Lambert 2016; De Luna et al. 2017; Finnerty et al. 2017; Crowell et al. 2018). A detailed discussion of plant defenses to herbivory is not within the scope of this chapter. Instead, we choose to highlight specific mammalian practitioners that exemplify

mechanisms adaptive in folivory. We encourage you to examine recent reviews of the ecological and evolutionary consequences of plant-herbivore interactions (Batzli 1985, 1994; Belsky 1986; Palo and Robins 1991; Coley and Barone 1996).

Leaves are difficult to digest and have poor nutritional value. In addition, many leaves contain potentially toxic phenolics and terpines. In spite of these obstacles, three species of marsupials subsist on seemingly unpalatable leaves of *Eucalyptus*: koalas (*Phascolarctos cinereus*; Figure 7.16), greater gliders (*Petauroides volans*), and common ring-tailed possums (*Pseudocheirus peregrinus*) of eastern Australia. These species have evolved a remarkable suite of anatomical, physiological, and behavioral adaptations to consume *Eucalyptus*. Of special interest among these is the koala (Figure 7.17). The bulk of the diet of koalas consists of only about 5 species of *Eucalyptus*. The koala's jaw is very powerful and is equipped with sharply ridged, high-cusped molars that finely grind *Eucalyptus* leaves. Koalas consume about 500 g of leaves each day. The stomach is small, and the small intestine is of intermediate length; the colon and cecum, however, are extremely long and wide (Figure 7.18). The cecum, which is the site of microbial fermentation, is the most capacious of any mammal, measuring 4 times the koala's body length. Hindgut microflora are thought to detoxify certain essential oils of *Eucalyptus*, about 15% of which pass through the alimentary canal without transformation or absorption (Eberhard et al. 1975). Toxic compounds are inactivated in the liver through the action of glucuronic acid and are then excreted (Lee and Martin 1988). The cecum also plays a vital role in absorption of water from *Eucalyptus* leaves: the water content of fecal pellets of koalas is low (about 48%),
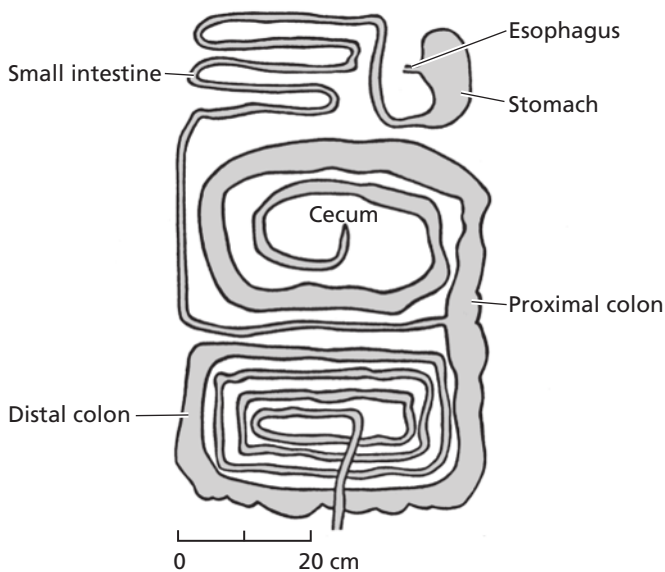
similar to that of camels and kangaroo rats (Schmidt-Nielsen 1964). The frugal water economy of koalas is essential because they do not drink free water and must rely on water derived from their folivorous diet.

Folivory is represented in about 12% of the genera of primates. With this group, notable folivores include the indris, howlers, langurs, gorillas, and colobus and leaf monkeys of Africa and Asia. The diet of gorillas (*Gorilla gorilla*), the largest of all primates, consists of about 86% leaves, shoots, and stems (Fossey and Harcourt 1977), yet their close relatives, the chimpanzees, feed mainly on fruit. Leaves are the staple in the diet of all species of colobus monkeys except Brelich's snub-nosed monkey (*Pygathrix brelichi*), which feeds on fruits such as wild cherries, pears, and cucumbers. Colobus monkeys have flexible food preferences. They consume fruits, flowers, buds, seeds, shoots, sap, and arthropods in addition to leaves. These monkeys are unusual, because, like ruminant cetartiodactyls and kangaroos, they possess a greatly modified forestomach and thus are able to ruminate. Colobus monkeys have large stomachs with a large upper, sacculated region where fermentation by microorganisms occurs and a lower region typified by high concentrations of digestive enzymes. Digestion is further enhanced by enzymes produced by large salivary glands augmented by mastication with high, pointed cusps on their cheekteeth.

Two-toed and three-toed sloths of South America (Genera *Choloepus* and *Bradypus*, respectively) feed almost exclusively on leaves, stems, and fruit. Like other leaf-eating mammals, sloths possess an extremely large, compartmentalized stomach containing cellulose-digesting bacteria. As in colobus monkeys, the sloth's stomach may be one-third its body mass. The colon and cecum of sloths are relatively simple. Feces and urine are passed only once per week, and thus the rectum is quite expanded—an adaptation for storing feces during prolonged periods between defecations.

Contrary to our stereotypical view of Order Carnivora, at least two species of "carnivores" practice folivory. The red panda (*Ailurus fulgens*) consumes mostly bamboo sprouts, roots, and fruit (Zhang et al. 2009). The giant panda (*Ailuropoda melanoleuca*) is well known for its consumption of bamboo shoots but feeds on only about 5 species out of the 20 available. Pandas are unique in possessing an extra "digit" on their forepaws (Schaller et al. 1989). This enlargement of one of the wrist bones acts as sort of a "thumb" to oppose the rest of the digits, enabling pandas to grip and manipulate slender pieces of bamboo with great dexterity. The carnassial teeth of *Ailuropoda* are well adapted for crushing and slicing fibrous plants. Because bamboo is low in nutritional value, giant pandas spend about 12 hours a day consuming up to 40 kg of bamboo, yet they digest less than 20% of what they eat. Much of the stem is passed through the gut relatively unchanged, resulting in many large feces.

Other notable arboreal folivores include the dermopterans (colugos) of Southeast Asia, the prehensile and South

Figure 7.17 Koala digestion. The digestive tract of the koala is well adapted for digesting fibrous leaves of *Eucalyptus*, the staple in its diet. The cecum, measuring up to 2.5 m (8 ft), is the site of microbial fermentation. *Adapted from Harrop and Hume (1980).*

A

B

C

D
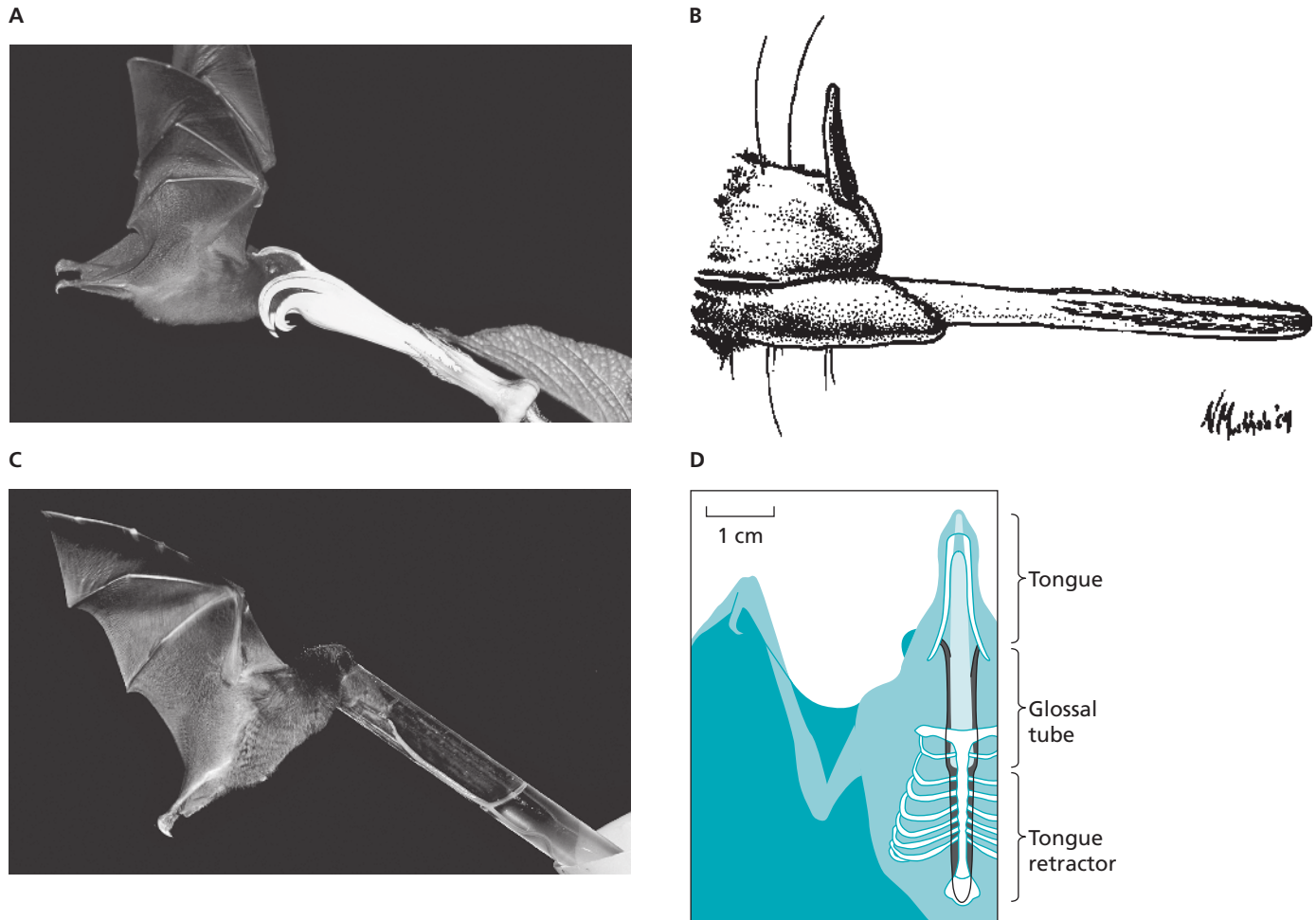
Figure 7.18 **Bat tongues.** Protrusible tongue of the tube-lipped nectar bat, *Anoura fistulata*. (**A**) *A. fistulata* pollinating the specialized flower of *Centropogon nigricans*; because of the long corolla, only *A. fistulata* can reach its nectar. (**B**) Lateral view of the noseleaf, lip, and partially extended tongue showing proximally facing papiillae. (**C**) *A. fistulata* feeding from a test tube filled with sugar water; note its tongue (*tan*) can extend to 150% of body length. (**D**) Ventral view of *A. fistulata*, showing tongue (*tan*), glossal tube and tongue retractor muscle (*black*), and skeletal elements (*white*). *Modified from Muchhala (2006) and Muchhala et al. (2005).*

American porcupines, tree hyraxes of Africa, bamboo lemurs of Madagascar, and about 18 species of rodents (Meier et al. 1987; Santini-Palka, 1994; Nowak 1999). Folivory in plant-visiting bats was once thought to be rare. However, leaf-eating may be quite common and more widespread than we realize. Within the Chiropterans, leaves are consumed by 17 species of Old World "flying foxes" (Family Pteropodidae) and 4 species of neotropical bats (Kunz and Ingalls 1994). Bats are known to masticate leaves of some 44 species of plants in 23 different families (Kunz and Diaz 1995).

Frugivory

Animals that exhibit adaptations to consume a diet of fruit, the reproductive part of plants, are referred to as **frugivorous** (meaning "fruit-eating"). Mammals from several families are known to specialize in the consumption of fruit: pteropodid and phyllostomid bats; phalangerids; tupaiids; and primates such as indrids, lorisids, cercopithecids, and

colobines; and the pongids (Emmons 1991). Because fruit can have a hard outer covering, the teeth of some frugivores are adapted for piercing and crushing. Mammals that subsist on softer fruits typically possess a reduced number of cheekteeth with a bunodont occlusal pattern. Frugivorous civets (Carnivora; Family Viverridae) are distributed across Southeast Asia (Nowak 2005). Although their dentition is adapted for a carnivorous diet, they consume primarily fruits (Nakashima et al. 2010; Nakabayashi et al. 2016). In a Bornean rainforest, civets were strictly nocturnal and consumed three different species of figs.

As mentioned earlier, many species of bats depend on plants as food. The frugivorous bats are distributed within two families: the Pteropodidae of the Old World tropics and the Phyllostomidae of the New World tropics (Fleming 1982, 1988, 1993; Fleming and Sosa 1994; Racey and Swift 1995; Dumont 2003; Patterson et al. 2003). Frugivorous bats are reported to dominate assemblages in lowland forests of the neotropics (Kalko 1998; Horsley et al. 2015).

No fruit- or nectar-feeding "microchiropterans" occur in the Old World (Nowak 1999). Bats play an essential role in the pollination of flowers (chiropterogamy) and dispersal of seeds. Because some seeds exhibit higher rates of germination after passing through the gut of a mammal, this method of dispersal is termed "chiropterochory." Frugivorous bats are either principal or partial pollinators and dispersers of close to 130 genera of tropical and subtropical plants. Bats are particularly important to those species of plants that blossom only at night (e.g., avocados [Genus *Persea*], balsa [*Ochroma lagopus*], durian [*Durio zibethinus*], *Eucalyptus*, figs [Genus *Ficus*], guava [*Psidium guajava*], kopok [*Ceiba pentandra*], mangoes [*Mangifera indica*], papaya [*Carica papaya*], and wild bananas [*Musa paradisiaca*]).

Old World flying foxes and fruit bats (see Chapter 21) are restricted to the tropical forests of Africa, Asia, and the Australian region, where succulent fruits are plentiful. Marshall (1985) reported that they feed on fruits of at least 145 plant genera in 50 families. Most species locate fruit by smell. Old World fruit bats possess comparatively few teeth, and the lower molars are reduced in number and possess large, flat grinding surfaces. The canines are the principal piercing teeth (see Figure 7.1). Rather than biting off and swallowing mouthfuls of fruit, the bats crush the pulp of ripe fruit in their mouth, swallow the juice, and spit out most of the pulp and seeds. They can bite into fruit while hovering, or they may hang onto a branch with one foot and press the fruit to their chest with the other foot and bite into it. If the fruit is small, they may carry it with them to a branch and hang their head downward while they consume it (Nowak 1999; Dumont 2003; Bonaccorso et al. 2014; Chen 2017). Most fruit bats crush pulp from soft fruits and may extract only the juice and reject the pulp and seeds or digest the pulp and excrete intact seeds. Because this activity often occurs at some distance from the harvesting site, seeds are dispersed great distances. Several species of Old World fruit bats, including the Egyptian rousette (*Rousettus aegyptiacus*), Wahlberg's epauletted fruit bat (*Epomophorus wahlbergi*), and the straw-colored fruit bat (*Eidolon helvum*) are principal agents of dispersal of the baobab (*Adansonia digitata*), an important tree in the African savanna (Start 1972; Nowak 1999).

Although phyllostomids may be viewed as generalists (see Chapter 21), over one half of the species consumes some fruit (Dumont et al. 2009; Freeman and Lemen 2010; Madrid-López et al. 2013). Most fruit-eating phyllostomids are in Subfamilies Carolliinae or Stenodermatinae of the neotropics or Brachyphyllinae of the Antilles (Gardner 1977; Findley 1993). Members of Subfamily Carolliinae possess reduced molars and consume ripe, soft fruits such as bananas and figs. In contrast, members of Subfamilies Stenodermatinae and Brachyphyllinae have more robust molars adapted for crushing fruit (see Figure 7.1). Species within Genus *Artibeus*, neotropical fruit bats, possess a short rostrum and a high coronoid process on the dentary, which supports a strong temporalis muscle and enhances a vertical chewing motion. Like many of the pteropodids,

Artibeus species bite chunks from fruit and crush the pulp for its juices with broad, flat posterior teeth. They eat their own weight in fruit each night, and food passes through their alimentary tract rapidly, in about 15–20 minutes. These species are important in the dispersal of seeds of tropical fruits. The Jamaican fruit-eating bat (*Artibeus jamaicensis*) is a generalist frugivore, consuming up to 92 taxa of plants, with figs forming a staple in its diet throughout the range (Gardner 1977; Fleming 1982, 1988; Handley et al. 1991; Kalko et al. 1996).

Nectarivory

Insects and hummingbirds are not the only animals that feed on flowers. Some mammals are also exquisitely adapted to feed on nectar and in the process transfer pollen. **Nectarivorous** (meaning "nectar-eating") mammals are represented by about 6 genera of bats, and the marsupial honey possums (see Figure 10.42). Their skulls are characterized by elongated snouts; small, weak teeth (bats); reduced numbers of teeth (honey possums); and poorly developed jaw musculature. The tongue is long, slender, and protrusile and typically has a brush tip consisting of many rows of hair-like papillae pointing toward the throat (Greenbaum and Phillips 1974; Hildebrand 1995). Bats of Subfamily Glossophaginae (Phyllostomidae) are the most specialized mammalian nectarivores. They are well adapted to feed on fruits, pollen, nectar, and insects (Fleming 1995; Freeman 1995; Flemming et al. 2009; Frick et al. 2014; Zalipach et al. 2016). Flowers of the *Agave* and the saguaro cactus (*Carnegia gigantea*) are a staple in the diet of the big long-nosed bat (*Leptonycteris nivalis*; Hensley and Wilkins 1988), a bat (20–25 g) with high energy demands. During feeding, *L. nivalis* crawls down the stalk of an *Agave*, thrusting its long snout into the corolla of the flower. It licks nectar with its tongue, which can be extended up to 76 mm. Big long-nosed bats emerge from feeding covered with pollen. They are agile flyers and form foraging flocks containing at least 25 bats that feed at successive plants. While feeding, bats circle the plants and take turns feeding on the flowers. Flocks show a cohesiveness typified by minimal antagonistic behavior. Flocking seems to confer the adaptive advantage of an increased foraging efficiency, which is critical for minimizing energy expenditure. Another phyllostomid regarded as an obligate pollen feeder is the Mexican long-tongued bat (*Choeronycteris mexicana*). Analysis of stomach contents of bats from Central America showed a majority of pollen grains from pitahaya (Genus *Lemaireocereus*), cazahuate (Genus *Ipomoea*), *Ceiba*, *Agave*, and garambulla (Genus *Myrtillocactus*; Arroyo-Cabrales et al. 1987).

Possibly the most specialized mammalian nectar-feeding bat is the recently described glossophagine tube-lipped nectar bat (*Anoura fistulata*), an inhabitant of the cloud forests of the Andes Mountains of Ecuador (Muchhala et al. 2005; Muchhala and Serrano 2015). This species coinhabits the cloud forests with two other glossophagines, the tailed tailless bat (*A. caudifer*) and the tube-lipped nectar

bat (*Anoura fistulata*). This unique bat possesses a tongue that extends 84.9 mm—150% of its body length and twice as long as its congeners (Figure 7.18). Its protrusile tongue is longer, relative to body length, than any other mammal—surpassed only by the chameleon among vertebrates. The morphology of its tongue is indeed unique. Whereas in other nectarivorous bats, the base of the tongue attaches to the base of the oral cavity, the tongue of the nectar bat passes back through the neck and attaches in the thoracic cavity, where its distal portion is surrounded by a sleeve of tissue (the glossal tube) that parallels the ventral surface, with the base inserting between the heart and sternum. *A. fisulata* is the exclusive pollinator of *Centropogon nigricans*, a plant that possesses corollas of matching length—80–90 mm. Both *A. fistulata* and pangolins (Pholidota: Manidae) possess glossal tubes to accommodate attachment of their long, protrusile tongues (Chan 1995). Tube-lipped nectar bats and pangolins represent excellent examples of convergent evolution—the evolution of similar morphologies (i.e., long protrusile tongues) by distantly related lineages as adaptive solutions to similar ecological pressures, in this case, availability of ant- and pollen-feeding niches (see Chapter 5 for additional examples of convergent evolution).

Parallel adaptations for nectarivory are well known in long-tongued fruit bats (Genus *Macroglossus*) and blossom bats (Genus *Syconycteris*; Flemming et al. 2009). Common blossom bats such as the southern blossom bat (*S. australis*) of eastern Australia feed on nectar and pollen of a variety of rainforest plants, such as cauliflorous (Genus *Syzigium*), *Banksia*, *Melaleuca*, *Callistemon*, and certain *Eucalyptus*. Blossom bats locate nectar and pollen with their large eyes and keen sense of smell. Blossom bats typically land on an inflorescence and gather pollen and nectar by use of their long snout and brush-tipped tongue—they do not hover while feeding, as do many other nectarivores. These bats are unique in that they do not consume pollen directly from the flower. Instead, their body hairs are covered with small, scale-like projections in which pollen lodges and is then consumed while the animal grooms its fur and wings after a foraging episode. As with other nectarivores and frugivores, pollen rapidly passes through the gut and appears in the feces 45 minutes after ingestion. The majority of protein in the diet of these bats is provided by pollen, whereas sugars in the nectar help to meet energy demands (Law 1992, 1993).

A species of marsupial is the premier terrestrial nectarivore. The honey possum (*Tarsipes rostratus*), the only species within the marsupial Family Tarsipedidae, is found only on the sand plain heaths of southwestern Australia (see Chapter 10). It weighs only 8–12 g (Figure 7.19). Unlike most mammals, this mouse-sized marsupial does not climb by the aid of claws but has digits that are expanded at the tip with short, nail-like structures adaptive in gripping branches. The honey possum locates food by smell, inserting its long snout into a flower and using its protrusile tongue (reaching some 25 mm beyond the nose), which has bristles at the tip to lick pollen from protruding anthers. The stomach is small and may act as a temporary storage compartment, the intestine is short, and there is no cecum. Pollen passes though the gut in about 6 hours.

In addition to chiropterans and other previously mentioned mammals, the following groups are important seed dispersers: primates, tapirs (Genus *Tapirus*), African elephants (*Loxodonta africana*), one-horned rhinoceroses (*Rhinoceros unicornis*), European badgers (*Meles meles*), and foxes (Genus *Dusicyon*).

Figure 7.19 **Nectarivore.** The honey possums, or noolbengers, inhabit the coastal sand plain heaths of southwestern Australia. With their thin tongue, bearing bristles and a tuft at the tip, honey possums lick nectar and pollen from the anthers of native plants, such as bottlebrush and *Banksia*. Honey possums are a significant pollinator of plants of southwestern Australia.

Figure 7.20 **Mycophagy.** Many species of sciurids, cricetids and the marsupial family Potoroidae consume a diet of fungi. Mycophagists such as long-nosed potoroos (*Potorous tridactylus*) are able to digest certain hypogeous fungi, thus accessing more of the fungi's available energy.

Gummivory

Animals that consume primarily plant exudates, such as resins, sap, or gums, are termed **gummivorous** (meaning "gum-eating") (Bearder and Martin 1980; Nash 1986). This peculiar dietary specialization occurs in 8 species of marmosets (Genus *Cebuella*), bush-babies (*Galago senegalensis*; Bearder and Martin 1980), pottos (Genus *Perodicticus*), slow lorises (*Nycticebus coucang*; Wiens et al. 2006), 4 species of petaurid gliders (Genera *Petaurus*), and Leadbeater's possum (*Gymnobelideus leadbeateri*; Oates 1984). All members of Family Cheirogaleidae (dwarf and mouse lemurs) feed on tree exudates; however, consumption of gum is only occasional for *Micocebus*, *Cheirogaleus*, and *Mirza*. Gums are a staple in the diet of *Phaner* and *Allocebus* (Viguier 2004). For example, the diet of the fork-marked mouse lemur (*Phaner furcifer*) of Madagascar consists of close to 90% gum exudates from the trunks and branches of trees. Lemurs use a "tooth comb" (formed by their procumbent lower incisors and canines) to scrape off gum released from the surface of a plant. During feeding, lemurs easily cling to the surface of the trunk by use of needle-sharp claws. They digest gums within the enlarged cecum, which houses symbiotic bacteria. Whereas lemurs are able to scrape off saps and gums exuded as a result of damage from wood-boring insects, marmosets are the only primates that actually gouge holes to liberate plant juices. The incisors of marmosets (Family Cebidae) are composed of thickened enamel on the outer surface and lack enamel on the inner surface, thus producing chisel-like instruments. By anchoring their upper incisors in the bark, marmosets use their lower incisors to gouge oval holes in the trunks of trees. These holes can measure 2–3 cm across, and certain trees can be riddled with channels of holes 10–15 cm in length (Tattersall 1982). As in lemurs, the claw-like nails of marmosets are essential adaptations for clinging to vertical trunks while feeding on sap, gums, and resins. Plant and insect exudates make up the bulk of the diet of petaurid gliders of Australia. Yellow-bellied gliders (*Petaurus australis*) obtain sap from *Eucalyptus* by biting out small patches of bark of the trunk or main branches. After the flow of sap dries up, they move on to a new area. As a result, some trees become heavily scarred after several years of feeding (Goldingay and Kavangah 1991).

Mycophagy

Animals that consume fungi are referred to as **mycophagous** (meaning "fungus-eating"). Fungi of various types are an important component in the diet of a diverse array of mammals, including herbivores, carnivores, and omnivores. Fogel and Trappe (1978) provide a thorough review of mycophagy in mammals, detailing both the specific taxa of fungi consumed by mammals and the mammalian groups known to exhibit mycophagy. Fungi preferred by mammals include the higher Basidiomycetes, Ascomycetes, and Phycomycetes (Endogonaceae) and lichens

(Maser et al. 1978). These groups of fungi are especially well represented in the diets of sciurids, murids, and members of the marsupial Families Potoroidae and Phalangeridae (Maser et al. 1978; Ure and Maser 1982; Maser et al. 1985; Maser and Maser 1987; Taylor 1992; Claridge and May 1994; Johnson 1994; Waters and Zabel 1995; Pastor et al. 1996; McIlwee and Johnson 1998; Mangan and Adler 1999; Orrock et al. 2003; Lehmkuhl et al. 2004; Izzo et al. 2005; Taylor and Southworth 2009;Vernes 2010; Teron and Hutchison 2013).

It is noteworthy that 22 species of primates consume fungi; these include marmosets, gorillas, bonobos, macaques, vervets, mangabeys, snub-nosed monkeys, marmosets, and lemurs (Hanson et al. 2006; Hilario and Ferrari 2010). For most, less than 5% of their feeding time is allocated to mycophagy. However, some primates spend from 12% to 95% of feeding time consuming fungi—namely, buffy tufted-eared marmosets (12%), Japanese macaques (14%), Goeldi's monkeys (29%), and 2 species of snub-nosed monkeys (95%).

Fungi constitute a principal component of the diet of mammals on a year-round basis (Maser et al. 1986; Currah et al. 2000), with seasonal peaks in consumption reflecting availability (Merritt and Merritt 1978). When ingested by mammals, sporocarps pass through the digestive tract and are excreted without morphological change or loss of viability (Trappe and Maser 1976), while the other tissues are digested. The rate of passage of spores varies from 12 to 24 hours in the Cascade golden-mantled ground squirrel (*Callospermophilus saturatus*) and the deer mouse (*Peromyscus maniculatus*), respectively (Cork and Kenagy 1989b). Both subterranean fungi and fungi growing under the bark of trees are important source of food for red squirrels (*Sciurus vulgaris*) (Moller 1983; Gurnell 1987). Caching of such fungi is common, and *S. vulgaris* may hang fungi on branches of trees next to the trunk at heights of up to 8 m; fungal stores will typically be short-lived, with most fruiting bodies gone after 2 weeks (Lurz and South 1998).

Fleshy fungi are 70%–90% water and provide protein and phosphorous to the consumer. Sporocarps of hypogeous (below-ground) fungi are reported to contain high concentrations of nitrogen, vitamins, and minerals (Cork and Kenagy 1989a; Mcilwee and Johnson 1998; Claridge et al. 1999; Azcon et al. 2001). Because fungi often contain complex carbohydrates associated with cell walls, many small mammals are unable to efficiently digest and access their nutritious material. Some mammals possess modifications of the digestive tract that enable them to use fungi as a primary food. Potoroids, however, possess an enlarged foregut supporting fermentation of food by microbial symbionts. Long-nosed potoroos (*Potorous tridactylus*) are able to digest much of the cell wall and sporocarps of certain hypogeous fungi, thus accessing more of the fungi's available energy (Claridge and Cork 1994; Figure 7.20). Vernes (2010) reported fungi in the diets of 6 marsupial species in northeast New South Wales, Australia. Mycophagous species included: the swamp wallaby
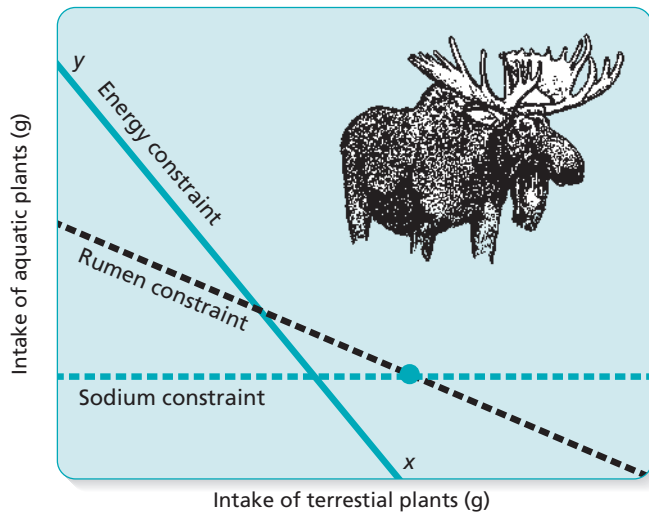
Figure 7.21 Moose feeding. The foraging constraints affecting daily feeding by moose involve (**1**) the need for sufficient energy (*solid line*), (**2**) the need for sufficient sodium intake (*dashed line*), and (**3**) the size of its rumen (*broken line*). Aquatic plants are bulkier but contain more sodium than terrestrial plants. The moose's average intake lies within the triangle defined by the three constraints, near the circle. *Data from Belovsky (1978).*

(*Wallabia bicolor*), the red-necked pademelon (*Thylogale thetis*), the parma wallaby (*Macropus parma*), the brush-tailed rock wallaby (*Petrogale penicillata*), and the rufous bettong (*Aepyprymnus rufescens*).

Certain coniferous and deciduous trees possess a relationship between their root systems and the mycelia of specific fungi. The combination of host and fungus is called a **mycorrhiza** (a mutualistic relationship): trees rely on filaments of the fungi to extract water and nutrients from the soil, and fungi derive nutrition from the sugars of the trees (Trappe and Maser 1976; Dubay et al. 2008). Mycorrhizal fungi do not produce aboveground fruiting bodies, and thus they rely on small mammals to disperse their spores. Many forest-dwelling small mammals, such as shrews, mice, voles, and squirrels, consume large quantities of spores of mycorrhizal fungi, which then pass unchanged through their digestive tracts. Detection of truffles by small mammals is primarily by olfaction (Pyare and Longland 2001, 2002). The dispersal of sporocarps by small mammals serves the essential function of reinoculating habitats for reestablishment of forests following natural catastrophes or deforestation (Green et al. 1999; Loeb et al. 2000; Pyare and Longland 2001, 2002).

OMNIVORY

Most mammals are **omnivorous** (meaning "everything-eating") and notably opportunistic. Each order of mammals contains omnivorous species; however, omnivory is best illustrated in opossums, primates such as humans and many monkeys, pigs, bears, and raccoons (see Figure 7.1). The dentition is versatile, adapted to process a variety of foods. Omnivorous mammals retain piercing and ripping cusps in the anterior teeth but typically have flat, broad cheekteeth with low cusps (bunodont) adapted for crushing food (see Figure 7.8). The stomachs of omnivores such as pigs (*Sus scrofa*) are comparatively simple. The small intestine is elongated, and the colon is large with many folds and bands of longitudinal muscle. The cecum of most omnivores is poorly developed due to the lack of fibrous plant material in the diet. Most bears, including black bears (*Ursus americanus*), brown bears (*U. arctos*), polar bears (*U. maritimus*), Asiatic black bears (*U. thibetanus*), sloth bears (*Melursus ursinus*), and sun bears (*Helarctos malayanus*) are opportunistic feeders and known to consume high-lipid foods (e.g., nuts, grasses and forbs, some tropical fruits, marine mammals, eggs, and reproducing insects) (Stirling and McEwan 1975; Mattson et al. 1992; Joshi et al. 1997; Gende et al. 2004; Steinmetz et al. 2013). The success of raccoons (*Procyon lotor*) in North America is a good example of a mammal that combines omnivory with opportunism to enhance survival. Although raccoons exhibit distinct food preferences, availability largely dictates selection. During spring and summer in eastern North America, *P. lotor* feeds mainly on animal matter, including insects, earthworms, snails, bird eggs, and small mammals. It also feeds on carrion and commonly visits creek edges to search for crayfish, frogs, fish, and other aquatic prey. During late summer, autumn, and winter, fleshy fruits and seeds, such as wild grapes, acorns, beechnuts, and berries, constitute the bulk of the raccoon's diet.

Foraging Strategies

The preceding discussion of dietary types illustrates many aspects of how mammals obtain their food. It also includes some general rules to describe the processes that occur when an animal, such as a mammal, forages for food. These rules apply to all foraging behavior, regardless of the type of diet—thus to nectarivorous bats searching for flowers and to coyotes looking for small mammals or fruit. In addition, when some mammals discover a food source, they hoard the food they find. We conclude the chapter with an examination of patterns of hoarding behavior. Predictions derived from many of the general rules concerning foraging behavior have been tested on a variety of birds, on some other vertebrates, and on insects such as bees. To date, although mammalogists maintain a consistent interest in foraging theory, fewer aspects of this theory have been thoroughly tested on mammals. Part of the problem may be that when the various foraging models are applied to some mammals (ungulates in particular), the models have

proved to be relatively poor predictors (Belovsky 1984; Owen-Smith 1993).

OPTIMAL FORAGING

Models of foraging behavior are created to generate testable predictions about such behavior, which can then be evaluated by empirical studies. One general theoretical framework for analyzing the foraging behavior of mammals is "optimal foraging"; models developed accordingly attempt to predict the combination of costs and benefits that will ultimately maximize the animal's fitness (Charnov 1976; Pyke et al. 1977; Cremona et al. 2015; Emerson et al. 2018). Optimal foraging models involve three types of issues (Stephens and Krebs 1986):

1. The decisions an animal makes while it forages: Should it eat a particular type of food or prey? Should it remain in one place to capture its prey (sit-and-wait behavior) or actively seek out prey (stalking)?
2. The currency involved: What is being maximized?
3. How the constraints or limits of the animal affect its foraging pattern: How large a prey item can it handle? Does the fruit have a hard or soft covering?

For mammals, foraging decisions depend a great deal on past evolutionary history: What particular morphological, physiological, and behavioral traits adapt the mammal for a particular type of diet? Much of this chapter has dealt with the adaptations of the dentition, skulls, and alimentary canals of mammals with respect to various types of diets, ranging from seeds utilized by heteromyids, gerbils, and chipmunks (Price and Correll 2001; Veech 2001; Ovadia and Dohna 2003; McAleer and Biraldeau 2006), invertebrates taken by moles (Catania 2012) to krill consumed by fur seals (Mori and Boyd 2004). Some mammals are omnivores—food generalists that consume a wide variety of food types. Others, such as koalas, are food specialists, being highly adapted to exploit a particular type of food.

Two types of currencies are generally considered when examining foraging behavior: energy (calories) and time. Should the animal minimize its time hunting to gain a fixed quantity of food, or should it maximize its energy intake in a fixed amount of time? A lion spots a potential prey. What "decision rules" does it use to determine its actions? How close is the prey, and how much energy will be needed to pursue and capture it? How big of a meal does it represent? What are the dangers in pursuing this particular prey? Given the time that it will take to pursue and subdue this prey, would the lion be better off if, instead, it went off in search of some other prey? The lion does not actually compute a cost-benefit analysis before acting, but we can use the economic model as a means of generating testable predictions about its behavior (Broekhuis et al. 2013).

Several key constraints influence a mammal's foraging strategy. The first are constraints related to the time spent traveling to find food—that is, search time (Dorning and Harris 2017). Consider the differences between an insectivorous bat that must find swarms or patches of insects and a nectarivorous bat searching for groups of flowers (Pleasants 1989; Jones 1990; Barclay and Brigham 1994; von Helversen and Winter 2003; Hemingway et al. 2017). For smaller mammals, the danger of starvation may be greater than for large mammals, and thus the constraint imposed by time and the need to regularly find food sources affects foraging decisions. The second constraint has to do with the fact that foods vary in how easily their energy "packets" can be extracted by a mammal—that is, handling time. Some foods, such as grasses, require almost no manipulation; they are snipped or chewed off and swallowed. By contrast, some fruits and seeds may require the animal to spend considerable time and energy to extract the nutrition. In an experiment that combined field and laboratory testing, oldfield mice (*Peromyscus polionotus*) made their food selections among millet, sunflower seeds, and peanuts based, in part, on handling time (Phelan and Baker 1992).

A third constraint is that mammals that are themselves potential prey must always balance the need for finding and consuming food with some degree of vigilance. Individual mammals may do this by keeping a wary eye or ear attuned to the surroundings as they feed. Group-living mammals may have various systems for detecting predators and alerting other members of the group. Meerkats (*Suricata suricatta*) feed in groups, and individual members take turns being the sentinel, watching for predators such as snakes or hawks. The sentinel is, of course, sacrificing valuable feeding time, and thus the meerkats rotate this duty to ensure that each individual has sufficient time for energy intake (Ewer 1968; Doolan and Macdonald 1996; Landre et al. 2001; Ford and Goheen 2015; Banasiak and Shrader 2016; Hefty and Stewart 2018; Esparza-Carlos et al. 2018.). Another way to reduce predation risk is to hoard food; by having food stores in a protected location, the mammal does not have to venture forth, exposing itself to potential predators. Hoarding behavior is discussed in more detail in the last section of this chapter. Fourth, some mammals have nutrient constraints. The contrasts between foregut and hindgut fermenters particularly exemplify this point. Moose (*Alces alces*) and Canadian beavers (*Castor canadensis*) must consume both sufficient energy and sufficient sodium to meet their daily needs (Belovsky 1978; Strules and DeStefano 2016), but the capacity of the rumen also must be considered (Figure 7.21). A central challenge for classical foraging theory pertains to patch-use decisions of large herbivores such as deer (*Odocoileus* spp.; Altendorf et al. 2001; Lingle 2002), caribou (*Rangifer tarandus*; Whittington et al. 2011); guanaco (*Lama guanicoe*; Marino and Baldi 2008), moose (Berger 2007; Gervasi et al. 2013), free-ranging bison, and domestic goats (Illius

et al. 2002; Fortin 2003; Courant and Fortin 2012; Shrader et al. 2012).

MARGINAL VALUE THEOREM

A second foraging behavior model examines how animals make decisions about their feeding sites; these are often called "patch models" (Wiens 1976; Bell 1991; Nonacs 2001; Searle et al. 2005; Ferraro et al. 2017; Makin et al. 2018). Many food items consumed by mammals are found in patches, or clumps. Some of the model's questions are associated with locating patches, devising search patterns within patches, and deciding when to leave a patch and search for another and when to return to a patch (if the resource is renewable, such as nectar). For example, if a wild pig locates some acorns, it initially moves from one acorn to the next rather rapidly. Soon, however, the patch becomes depleted and the acorns are more difficult to find. Mapping the path used to find acorns can provide insights concerning the pig's foraging decisions. Finally, at what point should the pig give up on that patch and attempt to locate another, perhaps more profitable, patch?

The marginal value theorem deals with the decisions about when to leave patches (Charnov 1976; Searle et al. 2005). The model relates the energy an animal spends moving between resource patches to the energy that can be obtained in that patch. At some point, the gain in energy relative to the costs of continued foraging in that patch becomes marginal; this is often referred to as the "giving-up time" (McNair 1982). Leaving a patch that is becoming depleted of food means the animal is confronted with the costs of searching for another patch and of traveling to it. The basic question is, based on diminishing returns within a patch, when should the animal leave?

Our discussion of foraging behavior can best be summarized by the following formula:

$$\text{Net rate of energy intake} = \frac{\text{Energy from food} - \left(\begin{array}{c}\text{Search} \\ \text{energy}\end{array} + \begin{array}{c}\text{Pursuit} \\ \text{energy}\end{array} + \begin{array}{c}\text{Handling} \\ \text{energy}\end{array} + \begin{array}{c}\text{Eating} \\ \text{energy}\end{array}\right)}{\begin{array}{c}\text{Search} \\ \text{time}\end{array} + \begin{array}{c}\text{Pursuit} \\ \text{time}\end{array} + \begin{array}{c}\text{Handling} \\ \text{time}\end{array} + \begin{array}{c}\text{Eating} \\ \text{time}\end{array}}$$

Exploring and testing the various components of this formula have been and will continue to be significant research problems for mammalogists. Feeding is, after all, of primary importance for fitness, measured as survival and reproductive success.

FOOD-HOARDING

During autumn in seasonal environments, certain mammals, such as squirrels, are commonly observed harvesting fallen nuts and establishing food stores in preparation for winter. This habit, called **food-hoarding**, or **caching**, has been reported for members of 6 orders and 30 families of mammals (Vander Wall 1990; Vander Wall and Jenkins 2003). Caching confers the advantage of providing a reserve food supply during lean periods. Further, the larder is isolated from competitors and offers protection from predators during feeding. Caching techniques, location, composition, season, and how food is used vary at both the individual and species levels. Caching is performed by employing either larder hoarding (concentration of all food at one site) or scatter hoarding (one food item stored at each cache site). Vander Wall (1990) documents the mammalian taxa that store food and summarizes their food-storing behavior (Table 7.1).

Most mammals that cache food are members of Orders Rodentia or Carnivora. Only one marsupial is reported to store food, the pygmy possum (*Burramys parvus*). The pygmy possum is the only mammal restricted to the alpine and subalpine zones of Australia. It is a true hibernator, and in autumn, it caches seeds and fruits of heathland shrubs as a food reserve for its winter dormancy.

Of the approximately 312 species of shrews, only 7 cache food. This behavior has been documented primarily in the laboratory with food provided *ad libitum* (Merritt and Vessey 2000; Kowalski and Rychlik 2018). Among shrews, the premier scatter-hoarder is the northern short-tailed shrew. European moles (*Talpa europaea*) collect and cache earthworms and insect larvae. After mutilating the head segments of earthworms, moles cache the worms in chambers and walls of galleries near the nest as food for the winter. When soil temperature increases in the spring, some of the remaining worms, trapped in the galleries, may regenerate a head and burrow to escape (Gorman and Stone 1990).

Members of five families of carnivores cache food: the canids, ursids, mustelids, hyaenids, and felids (Vander Wall 1990; Skelpkovych and Montevecchi 1996; deRuiter and Berger 2001; Mattson 2004; Careau et al. 2008; Lanszki et al. 2011; Inman et al. 2012; Cristescu et al. 2014; Balme et al. 2017; Willebrand et al. 2017). Groups of predators follow several distinctive caching patterns: (1) canids bury prey in shallow surface depressions; (2) felids and ursids do not excavate a hole but rather rake soil and leaf litter over the prey; (3) mustelids either cache the prey in their dens or, like canids, bury it in shallow surface pits; and (4) hyenas may submerge prey in water (Macdonald 1976; Elgmork 1982). Because the food items captured by these predators are usually single carcasses, these predators practice larder hoarding.

The most common hoarders are rodents. They store food in many different locations, usually for periods of more than 10 days. Larder- and scatter-hoarding techniques are employed to cache foods ranging from seeds and nuts to woody vegetation, roots, and invertebrates (Steele and Koprowski 2001; Geluso 2005; Thorington and Ferrell 2006; Vander Wall and Jenkins 2003; Hirsch et al. 2013; Dittel et al. 2017; Dittel and VanderWall 2018; Wang et al. 2018). As winter approaches, eastern chipmunks carry large amounts of food in their cheek pouches and cache

Table 7.1   Mammalian taxa known to store food and a summary of their food-storing behavior

Order Family	Dispersion*	Food Type†	Substrate/ Location‡	Storage Duration§
Marsupials				
Pygmy opossums (Burramydae)	L	S	N	L
Insectivores				
Shrews (Soricidae)	L	I, SM, A, Fi, S	N, B	L
Moles (Talpidae)	L	I	B, N	L
Primates				
Squirrel monkey (Cebidae)	S?	Mi	?	S
Green monkey (Cercopithecidae)	L?	Fr	C	S
Chimpanzee (Hominidae)	S?	Me	?	S?
Carnivores				
Foxes, wolves (Canidae)	S, L	SM, MM, Bi, E, Re	S, Sn, C	S, L
Bears (Ursidae)	S, L	LM	S, L	S
Weasels, mink (Mustelidae)	L	SM	B, N, S, C	S, L
Hyenas (Hyaenidae)	S	Ca	W	S
Tigers, bobcats (Felidae)	S	MM, LM	S, L, Sn, T	S
Rodents				
Mountain beaver (Aplodontidae)	L	V	B	S, L
Squirrels and chipmunks (Sciuridae)				
Chipmunks	L, S	S, Nu, Bu	B, N, S	L
Red squirrels	L	Co, Fu	L, F, T	L
Tree squirrels	S	Nu, Fr, Fu	S, T	L
Ground squirrels	L, S	S, Nu, V	B, S	L
Flying squirrels	S, L	Nu	S, L, T	L
Pocket gophers (Geomyidae)	L	Bu, Ro	B, Sn	L
Kangaroo rats (Heteromyidae)	L, S	S	B, S	L
Beavers (Castoridae)	L	WV	W	L
Mice, hamsters (Cricetidae)				
New World mice	L, S	S, Nu, I	B, S	L
Woodrats	L	V, S, Nu, Fr	N	L
Hamsters	L	S	B	L
Gerbils	L	S, Nu, Ro, V	B	L
Mole-rats	L	Bu, Ro, V	B	L
Voles and muskrats	L	V, Bu, Ro, WV	B, G, Sn, F	L
Old World rats and mice	L, S	S, Nu	B, S	L
Dormice (Gliridae)	L	Nu, Fr, Mi	C	L
Jerboas (Dipodidae)	L?	?	B	L?
Old World porcupines				
(Hystricidae)	S	?	S	?
Agoutis and acouchis				
(Dasyproctidae)	S	Nu, Fr	S	L
Octodonts (Octodontidae)	L	Bu	B	L
Tuco-tucos (Ctenomyidae)	L	Bu	B	L?
African mole-rats (Bathyergidae)	L	Ro, Bu	B	L
Lagomorpha				
Pikas (Ochotonidae)	L	V	G, B	L

From S. B. Vander Wall, Food hoarding in animals, *1990.*

*Dispersion patterns: L = larder; S = scattered.

†Food types: A = amphibians; Bi = birds; Bu = bulbs; Ca = carrion; Co = cones; E = eggs; Fi = fishes; Fr = fruit; Fu = fungi; I = invertebrates; LM = large mammals; Me = meat; Mi = miscellaneous; MM = medium mammals; Nu = nuts; Re = reptiles; Ro = roots; S = seeds; SM = small mammals; V = green vegetation; WV = woody vegetation.

‡Substrates and locations: B = burrow chambers; C = cavity or chamber (not in burrow); F = foliage; G = ground surface; L = litter; N = nest; Sn = snow; S = soil; T = tree trunk and branches; W = water.

§Storage duration: S = short term (generally <10 days); L = long term (generally >10 days).

the food in their burrows for winter use. Preferred items in their winter diet include hickory nuts (Genus *Carya*), beechnuts (Genus *Betula*), maple seeds (Genus *Acer*), acorns (Genus *Quercus*), and a long list of seeds of woody and herbaceous plants. Scatter-hoarding rodents store food items to be used later when food is scarce (Vander Wall 1991,

1993, 1995, 2000, 2006; Downs and Vander Wall, 2009; Zhang et al. 2014).

Gray squirrels (*Sciurus carolinensis*) are principal consumers of acorns of red and white oaks in eastern North America. Steele and colleagues (2001) have demonstrated the importance of embryo excision as a means of long-term

cache management by gray squirrels. Red oaks exhibit delayed germination of acorns and can be stored up to 6 months before they begin to germinate. Acorns of white oaks show no dormancy and germinate in autumn soon after the seeds fall; however, if the embryo is excised, these acorns will remain intact for up to 6 months. *S. carolinensis* cached significantly more acorns of red oak species than those of white oak species; it cached the latter after excision of the embryos. Squirrels excised embryos of red oaks only when the acorns began to germinate following winter. Naive captive gray squirrels, without previous experience with acorns, also cached red oak acorns over those of white oaks and attempted embryo excision on white oaks, which suggests a strong innate tendency for the behavior. Such attempts, however, are often unsuccessful, thus indicating that the behavior is likely perfected through learning (Steele et al. 2006).

Flying squirrels (*Glaucomys volans*) are more selective than eastern chipmunks; hickory nuts may comprise up to 90% of the nuts they store for the winter. Unlike chipmunks (Genera *Neotamias* and *Tamias*) and tree squirrels (Genus *Sciurus*), red (*Tamiasciurus hudsonicus*) and Douglas (*T. douglasii*) squirrels establish large surface middens to cache conifer cones and mushrooms (Fletcher et al. 2010; Archibald et al. 2013; Sundaram et al. 2017). Heteromyids cache primarily seeds, but some species also store fruit, dried vegetation, and even fungi (Rebar and Reichman 1983; Reichman et al. 1985; Reichman and Rebar 1985; Geluso 2005). Foods are cached in burrows or shallow pits on the surface of the ground near entrances to the burrow, or possibly grouped in small haystacks on the ground.

Some small mammals store food in scattered surface caches and underground chambers, whereas others concentrate their cache in a single or just a few larder sites. These foods are consumed during the winter when food supplies are scarce. Eastern woodrats (*Neotoma floridana*) gather and store large quantities of fruit, seeds, leaves, and twigs in large surface dens constructed of sticks (Wiley 1980). Perishability and nutrient content of food influence caching decisions of woodrats (Family Cricetidae; Post and Reichman 1991; Post et al. 1993, 2006; Torregrossa and Dearing 2009) and kangaroo rats (Heteromyidae; Reichman and Rebar 1985; Reichman 1991; Brown and Harney 1993; Jenkins and Breck 1998; Price et al. 2000).

Mole-rats (*Spalax microphthalmus*) of the steppes of Eurasia are noteworthy for establishing many storerooms up to 3.5 m in length, which they pack with rhizomes, roots, and bulbs. These large caches are essential for meeting the energy demands of mole-rats during the long winter on the steppes, when the ground surface is frozen and foraging is restricted. Beavers stockpile in submerged caches below the ice near their dens' woody vegetation, which remains a fresh and handy food supply through the winter. The phrase "busy as a beaver" refers to the energetic activity of beavers generating these food stockpiles. Among lagomorphs, only the pikas (Genus *Ochotona*) establish food caches, called "haypiles." Hay-gathering behavior is common to most species of pikas. The American pika (*Ochotona princeps*) collects green vegetation during late summer and autumn and establishes haypiles under overhanging rocks within talus (rubble or scree) deposits (see Chapter 16). Haypiles function as a source of food during winter as well as serving as a safeguard against an unusually harsh or prolonged winter (Conner 1983; Dearing 1997a,b; Smith 2008; Morrison et al. 2009; Varner and Dearing 2014). Size and placement of haypiles vary greatly among different species of pikas. The American pika establishes comparatively large haypiles, weighing up to 6 kg (Millar and Zwickel 1972), and up to 30 species of plants may be found in one haypile (Beidleman and Weber 1958). Daurian pikas (*O. dauurica*) inhabiting the steppes of northern Manchuria establish haypiles weighing 1–2.5 kg (Vander Wall 1990). Pallas's pikas (*O. pallasi*) make haypiles measuring up to 100 cm in height; these are placed on the ground over burrow entrances. They carry pebbles (up to 5 cm in diameter) in their mouth, placing them near the burrow entrance to prevent the hay from being scattered by the wind.

As noted above, most pikas establish impressive haypiles. However, within *O. princeps*, this caching behavior may be flexible and dependent on the length of winter. Talus in the Columbia River Gorge of Oregon is covered in moss year-round and experiences just a few weeks of persistent snowpack each year. Pikas in this habitat construct relatively small haypiles, if at all, and specialize on consuming moss (60% of their summer diet; Varner and Dearing 2014). Consuming moss allows pikas to forage within the confines of talus areas, which may reduce exposure to predators and thermal stress (Varner and Dearing 2013).

SUMMARY

- Just as mammals range in size from shrews to elephants, their food ranges from microscopic organisms to prey that is larger than the predator. Types of food range from those low in calorie content, such as grasses and nectar, to proteinaceous foods, such as insects, blood, and pollen. Food may be highly restricted, such as underground fungi available only during summer, or ubiquitous and available year-round, such as insects in tropical environments.

- Mammals have evolved many fascinating adaptations to procure food. Evolutionarily, the precursor of all mammalian feeding groups was represented by insectivores of the Triassic. Insectivores today include aerial forms (bats) and terrestrial forms (platypuses, shrews, moles, anteaters, echidnas, aardwolves, etc.). These mammals have one thing in common: teeth equipped with sharp cones and blades for crushing insect exoskeletons. Insectivorous mammals also possess additional adaptations that optimize their ability to capture and process prey, such as the toxic bites of shrews for immobilizing prey and the sensitive tactile organs (Eimer's organs) of some talpids for efficiently locating insects below ground.

- Mammals that feed primarily on flesh are called "carnivores" and include the canids, mustelids, felids, hyaenids, and dasyurid marsupials. Carnivorous mammals have sharp incisors and canines as well as a pair of carnassial teeth—a characteristic of meat-eaters. Carnivores possess a keen sense of smell and acute vision and hearing. Some carnivores such as canids rely on intelligence, social organization, and behavioral adaptability to optimize their hunting success. Carnivores hunt prey on land, in the air, and in the water. Three species of carnivorous mammal specialize in the consumption of blood: the vampire bats. The largest of all mammals, the baleen whales, consume the smallest prey: diatoms and krill.

- Herbivorous mammals consume plants and include the ungulates and gnawing mammals. The cetartiodactyls and perissodactyls possess high-crowned cheekteeth with transverse ridges, which are well adapted for shredding and grinding coarse plant material. Ungulates, rodents, and lagomorphs have microorganisms in their alimentary canals that break down and metabolize cellulose. The ruminant cetartiodactyls (foregut fermenters) have a very efficient but slow digestive process. The perissodactyls (hindgut fermenters) have a faster but less efficient digestion. Gnawing mammals (lagomorphs and rodents) and ungulates are unable to produce the enzyme cellulase. Thus, they ferment fibrous plant material using bacteria and protozoa in the alimentary canal. Rodents and lagomorphs possess large gnawing incisors followed by a conspicuous gap (diastema) and a battery of cheekteeth characterized by many peculiar patterns

adapted to consuming a diverse array of foods. Herbivorous mammals that consume seeds are called "granivores" and include mostly desert mammals in Family Heteromyidae. Leaf-eaters, or folivores, must work very hard for minimal nutritional reward. The koala of Australia, with its elongated cecum, and many species of primates, sloths, and the pandas are noteworthy folivores.

- Fruit-eating (frugivory) is characteristic of pteropodid and phyllostomid bats, phalangerids, and certain primates. Megachiropterans feed on fruits of some 145 genera of plants and are important pollinators of flowers and dispersers of plant seeds. This frugivorous niche is filled in the New World by the phyllostomids, notably the Genus *Artibeus*.

- Nectarivorous mammals are represented in about six genera: the flying foxes, the "microchiropterans," and the diminutive honey possums of Australia. Adaptations for consuming nectar and pollen include greatly elongated snouts and long, slender, protrusile tongues equipped with a brush tip for gleaning pollen and nectar from flowers. The champion nectarivore is arguably the tube-lipped nectar bat, *Anoura fistulata* of the Andes Mountains of Ecuador.

- Mammalian gummivores consume the exudates of plants, such as resins, sap, or gums. This unusual dietary specialization is represented by various marmosets, bush-babies, mouse lemurs, pottos, petaurid gliders, and Leadbeater's possum.

- Fungi are important in the diet of many insectivores, herbivores, carnivores, and omnivores, as well as the marsupial Families Potoroidae and Phalangeridae. Many species of rodents, called mycophagists, act as important consumers and dispersers of mycorrhizal fungal spores and thus contribute to forest succession. Further, some 8 groups of primates are reported to consume fungi; however, for most, less than 5% of their feeding time is allocated to mycophagy.

- Various models developed to explain foraging behavior have been tested for mammals. These include the optimal foraging theory, which models dietary decisions, the currency that is maximized (energy or time), and the constraints that affect feeding behavior. Patch models are used where food is distributed in clumps. The marginal value theorem makes predictions about when a mammal should give up feeding in one location and find another patch. These models have been applied to mammalian foraging with varying degrees of success.

- Food-hoarding, or caching, occurs in 6 orders and 30 families of mammals. The techniques, location, and composition of the cache and how the food is used vary greatly depending on the individual, species, and season.

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DISCUSSION QUESTIONS

1. What would the diet of primitive mammals likely have been? What modern mammals possess teeth like those of primitive mammals?

2. Compare the digestive systems of Cetrtiodactyla and Perissodactyla. Comment on their digestive efficiency and speed of processing food. How do the differences in processing food of foregut and hindgut fermenters relate to the ecology of ungulates?

3. How can you distinguish between the skull of an herbivore and that of a carnivore?

4. Of a group of mammals consisting of a bovid, mustelid, primate, and pinniped, which do you predict would have the shortest gut in proportion to its body length? Why?

5. Compare the feeding behavior of right whales to that of rorquals.

6. Explain the mechanism and adaptive significance of the toxic bite of the northern short-tailed shrew (*Blarina brevicauda*). Can you list the other species of "insectivores" that possess a venomous bite?

Environmental Adaptations

Land mammals reside in environments characterized by extremes in temperature, precipitation, and altitude. Marine environments also vary greatly in terms of water pressure at different depths. Different terrestrial mammals may be faced with temperatures ranging from close to –65°C in the Arctic to 55°C in Death Valley, California. Daily fluctuations during winter can be extreme; for example, in Montana, the temperature in one day can plummet from 6°C to –49°C. Summer is no relief for mammals, and a hot spell in western Australia can reach 38°C and last for 162 continuous days. Although marine mammals live in water, they also experience temperature variation ranging from –2°C near the poles to 30°C near the equator. So how do mammals cope with such extremes? This chapter focuses on the diversity of mammalian adaptations that enhance survival in variable environments.

For many years, the terms **warm-blooded** and **cold-blooded** were used to conveniently divide animals into two groups: the vertebrates (typified by high, constant body temperature) and the invertebrates (typified by variable body temperatures). These terms are inaccurate and unscientific, however, as well as being unclear. Thermoregulatory terminology can be tricky and ambiguous, so it should be well defined (Hainsworth 1981; Bartholomew 1982; Hill and Wyse 1989; McNab 2002; Pough et al. 2005; Merritt 2010). The ability of mammals to colonize inhospitable environments is due largely to their ability to use **endothermy**—the maintenance of a relatively constant body temperature by means of heat produced from inside (*endo*) the body. The degree of endothermy varies in both space and time. No animal maintains the same body temperature over all parts of its body. The term **homeothermy**, which refers to the regulation of a constant body temperature by physiological means, is more precise than endothermy (Hill and Wyse 1989). The term **ectothermy** refers to the determination of body temperature primarily by sources outside (*ecto*) the body. This is not necessarily a passive system, and many ectotherms employ behavioral means to regulate their body temperature; for example, lizards will bask in the sun or rest on a warm rock. A similar term, **poikilothermy**, emphasizes the variation in body temperature under environmental conditions, as opposed to focusing on the mechanism by

which the body temperature is maintained. Some examples of poikiotherms are clams, starfish, and many other invertebrates. Mammals and birds that are capable of dormancy—hibernation, daily torpor, and estivation—are referred to as **heterothermic**. In such cases, regulation of body temperature may vary on different parts of the body (regional heterothermy) or at different times (temporal heterothermy). Many species of bats, for example, exhibit temporal heterothermy: they maintain constant body temperature while foraging but permit their body temperature to approach ambient temperature when they rest.

Maintaining an internally regulated body temperature offers numerous benefits for mammals. Both mammals and birds have high metabolic rates—at least 8 times that of ectotherms. In terms of energy expenditure, maintaining such high body temperatures plus high levels of activity is costly, but it has the advantage of enhancing coordination of biochemical systems, increasing information processing, and speeding central nervous system functions. As a result, mammals have a refined neuromuscular system, which enhances their efficiency in capturing prey and escaping from predators. Mammals gain independence from temperature extremes in nature, can extend activity periods over a 24-hour period, and colonize many environments and ecological niches throughout the world. Mammals can match their thermoregulatory pattern to suit a given environment and thus take advantage of nutritional resources year-round.

Endothermy is thought to have evolved from an ectothermal condition probably two to three times in the Mesozoic era. Internal heat production probably evolved in the Late Triassic within the group of mammal-like amniotes in response to selective pressure favoring sustained activity and temperature regulation. The evolution of endothermy in mammals has been the subject of considerable debate (Bennett and Ruben 1979; Farlow 1987; Hayes and Garland 1995; Grigg et al. 2004; Kemp 2006; Lovegrove 2012; McNab 2012).

Heat Transfer between a Mammal and the Environment

Most placental mammals residing in thermally benign environments maintain their body temperature between 36° and 38°C (Cossins and Bowler 1987; McNab 2012). In general, the body temperature of birds is several degrees higher than that of mammals. Monotremes and marsupials, on the other hand, may have a core body temperature ranging from 30° to 33°C, but they thermoregulate quite well. To keep a constant body temperature, mammals must maintain a delicate balance between heat production (energy in) and heat loss (energy out)—thermodynamic equilibrium—to survive (Porter and Gates 1969). Heat is produced through metabolism of food or fat, cellular

metabolism, and muscular contraction. The factors affecting the exchange of energy between a mammal and the environment are sunlight (solar radiation), reflected light, thermal radiation, air temperature and movement, and the pressure of water vapor in the air (Figure 8.1). The properties of a mammal that influence the exchange of energy are metabolic rate, rate of moisture loss, thermal conductance of fat or fur, absorptivity to radiation, and the size, shape, and orientation of the body. Most of the heat produced by mammals is passively lost to the environment by **radiation**, **conduction**, and **convection** (air movement) to a cooler environment and by the **evaporation** of water. Mammals must adjust their energy balance to meet different demands in their environment.

Temperature Regulation

As mentioned in Chapter 6, mammals regulate body temperature by continuously monitoring outside temperatures at two locations: on the surface of the skin and at the hypothalamus. The hypothalamus, or mammalian "thermostat," is located in the forebrain below the cerebrum and operates by comparing a change in body temperature with a reference temperature, or set point. Each species may have a different **set point**, or comfort zone, which is set at the hypothalamus. For most eutherian mammals, heat is generated by muscle contraction (shivering), brown fat (nonshivering thermogenesis), and activity of the thyroid gland. In marsupials and monotremes, heat production is due primarily to the activity of skeletal muscle (Augee 1978; Nicol and Andersen 1993). For mammals residing in variable environments, body temperature is maintained around a given set point, with each mammal's set point determined by such factors as insulation, behavioral postures, activity levels, and microclimatological regimes.

Adaptations to Cold

Most eutherian mammals maintain a core body temperature of about 38°C. Monotremes and marsupials tend to show lower body temperatures, with echidnas and platypuses exhibiting normal body temperatures ranging from 28° to 33°C (Augee 1978; Geiser 2004; Grigg et al. 1989, 1992, 2003, 2004). For each species, a range of environmental temperatures, referred to as the **thermoneutral zone**, occurs within which the metabolic rate is minimal and does not change as ambient temperature increases or decreases. The upper and lower limits of the thermoneutral zone are referred to as the "upper" and "lower critical temperatures" (Figure 8.2). Decreasing environmental temperatures require that an animal increase its metabolic rate to balance

Sun 6000C

Thermal radiation from atmosphere

Direct solar radiation

Sky temperature 13C

Thermal radiation to sky

40C

Reflected light

27C

Thermal radiation

Rocks

Thermal radiation

Convection

Evaporation

Reflected light   50C

Thermal radiation

Evap.

Thermal radiation

20C

Soil

25C

Core body temperature 39C
Mean surface temperature of skin 32C
Hair on back 45C
Air temperature 30C
No wind movement

Conduction

Figure 8.1 **Energy exchange.** Illustration of the energy exchanges between an animal and its environment under warm conditions. *Adapted from Gordon (1982).*
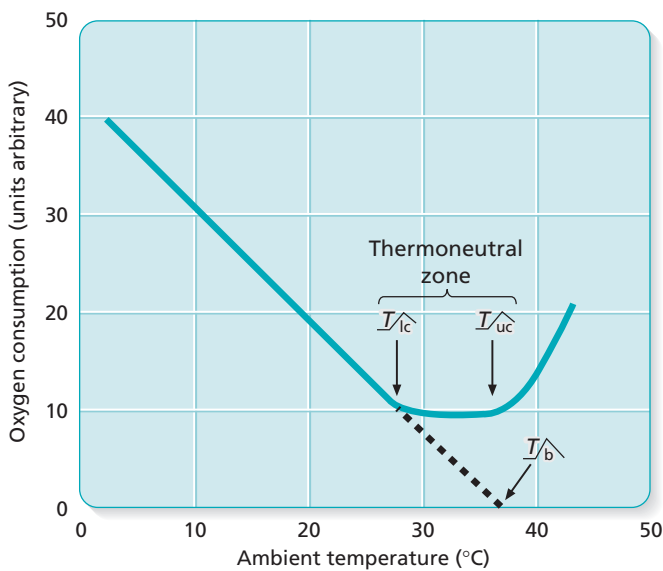
Figure 8.2 **Thermoneutral zone.** Relationship of oxygen consumption to ambient temperature in a hypothetical mammal. T_{lc} = lower critical temperature; T_{uc} = upper critical temperature; T_b = core body temperature. *Data from Bartholomew (1982).*

heat loss. The temperature at which this becomes necessary is called the **lower critical temperature**. This temperature varies from species to species and is seasonally adjusted by the interplay of insulation, behavioral attributes, and integration with the hypothalamus. As environmental temperatures decrease, adjustments in **thermal conductance** (the rate at which heat is lost from the skin to the outside environment) and metabolism are necessary if a species is to maintain euthermy. If this is not possible, death due to **hypothermia** (low body temperature) results. Thermal conductance (C) is expressed as the metabolic cost (MR), expressed in milliliters of oxygen per gram of body mass, for a given time interval per degree Celsius difference between body temperature (T_b) and environmental temperature (T_a):

$$C = MR/T_b - T_a$$
(McNab 1980b, 2002, 2012; Hill and Wyse 1989)

Some mammals and birds from polar regions are so well insulated that they can withstand the lowest environmental temperatures on earth (about –70°C; Figure 8.3) by simply increasing their resting metabolic rate (Scholander et al. 1950; Irving 1972). As we will learn later, however,
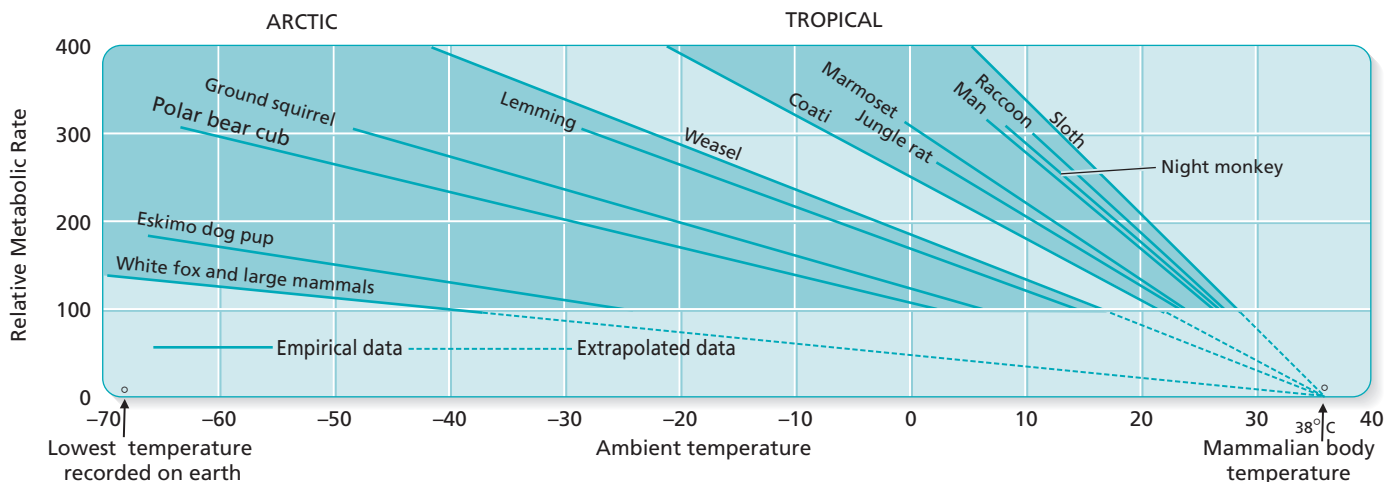
Figure 8.3 Metabolism and temperature. Metabolic rates of various mammals in relation to ambient temperature. The normal resting metabolic rate for each animal, in the absence of cold stress, is given the value 100%. Any increase at lower temperature is expressed in relation to this normalized value, making it possible to compare widely different animals. *Data from Scholander et al. (1950).*

some species can significantly decrease body temperature (undergo hibernation or torpidity) to combat seasonal decreases in food. To maintain body temperature within the thermoneutral zone when residing in cold environments, the individual must reduce the rate of heat loss to the environment. Mammals can achieve this reduction in many different ways: by being larger, possessing enhanced body insulation, changing peripheral blood flow, or modifying behavior (e.g., curling, **piloerection** [the fluffing of fur], nest-building, and huddling in groups). By modifying the pelage, for example, an animal can reduce the gradient of heat flow. Do not forget that hair is a principal means of conserving energy (see Chapter 6). Hair is a poor thermal conductor, so it greatly decreases the amount of body heat lost to the environment by decreasing thermal conductance (Speakman and Thomas 2003).

At the other end of the thermoneutral zone is the **upper critical temperature**, the temperature above which animals must dissipate heat by evaporative cooling to maintain a stable internal temperature. This zone is important to mammals residing in desert environments and is less variable than the lower critical temperature. Mammals employ many different mechanisms, such as seeking shelter in cooler underground burrows and restricting surface activity to hours of darkness, to avoid upper critical temperatures. Furthermore, evaporative cooling can be facilitated by pulmonary means, panting, sweating, spreading saliva, or using a form of dormancy called "estivation." If a mammal cannot combat an increase in temperature by dissipating heat through evaporation or by muscular activity of panting, its body temperature will keep increasing, ultimately resulting in death. The mechanisms used to cope with heat are examined later in the chapter.

ENERGY BALANCE IN THE COLD

Winter is a potentially stressful time for northern mammals (and for mammals from extreme southern latitudes), and they employ a wide array of adaptations to cope with the food shortages and cold stress that the season brings. The key to survival in the cold is to maintain energy balance (Wunder 1978, 1984). Two major features determine the energy needs of mammals in the natural environment: the physical environment and the activities of the mammal (i.e., type and level of behavior, growth, or production of young; Figure 8.4). To meet their energy needs, mammals must acquire energy—they must feed. Given a finite source of food during winter, mammals initially allocate energy to thermoregulation. Temperature regulation is essential for mammals to perform normal functions. For example, a mammal can freeze to death even with abundant food if it cannot assimilate that energy and produce heat fast enough to balance heat loss (turnover capacity). Also, even a mammal with a high heat-generating capacity will perish if there is not enough food (energy) available in the environment to meet its needs. In sum, mammals residing in cold regions must have sufficient food available and sufficient turnover capacity to meet their thermoregulatory needs.

AVOIDANCE AND RESISTANCE

Unlike many species of passerine (perching) birds inhabiting cold regions, most mammals do not undertake long migrations. They remain as residents during winter months and have evolved mechanisms of avoidance and resistance to cold (Table 8.1). Avoidance of cold entails energy conservation, whereas resistance requires energy expenditure—a debt that must be repaid (Speakman and Thomas 2003). Mammals rarely rely on a single mechanism to enhance
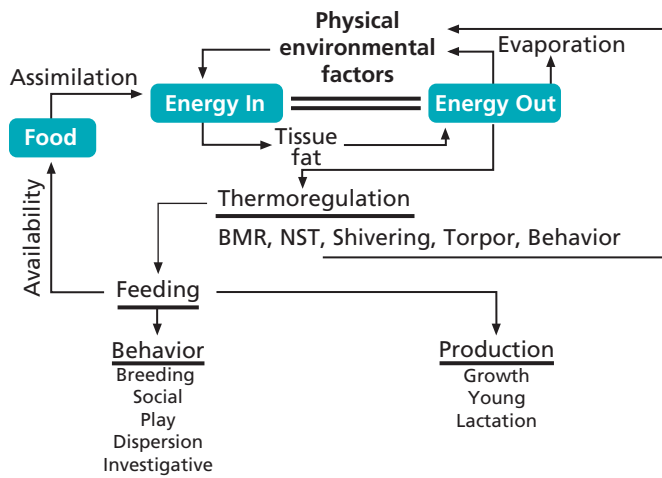
Figure 8.4 **Energy balance.** Conceptual model of avenues of energy balance for a small mammal, indicating a primary cascade for energy allocation. Lines represent both total energy flow and rate functions. *Adapted from Wunder (1978).*
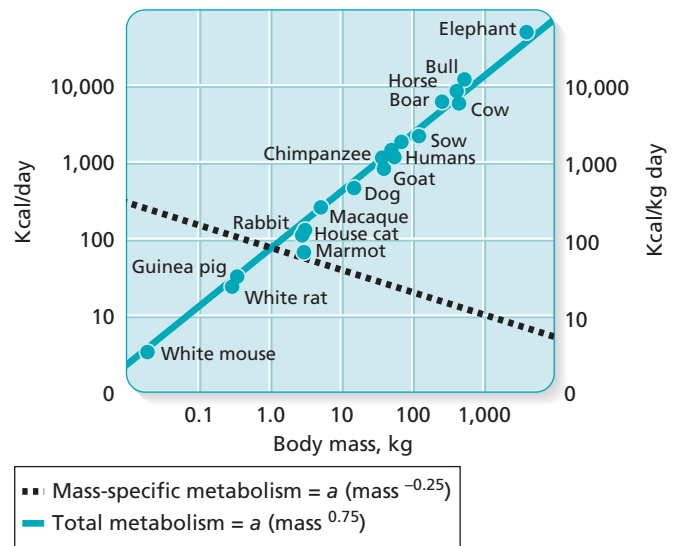
Figure 8.5 **Body size and metabolism.** Linear relationship comparing the log of body size in placental mammals with the log of total metabolism (*solid line*) and the mass-specific metabolism (*broken line*). *a* = proportionality constant (3.8) for placental mammals. *Data from Kleiber (1932).*

Table 8.1   Winter survival mechanisms of mammals
Avoidance
Body size
Insulation
Appendages
Coloration
Modification of microclimatic regime
Communal nesting
Construction of elaborate nests
Foraging zones
Food hoarding
Reduction in level of activity
Reduction in body mass
Dormancy
Resistance
Increase in thermogenic capacity through BMR, NST, shivering

Abbreviations: BMR = basal metabolic rate; NST = nonshivering thermogenesis.

survival in the cold but instead exhibit a suite of strategies that integrate behavioral, anatomical, and physiological specializations finely tuned to a particular habitat and lifestyle (Merritt and Zegers 2002). Thermoregulatory mechanisms vary according to taxon and the attributes of each species.

Avoidance of Cold

Body Size and Metabolism

Does a mammal's size enhance its energy conservation capacity in the cold? To answer this question, we must closely examine the relationship of body size and metabolism. Recall that in euthermic animals, heat production must equal heat loss, and heat loss is proportional to surface area. Resting, or basal, metabolic rate (BMR) is the volume of oxygen consumed per unit of time at standard temperature and pressure (STP) and is known for many species of mammals. McNab (1988) provides rates of basal metabolism and body masses for 320 species constituting 22 orders of mammals. MacMillen and Garland (1989) studied metabolic rates, body masses, climatic data, and latitudes for many species of rodents. Hill (1983) provides an excellent review of the thermal physiology and energetics of the rodent Genus *Peromyscus*.

It makes intuitive sense that larger animals require more food to maintain their body temperature and level of activity. Figure 8.5 (solid line) shows that larger animals consume more oxygen (they eat more food) than smaller animals—this is **total metabolic rate**. To compare oxygen consumption between animals of different sizes, metabolic rate is adjusted for body size and expressed as **mass-specific metabolic rate** (rate of oxygen consumption per gram of body mass). It is apparent that the mass-specific metabolic rate decreases as body size increases (see Figure 8.5, broken line). Given this relationship, we can estimate metabolic rate from the body mass of a species. The relationship of mass-specific and whole-animal metabolism is complex, and authors do not always agree on interpretation of this relationship (Packard and Boardman 1988; Hays and Shonkwiler 1996; Hays 2001; McNab 2002; Smith and Lyons 2011; Lomolino et al. 2012). The slope of the solid line in Figure 8.5 has a value of about 0.75; that is, the metabolic rate scales to body mass to the 3/4 power—this relationship is generally known as "Kleiber's law" (Kleiber 1932, 1961; Brody 1945; Brown and West 2000; Smil 2000;

West and Brown 2005). Glazier (2006:326) contends that "the 3/4-power law is not universal, and should at most be regarded as a statistical rule or trend, rather than as an inviolable law." Although variation in the metabolic scaling exponent has been demonstrated both within and between species, this equation is quite useful in estimating the metabolic rate of mammals of known body mass and has important ecological and evolutionary consequences.

The study of the consequences of a change in size, or in scale, is important in predicting the metabolic rates of mammals. Physiologists define **scaling** as the structural and functional consequences of a change in size or scale (Schmidt-Nielsen 1964; Calder 1984; Nagy 1987; McNab 1988, 2002; Withers 1992). As the size of an animal increases, volume and mass change more rapidly than does area. The change in proportions with increasing or decreasing body size is referred to as allometry and determines many patterns seen in body structure, metabolic rate, and heat flow. An excellent discussion of the relationship of body size and energy requirements is conducted by Speakman and Thomas (2003).

How do the above relationships of body mass and metabolism relate to the geographic distribution of mammals? As we will learn, several ecogeographic rules have been proposed to explain morphological variation on a geographic scale. The best known ecogeographic rule is **Bergmann's rule**. In 1847, Carl Bergmann (translated in James 1970) contended that "on the whole . . . larger species live farther north and the smaller ones farther south." Mayr (1956:105) restricted Bergmann's rule to variation within species, stating that "races of warm-blooded animals from cooler climates tend to be larger than races of the same species from warmer climates." Investigators testing the validity of Bergmann's rule have traditionally compared body size with latitude using latitude as proxy for temperature (Ashton et al. 2000). There is much debate concerning the interpretation and implications of Bergmann's research (Scholander 1955; Mayr 1963; Rosenzweig 1968; McNab 1971, 2002, 2010, 2012; Calder 1984; Lindstedt and Boyce 1985; Geist 1987; Ashton et al. 2000; Olcott and Barry 2000; Smith et al. 2002; Meiri and Dayan 2003; Ochocinska and Taylor 2003; Blackburn and Hawkins 2004; Rodriguez et al. 2006; Briscoe et al. 2015; Alhajeri and Steppan 2016; Gohli and Voje 2016; Brown et al. 2017; Sargis et al. 2018).

Bergmann's rule implies that some energetic advantage may be gained through a decreased surface-area-to-volume ratio. We can further generalize that the amount of heat loss depends on both the animal's surface area and the difference in temperature between its body surface and the surroundings. Large mammals, for example, have less heat loss than small mammals because of their large body mass relative to surface area. For example, visualize a mammal as a cube. With linear dimensions of 1 cm on each side, the cube has a surface of 6 cm^2 and a volume of 1 cm^3. Hence, the surface-area-to-volume ratio is 6:1. If you double the linear dimension of the cube, the total surface area in-

creases to 24 cm^2, and the new volume is 8 cm^3. Now the surface-area-to-volume ratio is 3:1. By doubling the length, heat conservation is enhanced by reducing surface area relative to volume. Granted, mammals are not cubes, but arguments in support of an energetic interpretation of Bergmann's rule follow this logic: a larger mammal has less total surface area per unit volume and thereby benefits from a reduced rate of cooling. This interpretation sounds rather convincing, but there are problems. Small mammals know little about per-gram efficiency and are concerned only with total food requirements; a larger mammal clearly requires more food—an obvious disadvantage for herbivores during winter. Interpretation of Bergmann's rule can be tricky. If we analyze body size of mammals distributed over a wide latitudinal range, we see mixed results. Rensch (1936) showed that 81% of North American species of mammals and 60% of European species of mammals were indeed larger at higher latitudes. However, McNab (1971) was critical of the work of Rensch (1936, 1938) because his data were derived from a field guide rather than from measurements of individuals from different localities. McNab (1971) found that of 47 North American species examined, only 32% (15/47) followed the trend predicted by Bergmann's rule, which was thus invalid. Geist (1987) concurred that Bergmann's rule was invalid; although body size of large mammals initially increased with latitude, it reversed between 53° and 63°N; small body size occurs at the lowest and highest latitudes. However, Ashton and coworkers (2000) isolated problems with the analysis of McNab (1971) and found broad support for Bergmann's rule for all orders and most families of mammals examined (78/110 species examined). Temperature and latitude were strong predictors of body size variation (Ashton et al. 2000; Freckleton et al. 2003). For Order Carnivora Dayan and associates (1991) reported only a minority of species that conform worldwide to Bergmann's rule. Meiri (2004) examined 44 species of Order Carnivora and found patterns of correlation between length of skull and geographic latitude. Investigators found a significant positive correlation between skull length and latitude in 50% of carnivore species examined. In sum, an analysis of the validity of Bergmann's rule must integrate many factors associated with the biology of a species, such as pelage, behavior, temperature and water-related factors, size and type of food, primary plant production, and morphology, to mention just a few (Rosenzweig 1968; McNab 1971, 2010, 2012; Burnett 1983; Steudel et al. 1994; Meiri 2004; Yom-Tov and Geffen 2006, 2011).

For carnivorous mammals, the long, thin shape of weasels (Genus *Mustela*) has distinct disadvantages in cold climates. Their shape exposes a large surface area to the cold air, and their unique feeding requirements dictate that they pursue prey through small crevices and a labyrinth of subterranean runways, which is energetically very expensive. Their mobility would be greatly compromised by a dense, heavy pelage; thus, a short fur is essential for optimal agility. Compared with woodrats (Genus *Neotoma*), weasels have about a 15% higher surface-area-to-mass ratio—they

cannot assume a spherical form by curling as woodrats can. As a result, cold-stressed weasels have metabolic rates 50%–100% greater than less slender mammals of comparable size. So, being long and skinny may facilitate capturing prey, but weasels pay a high energy cost in the form of a rapid rate of heat loss. As a result, weasels must consume more food to maintain energy efficiency (Brown and Lasiewski 1972; King 1989, 1990; McNab 1989).

Insulation

For mammals that reside in cold environments, the most direct method of decreasing heat loss is to increase the effectiveness of insulation (see Table 8.1). For mammals and birds, the best way to reduce thermal conductance is to possess fat, fur, or feathers between the body core and the environment (Withers 1992). Mammals residing in polar environments cope with cold by employing behavioral, physical, and physiological adaptations (Blix 2016). Insulation value increases with the thickness of fur (Figure 8.6) and is at maximum in such mammals as Dall sheep (*Ovis dalli*), wolves (*Canis lupus*), and arctic foxes (*Alopex lagopus*). The easiest way to understand the benefits of insulation is to think in terms of extending the limits of the lower critical temperature. The arctic fox, for example, has a lower critical temperature of –40°C, and at an environmental temperature of –70°C, it has elevated its metabolic rate only 50% above its normal metabolic rate. It is easy to understand that if an animal lowers its metabolic rate, it can get along with less food—a real plus if food is limited during winter months.

Some trade-offs are associated with insulation. The insulating value of fur is a function of its length and density;
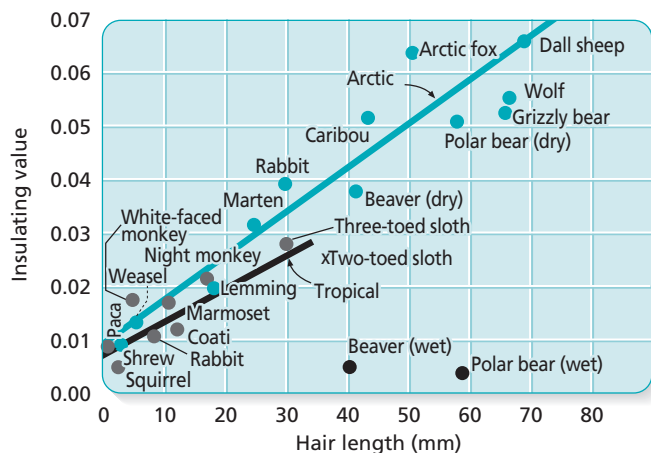
Figure 8.6 Length of fur. The insulating values of the pelts of arctic mammals (•) are proportional to the length of the hair. Pelts from tropical mammals (∞) have approximately the same insulating value as those of arctic mammals at short hair lengths, but long-haired tropical mammals like sloths have less insulation than arctic mammals with hair of the same length. Immersion in water greatly reduces the insulative value of hair, even for such semiaquatic mammals as the beaver and polar bear (µ). *Data from Scholander et al. (1950).*

some small mammals such as lemmings (Genera *Dicrostonyx*, *Lemmus*) have very long fur relative to body mass. A thick coat on predators such as weasels, however, would compromise their ability to forage in narrow crevices. Scholander (1955) contended that small mammals could not accumulate enough insulation in the form of fat or hair to cope with low winter temperatures without compromising agility. Research documenting the importance of pelage insulation in small mammals has focused primarily on Families Muridae and Soricidae (Churchfield 1990). When these groups were faced with cold stress, heat loss was reduced by increasing pelage insulation by 11%–19% during winter months. For small mammals, pelage changes may be useful in conserving energy and compensating for the large difference between body and environmental temperatures during winter (Bozinovic and Merritt 1992).

Sheriff and associates (2009) measured hair length and density for snowshoe hares (*Lepus americanus*) residing in the Kluane region of the Yukon. Body mass and body temperature of hares were similar between seasons; however, average resting metabolic rate and thermal conductance were, respectively, 20% and 32% lower in winter compared to autumn. Lower critical temperature was –10°C to –15° in winter and 0°C to –10°C in autumn. Guard hairs were 36% longer and 148% denser in winter compared to autumn. Downy hairs were of similar length but 128% denser in winter compared to autumn. Pelage dynamics of snowshoe hares represent an excellent example of seasonal acclimation to harsh winter temperatures.

Other small mammals that do not have a thick, long pelage must take advantage of stable microclimatic regimes below ground and may employ social thermoregulation to cope with cold. In contrast, larger mammals benefit greatly from insulation in the form of fat and fur. An excellent discussion of adaptation to cold by northern cervids is provided by Marchand (1996).

Large arctic mammals such as muskox (*Ovibos moschatus*), caribou (*Rangifer tarandus*), and wolves have long, dense fur as well as thick layers of fat beneath the skin. The muskox, in particular, is equipped with an immense cloak of coarse guard hairs over 30 cm in length and an underfur of thick, dense, silky wool (Figure 8.7). The hairs of the muskox are thicker at the tip than at the root so that they form an almost airtight coat. The animal's heat-losing extremities (tail and ears) are well hidden under the pelage. These heat-conserving adaptations permit the muskox to survive in the arctic tundra where winter temperatures commonly reach –40°C.

While insulating fur is a great advantage for thermoregulation in larger terrestrial mammals (Hudson and White 1985; Marchand 1996), aquatic mammals have a slightly different strategy. For example, muskrats (*Ondatra zibethicus*), water shrews (*Sorex palustris*), beavers (*Castor canadensis*), and northern fur seals (*Callorhinus ursinus*) can function in waters at 0°C because of structural modifications of their fur that trap air. Their skin stays dry, shielded from the water by a layer of air. This layer of air not only

Figure 8.7 **An immense fur coat.** Muskox are inhabitants of the arctic tundra of North America. They possess a massive dark brown coat composed mainly of long threads of high-quality wool. The outer coat is covered with long, coarse guard hairs. Heat-losing extremities are buried in the coat, an adaptation for survival in the arctic cold.

Figure 8.8 **Blubber.** Cross section of a frozen seal showing the thick layer of blubber. Of the total area in the photograph, 58% is blubber, and the remaining 42% is muscle, bone, and visceral organs. The measuring stick is graduated in inches.

helps with thermoregulation but also assists with buoyancy (Calder 1969; Catania et al. 2008; Gmuca et al. 2015). It is therefore easy to see that a polar bear (*Ursus maritimus*) with dry fur is far better off than one with wet fur. Fur is actually of limited value to an aquatic mammal. Body warmth is maintained because air is trapped between hair and the skin; if this air is displaced by water, the fur loses most of its insulating value, which falls close to zero when the fur becomes wet.

Because the thermal conductivity of water is almost 25 times greater than that of air, marine mammals must protect themselves from heat loss, particularly when inactive (Schmidt-Nielsen 1997). Air trapped in dry underfur acts as an effective insulator for some groups. Marine mammals such as whales (see Chapter 20), walruses, and seals (see Chapter 18) possess a particularly effective insulator: **blubber**. Consisting of collagen and elastic fibers embedded in an incompressible matrix of adipocytes, blubber is located below the dermis of the skin (see Figure 8.8). In addition to providing insulation, blubber acts to streamline the body (Koopman 1998; Mellish et al. 2007), adjust buoyancy (Beck et al. 2000; Biuw et al. 2003), provide an energy storage site, and support thermoregulation (Kanwisher and Sundnes 1966; Blix et al. 1979; Koopman 1998; Willis et al. 2005; Cornick et al. 2016; Ball et al. 2017; Guerrero and Rogers 2017), and may also provide a hydrodynamic function (Hamilton et al. 2004). The fat of marine mammals is entirely blubber; marine mammals have no visceral fat like other mammals. Thickness of blubber varies from 5 cm in small seals to 60 cm in the bowhead whale (*Balaena mysticetus*). In some cetaceans, such as the gray whale (*Eschrichtius robustus*), blubber is also an energy reserve during migration. The blubber of seals is a better insulator than that of whales because it contains less fibrous connective tissue (Bonner 1990). During winter, the layer of blubber in a
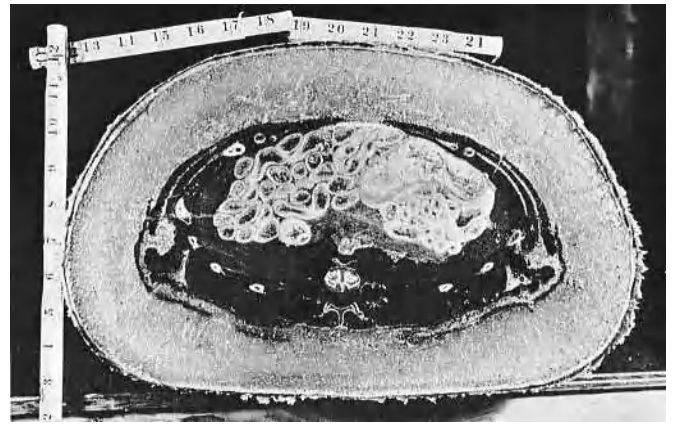
ringed seal (*Phoca hispida*) may account for 40% of its mass. Northern fur seals and other eared seals (Family Otariidae) are characterized by a dense covering of fur that traps air bubbles. Because they rely less on insulation in the form of blubber, they must remain active to maintain normal body temperature in frigid waters.

Activity on land, even with the air temperature at 12°C, can produce overheating, however, which may prove lethal. Marine mammals control overheating by remaining in the water, thus keeping their fur or skin moist; by panting; and also by waving their hind flippers, which are supplied with abundant sweat glands. Another way to control heating is by sleeping; in some species, sleeping reduces heat production by almost 25%. A southern elephant seal (*Mirounga leonina*) may reach 3,500 kg. This large, dark mass basking on pack ice in the Antarctic is subject to significant warming due to absorption of solar radiation. Blubber, permeated by blood vessels, is not passive insulation. For large elephant seals and Weddell seals (*Leptonychotes weddellii*) resting on pack ice, loss of heat is essential. In response to heat stress, these seals can increase the rate of blood flow through their skin by dilating special vessels that join arterioles directly to venules, bypassing the capillary beds. Because these bypasses (called "arteriovenous anastomoses") are very near the surface of the skin, the increased flow of blood permits heat to be lost to the environment. **White adipose tissue** is typically considered an organ associated with the storage of lipid that acts to insulate mammals inhabiting cold environments. Recent research, however, indicates that white adipose tissue serves as an important endocrine organ associated with metabolic and physiological regulation (Trayhurn et al. 2000). White fat secretes a signal protein called "leptin" that is important in processes of energy balance, reproduction, and immunity (Zhang et al. 1994).

Appendages

The fur thickness of northern mammals may increase as much as 50% during winter months. Appendages such as legs, tail, ears, and nose, however, are potentially great heat "wasters." They cannot be well insulated. Thus, to prevent heat loss from appendages, arctic land mammals permit temperatures at appendages to decrease, often approaching the freezing point. Appendages must be supplied with oxygen and kept from freezing, however, by circulating blood through them. This is done, without constant loss of heat from the extremity, by a process called **countercurrent heat exchange**, a form of peripheral heterothermy. This physiological mechanism shunts blood through a heat exchanger (the ***rete mirabile***, or "miraculous net"), which intercepts the heat on its way out and maintains the extremity at a considerably lower temperature than the core—the net result is a reduction of heat loss. As warm arterial blood passes into a leg, for example, heat is shunted directly from the artery to the vein and then carried back to the core of the body (Figure 8.9). As a consequence, the appendages of many northern mammals are maintained at comparatively cold temperatures. Anatomical studies have shown that the foot pads of arctic canids possess a massive arteriovenous plexus through which blood flow to and heat loss from the foot pads is controlled (Henshaw et al. 1972; Prestrud 1991; Prestrud and Pond 2003). To keep the extremities soft and flexible at such low temperatures, the fat in the feet of northern mammals must have very low melting points, perhaps 30°C lower than ordinary body fat (Storey and Storey 1988). Countercurrent heat exchange is well developed in the tail of beavers and ears of Japanese hares (*Lepus brachyurus*; Cutright and McKean 1979; Ninomiya 2000). In air at low temperature, loss of heat from the tail may be reduced to less than 2% of the resting metabolic rate. Then, when the animal is faced with higher temperatures, over 25% of the heat produced at resting metabolism can be dissipated through the tail (Coles 1969).

Countercurrent heat exchange also occurs in the respiratory passages of mammals. Heat recovery (heat exchange) in the respiratory system is slightly different from the countercurrent heat exchange process for the vascular system. For example, during inhalation, heat and water are added to air before it reaches the lungs. During exhalation, heat is typically lost to the environment due to warm air loss and evaporation of water. In the vascular system, heat exchange occurs at the same time between two channels, but in the respiratory system, the exchange occurs at different times in the same channel (Schmidt-Nielsen 1997). Caribou demonstrate the principle. When active, they produce a considerable amount of heat, which, due to their excellent insulation, may exceed their thermoregulatory requirements. Some must therefore be lost, or their body temperature would increase. When resting, however, caribou do not generate as much heat and must minimize heat loss to the environment. Caribou and other large mammals possess a flap of skin at the opening to the nasal passages.
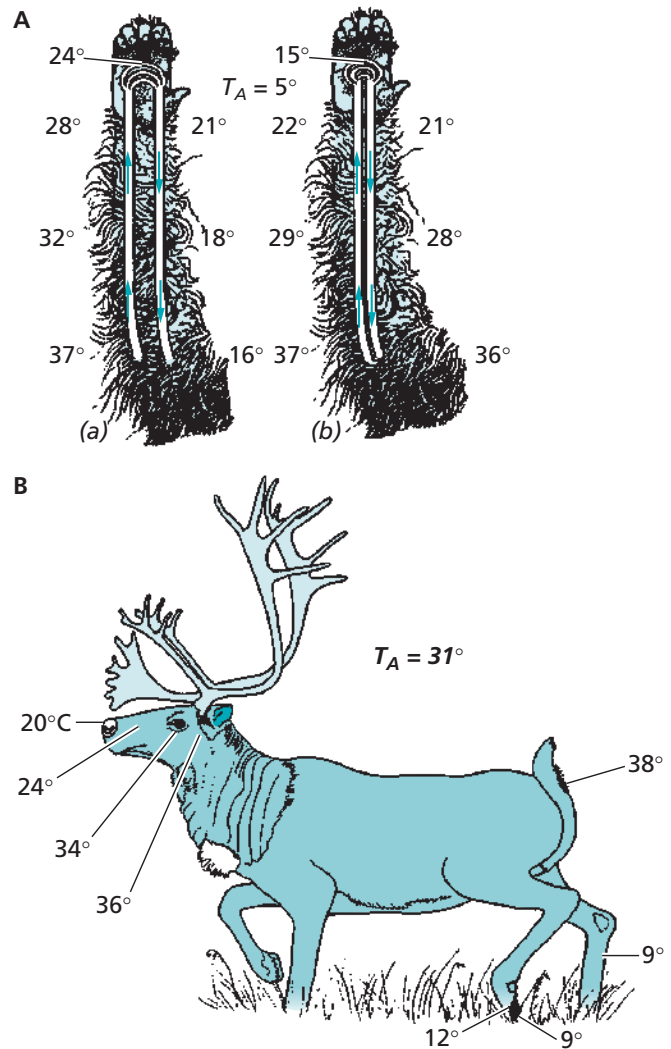
Figure 8.9 Countercurrent heat exchange. (**A**) A diagram of the circulation in a limb of a mammal showing hypothetical temperature changes of the blood in the absence (*a*) and presence (*b*) of countercurrent heat exchange (°C). Arrows indicate direction of blood flow. In (*b*), the venous blood takes up heat (thus cooling the arterial blood) all along its path of return, because even as it becomes warmer and warmer, it steadily encounters arterial blood that is even warmer. (**B**) Regulation of external body temperature in the caribou (°C). Temperature regulation is accomplished in part by countercurrent heat exchange. An intricate meshwork of veins and arteries acts to keep the temperature of the legs near that of the environment so heat is not lost from the body. *(A) Data from Hill and Wyse (1989).*

This flap of skin reduces the size of each opening to a small slit when the animal is inactive, thus minimizing heat loss from the lungs. When resting, the temperature of expired air is lower than body temperature. When exercising, the nostrils flare open, increasing the surface area of the mucous lining of the nose for heat exchange. The temperature of expired air during exercise for arctic species is therefore higher when the animal's heat production exceeds its requirements for temperature regulation. Thus, respi-

ratory heat exchange for large arctic species serves a dual function: minimizing heat loss while at rest and increasing heat loss during periods of activity (Scholander 1957; Hainsworth 1981).

Conservation of heat in species occupying cold regions can also be enhanced by reducing the length of the exposed extremity. **Allen's rule** states that the appendages of endothermic animals are shorter in colder climates than those of animals of the same species found in warmer climates (Allen 1877). By reducing unnecessary body surface area, animals can reduce heat loss. It seems logical from the standpoint of thermal physiology that a long nose and tail, as well as long ears and legs, tend to add unnecessarily to the body surface and would be great heat wasters for cold-adapted species (Scholander 1955). For instance, arctic foxes have small, rounded, densely furred ears, a reduced muzzle, and short, stubby legs. Foxes living in deserts, such as swift foxes (*Vulpes velox*) of the southwestern United States or the fennec (*V. zerda*) of North Africa, have large, elongated, thinly furred ears, and comparatively long legs (Figure 8.10). For species residing in hot climates, long appendages are a valuable commodity because they aid in the dissipation of heat. In four species of macaques (Cercopithecidae: *Macaca*) residing in Asia, relative tail length generally decreases with increasing latitude in accord with Allen's rule (Fooden 1997; Fooden and Albrecht 1999). However, as with Bergmann's rule, the validity of this generalization is debatable, and there are exceptions. For example, the body form of bush dogs (*Speothos venaticus*) in the tropics of South America is not unlike that of arctic foxes. Furthermore, the length of ears and tail in hares (Genus *Lepus*) follows Allen's rule, but that for rabbits (Genus *Sylvilagus*) does not (Stevenson 1986).

Coloration

Although northern mammals exhibit some fascinating anatomical specializations for coping with harsh winter climates, perhaps the most obvious trait defining them is their white pelage (Figure 8.11). **Gloger's rule** (Gloger 1833) states that "races in warm and humid areas are more heavily pigmented than those in cool and dry areas" (Mayr 1970:200). Three classic hypotheses for the functional significance of coloration in mammals include concealment, communication, and physiological processes (Caro 2005). Four major mammalian groups have been examined: Orders Primates, Carnivora, Lagomorpha, and Cetartiodactyla. Kamilar and Bradley (2011) analyzed a dataset of more than 100 primate species representing all major primate clades. Their finding provides strong support for the applicability of Gloger's rule for primates. Pigmentation in many mammals tends to be paler the closer the species habitat is to the arctic, with northern subspecies of animals generally being lighter in color than their southern counterparts (Flux 1970; Johnson 1984). Coloration of pelage of many arctic mammals either remains white year-round or changes to white during winter. Those whose pelage remains white year-round include the polar bear (actually their hairs are transparent and pigmentless), arctic hares (*Lepus arcticus*) of the far north, and northerly forms of the caribou and gray wolf. It is noteworthy that arctic hares in the far north change color seasonally, displaying a white coat in winter and brown coat in summer (Figure 8.12). Because hares are so well adapted to winter, the cost in energy of changing to brown during the short summer exceeds the benefits of permanent adaptation to winter.

By contrast, a seasonal color change (dimorphism) is seen in collared lemmings (Genus *Dicrostonyx*), Siberian hamsters (*Phodopus sungorus*), snowshoe hares, mountain hares (*Lepus timidus*), ermines and weasels (Genus *Mustela*),
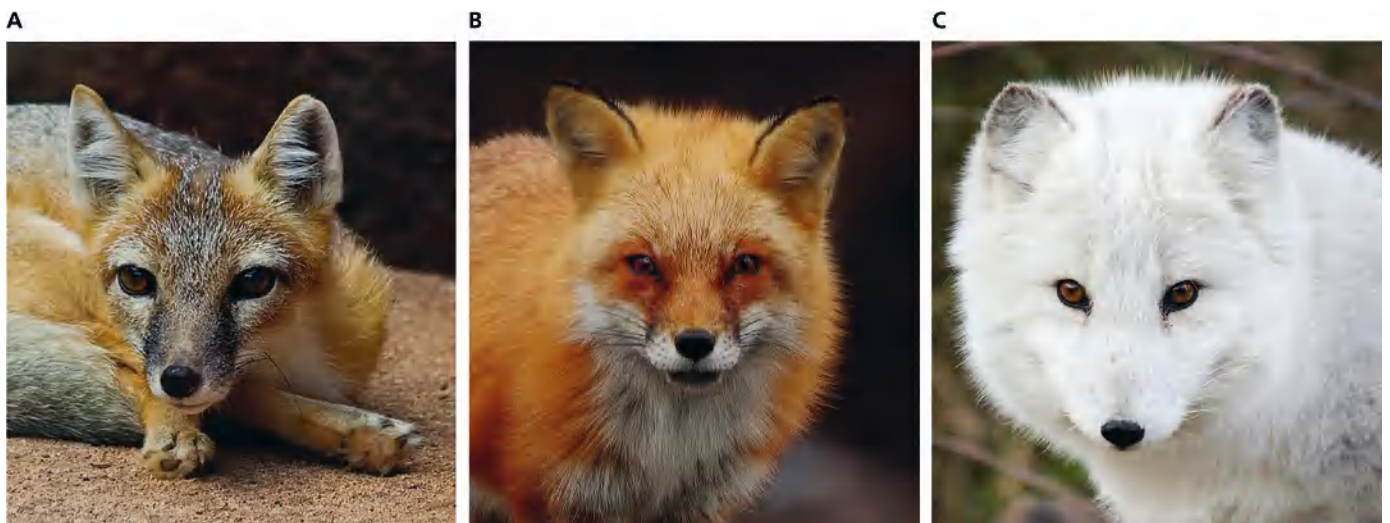
Figure 8.10 Ears and heat loss. The ears of foxes help to regulate body heat. (**A**) The swift fox (*Vulpes velox*) of the American Southwest has relatively long ears that help to dissipate heat. (**B**) The red fox (*Vulpes vulpes*) of temperate America possesses intermediate-sized ears. (**C**) In contrast, the relatively short ears of the arctic fox (*Alopex lagopus*) help to conserve heat in the cold.

Figure 8.11 **A white fur coat.** The polar bear has a circumpolar distribution. It is one of the largest terrestrial carnivores in the world, feeding primarily on seals and fish. The thick white coat is composed of hollow hairs that trap warm insulating air and also act as an efficient solar collector for this bear when it is wandering from ice floe to ice floe in search of prey. Although their unique hairs convey a thermal advantage, polar bears enhance survival in cold by possessing an enormous thermal inertia (large body size) and large stores of subcutaneous fat.

A

B

Figure 8.12 **Arctic hares in the far north.** *Lepus arcticus* reside on the arctic tundra the most northern distribution of all leporids. *Lepus arcticus* during winter (**A**) and in midsummer (**B**).

and arctic foxes. Species that undergo seasonal dimorphism accomplish the color changes in different ways. One is by molting. For example, in ermines and weasels, a complete molt is characterized by each hair being lost and a new, white (winter) hair replacing the old, brown (summer) hair. Snowshoe hares exhibit a different type of molt: rather than going through a complete molt pattern, only the tips of the winter hairs are white; the bases remain gray. The timing of molt patterns for the Old World mountain hares is most strongly influenced by length of day (photoperiod) but is also correlated with average ambient temperature and duration of snow cover (Angerbjörn and Flux 1995). Furthermore, species of mammals that show seasonal color changes do not change color over their entire geographic range. For example, the North American long-tailed weasel (*M. frenata*) shows seasonal color changes north of about 40°N latitude, but south of this zone, they remain brown year-round. Individuals residing in the zone of overlap between these color groups show gradations in color from white to pied or brown (Hall 1951).

The specific cue (proximate factor) that triggers the onset of molt is decreasing day length. In autumn, the optic nerve receives the stimulus, which is then transmitted to the hypothalamus. The factor that is ultimately responsible for establishing the duration of the winter coat is probably its thermal advantage, which accounts for the close correlation between molting and mean annual temperatures (Flux 1970; Johnson 1984). Temperature and photoperiod, however, are not the sole determinants of white winter coloration. Transplantation experiments have demonstrated that heredity as well as temperature are involved in controlling pelage changes in mammals (Kliman and Lynch 1992). The molt cycle is geared to changes in the environment by way of changes in the hormonal system (namely, the **endocrine glands**: thyroid, **pituitary**, adrenal cortex, and pineal) as mediated by the brain and the hypothalamus. The seasonal cycles of molt and reproduction are closely related and are coordinated by the neuroendocrine system. In spring, in addition to changes in pelage color,

density, and length, the brain signals the pituitary to secrete gonadotropins, which stimulate the gonads to prepare for the approaching breeding season. During spring, the hair follicles and testes of male weasels enlarge simultaneously; the testes begin to manufacture testosterone and sperm, and the hair follicles accumulate melanin and manufacture hair for a complete coat replacement (King 1989).

Why northern animals turn white in winter is not fully known. We assume that if the mechanism were not maintained by natural selection (if it did not confer an adaptive advantage more often than a disadvantage), it would disappear. We assume that the color white acts to conceal both predators and prey (Stoner et al. 2003a, 2003b). This adaptation may conceal polar bears from a potential victim. While actively searching for prey, however, a weasel is surely easily detected, even with a white pelage. It is possible that the weasel's white color in snowy regions may allow it to blend with its background (cryptic coloration) and thus avoid predation by hawks, owls, and foxes. Many questions concerning the adaptive nature of color changes in northern mammals have yet to be answered (Walsberg 1983, 1991; Marchand 1996). For example, what can be the explanation for the blue color phase that commonly occurs in arctic foxes inhabiting the Pribilof Islands and many coastal areas of Alaska and Canada? If color acts to camouflage these animals, why are they slate blue during winter? If this blue phase is not adaptive, then how did it evolve and how is it maintained in the population? If cryptic coloration is important to conceal predator from prey, why don't gray foxes (*Urocyon cinereoargenteus*), fishers (*Martes pennanti*), and martens (Genus *Martes*) turn white in snowy regions?

The color white may also convey a thermal advantage. According to the laws of physics, black-colored animals lose heat by radiation faster than white-colored ones. Following Gloger's rule, we therefore expect to find white animals occurring in cold regions. Some investigators have misinterpreted the pertinent physical laws, however. Radiation of heat from an animal's body is in the form of infrared energy, which is unrelated to visible coloration. All animals are therefore considered to be thermodynamic "blackbodies," meaning that they absorb all incident radiation and reflect none. The color of the fur and underlying skin may be important to the amount of heat absorbed from solar radiation—its peak intensity is in the visible range. When exposed to direct solar radiation, dark-colored skin or fur absorbs more incident energy than light-colored skin or fur. The conservation of this heat energy depends on the length and thickness of the fur, not on its color. Many small mammals, such as voles and shrews, show increases in pelage density and length during winter (Khateeb and Johnson 1971; Bozinovic and Merritt 1992).

Animals living in northern regions may possess not only white fur but also thicker, denser pelages. For example, mountain hares have a white winter coat that is twice the length and thickness of their summer coat and provides an insulatory advantage in cold (Flux 1970). Walsberg (1991) examined coat insulation and solar heat gain in three species of subarctic mammals that shift between white winter pelages and darker summer pelages (snowshoe hares, short-tail weasels [*Mustela erminea*], and Dzhungarian hamsters [*Phodopus sungorus*]). He contends that seasonal changes in coats of these species serve important roles in cryptic coloration, thermal insulation, and radiative heat gain. A white coat in winter does indeed result in a reduction in solar heat gain; however, this is not necessarily a result of increased heat reflectivity of the pelage or optical properties of the coat to solar radiation, but is rather a product of increased coat insulation (Walsberg 1991). Generalizations concerning the adaptive significance of different biogeograpical "rules" or trends must take into account that the survivability of northern mammals may not result solely from forces that maximize heat conservation.

For some animals, the thermal advantage of hair is not necessarily contingent on its color, density, or length; instead, it depends on the anatomy of the hairs and color of the skin beneath it. For many deer (Family Cervidae), insulation depends on the air contained by the highly medullated guard hairs that provide insulation (Johnson and Hornby 1980). Research with polar bears indicates that a combination of their transparent, pigmentless hair and black skin may enhance their heat-conserving abilities (Grojean et al. 1980; Walsberg 1983; Tributch et al. 1990). Pigmentless hair traps and transmits to the skin 90% of sunlight in the invisible ultraviolet portion of the spectrum but only 10% of the visible light. Energy in the form of heat from the ultraviolet light is absorbed by the dark skin to help warm the body, while the visible light is reflected as white color. The hairs of polar bears act like optical fibers, with ultraviolet light entering at one end and bouncing along the inside of the hair shaft to reach the dark skin, where it is absorbed. However, Koon (1998) reanalyzed the UV wave-guiding proposed by Grojean and colleagues (1980). Although the theory of fiber-optic polar bear hair is an "attractive theory," there is no direct evident to support it. The low UV reflection of the pelt may be best explained by direct evidence of absorption by hairs of the polar bear (Koon 1998).

Modification of Microclimatic Regime

In northern regions, nonhibernating small mammals, particularly those of the rodent Families Cricetidae and Sciuridae (e.g., flying squirrels, Genus *Glaucomys*), construct elaborate nests and engage in communal nesting (Cricetidae: Madison et al. 1984a; West and Dublin 1984; Wolff 1989; Bazin and MacArthur 1992; Sciuridae: Muul 1968; Stapp et al. 1991; Stapp 1992; Merritt et al. 2001). The greatest gain from huddling should accrue to small mammals with a large surface-area-to-mass ratio and a limited capacity for increasing the insulation value of their pelage. But not only small mammals use huddling. In one study, 23 raccoons (*Procyon lotor*) were reported occupying one winter den (Mech and Turkowski 1966). During winter, female striped skunks (*Mephitis mephitis*) formed a communal nest with other females or with a single male (Wade-Smith and Verts 1982). Communal denning has adaptive value for

winter survival and reproductive success, especially in northern latitudes. For example, in Alberta, an average of 6.7 striped skunks occupied communal dens with females more common in dens than males (Gunson and Bjorge 1979). Recently, den-sharing was reported in striped skunks during summer, autumn, and winter (Theimer et al. 2016). Huddling confers an important adaptive advantage for California sea lions (*Zalophus californianus*) residing on San Nicolas Island, California. California sea lions are highly communal and congregate in large numbers on coastal rookeries. By employing an infrared temperature monitor, investigators found that sea lion huddling behavior increased in colder weather (Liwanag et al. 2014). Aggregation serves an important social role in addition to influencing changes in microhabitat and consequently thermal conditions (Liwanag et al. 2014).

Both nest-building and huddling conserve body heat through reductions in thermal conductance. Huddling in groups reduces each individual's exposed surface, thus reducing the cold stress and the metabolic requirement for heat production. Studies traditionally employed laboratory-based calorimetry to demonstrate energy savings of communal nesting during winter (Glaser and Lustick 1975; Martin et al. 1980; Casey 1981; Kotze et al. 2008); Merritt and Zegers 2014). Other studies have linked laboratory experimentation with field-derived data on nesting habits by employing radiotracers, radiotelemetry, and thermal imaging methods (Madison et al. 1984a; Andrews and Belknap 1986; Arnold 1993; Boyles et al. 2008).

When muskrats huddle in a group, a major part of each individual's body surface is in contact with a neighboring animal (Figure 8.13). Curling and retracting the extremities reduce heat loss, and microclimatic modification in the form of an elaborate, well-insulated nest below ground and snow cover (subnivean) adds greatly to energy savings. Sealander (1952) showed that at low temperatures, mice of the Genus *Peromyscus* formed a "communal" group. Those at the bottom of the group enjoyed temperatures well above ambient levels, but by continually shifting position, each mouse in the huddle was periodically rewarmed and thus avoided hypothermia. Because heat loss by conduction or convection varies in direct proportion to the amount of surface area exposed, the energy savings of huddling can be easily calculated (Marchand 1996; Nunez-Villegas et al. 2014; Nowack and Geiser 2016). Vickery and Millar (1984) provided a model for predicting the energy advantages and disadvantages of huddling. When applying their data on *Peromyscus*, they found that huddling confers a distinct energy savings for mice subjected to ambient and nest temperatures well below thermoneutrality.

Many species of small mammals (principally rodents of Subfamilies Arvicolinae and Cricetinae) form aggregations during winter to conserve energy (Merritt 1984; Pillay and Rymer 2017). Rodents construct elaborate nests of grasses and herbs either under the litter, on the ground, or within a hollow tree or log. During the winter in northern regions, these nests are commonly located within the subnivean
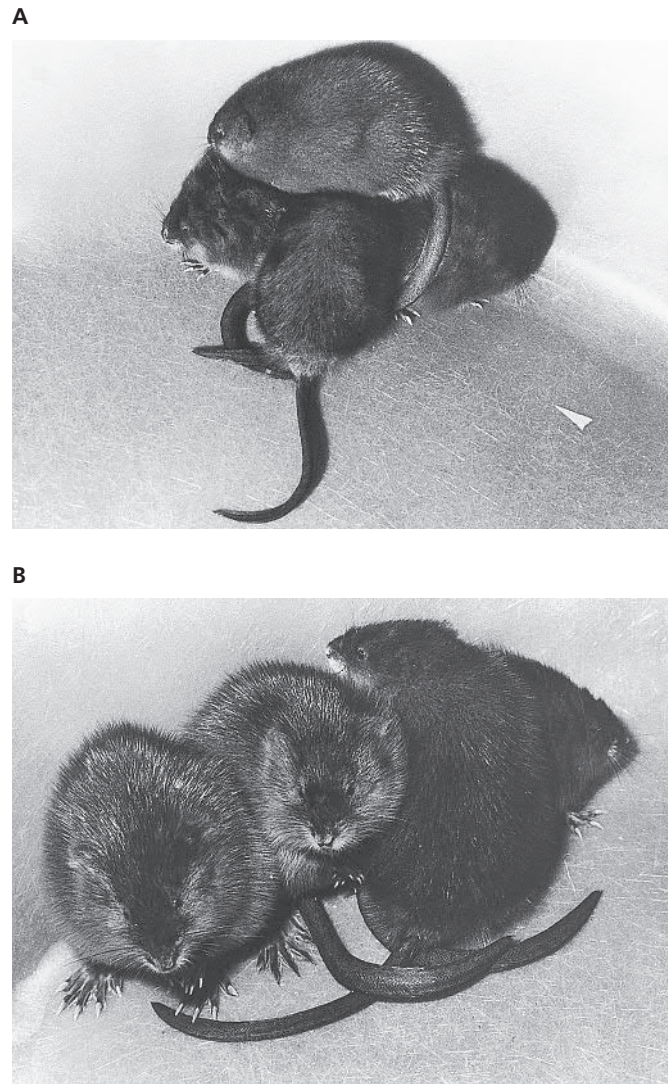
Figure 8.13 **Social thermoregulation.** Examples of (**A**) close and (**B**) loose aggregation responses of muskrats exposed to a temperature of 5°C.

(below snow) environment, which aids in insulating the nest site from fluctuating supranivean (above snow) temperatures. Radiotelemetry studies demonstrated that up to 6 muskrats may inhabit the same winter lodge in the marshes of Manitoba, Canada (MacArthur and Aleksiuk 1979). The resting metabolic rate of a group of 4 muskrats huddling in such a lodge during winter with an environmental temperature of –10°C shows up to a 13% energy savings over that of a single animal. In northern latitudes, aggregations of at least 6 muskrats are common. The physical structure and communal use of beaver lodges in southeastern Manitoba were assessed by Dyck and MacArthur (1993). Winter air temperatures outside the lodges reached a low of –41.4°C, but temperatures within the chambers of occupied lodges did not fall below 0°C. The mean monthly temperature of the nesting chamber consistently exceeded the mean monthly exterior air and water temperatures. The ameliorated microclimate within the

lodges also facilitates periodic rewarming of foraging beavers, thus minimizing thermoregulatory costs during rest. Nests of taiga voles (*Microtus xanthognathus*) occupied by 5 to 10 individuals remained between 7° and 12°C warmer than ground temperature within the subnivean environment and as much as 25°C warmer than supranivean temperatures (Figure 8.14). Furthermore, nests were not completely vacated, so that foraging voles returned to a warm nest (Wolff 1980; Wolff and Lidicker 1981). Huddling by deer mice and voles may reduce energy requirements in the cold by as much as 16%–36% (e.g., Gebczynska and Gebczynski 1971; Vogt and Lynch 1982; Andrews and Belknap 1986). For white-footed mice (*Peromyscus leucopus*), a combination of torpor and huddling of 3 individuals within a nest at an ambient temperature of 13°C resulted in a daily energy savings of 74% compared with nontorpid, individ-

A

B

Figure 8.14 **Nest temperatures of taiga voles.** (**A**) Daily mean air temperature, ground temperature, and temperature in the nest of the taiga vole from 15 October to 1 December 1977, at a site 155 km northwest of Fairbanks, Alaska. The daily ranges of nest temperature are shown by the vertical bars. Increasing ground temperatures after 20 October were due to progressively deeper snow cover. (**B**) The communal winter midden-tunnel system and activities of a group of taiga voles. *Data from Wolff and Lidicker, Jr. (1981).*

ual mice without a nest (Vogt and Lynch 1982). Aggregate nesting during winter is common for *Peromyscus* species (Madison et al. 1984b; Wolff and Durr 1986). The average daily metabolic rate of deer mice (*P. maniculatus*) is also lower in winter (Merritt 1984). When *P. maniculatus* and *P. leucopus* are **syntopic** (live within the same locality) in the Appalachian Mountains of Virginia, radiotelemetry studies have shown that *P. maniculatus* prefers nesting high in large, hollow trees, year-round, whereas *P. leucopus* uses both ground and tree nest sites in summer but shifts to underground nest sites in winter (Wolff and Durr 1986). Radiotelemetry studies have demonstrated that both species nest together during winter months (Wolff 1989).

The greatest gain from huddling should logically accrue for small mammals that possess a large surface-area-to-mass ratio and a limited capacity for increasing the insulation value of their pelage. Huddling reduces each individual's exposed surface, thus reducing the cold stress and the metabolic requirement for heat production. Most tree squirrels are solitary and euthermic during winter. Southern flying squirrels (*Glaucomys volans*), however, form "huddles" of up to 20 individuals (but groups fewer than 10 are more common) in hollow trees to conserve energy during winter (Merritt et al. 2001). For example, a group of 6 southern flying squirrels in New Hampshire, huddling within a wooden nest box and surrounded by temperatures of 6°C, reduced their energy expenditure by 36% (Stapp et al. 1991).

Although nesting aggregations are most commonly reported in rodents, social thermoregulation also is reported in marsupials (Morton 1978, Canals et al. 1989; Tomlinson et al. 2014), bats (Dunz 1982; Roverrun and Chappell 1991; Kurta 1995; Boyles et al. 2008; Boratynski et al. 2012; Sugita and Ueda 2013; Russo et al. 2017), primates (Schino and Troisi 1990; Genoud et al. 1997; Perret 1998; Gestich et al. 2014; Kelley et al. 2016; Eppley et al. 2017), and insectivores (Dryden et al. 1974; Genoud 1985, 1988; McDevitt and Andrews 1995; Merritt and Zegers 2014). Most species of shrews do not employ social thermoregulation to conserve energy; however, exceptions do occur. Recently, Merritt and Zegers (2014) examined metabolic shifts and group-nesting of least shrews (*Cryptotis parva*) residing in prairie habitats of Illinois. Oxygen consumption was measured in groups ranging from 1 to 8 at ambient temperatures of 4°, 14°, 24°, and 34°C. At 24 °C, individuals huddling in groups of 2 and 8 experienced metabolic expenditures reduced by 49% and 53%, respectively, when compared to that of solitary individuals. At 4°C, those energy reductions were 26% and 54% respectively for individual huddling in groups of 2 and 8. An inverse relationship between metabolic rate and numbers of huddling individuals, at ambient temperatures below thermoneutrality (34°C), supports the classical explanation that reduction in metabolic rate is attributable to a reduction of surface-to-volume ratio.

Conservation of heat by a group of huddling animals is greatest when the nest is well insulated. Researchers have evaluated the thermal capacity of nests by calculating their

shape, thickness of the nest wall (Wolfe 1970; Wolfe and Barnett 1977; Redman et al. 1999), and composition (King et al. 1964; Layne 1969). The resistance of nests to heat loss can also be measured quantitatively (Wrabetz 1980). Interspecific differences in nest-building behavior were correlated with available microhabitat and nest site preferences (Layne 1969). King and colleagues (1964) demonstrated a geographic correlation in the amount of nest material used by Genus *Peromyscus*. Northern forms used more nesting material under constant temperatures than did southern forms. Sealander (1952) demonstrated a seasonal difference in nest-building behavior: *P. leucopus* and *P. maniculatus* constructed more elaborate nests during winter than in summer, with winter nests conferring greater resistance to low temperatures. Pierce and Vogt (1993) employed outdoor enclosures and demonstrated that *P. leucopus* and *P. maniculatus* from northern New York constructed larger nests during winter compared with other times of the year. *P. maniculatus* constructed the largest nests.

Foraging Zones

Small mammals such as shrews and voles are active during midwinter and most do not undergo physiological heterothermy (Wunder 1985; Merritt 1995). The thermal regime of the foraging zone, therefore, is crucial in dictating energy budgets of these winter-active mammals (Chappell 1980). The climatological regime of the foraging and nesting sites of shrews, voles, and mice has been examined during winter in Michigan (Pruitt 1957), Ontario (Randolph 1973), and Pennsylvania (Merritt 1986). In mixed deciduous forests, many small mammals forage in tunnels within soil covered by a rich layer of leaves. During winter, this foraging zone provides a stable, comparatively warm thermal regime. Snow covering the ground also provides additional insulation. Although ambient temperatures may reach –29°C in mid-January, the minimum temperature at the soil-leaf litter interface is about –4°C and 1°C within a subsurface tunnel (Figure 8.15). Snow cover is an integral part of the life of small mammals (Merritt 1984; Marchand 1996). The presence of a sufficient depth of snow, called the **heimal threshold** (Pruitt 1957), insulates the subnivean environment against widely fluctuating environmental temperatures. High mortality rates among red-backed voles (*Myodes gapperi*) and white-footed mice during midwinter are attributable to a lack of snow cover to insulate the forest floor (Pruitt 1957; Beer 1961; Fuller et al. 1969).

The period of autumn freeze is also crucial to the survival of small mammals due to great fluctuations in temperatures in their foraging zone. This period was found to
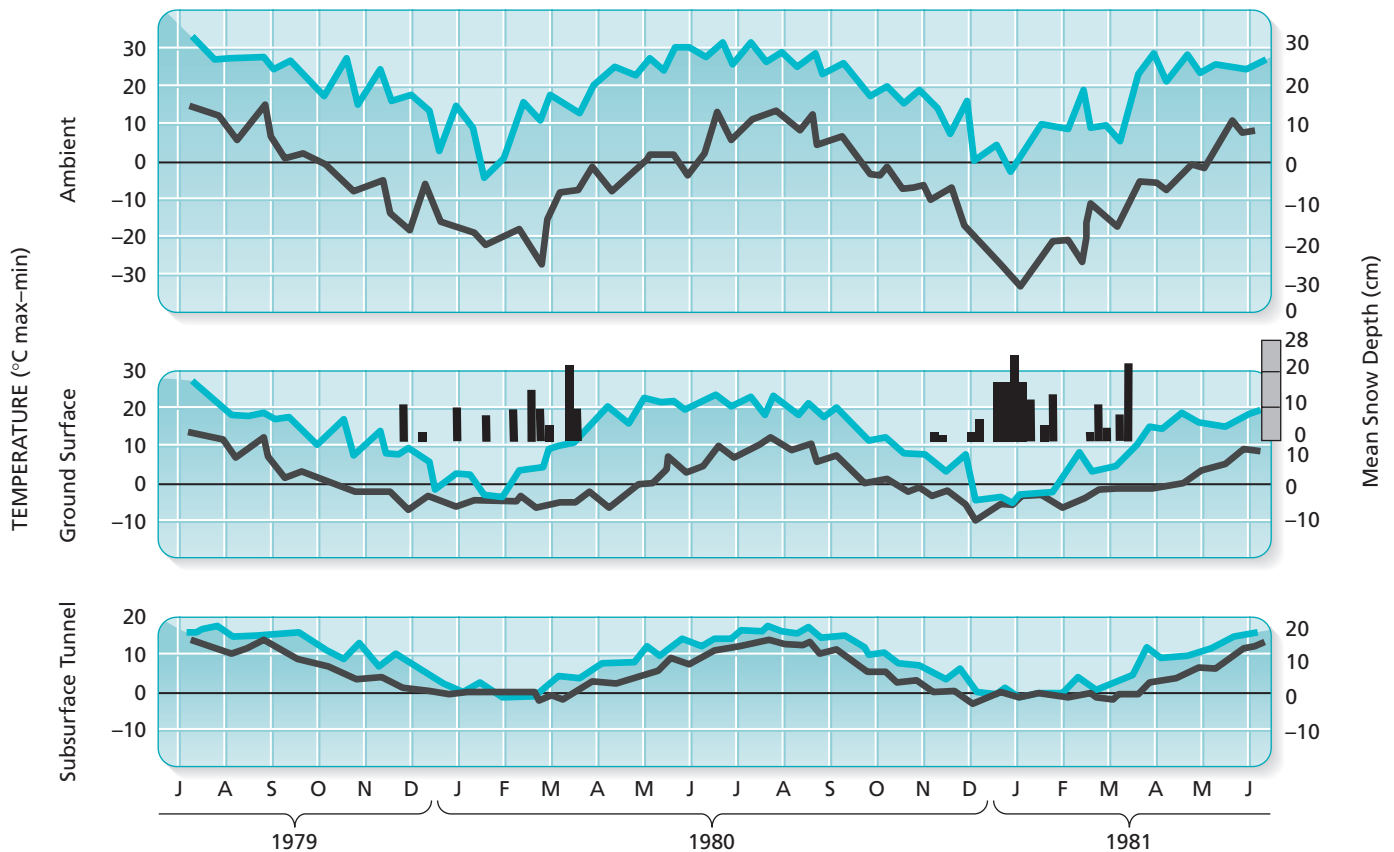
Figure 8.15 Thermal zone of small mammals. Maximum and minimum temperatures recorded on an Appalachian Mountain site from July 1979 to June 1981. Temperatures are recorded from 1.5 m above ground surface (ambient), at ground surface, and in a subsurface tunnel. Snow depth is shown by shaded bars. *Data from Merritt (1984).*

produce increased mortality rates in small mammals studied in the Rocky Mountains of Colorado (Merritt and Merritt 1978). Snow thickness in autumn was insufficient to insulate soil against fluctuating ambient temperatures, which may reach –20°C. Within the stable foraging zone, many species of small mammals establish caches of food to ensure that a predictable, quick energy source is readily available during winter, when food is scarce. Food-hoarding is reported for 6 orders and 30 families of mammals, with most practitioners found in Orders Rodentia and Carnivora. Because hoarding behavior is so important in the biology of mammals, a detailed discussion of this topic is provided in Chapter 7.

Reduction in Level of Activity

Daily and seasonal temperature changes influence activity patterns of winter-active small mammals. Nonhibernating species residing in seasonal environments must secure adequate nourishment during winter to maintain a constant high body temperature. Among winter-active mammals, shrews are characterized by rapid heat loss due to their large surface-area-to-volume ratio, high metabolic rate, and resulting high caloric requirements. We would therefore intuit that they are poor candidates for enduring cold stress. The northern short-tailed shrew (*Blarina brevicauda*) of eastern North America conserves energy by using cached food reserves and avoids cold environmental temperatures by restricting foraging and nesting to zones characterized by stable microclimates. Because temperature changes influence the activity of invertebrates within the soil, foraging by soricid predators may also be influenced. Churchfield (1982) used time-lapse photography to analyze the influence of temperature on the activity and food consumption of *Sorex araneus*. Shrews were active throughout the day and night with peaks in activity every 1–2 hours. Activity outside the nest in summer was 28% but dropped to 19% during winter, concomitant with a decrease in food consumption. Martin (1983) showed an annual activity range for *B. brevicauda* of 7%–31% of the day. Daily activity during winter was greatly reduced, averaging only 11.6% during the coldest months. *Blarina* spent 80%–90% of the day resting in its nest at a low metabolic rate, sleeping for long periods, and being intermittently highly active. The reduction in caloric intake and foraging activity during winter represents a survival tactic for coping with cold. In contrast, seasonal metabolism of *B. brevicauda* increases from a low in summer to a maximum in autumn and winter. Northern short-tailed shrews may depart from the typical metabolic profile of shrews due to their proclivity for hoarding food (Merritt 1986).

Unlike the case for Genus *Blarina*, for many rodents food is severely limited during winter months. For species of *Peromyscus* inhabiting northern latitudes, torpidity combined with communal nesting is important to conserving energy. For example, in western Kansas, *P. leucopus* spent 72% of the day in the nest during winter, compared with 28% of the day in summer (Baar and Fleharty 1976). During winter, when the cost of thermoregulation is highest and food resources are lowest, available energy must be used to maintain metabolism. Energy loss can be minimized in part by curtailing locomotor activity. For meadow voles (*Microtus pennsylvanicus*), cold temperatures during winter, especially at night, may select for more diurnal activity. During winter, voles demonstrate increased movements on warm days or forage below a mantle of snow. When there is no insulating blanket of snow, low temperatures stimulate the use of nests and inhibit activity in voles (Madison 1985). Hottentot golden moles (*Amblysomus hottentottus*) residing at high elevations (1,500 m) in the subtropical savannah of South Africa are exposed to cold and shortages of food during winter. These fossorial mammals cope with seasonal stressors by restricting activity to shorter, more intense periods and by decreasing thermal conductance by increasing pelage insulation (Scantlebury et al. 2005).

Reduction of Body Mass

Small mammals, notably voles and shrews inhabiting seasonal environments, are reported to undergo a general decline in body mass during winter. This overwinter mass decline, called **Dehnel's phenomenon** (Dehnel 1949), is thought to confer the adaptive advantage of decreasing caloric needs during winter when food resources are limited (Merritt and Merritt 1978; Hyvärinen 1984; Merritt 1984, 1995; Yaskin 1984; Churchfield 1990; McNab 1991; Churchfield et al. 1995; Taylor 1998; Hays and Lidicker 2000). For shrews, reduction of body mass and length is accompanied by a reduction of brain mass and skull depth, as well as a decline in most internal organs. As a result, these changes may lead to a decrease in mass-specific metabolism and food consumption during winter. Some northern species—namely, collared lemmings (*Dicrostonyx groenlandicus*) (Nagy 1993) and northern short-tailed shrews—depart from this trend, however, and gain mass during winter. Genus *Peromyscus* does not conserve energy in this way during winter: Its ability to undergo torpor, coupled with communal nesting, food-hoarding, and use of elaborate nests, aids considerably in conserving energy during winter. The cues for such fluctuations in mass are complex and include photoperiod, environmental temperature, and availability of food. The common shrew (*Sorex araneus*) in Eurasia also demonstrates body mass decreases during winter. Declines in body mass of shrews can be significant—*S. araneus* residing in Great Britain, Poland, and Finland lose up to 45% of body mass (Pucek 1965; Hyvärinen 1969; Churchfield 1982), and *Sorex cinereus* in North America showed a decline of 53% in body mass from early summer to winter (Merritt 1995). Churchfield (1990) indicated that a latitudinal gradient may exist for changes in body mass of shrews. Small size during winter confers an energy advantage by reducing food requirements. A small mammal eats less food and has a greater assimilation efficiency than a large one; consequently, it can reduce foraging time during cold and thus conserve energy. Although small body mass in winter decreases food

requirements, it will reduce cold tolerance due to an increase in surface-area-to-volume ratio.

The survival mechanisms discussed here have one thing in common: they pertain to animals that are active during most of the winter and thus must forage to find food to maintain a high body temperature. Even small mammals that exhibit short-term torpidity, such as *Peromyscus*, are quite thermolabile—because their body temperature decline is slight, they can quickly elevate their body temperature, forage on cached food, and then rewarm in a communal nest. As depicted in our model of the energy budget (see Figure 8.4), thermoregulation is the highest priority: if a mammal cannot maintain euthermy, it cannot conduct other activities. But some small and medium-sized mammals residing in northern environments are quite lethargic during winter. They solve the problem of scarcity of food and low temperature by entering a prolonged and controlled state of dormancy called "torpor," or "hibernation."

Dormancy

Small mammals, such as bats and rodents, maintain high body temperature when active but are able to save energy by temporarily abandoning euthermia. **Dormancy** is defined as a period of inactivity characterized by a reduced metabolic rate and lowering of body temperature. **Torpor** is a form of dormancy characterized by a lowering of body temperature, metabolic rate, respiration, and heart rate. During the winter, torpor is referred to as "hibernation," and during the summer, it is called "estivation." Torpor that occurs daily is logically called "daily torpor." These energy-conserving responses are sometimes grouped as forms of **adaptive hypothermia** (Bartholomew 1982). Unfortunately, "hibernation biologists" have difficulty agreeing on consistent terminology. The difference between these patterns should be treated as points along a continuum because one condition may shade imperceptibly into another. To understand these concepts, we must first establish some definitions. Our terms follow Bartholomew (1982), French (1992), Geiser and Ruf (1995), Barclay and colleagues (2001), Geiser (2004), Grigg and colleagues (2004), and Geiser and Brigham (2012).

The energy savings for mammals coping with cold depend on their drop in body temperature and length of time spent in a state of dormancy. Torpor is a type of dormancy in which body temperature, heart rate, and respiration are not lowered as drastically as in true hibernation. Body temperature declines markedly but not usually below 15°C. The lowest range of tolerable body temperatures during torpor is about 10° to 22°C (Wang and Wolowyk 1988). Patterns of torpor may extend for a period of hours or several days. Daily torpor is a response of small mammals to an immediate energy emergency. Examples of animals that undergo daily torpor are species of rodents (namely, *Peromyscus*), many marsupials, insectivores, bats, and some primates (Nestler et al. 1996). Torpor is a quite plastic condition and can provide significant energy savings for animals

coping with cold stress (Bartholomew 1982). Torpidity is certainly not a primitive physiological trait; rather, it is a unique feature adaptive for survivorship in seasonal environments. The ability of many rodents to undergo periodic bouts of torpor during winter is well known (Lyman et al. 1982; French 1992). This strategy aids in combating cold stress and scarcity of food during winter and is commonly accompanied by other energy-saving strategies. It is noteworthy that the ability to abandon homeothermy for torpor has never been shown in voles and most shrews, which must continue to forage under coldest conditions (Wunder 1985; Churchfield 1990).

Hibernation is defined as a profound dormancy in which the animal remains at a body temperature ranging from 2° to 5°C for periods of weeks during winter. Body temperature of mammals may reach as low as –6 °C without resulting in death due to freezing. Little brown bats (*Myotis lucifugus*) were exposed for durations of 30 minutes to 6 hours to temperature extremes ranging from –3° to –9°C (Hurst and Wiebers 1967). Of 3 bats whose body temperature reached –6°C, 2 died during the experimental run, and a third bat whose body temperature reached –6°C lived for 3 days following exposure. Bats subjected to –4°C lived for an indefinite period of time. Barnes (1989) measured core body temperatures as low as –2.9°C in hibernating arctic ground squirrels (*Urocitellus parryii*) held in outdoor burrows near Fairbanks, Alaska. Hibernation is also referred to as "seasonal torpor," "deep hibernation," or "true hibernation." Animals that undergo hibernation include ground squirrels, marmots, and hedgehogs. No mammal remains continuously in a dormant state during the entire period of hibernation, however, and the length of the period of hibernation varies with ambient temperature, body size, and species. We defer treatment of estivation (a form of shallow torpor typified by desert small mammals) for the later discussion of how mammals cope with heat.

Dormancy is exhibited by some 7 orders of mammals (marsupials, insectivores, elephant shrews, bats, primates, rodents, and carnivores) and at least 6 groups of birds (swifts, goatsuckers, hummingbirds, sunbirds, manakins, and colies) (Merritt 2010). Representative birds and mammals and their sizes are given by Hudson (1978), Lyman and colleagues (1982), Geiser and Ruf (1995), and Barclay and coworkers (2001). All mammals exhibiting adaptive hypothermia have a hypothalamic set point below which they do not allow body temperature to fall. For example, in very cold environments, for most species, the lowest temperature for hibernation may be regulated at just a couple degrees above freezing. For species in slightly warmer environments, body temperatures range slightly higher (5°C–10°C), and for species that employ torpor only for short-term emergencies, body temperatures range from 10°C to 15°C. When challenged in such a way, these animals must arouse from torpor and restore their body temperature all the way to normal before reentering the state of hibernation. In terms of energy, this can be very costly.

The largest mammals to undergo true hibernation are marmots (Genus *Marmota*), which weigh about 5 kg (Lee et al. 2016; Armitage 2017). Hibernation is not possible or even necessary in very large mammals because of the large amount of energy necessary for arousal (Morrision 1960). Also, due to their size, large mammals can store sufficient energy in the form of internal fat to meet winter demands. Bears have been thought to be marginal hibernators since they shelter in dens for up to 5–7 months; plus, the birth of young occurs while the female is hibernating. But contrary to popular belief, bears do not exhibit "true" hibernation. Instead, they undergo a period of **winter lethargy**, or shallow torpor, with a decrease in body temperature of only 5°–7°C below their active level of 38°C (Craighead et al. 1976; Rogers 1981; Watt et al. 1981; Hissa et al. 1994; Hissa 1997; Harlow et al. 2002, 2004; McNab 2008; Heldmaier 2011). Toien and colleagues (2011) examined independence of metabolic suppression from body temperature of American black bears (*Ursus americanus*) residing in south-central interior Alaska. In this region black bears are known to "hibernate" for 5 to 7 months, during which time they do not eat, drink, urinate, or defecate; metabolism and body temperature are suppressed to 25% of basal rates, and body temperature ranges from 30 to 36 °C. Heart rates were reduced from 55 to as few as 9 beats per minute (bpm). Following emergence from dens in spring, bears maintained a reduced metabolism for up to 3 weeks; this suppressed metabolism during "hibernation" was independent of a lowered body temperature. Robbins and coworkers (2012) compared hibernation in brown bears (*Ursus arctos*) and American black bears to the energetic costs for summer-fall fasting of polar bears. Although polar bears that were confined to dens and therefore were truly hibernating expended energy at the same rate per unit mass as did brown bears and black bears, daily mass losses, energy expenditure, and losses of lean mass were approximately twice as high as in fasting, active polar bears than in hibernating brown or black bears. Increases in global warming and resulting ice-free duration in more southern regions of the arctic will likely extirpate some polar bear populations (de la Guardia et al. 2013). For northern regions, global climate changes may require increases in the amount of fat necessary to withstand longer summer-fall fasts necessary for producing large, robust cubs (Hunter et. al 2010; Regehr et al. 2007, 2010).

Do bears exhibit periodical arousals during winter? Some investigators contend that bears do not engage in bouts of arousal during winter lethargy (Nelson et al. 1973; Nelson 1980; Hissa et al. 1994). In contrast, Harlow and coworkers (2004) suggest that bears engage in bouts of muscle activity during the winter denning period; these result in retention of muscle strength without elevating their core body temperature and without arousing from shallow torpor (Harlow et al. 2004). In terms of energy, it makes good sense to maintain a comparatively high body temperature for large mammals such as bears. Members of Order Carnivora do not exhibit true hibernation; however, as seen above, some species undergo inactivity and depression of body temperature during winter periods. For example, winter torpor has been observed in Japanese badgers (*Meles anakuma*) (Yamamoto 1997; Kaneko 2001; Tanaka 2005; Newman et al. 2011), American badgers (*Taxidea taxus*), striped skunks, and raccoon dogs (*Nyctereutes procyonoides*) residing at northern latitudes (Harlow 1981; Korhonen and Harri 1984; Mutch and Aleksiuk 1977). Striped skunks enter spontaneous daily torpor with body temperature reaching 26°C—the lowest torpid body temperature recorded for any carnivore (Hwang et al. 2007).

Mammals capable of adaptive hypothermia are found in all mammalian Subclasses— Prototheria, Metatheria, and Eutheria. True hibernation has not been reported for members of Orders Cetacea, Cingulata, Carnivora, Tubulidentata, Lagomorpha, Perissodactyla, or Cetartiodactyla. The short-nosed echidna (*Tachyglossus aculeatus*) and 15 species of marsupials undergo adaptive hypothermia (Geiser and Ruf 1995; Grigg and Beard 2000; Nicol and Andersen 2000; Morrow et al. 2016). Temporal heterothermy (hibernation and torpor) have been reported in many marsupial species (Riek and Geiser 2014; Stawski et al. 2015; Kortner et al. 2016; Swoap et al. 2017; Wacker et al. 2017). Marsupials capable of torpor range in size from Giles's planigale (*Planigale gilesi*, 8 g) to the western quoll (*Dasyurus geoffroii*, 1 kg). Of Orders Afrosoricida and Eulipotyphla, only the hedgehogs (Genera *Erinaceus* and *Aethechinus*) and some tenrecs of Madagascar hibernate, as do the golden moles (Family Chrysochloridae). In Europe, hedgehogs have been a principal subject of hibernation studies (Webb and Ellison 1998). Recently, body temperature of free-ranging desert hedgehogs (*Paraechinus aethiopcus*) was documented across seasons in the deserts of Saudi Arabia (Boyes et al. 2017). Modal body temperatures (35°–36.5°C) were slightly below normal for mammals. These temperatures were slightly cooler than maximum Tb's recorded for most desert-adapted mammals. For free-ranging Ethiopian hedgehogs (*Paraechinus aethiopicus*) basking behavior during winter represents a form of energy conservation (Baker et al. 2016).

Shrews do not hibernate, but some may undergo shallow torpor (Fons et al. 1997). Two metabolic levels characterize Family Soricidae (Vogel 1976; Nagel 1977; Genoud 1988; Merritt 2010).Subfamily Crocidurinae (white-toothed shrews) has a low metabolic rate and low body temperature and undergoes torpor. In contrast, Subfamily Soricinae (red-toothed shrews) exhibits high metabolic rates and elevated body temperatures and cannot undergo torpor (Churchfield 1990; Merritt 1995). The different metabolic levels of the two subfamilies represent evolutionary responses to different climates: white-toothed shrews are adapted to warmer, more southern latitudes, whereas red-toothed shrews have evolved in more northerly latitudes.

Bats avoid cold by hibernating, migrating, or doing both. The picture of temperature regulation in the microchiropterans is more complicated, however (O'Farrell and Studier 1970; Lyman et al. 1982; Thomas 1995; Altringham 1996; Neuweiler 2000; Ayala-Berdon et al. 2017; Barclay

et al. 2017). Bats of Family Vespertilionidae (see Chapter 21) are well-known hibernators, and most species occurring in the temperate zones spend the winter in caves for this purpose. Vespertilionid bats in temperate regions typically hibernate from October to April. In a hibernation site (hibernaculum), the ambient temperature may be near 5°C, and the bats are in deep hibernation, maintaining a body temperature of about 1°C above the ambient. This period is punctuated with occasional arousals during which the animal urinates, drinks, or changes location. Arousals occur every 1–3 weeks and last for only a few hours each time. The arousals are very similar to those exhibited by sciurid rodents. In preparation for winter, temperate zone bats may establish body fat in autumn equal to one-third of their body mass. In summer, shallow daily torpor (lasting for only a few hours) may occur during the day while bats are roosting. Body temperature rises again before feeding at dusk. Winter hibernation in bats differs from short-term torpor largely in the length of dormancy and the temperature decrease.

The duration of hibernation for bats also differs widely among species and within a species, depending on the geographic area. In the northeastern United States, for example, cavernicolous bats (those that occur in caves or abandoned mines) such as the little brown bat (*Myotis lucifugus*) hibernate for 6–7 months. Periods of hibernation for bats in warmer areas are considerably shorter. The larger fruit bats (Family Pteropodidae) are euthermic and maintain body temperature between 35° and 40°C (Ransome 1990; McNab and Bonaccorso 1995). Some small-bodied tropical and subtropical pteropodids employ torpor to offset energetic constraints (Barclay et al. 2017). Free-living big brown bats (*Eptesicus fuscus*) residing in a building in Indiana showed a different pattern of thermoregulation than little brown bats. Torpor bouts lasted on average 5 hours. There was a significant correlation between roost temperature and length of the euthermic period; a larger proportion of bats aroused on warm days, which suggested that big brown bats may be taking advantage of warm nights to forage. During arousals when in hibernation, big brown bats and other noncavernicolous bats may utilize partial passive rewarming (Halsall et al. 2012). Bartholomew and colleagues (1970) reported torpor in smaller species of fruit bats (the common tube-nosed fruit bat, *Nyctimene albiventer* and the unstriped tube-nosed bat, *Paranyctimene raptor*), and Coburn and Geiser (1996) described torpor in the southern blossom bat (*Syconycteris australis*; Figure 18.16). When food was withheld, blossom bats remained in torpor from 1 to 10 hours at a body temperature of about 18°C.

Torpor in primates is limited to the small lemurs of Madagascar. Mouse lemurs (Genus *Microcebus*), the smallest primates, range in mass from 29 to 63 g and exhibit an average body temperature during torpor of 24.9°C (Ortmann et al. 1996). Madagascar fat-tailed dwarf lemurs (*Cheirogaleus medius*) showed a wide daily fluctuation in body temperature of almost 20°C, closely tracking air temperature of their tree holes (Dausman et al. 2004). Energy

Figure 8.16 **The frugivorous southern blossom bat (Syconycteris australis) of Australia.** This species is one of many bats that enter torpor.

savings in the form of heterothermy (i.e., daily torpor) has been confirmed only in Family Cheirogaleidae (*Cheirogaleus*, *Microcebus*, *Allocebus* and *Mirza*) of the Malagasy lemurs and the southern lesser bushbaby (*Galago moholi*) of Family Galagonidae (Dausmann 2014).

The greatest number of hibernators is found in Order Rodentia, specifically squirrels (Family Sciuridae). Rodents also show the greatest variation in length of dormancy. Within this group, we see a continuous integration between daily and seasonal torpor. Ground squirrels and marmots undergo periods of deep hibernation (Barnes 1989; Armitage et al. 1990; Ferron 1996; Buck and Barnes 1999a; Barnes and Buck 2000; Lee et al. 2016; Armitage 2017). Body temperature in marmots decreases from about 39°C during summer to between 2° and 8°C during deep hibernation. The lowest body temperature reported for hibernating marmots is about 4°C (Ferron 1996). Typically, the heartbeat slows from 100 to 15 bpm, and oxygen consumption falls to a tenth of the normal rate. Marmots may

breathe only once every 6 minutes when in deep hibernation; hibernating animals lose 30% of their weight by mobilizing body fat during winter. It is noteworthy that, with the exception of the woodchuck (*Marmota monax*), all species of the Genus *Marmota* are social and hibernate in groups (Arnold 1988; Armitage 2017).

Richardson's ground squirrels (*Urocitellus* [*Spermophilus*] *richardsonii*) of northwestern North America also undergo periods of deep hibernation. Adult squirrels may enter hibernation as early as mid-July and emerge 8 months later, in mid-March. During much of their long period of hibernation, body temperature is about 3°–4°C and increases to about 38°C for their 4-month active phase. Like the torpor in many hibernators, torpor in ground squirrels during winter is interrupted by frequent intervals of rewarming to euthermy, and entry and arousal show a stepped progression in body temperature. Hibernation has been well studied in different ground squirrels, especially in golden-mantled (*Callospermophilus* [*Spermophilus*] *lateralis*), Richardson's (*Urocitellus richsonsonii*), arctic (*Urocitellus* [*Spermophilus*] *parryii*), and 13-lined (*Ictidomys* [*Spermophilus*] *tridecemlineatus*) ground squirrels (Wang 1979; Michener 1992; Barnes 1989; Healy et al. 2012; Kisser and Goodwin 2012). The "champion" of hibernators is the arctic ground squirrel; it will be discussed in detail later in this section.

Cricetids commonly survive cold by employing daily torpor coupled with communal nesting. Because their body temperatures are not as depressed as those of such deep hibernators as ground squirrels, they show a great deal of thermolability. All members of Genus *Peromyscus* probably undergo some form of dormancy. Torpor occurs diurnally and lasts for less than 12 hours (Hudson 1978). Thus, *Peromyscus* may be active on a warm day in mid-January in the north, but when ambient temperatures reach about 2°–5°C, these small rodents may rapidly decrease body temperature to 13°C and undergo short-term torpor. The lability of body temperature in *P. leucopus* seems greater than that of other species of the genus (Hart 1971).

Hibernation (deep torpor) is reported for zapodids (Genera *Zapus* and *Napaeozapus*; Brower and Cade 1966; Muchlinski 1980). In the Wasatch Mountains of Utah, the period of hibernation of *Z. princeps* ranges from early September to late July depending on elevation of the hibernacula (Cranford 1978). A summer active period of about 87 days spanned the period between snow melt in early summer and the beginning of the autumn snowfall season. Mice hibernated at an average depth of 59 cm, with no food caches. The mean soil temperature during hibernation was 4.6°C, and emergence from hibernation was cued by increasing soil temperature (Figure 8.17). Northern birch mice (*Sicista betulina*) of northern and eastern Eurasia undergo daily torpor in response to cold. They decrease body temperature to about 4°C and wake spontaneously at night to feed. Most hamsters (namely, golden or Syrian and Turkish—*Mesocricetus auratus*, *M. brandti*) do not readily hibernate or exhibit torpor. On the other hand, Siberian hamsters (*Phodopus sungorus*) undergo periodic daily torpor
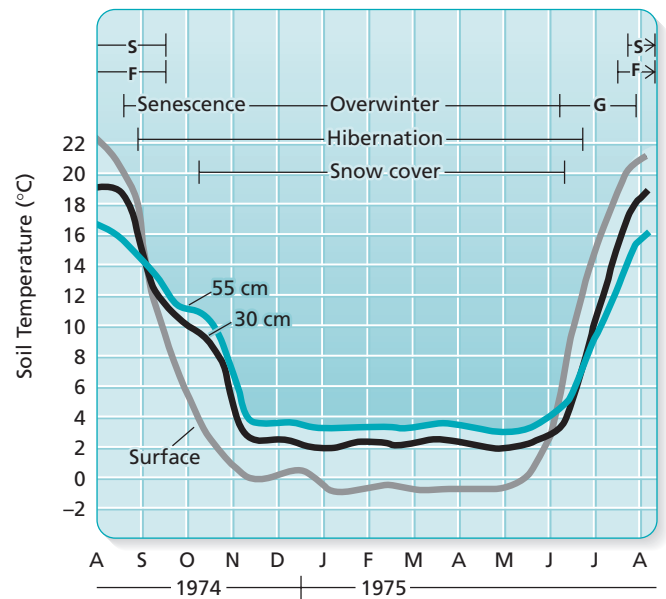
Figure 8.17 Soil temperatures in a montane environment. Daily average soil temperatures at the surface, 30 cm, and 55 cm depth at 2,900 m in Albion Basin, Alta, Utah, from 15 August 1974 to 15 August 1975. The lines are plotted through the weekly mean. *Abbreviations:* G = plant growth; F = flowering; S = plants setting seed. *Data from Cranford (1978).*

with body temperature near 19°C. Color change and torpor in these hamsters are quite variable; some individuals turn white in winter and exhibit torpor, whereas others remain brown and do not enter torpor. Dormice (Genera *Glis* and *Eliomys*) also undergo hibernation in response to food deprivation (Wilz and Heldmaier 2000).

The **cycle of dormancy** can be divided into three phases: entrance, period of dormancy, and arousal (Hudson 1973). An excellent example of the cycle of dormancy is that measured for the arctic ground squirrel (*Urocitellus* [*Spermophilus*] *parryii*; Barnes 1996; Boyer and Barnes 1999; Sheriff et al. 2012; Williams et al. 2012) and for Richardson's ground squirrel (*S. richardsonii*; Wang 1978, 1979). Many mammals prepare for **entrance** to winter dormancy by putting on fat. For example, the woodchuck of North America begins putting on weight in midsummer. Just prior to hibernation, its weight is about 30% greater than in early summer. In autumn, after lining its hibernaculum with leaves and grasses, the obese woodchuck moves into its den, plugs the entrances, and curls up into a tight ball. The earthen plug is important for maintaining proper temperature and humidity in the den during winter. Increase in body mass among hibernators before dormancy can be impressive, reaching 80% in golden-mantled ground squirrels (*Callospermophilus lateralis*), for example. During entrance, animals decrease heart rate, blood pressure, and oxygen consumption and finally exhibit a decline in body temperature. For some species, the environmental cues that signal preparation for hibernation are associated with the time of year and are induced by a combination of low

Figure 8.18 **Period of dormancy of the arctic ground squirrel.** The arctic ground squirrel (*Urocitellus[Spermophilus] parryii*) of northern Alaska undergoes seasonal hibernation. During deep hibernation the minimum body temperature falls to –2°C. Details of this period of hibernation are described in Figure 8.19 and in the text.

temperature and lack of food. For others, entrance into dormancy may occur without an external stimulus. For such species, the duration of the daily light and the temperature cycle may synchronize to maintain the annual rhythm of dormancy. For arctic ground squirrels, entrance into hibernation begins in autumn with stepped periods of torpor alternating with periodic rewarming bouts reaching euthermy (Figure 8.18). The soil temperature during the period of entrance is about 0°C.

The **period of dormancy** is signified by a leveling off of the body temperature in late autumn. During the season of hibernation, arctic ground squirrels demonstrate 12 bouts of torpor with durations of 1–3 weeks each. Bouts are separated by regular episodes of arousal (Figure 8.19A) in which the body temperature returns to normal (that is, euthermic) levels (about 37°C). During hibernation, minimum body temperature falls to –2°C, whereas temperature of the surrounding soil is –10° to –15°C. **Arousal** from hibernation occurs in spring. To reduce energy expenditure during arousal, some hibernators employ passive rewarming. This is achieved by basking in the sun or practicing social thermoregulation and can be facilitated by an increase in surrounding ambient temperature (Geiser et al. 2004).

Changes in body temperature of a specific episode of torpor of the arctic ground squirrel are illustrated in Figure 8.19B. Each arousal episode includes three phases: (1) rewarming from torpor, (2) 24 hours of normal high body temperature, and (3) a slow cooling into torpor. Periods of arousal account for most of the energy used during dormancy. Energy costs associated with arousal from –2° to 37°C include (1) the cost of warming from hibernation to 37°C, (2) the cost of sustaining euthermy (37°C) for several
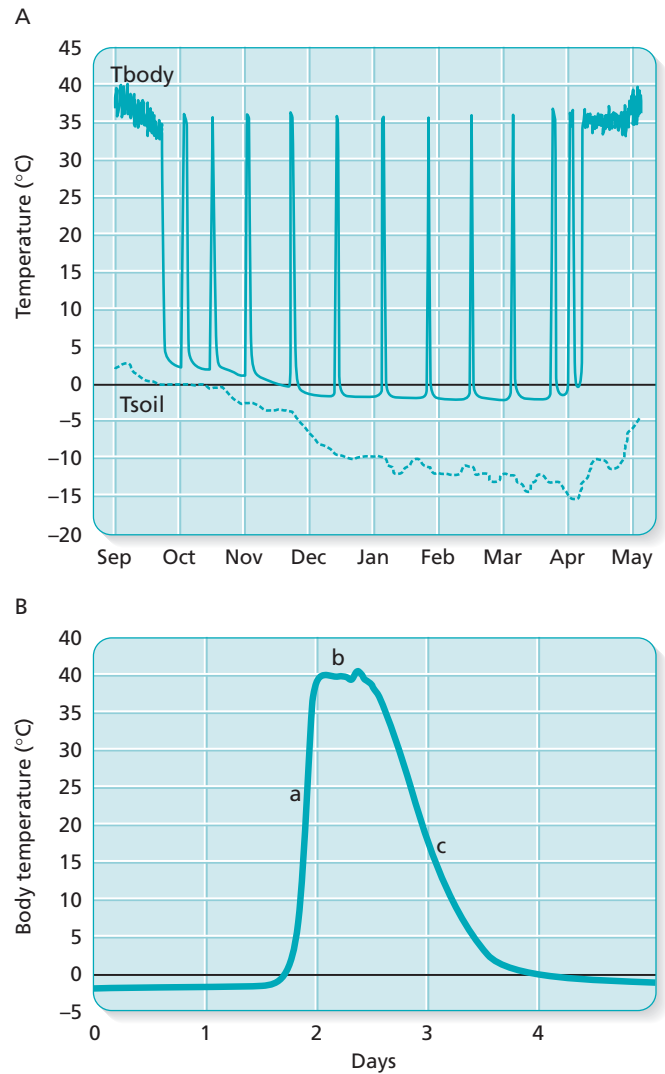
Figure 8.19 **Hibernation in the arctic ground squirrel.** (**A**) The period of seasonal hibernation of the arctic ground squirrel (*Urocitellus [Spermophilis] parryii*) residing in northern Alaska. Note the numerous bouts of torpor and episodes of arousal, as well as the extreme decrease in core body temperature occurring during deep torpor. (**B**) Each arousal episode includes three phases: (*a*) rewarming, (*b*) euthermia, and (*c*) cooling. *Adapted from Boyer and Barnes (1999).*

hours, and (3) the cost of maintaining a metabolic rate above torpor as the body temperature slowly declines during reentry into torpor. For the entire period of dormancy, these three metabolic phases account for an average of about 83% of the total energy used by a squirrel (e.g., *Urocitellus* [*Spermophilus*] *richardsonii*; Wang 1979). Energy for arousal from hibernation is provided principally by nonshivering thermogenesis in brown adipose tissue augmented by shivering. This energy expense seems rather wasteful, and the function of such periodical arousals is not well understood.

Why do mammals arouse from hibernation in the middle of winter? Many hypotheses have been forwarded to explain this phenomenon. It is possible that periodic arousal permits hibernators to assess environmental con-

ditions conducive to emergence. Some scientists contend that arousals are related to retention of memory and that retention of memory requires slow-wave electrical activation, which does not occur at low body temperatures characteristic of hibernation (Heller and Ruby 2004); therefore, periodic arousals during hibernation are necessary to provide conditions appropriate for slow-wave electrical activation and retention of memory. Further, periodic arousals may function to (1) permit hibernators to assess environmental conditions conducive to emergence; (2) respond to a buildup of metabolic byproducts that must be expelled periodically by defecation and urination; (3), mediate evaporative water loss; or (4) are necessary for conducting some endogenous repair functions that require mitochondrial RNA and protein synthesis, which are not possible at a low body temperature. Due to the high energetic cost of the arousal, there must be some evolutionary benefit for this phenomenon; however, as of now, functions of mammalian arousals remain a mystery (Bouma et. al. 2010; Heller et. al 1993; Heller and Ruby 2004; Malan 2010).

Resistance to Cold

Increase in Thermogenic Capacity

Mammals employ many different tactics of energy conservation to avoid cold stress. If cold stress persists, however, mammals must resist it by processes that generate heat and thus require energy (see Table 8.1). The major ways in which endotherms increase heat production are muscular activity and exercise, involuntary muscle contractions (shivering), and nonshivering thermogenesis (see Figure 8.4). The most conspicuous mechanism by which endotherms increase heat production is by muscular activity from locomotion or shivering; however, the means need not be apparent for the rate of heat production to increase (Bartholomew 1982; Korhonen et al. 1985; Kleinebeckel and Klussmann 1990; Schmidt-Nielsen 1997; May 2003; Hohtola 2004; Rose and Ikonomopoulou 2005). Whereas shivering is well documented for marsupials, humans, canids, felids, selected rodents, lagomorphs, and ungulates as well as many species of birds, small mammals residing in variable environments employ a means of heat production called **nonshivering thermogenesis**, which does not involve muscle contraction (Smith and Horwitz 1969; Jansky 1973; Girardier and Stock 1983; Trayhurn and Nicholls 1986; Cannon and Nedergaard 2004; Luna et al. 2012; Oelkrug et al. 2015; Li et al. 2016). **Brown adipose tissue**, the site of nonshivering thermogenesis, was first observed by Conrad Gesner in 1551 in the interscapular area of the Old World marmot (*Marmota alpina*). Brown fat, once referred to as the "hibernating gland," is found in all hibernating mammals and is the primary thermogenic tissue of cold-adapted small mammals (especially rodents and shrews). It is also well developed in newborn species of mammals, including humans. Within mammals, brown fat

has been reported in many species spanning nine orders: Dasyuromorphia, Chiroptera, Afrosoricida, Eulipotyphla, Rodentia, Lagomorpha, Cetartiodactyla, Carnivora, and Primates. The wide occurrence of nonshivering thermogenesis in small mammals was reviewed by Heldmaier (1971), Jansky (1973), Scantlebury and colleagues (2008), and Ruff and coworkers (2012). While monotremes do not possess brown adipose tissue (Hayward and Lisson 1992), researchers have isolated brown adipose tissue in some species of marsupials (Hope et al. 1997; Wallis 1979; Clements et al. 1998; Rose et al. 1999). For most carnivorous marsupials, however, endogenous heat production is accomplished primarily by shivering thermogenesis (Geiser 2003). Although Oliphant (1983) reported the presence of brown adipose tissue in ruffed grouse and chickadees, microanatomical studies based on multilocularity, increased vascularity, mitochondrial density, and cytochrome-c oxidase activity indicate that birds do not possess functional brown fat (Olson et al. 1988; Saarela et al. 1989, 1991; Brigham and Trayhurn 1994).

Unlike white adipose tissue, which is characterized by a single large droplet of fat with a peripheral nucleus (Pond 1978), brown fat contains many small droplets (multilocular) with a centrally located nucleus. Brown fat also differs from white adipose tissue in being highly vascular and well innervated. The cells contain many mitochondria, whereas white fat cells have comparatively few. Brown fat is capable of a far higher rate of oxygen consumption and heat production than white fat is. The reddish-brown color of brown fat is derived from iron-containing cytochrome pigments in the mitochondria, the essential part of the oxidizing enzyme apparatus of brown adipose tissue. White fat serves primarily as insulation and a storage site for food and energy. Brown fat, with its rich supply of mitochondria, serves as a miniature internal "blanket" that overlies parts of the systemic vasculature and becomes an active metabolic heater applied directly to the bloodstream (Wunder and Gettinger 1996). Deposits of brown fat can be rather diffuse but are principally found in the interscapular, cervical, axillary, and inguinal regions in close proximity to blood vessels and vital organs (Hyvärinen 1994).

Temperature receptors in the skin sense cold and send impulses to the preoptic area of the hypothalamus—the "mammalian thermostat" located in the brain. Impulses are then relayed along the sympathetic nerves to the brown adipose tissue, where nerve endings release the neurohormone **norepinephrine**. At the brown adipose tissue, norepinephrine activates an enzyme (lipase) that splits triglyceride molecules into glycerol and free fatty acids. In the brown fat cell, the mitochondrial respiration is "uncoupled" from the mechanism of adenosine triphosphate (ATP) synthesis so that the energy of oxidation of the fatty acids is dissipated as heat instead of being used for ATP synthesis. A special protein, called **thermogenin**, is responsible for the uncoupling (Himms-Hagen 1985). When bats arouse from hibernation, the brown fat pad is much warmer than the rest of the body (Hayward and Lyman 1967; Figure 8.20). The close

A

Interscapular
brown fat

B

Head

Brown
fat

Wing   Wing
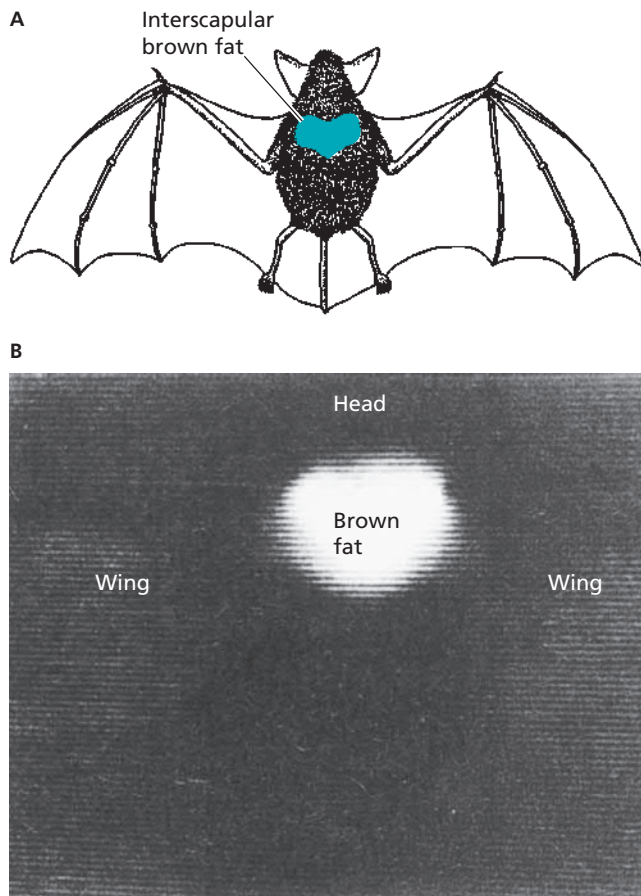
Figure 8.20 Brown fat. (**A**) Diagram showing the position of interscapular brown fat in the big brown bat (*Eptesicus fuscus*); (**B**) photograph taken with heat-sensitive film indicating that the temperature of interscapular brown fat in the big brown bat is high during arousal from hibernation. *Adapted from Hayward and Lyman (1967).*

proximity of Selzer's vein just beneath the interscapular brown fat permits rapid passage of warmed venous blood directly to the heart and brain with a minimum of heat loss.

Research on northern small mammals has shown that dramatic increases in metabolic rate in cold are due to nonshivering thermogenesis (Gebczynski and Taylor 2004). Nonshivering heat production usually tracks environmental temperatures, falling to the lowest rates in spring and summer, increasing in autumn, and peaking in winter. Typically, small mammals demonstrate a significant inverse relationship between nonshivering heat production and environmental temperature. Wunder and colleagues (1977) showed a 29% increase in oxygen consumption for prairie voles (*Microtus ochrogaster*) in winter compared with summer. Alaskan red-backed voles (*Myodes rutilus*) exhibited a 96% increase in metabolism in winter. Although species of *Peromyscus* commonly employ many different survival adjustments (Merritt 1984), they are adept at increasing metabolism during winter. Maximum metabolism for *Peromyscus* from Iowa and Michigan ranged from a 24% to a 70% increase over summer rates (Lynch 1973; Wickler 1980, respectively). Shrews

typically show very high rates of nonshivering heat production. For example, for masked shrews (*Sorex cinereus*) residing in Pennsylvania, nonshivering thermogenesis in winter was almost twice that measured in summer—an increased capacity of 182% (Merritt 1995). Maximum metabolism, resting metabolic rate, and nonshivering thermogenesis were compared for 12 species of shrews from tropical and temperate regions (Sparti 1992). Maximum metabolism, and consequently improved cold tolerance, was pronounced in temperate species. Smith and Horwitz (1969) found a direct correlation between mass of brown fat and nonshivering thermogenesis. Like nonshivering thermogenesis, monthly changes in the mass of brown fat are inversely related to minimum environmental temperature for many species of voles, mice, and shrews (Merritt and Zegers 2002).

Adaptations to Heat

To survive in deserts, mammals must cope with a variety of demanding environmental challenges, such as intense heat during the day, cold nights, paucity of water and cover, and a highly variable food supply. Desert ecosystems are widespread and abundant—35% of the earth is covered with deserts. Mammals have successfully colonized desert ecosystems, as evidenced, for example, by the rich and diverse fauna of heteromyid and dipodid rodents (see Chapter 16) in the deserts of North America and the Old World, respectively (Schmidly et al. 1993; Wilson and Reeder 2005). An excellent review of studies examining adaptations of mammals to desert environments is provided by Degen (1997) and Tracy and Walsberg (2002).

The challenges faced by mammals in desert environments are even more severe than those encountered in cold regions. Water as well as food is scarce, and the problem in temperature regulation is reversed. When we considered cold stress to mammals, we assessed the role of thermal radiation, conduction, convection, and other environmental influences on heat transfer between an individual and the environment, and then we focused on the many mechanisms employed to reduce heat flow to the environment (see Figure 8.1). Recall that small mammals in cold regions reduced heat loss by up to 19% by increasing pelage insulation. Increased insulation reduced the gradient between the warm core of the body and the outside environment. In desert environments, however, the gradient between the internal and environmental temperatures is reversed. In some deserts, mammals may have to cope with air temperatures that reach 55°C and ground temperatures that exceed 70°C. Unlike arctic mammals concerned with conserving heat, desert mammals must dissipate heat or avoid it to maintain euthermy. Our discussion now focuses on the complex anatomical, physiological, and behavioral adaptations that enhance the survival of mammals in desert ecosystems.

Water is essential for survival. It constitutes 70% of the body mass of mammals, and water loss must be balanced by water gain. In mammals, **osmoregulation**—the maintenance of proper internal salt and water concentrations—is performed principally by the kidney. In addition to producing a concentrated urine, desert mammals cope with a lack of water by producing very dry feces. Evaporation, occurring mostly from the respiratory tract, is the major avenue of water loss but is also an important device for cooling. In this section, we examine evaporation across the skin and from respiratory passages and the ways in which mammals keep cool in xeric (very dry) environments by employing evaporative cooling. Temperature regulation is also influenced by changes in insulation, appendages, metabolic rate, and body size. Mammals achieve water balance by eating succulent vegetation, drinking available water, and "metabolically" converting food into water (Nagy and Peterson 1980; Morton and MacMillen 1982; MacMillen and Hinds 1983; Walsberg 2000; Tracy and Walsberg 2002). Last, we will discuss a form of dormancy called "estivation," which mammals residing in hot environments employ to survive heat and reduced food availability.

WATER ECONOMY

The Mammalian Kidney

Most of the elimination of excess water and soluble salts, urea, uric acid, creatinine, and sulfates occurs in the kidney. Mammalian **kidneys** are paired, bean-shaped structures located within the dorsal part of the abdominal cavity (Figure 8.21). The kidney in cross section displays the following areas and structures. The outer **cortex** contains the renal corpuscles, convoluted tubules, and blood vessels.

Masses of cortical tissue fill in between the pyramids of medullary tissue. The inner **medulla** is divided into triangular wedges called **renal pyramids**. Their broad bases are directed toward the cortex, and narrow apices (**renal papillae**) are oriented toward the center of the kidney, opening into the **calyx** and expanded **pelvis**. Ducts leading into the pelvis, the **ureters**, empty into the **urinary bladder**, which functions as a storage organ for urine. Another duct, the **urethra**, drains the bladder and carries its contents to the outside.

Nephrons (about 1.5 million in each kidney) are the functional units of the kidney and consist of a closed bulb, **Bowman's capsule** (or glomerular capsule), connected to a long coiled tube. Tubules of the various nephrons empty into collecting ducts that discharge into the pelvis of the kidney and then connect to the ureter. A microscopic mass of capillaries called the **glomerulus** is enclosed within the capsule. The capsule plus the inner glomerulus is called a **renal corpuscle**. Blood reaches the kidney via the large renal artery, a branch of the descending aorta. The blood arrives at the glomeruli by afferent arterioles. The blood is collected from the glomeruli by a number of venules and leaves the kidney by way of renal veins making their way to the inferior vena cava. Blood vessels enter a convoluted network within the glomerular capsule, then move around proximal and distal convoluted tubules and the **loop of Henle**, finally emptying into a branch of the renal vein. Exchange of substances takes place through active transport and osmosis almost exclusively between blood capillaries and nephrons.

The mammalian kidney performs many different roles including glomerular filtration, tubular reabsorption, and tubular secretion. These functions are well described by Hill and Wyse (1989) and Schmidt-Nielsen (1997). For mammals residing in desert environments, the ability to
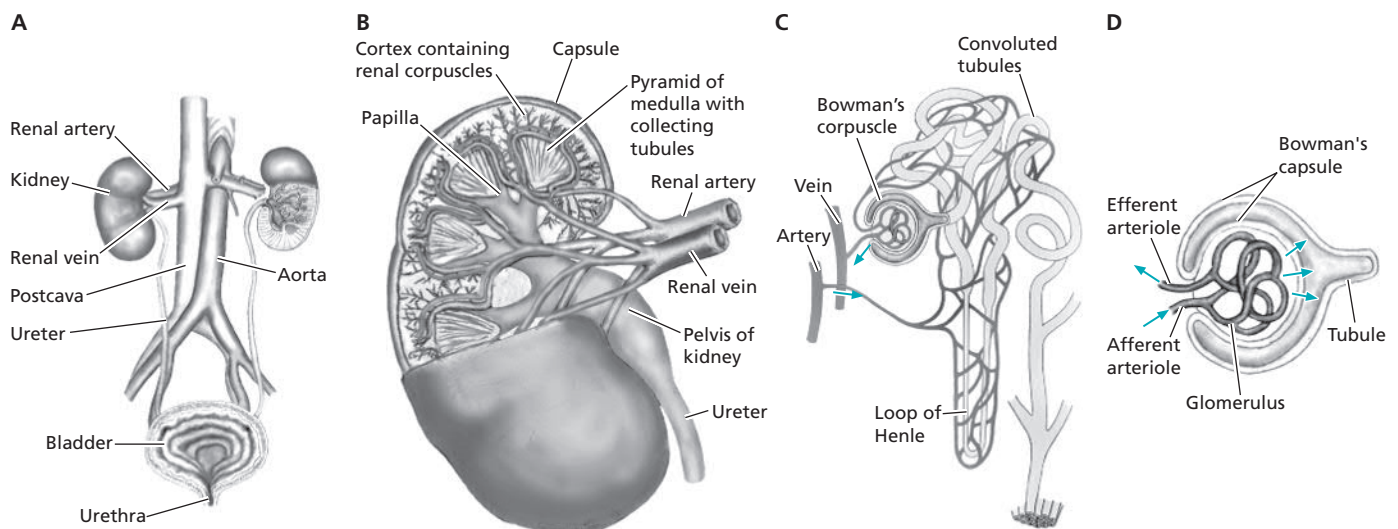
Figure 8.21 **The human excretory system.** (**A**) Ventral view of the entire system; (**B**) median section of one kidney; (**C**) relationship of Bowman's corpuscles, tubules, and blood vessels; (**D**) a single Bowman's corpuscle and adjacent tubule (shown also in cross section); solid arrows show flow of blood, broken arrows show the excretory path; (**C**) and (**D**) are diagrammatic and much enlarged. *Adapted from Storer et al. (1979).*

concentrate urine is paramount and closely tied to the function of the kidney (Fielden et al. 1990a; Degen 1997). Because of the urine-concentrating ability of kidneys, mammals are able to produce urine that is hyperosmotic to that of blood plasma—up to 25 times the concentration of plasma. Understandably, the highest urine concentrations are found in mammals residing in desert habitats (Yousef et al. 1972; French 1993). The concentrating ability of the mammalian kidney in different species is closely related to the respective lengths of their loops of Henle and the collecting ducts that transverse the renal medulla. The prominence of the medulla is commonly expressed as the relative medullary thickness (RMT), an important index of kidney adaptation (Sperber 1944). RMTs of mammals residing in arid areas are greater than those of mammals from more mesic environments (those with more moisture). The relationship between RMT and the kidney's maximum urine-concentrating capacity was first quantified by Schmidt-Nielsen and O'Dell (1961) and has proven very useful as a means of comparing kidney function in mammals. The anatomy of the papilla of the medulla can be compared visually for different species (Figure 8.22). In

desert-adapted small mammals, the papilla may extend beyond the margins of the renal capsule into the ureter. This extension is pronounced in small desert rodents (MacMillen and Lee 1969; Altschuler et al. 1979; Diaz and Ojeda 1999), shrews (Lindstedt 1980), and bats (Geluso 1978), suggesting that these species possess very powerful kidneys. In contrast, aquatic mammals, such as beavers, aquatic moles, water rats, and muskrats, have very short loops (shallow papillae) and produce less concentrated urine.

Urine and Feces

Comparative studies of renal function and morphology in mammals indicate a direct relationship between the ecological distribution of a species and its ability to conserve urinary water. The ability to concentrate urine in mammals is associated with long loops of Henle and tubules in the kidney, which enhance the countercurrent exchange function. Species that reside in arid habitats tend to possess kidneys better adapted for water conservation. Representatives are found in Orders Diprotodontia (Family Macropodidae), Chiroptera, Cingulata (Family Dasypodidae), Rodentia (Families Muridae, Cricetidae, Octodontidae, Heteromyidae, Sciuridae), and Lagomorpha (Family Leporidae). Most mammals lose water by excretion in the urine and elimination in the feces. But the preceding groups have the ability to produce relatively dry feces and concentrated urine. Thus, the average values for maximum urine concentration in desert heteromyids is superior to those of most mammals and comparable to those of other desert-adapted small mammals, such as dipodids from Asia and North Africa (see Chapter 16) and murids from Australia and southern Africa (French 1993). For example, the laboratory white rat can produce urine with twice the osmotic concentration that humans can achieve. The dromedary camel (*Camelus dromedarius*), and even dogs and cats, have a urine-concentrating equivalent to that of the white rat. As expected, the amount of water loss from feces is quite low for desert mammals. The feces of Merriam's kangaroo rat (*Dipodomys merriami*) are over 2.5 times as dry as those of white rats (834 versus 2,246 mg of water/g of dry feces). Furthermore, heteromyids commonly decrease fecal water loss by assimilating over 90% of the food they ingest. Desert rodents (e.g., kangaroo rats, sand rats, and jerboas) produce urine concentrations of 3,000–6,000 mOsm/L; Australian hopping mice (*Notomys alexis* and *N. cervinus*) can produce urine concentrations of over 9,000 mOsm/L (MacMillen and Lee 1969, 1970). Intuitively, we think of heteromyid rodents such as kangaroo rats and pocket mice as leaders in water conservation. Many other small mammals, however, such as pallid bats (*Antrozous pallidus*), canyon and house mice (*Peromyscus crinitus* and *Mus musculus*), golden hamsters (*Mesocricetus auratus*), Chaotung voles (*Eothenomys olitor*), and the subterranean Talas tuco-tuco (*Ctenomys talarum*) have evaporative water losses equivalent or greater to that of many desert-dwelling heteromyids (Baldo
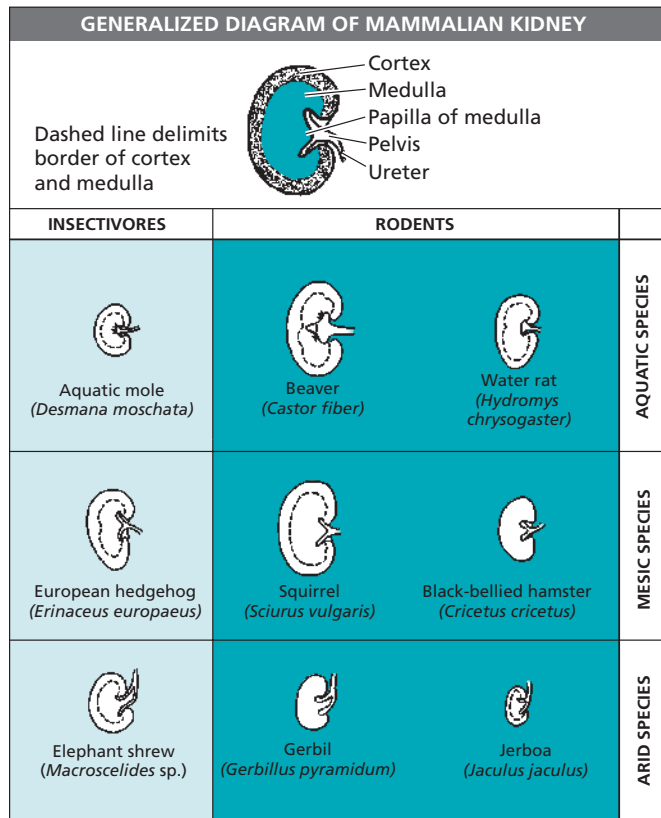
Figure 8.22 The kidneys of select mammals. Aquatic species show little or no development of the papilla of the medulla. Genera *Desmana* and *Hydromys* lack the papilla. Genus *Castor* has two very shallow papillae. Mesic species have papillae. The papilla is especially well developed in arid species, so much so that it often penetrates well into the ureter (e.g., Genera *Macroscelides*, *Gerbillus*, and *Jaculus*). *Adapted from Hill and Wyse (1989).*

et al. 2015). In addition, huddling thermogenesis is crucial in reducing evaporative heat loss in bats such as Natterer's bat (*Myotis nattereri*; Boratynski et al. 2015). Evaporative water loss, economy, and partitioning at ambient temperatures from 14° to 33° C was examined for the monito del monte (*Dromiciops gliroides*) occurring in temperate rainforests of Chile. The evaporative water loss of *D. gliroides* was typical for a marsupial of its body mass and phylogenetic position (Withers et al. 2012). For another marsupial, the spectacled hare-wallaby (*Lagorchestes conspicillatus*), Bradshaw and colleagues (2001) noted the lowest mass-specific rate of water turnover reported for any mammal.

An additional way that desert rodents economize water loss is by producing a highly concentrated milk. The milk of Merriam's kangaroo rat averages 50.4% water—a concentration comparable to that produced by seals and whales (Kooyman 1963). Furthermore, it has been demonstrated that in desert rodents, canids, and kangaroos, mothers reclaim water by consuming the dilute urine and feces of their young. This behavior may regain about one-third of the water originally secreted as milk (Baverstock and Green 1975).

Diet

Because free drinking water is not available for desert mammals, they must obtain water from other sources, such as succulent plants, the body fluids of their prey, or seeds. Such food sources require that animals subsist on **metabolic water**, which is created in the cells by the oxidation of food, especially carbohydrates (Frank 1988; Hill and Wyse 1989; Degen 1997; Walsberg 2000; Tracy and Walsberg 2002). Some desert mammals consume succulent plants and insects for a source of water. Desert woodrats (*Neotoma lepida*) and cactus mice (*Peromyscus eremicus*) of southwestern North America consume large quantities of cactus (Genus *Opuntia*) as a source of both food and water. In addition, cactus is a staple in the diet of other xeric-adapted mammals, such as northern pocket gophers (*Thomomys talpoides*) inhabiting the dry short-grass prairies of Colorado (Vaughan 1967). Gophers and cricetids such as woodrats have evolved the ability to metabolize oxalic acid, an abundant compound of cactus that is toxic to other mammals. Some desert mammals depend on moist food such as cactus. Others rely primarily on dry seeds or halophytic plants (those that grow in salty soils), and their intake of water is quite minimal. Kangaroo rats, pocket mice of southwestern North America, and fat sand rats (*Psammomys obesus*) of the Sahara-Arabian deserts are able to subsist on dry food only and do not require water.

Halophytic plants of the Family Chenopodiaceae form a staple in the diet of many desert-dwelling small mammals but are, by definition, extremely high in salt concentrations (Degen 1997; Degen et al. 2000). Many small mammals that consume halophytes possess kidneys that produce highly concentrated urine. Fat sand rats obtain water from the leaves of the saltbush (*Atriplex halimus*). These gerbillid rodents are unusual in being diurnal and wholly herbivorous, whereas other members of the family are nocturnal and granivorous. Genus *Psammomys* scrapes off the outer surface of leaves with its teeth before consuming them—negligible amounts of leaf are scraped from moist plants and substantial amounts from dry plants (Kam and Degen 1992). Leaves possess up to 90% water but have high concentrations of salts and oxalic acid. To consume this plant material, the rat must produce urine with extremely high concentrations of salt as well as be able to metabolize large concentrations of oxalic acid. A parallel development occurs in the chisel-toothed kangaroo rat (*Dipodomys microps*), an inhabitant of shrub habitats of western North America. This heteromyid harvests leaves of the chenopod (*A. confertifolia*) rather than foraging on seeds, as do most heteromyids. The epidermis of *Atriplex* leaves is high in electrolyte concentration, but the more internal parenchyma is low in electrolytes and high in starch. *D. microps* is able to consume the inner tissue by shaving off the peripheral epidermis, thus minimizing its consumption of salt. These kangaroo rats can perform such a task because they possess lower incisors that are broad, flattened anteriorly, and chisel-shaped, thereby permitting access to the plant's inner tissue. Because other sympatric kangaroo rats lack this adaptation, they cannot exploit this unique food resource and must rely on unpredictable seed crops (Kenagy 1972). Many other species exhibit tolerance for high levels of salt in their food or water including highland desert mice (*Eligmodontia typus*) of South America, fawn hopping-mice (*Notomys cervinus*) and Tammar wallabys (*Macropus eugenii*) of Australia, and western harvest mice (*Reithrodontomys megalotis*) of western North America, to mention just a few.

Desert carnivores and insectivores meet their moisture requirements by relying on their food rather than on free water. Southern grasshopper mice (*Onychomys torridus*) of hot, arid valleys and shrub deserts of southwestern North America consume primarily arthropods, including scorpions, beetles, and grasshoppers. Studies of water balance demonstrate that grasshopper mice can be maintained in the laboratory for more than 3 months on a diet of only fresh mouse carcasses. Grasshopper mice are able to survive the arid conditions of the desert because of their preference for animal foods high in water content (Schmidt-Nielsen 1964). Kit foxes, badgers (*Taxidea taxus*), coyotes (*Canis latrans*), desert hedgehogs (*Hemiechinus auritus*), fennecs, and the Australian mulgara (*Dasycercus cristicauda*) are also able to subsist on a meat diet with minimal supplementation by free drinking water. Fennecs, xeric-adapted canids inhabiting the deserts of northern Africa, maintained water balance for a minimum of 100 days when fed only mice and no drinking water (Noll-Banholzer 1979).

In East Africa, many plains antelope are able to endure long periods of intense heat without drinking water. Two examples of nonmigratory ungulates, the eland (*Taurotragus oryx*) and oryx (*Oryx beisa*), are able to survive indefinitely without drinking water in an ecosystem typified by environmental temperatures reaching 40°C. A critical part of their ability to survive without drinking water is contingent on the

fact that they can use metabolic water. Elands consume large quantities of the leaves of *Acacia*, which contain about 58% water. Oryx feed primarily on grasses and shrubs, a staple being the shrub *Diasperma*. Leaves of this shrub fluctuate in water content. During the day, when air temperature is high and humidity low, the leaves contain only 1% water; at night, they increase to 40% water due to decreased temperature and increased relative humidity. The oryx takes advantage of the variable water content of *Diasperma* by consuming it only late at night when water content is highest. During other hours, oryx opportunistically consume more succulent species of plants according to availability.

TEMPERATURE REGULATION

Evaporation

Metabolic processes, such as kidney function, all require energy. Changes in metabolic processes produce heat, and in desert environments, internal heat must be lost or an individual overheats and dies. **Evaporative cooling**, the major mechanism employed by mammals to reduce body temperature, is very effective as long as an animal has an unlimited supply of water. Evaporative cooling is relatively simple. When mammals cool by evaporation, they take advantage of a physical property of water's ability to absorb a great deal of heat when it changes state from a liquid to a vapor. In desert ecosystems, however, heat is intense and water scarce, so evaporative cooling is of limited utility except as a short-term response to a temperature crisis. In terms of thermal stress, it is clearly maladaptive for a kangaroo rat to venture into the desert sun. For such a small mammal to maintain normal body temperature under such circumstances, it would have to evaporate 13% of its body water per hour. This would be highly taxing, as most species die when they lose 10%–20% of their body water. As we know from discussing how mammals cope with cold, many factors can modify the direct influence of environmental stressors. Although evaporative cooling requires some trade-offs, it represents a major line of defense for mammals combatting heat.

We now focus on four major mechanisms of water loss known as **insensible**, or **transpirational**, **water loss.** This water loss occurs by diffusion through the skin and from the surfaces of the respiratory tract. It includes sweating, panting, saliva-spreading, and respiratory heat exchange (Hill and Wyse 1989). Keep in mind that small mammals are limited by body size in the extent to which they can store and lose heat. As we will learn later, selection of cool and saturated microclimates represents a crucial strategy for conserving water by small mammals residing in xeric ecosystems.

Sweating

For many mammals, water loss occurs through the skin by way of sweat glands. There are two types of sweat glands: **apocrine** (found on the palms of the hands and bottom of the feet; they do not secrete for thermoregulation) and **eccrine** (distributed throughout the body; they secrete for evaporative heat loss). Water released from eccrine sweat glands evaporates from the surface of the skin, cooling it and the underlying blood. Sweating in response to overheating occurs only in primates and several species of ungulates; it does not occur in rodents and lagomorphs. For humans working in a hot, dry environment, as much as 2,000 mL/h of water may be produced by eccrine sweat glands and lost by evaporation. Sweating appears to have evolved in mammals whose fur does not represent an appreciable barrier to surface evaporation, but the mechanism is not quite so simple. For animals that sweat, such as camels, the insulative barrier provided by the pelage takes on special significance. It is noteworthy that eastern grey kangaroos (*Macropus giganteus*) do not sweat, but instead rely on conductance through peripheral vascular adjustments and evaporative heat loss for thermoregulation, which is divided almost equally between panting and arm licking, at ambient temperatures below 33°C (Dawson et al. 2000).

Panting

Humans sweat to increase cooling by evaporation. In contrast, canids possess very few sweat glands and cool primarily by **panting**—a rapid, shallow breathing that increases evaporation of water from the upper respiratory tract. Panting is a common method of evaporative cooling for many carnivores and smaller ungulates, such as sheep, goats, and many small gazelles (Schmidt-Nielsen et al. 1970a). All mammals lose some heat as a result of evaporation of water from their respiratory passages. Inspired air is cooler and less humid than expired air; thus, heat is released from the evaporatory surface in both warming and humidifying the air. Water (and heat) is conserved during expiration when the warmed, moist expired air meets the cooler respiratory surfaces.

Sweating versus Panting

A major difference between sweating and panting is that the panting animal provides its own air flow over the moist surfaces, thus controlling the degree of evaporative cooling. A sweating animal has minimal control over the degree of evaporation. Another shortcoming of sweating is that sweat contains large amounts of salt. A profusely sweating human may lose enough salt in the sweat to become salt deficient. This is why we are reminded to drink lots of liquid and limit strenuous exercise outside on very warm days. In contrast, panting animals do not lose any electrolytes and do not become sodium-stressed (Dawson et al. 2000). Panting does, however, have some drawbacks. The muscular energy associated with panting generates more heat than sweating, thus adding to the heat load.

Second, the increased ventilation generated by panting can result in severe respiratory alkalosis—an elevation of serum pH attributable to excess removal of carbon dioxide.

Cool Brains

Panting has the major advantage of allowing an animal under sudden heat stress (e.g., a gazelle pursued by a cheetah) to maintain a high body temperature and yet keep its brain at a lower temperature. Taylor (1972) and Mitchell and coworkers (1997) described this fascinating adaptation in cetartiodactyls. The brain is kept cooler than the body by the now familiar mechanism of countercurrent heat exchange. Arteries carrying warm blood from the heart toward the brain come into intimate contact with venous blood cooled by evaporation of water from the walls of the nasal passages within the **cavernous sinus**—a network of small vessels immersed in cool venous blood located in the floor of the cranial cavity where heat exchange occurs (Figure 8.23). The venous blood from the nasal passages cools the warmer arterial blood heading toward the brain. As a result, the brain temperature may be 2° or 3°C lower than the blood in the core of the body (Baker 1979). Taylor and Lyman (1972) found that the small Thomson's gazelle (*Gazella thompsonii*) of East Africa, when running for 5 minutes at a speed of 40 km/h, exhibited a core body temperature of 44°C, but its brain was maintained at the cooler level of 41°C. Other devices may augment cooling of the brain due to panting. Cabanac (1986) described the cooling of the brain from venous blood returning from facial skin, exchanging with warm arterial blood within the cavernous sinus and influencing the temperature of the brain.

Cooled arterial blood to brain (40°C)

Brain

Arterial blood from heart (43°C)

Evaporation in nasal passages

Heat exchange in cavernous sinus

Cool venous blood from nasal passages
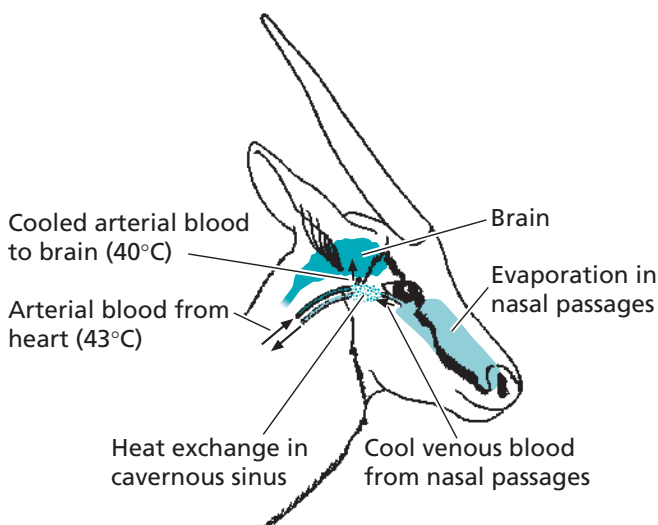
Figure 8.23 Cool brains. Schematic representation of the anatomical arrangement that promotes cooling of the brain in certain mammals. Dark vessels symbolize arterial blood flow, and light vessels, venous blood flow. In the cavernous sinus, the two flows are in intimate juxtaposition. *Adapted from Taylor and Lyman (1972).*

Saliva-Spreading

When faced with heat stress, many rodents and marsupials spread saliva on their limbs, tail, chest, or other body parts. Grooming saliva assists in evaporative heat loss. This technique is less effective than sweating for evaporative cooling because the fur must be soaked with saliva before heat can be lost from the underlying surface of the skin. Furthermore, this technique is effective for only a short time. Because of their small size, most rodents have limited supplies of internal water to replenish the high rates of loss. Nonetheless, many rodents rely solely on saliva-spreading for evaporative cooling. This mechanism is especially useful when heat stress is relatively short—for example, to prevent excessive hyperthermia while searching for cool refuge sites.

Secretion of saliva, like sweating and panting, is controlled by the hypothalamus. An increase in body temperature from a set point between 37° and 38.5°C is detected at preoptic tissues of the anterior hypothalamus and results in the activation of a salivary control center in the brainstem. Saliva then flows from the submaxillary and parotid glands (the salivary glands); saliva-spreading thereby decreases or stabilizes the rising body temperature, which, in turn, signals the hypothalamus by a negative feedback mechanism. Certain nondesert rodents have been shown to increase evaporative heat loss to more than 100% of heat production, and at least half of this evaporative cooling is due to saliva-spreading.

Respiratory Heat Exchange

Earlier, we discussed the importance of respiratory countercurrent heat exchange as a mechanism for conserving heat loss from respiratory passages in cold environments. Now, we see how water can be saved by evaporation in the lungs for animals residing in desert ecosystems. Many desert mammals, such as kangaroo rats (*Dipodomys*), are able to cool expired air and thus reduce the amount of water lost to the environment. A brief discussion of the cycle of respiration helps elucidate this process of water conservation. As air is inhaled, it passes over moist tissues in the nasal passages where it is warmed and humidified. As the relatively dry air passes over the moist tissues of the nasal passages, these tissues are cooled due to evaporation, and heat is transferred from them to warm the inhaled air. During exhalation, the returning warm, saturated air from the lungs condenses on the cool walls of the nasal passages, thus conserving water. This countercurrent exchange—evaporation on inhalation and condensation on exhalation—conserves both water and energy. Kangaroo rats are extremely efficient at cooling expired air because of the unique morphology of their nasal passageways (Schmidt-Nielsen et al. 1970b). Compared with another desert inhabitant, the cactus wren (*Campylorhynchus brunneicapillus*), the nasal passages of the kangaroo rat are very narrow with a large wall surface, which enhances heat

exchange between the air and the nasal tissues (Figure 8.24). In birds such as the cactus wren, the passageway for airflow is wider and shorter and thus the surface area for contact is smaller. As a result, the nasal passageways of the cactus wren are less efficient at heat exchange than those of the kangaroo rat.

Depending on the ambient temperature and humidity, about 65%–75% of the water vapor added to inspired air is recovered in the kangaroo rat's nasal passage during exhalation (Figure 8.25). Kangaroo rats may inspire air that is at about 15° and 30°C and 25% saturated with water vapor (these are arbitrarily selected air temperatures and humidity levels). In Figure 8.25, the shaded bars indicate the
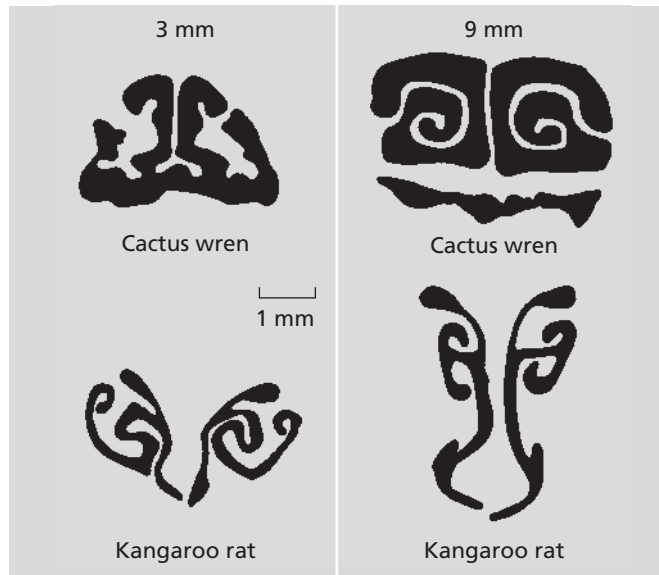
Figure 8.24 Comparative anatomy of nasal passages. Cross sections of the nasal passageways of the cactus wren and kangaroo rat. The passages are wider and the wall area smaller in the bird than in the mammal of the same body size (about 35 g). In both animals, the profiles were obtained at a depth of 3 mm and 9 mm, respectively, from the external openings. *Adapted from Schmidt-Nielsen (1972).*
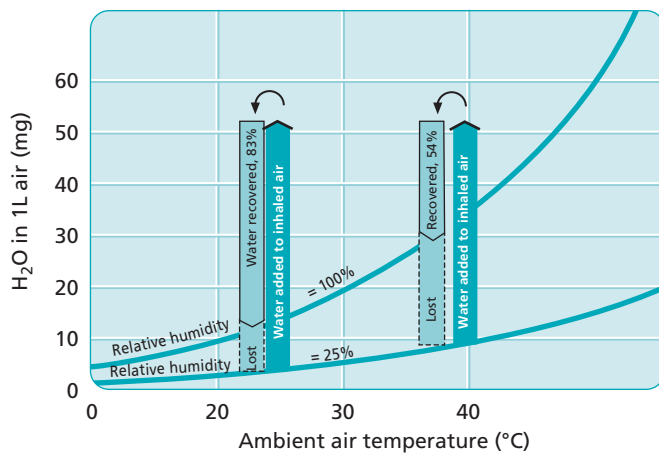
Figure 8.25 Respiratory water exchange. Diagram showing the recovery of water from exhaled air in the kangaroo rat. *Data from Schmidt-Nielsen et al. (1970).*

amount of water vapor that must be added to 1 L of outside air as it is inhaled and brought to saturation at the body temperature of 38°C. The unshaded bar next to each shaded bar is the corresponding temperature of exhaled air under the selected conditions. If air is inhaled at 15°C, for example, it will be exhaled at 13°C. In this case, the cooling of the exhaled air causes the recondensation (recovery) of about 83% of the water that was added on inhalation; note that only about 17% of the water needed to saturate the respiratory air is lost by the animal. At 30°C, less water is recovered, but even so, 54% of the evaporated water is saved compared with what would be lost had the air been exhaled at body temperature. By cooling expired air, kangaroo rats reduce the amount of water lost. As shown by the shaded bars in the figure, the amount of water lost and recovered depends on the saturation deficit between inspired air (25% humidity) and expired air (100% humidity) plus the air temperature of the inspired air. Expired air is always saturated, and thus its water content is directly related to its temperature.

Evaporation of water from the respiratory passages and through the skin (cutaneous) is a major avenue of water loss for small mammals residing in dry habitats (French 1993). For example, of the total water lost by Merriam's kangaroo rat, 84% is due to evaporation in the respiratory tract, and only 16% is lost through the skin (Chew and Dammann 1961). The orange leaf-nosed bat (*Rhinonycteris aurantius*) of northern Australia has a rate of pulmocutaneous evaporation that is more than double that of other bats, and about 7 times that measured in rodents of similar body mass (Baudinette et al. 2000; Tracy and Walsberg 2001). Desert-adapted species of rodents and many species of bats are able to reduce evaporative losses either by nasal heat exchange or by residing in humid microenvironments, such as subterranean burrows and caves, respectively. Living in such saturated microhabitats helps to reduce the vapor pressure deficit between the evaporating surface and the surrounding air.

Insulation

Earlier, we discussed how animals residing in cold environments used their pelage to decrease the flow of heat from the body to the environment. In contrast, animals adapted to hot climates use their fur to minimize the rate of heat they absorb from the environment. Dromedaries must cope with surface temperatures of 70°C, and Merino sheep with temperatures as high as 85°C. Because the core body temperature of these ungulates is about 40°C when they are heat-stressed, the temperature gradient between the surface of the pelage and the body core is extremely steep. A shallower gradient in the opposite direction exists between core and skin if sweating occurs, as it does in camels. The maintenance of these two opposing temperature gradients is an essential component of the temperature regulation process of mammals residing in hot environments.

Pelage insulation not only retards movement of heat from the environment to the skin but also prevents large amounts of heat in the form of incident solar radiation from reaching the skin. The heat returns to the environment from the surface of the hair by convection and radiation (see Figure 8.1). The reduction of surface temperature due to forced convection and air movement is significant and decreases the steepness of the thermal gradient across the pelage, thus reducing the heat load on the animal. In addition, the steepness of the gradient from the surface of the pelage to the skin is affected by the quality of the hair. For example, many mammals residing in arid regions have sleek, glossy, light-colored pelages that reflect many of the wavelengths of sunlight, thus reducing heating due to solar radiation.

Furthermore, the pelage of a mammal is not uniformly distributed. Guanacos (*Lama guanacoe*) reside in regions of South America characterized by intense solar radiation and high air temperatures. They possess gradations in pelage ranging from bare skin at the axilla, groin, scrotum, and mammary glands to thick pelage on the dorsum. These bare and sparsely furred areas, seen also in many desert antelopes, serve as **thermal windows** through which some of the heat gained from solar radiation can be lost by convection and conduction (Morrison 1966). In terrestrial mammals such as guanacos, African elephants (*Loxodonta africana*; Phillips and Heath 1992), camels (Abdoun et al. 2102), and woodchucks (Phillips and Heath 2001), thermal windows typically represent bare or sparsely haired thermoregulatory surfaces. These sites are located mainly in the appendages, which permit heat loss by increased peripheral blood flow (Williams 1990; Klir and Heath 1992). For amphibious pinnipeds, dissipation of heat is crucial when exposed to external thermal stress following haul-out (coming onto land to breed or give birth). These mammals possess thermal windows distributed throughout their body surfaces (Oritsland et al. 1974; Mauck et al. 2003; Willis et al. 2005), which act as efficient dissipaters of heat during thermal stress. Such regions represent sites of convective heat loss associated with varying cutaneous blood flow. When seals leave the water, they are exposed to high ambient temperatures, and vasodilation of vessels leading to the periphery results in an increased blood flow to the skin. The numerous arteriovenous anastomoses of seals facilitate dissipation of heat via increased cutaneous blood flow (Bryden and Molyneau 1978). This mechanism can be accurately tracked using infrared thermography, which has been employed to isolate the appearance, distribution, and development of thermal windows on the head, trunk and extremities of harbor seals (*Phoca vitulina*), harp seals (*P. groenlandicus*), and gray seals (*Halichoerus grypus*; Mauck et al. 2003) (Figure 8.26). It is noteworthy that the functional significance of anatomical specializations such as thermal windows is commonly augmented by behavioral techniques. For example, otariids and walruses (*Odobenus rosmarus*) respond to changing environmental temperatures by adjusting posture and manipulating the
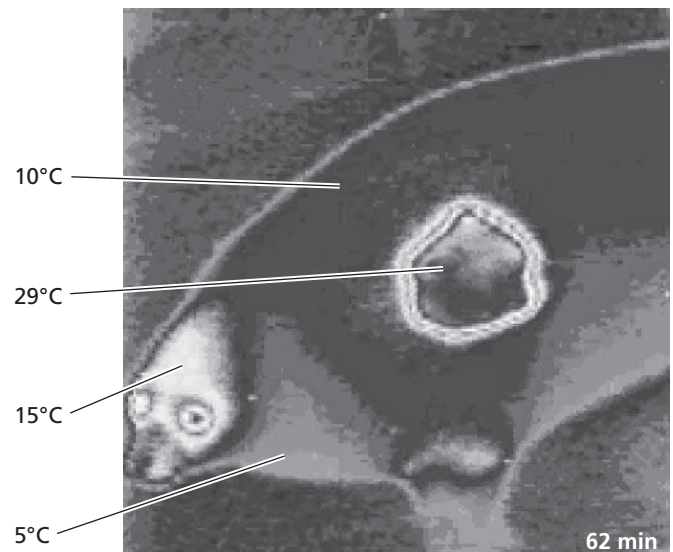
Figure 8.26 Thermal windows. Infrared thermogram of a harp seal (*Pagophilus groenlandicus*) obtained 62 minutes after leaving the water. The large thermal window on the left side of the seal is clearly visible and exhibits temperatures up to approximately 24°C higher than those of the rest of the body surface. The thermal windows are separated from the surrounding areas by narrow but regular transition zones grading to lower temperatures. *Adapted from Mauck et al. (2003).*

exposed surface area of their flippers to ambient air. These behavioral adjustments may be used to conserve or to dissipate heat in order to regulate energy balance (Fay and Ray 1968; Campagna and LeBoeuf 1988; Beentjes 1989, 2006). Horns, found in Family Bovidae (see Chapter 19), also serve as thermal windows for species residing in many different climates. Because horns are often richly vascularized, under certain circumstances they exhibit local vasodilation and serve as sites of heat loss, similar to bare patches on the coats of desert mammals.

Studies of the insulation of small desert rodents indicate a trend toward increased insulation. McNab and Morrison (1963) examined Genus *Peromyscus* from arid and mesic environments and concluded that desert subspecies showed a marked increase in insulation compared with their nondesert relatives. When the body temperature is less than the ambient temperature (e.g., during summer in desert ecosystems), it is advantageous for a mammal to have fur of a low conductance so as to slow the inward conduction of heat. The body temperature of desert rodents decreases at night; during the day, heat is a gradually stored in the fur, with a concomitant rise in body temperature.

Appendages

In the discussion of adaptations to cold, the physiological mechanism called "peripheral heterothermy" via countercurrent heat exchange was examined (see Figure 8.9). These vascular arrangements, in which arteries and veins are

closely juxtaposed, are widely reported to occur in the appendages of species that display regional heterothermy. The extent to which such a system can work for animals coping with heat stress depends on several properties of the countercurrent exchanger. Cooling of the outgoing arterial blood in the appendages is promoted by a high degree of contact between arteries and veins and by a relatively slow rate of blood flow through the exchanger. The arms of humans, the flippers of dolphins, and the limbs of tropical mammals such as sloths have a unique arrangement of countercurrent exchange. They possess two sets of veins: one superficial and distant to the major arteries, and the other deep and part of the exchange system. By changing the return of blood along these two venous systems, a mammal can emphasize heat dissipation or conservation in its extremity according to its thermal needs. The large ears of black-tailed jackrabbits (*Lepus californicus*) are excellent heat dissipators. Most excess heat generated during activity may be lost by dilation of the arteries in the ears (Hill et al. 1980). Thermal conductivity of the heat exchange system of jackrabbits is reported to be about ten times greater for animals at 23°C than at 5°C. Hart (1971) provides an excellent review of studies confirming the importance of appendages as dissipators of heat for desert mammals.

Metabolic Rate

Seed-eating rodents residing in desert ecosystems tend to exhibit low basal metabolic rates. Examples include heteromyids of North America (McNab 1979a; Hinds and MacMillen 1985; French 1993) and murids of Australia (MacMillen and Lee 1969, 1970) and Asia (Shkolnik and Borut 1969). French (1993) summarized the factors related to energy consumption in heteromyid rodents. They may use low metabolic rates to reduce overheating when they occupy a closed burrow system or to cut pulmonary water loss in a dry environment. Metabolic rates of heteromyids are about a third less than those of other mammals when at rest. In addition, metabolic reductions are possible when species estivate during times of food scarcity.

Body Size

Earlier, we used the analogy of the mammal as a cube to help illustrate the energy implications of surface-area-to-volume ratios. Now we consider the implications of body size for mammals coping with heat rather than cold. Animals living in hot environments gain heat from two sources: (1) the environment, through conduction and convection plus radiation from ground and sun (see Figure 8.1) and (2) metabolic heat gain. A mammal's **heat load** (the sum of the environmental and metabolic heat gain) is therefore roughly proportional to its body surface area. Because small mammals have a much larger surface-area-to-volume ratio, they lose heat more readily than large mammals. Us-

ing the surface relationship, we can estimate the quantity of water required to dissipate a certain heat load. A small mammal such as a kangaroo rat would need to evaporate a great deal more water (relative to body size) to eliminate its heat load than would a large mammal (Figure 8.27). To avoid this, as we shall see, small mammals escape the heat (curtail the heat load) by retreating to underground burrows during the day. In addition, desert mammals can decrease their body temperature to conserve water and decrease heat load.

DORMANCY

As we learned earlier, many mammals pass through unfavorable climatic periods by becoming inactive. A period of dormancy in reaction to cold is called "torpor" and "hibernation." A similar period in reaction to dry or hot conditions is called **estivation.** Estivation occurs in marsupials and insectivores but is most common among the rodents. It occurs at relatively high body temperatures, and the animals seem somewhat lethargic rather than torpid. If body temperatures are not measured, estivation may go unnoticed. For example, the eastern pygmy possum (*Cercartetus nanus*), an Australian marsupial, is able to eat and exhibit normal mobility at a body temperature as low as 28°C. Little pocket mice (*Perognathus longimembris*) exhibit a wide repertoire of behaviors while in estivation, ranging from eating at 23°C to shifting postures at temperatures as low as 6°C (Figure 8.28). Typically, rodents capable of dormancy have narrow thermoneutral zones (28°–35°C) and
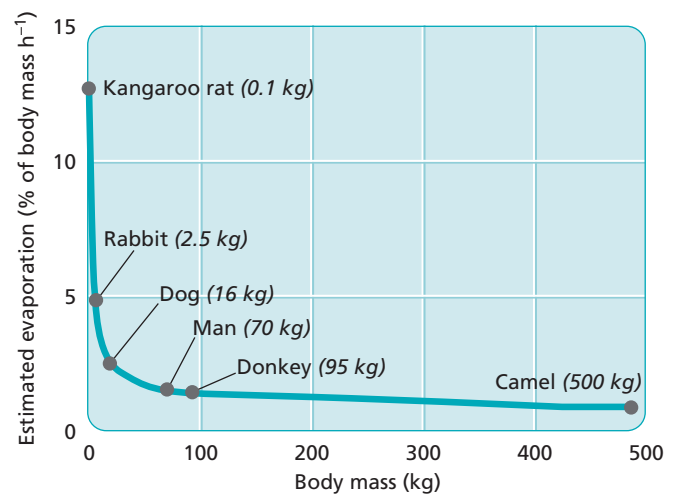
Figure 8.27 Evaporation in relation to body mass. Estimated evaporation compared with body mass of different mammals. For a mammal to maintain a constant body temperature under hot desert conditions, water must be evaporated in proportion to the heat load. Because of the larger relative surface area of a small animal, the heat load, and therefore the estimated evaporation in relation to the body size, increases rapidly. The curve is calculated on the assumption that heat load is proportional to body surface. *Data from Schmidt-Nielsen (1964).*
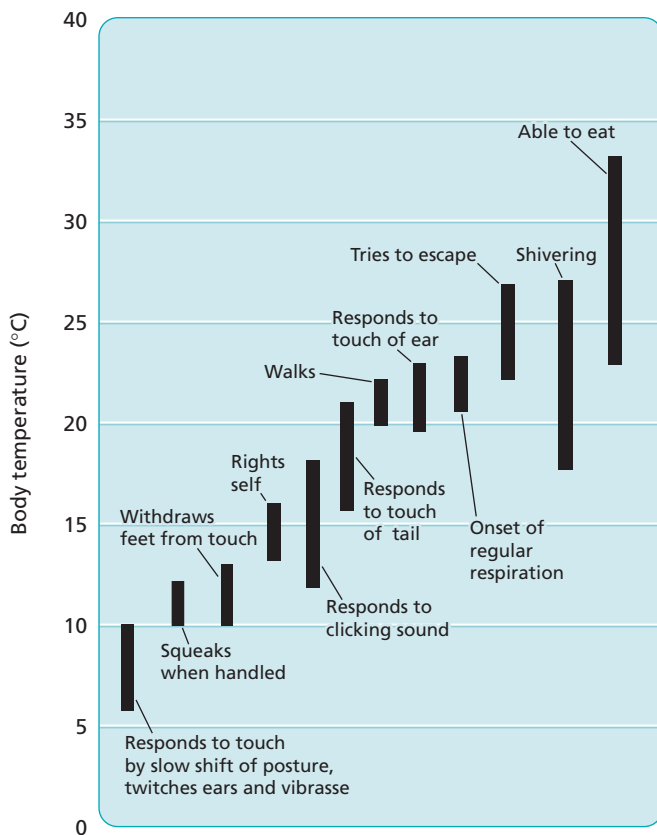
Figure 8.28 **Body temperature and behavior.** Range of minimal body temperatures for various patterns of behavior exhibited by the little pocket mouse during arousal from hibernation. *Data from Bartholomew and Cade (1957).*

Figure 8.29 **Torpor in the cactus mouse.** Pattern of changes in oxygen consumption and body temperature in the cactus mouse during entry into and arousal from torpor at an ambient temperature of 19.5°C. The standard consumption line is for active mice at an ambient temperature of 20°C. The cycle of torpor was initiated by deprivation of food and water. *Data from MacMillen (1965).*

low basal metabolic rates. Estivation has not been as intensely studied as hibernation.

Among heteromyids, estivation is reported for all species of pocket mice and kangaroo mice (Genera *Perognathus*, *Chaetodipus*, and *Microdipodops*) but is poorly developed in the kangaroo rats (Genus *Dipodomys*; French 1993). Within heteromyids, two basic dormancy "profiles" occur: (1) those species that forage year-round and employ shallow torpor to cope with energy emergencies (e.g., species of Genus *Chaetodipus* that tolerate body temperatures of 10°–12°C for less than 24 hours) and (2) those species of Genus *Perognathus* (e.g., the Great Basin pocket mouse, *P. parvus*) that use supplies of cached seeds during dormancy and may last for up to 8 days at a body temperature as low as 2°C. A thorough discussion of dormancy in Family Heteromyidae is provided by French (1993). Some of the smallest rodents in the world, pygmy mice (Genus *Baiomys*; adults = 9 g) of southwestern North America, undergo bouts of estivation. If food and water are limited, these small mice readily decrease body temperature from 38° to 20°C. Periods of estivation are reported for species of Genus *Peromyscus* inhabiting hot regions. The cactus mouse (*P. eremicus*), an inhabitant of deserts of southwestern North America, undergoes torpor (estivation) in summer and winter in response to limited food and water (Figure 8.29). Cactus mice

remain in burrows during the driest part of the summer and enter torpor in response to food and water shortages at environmental temperatures of about 30°C. Under laboratory conditions, when deprived of food and water, *P. eremicus* enters torpor at an ambient temperature of 19.5°C, maintaining a body temperature of about 22°C for several hours. Body temperature does not drop below 15°C during torpor (MacMillen 1965). From the preceding discussion, it is apparent that rodents exploit many different adaptive patterns in dormancy, with the ultimate goal of saving energy in unpredictable environments.

Case Study of Estivation

Kangaroo mice can be used to illustrate the energy savings accrued by estivation. These small heteromyid rodents (10–14 g) occur in the Upper Sonoran sagebrush desert of western North America. Seeds, a staple in their diet, are gleaned from the sand and hoarded in underground burrows. Although environmental temperatures may range from 0° to 30°C, kangaroo mice rarely experience drastic changes in temperature due to their fossorial (burrow-digging) and nocturnal habits. In most deserts, seed production is quite seasonal and limited to very brief periods. As a result, strict homeothermy for granivorous rodents such as kangaroo mice would be a waste of energy. Kangaroo mice therefore cope with such environmental unpredictability by exhibiting great thermolability; duration and frequency of estivation are contingent on the availability of seeds and environmental temperature. For example, when food is in excess and environmental temperatures high, kangaroo mice exhibit homeothermy; if food is limited and temperatures unfavorable, they shift into heterothermy
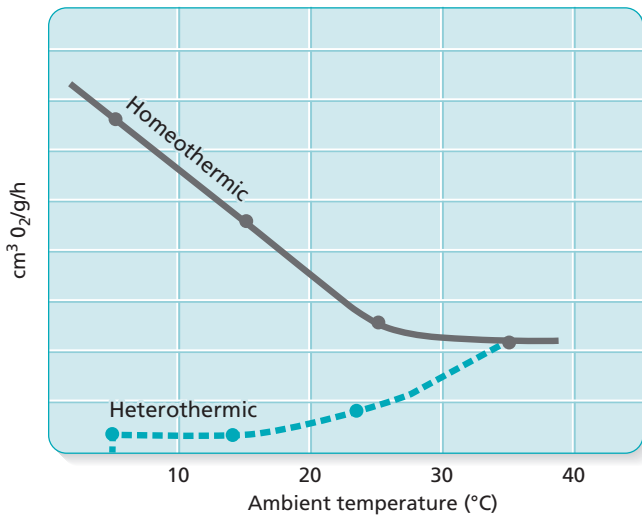
Figure 8.30 Torpor and euthermy in the kangaroo mouse. The effects of ambient temperature on the oxygen consumption of kangaroo mice when maintaining normally high body temperatures and when in torpor. The points are mean values. *Data from Brown and Bartholomew (1969).*

Figure 8.31 Soil temperature changes in deserts. Diagram showing the range of temperature compared with the depth of the soil. Temperature fluctuations are less extreme below the surface of the desert at depths typical of burrows of kangaroo rats. A temperature of 25°C represents an "average" burrow temperature. *Data from Schmidt-Nielsen (1964).*

(estivation). Periods of estivation may last for only a few hours or for several consecutive days, and the more time they spend in dormancy, the less food they need. Brown and Bartholomew (1969) measured the influence of environmental (ambient) temperature on the energy needs (oxygen consumption) of homeothermic and torpid kangaroo mice (Figure 8.30). At ambient temperatures of 5°–25°C, the body temperatures of mice were 32°–37°C when they were homeothermic, but during torpor, their body temperatures were just 1° to 3°C above ambient levels. As shown in the figure, the vertical distance between the "homeothermic" and "torpid" lines represents the energy savings per unit time of torpor at that temperature.

AVOIDANCE OF HIGH TEMPERATURES

Unlike large mammals, small mammals avoid extreme temperatures in desert ecosystems by adhering to fairly definite periods of activity. With the exception of ground squirrels and chipmunks, all desert rodents of North America are nocturnal and fossorial. Small mammals optimize survival by residing in burrows below ground during the heat of the day. For a typical desert ecosystem, the temperature of the air in the burrow is mild compared with the extremes that occur on the surface (Figure 8.31). Heteromyids search for seeds at night when it is cool and spend the day in relatively cooler and more humid burrows. They are seldom exposed to air with high temperatures. Within burrow environments, the air is saturated with water vapor. This is essential for granivorous rodents for two reasons: first, the seeds gathered on the dry surface absorb water when stored in the burrow, and; second, evaporative water loss is reduced considerably while the rodent is in its

burrow because there is no saturation deficit. However, not all desert-dwelling small mammals conform to the above generalizations. Merriam's kangaroo rats are an exception. These small heteromyids reside in much hotter summer burrows, which sometimes exceed 35°C. They have much higher thermal tolerances than previously known, and are active immediately following sundown. Further, their burrows are not persistently humid but may be quite dry, and they are known to consume insects and succulent vegetation, a key to enhancing their survival in harsh desert environments (Tracy and Walsberg 2002).

Diurnal desert rodents must devise other ways to cope with heat stress. Studies of antelope ground squirrels (*Ammospermophilus leucurus*) in the deserts of southern California have elucidated some unique tactics for surviving heat stress (Chappell and Bartholomew 1981; Figure 8.32). Ground squirrels foraging on the surface of the ground during midday in summer are faced with temperatures approaching 43°C. Daily foraging therefore assumes a bimodal activity pattern, with most activity taking place during midmorning and late afternoon. During the day, body temperature is quite labile, varying from 36.1° to 43.6°C. Squirrels use fluctuating body temperature to store heat during their periods of activity. High temperatures limit the time that squirrels can be active in the open to no more than 9–13 minutes. During this time, they move rapidly from one patch of shade to the next, pausing only to seize food or monitor predators. Exposure to midday temperatures is minimized by running or "shuttling" between foraging and cooling sites. The body temperature of the antelope ground squirrel shows a pattern of rapid oscillations, rising while the squirrel is in the sun and dropping when it retreats to its burrow (Vispo and Bakken 1993; Hainsworth 1995; Degen 1997). In addition, ground squirrels
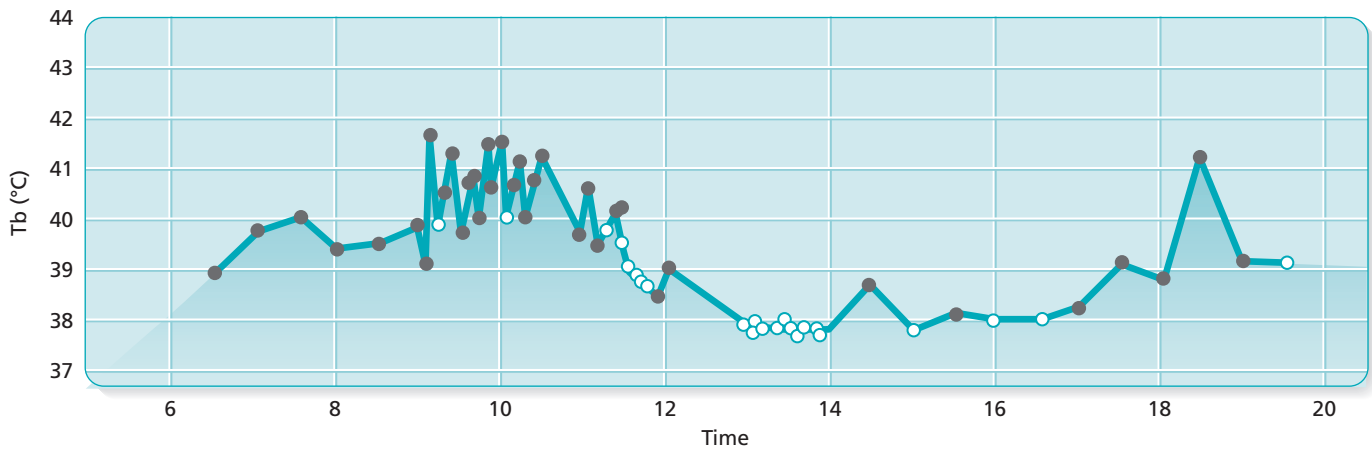
Figure 8.32 **Activity and body temperature of the antelope ground squirrel.** Short-term cycles of activity and body temperature of *Ammospermophilus leucurus*. Active (λ); inactive (μ). *Data from Chappel and Bartholomew (1981).*

Figure 8.33 **The heat shield.** The cape ground squirrel (*Xerus inauris*) resides in hot deserts of southern Africa and uses its tail as a parasol. (**A**) The erected tail covers the entire dorsal surface of the sitting squirrel. (**B**) The tail is held over the back of a horizontally positioned squirrel shading its head and body from the sun.

employ their tail as a sort of parasol, or "heat shield." As shown in Figure 8.33, the cape ground squirrel (*Xerus inauris*), an inhabitant of the hot arid regions of southern Africa, holds its wide, flat tail tightly over its back with the white ventral surface upward. In this position, the tail shades a large portion of the animal's back, thus lowering the effects of solar radiation on body temperature. On a hot day, to maintain their body temperature below 43°C, squirrels must retreat to burrows every few minutes. Burrows deeper than 60 cm usually have temperatures between 30° and 32°C. Ground squirrels and other rodents do not sweat or pant. Instead, they use this combination of transient heat storage and passive cooling in a deep, saturated burrow to permit activity during daylight hours when heat is extreme (Figure 8.33). As will be explained in the following section, antelope ground squirrels employ a strategy for coping with heat that is very similar to that of camels—namely, saving water by allowing their body temperature to rise until the heat can be dissipated passively. The major dif-

ference between these squirrels and camels is a function of body mass. The large camel can store heat for an entire day and cool off at night, whereas the antelope ground squirrel goes through the same cycle many times during the day.

The Dromedary

The biology of camels (see Chapter 19) has been reviewed by Gauthier-Pilters and Dagg (1981), Yagil (1985), Kohler-Rollefson (1991), and Abdoun and colleagues (2012). The dromedary, touted as the "ship of the desert," occurs in semi-arid and arid regions of the Old World. Camels take long journeys, some lasting from 2 to 3 weeks, with no opportunity to drink water. In the Sahara, dromedaries often remain without drinking water from October to May, existing solely on water content in the forage. During such arduous trips, they are faced with severe problems of water conservation and temperature regulation. As a result, they have evolved unique mechanisms to cope with desert ecosystems.

   One interesting mechanism employed by camels in coping with intense heat and lack of water of arid regions is their ability to vary body temperature as a device for saving water (Schmidt-Nielsen et al. 1957). Researchers have studied the daily cycle of body temperature in camels that received water and those that were dehydrated (Figure 8.34). Camels given water show a very small daily fluctuation in body temperature, ranging from 36°C in the early morning to a maximum of 39°C by midafternoon. If a camel is deprived of water, however, the daily variation in body temperature triples—falling to 34.5°C at night and climbing to 40.5°C during the day. This temperature variation is important because when camels are dehydrated, they can lose excess heat at night through radiation, conduction, and convection to a cooler environment, thus saving water. This results in a change in body temperature for dehydrated camels of about 6°C; for camels with water, the change is only half of this (see Figure 8.34). To determine
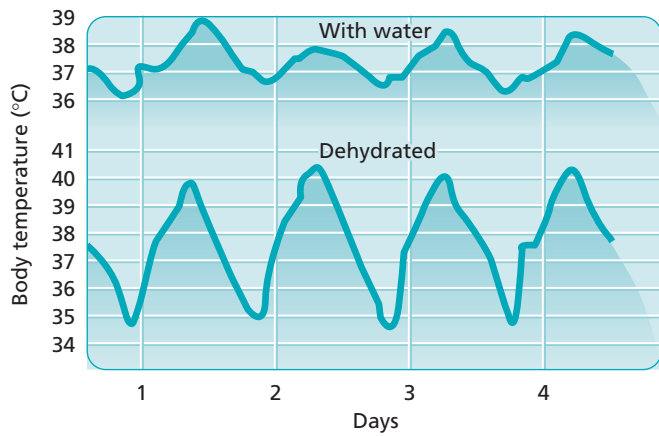
Figure 8.34 **Heat storage and loss in the dromedary.** Diagram showing the relationship of changes in body temperature compared to heat storage and loss in the dromedary. Camels store more heat when water availability is restricted. *Data from Schmidt-Nielsen et al. (1957).*

how much water camels can conserve by storing heat during the day and losing it later that night by nonevaporative means, we use the following calculations. About 0.9 cal is required to increase each gram of tissue 1.0°C. A 500-kg camel that increases its temperature by 6°C can therefore store 2,700,000 cal of heat in its body. If this heat had to be lost entirely by evaporation (each milliliter of water dissipates about 580 cal), however, a total of 4,655 mL of water would be required. Thus, a camel would have to evaporate about 4.5 L of water to maintain a stable body temperature at the nighttime level. By tolerating a high body temperature during the day, camels can therefore conserve considerable amounts of water.

Camels can tolerate a water loss greater than 30% of their body mass, whereas a 15% loss is lethal in most other mammals. Their toleration of dehydration appears to be related to their ability to maintain blood plasma volume near normal levels during dehydration. They can rehydrate quickly, taking in water equal to 30% of their body mass within a matter of minutes. Camels have an impressive ability to concentrate urine and absorb water from fecal material. Their kidneys can produce urine with a high chloride content; dromedary camels can drink a sodium chloride solution even more concentrated than seawater without ill effect.

Many of their morphological, behavioral, and physiological adaptations enhance survival during periods of heat. As a result of its thick pelage, much of the solar energy that strikes a camel's fur never reaches its skin. During summer, the surface of its fur can reach 70° to 80°C, but skin temperature stays at only 40°C. Abundant sweat glands release secretions onto the skin surface beneath the hair, and evaporative cooling aids temperature regulation. The combination of a thick pelage and high body temperature reduces the rate of heat gain to the core of the body, slows the rate of sweating needed, and thus conserves water. During the day, camels must resort to evaporative cooling

through sweating and panting, coupled with deep, slow breathing to eliminate heat and reduce respiratory water loss. A thick fur coat protecting the evaporative surface of the bare skin from unrestrained access by environmental heat could also reduce the vaporization of sweat. So the camel has evolved an optimal thickness for its pelage: it is not so thick or dense as to interfere with dissipation of vaporized water from the skin to the atmosphere, nor is it so thin as to provide inadequate protection. It seems counterintuitive that wearing a fur coat on a hot day may enhance thermoregulatory ability, but it works for camels. The deserts of northern Africa are cold in the winter, and camels have an extremely thick fur. In summer, camels shed their winter coat but retain hair of up to 6 cm long on the back and 11 cm on the hump. On the venter (abdomen) and surface of legs, the hair is only 1.5–2.0 cm long. As in guanacos and other large mammals, the lightly furred areas of camels act as thermal windows for heat loss.

The morphological peculiarities of camels couple with behavior to enhance water conservation and temperature regulation. Early in the morning, camels lie down on surfaces that have cooled overnight by radiation. They tuck their legs beneath the body with their ventral surface of short fur in contact with the cool ground. In this position, a camel exposes only its well-furred dorsum and flanks to the hot sun and places its lightly furred legs and venter in contact with cool sand, thus conducting heat away from the body. Camels also form group huddles during the day, in which they lie closely together. The side-by-side contact prevents solar radiation from permeating the body of each animal and raising its body temperature.

The ability of the dromedary to withstand heat and dryness does not depend on water storage in its hump but rather on numerous physiological mechanisms aimed at water conservation. It is a popular misconception that the camel's hump is filled with water. Actually, the hump is filled with fat bound together by fibrous connective tissue. Contrary to myth, this fat does not help much as a source of energy for long travels in the desert or as a lightweight method of carrying water (Hill and Wyse 1989). To understand the costs and benefits of fat stored in the camel's hump, the amount of water gained and lost in breaking down (catabolizing) lipids or carbohydrates must be assessed. Consider the production of metabolic water in relation to respiratory water loss. For temperatures and humidities of a desert environment, camels actually lose more water across the lungs in obtaining oxygen to oxidize fats than they gain from the oxidation of those fats. In reality, the breakdown of fat to derive energy actually imposes a water deficit.

Other Desert Ungulates

Desert antelopes (e.g., oryx, gazelles, and elands) possess a number of adaptations for coping with heat and dehydration (Taylor 1972; Figure 8.35). The pallid color and glossy fur of the desert antelope reflect direct sunlight, and the fur is ex-
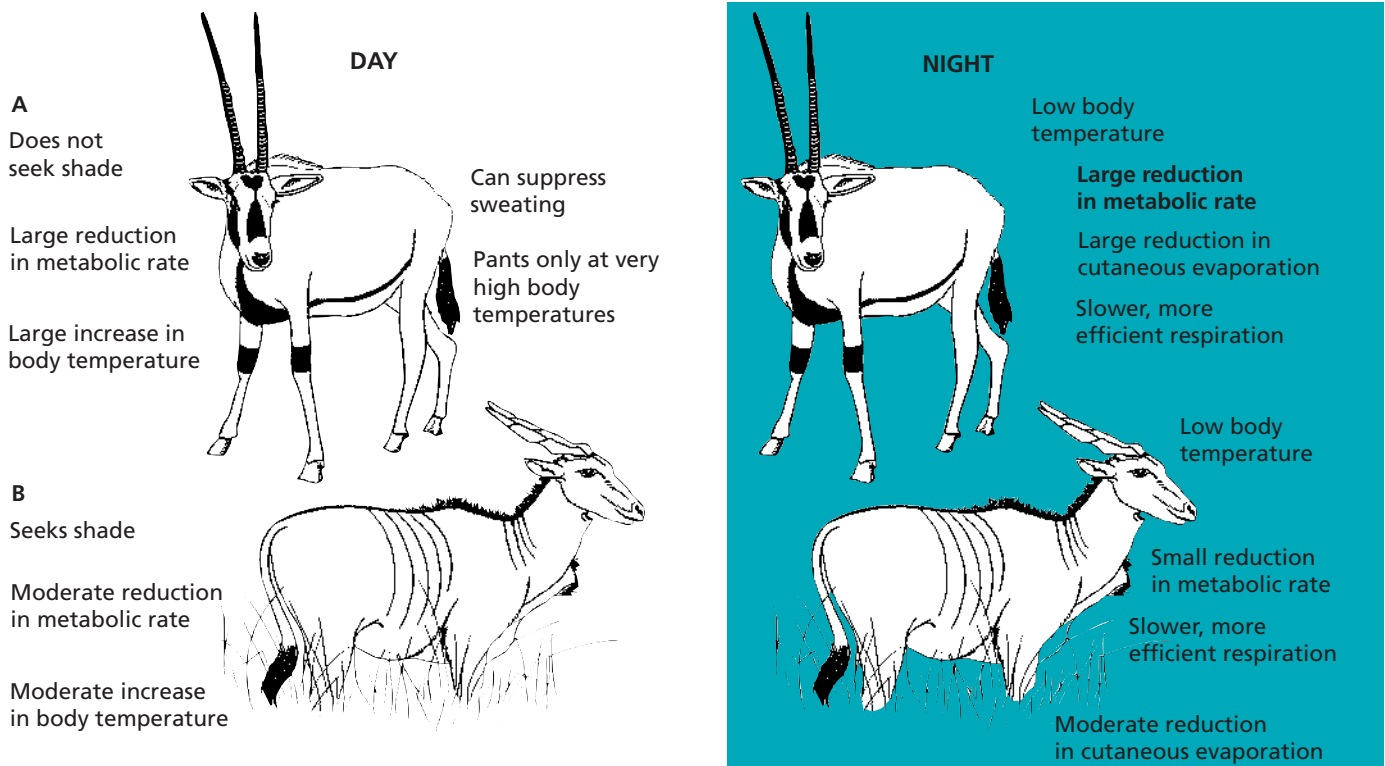
Figure 8.35 Water conservation in antelopes. Adaptations for water conservation in two nondrinking east African antelopes: (**A**) the oryx; (**B**) the eland. Figures on the left are for daytime; figures on the right are for night. *Adapted from Taylor (1970) and Gordon (1982).*

cellent insulation against the heat. Heat is lost by convection and conduction from the venter, where the pelage is very thin. Unlike the dromedary, the antelope's coping mechanisms are independent of drinking water. Elands search for shade during the heat of day, whereas dromedaries remain in the full sun all day, with relief from heat not coming until evening. Elands and oryx both pant at high temperatures and can reduce their metabolic rates to conserve water. Furthermore, evaporation through the skin is reduced by 30% in elands and by 60% in oryx. Evaporative water loss through the respiratory tract is also reduced. In comparison to camels, oryx can reduce daytime evaporative water losses by suppressing sweating completely, even when very hot. The fat tissue in elands and dromedaries is localized in the hump rather than dispersed uniformly under the skin, where it would impair heat loss by radiation. The water requirements of antelopes are negligible, plus their ability to conserve

water is greatly enhanced by their production of concentrated urine and dry feces. The deserts of the Arabian Peninsula are characterized by unpredictable rainfall and summer ambient temperatures that exceed 45°C; such habitats are arguably the most inhospitable environments for mammals. Yet such habitats are home to Arabian oryx, Nubian ibex (*Capra ibex*), mountain gazelles (*Gazella gazella*), and sand gazelles (*G. subgutturosa*). How do these ungulates cope with such extremes? Gazelles (*G. thomsonii* and *G. granti*) residing in arid savannahs of eastern Africa show very low values for evaporative water loss as a method of water conservation (Taylor 1970); however, their frugality is five time higher than the value for sand gazelles (Ostrowski 2006). Such low evaporative water loses indicates that sand gazelles have evolved a remarkable capacity to reduce water expenditures, a principal reason for their success in the deserts of Saudi Arabia.

SUMMARY

- The evolutionary success of mammals derives from their sophistication in form, function, and especially behavior.

- Mammals are widely distributed throughout the Earth, ranging from tundra to deserts, with each environment characterized by different extremes in climate. As a result of such strong selection pressures, mammals have evolved a unique suite of mechanisms to enhance survival. These adaptive strategies are diverse and highly sophisticated, with variation exhibited at the levels of ecosystem and species and between individuals.

- Basic terminology in the physiology of environmental adaptation includes "endothermy," "homeothermy," "euthermy," "heterothermy," and "poikilothermy," as well as ambiguous terms such as "warm-" and "cold-blooded." Most mammals maintain their body temperatures between 36° and 38°C. To do this, they must balance heat gain and heat loss against such forces as radiation, conduction, convection, and evaporation. The equilibrium maintained by mammals is achieved through interaction with the environment by the mammalian thermostat—the hypothalamus—with its species-specific set points. Each species has unique coping mechanisms and peculiarities in its thermoneutral zone, thermal conductance, and metabolic rate. These characteristics and the important concept of countercurrent heat exchange help determine the distribution of species as well as such long-standing "biogeographic rules" as Bergmann's, Allen's, and Gloger's.

- Mammals employ several mechanisms to defend against cold, including (1) behavioral mechanisms (communal nesting, nest construction, food hoarding, foraging dynamics, and activity patterns) and (2) anatomical and physiological mechanisms (body mass reduction during winter, decrease in thermal conductance, nonshivering heat production, and dormancy).

- The challenges faced by mammals in desert environments are even more severe than those for species residing in the cold. Water is essential for the survival of all animals, so the role of water economy and the anatomy and physiology of the mammalian kidney are crucial to desert animals. Desert mammals conserve water by eating succulent plants and using metabolic water. Certain small mammals also have ingenious mechanisms for consuming halophytic plants. In addition to conserving water, xeric-adapted mammals regulate body temperature through evaporative cooling by sweating, panting, saliva-spreading, and respiratory heat exchange.

- As we have seen with mammals faced with cold, mammals residing in hot environments possess certain adaptive strategies that enhance their survival, including unique patterns in insulation, appendages, metabolic profiles, and body size. Just as animals in the cold use hibernation, desert mammals employ estivation to avoid heat and lack of water. Certain mammals epitomize the ability to survive in heat— namely, heteromyid and dipodid rodents, dromedaries, and desert antelopes.

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DISCUSSION QUESTIONS

1. Distinguish among the following terms: homeothermy, ectothermy, poikiothermy, heterothermy.

2. Small mammals are common inhabitants of deserts and mountains. Describe the different adaptations they employ to maintain homeothermy in each environment.

3. Explain why it is advantageous for certain small mammals to abandon homeothermy during brief or extended periods of their lives.

4. Explain nonshivering thermogenesis. Track this heat-producing mechanism for a small mammal from its initiation in nature to its function in maintaining homeothermy.

5. Compare the advantages and disadvantages of the color white for animals residing in northern environments.

6. What are the benefits of having a larger body size in the Arctic? Compare the advantages and disadvantages of body size in terms of mass-specific metabolism and total energy needs.

7. Define countercurrent heat exchange. What are the advantages of this mechanism for a caribou of the Arctic and a sloth of Panama?

8. Define thermal conductance. Compare the benefits of a thick fur coat for a lemming in the Arctic with that of a dromedary in the Sahara Desert.

9. Compare the different types of dormancy in mammals: hibernation, torpor, and estivation. Provide a definition for each type and give examples of different mammals that fit into each category. What are the advantages and disadvantages of dormancy?

10. Describe the cycle of hibernation of a ground squirrel residing in northern Montana. Compare hibernation in this ground squirrel with estivation of a kangaroo mouse residing in the desert of California.

11. List the different water conservation strategies employed by desert mammals.

12. Discuss four major mechanisms of evaporative cooling (insensible water loss).

Reproduction

Reproduction is the process by which organisms produce new individuals, passing on genetic material and thus maintaining the continuity of the species and of life. All mammals reproduce sexually by way of internal fertilization; the sexes are separate, and a given individual normally has the sex organs and secondary sexual characteristics of only one gender.

As you will see in this chapter, mammals vary greatly in the structure and function of their reproductive system. The monotremes lay eggs and incubate their young, and as is the case for most reptiles and birds, monotremes have a **cloaca**—a common opening for the urinary and reproductive tracts. In addition, as with birds, only the left ovary is functional in monotremes; they do, however, have true mammary glands but lack nipples (Hughes et al. 1975; Griffiths 1978; Griffiths et al. 1988; Grant 1995; Strahan 1995; Rismiller and McKelvey 2000; see Chapter 10).

The marsupials, or pouched mammals, like the monotremes, possess a cloaca. The placenta in these animals is not very efficient due to the limited contact between the maternal and fetal blood supply. As a consequence, marsupials undergo a very brief gestation period and a prolonged period of nursing. The young are born in an altricial (poorly developed) state and require a long period of development in the pouch (**marsupium**) of the mother (Padykula and Taylor 1982; Dawson 1995; Tyndale-Biscoe 2005; Coulson and Eldridge 2010)—although a few species do not have a pouch. The eutherian mammals, commonly called "placental mammals," have made a major advance in the evolution of their reproductive patterns. A key innovation was the appearance of a highly sophisticated placenta that facilitates efficient respiratory and excretory exchange between the maternal and fetal circulations. Unlike the marsupials, the eutherian mammals exhibit a longer gestation period and a shorter period of nursing or lactation. Furthermore, at birth, the young are more highly developed (precocial) than are young marsupials.

Mammals vary widely in the complexity of their reproductive patterns, but it is incorrect to interpret the seemingly more primitive reproductive patterns of the monotremes and marsupials as being less successful than those of eutherians. The success of a species can be evaluated only case by case and in the context of its specific ecological

relationships. Many examples exist of successful groups of noneutherian mammals, one of which—the Virginia opossum (*Didelphis virginiana*)—is well known (Figure 10.18). This marsupial originated in South America and has colonized environments as far north as Ontario, Canada, within only a short time. The opossum has an unusually rapid life history for its body mass, relatively fast maturation followed by a condensed period of rapid reproduction, and early **senescence** and death (Bielby et al. 2007). Both female and male opossums are sexually mature in the first year following birth (Sunquist and Eisenberg 1993); 13 days following parturition, 4–25 embryo-like young, the size of honeybees, emerge. These young are pink-skinned, hairless, and blind; each weigh about 0.13 g and are about 13 mm long. Most opossums survive to breed for only 1 year, which includes 2 breeding seasons. In the southern part of their range the average litter size is about 7; this results in an average lifetime reproductive output of 14 young per female (Sunquist and Eisenberg 1993). This reproductive potential yields a high yearly per capita population growth rate.

The variations in reproductive patterns of mammals seem endless. For example, gestation ranges from 10 to 14 days in some dasyurid marsupials to over 650 days in elephants. Lactation varies from only 4 days in pinnipeds such as the hooded seal (*Cystophora cristata*) to over 900 days in chimpanzees (*Pan troglodytes*) and orangutans (*Pongo pygmaeus*; Hayssen et al. 1993). Most mammals give birth to between 1 and 15 young per litter, and intervals between births may range from 3 to 4 weeks in rodents to as long as 3 to 4 years or more in sirenians, elephants, and rhinos (Hayssen et al. 1993). Voles (Order Rodentia: Cricetidae) may hold the record for biotic potential: the meadow vole (*Microtus pennsylvanicus*) of the North American grasslands may produce up to 8 or 9 litters of 5 to 8 young in a single year. As a result, a single female may potentially produce up to 72 offspring during one breeding season. Bailey (1924) reported that a captive female meadow vole produced 17 families in a single year. Naked mole-rats (*Heterocephalus glaber*; Family Bathyergidae) of Africa have the largest mean litter size of all wild mammals—up to 28 young (Sherman et al. 1999). Variation in reproductive patterns may be explained by assessing environmental factors and the risk of raising young in highly seasonal environments. Hayssen (2008a, 2008b) assessed patterns of reproduction in squirrels (Family Sciuridae) related to body size, ecological profile, phylogeny, and latitude. For 171 species, litter size varied from 1 to 9.7, with an average litter size of about 3.5. The marmotine ground squirrels are distinctive in having larger litter sizes and shorter gestation and lactation than squirrels overall. Hayssen and colleagues (1993) presented a thorough review of the numerous reproductive strategies employed by mammals.

To examine the variation in reproductive patterns in mammals, we divide this chapter into six parts. First, we concentrate on the role of the male and the female in the production of **gametes** (sperm produced by the testes of the male and ova produced by the ovaries of the female). The next five phases deal with the female body and include fertilization, implantation, gestation, parturition, and lactation. As we discuss each process, remember that each species of mammal has evolved a unique reproductive capacity for coping with the selective forces of the environment in which it resides.

The Reproductive Systems

THE MALE REPRODUCTIVE SYSTEM

The reproductive system of males comprises paired testes, paired accessory glands, a duct system, and a copulatory organ.

Testes

The **testes** (sing., *testis*) are the site of production of sperm (the male gametes) and the synthesis of male sex hormones, chiefly testosterone (Figure 9.1). The paired testes of mammals are oval-shaped and may be suspended in a pouch-like, skin-covered structure called the **scrotum**. The position of the testes in mammals varies considerably. In many species (e.g., some bats and many rodents), the testes migrate from the body cavity into the scrotum during the breeding season and afterward are withdrawn into the inguinal canal. In some mammals (e.g., monotremes, some insectivores, anteaters, tree sloths, armadillos, manatees and dugongs, all the seals except the walruses, whales, hyraxes, and elephants), the testes are always in the abdominal cavity. The testes remain in the scrotum permanently in most primates, cetartiodactyls, perissodactyls, and carnivores. It is possible that the temperature of the abdominal cavity is too high to permit development of sperm (**spermatogenesis**), and thus the scrotum allows for cooling of the testes. Temperature may not be the only critical factor for spermatogenesis, however, and a number of environmental factors interact to initiate and end spermatogenesis (van Tienhoven 1983; Hadley 1988; Kunz et al. 1996).

Spermatogenesis, the production of spermatozoa by the process of meiosis, occurs within the **seminiferous tubules** of the testes. Within these tubules, spermatozoa mature by passing through several stages of development and are nurtured by **Sertoli cells** (see Figure 9.1). Surrounding the tiny, coiled tubules within the testes are microscopic interstitial cells (**Leydig cells**), which are the site of secretion of the male hormone, **testosterone**. The secretions of Sertoli and Leydig cells provide an optimal microenvironment for spermatogenesis (Gordon 1982; Hadley 1988).

A

Epididymis

Spermatic cord

Capsule of testis

Septum

Vas deferens

Seminiferous tubules

B

Interstitial cells

C

Spermatids

Sperm cells

Secondary spermatocyte

Primary spermatocyte

Sertoli cell

Basement membrane
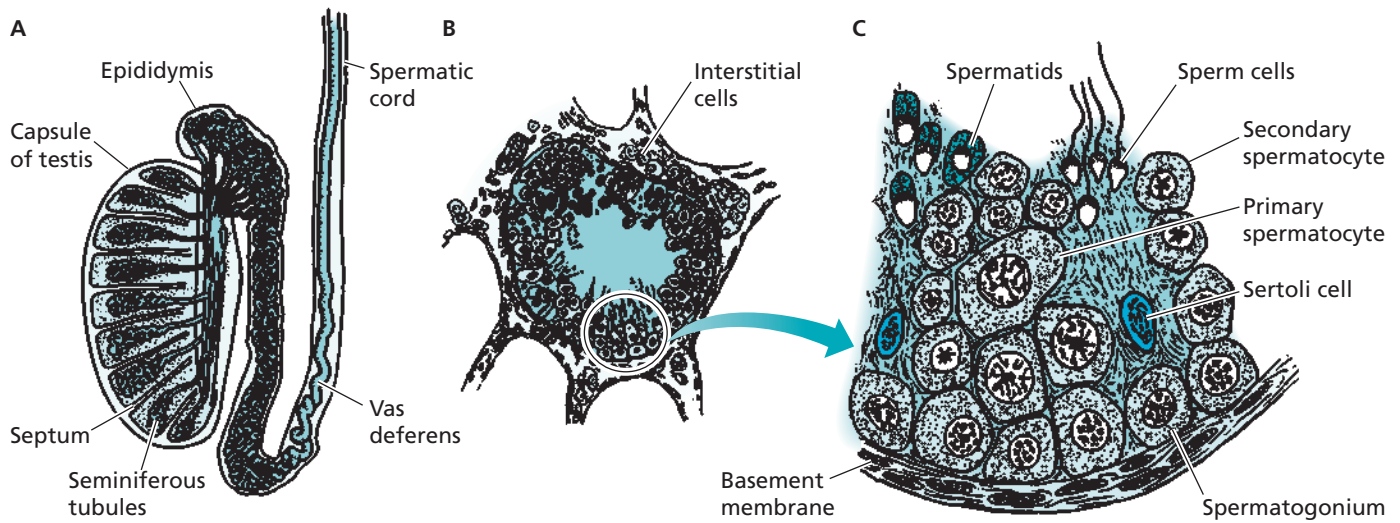
Spermatogonium

Figure 9.1 Mammalian testes. Section of the mammalian testis showing coils of (**A**) seminiferous tubules containing spermatozoans (**B**) in various stages of development. (**C**) The composite cross section of a seminiferous tubule shows spermatogonia near the basement membrane, progressing from spermatocytes to spermatids with mature spermatozoa (sperm cells) located near the lumen of the tubule. See Curtis (1975) and Hickman et al. (2004) for a description of the maturational process within the seminiferous tubule. *Adapted from Curtis (1975).*

Ducts and Glands

After the sperm are mature, they must be transported to the exterior by a series of ducts (Figure 9.2). On leaving the seminiferous tubules, sperm are collected in the **epididymis**, a highly coiled tube located on the surface of each testis. This tube serves both as a duct for passage of sperm and as a brief storage site where sperm and all glandular secretions are nourished prior to ejaculation. After the epididymis leaves the testis, its shape changes, becoming enlarged and straight to form the **ductus deferens** (vas deferens), which passes to the urethra. Near the junction of the ductus deferens and the urethra, three different glands add secretions to the seminal fluid: the paired **seminal vesicles** (vesicular glands), a single **prostate gland**, and paired **bulbourethral glands** (Cowper's glands). Additional accessory glands, such as the paired **preputial glands** and **ampullary glands**, contribute their products to the seminal fluid (**semen**). Considerable variation in reproductive glands occurs among species of mammals, and not all species possess all the glands listed. In some animals, **coagulating glands** produce a substance that coagulates the secretions of the seminal vesicles. Following copulation, fluid from this gland contributes to formation of a **copulation plug**, which blocks the entrance to the female's vagina. Presence of this plug often indicates that a female has mated; it may persist for up to two days following copulation. The copulation plug is thought to be important in retaining the spermatozoa and preventing their loss from the female tract. Copulation plugs have been noted in many species of rodents and in some bats, insectivores, and marsupials (Austin and Short 1972a; Martin et al. 2001). In ad-

Medulla

Kidney

Sinus

Cortex

Papilla

Pelvis

Coagulating gland

Ureter

Ampullary gland

Vesicular gland

Prostate gland

Urinary bladder

Cowper's gland

Urethra

Vas deferens

Preputial gland

Testis

Penis

Epididymis
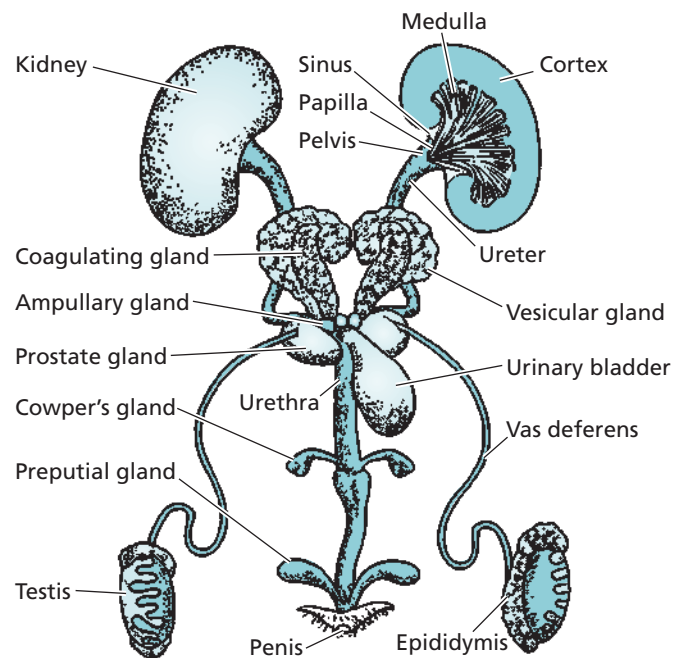
Figure 9.2 Male urogenital system. Composite diagram of the male urogenital system of the rat (*Rattus norvegicus*). *Adapted from DeBlase and Martin (1981).*

dition to nourishing sperm, acting as a lubricant and, for some species, helping to form a copulation plug, glandular secretions enhance the alkalinity of the semen so as to protect the sperm from the acidic environment present in the male urethra and female vagina.

The Penis

Transfer of male sperm to the body of the female is facilitated by the highly vascular, erectile **penis**. The penis is composed of cylindrical bodies, the **corpora cavernosa**, which become filled with blood during sexual excitation, thus causing the organ to become erect. The sperm pass during coitus through the urethra, which is also used for urination. In some mammals (e.g., all carnivores, most primates, rodents, bats, and some insectivores), the tip of the penis (**glans penis**) may include a complex bony structure, the **os penis**, or **baculum** (Figure 9.3; also see Figure 18.6). Mammalogists identify different species by this structure as well as use it as an index of approximate age of an individual (Burt 1960). The glans penis shows many different configurations, such as the bifurcated penis of some monotremes and marsupials and the corkscrew shape in the domestic pig. These configurations are compatible with the vagina of females of the same species. Furthermore, the penis of different mammals may be situated either anterior (most eutherian mammals) or posterior (marsupials, rabbits, hares, and pikas) to the scrotum. In mammals such as monotremes and marsupials, the penis is situated in a sheath within the cloaca, and in marsupials, it may be directed posteriorly (Biggers 1966).

THE FEMALE REPRODUCTIVE SYSTEM

The reproductive organs of females consist of a pair of ovaries, which produce the eggs and certain hormones; a pair of **oviducts** (Fallopian tubes), which act as the channel for travel of the ova from the ovary to one or two enlarged **uteri** (sing., *uterus*), the site of embryonic development; and a **vagina**, the opening to the outside of the body. A **cervix** (pl., *cervices*) connects the uterus and vagina (Figures 9.4).

The Ovary

The primary reproductive organ of the female is the **ovary**. In mammals, the ovaries are a pair of small, oval bodies that lie slightly posterior to the kidneys. They produce the female gametes, called **ova** (sing., *ovum*), and certain hormones. As within the testes of the male, chromosome reduction occurs in female gametes within the ovary. Immediately under the surface of the ovary is a thick layer of spherically grouped cells called **follicles** (Figure 9.5), each of which encloses a single egg. At birth, large numbers of follicles are present in the female mammal (about 2 million in the ovaries of humans), but the number decreases steadily with age. The ovarian follicle is the source of three types

A

B
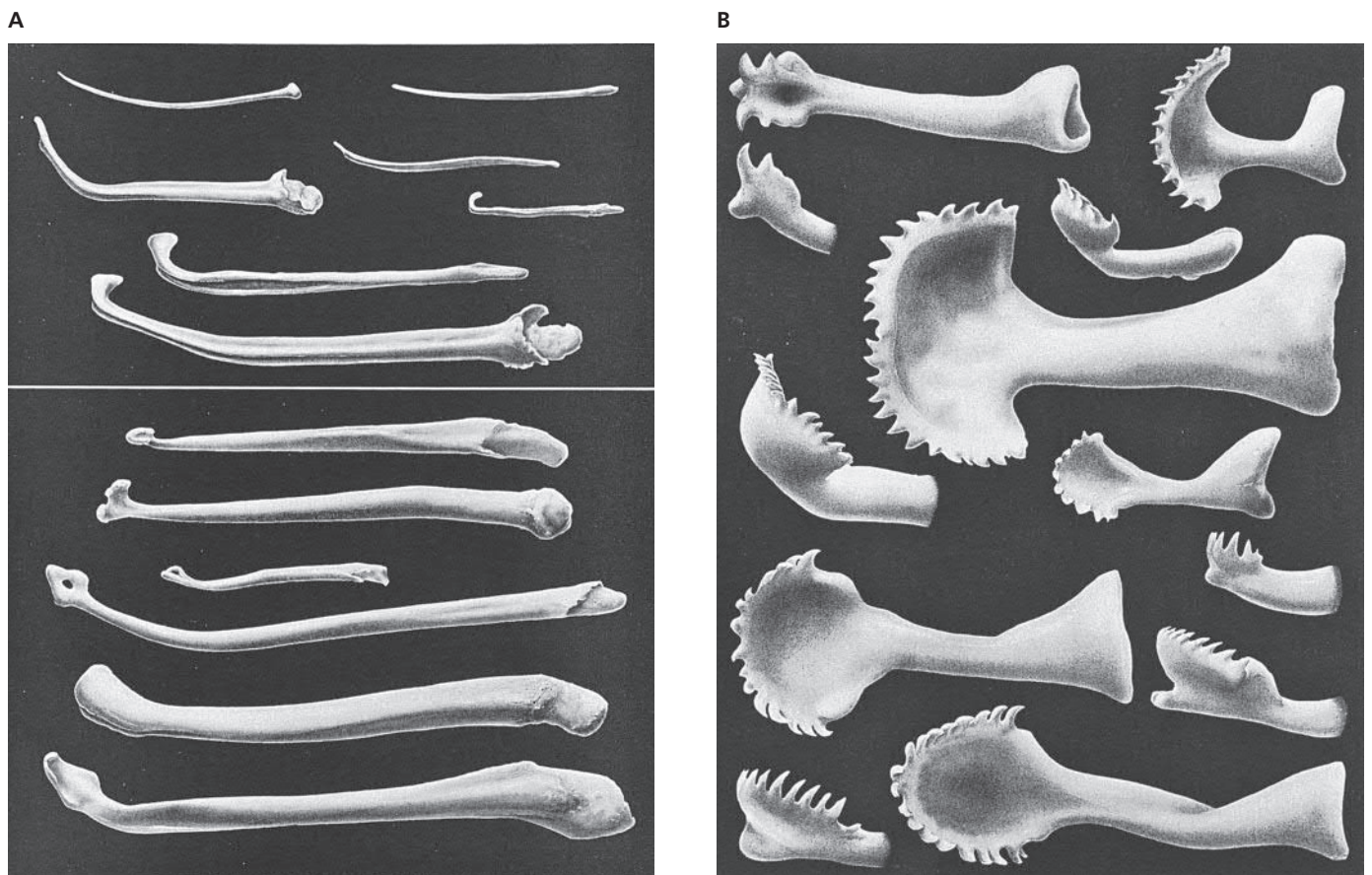
Figure 9.3 **The baculum.** Representative bacula of the Families (**A**) Mustelidae and Mephitidae and (**B**) Sciuridae.
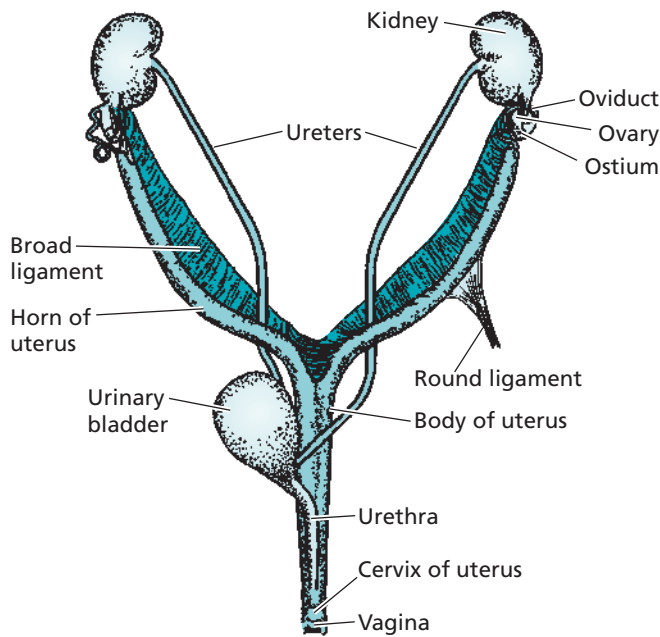
Figure 9.4 Female urogenital system. Composite diagram of the female urogenital system of the cat (*Felis catus*). *Adapted from Leach (1961).*

Figure 9.5 Mammalian ovary. Composite diagram of the mammalian ovary showing the progressive stages in the differentiation of a Graafian follicle shown on the left. The mature follicle may become atretic (*top*) or ovulate and undergo luteinization, as on the right. Insets show magnification of cellular components in each region of the ovary. *Adapted from Turner (1966).*

of gonadal steroids: androgens (masculinizing), estrogens (feminizing), and progestins. The amounts of each class of steroid vary throughout the reproductive cycle of the female (Albrecht and Pepe 1990; Strauss et al. 1996).

Ovulation

As the egg matures and the surrounding follicle enlarges, they move closer to the surface of the ovary. **Ovulation** occurs when the follicle bursts, releasing the egg, which penetrates the surface of the ovary and passes into the oviduct, where it may be fertilized if sperm are present (Tyndale-Biscoe 2005). Some sperm may reach the site of fertilization (typically, the oviduct) within a few minutes, but for the most part, it takes several hours for **capacitation** (the physiological changes in the sperm that facilitate penetration of the covering of the egg) to take place (Austin and Short 1972c). For some species of mammals, however, the period between insemination and actual fertilization may be delayed for up to 12 months—a phenomenon called "delayed fertilization" (discussed in detail in "Reproductive Variations" in this chapter). If fertilization does not occur, the egg enters the uterus and degenerates.

The development of follicular cells is controlled by the action of **follicle-stimulating hormone** (**FSH**) and **luteinizing hormone** (**LH**) produced by the anterior pituitary gland (Figure 9.6). Ovulation is induced by high levels of LH. Under the influence of these hormones, the ruptured follicle fills with yellow follicular cells and is called the **corpus luteum** (pl., *corpora lutea*), or "yellow body." The corpus luteum continues functioning during early pregnancy and produces the female hormone **proges-**

terone. This hormone promotes growth of the uterine lining (**endometrium**) and makes possible the implantation of the fertilized egg (Stouffer 1987; Keys and Wiltbank 1988; Nelson 1995). Progesterone also stimulates development of the mammary glands. Inactive corpora lutea eventually degenerate into **corpora albicans**, or "white bodies," visible on the surface of the ovary. An examination of the number of corpora lutea and corpora albicans in the ovaries can reveal a great deal about the reproductive history of a particular female (Perry 1972). The number of corpora lutea is related to the number of ova that have been ovulated and can be used to estimate the number of embryos that were produced. The major female hormone secreted by the developing follicles is **estradiol** (a form of **estrogen**), under the control of the FSH (see Figure 9.6). Estrogen is essential in promoting the proliferation of the endometrium. As the corpus luteum disintegrates, no more progesterone is produced, which in turn causes the "sloughing off" of the endometrium. Although this sloughing off and regrowth of the endometrium oc-
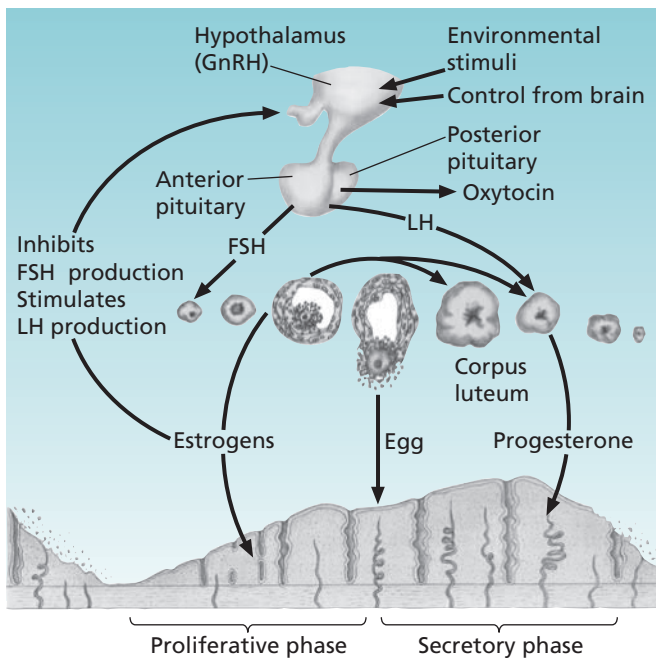
Figure 9.6 **Estrous cycle.** Hormones influence the estrous cycle of a mammal. Follicle-stimulating hormone (FSH) secreted by the anterior pituitary gland initiates the onset of follicular development. During the proliferative phase of the cycle, FSH and luteinizing hormone (LH) further the maturation of the follicle. Estrogens secreted by the follicular cells surrounding the egg cause thickening of the endometrium and further follicular growth, while also inhibiting the production of FSH. When the egg is mature, the enlarged follicle bulges from the surface of the ovary and bursts, releasing the egg (ovulation). Ovulation, induced by high levels of LH, initiates the secretory phase of the cycle. The egg passes into the oviduct, where, if it is fertilized, it implants into the endometrium. Unfertilized eggs enter the uterus and degenerate. Under the influence of LH, the ruptured follicle fills with yellowish cells and is called the "corpus luteum." The corpus luteum produces high levels of progesterone and estrogens that strongly inhibit gonadotropin-releasing-hormone (GnRH) secretion by the hypothalamus, thereby inhibiting secretion of FSH and LH necessary to permit maturation of new follicles. High levels of estrogens and progesterone stimulate the uterus to thicken, making final preparations for gestation. Progesterone also stimulates growth of the mammary glands. *Data from Gunderson (1976).*

curs cyclically in all mammals, it is most pronounced in primates. In some mammals, for example, in dogs and cats, a false pregnancy, or **pseudopregnancy**, may occur. This results from the maintenance of the corpus luteum, without fertilization, beyond the time of normal regression. Mammals exhibiting a false pregnancy behave as if they are pregnant, even though they are not.

The Estrous Cycle

All female mammals except higher primates restrict copulation to specific periods of the sexual cycle. Periods of reproduction are controlled by hormones and by the nervous system and are regulated by environmental and social cues (Bronson 1989). In nonprimates, a period of brief receptivity shortly before and after ovulation is called **estrus** (adj., *estrous*), or **heat**. In the majority of mammals, ovulation is **spontaneous**—that is, it occurs without copulation (Nelson 2000; Carlson and Gese 2008; Rasweiler et. al 2011) (Figure 9.7). Spontaneous ovulation tends to occur in gregarious species where breeding seasons are long or continuous and estrous cycles are asynchronous (Conaway 1971; Flowerdew 1987). Bouchie and associates (2006) noted that cape ground squirrels (*Xerus inauris*) appeared to be spontaneous ovulators; neither the presence of males nor copulation appeared to be necessary for ovulation to occur. As mentioned in the breakout box, the "big-bang" breeders among mammals include American didelphids (*Marmosa*, *Marmosops*, and *Monodelphis*), and three groups of Australian dasyurids, the antechinuses, phascogales, and northern quolls (Cockburn 1997; Oakwood et al. 2001; Shimmin et al. 2002; Leiner et al. 2008; Mutton et al. 2017). Among these mammals, we know the most about the brown antechinus (*Antechinus stuartii*). They are monoestrous and ovulation is spontaneous. They are reported to have only 1 breeding season per year; young are weaned when 4–5 months old, and reach sexual maturity in the year following their birth. They exhibit a short annual mating period that terminates by the abrupt death of all males (Woolley 1966) (see breakout box). Woolley (1984, 1990, 1991), McAllan (2003), Tydale-Biscoe (2005), Foster and coworkers (2008), and many others provide excellent discussions of the antechinuses and other "big-bang" breeders.

In contrast to spontaneous ovulation, **induced ovulation** occurs if release of the ovum is triggered by the act of copulation. Many investigators suggest, however, that these two strategies for ovulation cannot be separated and instead represent a continuum (Weir and Rowlands 1973). Mammals known to be induced ovulators include several species of carnivores, some rodents, some insectivorans, most rabbits, and some ground squirrels (Asa 1998; Valdespino et al. 2002). For several species of carnivores, male stimulation has been suspected for three nondomestic canids—for example, maned wolves (*Chrysocyon brachyurus*; Velloso et al. 1998), island foxes (*Urocyon littoralis*; Asa et al. 2003), and bush dogs (*Speothos venaticus*; DeMatteo et al. 2006). Some desert rodents and montane voles (*Microtus montanus*) may also exhibit induced ovulation in response to the occurrence of green vegetation and associated nutritional factors in their diet (Beatley 1969; Reichman and Van De Graaff 1975; Negus and Berger 1977; Kenagy and Bartholomew 1985). Jackson and Bennett (2005) reported induced ovulation of the Natal mole-rat (*Cryptomys hottentottus*), a social subterranean rodent occurring in the KwaZulu-Natal Midlands of South Africa.

During the breeding season, the time span from one period of estrus to the next is called the **estrous cycle** (Gunderson 1976; Withers 1992; Kunz et al. 1996). A species that has one such cycle per year, as is true for some carnivores, is termed **monestrous**. Other species, including rodents, rabbits, hares, and pikas, are **polyestrous**, meaning

Big-Bang Breeders: Semelparous Mammals

A

B

The marsupial genus *Antechinus*. Of all the marsupial carnivores of the family Dasyuridae, the genus *Antechinus* is the most numerous and widespread in Australia. (**A**) The brown antechinus (*Antechinus stuartii*) exhibits a rare reproductive behavior: it reproduces only once in its, lifetime, and all females come into estrus at the same time just once a year. After mating, all the males die. (**B**) Brown antechinus and young.

The semelparous, or "big-bang" breeders, among mammals include American didelphids (Genera *Marmosa*, *Marmosops*, and *Monodelphis*) and three groups of Australian dasyurids (the antechinuses, phascogales, and northern quolls). Among these mammals, we know the most about the brown antechinus (*Antechinus stuartii*). The brown antechinus is a small insectivorous dasyurid marsupial that inhabits the forests of eastern Australia. These small dasyurids range in mass from 17 to 71 g—the males are typically 20% to 100% heavier than the females. Day length acts as the trigger for the onset of reproductive activity, which begins in August in southern Australia and September in southern Queensland. All animals mate in the first breeding season when males have reached 11 to 12 months of age. Males become active and aggressive during the breeding season. During the short 2-week breeding season, as many as 20 males may aggregate in a tree cavity where females visit them. During this time, copulation is intense and prolonged, generally occurring for about 6 hours, with a few of the males mating many times. At the end of the 2-week mating season, not a single male is left alive. Death of males results from stress associated with social demands of the mating season during which time they stop feeding and live on their fat reserves while seeking every opportunity to mate.

What accounts for this sudden death in *Antechinus*? It is believed that increased physiological stress resulting from heightening activity, aggression, and competition for mates is the culprit. Increasing levels of testosterone and other androgens evidently depress plasma-corticosteroid-binding globulin resulting in a rise in corticosteroid concentration. The trauma associated with stress and endocrine changes causes suppression of the immune system, major ulceration of the gastric mucosa, increased vulnerability to parasites of the blood and intestines, and bacterial infections of the liver. Pregnant females live on following the death of the males. Following a gestation of about 4 weeks, a litter of 6 to 10 tiny young weighing about 16 mg each is born.

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they have several cycles a year. In general, several stages may be seen during a given estrous cycle. As an individual moves from **anestrus** (the nonbreeding, quiescent condition) to **proestrus** (the beginning stage), the uterus begins to swell, the vagina enlarges, and ovarian follicles grow in response to several hormones—the animal is said to "come into heat." The ova are usually discharged from the ovary late in this estrous stage, which may be followed by **fertilization**, the successful union of sperm and egg to form a zygote, and implantation, in which the embryo adheres to the uterine wall. Gestation represents the period of development within the uterus. The period of lactation (production of milk by the mammary glands) is reported to "block" the start of an-

other estrous cycle; however, in certain mammals, parturition (birth) is followed immediately by another estrous cycle (postpartum estrus). Many members of the rodent Family Cricetidae are known to ovulate within an hour after parturition. If, however, mating does not occur, the female enters the normal condition of **metestrus**, followed by anestrus. Periods between mating in polyestrous species are termed **diestrus**; this is when the reproductive system recycles to the proestrous condition. Mammalogists can determine the different estrous periods by using the **vaginal smear technique**, which identifies specific cell types associated with a certain phase of the cycle (Kirkpatrick 1980). In humans and Old World primates, the ovarian and uterine cycles are

A

Ovulation
Copulation
Fertilization
Implantation
Gestation
Parturition
Lactation

B

Copulation
Ovulation
Fertilization
Implantation
Gestation
Parturition
Lactation

C

Copulation
Delay
Ovulation
Fertilization
Implantation
Gestation
Parturition
Lactation

D

Ovulation
Copulation
Fertilization
Delay
Implantation
Gestation
Parturition
Lactation

Figure 9.7 **Reproductive events.** (**A**) Spontaneous ovulation is the usual sequence of reproductive events occurring in eutherian mammals. Several different groups show variation on this general sequence, including (**B**) induced ovulation exhibited by cats and some rodents, (**C**) delayed fertilization displayed by certain insect-eating bats, and (**D**) delayed implantation shown in a diverse array of groups. Delayed development, exhibited by the neotropical fruit bat, and embryonic diapause, exhibited by almost all kangaroos, wallabies, rat kangaroos, pygmy possums, feathertail gliders and honey possums, are not shown in this figure.

different and are called "menstrual" rather than "estrous" cycles (Nadler 1975; Guyton 1986).

The Female Duct System and External Genitalia

The female duct system consists of paired oviducts (or Fallopian tubes), one or two uteri, one or two cervices, and the vagina (see Figure 9.4). The external genitalia include the **clitoris**, the **labia majora**, and **labia minora**. The clitoris is the embryonic homologue of the penis, and in those species where males possess a baculum, females possess a small bone, the **os clitoris**, in the clitoris.

The architecture of the **female reproductive** tract also varies considerably in mammals. The monotremes and mar-supials (Chapter 10) do not possess true vaginae. In the monotremes, the paired uteri and oviducts empty into a **urogenital sinus**, as do liquid waste products. This sinus passes into the cloaca. The female reproductive tract of marsupials is referred to as **didelphous**, meaning that the uteri, oviducts, and vaginal canals are paired. During copulation, the forked penis of the male delivers sperm to the paired uteri of the female. In more advanced marsupials, such as the kangaroos, two lateral vaginae are used to conduct sperm, and a medial vagina functions as the birth canal.

In eutherian mammals, four principal uterine types occur that are based on the relationship of the uterine horns (Figure 9.8). A **duplex** uterus is found in lagomorphs, rodents, aardvarks, and hyraxes and is characterized by two uteri, each with a cervix opening into the vagina. A **bipartite** uterus is typical of whales and most carnivores. Here,
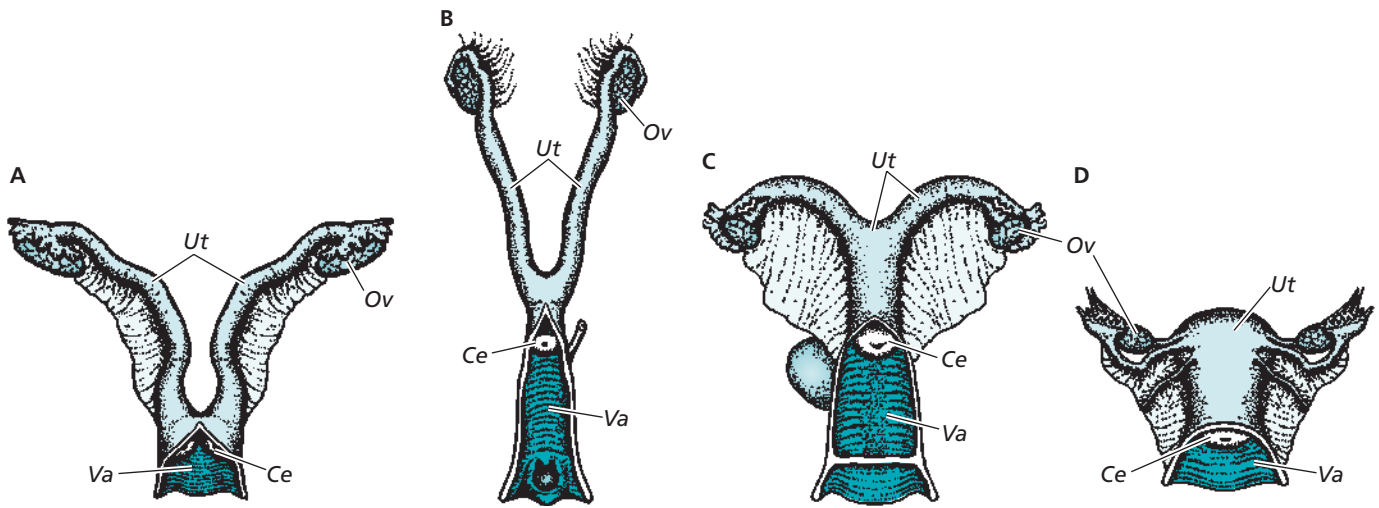
Figure 9.8 Types of uteri. The degree of fusion of the uterine horns varies among different groups of eutherian mammals. (**A**) A duplex uterus occurs in rodents, rabbits and hares, aardvarks, and hyraxes; note the separate horns and distinct cervix of each. (**B**) Most carnivores and whales exhibit a bipartite uterus. (**C**) Insectivores, most bats, primitive primates, pangolins, some carnivores, elephants, manatees and dugongs, and most ungulates possess a bicornuate uterus. (**D**) A simplex uterus is typified by higher primates, some bats, anteaters, tree sloths, and armadillos. *Abbreviations:* Ut = uterus, Ce = cervix, Ov = ovary, Va = vagina. *Adapted from Ramsey (1982).*

the horns of the uterus are separate but enter the vagina by a single cervix. The most widespread condition is called the **bicornuate** uterus, which is found in the insectivores, most bats, primitive primates, pangolins, some carnivores, elephants, manatees and dugongs, and most ungulates. The uterine horns are Y-shaped, being separated medially but fused distally, where they form a common chamber, the body, which opens into the vagina through a single cervix. The last type of uterus is called **simplex**, in which all separation between the uterine horns is lacking, and the single uterus opens into the vagina through one cervix. This condition is seen in some of the bats, higher primates, and xenarthrans.

Implantation

Fertilization usually occurs shortly after ovulation in the oviduct. **Implantation** is the attachment of the embryo to the uterine wall. Cleavage of the **zygote**, or fertilized egg, occurs as it passes down the oviduct toward the uterus, propelled by ciliary action and rhythmic muscular contractions (peristalsis). Next, the blastocyst (the embryo at the 32- to 64-cell stage) implants on the wall of the uterus. The uterus of mammals is characterized by a thick muscular wall (the **myometrium**) surrounding the highly vascular endometrium—the specific site of implantation. The anterior pituitary gland (which produces FSH and LH) and the corpus luteum (which produces progesterone) both prepare the endometrium for implantation. The blastocyst differentiates into the embryo and the trophoblast (Figures 9.9 and 9.10). On contact with the lining of the uterus, the cells of the trophoblast region proliferate rapidly, producing en-
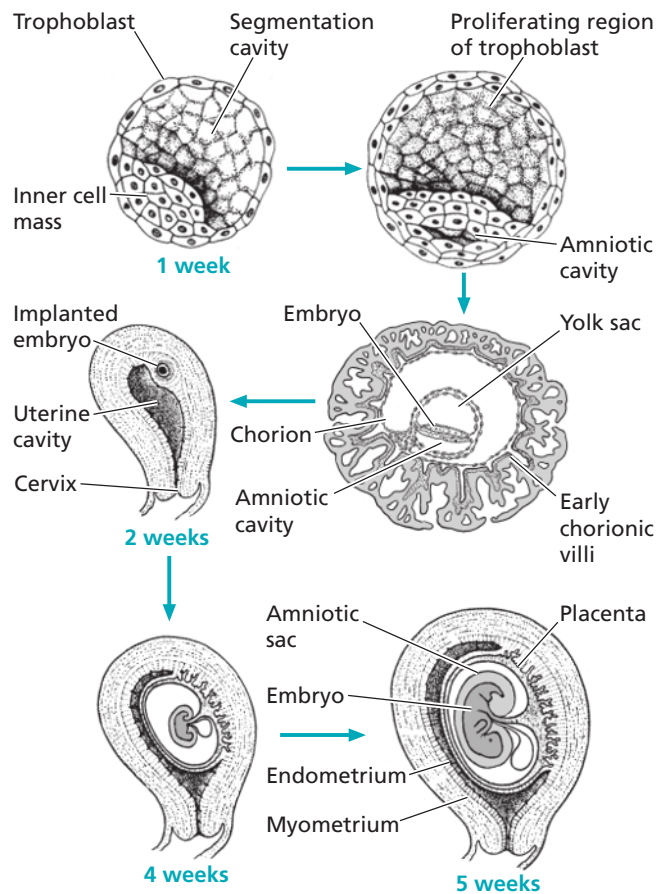
Figure 9.9 Human embryo. Diagram showing the early development of the human embryo and its extraembryonic membranes. *Adapted from Hickman et al. (2004).*

A

Vascular yolk-sac chorion

Yolk sac

Nonvascular yolk-sac chorion

Amnion

Extra-embryonic coelom

Allantois

B

Amniotic cavity

Amnion

Extraembryonic coelom

Yolk sac

Chorion

Allantois

Villi

Allantoic mesoderm
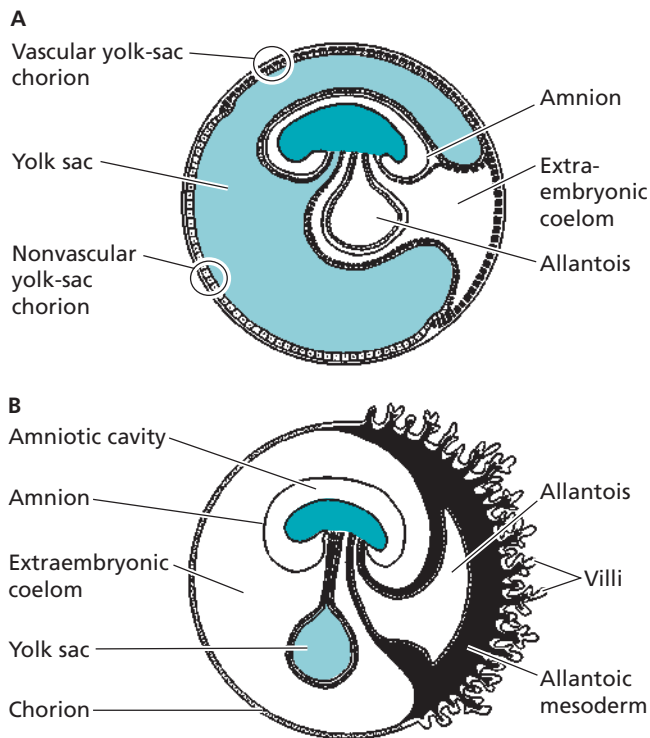
Figure 9.10 Embryo and extraembryonic membranes. Diagram showing the embryo and extraembryonic membranes of (**A**) a metatherian (kangaroo) and (**B**) a eutherian mammal. Note the metatherian's greatly enlarged yolk sac, which serves the nutritional needs of the developing embryo. In the eutherian mammal, extensive chorionic villi penetrate the endometrium and provide mechanical strength and increased surface area for rapid and efficient exchange of nutrients, gases, and waste products between the maternal and fetal blood supplies. *(A) Adapted from Torrey and Feduccia (1979). (B) Adapted from Balinsky (1975).*

zymes that break down the **decidua**—the uterine mucosa in contact with the trophoblast. This permits the blastocyst to sink into the vascularized endometrium, and subsequently it is surrounded by a pool of maternal blood. At this point, the trophoblast thickens, extending thousands of fingerlike roots (**villi**) that penetrate the lining of the endometrium. The trophoblast further invades the decidua, eventually contributing to the formation of the placenta. The more invasive the trophoblast, the larger the area of decidua through which both the embryo and placenta obtain nutrients, oxygen, water, ions, and hormones from the mother and discharge waste products. The degree of intimacy between the maternal and embryonic parts of the placenta varies in different mammals, and mammalogists employ these differences to help define various groups of mammals.

The Placenta

The placenta, a complex of embryonic and maternal tissues, performs several essential functions during pregnancy. It (1) physically anchors the fetus to the uterus,

(2) transports nutrients from the circulation of the mother to the developing fetus, (3) excretes metabolites of the fetus into the maternal compartment, and (4) produces hormones that regulate the organs of the mother and fetus. Because both the placenta and embryo are genetically alien to the mother, uterine tissue should reject the embryo. This does not happen because the placenta has evolved the ability to suppress the normal immune response that the mother's body would ordinarily mount against it and the embryo. This ability of the embryo to become an **allograft** (successful foreign transplant) is attributed to the production by the chorion of essential lymphocytes and proteins that block the mother's immune response by suppressing the formation of specific antibodies (Adcock et al. 1973; Strauss et al. 1996).

Although eutherians are often referred to as "placental" mammals, marsupials also have a placenta, albeit not one as efficient as that found in the eutherians. Most metatherians have only a choriovitelline placenta in which the yolk-sac cavity is greatly enlarged to form the placenta; it serves the nutritional needs of the developing embryo. Compared to eutherians, the placentae of most metatherians lack extensive villi and have a comparatively weak mechanical connection to the uterine lining (Figure 9.11). The embryo of metatherians does not implant deeply in the endometrial mucosa but merely sinks into a shallow depression of the mucosa. The surface area for adhesion and absorption is increased by a slight wrinkling of the surface of the embryo that lies against the endometrium. Besides nutrition provided by the enlarged yolk sac, the developing embryo gains a limited amount of nutrition in the form of "uterine milk" derived from the uterine mucosa. The system of nourishment to the embryo from the mucosa is comparatively inefficient.

We can delimit four types of metatherian placentae based on the degree of apposition between the fetal and maternal tissues and the structure of the chorion and allantois (Austin and Short 1976; Hughes 1984; Mossman 1987; Tyndale-Biscoe and Renfree 1987; Dawson 1995). Within the metatherians, the most common type of arrangement of fetal and maternal tissues is seen in eastern gray kangaroos (*Macropus giganteus*; Dawson 1995). Here, the highly vascularized wall of the yolk-sac cavity is intimately connected with the maternal endometrial mucosa (see Figure 9.11). This kind of placenta is also found in other members of Diprotodontia and in the Didelphimorphia (American opossums). The dasyurids show a variation on the latter condition in which the allantois and chorion are opposed early in development and then retreat without forming a placental structure. The koala (*Phascolarctos cinereus*) and coarse-haired wombat (*Vombatus ursinus*) demonstrate an apposed, nonvascular, chorioallantoic placenta but still retain a vascular choriovitilline placenta. Here the large yolk-sac cavity retains its role as the primary surface for gas exchange and absorption of nutrients.

The placenta of the bandicoots (Order Peramelemorphia: Family Peramelidae) shows the greatest similarity to the
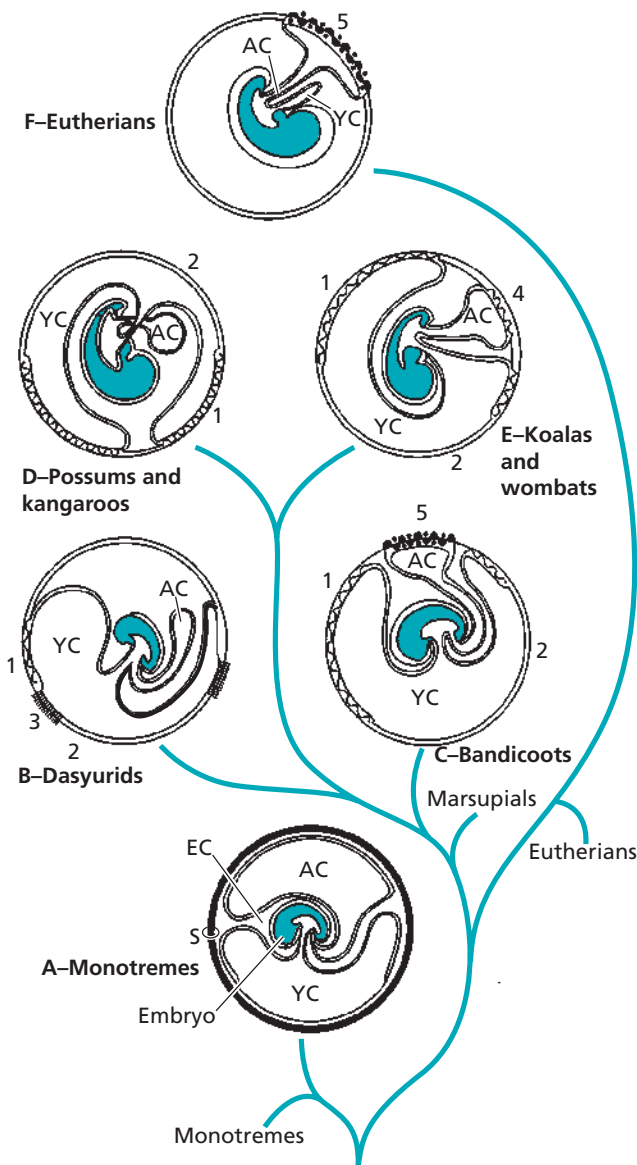
Figure 9.11 **Types of placentation in marsupials and eutherians.** *Key:* 1 = vascular choriovitilline placenta; 2 = nonvascular choriovitilline placenta; 3 = syncytialized choriovitilline placenta; 4 = apposed (nonvascular) chorioallantoic placenta; 5 = syncytialized (vascular) chorioallantoic placenta; AC = allantoic cavity; EC = extraembryonic coelom; S = shell; YC = yolk-sac cavity. *Adapted from Sharman (1976), Austin and Short (1976), and Pough et al (2005).*

Figure 9.12 **Mammalian placental structures.** Two types of mammalian placental structures as seen in a transitional stage of an implanted embryo of a cat. Both a choriovitilline placenta and a chorioallantoic placenta are present at this stage. The chorioallantoic placenta grows outward and takes over the function of the choriovitilline placenta. *Adapted from Pough et al. (2005).*

eutherian placental condition. Bandicoots possess a true "syncytialized" vascular chorioallantoic placenta yet still retain a vascular choriovitilline placenta (see Figure 9.11). In bandicoots, the allantois is large and highly vascular. The position of the embryo, close to the highly vascularized endometrial mucosa, promotes exchange of materials across allantoic membranes. However, the allantois of bandicoots lacks villi, thus compromising the surface area available for exchange of materials between fetal and maternal bloodstreams. Nutrition to the embryo is augmented by "uterine

milk" absorbed across the choriovitilline membranes. In sum, the arrangement of placental membranes in the bandicoots results in a less effective transfer of substances between the fetus and material circulations. Unlike metatherians, all eutherian mammals possess a **chorioallantoic placenta** (see Figure 9.10), which develops from the combination of the embryonic membranes, an outer chorion, and an inner vascularized allantois. The choriovitilline placenta is short lived, and a complex "syncytialized," vascular chorioallantoic placenta is the functional one for most of gestation (Figure 9.12). In this case, the blastocyst adheres to the endometrium and then sinks very deeply into it, forming a strong adhesion. This adhesion is enhanced by the rapid growth of **chorionic villi** (finger-like projections of capillaries from the outermost embryonic membrane) that penetrate the endometrium. The uterus becomes highly vascularized at the point of attachment of the developing embryo. It is important to note that although the maternal and fetal circulations are in close contact, these two blood systems are not fused. Fetal blood does not circulate in the mother, and maternal blood does not circulate in the fetus. The complex, extensive network of villi provides not only mechanical strength but also an increased surface area for rapid and efficient exchange of nutrients, gases, and waste products between the maternal and fetal blood supplies. A human placenta is reported to possess about 48 km of villi (Bodemer 1968).

The four types of placentas are classified according to the distribution of villi permeating the endometrial lining of the uterus (Ramsey 1982; Figures 9.13 and 9.14). Lemurs, nonruminating cetartiodactyls, pangolins, and perissodactyls have a placenta that is **diffuse**, with villi scattered evenly throughout the uterus. A **cotyledonary placenta**,

found in ruminating cetartiodactyls, is characterized by more or less evenly spaced patches of villi throughout the uterus. Carnivores have a **zonary placenta**, which has a continuous band of villi within the uterus. Many groups, including insectivores, bats, most primates (including humans), some rodents, rabbits and hares, and pikas, have a placenta referred to as **discoidal**, in which villi occupy one or two disc-shaped areas within the uterus. A variation on the discoidal arrangement is the **cup-shaped discoid** found in most rodents.

Mammalian placentas are also categorized by an assessment of the speed and efficiency with which nutrients,

oxygen, and waste material are exchanged between maternal and fetal blood supplies. Recall that as the blastocyst sinks into the endometrium and implantation proceeds, the chorionic villi grow farther into the endometrium. The uterus becomes greatly vascularized in the area of the implantation. Such an arrangement increases the surface area, allowing a more rapid interchange between the maternal and fetal circulation. Exchange rates depend on the number and thickness of capillary walls, connective tissue, and uterine and chorionic (fetal) epithelial tissues. Six arrangements are generally recognized (Figure 9.15):
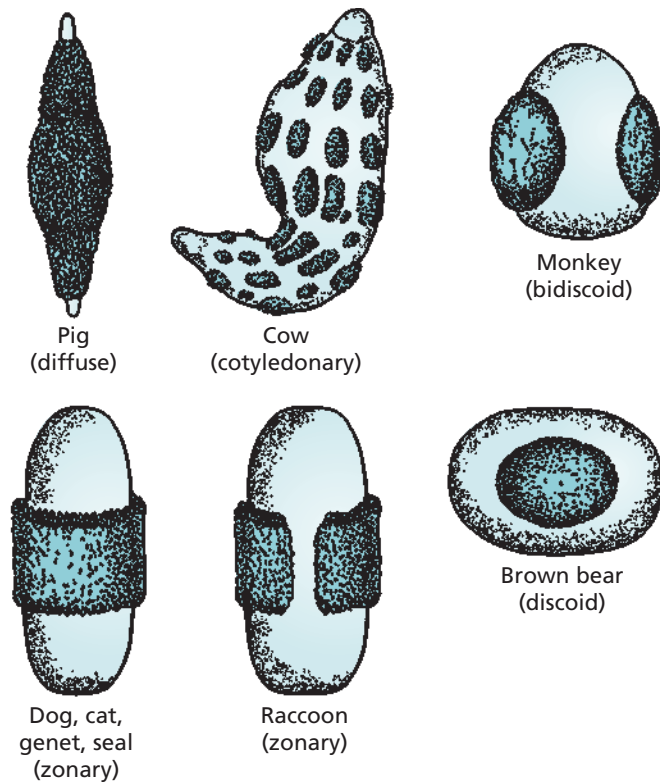
1. An **epitheliochorial** system is typified by having six tissue layers, with the villi resting in pockets in the endometrium. This system occurs in pigs, lemurs, horses, and whales.
2. The **syndesmochorial** system has one less layer because the epithelium of the uterus erodes at the site of attachment, thus reducing the separation of the maternal and fetal bloodstreams. This system is found in ruminating cetartiodactyls, such as cows, sheep, and goats.
3. Even further erosion of the maternal tissue is exemplified by the **endotheliochorial** system of the carnivores. Here, the chorion of the fetus is in direct contact with the maternal capillaries.
4. In the **hemochorial** system seen in advanced primates (including humans), insectivores, bats, and some rodents, no maternal epithelium is present, and the villi are in direct contact with the maternal blood supply.
5. In an **endothelioendothelial** system, maternal and fetal capillaries are next to each other, with no connective tissue between them.
6. The greatest destruction of placental tissues and least separation of fetal and maternal bloodstreams occur in the **hemoendothelial** system in which the fetal capillaries are literally bathed in the maternal blood supply. This system occurs in some rodents, rabbits, and hares (Austin and Short 1972b; Gunderson 1976; Ramsey 1982; Pough et al. 2005).

Figure 9.13 **Placental villi.** The shape and distribution of placental villi vary among different groups of mammals. *Adapted from Ramsey (1982).*
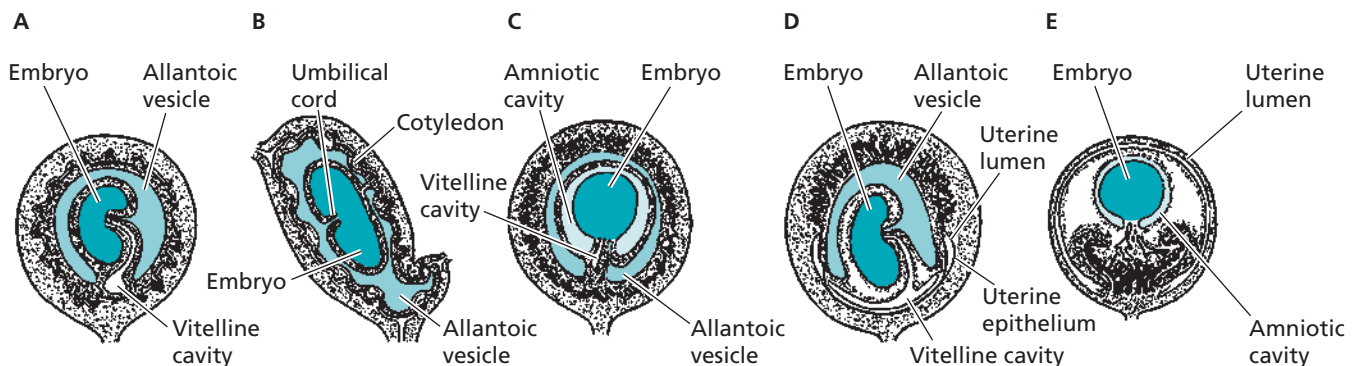
Figure 9.14 **Types of placentae.** Sectional views of different types of mammalian placentae: (**A**) diffuse; (**B**) cotyledonary; (**C**) zonary; (**D**) discoid; (**E**) cup-shaped discoid. Views (**A**), (**B**), and (**D**) are sagittal; views (**C**) and (**E**) are transverse sections. *Adapted from DeBlase and Martin (1981).*
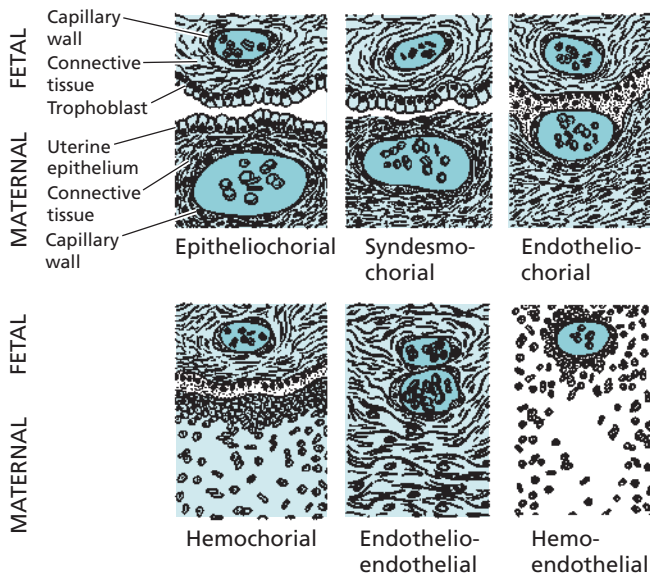
Figure 9.15 **Internal structure of the placenta.** Diagram showing variation in the number of tissue layers separating maternal and fetal blood supplies in different systems of placental mammals. The number varies from one layer in a hemoendothelial system to six layers in an epitheliochorial system. *Adapted from Ramsey (1982).*

Those of you who have observed the birth of pets or livestock (or even witnessed the birth of children) may have noticed the appearance of the "afterbirth," which is the expelled placenta and extraembryonic membranes. Sometimes the afterbirth is expelled with the young shortly thereafter. Mammals such as pigs, lemurs, horses, and whales possess the epitheliochorial type of placenta, which provides the least intimacy between maternal and fetal membranes. In such cases, the placentas are termed **nondeciduous**, and due to the minimal attachment of villi in the uterine wall, they can pull away from the wall of the endometrium at birth without causing any bleeding. Mammals such as armadillos, sloths, anteaters, rodents, carnivores, and primates have more intimate associations between the endometrial and fetal bloodstreams. Such placentas are termed **deciduous** and are typified by the hemoendothelial system. As a result of this close attachment, extensive erosion of the uterine tissue takes place at parturition. A portion of the uterine wall is actually torn away when the placenta separates at delivery. Bleeding occurs because some blood vessels and connective tissue of the uterine wall are shed with the placenta. Hemorrhaging following birth soon stops due to the collapse of the uterus by contractions of the myometrium (the smooth muscle layer of the uterus), which tends to constrict the blood vessels. The previous site of attachment of the fetus on the uterine wall is evidenced by a pigmented area called a **placental scar**. Placental scars form in rodents, shrews, carnivores, bats, rabbits, hares, and pikas, for example, and are useful in studying an individual's reproductive history (Lidicker 1973). Females that are **nulliparous** (never hav-

ing been pregnant) show no evidence of placental scars, whereas a female that is termed **parous** has scars indicating prior parturition. A **multiparous** individual has placental scars of different ages, thus indicating that several fetuses or litters were produced.

The Trophoblast

The reproductive patterns of marsupials and eutherians are very different. Marsupials bear embryonic (altricial) young after a brief gestation, whereas eutherians produce precocial young following a comparatively long period of gestation. One explanation for this difference is the evolution of the trophoblast and its importance in preventing immunorejection between the fetus and mother (Lillegraven 1975, 1987; Luckett 1975; Eisenberg 1981; Tyndale-Biscoe and Renfree 1987; Vaughan et al. 2000). Recall that the **trophoblast** (see Figure 9.9), the embryonic contribution to the placenta, greatly enhances fetal development by efficiently transferring nutrients and dissolved gasses between the fetal and maternal circulations. The trophoblast also prevents the immunorejection response from developing between the fetal and maternal circulatory systems. During early gestation in marsupials, membranes of the eggshell act as a barrier between antigen-bearing parts of the embryo and the uterine fluid, thus preventing immunorejection. Late in gestation, however, shell membranes are shed, leaving the embryo and maternal systems vulnerable to immunological attack. To circumvent rejection, marsupials have evolved abbreviated gestation periods. In contrast, although eutherians lack shell membranes, early stages of the zygote are protected from mixing with maternal blood by the **zona pellucida**—a noncellular layer surrounding the zygote. Later in development, immunorejection is prevented by the trophoblast and the decidua. Throughout gestation, a close association of uterine and fetal tissues is maintained, yet the trophoblast provides a constant "line of defense" against the mixing of fetal and maternal tissues. As a result, the trophoblastic tissues have permitted eutherians to evolve longer periods of gestation, thus giving rise to the production of more precocial young and a decrease in the length of the energetically expensive period of lactation. The "appearance" of the trophoblast is of central importance in favoring the evolution of structural diversity and adaptive radiation of eutherian mammals.

Gestation

The period of time from fertilization until the birth of the young is referred to as **gestation**. This period of intrauterine growth also varies greatly within mammals. The prototherian mammals (monotremes) lay eggs (that is, they are oviparous) that hatch outside the body, so, by definition, gestation does not even occur in monotremes. By contrast, the therian
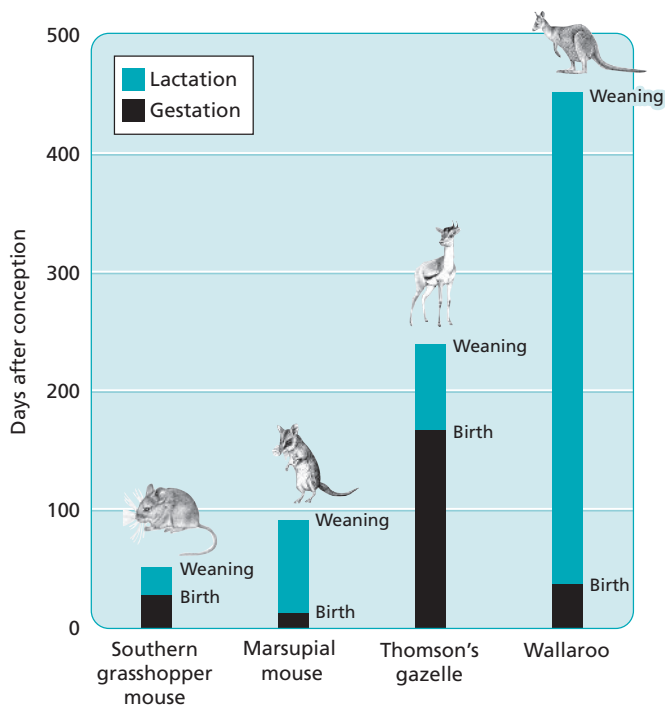
Figure 9.16 Gestation and lactation. Diagram comparing the periods of gestation and lactation of marsupial and placental mammals. Note that marsupials have a shorter interval of gestation and longer period of lactation than similarly sized species of placental mammals. *Data from Hickman (1997). All rights reserved.*

Figure 9.18 Young Virginia opossums. Photograph showing eight one-week-old Virginia opossums attached to the teats within the pouch of the mother.

Figure 9.17 Long-nosed bandicoot. The shortest gestations periods are found in marsupials such as the northern brown bandicoot (*Isodon macrou*) and the long-nosed bandicoot (*Perameles nasuta*).

mammals (Infraclasses Metatheria and Eutheria) bear live young (they are viviparous) and retain the embryo within the body. They therefore have a gestation period.

Marsupials bear altricial young following a brief gestation period, and lactation is protracted compared with similarly sized placental mammals (Figure 9.16; Tyndale-Biscoe and Renfree 1987; Dawson 1995; Tyndale-Biscoe 2005). The shortest gestation periods are found in the mar-

supials. The northern brown bandicoot (*Isodon macrou*) and the long-nosed bandicoot (*Perameles nasuta*; Figure 9.17) have one of the shortest gestation periods among mammals (ca. 12.5 days); however, young bandicoots are relatively precocial at birth. This fact suggests that the choriovitilline placenta is less efficient than the chorioallantoic placenta (Padykula and Taylor 1982). The Virginia opossum also has a very short gestation—only about 12.5 days (Harder et al. 1993). Following this brief period of intrauterine development, from 4 to 25 embryo-like young (the size of honey bees) emerge from the birth canal. The young are altricial, and each weighs only about 0.13 g—an entire litter can fit into a teaspoon. Although altricial, the young have well-developed, muscular forelegs with sharp claws and can move hand over hand, up the hair of the mother's belly and into her pouch—traveling up to 50 mm in about 16.5 seconds. After reaching the mother's pouch, each pup takes hold of one of the 13 available nipples (Figure 9.18), which then enlarges, forming a bulb within the mouth of the suckling young. They remain attached to the nipple until about 2 months later, when they are weaned.

Although as many as 25 young are born, the entire litter cannot survive. Pouched young average about 8 in number and, following weaning, ride on the mother's back for another month (McManus 1974; Gardner and Sunquist 2003).

The length of gestation, which varies according to taxonomic group, is correlated with body mass, the number of young per litter, and the degree of development of the young (Eisenberg 1981; Dawson 1995). A prime example of a mammal with a large body mass and the record holder for the longest gestation period (about 22 months) is the African elephant (*Loxodonta africana*). Bats are rather unusual among small mammals in displaying a comparatively long gestation period. Pregnancy generally lasts from 3 to 6 months, and most bats have only 1 young per litter (O'Shea et al. 2010). Some species, however, such as the red bat (*Lasiurus borealis*), produce litters of up to 5 young (Hayssen et al. 1993; Altringham 1996).

Body mass is not always the best predictor of gestation period. The blue whale (*Balaenoptera musculus*) is the largest animal that has ever lived. So it might be expected to have the longest gestation period. This huge mammal (about 130,000 kg), however, has a gestation period of only 10–12 months, similar to that of a horse. Orders Pilosa (anteaters and sloths) and Cingulata (armadillos) are known to have longer gestation periods than predicted by body mass (McNab 1985). The two-toed sloth (*Choloepus didactylus*) of the neotropical region weighs about 9 kg but has a gestation period of almost 11 months. This is about 4 months longer than the wapiti, or elk (*Cervus elaphus*), which weighs 22 times more (Hayssen et al. 1993; Vaughan et al. 2000). Other groups of mammals that do not exhibit longer gestation periods as body mass increases are the marsupials, whales and dolphins, higher primates, elephant shrews, and hystricomorph rodents (porcupines, guinea pigs, capybara, agoutis, pacas, cane rats and allies; Sadleir 1973; see Chapter 16).

Primates tend to exhibit long gestation periods compared with other mammals of similar body size. Some of the smaller primates, such as the lemurs, lorises, and marmosets, have gestation periods ranging from 60 to 200 days. Larger primates, such as gorillas, have gestation periods lasting about as long as that of humans (280 days). Newborn primates are precocial but require long periods of maternal care and lactation. These extended periods of care-giving appear to be important in the evolution of socialization in higher primates. In addition to body mass, environmental factors such as latitude, ecosystem, and seasonality influence the length of gestation period and litter size in mammals.

Reproductive Variations

For most mammals, fertilization occurs within several hours of insemination. The fertilized egg becomes implanted in the uterus, and development continues until birth. Thus, we define the gestation period as the interval between fertilization and parturition. Mammals may exhibit modifications that lengthen the fertilization or gestation period, including delayed fertilization, delayed development, delayed implantation, and embryonic diapause (Weir and Rowlands 1973; Gaisler 1979; Nowak 1994; Orr and Zuk 2014).

DELAYED FERTILIZATION

Many animals residing in seasonal environments employ special mechanisms to optimize survival. Bats of Families Vespertilionidae and Rhinolophidae, which occupy temperate zones of the New and Old Worlds, exhibit reproductive tactic called **delayed fertilization** or delayed ovulation (Wimsatt 1945; Austin and Short 1972a; Oxberry 1979; Racey 1982; Nowak 1994; Bernard and Cumming 1997; Neuweiler 2000; Orr and Zuk 2013; see Figure 9.7). Copulation takes place in September or October before hibernation commences. Follicular growth has occurred in the ovary, but ovulation does not happen at this time. The sperm are immotile and stored in either the uterus or the upper vagina, and then both sexes enter hibernation. When the female emerges from hibernation in the spring, the eggs are ovulated, spermatozoa become motile, and fertilization takes place. It is noteworthy that some bats do copulate during the period of hibernation, especially species in Genera *Myotis* and *Corynorhinus*. Implantation of the blastocyst occurs about a week after fertilization (Kunz 1982). The gestation period may last for 50–60 days, as in the silver-haired bat (*Lasionycteris noctivagans*) and little brown bat (*Myotis lucifugus*; Wimsatt 1945; Kunz 1982; Gustafson and Damassa 1985; Hayssen et al. 1993). Young are born in early summer, when insects are abundant. Delayed fertilization is advantageous for northern species of bats because it provides young with more time to build critical body mass to sustain their long period of hibernation.

While delayed fertilization is most common in temperate species of bats that undergo hibernation, mammalogists have found sperm storage in bats that reside in tropical regions and that apparently do not undergo true hibernation. Tropical species may store sperm as an adaptive strategy synchronized with the availability of food (Racey 1982).

DELAYED DEVELOPMENT

Delayed development differs from delayed fertilization in that the blastocyst implants shortly after fertilization, but development is very slow. A fertilized blastocyst implants in the uterus in summer but may have a 7-month period of development or gestation. Delayed development is reported for both pteropodids (Old World fruit bats traditionally called "megachiropterans"; see Chapter 21) as well as other bat families (Racey 1982). The Jamaican fruit-eating bat (*Artibeus jamaicensis*; Figure 9.19) employs delayed develop-

Figure 9.19 Jamaican fruit bat. *Artibeus jamaicensis* is in Family Phyllostomidae. This species and other micro- and megachiropterans employ delayed development. *A. jamaicensis*, a fruit-eating bat, is native to Mexico, Central America to northwestern South America, as well as the Greater and many of the Lesser Antilles.

ment as a unique mechanism to synchronize the birth of young with the end of the dry season, when the availability of large fruits is at its peak (Fleming 1971; Racey 1982). The Old World insectivorous little long-fingered bat (*Miniopterus australis*) also exhibits delayed development (Richardson 1977). The reproductive delay in this species is reportedly in response to unpredictable availability of insects. Other species of bats reported to undergo delayed development are the California leaf-nosed bat (*Macrotus californicus*; Bradshaw 1961, 1962); the Philippine pygmy fruit bat (*Haplonycteris fischeri*; Heideman 1988, 1989); the Luzon fruit bat (*Otopteropus cartilagonodus*; Heideman et al. 1993); the greater musky fruit bat (*Ptenochirus jogori*; Heideman and Powell 1998); the rufous horseshoe bat (*Rhinolophus rouxii*), the greater short-nosed fruit bat (*Cynopterus sphinx*); the Argentine brown bat (*Eptesicus furinalis*); and the silver-tipped myotis (*Myotis albescens*) (Racey 1982).

DELAYED IMPLANTATION

In **delayed implantation**, ovulation, copulation, fertilization, and early cleavage of the zygote up to the blastocyst stage occur normally (see Figure 9.7). Development of the blastocyst is arrested, however, and each blastocyst floats freely in suspended animation in the reproductive tract until environmental conditions become favorable for implantation. During this free-floating stage, the blastocyst is

encased in a protective coat (called the "zona pellucida") until the optimal time for its development. Eventually implantation occurs, and development proceeds normally (Enders 1963). Delayed implantation is either **obligate**, as in armadillos, in which the delay occurs as a normal, consistent part of the reproductive cycle, or **facultative**, as when rodents or insectivores are nursing a large litter or are faced with extreme environmental conditions. Daniel (1970) and Mead (1989) discussed delayed implantation in detail.

Although delayed fertilization and delayed development occur only in bats, delayed implantation is seen in many diverse groups, including insectivores, rodents, bears, mustelids (weasels and allies), seals, armadillos, certain bats, and European and Siberian roe deer (*Capreolus capreolus* and *C. pygargus*). Delayed implantation is a rule in the pinnipeds (Atkinson 1997; Laws et al. 2003). Delayed implantation occurs in the Old World vespertilionids—the lesser long-fingered bat (*Miniopterus fraterculus*) and Schreiber's long-fingered bat (*M. schreibersii*; Kimura and Uchida 1983). The length of gestation in *M. schreibersii* varies geographically, and differences may in part reflect local environmental conditions (Racey 1982). For many species of bats, timing of implantation may be contingent on endocrine controls for different populations (see Nowak 1994; Neuweiler 2000).

Delayed implantation was probably first reported in the mid-1600s, as described in the "field notes" of the English physician William Harvey, who joined King Charles I on hunting trips for European roe deer (see Gunderson [1976] for a discussion of the historical account). Many different mammals employ delayed implantation, and this reproductive strategy varies widely even within the same genus (Sandell 1984; King 1990). As noted, roe deer are the only ungulates that exhibit delayed implantation. Following the rut in July and August, implantation is delayed until December or January, and the young are born in the spring (April–June). The gestation period is between 264 and 318 days (Hayssen et al. 1993; Danilkin 1995; Sempéré et al. 1996). In North America, the black bear (*Ursus americanus*) exhibits delayed implantation. In Pennsylvania, for example, black bears mate during the summer, usually sometime from early June to mid-July. After the ova are fertilized, implantation of the blastocyst in the uterine wall is delayed for up to 5 months. Young are born in winter dens in mid-January, following an "actual" gestation period of about 60–70 days (Pelton 1982; Alt 1983; Hellgren et al. 1990; Hayssen et al. 1993). Mustelids also represent excellent examples of delayed implantation (King 1983; Mead 1989; Ferguson et al. 2006). Species of Carnivora are known to shorten gestation period so that reproduction can occur during the short window of time that favors environmental conditions. Some species of carnivores lengthen gestation periods to cope with long winters; this occurs not by decelerating intrauterine growth but by delaying implantation (Heldstab et al. 2018). Although great variation occurs among different species of mustelids, the eastern spotted skunk (*Spilogale putorius*) and other mephitids seems to

Figure 9.20 **Delayed implantation.** The postponement of embedding of the blastocyst in the uterine epithelium for several days or months is practiced by many diverse mammalian groups, including insectivores rodents, bears, mustelids, seals, armadillos, certain bats and two species of roe deer. The eastern spotted skunk (*Spilogale putorius*) is one of the smallest of the New World skunks. In addition to undergoing delayed implantation, these fascinating mustelids display a unique acrobatic feat of performing a "handstand" on their forefeet as a defense behavior.

represent a fairly typical example of delayed implantation (Mead 1968) (Figure 9.20). Female spotted skunks enter estrus in September and mate in September or October. The zygotes undergo normal cleavage but stop at the blastocyst stage, at which time they float freely in the uterus for about 6.5 months. After implantation, gestation lasts only about a month, and young are usually born between April and June. The total period of pregnancy takes 210–260 days. Of all mammals, the fisher (*Martes pennanti*) has the most protracted delay to implantation. Fishers breed between March and April. Following a 9-month delay, blastocysts implant in January or February, and most births occur in March and early April (Wright and Coulter 1967; Powell 1993; Frost et al. 1997). The total pregnancy lasts between 327 and 358 days, about the same as that of the blue whale (Hayssen et al. 1993).

The adaptive advantage of delayed implantation is poorly understood (King 1984). Two closely related species of weasels residing in the same habitat may exhibit very different reproductive patterns. For example, in eastern North America, the long-tailed weasel (*Mustela frenata*) and the least weasel (*M. nivalis*) may occupy the same habitat, but the former demonstrates delayed implantation, and the latter does not. Many mammalogists believe that by delaying the arrival of the young until spring, when hunting is easiest

because small mammals are plentiful, the long-tailed weasel optimizes the likelihood of survival of its young. But why does the smaller least weasel not show such a delay?

The nine-banded armadillo (*Dasypus novemcinctus*) of the New World is another interesting example of variation in reproductive biology (Prodohl et al. 1996). Armadillos in the southern United States breed in July or August. Their copulatory position is rather unusual for a quadruped mammal—the female assumes a mating position on her back. Implantation is delayed until November, followed by a gestation period of about 4 months. In late February, the litter is born and comprises identical quadruplets, all of one sex; they all come from a single fertilized ovum—a phenomenon called **monozygotic polyembryony**—and all the young have exactly the same genetic makeup. Delayed implantation in this case seems to serve to time the birth of the litter for the spring flush of invertebrate food—the staple in the diet of armadillos (Lowery 1974).

EMBRYONIC DIAPAUSE

Many marsupials undergo a condition called **embryonic diapause** in which the blastocyst enters a state of dormancy; during this time division and growth of the cells may cease or continue at a slow pace until a signal is received from the mother (Renfree and Shaw 2000; Tyndale-Biscoe, 2005; Oates et al. 2007). Embryonic diapause is similar to the process of delayed implantation for placental mammals. Among marsupials, embryonic diapause is reported to occur in almost all kangaroos, wallabies, rat-kangaroos, pygmy possums, feathertail gliders (*Acrobates pygmaeus*) and honey possums (*Tarsipes rostratus*). Western gray kangaroos (*Macropus fuliginosus*), Lumholtz's tree kangaroos (*Dendrolagus lumholtzi*), and musky rat kangaroos (*Hypsiprymnodon moschatus*) are not known to exhibit embryonic diapause. Endocrine control of embryonic diapause has been intensively studied in the tammar wallaby (*Macropus eugenii*) (Sharman and Berger 1969; Tyndale-Biscoe and Renfree 1987; Gordon et al. 1988; Tyndale-Biscoe 2005).

Embryonic diapause is common in red kangaroos (*Macropus rufus*), residents of arid regions of Australia (Figures 9.21 and 9.22). Both red kangaroos and euros (= common wallaroos, *M. robustus*) are opportunistic breeders—that is, reproduction is finely tuned to climatic changes. At a given time, an adult female red kangaroo simultaneously nourishes three young (called "joeys"): (1) one "weaned" joey that runs at the heel of the mother and occasionally suckles from an elongated teat from outside the pouch; (2) a nursing, pouch young attached to another teat inside the pouch, and (3) a tiny blastocyst lodged in one of the two uteri of the female (see Figure 9.22). For red kangaroos, the first pregnancy of the season is followed by a gestation period of about 33 days. The joey is born in a very altricial state yet makes its way to the pouch and attaches to a nipple. Under favorable conditions, adult females will breed continuously throughout the year. The presence of the suckling
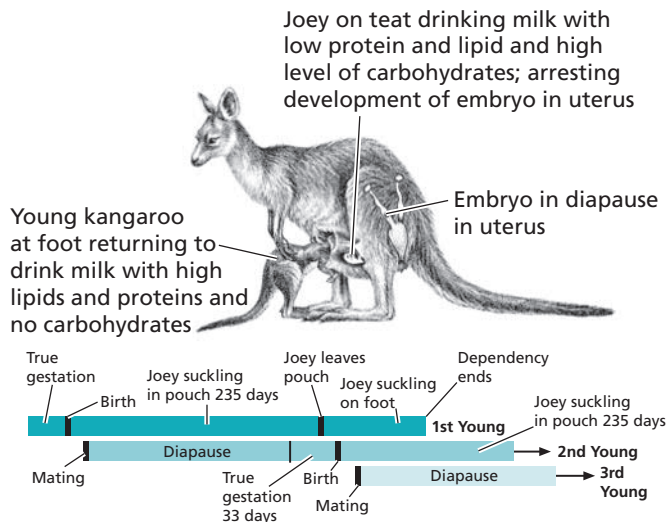
Figure 9.21 Embryonic diapause. Illustration showing embryonic diapause in the red kangaroo (*Macropus rubrus*). The complex reproductive pattern of many kangaroos may result in having three young in different stages of development dependent on the mother at one time.

Figure 9.22 Red kangaroo. The red kangaroo (*Macropus rufus*) is the largest member of the family Macropodidae. In these arid-adapted kargaroos, green herbage determines the proportion of females that breed and the survival of their young. This species and other species of kangaroos and wallabies undergo embryonic diapause, a period of arrested development of an embryo at the stage of the blastocyst (70- to 100-cell stage).

young causes the development of the new embryo to be arrested between the 70- and 100-cell stage. This period of embryonic diapause may last about 240 days, during which time the joey is growing in the pouch (Dawson 1995; Tyndale-Biscoe 2005). When the young at foot is about 1 year old, it is fully weaned yet still associates with its mother. When the young in the pouch reaches 200 days of age, development of the blastocyst resumes, and it is born soon after the older joey has been permanently excluded from the pouch. At this point, the mother may again mate and be-

come pregnant; however, because of suckling of the new pouch joey, the development of the new embryo is arrested. If the pouch young dies, normal embryonic development of the blastocyst resumes almost immediately so that a new individual is born about a month later.

Red kangaroos are commonly faced with extreme drought and dwindling supplies of green herbage, which greatly influence their reproductive activity. Young on the foot are first to feel the stress of drought. Their diet is changing from mother's milk to herbage; they exhibit a very high metabolism (twice as high as the mothers) and pronounced evaporative heat loss when exposed to high summer temperatures (Munn and Dawson 2001). Moreover, during periods of drought in which forage is low in protein and water, young kangaroos cannot meet their energy needs and mothers are not able to provide sufficient milk for their rapidly growing young. At such times, young at the foot may perish; however, the mother still carries a small joey in the pouch. As the drought continues, her late stages of milk production will decline, and the pouch young may die. The loss of the pouch young triggers the development of the uterine blastocyst. If the drought persists, she may produce a succession of young that she cannot nourish in the pouch. If the drought lasts for more than 6 months, red kangaroos and euros will eventually cease to breed altogether (Sharman 1963; Sharman and Clark 1967; Tyndale-Biscoe 2005). However, if rain occurs and plants grow, the milk production of the mother will increase, and the young will continue to develop to the end of the pouch life.

The reproductive plasticity in the form of embryonic diapause of red kangaroos and euros is truly remarkable—females breed well into a drought and can take immediate advantage of any improvement in climatological conditions shortly after they occur. This turnaround time is rapid; euros and red kangaroos are reported to have small young in their pouches very soon after the drought breaks (Tyndale-Biscoe 2005).

The suite of reproductive interactions outlined here is induced by the joey, whose suckling produces nervous stimulation of the hypothalamus. As a result, release of FSH and LH by the pituitary gland is inhibited, thereby reducing follicular development and subsequent ovulation. The production of estrogen and progesterone by the corpus luteum is suppressed by the increase in prolactin. Red kangaroos represent an excellent example of **biological control** of reproductive output—the suckling joey represents the proximate cause of embryonic diapause, yet the ultimate controls are the selective pressures exerted by the environment.

Parturition

Before we begin our discussion of parturition, reviewing some terms concerning the developmental stages of young will be helpful. Newborn mammals can be categorized into

two groups based on their degree of development. **Altricial** young are born hairless, blind, and essentially helpless. Rabbits, carnivores, and many rodents bear altricial young. **Precocial** young are born fully haired, with eyes open, and are able to get up and walk around shortly after birth. Good examples of precocial young are hares, many large grazing mammals (the ungulates), cetaceans, hyraxes, some rodents, and some primates.

Parturition, or birth, results when the fetus has completed its period of intrauterine growth. The mechanisms that act to terminate gestation and initiate parturition vary among species, are complex, and are not well understood (Gordon 1982; Pough et al. 1996). During the last part of gestation, the adrenal gland of the fetus begins to secrete **adrenocortical hormones**, such as **cortisol**, which initiates parturition. At this time, the placental secretions of estrogen increase and progesterone decreases. As a result of these hormonal changes, the placenta produces hormones called **prostaglandins**, which increase contractions of the uterus. The pressure of the fetus on the cervix then stimulates production of the hormone **oxytocin**, which is produced by the posterior pituitary gland. Oxytocin also increases uterine contractions and stimulates milk "letdown." **Relaxin**, a hormone produced by the corpora lutea, softens the ligaments of the pelvis so it can spread to allow the fetus to pass through the birth canal. After dilation of the vagina, rhythmic contractions of the uterus gradually force the fetus through the vagina to the outside. If the fetal membranes are not ruptured in the birth process, the mother tears them from the young, thus permitting the newborn to breathe. The mother usually severs the umbilical cord and consumes the placenta.

Lactation

DEFINITION AND PHYSIOLOGY

Lactation, the production of milk by the mammary glands, is the quintessential feature of Class Mammalia and is a crucial element in the life-history strategies of all mammals whether monotreme, marsupial, or eutherian. Lactation has an ancient origin and long evolutionary history (Hayssen and Blackburn 1985; Oftedal 2011). Probably the most well-known characteristic of a mammal is its **mammae** or breasts—the word *mammal* is derived from the Latin word *mammalis*, meaning **breasts**. In females, these specialized skin glands produce milk to nourish the young; in males, they are usually rudimentary and nonfunctional. It is noteworthy, however, that lactation in males has been reported in a population of Dayak fruit bats (*Dyacopterus spadiceus*) from Malaysia (Francis et al. 1994).

Although the process is more complicated than we can cover here, lactation, like the estrous cycle, pregnancy, and parturition, is regulated by hormones as well as the presence of the suckling young. During pregnancy, high levels of the ovarian hormones estradiol and progesterone circulate in the blood and cause enlargement of the mammary glands, making them structurally ready to secrete milk. The actual production of milk does not take place until after parturition. Following parturition and the expulsion of the placenta, the estradiol concentration in the blood decreases. This decrease, in turn, signals the **anterior pituitary gland** to secrete the **lactogenic hormone**, or **prolactin.** Prolactin stimulates milk production but does not by itself cause the delivery, or letdown, of milk. Suckling by the newborn stimulates nerve receptors in the nipples. This information is transmitted to the hypothalamus and then to the posterior pituitary gland. This gland then releases oxytocin, the same hormone that is associated with uterine contractions during birth. Oxytocin stimulates the alveoli of the breasts to eject milk into the ducts, thus enabling the newborn to remove the milk by suckling. Prolactin is also important in inducing maternal behavior in females and, interestingly, sometimes in males.

COMPOSITION OF MILK

Milk contains fats, proteins (especially casein), and **lactose** (or milk sugar), as well as vitamins and salts. It provides nutrition for the growth of the newborn, transmits passive immunity, and may support the growth of symbiotic intestinal flora (Jensen 1995). The first product released by the mammary gland following birth is called **colostrum**, a protein-rich fluid containing antibodies that confer the mother's immunity to various diseases to the young. Other important milk proteins, such as **lysozyme** and **interleukin**, are present in milk throughout lactation. Lysozyme is reported to kill bacteria and fungi, protecting young animals from infection. The composition of milk varies greatly among groups of mammals (Jenness and Studier 1976; Oftedal 1984; Oftedal et al. 1987, 1988, 2000; Hayssen 1993; Kunz and Stern 1995; Riet-Sapriza et. al. 2012; Hood et al. 2014; Power et al. 2018). Mammals residing in northern environments have extremely high-fat, high-protein milk. The young of these species must increase weight rapidly to combat the cold after they are weaned and disperse. The milk of whales and seals, for example, may contain 40%–61% fat and 11%–12% protein—some milks are 12 times higher in fats and 4 times richer in protein than that of the domestic cow (Iverson 1993; Jensen 1995; Boness and Bowen 1996; Iverson et al. 1997; Mellish et al. 1999; Donohue et al. 2002; Riet-Sapriza et al. 2012). Thus, the milk of the hooded seal (*Cystophora cristata*) contains about 61% fat and 11% protein, and as a result, pups may gain 20.5 kg in their short 4-day nursing period (Bowen et al. 1985). The extent to which young depend on milk for nutrition also varies greatly. Rodents, such as voles and mice, and ground squirrels rely entirely on milk until they are weaned (Oswald and McClure 1990; Rogowitz 1998; Skibiel and Hood 2013). In contrast, many young ungu-
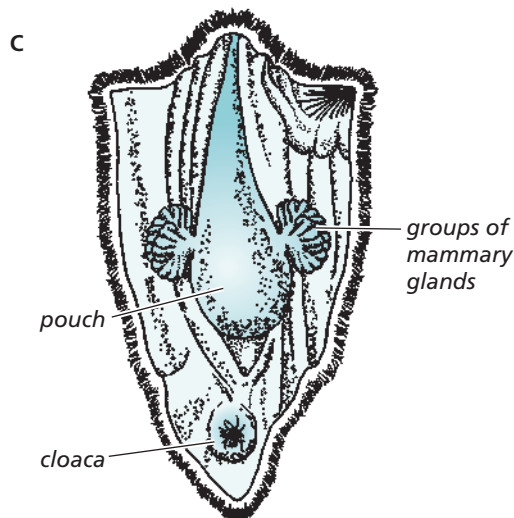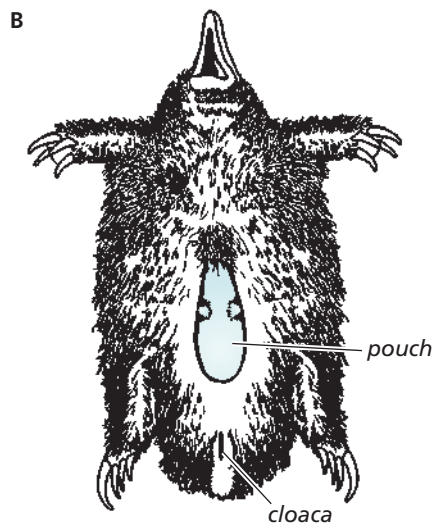
Figure 9.23 **An egg-laying mammal.** (**A**) Photograph of a young echidna between 2 and 4 months of age; (**B**) lower surface of brooding female; (**C**) dissection showing a dorsal view of the pouch, mammary glands, and two tufts of hair in the lateral folds of the mammary pouch from which the secretion flows. *Adapted from Nowak (1991).*

lates, such as New World deer (Genus *Odocoileus*), consume grass only a few days after birth, well before weaning occurs. Marsupials, bats, and primates have periods of lactation that are 50% longer than those of other mammals of similar body size (Hayssen et al. 1993; Hayssen and Kunz 1996). In many species of mammals, the composition of milk changes during the course of lactation. Milk that is produced during early stages of lactation and as weaning approaches often possesses more protein and less sugar than that delivered to young during the interim stages.

In addition to producing milk with different nutritive values, red kangaroos and wallaroos (Genus *Macropus*) may produce two milks of completely different characteristics at the same time (Dawson 1995; Tyndale-Biscoe 2005). During the earlier discussion of embryonic diapause in red kangaroos, we noted that the mother could simultaneously have two young, widely separated in age, both feeding on her milk. Because each joey has different requirements for nourishment, the mother must produce two different kinds of milk—two active teats are required for the nursing young. Oxytocin, the milk-letdown hormone, is elicited by different suckling stimuli. The first kind of milk is very dilute and is secreted for the newborn joey that exerts a slight sucking pressure. This young requires little nourishment as it is growing slowly and its metabolic rate is low. As this youngster develops and subsequently is at foot, it requires a more concentrated milk and higher levels of protein to meet its energy demands for thermoregulation and to support its rapid growth rate. Early milk of kangaroos is more dilute than that of humans' or cows' milk, while late-stage milk of kangaroos is similar to that of seals.

All female mammals except the monotremes (platypus and echidnas) have teats, or nipples, to facilitate the transfer of milk to the young, but their arrangement and number vary greatly. Female echidnas (Genera *Tachyglossus* and
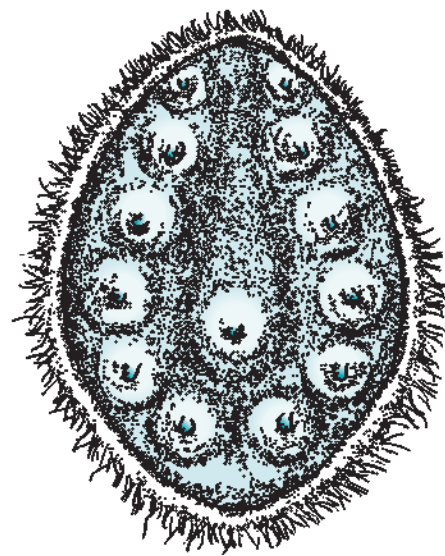
Figure 9.24 **The marsupium.** The opened pouch of the Virginia opossum has a horseshoe-shaped arrangement of mammae. *Adapted from Merritt (1987).*

Zaglossus) typically lay a single egg that is transferred from the cloaca directly into the abdominal pouch, where it is incubated for about 10 days (Figure 9.23). Because platypuses (*Ornithorhynchus anatinus*) do not have pouches, they keep their eggs (usually 2, each about the size of a robin's egg) in a nest within a burrow, where they are incubated for about 2 weeks. Meanwhile, the embryo is nourished from the yolk. Because monotremes lack true nipples, after "hatching" the young (about the size of a raisin) suck milk that drains from the mother's mammary glands onto tufts of hair located on her abdomen, or in the pouch in the case of the echidna. In monotremes, the milk flows from pores in the skin rather than from nipples.

Marsupials generally have a circular arrangement of nipples in a pouch. The opossum has 13 nipples: 12 arranged in a U-shape, and the 13th located in the center (Figure 9.24; also see Figure 10.12). The numbers of mammary glands or teats also vary among groups of mammals and are usually correlated with the size of the litter. The number of mammary glands ranges from 2 in many species of mammals to 29 in the tailless tenrec (*Tenrec ecaudatus*) of Madagascar. This latter species may be the most prolific mammal, with litters of as many as 32 young, but the average litter is between 15 and 20 (Louwman 1973; Eisenberg 1975; Nicoll 1983; Nicoll and Racey 1985). As mentioned earlier, naked mole-rats are a rival in maximizing fecundity (Sherman et al. 1999). Eutherian mammals typically have mammae arranged in two longitudinal ventral rows. Domestic pigs have large litters and, hence, have two rows of teats spanning all the way from near the forelimbs to between the hind limbs. Primates possess a pair of pectoral mammae, and horses have a pair of abdominal teats. The length of lactation varies greatly among mammals, ranging from only 4 days in hooded seals to more than 900 days in orangutans (*Pongo pygmaeus*). The record for "fastest developer" goes to the streaked tenrec (*Hemicentetes semispinosus*), whose young are weaned in about 5 days and begin breeding as early as 3–5 weeks of age (Hayssen et al. 1993; Sherman et al. 1999).

SUMMARY

- Mammals reproduce sexually, and fertilization is internal.
  - In the **male reproductive system,** the testes function to produce sperm (the male gametes) and to synthesize the male sex hormone (testosterone).
  - Testes in mammals are oval-shaped and may or may not be suspended in a pouch-like sac called a "scrotum."
  - Sperm are produced in the seminiferous tubules of the testes and travel by a series of ducts.
  - The ducts receive glandular secretions to the spermatozoa to form semen, which passes from the body via a canal (the urethra) into the highly vascular, erectile penis.

- The female reproductive system consists of a pair of ovaries that produce the ova and the female hormones, estrogen and progesterone.
  - Ovulation occurs when the follicle housing the ovum within the ovary bursts, releasing the egg into the oviduct.
  - The development of follicular cells is precipitated by the follicle-stimulating hormone and the luteinizing hormone produced by the anterior pituitary gland.
  - Follicular cells secrete estradiol (a form of estrogen), which causes a thickening of the endometrium in preparation for implantation of the egg.
  - Ovulation is induced by high levels of luteinizing hormone. Stimulation of corpora luteum development is accomplished by luteinizing hormone.
  - The corpus luteum, from the follicular cells, produces the hormone progesterone, which combines with estrogens to promote the growth of the uterine lining and makes possible the implantation of the fertilized egg.

- Progesterone also stimulates mammary gland development and maintenance of pregnancy.

- Estrus, or heat, represents the period of receptivity to copulation shortly before and after ovulation.

- Ovulation may be spontaneous, as in most mammals, or induced, as in rabbits, many carnivores, and some ground squirrels.

- The female duct system consists of paired oviducts, one or two uteri, one or two cervices, and the vagina.
  - Much variation occurs in this system among mammals.
  - Four principal types of uteri based on the relationship of the uterine horns exist: duplex, bipartite, bicornuate, and simplex.
  - Implantation occurs when the embryo attaches to the endometrium, or the lining of the uterine wall.
  - The highly vascular endometrium passes nutrients and gases to and receives wastes from the extraembryonic tissues, which are called the "placenta."
  - The relationship of the yolk sac to the developing embryo is the means of categorizing all mammalian placentas as either choriovitilline (most marsupials) or chorioallantoic (the bandicoots and all eutherian mammals).
  - Placentas can also be classified by distribution of villi; speed and efficiency of exchange of nutrients, oxygen, and waste materials; and the intimacy of the placenta with the uterine wall.

- The period from fertilization until birth of the young is called "gestation."

∘ Ovulation has a relatively low energetic cost (Bronson 1985; Bronson and Manning 1991); however, late gestation and especially lactation increase energy demand, especially for large litters (Moen 1978; Oftendal 1985; Mauget et al. 1999).

∘ The gestation period for marsupials is short, and lactation is protracted, whereas the reverse is true for eutherian mammals.

∘ Typically, variation in the length of gestation is correlated with body mass, the number of young per litter, and the degree of development of the young.

∘ Larger animals tend to have longer periods of gestation.

• Modifications in the length of fertilization or gestation, however, are exhibited by many mammals.

∘ These reproductive variations include delayed fertilization (in bats of temperate zones), delayed development (in some bats in Neotropical areas), delayed implantation (in some insectivores, rodents, bears, weasels and allies, seals, armadillos, and roe deer), and embryonic diapause (in kangaroos and some wallabies).

• Parturition, or birth, occurs when the fetus has completed its period of intrauterine growth.

∘ The degree of development of the newborn may be altricial or precocial.

∘ Processes associated with parturition are influenced by a variety of hormones, including oxytocin and relaxin.

• The production of milk to nurse the newborn is called "lactation" and is aided by the hormones oxytocin and prolactin.

∘ Milk is composed of fats, proteins, and milk sugar.

∘ The composition of milk varies greatly among mammals, ranging from only 0.2% fat in black rhinos (*Diceros bicornis*) to as high as 61% fat in hooded seals (*Cystophora cristata*).

∘ Kangaroo mothers may produce two kinds of milk to nurse two joeys of differing ages.

• The number of mammae also varies greatly in mammals, ranging from 2 in many species to 29 in the tailless tenrec (*Tenrec ecaudatus*).

• Monotremes do not have true nipples or mammae.

∘ Their young suck milk that drains from mammary glands onto tufts of hair on the mother's abdomen.

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DISCUSSION QUESTIONS

1. Trace the movement of spermatozoa from their origin and development in the seminiferous tubules of the testes to release at the penis.

2. Describe and give the function(s) of the following structures of the female reproductive system: ovaries, uterus, vagina, and mammary glands. How do these structures vary among monotremes, marsupials, and eutherian mammals?

3. Describe and distinguish the patterns in reproduction in monotremes, marsupials, and eutherian mammals. What aspects of reproduction are universal in Class Mammalia but not found in other vertebrates?

4. What reproductive attributes enhance survival of young residing in northern environments? List some such species, and state how the female makes physiological adjustments to enhance the survival of her young.

5. Delayed implantation is a common reproductive phenomenon for members of the Family Mustelidae (weasels and allies). The occurrence of this reproductive strategy varies widely among closely related species residing in similar environments. How can you explain this disparity, and how does it fit with the theory of natural selection?

6. Many mammals such as the opossum are known to produce more young that can be supported by the number of the mother's mammae. This attribute seems maladaptive. Explain this apparent waste of energy.

PART 3

Adaptive Radiation and Diversity

We discussed aspects of the diversity of structure and function in mammals in Part 2. In this part, which includes Chapters 10 through 21, we explore the life-history characteristics, morphology, fossil history, and conservation of living orders and families of mammals. There are about 6,400 extant mammalian species currently recognized throughout the world (Burgin et al. 2018). Traditionally, 10,000 species of birds have been recognized, but new research suggests there may be as many as 18,000 (Barrowclough et al. 2016). There are about 33,000 species of fishes. The number of vertebrate species is small compared with the 85,000 species of living mollusks, or the estimated tens of millions of species of insects.

Structurally and functionally, however, mammals are quite diverse. Consider the difference in size between the smallest and largest living species of birds. The largest, heaviest bird is the ostrich (*Struthio camelus*); adults weigh about 135 kg. The smallest hummingbirds (Family Trochilidae) weigh about 3 g (or 0.003 kg). Although this is a difference of 4.5 orders of magnitude, consider the mass difference between the largest mammal, a blue whale (*Balaenoptera musculus*), at about 160,000 kg (160,000,000 g), and one of the smallest mammals, either a pygmy shrew (*Sorex hoyi*) or Etruscan shrew (*Suncus etruscus*) at about 3 g—a range of over 7 orders of magnitude. Body size is just one characteristic that results from numerous selective factors operating through evolutionary time. In Part 3, we highlight not only the pronounced differences in structural and functional adaptations within the various mammalian orders but also the many examples of parallel or convergent evolutionary adaptations evident among phylogenetically distant groups. Environmental constraints force many otherwise unrelated taxa to adapt to similar problems in similar ways and, through time, to develop similar morphological features.

Classification

Class Mammalia is divided into 2 Subclasses of extant taxa, based primarily on reproductive characteristics: Prototheria and Theria. Prototherians are a small group of only 4 or 5 living species in Order Monotremata. Therians make up the vast majority of mammals, and are divided into 2 Infraclasses: the metatherians and the eutherians. Metatherians are more commonly referred to as "marsupials," whereas eutherians are typically called "placental" mammals. The approximately 330 extant species of marsupials, along with the monotremes, make up about 6% of the world's mammalian fauna. The remainder is made up of eutherians.

Numerous new mammalian species have been described since 1990. Taxonomic revisions have been based on a variety of genetic techniques as well as morphological approaches, and the number of recognized extant species has increased from about 4,600 in 1993 to 6,400 in 2018. Also, the enormous amount of taxonomic work during this period has resulted in some major revisions to orders and families (Table 10.1). The conservation status of species noted in the text as being considered **endangered** (defined as in danger of extinction and whose survival is unlikely if causal factors continue) or **threatened** (i.e., vulnerable, and likely to move into the endangered category in the near future if causal factors continue) is taken from the International Union for Conservation of Nature and Natural Resources (IUCN) Red Data List (2018), at www.iucnredlist.org.

Table 10.1 Class Mammalia		
Subclass Prototheria		
Order Monotremata		
Families	Ornithorynchidae	Duck-billed platypus
	Tachyglossidae	Echidnas
Subclass Theria		
(Infraclass Metatheria)		
Superorder Ameridelphia		
Order Didelphimorphia		
Family	Didelphidae	American opossums
Order Paucituberculata		
Family	Caenolestidae	Shrew or rat opossums
Superorder Australidelphia		
Order Microbiotheria		
Family	Microbiotheriidae	Monito del monte
Order Dasyuromorphia		
Families	Myrmecobiidae	Numbat
	Dasyuridae	Marsupial mice, Tasmanian devil
	Thylacinidae (recently extinct)	Thylacine
Order Peramelemorphia		
Families	Peramelidae	Bandicoots and echymiperas
	Thylacomyidae	Bilbies
	Chaeropodidae (recently extinct)	Pig-footed bandicoot
Order Diprotodontia		
Families	Phascolarctidae	Koala
	Vombatidae	Wombats
	Burramyidae	Pygmy possums
	Phalangeridae	Cuscuses, brushtail possums
	Acrobatidae	Feathertail glider, feathertail possum
	Tarsipedidae	Honey possum
	Petauridae	Striped possum, gliding possum
	Pseudocheiridae	Ringtail possums
	Hypsiprymnodontidae	Musky rat-kangaroo
	Potoroidae	Potoroos, bettongs
	Macropodidae	Kangaroos, wallabies, pademelons
Order Notoryctemorphia		
Family	Notoryctidae	Marsupial moles
(Infraclass Eutheria)		
Superorder Afrotheria		
Order Afrosoricida		
Suborder Tenrecomorpha		
Families	Tenrecidae	Tenrecs, shrew tenrecs
	Potamogalidae	Otter shrews

Suborder Chrysochloridea		
Family	Chrysochloridae	Golden moles
Order Macroscelidea		
Family	Macroscelididae	Sengis
Order Tubulidentata		
Family	Orycteropodidae	Aardvark
Order Hyracoidea		
Family	Procaviidae	Hyraxes
Order Proboscidea		
Family	Elephantidae	Elephants
Order Sirenia		
Families	Dugongidae	Dugong
	Trichechidae	Manatees

Superorder Xenarthra
Order Cingulata		
Families	Dasypodidae	Long-nosed armadillos
	Chlamyphoridae	Other armadillos
Order Pilosa		
Families	Bradypodidae	Three-toed sloths
	Megalonychidae	Two-toed sloths
	Myrmecophagidae	True anteaters
	Cyclopedidae	Silky anteater

Superorder Euarchontoglires
Grandorder Archonta
Order Scandentia		
Families	Ptilocercidae	Pen-tailed treeshrew
	Tupaiidae	Treeshrews
Order Dermoptera		
Family	Cynocephalide	Colugos
Order Primates		
[Suborder Strepsirrhini]		
Families	Cheirogaleidae	Dwarf lemurs, mouse lemurs
	Lemuridae	Lemurs
	Lepilemuridae	Sportive lemurs
	Indriidae	Indrid lemurs, sifakas
	Daubentoniidae	Aye-aye
	Lorisidae	Lorises, potto
	Galagidae	Bushbabies, galagos
[Suborder Haplorrhini]		
Families	Tarsiidae	Tarsiers
	Cebidae	New World monkeys
	Aotidae	Night monkeys
	Callitrichidae	Tamarins and marmosets
	Pitheciidae	Titis, sakis
	Atelidae	Howler monkeys
	Cercopithecidae	Old World monkeys
	Hylobatidae	Gibbons, siamang
	Hominidae	Gorilla, chimpanzees, orangutan, humans

Grandorder Glires
Order Lagomorpha		
Families	Ochotonidae	Pikas
	Leporidae	Rabbits, hares
Order Rodentia		
[Suborder Castorimorpha]		
Families	Castoridae	Beavers
	Geomyidae	Pocket gophers
	Heteromyidae	Kangaroo rats, kangaroo mice
[Suborder Myomorpha]		
Families	Dipodidae	Jerboas
	Zapodidae	Jumping mice
	Sminthidae	Birch mice
	Platacanthomyidae	Spiny mice, soft-furred tree mice
	Spalacidae	Zokors, bamboo rats, blind mole-rats
	Calomyscidae	Mouse-like hamsters
	Nesomyidae	Madagascar rats and mice
	Cricetidae	Voles, mice
	Muridae	Old World rats and mice

(continued)

[Suborder Anomaluromorpha]			
Families		Anomaluridae	Scaly-tailed squirrels
		Pedetidae	Springhares
[Suborder Hystricomorpha]			
Families		Ctenodactylidae	Gundis
		Diatomyidae	Laotian rock rat
		Bathyergidae	Mole-rats
		Hystricidae	Old World porcupines
		Petromuridae	Dassie rat
		Thryonomyidae	Cane rats
		Erethizontidae	New World porcupines
		Chinchillidae	Viscachas, chinchillas
		Dinomyidae	Pacarana
		Caviidae	Cavies, Patagonian "hare," guinea pigs, capybara
		Dasyproctidae	Agoutis, acouchis
		Cuniculidae	Pacas
		Ctenomyidae	Tuco-tucos
		Octodontidae	Viscacha rats, coruro
		Abrocomidae	Chinchilla rats
		Echimyidae	Spiny rats
		Capromyidae	Hutias
		Heptaxodontidae (recently extinct)	Giant hutias
[Suborder Sciuromorpha]			
Families		Aplodontiidae	Mountain beaver
		Sciuridae	Squirrels
		Gliridae	Dormice

Superorder Laurasiatheria
Grandorder Lipotyphla

Order Eulipotyphla			
Families		Solenodontidae	Solenodons
		Soricidae	Shrews
		Talpidae	Moles, shrew-moles, desmans
		Erinaceidae	Hedgehogs, gymnures

Grandorder Ferae

Order Carnivora			
Suborder Feliformia			
Families		Felidae	Cats
		Herpestidae	Mongooses
		Hyaenidae	Hyenas, aardwolf
		Viverridae	Civets, genets
		Nandiniidae	African palm civet
		Prionodontidae	Linsangs
		Eupleridae	Madagascar mongooses
Suborder Caniformia			
Families		Canidae	Dogs, foxes, wolves
		Ursidae	Bears
		Mustelidae	Weasels, otters, badgers
		Mephitidae	Skunks
		Odobenidae	Walrus
		Otariidae	Eared seals
		Phocidae	Earless seals
		Procyonidae	Raccoon, coati
		Ailuridae	Red panda
Order Pholidota			
Family		Manidae	Scaly anteaters (pangolins)

Grandorder Euungulata

Order Perissodactyla			
Families		Equidae	Horses, asses, zebras
		Tapiridae	Tapirs
		Rhinocerotidae	Rhinoceroses
Order Cetartiodactyla			
[Suborder Suiformes]			
Families		Suidae	Pigs, warthogs
		Tayassuidae	Peccaries
[Suborder Tylopoda]			
Family		Camelidae	Camels, llamas

[Suborder Ruminantia]		
Families	Tragulidae	Chevrotains
	Giraffidae	Giraffe, okapi
	Moschidae	Musk deer
	Cervidae	Deer
	Antilocapridae	Pronghorn antelope
	Bovidae	Antelope, sheep, goats, bison, cattle
[Suborder Whippomorpha]		
Family	Hippopotamidae	Hippopotamuses

Infraorder Cetacea
Parvorder Mysticeti

Families	Balaenidae	Bowhead whale, right whales
	Balaenopteridae	Rorquals
	Eschrichtiidae	Gray whale
	Neobalaenidae	Pygmy right whale

Parvorder Odontoceti

Families	Delphinidae	Dolphins
	Monodontidae	Narwhal, beluga
	Phocoenidae	Porpoises
	Physeteridae	Sperm whale
	Kogiidae	Pygmy whale, dwarf sperm whale
	Platanistidae	South Asian river dolphin (susu)
	Iniidae	South American river dolphin (boto)
	Lipotidae	Chinese river dolphin (baiji)
	Pontoporiidae	La Plata river dolphin (franciscana)
	Ziphiidae	Beaked whales

Grandorder Chiroptera
Order Chiroptera
[Suborder Yinpterochiroptera]

Families	Pteropodidae	Old World fruit bats
	Hipposideridae	Leaf-nosed bats
	Rhinonycteridae	Trident bats
	Rhinolophidae	Horse-shoe bats
	Rhinopomatidae	Mouse-tailed bats
	Craseonycteridae	Kitti's hog-nosed bat
	Megadermatidae	False vampire bats
[Suborder Yangochiroptera]		
Families	Emballonuridae	Sac-winged, or sheath-tailed, bats
	Nycteridae	Slit-faced bats
	Mystacinidae	Short-tailed bats
	Thyropteridae	Disk-winged bats
	Furipteridae	Smoky bats
	Noctilionidae	Fishing bats
	Mormoopidae	Leaf-chinned bats
	Phyllostomidae	New World leaf-nosed bats
	Myzopodidae	Sucker-footed bats
	Natalidae	Funnel-eared bats
	Molossidae	Free-tailed bats
	Miniopteridae	Long-fingered bats
	Cistugidae	Wing-gland bats
	Vespertilionidae	Common bats

TOTAL: Orders = 27; Extant Families = 156

CHAPTER 10

Orders: Monotremata and Marsupials

Monotremes and marsupials can be distinguished from eutherian mammals (or "placentals" as they are commonly called) on the basis of reproductive characteristics. Monotremes are the only extant mammals that are **oviparous**. Like birds and some other vertebrates, they lay eggs. Marsupials give birth to live young (they are **viviparous**) but are characterized by a very brief intrauterine **gestation** period. This results in reduced parental "investment," in terms of energy expenditure, in **neonates** (newborns). Maternal investment in lactation is high, however. In this chapter, we explore various aspects of form and function in these two lineages.

Monotremata

As noted in Chapter 4, mammals evolved from synapsid ancestors that appeared in the Carboniferous period. Monotremes (Subclass Prototheria) differ significantly from marsupials and eutherians (Subclass Theria) in their retention of various ancestral synapsid features. Extant monotremes are represented by two families (Figure 10.1). The Ornithorhynchidae is **monotypic** (a group that includes a single taxon) and includes only the duck-billed platypus (*Ornithorhynchus anatinus*). The Family Tachyglossidae includes the short-beaked echidna (*Tachyglossus aculeatus*) and the western long-beaked echidna (*Zaglossus bruijni*). Two additional species in New Guinea, the eastern long-beaked echidna (*Z. bartoni*) and Sir David's long-beaked echidna (*Z. attenboroughi*), were recognized by Flannery and Groves (1998) based on characteristics of the claws and cranium, with the latter species described from a single specimen collected in the Cyclops Mountains of Papua in 1961. Although no additional specimens were collected during a 2007 survey, Baillie and colleagues (2009) suggested that a population of *Z. attenboroughi* remains. However, the single specimen collected to date may be just an unusual morphologic variant of *Z. bartoni*.

The ordinal name Monotremata ("one opening") refers to the **cloaca**, a common opening for the fecal, urinary, and reproductive tracts. The most notable ancestral feature of monotremes is the structure of their reproductive tract and the fact that young hatch from small, somewhat rubbery-shelled eggs. The female reproductive tract includes separate uteri with large ovaries that produce large follicles during the breeding season (Figure 10.2). The uteri have separate openings into the urogenital sinus that leads to the cloaca. After an egg is shed into the infundibulum, it passes to the fallopian tube, where fertilization occurs. The shell is deposited in the oviduct over a period of about two weeks and is composed of three iden-

tifiable layers (see Griffiths 1978, 1989 for details). Nutrient material is absorbed through the shell. The early cleavage stages of the egg are **meroblastic**, that is, restricted to the anterior end (as opposed to holoblastic in which cleavage occurs throughout). The first cleavage furrow divides the germinal disk into two areas of unequal size. The second cleavage is perpendicular, so that at the four-cell stage, two large cells and two small cells (**blastomeres**) occur on the top of the yolk. Meroblastic eggs also occur in reptiles and birds.

Monotreme eggs are small, about 16 mm long and 14 mm wide. They are incubated for 10–11 days. During the final stages of incubation, a sharp egg tooth forms at the end of the snout of a developing young, which it uses to free itself from the egg, again as in birds and reptiles. Neonatal monotremes are structurally similar to newborn marsupials (Griffiths 1989). Development in both is rudimentary, although the forelimbs and shoulder muscles are well developed. Once eggs hatch, as in all other mammals, the young are nursed. Monotremes have mammary glands, but unlike other mammals, they have no teats. Milk is secreted from pores on the belly of the platypus and from paired glandular lobes in the pouch of echidnas. The structure of the mammary glands is identical in monotremes and marsupials (Griffiths et al. 1973), and the process of lactation in monotremes is as "sophisticated and highly evolved" (Griffiths 1989:424) as in any other mammal.
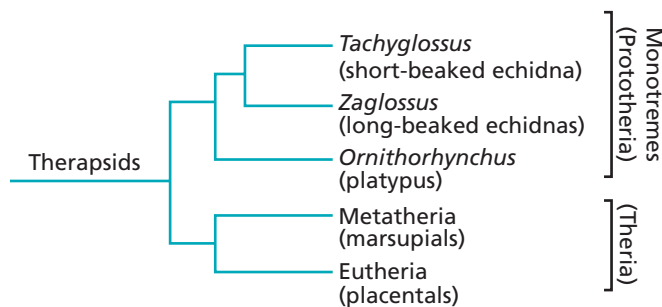
Figure 10.1 Monotreme phylogeny. *Redrawn and adapted from Westerman and Edwards (1992) and Warren et al. (2008).*
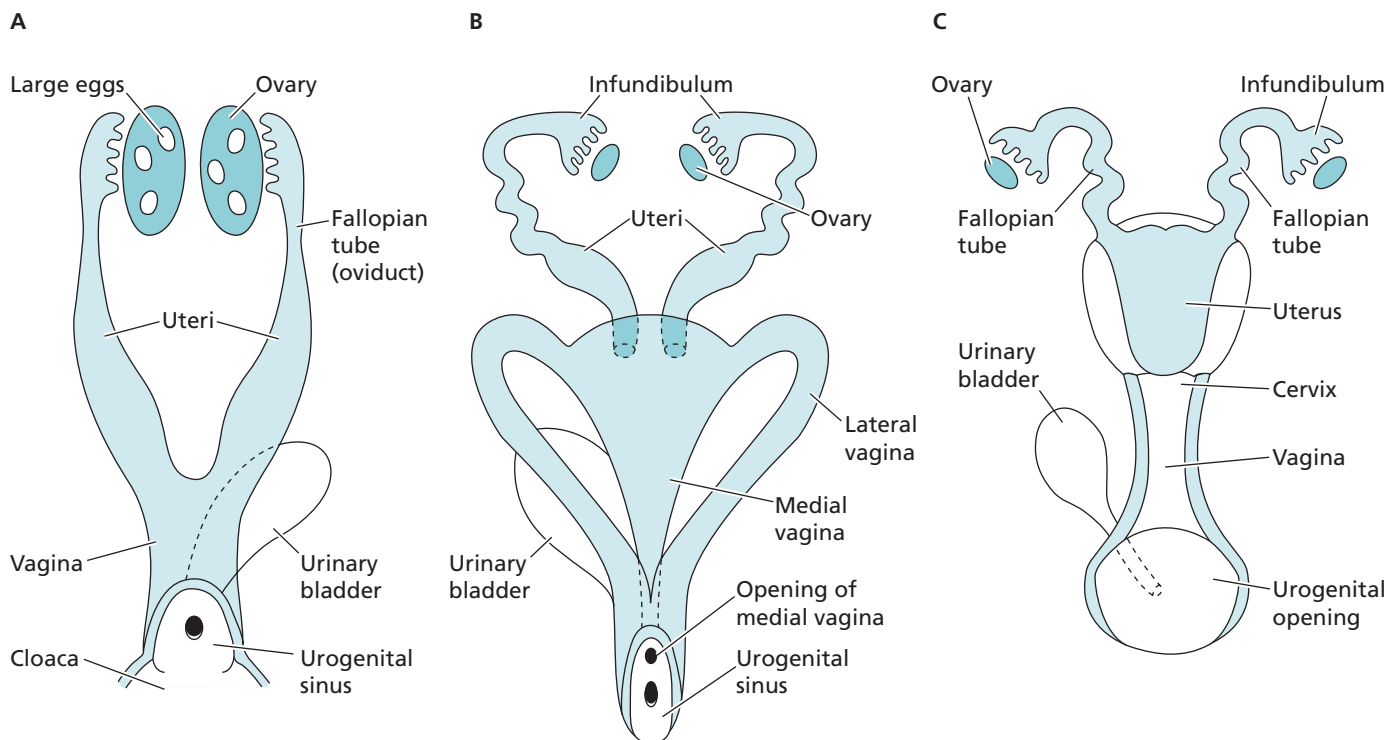
Figure 10.2 Female reproductive tracts. The structure of female reproductive tracts varies in the three groups of mammals: (**A**) prototherians (monotremes); (**B**) metatherians (marsupials); (**C**) eutherians ("placentals").

A

Scapula Clavicle

Precoracoid

Coracoid

Sternum

Interclavicle

B

Scapula Clavicle

Precoracoid

Coracoid

Sternum

Ribs

C

Scapula Spine

Coracoid
process

Sternum Clavicle
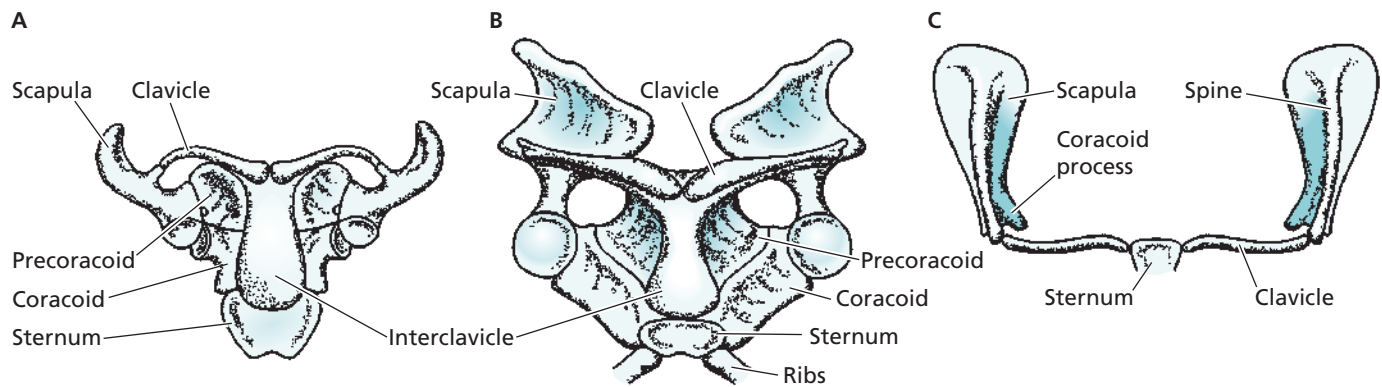
Figure 10.3 **Reptile-like pectoral girdle in monotremes.** Pectoral girdles in a (**A**) therapsid reptile, (**B**) short-beaked echidna, and (**C**) muskrat, a eutherian mammal. Monotremes have pectoral girdles very similar to ancient reptiles. *Adapted from Hyman (1942).*

Besides laying eggs, monotremes retain several other reptilian features. The pectoral girdle (Figure 10.3) has a corocoid, precoracoid, and interclavicle bone, as in primitive therapsid reptiles. Although they are homeotherms, the body temperature of monotremes is about 32°C—lower than that of therians. The chromosomes are unique among mammals in their mix of normal macrochromosomes and microchromosomes and in their meiotic division. The 3 extant genera of monotremes are unique among vertebrates in their sex chromosomes. Instead of the typical XX pattern in females and XY in males, there is a chain of 10 X-chromosomes in females and 5 X- plus 5 Y-chromosomes in males during meiosis. Nonetheless, the mechanism of sex determination in monotremes remains unresolved (Grutzner et al. 2004; Ferguson-Smith and Rens 2010). Sperm are **filiform** (thread-like) and reptilian in structure, as is the anatomy of the testes (Carrick and Hughes 1978). Lin and Jones (2000) described the ultrastructure of spermatid development in the platypus. Acrosomal development is reptilian, other features are the same as mammals, and some, including nuclear condensation, are unique to monotremes. Warren and coworkers (2008) reported a genome sequence for the platypus, the first for a monotreme.

MORPHOLOGY

Monotremes exhibit a "**mosaic evolution**," given their relatively specialized mammalian features and numerous retained archaic reptilian characteristics. Although they are diverse in their outward appearance, the two monotreme families share several characteristics. The cranial features of monotremes are unique, with adults having indistinct sutures. Unlike in therian mammals, the jugal bone is reduced or absent. The zygomatic arch is made up of the maxilla and squamosal bones. The dentary bone is greatly reduced, and adults are **edentate** (without teeth). With their elongated rostrum, lack of teeth, and high-domed cranium, monotreme skulls appear birdlike (Figure 10.4). The **cochlea** (semicircular canals of the inner ear) of

monotremes are also unique among mammals because they are not coiled.

Monotremes have several other distinctive features. As in marsupials, **epipubic bones** (attached to the pelvic girdle and projecting forward) occur in both sexes. Adult males have a large, horn-like medial spur on the ankle. In the platypus, this spur connects to a poison gland (see Family Ornithorhynchidae, discussed below). Details of the skull and postcranial skeleton of the platypus and echidnas can be found in Grant (1989) and Griffiths (1989), respectively. Monotremes, like marsupials, have no **corpus callosum**, a bundle of nerve fibers that integrate the two hemispheres of the brain. Also as in marsupials, the hypothalamus and pituitary of neonatal monotremes are not completely developed (Ashwell 2012). Males have a baculum, permanently abdominal testes, and no scrotum.

FOSSIL HISTORY

Monotremes may have diverged from therian mammals as long as 230 mya (van Rheede et al. 2006) in the Mesozoic. Rowe and colleagues (2008) suggested the platypus and echidna lineages diverged by the early Cretaceous about 115 mya. An early, undifferentiated Cretaceous monotreme, *Teinolophos trusleri*, was dated from 108 to 115 mya (Rich et al. 2001, 2005; Rowe et al. 2008). Rich and colleagues (2016) described the mandible and dentition of *T. trusleri*. Fossil evidence of Australian ornithorhynchids extends from the Cretaceous (Woodburne and Tedford 1975; Archer et al. 1978, 1992). Archer and coworkers (1985) described *Steropodon galmani*—the first Mesozoic mammal from the early Cretaceous of Australia—based on a partial lower jaw. Originally considered to be an ornithorhynchid, it was placed in its own Family Steropodontidae by Flannery and colleagues (1995). In addition to the sole extant ornithorhynchid, there are four known fossil species. The oldest Australian fossil is *Obdurodon insignis* from the late Oligocene (Woodbourne and Tedford 1975). The mid-Miocene fossil, *O. dicksoni*, was discussed

A

B

Figure 10.4 Monotreme skull morphology. (**A**) Dorsal view of the skull of a duck-billed platypus; (**B**) dorsal view of the skull and mandible of a short-beaked echidna.

by Musser and Archer (1998). The most recently discovered fossil ornithorhynchid, possibly from the mid-Miocene and the largest known, is *O. tharalkooschild* (Pian et al. 2013). The first evidence of a non-Australian fossil monotreme was a platypus, *Monotrematum sudamericanum*, from the early Paleocene of southern Argentina (Pascual et al. 1992; Pascual and Goin 2002). The earliest tachyglossid, *Megalibgwilia ramsayi*, is from the early to mid-Miocene of Australia (Griffiths et al. 1991). *Kryoryctes cadburyi*, known only from a partial humerus bone from Victoria, Australia, has been dated to 106 mya. It may be a stem monotreme—if it actually is a monotreme (Pridmore et al. 2005). Musser (2003) provided an excellent review of the fossil history of monotremes.

ECONOMICS AND CONSERVATION

Although certainly of intrinsic interest to mammalogists and the general public, monotremes have no economic importance. In the early days of Australian colonization, the platypus was hunted for its fur, but this was never a major industry. The platypus is neither threatened nor endangered, but overall population density is believed to be declining (IUCN 2018). The potential exists for habitat loss from stream erosion, reduced water quality, introduced species such as the red fox (*Vulpes vulpes*), and other factors (Grant and Temple-Smith 2003). The short-beaked echidna is the most geographically widespread monotreme and populations generally are stable. Populations of the eastern

long-beaked echidna, however, are declining, and the species is considered threatened, whereas both the long-beaked echidna and Sir David's long-beaked echidna are critically endangered (IUCN 2018).

FAMILIES

Ornithorhynchidae

As noted, the semiaquatic, semifossorial platypus is the sole extant ornithorhynchid. It occurs in freshwater lakes and rivers at both high and low elevations along the east coast of Australia and throughout Tasmania. Its physical appearance is so unusual among mammals (Figure 10.5) that the first specimen brought to London in 1798 was believed to be a hoax. Adult males average 50 cm in total length and 1.7 kg in body mass; females are about 25% smaller. Short, dense fur covers all but the bill, feet, and underside of the tail. Dorsal pelage is reddish-brown to brown with a lighter venter. The distinctive bill is unique among mammals and quite unlike that of a true duck. It is soft, pliable, and very sensitive and has nostrils at the tip. The bill is highly innervated both for tactile reception and to sense electric fields generated by the muscle contractions of prey (Scheich et al. 1986; Manger and Pettigrew 1996; Proske et al. 1998—see box). The small eyes and ears are situated in a groove extending from the bill. During a dive, this groove closes, and the platypus relies on the sensitivity of the bill to locate prey. Unlike those of eutherians, the eyes of a platypus retain scleral cartilage, double cones,
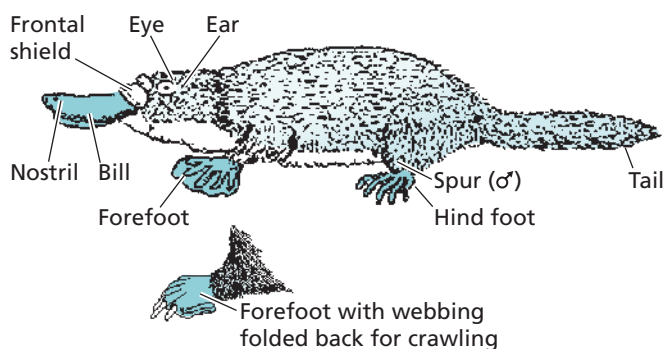
Figure 10.5 **External features of the duck-billed platypus.** The external anatomy of the duck-billed platypus is unique. *Adapted from Walton and Richardson (1989, vol. 1B).*

and cone droplets (Zeiss et al. 2011)—features found in early tetrapods such as amphibians. Well-developed electroreceptivity may have occurred as far back as the early Cretaceous (Asahara et al. 2016) as an adaptation for foraging in turbid waters.

Feet of the platypus are **pentadactyl** (five-toed), and the **manus** (forefoot) is webbed (Figure 10.6). Webbing is folded back when the platypus is on land. Nonetheless, terrestrial locomotion is energetically demanding (Fish et al. 2001). The long, sharp claws are used for burrowing. The medial spur on the hind limb connects to a large venom gland located in the thigh (Figure 10.7). Spurs are strong, sharp, and about 12 mm long. The function of the spur may be related to competition between males during the breeding season. People who have been accidentally envenomated in the hand

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Platypus Bill

Electroreception occurs in many vertebrates, but primarily in fishes. Most electric fields that are sensed in the environment are from other organisms, usually potential prey species. Monotremes are among the very few mammals known to use electroreception, with signals conducted by the trigeminal nerve pathways. This nerve complex is much more developed in the platypus than in echidnas. As noted, the bill of a platypus is soft, pliable, and very sensitive—it is the main sensory organ for navigation and locating food, and it is highly structured and complex. The skin is a mosaic of mechanical and electrical receptors located on both the dorsal and ventral surfaces. There are an estimated 40,000 cells in the bill that sense electric fields as a platypus moves its head from side to side while foraging—about 10 times more than occur in the beak of echidnas. The mechanoreceptors have a more uniform distribution across the bill and are clustered toward the edges, at the base of a mobile column of flattened, keratinized cells called "push rods." Upon contact with an object, the column moves upward or downward to stimulate receptors at the base; these touch receptors evoke a reaction in the brain. Four types of receptors are associated with the push rods: central and peripheral chain receptors, Merkel receptors, and paciniform receptors—each with its own function. Additionally, the

skin of the platypus bill contains erectile tissue. Blood engorgement might facilitate contact between push rods and the external environment. Also, contractile tissue around the tip of the push rods can restrict movement of the rods—perhaps when the animal leaves the water. Because platypuses are so specialized, they are highly vulnerable to habitat modifications. Many human-induced changes that cause habitat fragmentation in eastern Australia have resulted in local reductions in populations of this fascinating mammal, although they are currently not considered threatened or endangered.

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Figure 10.6 **Duck-billed platypus.** From an 1808 watercolor and gouache painting by John Lewin.
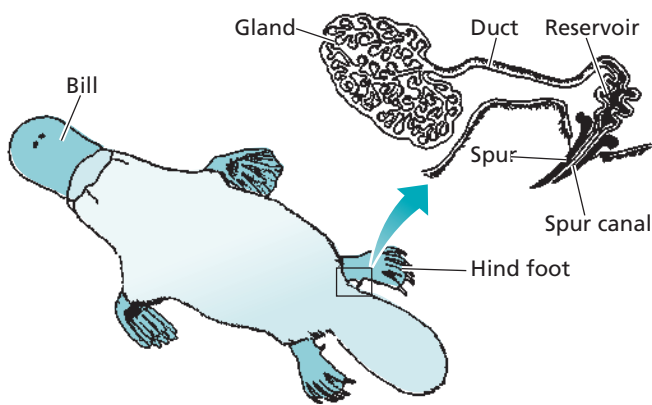
Figure 10.7 **Venom gland in the duck-billed platypus.** Anatomy of the venom gland associated with the spur on the hind limb of the male platypus. *Adapted from Walton and Richardson (1989, vol. 1B).*

experienced "immediate and intractable pain and marked swelling" (Fenner and Williamson 1996:438). Considerable research has been done to elucidate the chemical structure of platypus venom; it contains numerous unique peptides and proteins (Koh et al. 2009; Kita 2012). Whittington and coworkers (2010) identified 83 novel genes for platypus venom.

Prey consists of a diverse array of benthic invertebrates (Klampt et al. 2016). McLachlan and colleagues (2010) found benthic invertebrates from 16 orders and 55 families in the cheek pouches of platypuses from Kangaroo Valley, New South Wales, Australia, with variation between winter and summer diets. Food obtained during a dive is stored in two large internal cheek pouches, opening from the back of the bill. Smaller prey items are sifted from the substrate by the complex bill apparatus; larger prey is cap-

tured individually. Limited oxygen-storage capacity limits dives to shallow waters and durations of a minute or less.

Unlike echidnas, platypus neonates have three molariform teeth in each quadrant. These are shed before young emerge from the burrow. Adults lack functional teeth and instead have a series of horny pads and sharp, shearing ridges for most of the length of each jaw. These pads grind food before it is swallowed. A platypus also uses its flattened tongue to mash food against the palate while the animal floats on the surface.

Burrows are built in stream banks and generally are simple, although those constructed by females for nursing are 20–30 m long, with a nest chamber at the end. Unlike echidnas, the platypus has no pouch. Females curl their bodies around the eggs to incubate them—a process that takes less than 2 weeks. Average litter size is 2 and eggs are about 14 × 17 mm in size. As with birds, only the left ovary is functional. The young are not carried after hatching and remain in the burrow during the 4- to 5-month nursing period. Milk is secreted from the mammary glands onto distinct, protruding tufts of fur.

Gongora and colleagues (2012) found low rates of gene flow and significant genetic divergence of populations in different geographic areas. Similarly, Martin and colleagues (2018) found little gene flow throughout the species range, and radio-tracked platypuses in the Severn River area of Australia had very localized monthly movements (Bino et al. 2018). Grant (2015) provided a thorough review of the ornithorhynchids.

Tachyglossidae

The short-beaked echidna (Figure 10.8) occurs throughout Australia, New Guinea, and Tasmania in forest, scrub,

Figure 10.8 **External morphology of echidnas.** (**A**) The beak is much shorter and straighter in the short-beaked echidna (*Tachyglossus aculeatus*), and there are more spines than in long-beaked echidnas, such as in (**B**) this mounted specimen of an eastern long-beaked echidna (*Zaglossus bartoni*).

and desert habitats and is the most widely distributed endemic mammal in Australia. Because of morphological variation throughout their range, several subspecies of short-beaked echidna have been described (Morrow et al. 2009). The long-beaked echidnas are restricted to forested highland areas of New Guinea. Maximum body mass is about 6 kg in *Tachyglossus* and 16 kg in *Zaglossus bartoni*. Both genera have a long "beak" that, like the platypus, contains electroreceptors and tactile receptors at the tip, as well as a long, extensible tongue. Electroreception is less developed in echidnas than in the platypus, however. Enlarged submaxillary salivary glands produce mucus that coats the tongue and makes it sticky. Presence of echidnas in an area can be detected by the holes made in soil by the beak as they forage. Guard hairs on the back and sides of the body are modified to form barbless spines up to 6 cm long. The western long-beaked echidna has much thicker hair and fewer spines than *T. aculeatus*. Large, scoop-like claws on the feet enable echidnas to break into anthills and to burrow in a rapid, powerful manner. The number of claws on the fore- and hindfeet differ among the species of *Zaglossus*. They are active anytime during the day or night

but avoid extremes of temperature, with reduced activity and shorter digging bouts in the summer compared to spring (Clemente et al. 2016). Male short-beaked echidnas have home ranges about twice the area of females; Nicol and coworkers (2011) found no relationship between body weight and home-range size. Likewise, Opiang (2009) found that home-range sizes for *Z. bartoni* were not related to body weight, age, or sex. Because of their low metabolic rate, echidnas have smaller home-range sizes than would be predicted for their body weight.

Using its sticky tongue, which can be extended 18 cm, *Tachyglossus* (meaning "rapid tongue") consumes ants, termites, and other insects, which are ground to a paste between the tongue and spiny palatal ridges. Their most common prey are ants of Genus *Iridomyrmex*. Short-beaked echidnas use monounsaturated fatty acids from these ants for energy during winter hibernation (Falkenstein et al. 2001), which may last 3 to 4.5 months. They can also enter short-term, daily **torpor**. The high amount of monounsaturated lipids in their cellular membranes is thought to be a significant factor in the exceptionally long life span of *T. aculeatus*, which may reach 50 years (Hulbert et al. 2008, 2010). *Zaglossus* (meaning "long tongue") feeds primarily on earthworms.

Unlike those on the platypus, the ankle spurs on male echidnas do not function, nor do echidnas have teeth at any stage of development. Also, echidnas have a pouch in which the eggs—13 to 17 mm in diameter—are incubated and hatched, again unlike the platypus. Echidnas in Australia mate during winter, that is, from June through early September. Gestation is about 23 days (Rismiller and McKelvey 2000, 2009). The mammary glands converge to two small areas in the pouch, the milk areolae, where neonates cling to surrounding fur to nurse. Young remain in the pouch 45–50 days (Beard and Grigg 2000) until their spines begin to develop. Nicol (2015) provided a comprehensive review of the family.

Marsupials

Marsupials get their name from the female's abdominal pouch, or **marsupium**. This is a poor diagnostic feature, however, because not all marsupials have a marsupium (and, as we have seen, a pouch also occurs in echidnas). Nevertheless, the pouch is probably a derived condition in marsupials (Tyndale-Biscoe and Renfree 1987). Marsupials are best distinguished from eutherians on the basis of their reproductive mode—specifically, the relatively small maternal energy investment in **altricial** (undeveloped) young prior to birth. In fact, no marsupials have litters that weigh more than 1% of the mother's body mass (Russell 1982). In contrast, small eutherians, such as rodents or insectivores, may have litters that weigh 50% of the mother's body mass. However, maternal investment in lactation is
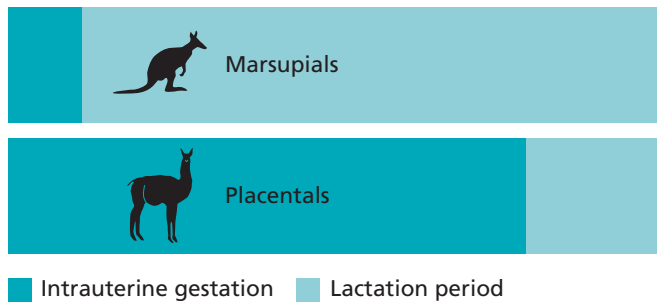
Figure 10.9 Lactation and gestation in therians.
Relative lengths of gestation and lactation differ significantly in marsupials and eutherians. Most energy expenditure in marsupials occurs during lactation. The total amount of time that young are dependent varies with the size of the species. *Adapted from Kirsch (1984a).*

much greater in marsupials (Figure 10.9), so by the time young are weaned, total investment in a litter by marsupials and eutherians of similar body weight may be similar. Renfree (1993:450) noted that "marsupials have, in effect, exchanged the umbilical cord for the teat." In addition to differences in their reproductive characteristics, marsupials differ from eutherians in many skeletal and anatomical features (Table 10.2). The two groups also have different dental characteristics. Unlike eutherians, marsupials characteristically have a well-developed "stylar shelf" on the upper molars, as well as a "twinned" hypoconulid and entoconid in the lower molars (Figure 10.10).
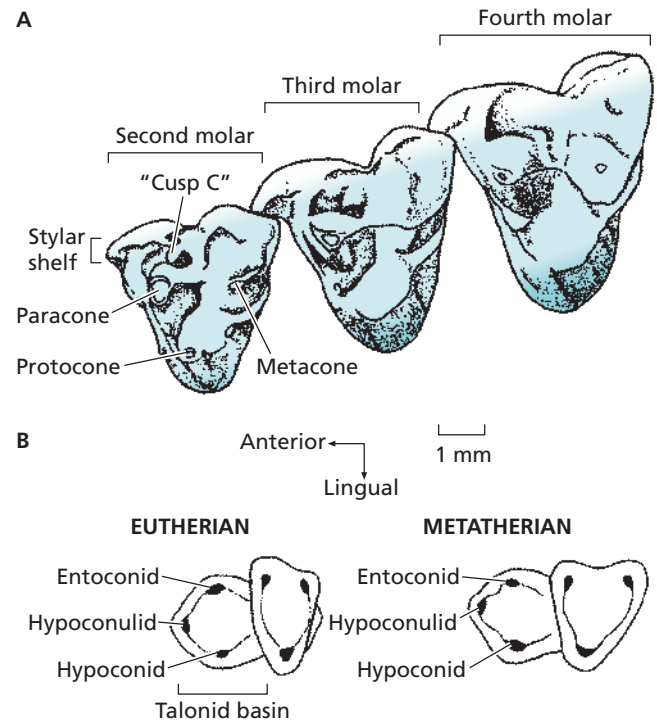
Figure 10.10 Marsupial molar morphology. (A) Left upper molars 2–4 of a primitive marsupial showing the characteristic stylar shelf with large Cusp C on the labial (cheek) side and large size of the metacone relative to the paracone; (**B**) lower molars, showing the hypoconulid closer to the entoconid ("twinned") than to the hypoconulid in a marsupial (*right*). In a placental, the hypoconulid is equidistant from the entoconid and hypoconid. *Adapted from data in Archer (1984a).*

Table 10.2 General skeletal and anatomical differences between metatherian (marsupial) and eutherian ("placental") mammals

Metatherians	Eutherians
Braincase small relative to body size; minimal development of neocortex; no corpus callosum	Braincase relatively large; greater complexity of neocortex; corpus callosum present
Auditory bullae usually absent, if present, formed primarily from alisphenoid bone	Auditory bullae present, formed from tympanic bone
Large vacuities often present in posterior part of palate	Palatal vacuities absent or small
Jugal bone large; jugal and squamosal bones articulate with dentary bone in mandibular fossa	Jugal bone does not articulate with dentary in mandibular fossa
Angular process of dentary inflected 90° (i.e., is perpendicular to the axis of the dentary), except in koala and honey possum	Angular process of dentary not inflected
Primitive dental formula 5/4, 1/1, 3/3, 4/4 = 50. Last premolar is the only deciduous tooth	Primitive dental formula 3/3, 1/1, 4/4, 3/3 = 44. Incisors, canines, and premolars are deciduous
Epipubic bones occur in both sexes	Epipubic bones do not occur
Female reproductive tract bifurcated; tip of penis (glans) bifurcated	Reproductive tract and glans penis not bifurcated
Marsupium often present enclosing teats; opens either anteriorly or posteriorly	Marsupium not present
Scrotum anterior to penis, except in the mole *Notoryctes*; baculum never present	Scrotum posterior to penis; baculum sometimes present

Several life-history characteristics of marsupials differ from those of eutherians, at least in matter of degree (Lee and Cockburn 1985). For example, marsupials generally have basal metabolic rates about 30% lower than comparably sized placentals. Except for bandicoots, they also have slower postnatal growth. Brain size relative to body size is smaller in marsupials, especially in large species, as is the range of body size itself. For example, the difference in body mass between the smallest living marsupial, the long-tailed planigale (*Planigale ingrami*—average adult body mass 4 g), and the largest, the red kangaroo (*Macropus rufus*—average mass of males 66 kg), is about 4 orders of magnitude (5 orders of magnitude if the 2,786 kg Pleistocene *Diprotodon* is considered; Wroe et al. 2004). This is less pronounced than the extremes in placentals, 7 orders of magnitude difference between pygmy shrews and blue whales. Nor have marsupials evolved marine adaptations (like cetaceans), true flight (like bats), or fossorial herbivory (like pocket gophers). Nonetheless, a fascinating array of behavioral and morphological adaptations occurs among the 7 orders and approximately 330 species of living marsupials.

REPRODUCTIVE SYSTEM

Female marsupials have a **bifurcated** (paired) reproductive tract. Two lateral vaginae lie on either side of a medial vaginal canal, or sinus (see Figure 10.2), and the uterus is duplex. The scrotum is anterior to the penis in almost all male marsupials. In marsupial moles (Notoryctidae), the testes are abdominal; testes are scrotal in wombats (Vombatidae) only during the breeding season. The two prongs of a male's bifid penis probably are compatible with the lateral vaginae of females during copulation. During copulation, sperm travel up the lateral vaginae. If fertilization occurs, the zygote(s) implant(s) in the uterus (uteri). Following a short gestation period, **parturition** (birth) occurs through extension of the medial vaginal canal, not through the lateral vaginae.

Most marsupials have a **choriovitilline** (yolk-sac) placenta (see Chapter 9). Unlike the **chorioallantoic** placentae of placentals, choriovitilline placentae have no **chorionic villi** (finger-like projections of capillaries from the embryonic membrane). Because of the tremendous surface area they provide, villi enhance both nutrient exchange and the strength of fetal attachment. Maternal-fetal exchange is also enhanced by wrinkling of the endometrium (wall of the uterus) after implantation. Among marsupials, only bandicoots (Peramelemorphia) and koalas (Phascolarctidae) have chorioallantoic placentae, but they lack villi. Renfree (2010) provides a thorough review of maternal-fetal interactions in marsupials.

Marsupial gestation periods are very short—12–13 days in some didelphids and bandicoots—and sometimes shorter than the interval between maternal estrous periods (Hsu et al. 1999). At parturition, neonates are tiny, often weigh-
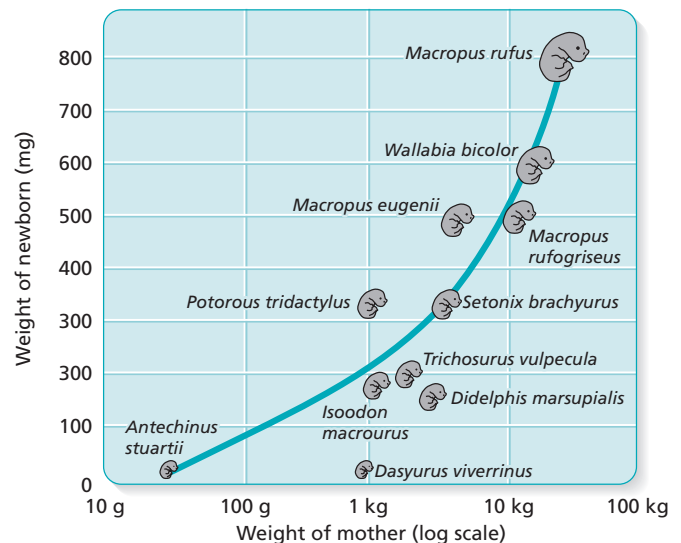
Figure 10.11 **Small size of newborn marsupials.** Body weight of neonatal marsupials is extremely low, never more than 1 g. An entire litter never weighs more than 1% of the mother's body mass. *Adapted from Tyndale-Biscoe (2005).*

ing only a few milligrams, and never more than 1 g (Figure 10.11); development of neonatal organ systems is just beginning. Despite their mostly altricial features, the forelimbs and shoulder muscles of neonatal marsupials are well developed, and the forefeet have deciduous claws. These features allow newborn marsupials to climb from the vaginal opening and through the mother's pelage to reach a nipple where development continues. The lack of specialized limbs such as hooves, flippers, or wings in adult marsupials may be related to the functional importance of these muscular, clawed forelimbs in neonates (Keyte and Smith 2010; Kelly and Sears 2011).

Once neonates are attached to a nipple, the teat swells, keeping the developing young in place during the early stages of the prolonged lactation period. This phase may be two-thirds of the lactation period in larger species, but one-third or less of that period in smaller species, especially those without a marsupium. During the next phase of lactation, the altricial young are left in the nest while the mother forages. This phase continues until the young are weaned (Harder et al. 1993). Thus, "Marsupials have evolved a different but highly successful reproductive strategy when compared with eutherian mammals, in that their major reproductive investment is placed in lactation rather than gestation and placentation" (Tyndale-Biscoe and Renfree 1987:371).

As noted, not all marsupials have a marsupium. The numbat (*Myrmecobius fasciatus*), some New World opossums (Didelphidae), rat opossums (Caenolestidae), the bushy-tailed opossum (Glironiidae), and many small marsupial mice (Dasyuridae) have no pouch. In other didelphids and dasyurids, there is simply a fold of skin on either side of the teats. Pouches often are best developed in arboreal species and those that either burrow or jump. Pouches may open
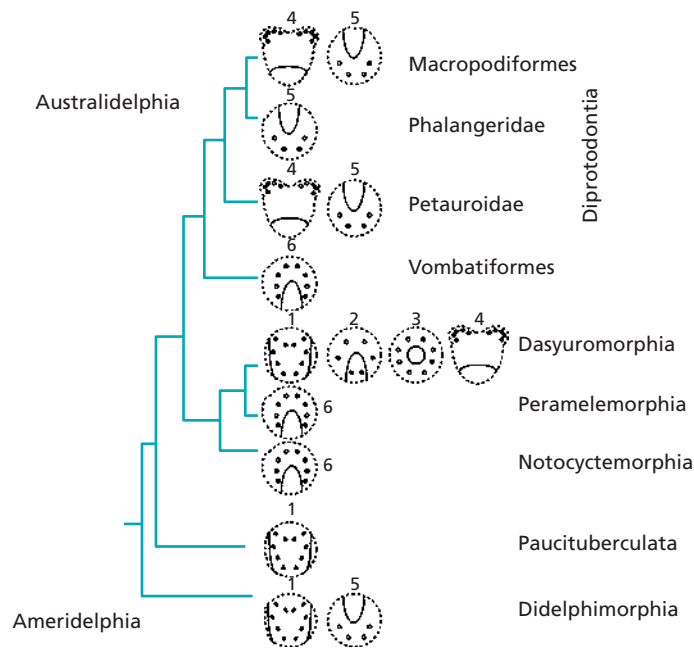
Figure 10.12 **Pouch types found in marsupial orders.** Solid and open circles indicate teats that are external or internal, respectively, to the pouch fold. Solid and dashed lines demarcate the pouch opening and covered areas, respectively. *Redrawn from Edwards and Deakin (2013).*

anteriorly or posteriorly (Russell 1982; Figure 10.12). Also, the condition and appearance of the pouch differs depending on the stage of the reproductive cycle. Woolley (1974) found no relationship between the structure of the marsupium and several life-history characteristics. Indeed, Kirsch (1977) argued that the pouch may have evolved independently in different marsupial lineages. The duration of pouch life and the time of weaning depend on several factors, including maternal body mass, litter size, and number of litters per year.

FOSSIL HISTORY

Early Metatherians

As shown in Figure 5.12, marsupials form a monophyletic group (Marsupialia) within the larger clade Metatheria. Although marsupials are the only living metatherians, a rich fossil record reaching back to the Cretaceous documents considerable diversity among nonmarsupial metatherian taxa. Luo and colleagues (2003) described the scansorial *Sinodelphys* from the Early Cretaceous (125 mya) of China as the oldest metatherian and argued for an Asian origin of the group. However, a phylogenetic analysis by Bi and coworkers (2018) suggests that *Sinodelphys* is a eutherian. If correct, this renders taxa such as the poorly known *Holoclemensia* from North America among the oldest (ca. 110 mya) metatherians (Figure 10.13). The metatherian affinities of *Holoclemensia* (represented by only three molars) have been controversial (Wroe and Archer 2006), but two

other Early Cretaceous taxa from North America, *Oklatheridium* and *Atokatheridium* (also known only from teeth), are the oldest known members of the metatherian clade Deltatheroidea (Williamson et al. 2014). Also found in the Early Cretaceous of North America is a lower jaw of *Kokopellia*, the oldest representative of Marsupialiformes (the clade that includes marsupials). If *Sinodelphys* is a eutherian, and the oldest metatherian fossils are North American, the continent on which metatherians arose is much in doubt. Also uncertain is where they may have been during the 50-my "ghost lineage" period that separates *Holoclemensia* and other Early Cretaceous taxa from the oldest eutherian, the Chinese *Juramaia* (ca. 160 mya).

Although *Oklatheridium* and *Atokatheridium* are North American, many deltatheroideans occur in Asian deposits of the Late Cretaceous. The best studied is *Deltatheridium*, from approximately 80 mya in Mongolia, and represented by skulls, jaws, and several postcranial bones (Rougier et al. 1998). About the size of a small opossum, *Deltatheridium* had prominent canines and sharp-pointed molar cusps, which suggest a carnivorous diet (perhaps including small dinosaurs; Elżanowski and Wellnhofer 1993). This animal resembles marsupials in its 3 premolars and 4 molars, replacement of only the last premolar, inflected angular process, and wide stylar shelf. Unlike marsupials, however, *Deltatheridium* lacked stylar cusp C and a twinned hypoconulid-entoconid; its incisor formula was 4/3 rather than 5/4 as in primitive marsupials. Nine genera of deltatheroideans have been described, including one (*Nanocuris*) that survived to near the Cretaceous-Paleogene (K-Pg) boundary in North America (Wilson and Riedel 2010).
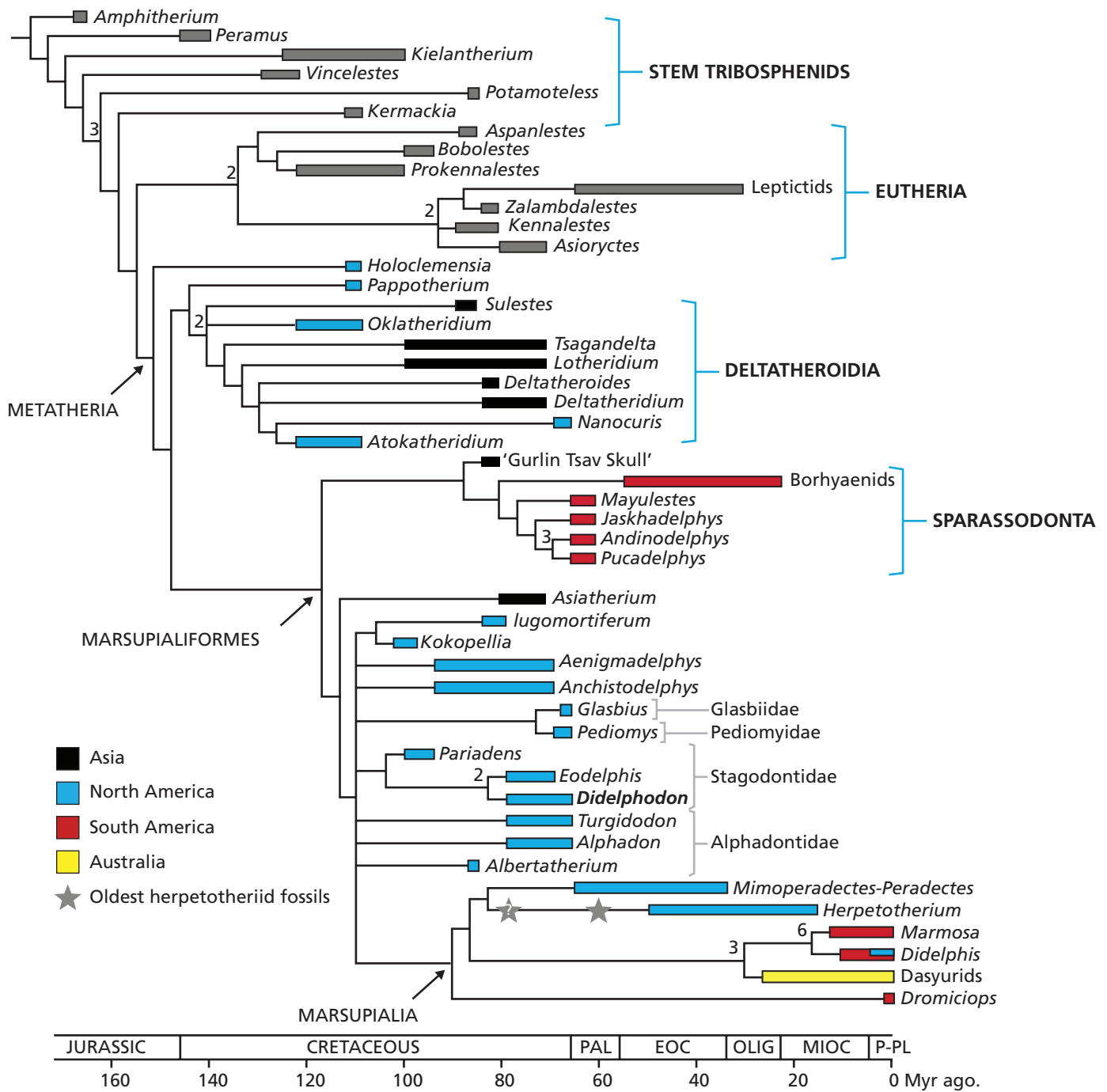
Figure 10.13 **Phylogeny of selected metatheria taxa.** Based on parsimony analysis of 164 anatomical characters. Thin lines are branches of the phylogeny. Thickened portions of branches indicate the temporal ranges of taxa named at the tips; shading patterns indicate geographic distributions. *Redrawn from Wilson et al. (2016).*

Marsupialiformes

The sister-group of Deltatheroidea in most modern phylogenetic analyses is Marsupialiformes, consisting of many **stem lineages** and the modern **crown group** Marsupialia (Figure 10.13). Over 40 extinct genera of nonmarsupial marsupialiforms have been recognized from the Late Cretaceous (ca. 95 mya) through the Miocene (ca. 5 mya), most from North America, but a few key groups were from South America and

Eurasia. Phylogenetic relationships among them have been difficult to resolve, and little consensus exists on the branching structure of Marsupialiformes, including the boundaries of Marsupialia. Here we describe some of the best-known groups, their possible role in ancient ecosystems, and their implications for marsupial origins. For a more detailed recent summary, see Williamson and colleagues (2014).

The record begins with a complete, 2-cm jaw of rat-sized *Kokopellia* from Utah, showing cheek teeth with

Figure 10.14 *Didelphodon vorax.* Skeletal reconstruction of a stagodontid marsupialiform in the Rocky Mountain Dinosaur Resource Center, Woodland Park, CO. The body length is approximately 30 cm.

many marsupial traits, but lacking stylar cusp C and a twinned entoconid-hypoconulid (Wroe and Archer 2006). Twinning appears in the mouse-size, terrestrial *Asiatherium* from Mongolia, one of the few Cretaceous metatherians known from a complete skeleton (Rose 2006). *Pariadens*, represented by a partial lower jaw with three molars from the Late Cretacous of Utah, was a larger animal that also showed twinning. *Pariadens* may have been an early representative of Stagodontidae, which includes the well-studied genera *Didelphodon* (Figure 10.14) and *Eodelphis* from North America—semiaquatic predator-scavengers that were among the largest (opossum-sized, up to 5.2 kg) mammals of the Late Cretaceous (Wilson et al. 2016). *Maastrichtidelphys* (a single molar) is one of very few Late Cretaceous marsupialiforms from Europe (Martin et al. 2005).

Several species of *Alphadon* have been described from teeth found at Late Cretaceous sites across western North America, suggesting animals resembling small opossums. These teeth are similar those of primitive marsupials in many ways, including presence of stylar cusp C, and were once taken as evidence that *Alphadon* approximates the ancestral marsupial (Wroe and Archer 2006). Phylogenetic analyses and uncertainty about dental formulae now make this position unlikely, but there is some consensus that *Alphadon* is closer to the marsupial root than other marsupialiforms described above. Indeed, some authors still consider *Alphadon* and the taxa described next to be marsupials.

Glasbius, from the Late Cretaceous of North America, had bunodont molars suggesting a frugivore diet—perhaps optimal for the presumably high metabolism of such a small (<50 g) mammal (Williamson et al 2014). Phylogenetic analyses have persistently linked *Glasbius* with the South American omnivore *Roberthoffstetteria* from across the K-Pg boundary in the Paleocene, forming the clade Glasbiidae. At least three, and perhaps as many as five, Late Cretaceous genera from North America constitute Pediomyidae, known mostly from teeth and jaw fragments. Remains of this diverse group are widespread and relatively abundant in many of the faunas where they occur. Tooth structure suggests that smaller species were insectivores, while larger forms show molar adaptations for crushing and shearing consistent with a more diverse diet (Williamson et al. 2014).

A group of fossils from the Paleocene of South America signals the first appearance of what may be a distinct clade of Gondwanan marsupialiforms. Several of these (e.g., *Pucadelphys*, *Andinodelphys*, *Mayulestes*), are from the rich Tiupampa site in Bolivia. *Pucadelphys* had a long tail and was capable of both digging and climbing; *Mayulestes* had a **prehensile** tail and was arboreal (Rose 2006). These genera are often associated phylogenetically with the diverse clade Sparassodonta. More than 20 genera of sparassodonts have been recognized from Paleocene through Pliocene deposits. They were mostly medium-large, scansorial or terrestrial carnivores, including some cursorial (Borhyaenidae) and saber-tooth forms (Thylacosmilidae) (Figure 10.15).

There is some consensus that two groups of Northern Hemisphere marsupialiformes from the Paleogene—herpetotheriids and peradectids—form the sister group(s) to, or are perhaps part of, Marsupialia (Luo et al. 2003, Horovitz et al. 2009, Williamson et al. 2014, Wilson et al. 2016). *Peradectes* and *Mimoperadectes* were widespread in North America during the Paleocene and Eocene, and a spectacularly preserved skeleton of the former was recovered from the famous mid-Eocene Messel shale deposits of Germany. Herpetotheriidae includes some 10 genera, mostly from Eocene-Miocene sites in Europe, southern Asia, North America, and Africa. However, there is some evidence that the group includes representatives from the Paleocene and Late Cretaceous (Willliamson et al. 2014, Wilson et al. 2016). Peradectids and herpetotheriids were similar to small, generalized opossums.

Marsupialia

We describe the fossil record of living marsupial groups later in this chapter. Approximately 40 genera of Cenozoic marsupials occur in South America; their affinities to extant taxa are unclear. Many of these represent the metatherian contribution to Simpson's (1980) "splendid isolation" phase of mammal evolution in South America. Again, we discuss only a sample of well-studied representatives; Goin and coworkers (2016) provide a more complete review.

Some 24 genera constitute Polydolopidomorphia (see Figure 5.12), with representatives spanning much of the Cenozoic. *Epidolops*, from the early Eocene of Brazil, was a squirrel-sized omnivore with procumbent incisors separated by a diastema from enlarged pairs of anterior cheek teeth. The 6 genera of polydolopids (e.g., *Polydolops*), dating from the Late Paleocene to Oligocene, were morphologically similar to *Epidolops*. Argyrolagoidea includes the Eocene *Groeberia*, a chewing herbivore similar to rodents, and the Pliocene *Aryrolagus*, with enlarged hind limbs resembling a jerboa. Beck's (2017) detailed phylogenetic analysis suggested that *Epidolops* and polydolopids lie outside Marsupialia.

Figure 10.15 **Carnivorous sparassodonts from South America.** (**A**) *Thylacosmilus atrox* (Thylacosmilidae), a marsupialiform sabertooth from the Pliocene of Argentina. The total length of skull is about 23 cm. (**B**) *Lycopsis longirostris*, a terrestrial predator from the Miocene of Argentina and Colombia.

Metatherian Paleobiology

Cretaceous metatherians were mostly small- to medium-sized (ca. 10–2,000 g) components of dinosaur-dominated faunas. Deltatheroideans were carnivorous, and limited evidence suggests scansorial or arboreal locomotion. In contrast, early marsupialiformes were insectivore-omnivores, and some (e.g., *Asiatherium*) were clearly terrestrial. Tooth morphology indicates specialized diets for some pediomyids (crushing), stagodontids (durophagy), and *Glasbius* (seeds and fruit). The distribution of Cretaceous fossils (Figure 10.16) supports an early diversification

of metatherians in the Northern Hemisphere, with dispersal among North America, Asia (deltatheroideans, *Asiatherium*), and Europe (*Maastrichtidelphys*). Metatherian diversity peaked in North America ca. 75 mya, declined slightly until the K-Pg boundary (66 mya), and then plummeted in the Paleogene as eutherians came to dominate local faunas. Nevertheless, North America may have been home to the marsupial ancestor, in that likely marsupial sister groups such as peradectids and herpetotheriids flourished there throughout the Paleogene (Williamson et al. 2014, Wilson et al. 2016).

In some fashion, metatherians reached South America shortly after the K-Pg boundary, as evidenced by the sparassodonts (e.g., *Pucadelphys*) and several other genera known from the Early Paleocene. Nearly 50 genera of Eocene metatherians are recognized, including the oldest representatives of extant clades Didelphimorphia, Paucituberculata, and Microbiotheria. About 20 genera occurred in the Oligocene and 17 in the Miocene; these periods hold the greatest diversity of carnivorous borhyaenoid sparassodonts (15 genera) and caenolestoid paucitubercuates (7 genera). Relatively few extinct genera are known from the Pliocene, when the Great American Biotic Interchange took place (see Chapter 5), but this period includes the ancestors of the 23 living genera of South American marsupials (Goin et al. 2016).

Fossils of some ten metatherian genera occur in Early Eocene deposits of Seymour Island, near the tip of the Antarctic Penninsula. These include several stem metatherians, polydolopidomorphs, and microbiotheres (Gelfo 2015). In Australia, the definitive marsupial fossil record begins with several genera from the Early Eocene Tingamarra Fauna of southeastern Queensland. One of these (*Tingamarra*) has affinities with more basal South American groups, and others (*Djarthia*, *Thylacotinga*) are probable members of Australidelphia (Goin et al. 2016), but their precise phylogenetic positions remain uncertain. The evidence that these provide about the timing of marsupial dispersal to Australia is discussed in Chapter 5. Representatives of extant Australian marsupial lineages began to appear in the Late Oligocene.

DIVERSITY OF LIVING MARSUPIALS

Modern taxonomy of marsupials dates from Aplin and Archer's (1987) "syncretic" classification based on morphological and molecular phylogenies estimated for living and fossil forms. The result has been a stable set of 7 extant orders with 19 extant families that subsequent research has repeatedly demonstrated as monophyletic (Figure 10.17). Among these are the New World opossums (Didelphimorphia: Didelphidae) and rat opossums (Paucituberculata: Caenolestidae), which Aplin and Archer (1987) united as "ameridelphians." However, recent phylogenetic work (Beck 2008; Meredith et al. 2008, 2011; Mitchell et al. 2014; May-Collado et al. 2015, Duchêne et al. 2018) fails to resolve
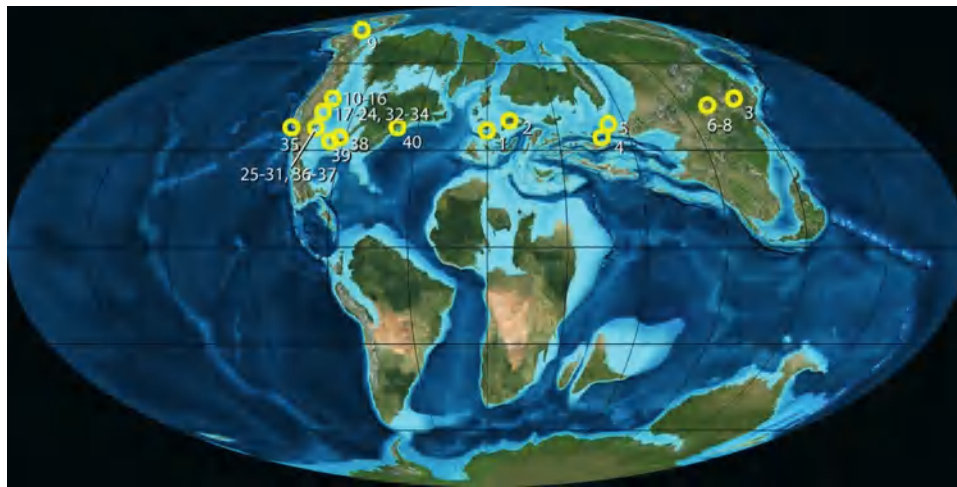
Figure 10.16 Late Cretaceous metatherian localities. Circles indicate localities from which Late Cretaceous metatherian fossils have been recovered. *Redrawn from Williamson et al. (2014).*

"Ameridelphia" as monophyletic. Following Szalay's (1982) demonstration that microbiotheres (of which *Dromiciops gliroides* from Chile is the only extant species) share a derived ankle-joint morphology with Australasian forms, most authors place these taxa in the clade Australidelphia. Despite lingering uncertainty over the position of *Dromiciops* among australidelphians (see May-Collado et al. 2015), molecular analyses have converged mostly on a sister-group relationship between microbiotheres and a clade of all Australasian orders ("Eomarsupialia" of Archer 1984a). Within the latter is a basal divergence between Agreodontia and Diprotodontia. Agreodontia comprises the carnivore-omnivore orders Notoryctemorphia (marsupial moles), Dasyuromorphia (dasyurids, numbat, and extinct thylacines), and Peramelemorphia (bandcoots and bilbies). Diprotodontia contains 11 predominantly herbivorous families. Relationships among agreodontian orders have not been consistently resolved. Within Diprotodontia, wombats and koalas (Vombatiformes) are sister to a clade of 3 other groups, but relationships among the latter are unclear. Phalangeroids and petauroids were long united as Phalangeriformes ("possums"), but there is little support for this in recent molecular studies. Petauroids most often appear as sister to Macropodiformes (kangaroos and relatives).

Didelphimorphia

This order includes the single extant family Didelphidae with 18 genera and 111 species (Voss and Jansen 2009, Burgin et al. 2018). They have a strictly New World (mostly Neotropical) distribution. Several new species have been described in the past decade, including members of *Monodelphis* (Pavan et al. 2012, 2017; Voss et al. 2012), *Lutreolina* (Martinez-Lanfranco et al. 2014), and *Marmosops* (Diaz-Nieto et al. 2011, Diaz-Nieto and Voss 2016). Although "Caluromyidae" and "Glironiidae" have sometimes been
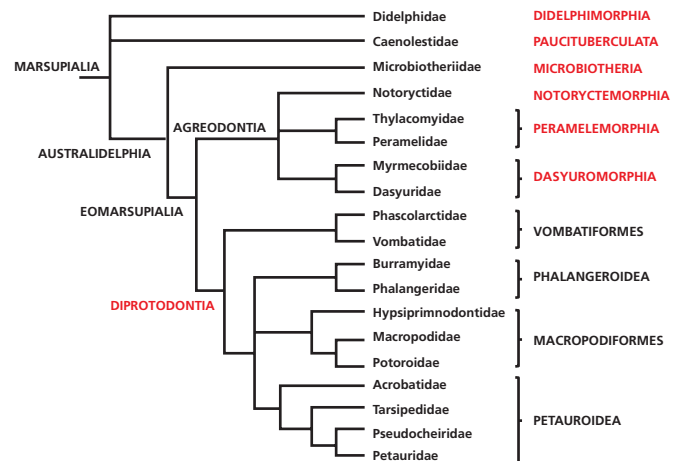
Figure 10.17 Phylogeny of living marsupial orders and families. Family names are at the tips of branches; order names are shown in red. *Based on Beck (2008), Meredith et al. (2008, 2011), Mitchell et al. (2014), May-Collado et al. (2015), and Duchêne et al. (2018).*

recognized as distinct families, Voss and Jansa (2009) and most subsequent authors retain these groups at their traditional subfamily rank.

Morphology. Didelphimorphs are the most generalized marsupials (Marshall 1984), retaining many **plesiomorphic** characteristics believed to approximate the structure of ancestral metatherians. These characteristics include pentadactyly (5 free digits on each foot) and the primitive metatherian dental formula (5/4, 1/1, 3/3, 4/4 = 50) on teeth adapted for omnivory. The full set of incisors is termed "polyprotodont" to distinguish it from the derived "diprotodont" (two front teeth) conditions of paucituberculates and diprotodontians. Didelphimorphs have a long rostrum and a well-developed sagittal crest. Body masses range from 10 g in pygmy opossums *Chacodelphys* to 3 kg in *Didelphis*

Figure 10.18 Virginia opossum, *Didelphis viriginiana*. This is the largest living didelphid and the only one that has extended its range from the neotropics into North America. Note the arboreal position of the animal.

viriginiana (Voss and Jansa 2009; Figure 10.18). The marsupium is well developed in some genera, but absent or poorly developed in others. Most have long, sparsely haired, prehensile tails to accommodate their semiarboreal habits, and an opposable **pollex** (thumb or first digit on the forefoot). Some species, including the Patagonian opossum (*Lestodelphys halli*), which has the southernmost distribution of any didelphid, as well as several species of mouse opossums, have **incrassated** tails; that is, they store fat in the base of their tail for periods of torpor.

Fossil History. Goin and colleagues (2016) considered the Paleocene-Eocene peradectids as early didelphimorphians, but not all phylogenetic analyses support this. Other Paleogene fossil families (e.g., Protodidelphidae, Derorhynchidae, Sternbergiidae) and genera (e.g., *Incadelphys*) are *incertae sedis* (i.e., of uncertain taxonomic placement), and their relationship to didelphimorphians is unclear. Some authors (e.g., Goin et al. 2016) include the fossil Family Caroloameghiniidae (Eocene) within Didelphimorphia, though others consider them paucituberculates. *Caroloameghinia* was a squirrel-sized arboreal frugivore (Croft 2016). The Miocene-Pliocene *Sparassocynus* (Sparassocynidae) was a small carnivore of Argentinian steppes (Reig and Simpson 1972). Cenozoic fossils from Europe and North America often recognized as didelphimorphs are peradectids (e.g., *Peradectes*, *Mimoperadectes*) and herpetotheriids (e.g., *Peratherium*, *Herpetotherium*). The last pre-Pleistocene representatives in the northern hemisphere are Miocene herpetotheriids, *Amphiperatherium* from Spain (Furió et al. 2012) and *Herpetotherium* from Nebraska (Bailey 2004).

Economics and Conservation. The Virginia opossum is one of the few didelphids eaten by humans. It also is taken as a fur-bearer and occasionally by sport hunters in North America (Gardner and Sunquist 2003). In general, however, it is of minor economic importance for fur, for sport, or as a poultry depredator. Some species (e.g., members of *Didelphis*) are reservoirs for zoonotics such as Chagas disease (Roman et al. 2018). The gray short-tailed opossum (*Monodelphis domestica*) has become an important model organism for research on development, the immune system, and cancer. This small (80–120 g), pouchless didelphid from rainforest-scrub habitats south of the Amazon River is relatively easy to breed in captivity. Like all marsupials, its neonates have underdeveloped organ systems comparable to early *in-utero* stages of placental mammals. These features make *M. domestica* ideal for laboratory research (Wang et al. 2009). Loss of tropical habitat adversely affects certain Central and South American didelphimorphs. Handley's slender mouse opossum (*Marmosops handleyi*) is critically endangered (although see Diaz-Nieto et al. 2011), as is the single-striped opossum (*Monodelphis unistriata*), both known from only two specimens taken in areas experiencing habitat loss. The red-bellied gracile mouse opossum (*Cryptonanus ignitus*), known only from the type specimen, has likely been extinct since the 1960s when its forest habitat in Argentina was converted to agriculture.

Didelphidae

This family is almost exclusively neotropical. The only extant marsupial north of Mexico, the Virginia opossum (*Didelphis virginiana*), ranges from British Columbia south through much of the United States, Mexico, and Central America. Other didelphids occur from Mexico south to southern South America and on islands in the Lesser Antilles. Voss and Jansa (2009) organize didelphid diversity into subfamilies Glironiinae, Caluromyinae, Hyladelphinae, and Didelphinae. Glironiinae includes only the medium-sized (ca. 140 g), arboreal bushy-tailed opossum (*Glironia venusta*) found in humid, tropical forests of Ecuador, Peru, Bolivia, and Brazil. Caluromyinae comprises the medium-sized (190–500 g), nocturnal, arboreal woolly opossums (*Caluromys*, 3 species) and black-shouldered opossum (*Caluromysiops irrupta*). These species are forest inhabitants of southern Mexico, Central America, and north-central South America. Hyladelphinae contains only Kalinowski's mouse opossum (*Hyladelphys kalinowskii*), a tiny (10–20 g) denizen of lowland forests of Amazonia.

Didelphines (14 genera, 105 species) occur in almost all habitats from deserts to tropical forests and at elevations up to 3,400 m. Some are terrestrial burrowers, although many are semiarboreal and inhabit tree dens. Generally solitary, most didelphines are opportunistic feeders, their diet dependent upon seasonal forage availability. Gestation periods are usually less than 2 weeks; neonates weigh about 0.1g (see Figure 10.11). Within *Didelphis*, mean litter size is 4–9 and increases with increasing latitude, while the length of the breeding season decreases (Rademaker and Cerqueira 2006; Goin et al. 2016).

Didelphids and caenolestids have paired sperm—joined side-by-side in didelphids and head-to-head in caenolestids (Figure 10.19). Although unpaired in the testes, sperm become coupled in the epididymis (Tyndale-Biscoe and Renfree 1987), then again separate in the female's oviducts. Although this phenomenon has been known for over 100 years, its significance is uncertain. Taggart and coworkers (1993) suggested that pairing in *Monodelphis domestica* aligns flagellae for enhanced motility. Moore and Moore (2002) note that after unpairing in the oviduct, one sperm cell becomes disabled while the other retains normal motility. They argue that pairing represents a case of "green beard selection" in which two sperm cells (which share many genes) cooperate to increase the likelihood of successful fertilization by one while the other is sacrificed. Because didelphids and caenolestids are not sister clades among living marsupials, and given the difference between

Figure 10.19 **Paired sperm in New World marsupials.**
Two families of marsupials have paired sperm, a feature unknown in any other mammal. Lateral view of the anterior ends of sperm pair typical of (**A**) a didelphid and (**B**) a caenolestid. *Abbreviations*: h = head; n = anterior portion of neck; a = acrosome. *Adapted from Tyndale-Biscoe (2005).*

them in sperm-pair morphology, sperm pairing probably evolved independently in the two groups.

As with all marsupials, reproduction is timed so that the young leave the pouch when resources are optimal. Several didelphids (*Monodelphis dimidiata*, *Gracilianus microtarsus*, *Gracilianus agilis*, *Marmosops incanus*, and *Marmosops paulensis*) show **semelparity**, a life-history strategy in which all or most males die after mating and females after weaning (Lopes and Leiner 2015). The most specialized didelphid is the yapok, or water opossum (*Chironectes minimus*), the only marsupial adapted for an aquatic habitat (Galliez et al. 2009) and a diet of small aquatic vertebrates. The hind feet are webbed, and the female's marsupium becomes watertight during dives.

Chemisquy and colleagues (2015) performed a phylogenetic comparative analysis of didelphid tooth evolution, asking whether the **occlusal** surface shapes of molars (Figure 10.20A) are more strongly influenced by diet or phylogeny. As pointed out in Chapter 4, many aspects of tooth morphology are dietary adaptations (e.g., sectorial molars for shearing in carnivorans, lophodont molars for grinding vegetation in kangaroos and elephants). Didelphids utilize a relatively restricted range of food types, from predominately fruit (e.g., woolly opossums, *Caluromys*) to predominantly vertebrate prey (e.g., thick-tailed opossums, *Lutreolina*), with more generalized omnivore-insectivores in between. Vieira and Astúa de Moraes (2003) classified didelphid genera into 5 diet categories (I–V) reflecting this frugivore-carnivore continuum (Figure 10.20B). All didelphid molar surfaces resemble the primitive tribosphenic pattern of early mammals (Chapter 4). Chemisquy and colleagues (2015) measured the position of 26 landmarks on digitized images of occlusal surfaces of first and third upper and lower molars from 13 extant and 3 extinct didelphid genera, then aligned landmarks among taxa using a geometric morphometric technique (see "Specimen-Based Studies" in Chapter 2). They reconstructed ancestral molar shapes on the phylogeny of Voss and Jansa (2009) with the "spatial optimization using parsimony" method and assessed correlations among molar shape, diet, and phylogeny using "canonical phylogenetic ordination" (Figure 10.20C). The latter method determines what fraction of the total variation in the occlusal shape of each tooth is explained by variation in diet versus variation in phylogenetic position. Phylogeny explained most (62%–76%) of the variation in molar shape, whereas diet explained only 10%–22%. Chemisquy and coworkers (2015) suggest that a possible explanation lies in the functional importance of transverse shearing crests for processing insect food, even in species with diets having a small proportion of insects (e.g., those in categories I and V). If key aspects of molar anatomy are thus constrained by an insect dietary component in all didelphids, the limited variation in shape observed may be a balance between adaptive (e.g., longitudinally oriented metacristae in the carnivorous *Lutreolina* clade) and nonadaptive (e.g., driven by genetic drift) phylogenetic divergence.
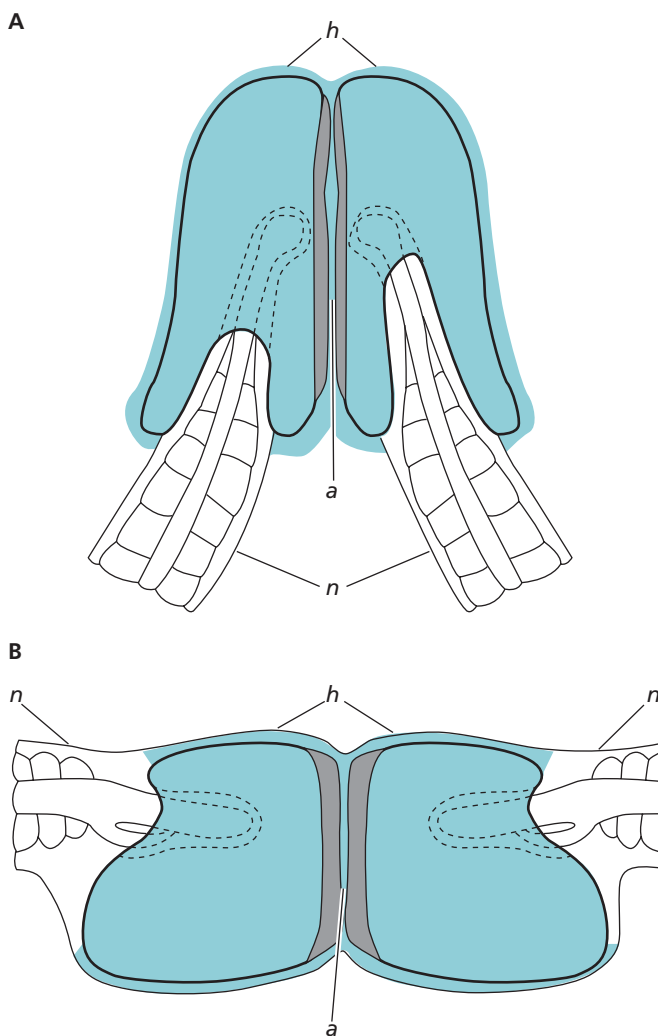
A

Caluromys **I**

Monodelphis **IV**
Marmosa **II**

Marmosops **II**
Thylamys **IV**
Lestodelphys **V**
Gracilinanus **II**
Cryptonanus **II**

Metachirus **IV**
Chironectes **V**
Philander **IV**
Didelphis **III**
Thylophorops **V**
Lutreolina **V**
Hyperdidelphys **V**

B

C

Monodelphis   Thylamys   Lestodelphys

Metachirus   Chironectes

Didelphis   Thylophorops
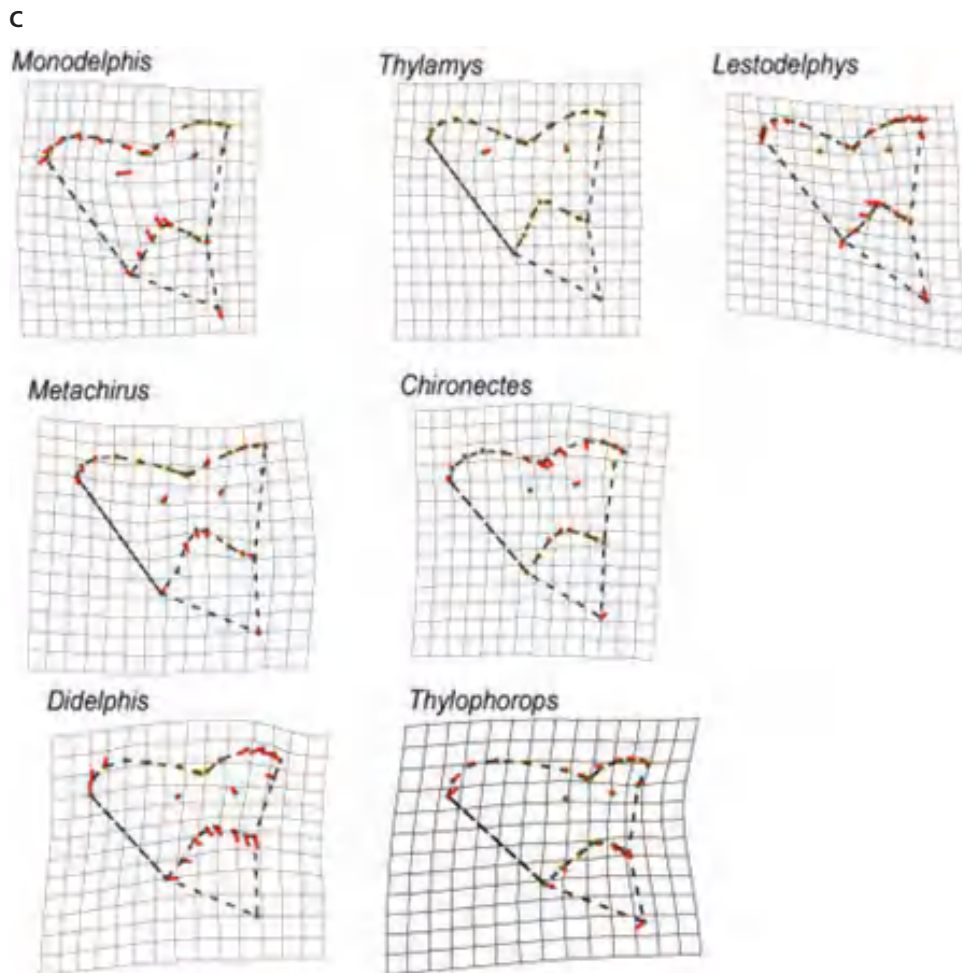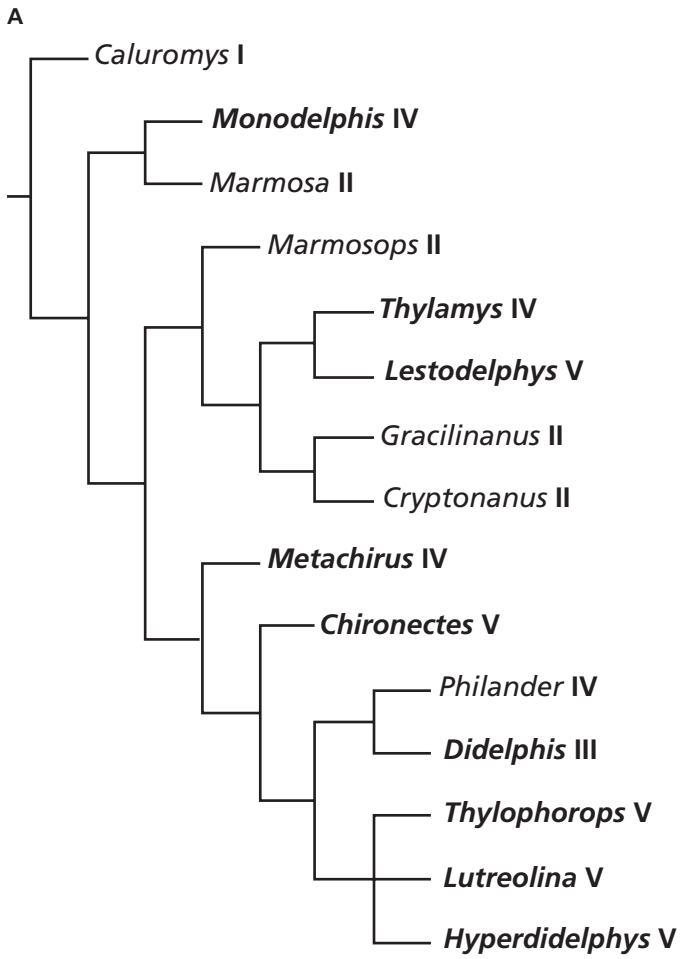
Paucituberculata

The single family, Caenolestidae, within this order contains three genera and seven species of "shrew," or "rat," opossums. The five species of *Caenolestes* occur in dense vegetation in cold, wet, high-elevation forests and meadows of northwestern South America. *Caenolestes sangay*, the eastern caenolestid from Ecuador, is the most recently described species (Ojala-Barbour et al. 2013). The Peruvian shrew opossum, or Incan caenolestid (*Lestoros inca*), inhabits the Andes Mountains of southern Peru, whereas the rare Chilean shrew opossum or long-nosed caenolestid (*Rhyncholestes raphanurus*)—the southernmost member of the family—occurs in moist, low-elevation forests of south-central Chile (including Chiloé Island) and nearby Argentina. Caenolestids are primarily nocturnal, insectivorous or omnivorous, and terrestrial. Like didelphids, caenolestids have spermatozoa that pair within the epididymis, though the alignment of pairing differs in the two groups (see Figure 10.19).

Morphology. Caenolestids are small and shrew-like in appearance (Figure 10.21). They have a long rostrum and small eyes, and the hind limbs are longer than the forelimbs. Adults weigh about 20–40 g. Total length is about 10–25 cm, half of which is the long, fully haired tail. They have a Type I pouch (Figure 10.12) with essentially no marsupium. The dental formula is 4/3–4, 1/1, 3/3, 4/4 = 46–48. The enlarged, procumbent first lower incisors (caenolestids are diprotodont) have enamel only on the anterior surface, and the lower canines are vestigial. (Note that I_1 "diprotodonty" in caenolestids is not homologous to that in diprotodontians, which involves the second lower incisors.) The deciduous last premolars do not develop into functional teeth and are lost early in development (Luckett and Hong 2000, Forasiepi and Sánchez-Villagra 2014).

Fossil History. The earliest known fossil paucituberculates are from the Early Eocene (e.g., *Riolestes*). Paucituberculates were much more diverse during the first half of the Cenozoic than they are today. Goin and coworkers (2016) recognized three extinct families and ten genera from the Eocene to Miocene, and Abello (2013) provided a phylogenetic analysis of these taxa. Extinct paucituberculates were mostly insectivores, but abderitids had adaptations for frugivory. Four genera of caenolestids are known from the Eocene through Pliocene, but there is no pre-Holocene record of the extant genera.

Economics and Conservation. Relatively little is known about most caenolestids. The long-nosed caenolestid (*R. raphanurus*) has been found at less than 25 locations (Mar-

Figure 10.21 A South American caenolestid. The rat opossum Rhyncholestes raphanurus.

tin 2011). The blackish shrew opossum (*Caenolestes convelatus*), Andean caenolestid (*C. condorensis*), and eastern caenolestid (*C. sangay*)—each known from only a few specimens—are considered vulnerable due to habitat loss.

Microbiotheria

The single family in this order, Microbiotheriidae, contains only one extant species. The monito del monte— "little monkey of the mountains," *Dromiciops gliroides* (Figure 10.22)—is nocturnal and arboreal and inhabits temperate rain forests of south-central Chile and adjacent Argentina. Its distribution is associated with beech (*Nothofagus*) and bamboo (*Chusquea*) forests, though it also occurs in second-growth myrtle (*Myrtus*) forests (Fontúrel et al. 2012). Its distinctive, round nests are found in fallen logs, tree cavities, and thickets. Nests are often lined with leaves of water-resistant Chilean bamboo. Prior to **hibernation**, fat accumulates in the base of the incrassated, prehensile tail. Enough fat may be stored in a week to double an individual's body mass. The species also exhibits short periods of daily torpor, reducing their metabolic rate up to 92% depending on food availability and ambient temperature (Nespolo et al. 2010). *Dromiciops* is omnivorous (Celis-Diez et al. 2012), but as a frugivore it plays a critical ecosystem role in dispersing the seeds of many native plants in its feces (Amico et al. 2009). Unlike the other New World marsupials, *Dromiciops* does not have paired sperm (Tyndale-Biscoe 2005).

Figure 10.20 Diet and molar evolution in Didelphidae. (**A**) Phylogeny of selected didelphid genera from Voss and Jansa (2009) with dietary categories from Vieira and Astua de Moraes (2003) at each tip. Categories form a continuum from mainly frugivorous (I) to mainly carnivorous (V), with omnivore-insectivore diets intermediate (II-IV). (**B**) A short-tailed opossum (Monodelphis domestica). Members of this genus have a high proportion of vertebrate prey in their diet. (**C**) Deformation grids showing the molar shapes of selected tips. (**A**) and (**C**) redrawn from Chimisquy et al. (2015).

Figure 10.22 **Monito del monte.** *Dromiciops gliroides,* the only living member of Microbiotheria.

Figure 10.23 **Skull of *Dromiciops*.** (**A**) Dorsal, (**B**) lateral, and (**C**) ventral views of the skull of a monito del monte (*Dromiciops gliroides*). Note the five upper incisors in an arc-shaped pattern, large palatal vacuities, and inflated auditory bullae (highly unusual in a marsupial). *Adapted from Marshall (1978).*

Morphology. These small (16–30 g), mouse-like animals have a maximum head and body length of 13 cm. The well-furred, prehensile tail is also about 13 cm long. The fur is short and thick, and a well-formed pouch is evident in females. The soles of the hind feet have 5 distinct, transverse pads, or ridges. Females are significantly heavier than males (Franco et al. 2011), but males have larger home ranges (Celis-Diaz et al. 2012). The dental formula is the same as in didelphids (5/4, 1/1, 3/3, 4/4 = 50). The skull is noteworthy for its greatly inflated auditory bullae, unlike any other marsupial (Figure 10.23). Giannini and colleagues (2004) discussed the postnatal ontogeny of the *Dromiciops* skull based on 14 cranial dimensions. Recent analyses of morphological (Martin 2018) and molecular (Súarez-Villota et al. 2018) data confirm the existence of a just a single *Dromiciops* species.

Fossil History. Most authors since Marshall and de Muizon (1988) accept *Khasia*—teeth from the Paleocene of Brazil—as the oldest microbiothere, but Goin and coworkers (2016) consider it a pediomyid. Eocene representatives include the larger woodburnodontids and smaller microbiotheriids (including some from Antarctica); the latter diversified in the Miocene but declined to the single species of *Dromiciops* in the later Neogene.

Economics and Conservation. The seed-dispersing role of *Dromiciops* (Fontúrel et al. 2012) has been recognized as a critical ecosystem service that helps maintain biodiversity in South American temperate rainforests. There are no known negative impacts on humans. *D. gliroides* is considered near threatened, with population trends decreasing as a result of habitat loss (Martin et al. 2015).

Dasyuromorphia

Dasyuromorphians are small to medium-sized Australasian marsupials that include three families of carnivore-insectivores (Dasyuridae, Myrmecobiidae, and Thylacinidae). Most of the extant species are dasyurids. With the recent extinction of the thylacine (*Thylacinus cynocephalus*), the Tasmanian devil (*Sarcophilus harrisii*) is the largest living carnivorous marsupial. Unfortunately, populations of devils have declined over 60% because of Devil Facial Tumour Disease (DFTD), a fatal, contagious cancer that has spread rapidly since its emergence in 1996 (Hawkins et al. 2008). Malignant tumors occur on the face, jaw, and oral cavity and are spread by biting during social interactions. Devils usually die within 6 months of the appearance of **lesions** (Murchison et al. 2012). Resistance to the disease is limited by the low genetic diversity of devils, especially in the major histocompatability complex (Hamede et al. 2012).

Morphology. Like didelphids, dasyuromorphians have teeth that resemble those of primitive marsupials. Canines are well developed; carnivorous species such as the Tasmanian devil and quolls (*Dasyurus*) have specialized **sectorial** (blade-like, shearing) molar cusps. Tails are usually long, often held erect, and never prehensile.

Fossil History. Thylacinid and dasyurid fossils appear in Australia by the late Oligocene; myrmecobiids have no pre-Pleistocene fossil record. Phylogenetic dating estimates based on morphological and molecular data suggest that dasyurids and myrmecobiids are sisters apart from thylacinids and place divergences among the 3 families some 30–40 mya in the early Oligocene or late Eocene (Kealy and Beck 2017; Feigin et al. 2018).

Thylacinidae

This family included the recently extinct Tasmanian "tiger, wolf, or thylacine" (Figure 10.24). Thylacinids were quite diverse during the Oligo-Miocene, and 13 fossil species in 9 genera have been described (Archer and Hand 2006). Thylacines are an oft-cited example of evolutionary convergence with placental canids, though Janis and Figueirido (2014) showed that thylacines had a less specialized forelimb structure than placental pounce-pursuit or ambush predators. Holocene fossil thylacines (and Tasmanian devils) occurred throughout Australia and New Guinea; White and colleagues' (2018b) statistical analysis suggested that both species went extinct on the Australian mainland approximately 3,200 years ago. Thylacines were common in Tasmania prior to European colonization, but soon came into conflict with humans because they preyed on domestic livestock (Wroe et al. 2005). Thylacine populations rapidly declined throughout the 1800s and early 1900s because of predator control programs, habitat loss, and competition with the dingo (Johnson and Wroe 2003). The Australian government placed a bounty on thylacines in 1888 (Figure 10.25), and the last captive individual died in the Hobart Zoo in 1936. Ironically, the species was given complete legal protection by the Tasmanian government a few years later. Carlson and coworkers' (2018) modeling study estimated that thylacines went extinct in the wild between 1936 and 1943, despite unconfirmed sightings that are still periodically reported. Prior to extinction, thylacine populations apparently had very limited genetic diversity, both on the mainland and in Tasmania (Menzies et al. 2012; White et al. 2018a). The phylogenetic relationships of thylacinids have received much attention, including some of the earliest (Thomas et al. 1989; Krajewski et al. 1992, 1997) and most extensive (Miller et al. 2009; Feigin et al. 2018) analyses of "ancient DNA." The latter confirm

Figure 10.25 **A hunter and dead thylacine.** Lethal control by humans was a factor in the extinction of thylacines. *Victor Prout may have taken this photo in 1869.*

that thylacinids are sister to a clade of myrmecobiids + dasyurids.

Myrmecobiidae

This monotypic family includes only the numbat (*Myrmecobius fasciatus*), which is highly specialized for a diet of ants and termites (**myrmecophagy**). Numbats were extirpated from New South Wales by 1857 and South Australia by 1924 (Archer 1978). The species is now restricted to isolated populations in arid, scrub woodlands in southwest Western Australia. Introduced predatory red foxes (*Vulpes vulpes*) and feral cats have reduced numbat populations to less than 1,000 individuals, and they are listed as endangered by the IUCN. Reintroduction of numbats into areas of their former range in New South Wales and South Australia have been initiated, but their long-term success hinges on protection from introduced predators (Hayward et al. 2015). Numbats forage diurnally, which is unusual among marsupials. They are active about 5 hours a day as they search for prey in hollow logs, but spend the night in tree cavities and burrows (Cooper and Withers 2004, 2005). Despite their inhabiting an arid habitat, the ability of numbats to concentrate urine is no greater than that of other dasyuromorphs. Apparently, their diet supplies adequate amounts of water (Cooper and Withers 2010). They are solitary except during the breeding season. The gestation period is 2 weeks and the usual litter size is 4. They

Figure 10.24 **A captive pair of thylacines in 1902.** The recently extinct *Thylacinus cynocephalus* was the largest modern species of carnivorous marsupial, with a body mass of 15–35 kg.

have no marsupium, and neonates cling to curly hair on the abdomen as they hang from the teats.

Numbats reach about 44 cm in total length, with the fully furred tail equal to the head and body length (Figure 10.26). Adults weigh up to 700 g. The reddish or grayish brown pelage has 7 transverse white and black stripes on the dorsum, and there is a black eye stripe. Like other myrmecophageous mammals, they have an elongated, tapered rostrum and tongue to take ants and termites. Their tongue can be extended 10 cm—close to half their head and body length. Numbats have small, degenerate, peg-like teeth. They also have **supernumerary** (additional) cheek-teeth, for a total of up to 52 teeth—more than any other metatherian. Like many other marsupials, both sexes have a large presternal gland on the upper chest, probably used to mark territories (Friend 1989).

Dasyuridae

This large, diverse family (17 genera and 76 species) is the most structurally and functionally generalized of the Australasian marsupials. Based on DNA sequence analysis, Krajewski and colleagues (2000a) and many subsequent studies confirmed that the family is monophyletic. Dasyurids range in size from the smallest marsupials, the tiny Pilbara ningaui, and other marsupial "mice," to the largest extant marsupial carnivore, the Tasmanian devil (Figure 10.27). Dasyurids occur throughout Australia and New Guinea, where they occupy all terrestrial and semiarboreal habitats from deserts to high-elevation rainforests. They are primarily nocturnal or **crepuscular** (active at dawn and dusk) and solitary.

The 42–46 teeth of dasyurids are specialized for a carnivorous or insectivorous diet. The marsupium usually is poorly developed or absent. In several species of *Antechinus*, males exhibit a mass die-off after mating in the first year of life. Male mortality results from effects of high levels of testosterone and cortisol on multiple organ systems. Females survive to raise litters and can mate again the following year (Naylor et al. 2008). Multiple paternity has been confirmed in dasyurids, including the tiger quoll (*Dasyurus maculatus*), by Glen and coworkers (2009). Dorph and McDonald (2017) used quantitative analysis of recordings to demonstrate that eastern quolls (*Dasyurus viverrinus*) have a 5-type repertoire of distinct vocalizations employed during aggressive encounters among conspecifics

Incrassated tails occur in several genera that inhabit deserts, including dunnarts (*Sminthopsis*), pseudantechinuses (*Pseudantechinus*), and mulgaras (*Dasycercus*). Molecular analyses by Pavey and colleagues (2011) confirmed the brush-tailed mulgara (*D. blythi*), partially sympatric with *D. cristicauda* and formerly considered synonymous, as a distinct species. In contrast, Umbrello and coworkers (2017) rejected the genetic distinctness of *Pseudantechinus roryi* from *P. macdonnellensis*. These and other studies suggest that current species-level taxonomy within Dasyuridae is imprecise. Masters and Dickman (2012) concluded that *D. blythi* could survive the harsh, arid conditions of central Australia because of its flexible feeding habits, deep burrows, and ability to enter torpor and endure large fluctuations in body condition. Krajewski and colleagues (2000b), Krajewski and Westerman (2003), and Westerman and coworkers (2016) provided extensive analyses of DNA sequences from most dasyurids and confirmed earlier results that living species are divided between two major phylogenetic branches, each with two constituent clades: Dasyurinae (quolls and relatives, plus antechinuses and relatives) and Sminthopsinae (dunnarts and relatives, plus planigales). Molecular dating suggests that dasyurines and sminthopsines diverged in the mid-Oligocene, but radiations

Figure 10.26 External features of a numbat. The endangered numbat (*Myrmecobius fasciatus*) is distinctively striped. Like all species of ant and termite eaters, it has a long, extensible tongue.

Figure 10.27 Tasmanian devil. *Sarcophilus harrisii* is the largest extant marsupial carnivore. This species is currently endangered due to spread of devil facial tumor disease.

within them were delayed until the mid-Miocene. Both episodes of cladogenesis coincide with climatically induced changes in habitat across Australia.

Several dasyurids are endangered, including the southern dibbler (*Parantechinus apicalis*), northern quoll (*Dasyurus hallucatus*), eastern quoll (*Dasyurus viverrinus*), and Tasmanian devil (*Sarcophilus harrisii*). The Kangaroo Island dunnart (*S. aitkeni*) is critically endangered, with perhaps fewer than 500 individuals left in the wild. Several other species of dasyurids are threatened, mostly by a combination of habitat degradation and invasive species.

Peramelemorphia

Bandicoots (Peramelidae) and bilbies (or rabbit-eared bandicoots—Thylacomyidae) occur throughout Australasia. All living species are terrestrial omnivores, feeding on invertebrates, small vertebrates, and plant material; the recently extinct pig-footed bandicoot (*Chaeropus ecaudatus*) was herbivorous. Bandicoots occupy a variety of habitat types from arid deserts to tropical rainforests and jungle, often at high elevations.

Peramelemorphians are unusual among marsupials in having chorioallantoic placentae. Unlike eutherians, however, the placentae have no villi; thus, gestation periods in these species are no longer than in other metatherians. In fact, both the northern brown bandicoot (*Isoodon macrourus*) and the long-nosed bandicoot (*Perameles nasuta*) have gestation periods of 12.5 days—the shortest known among mammals.

There has been considerable debate about the phylogenetic relationships and classification of peramelemorphians. Westerman and colleagues (2012) provided a robust assessment of living forms based on nuclear and mitochondrial DNA sequences. Bilbies (*Macrotis*, Thylacomyidae) are sister to all other extant bandicoots (Peramelidae). The recently extinct pig-footed bandicoots (*Chaeropus*, Chaeropodidae), are sister to living bandicoots and bilbies.

Morphology. Peramelemorphians have a short, compact body, with a long, pointed rostrum. All are adapted for digging with strong claws on the second, third, and fourth digits of the forefeet. All species are **syndactylous**, with the second and third hind digits joined in a common skin sheath, a convergent trait shared with diprotodontians. Hind limbs are larger than forelimbs, and the hind feet have a well-developed claw on the enlarged fourth digit

Dr. Patricia Woolley—A pioneer in marsupial biology

Dr. Patricia Woolley, a pioneer in marsupial biology.

Born in 1932 in Denmark, southern Western Australia, Pat Woolley has been a pioneer in the study of marsupials for decades, overcoming many obstacles along the way. She began her university studies in mathematics and physics at the University of Western Australia in Perth, but soon changed her major to zoology. Upon graduating in 1955, she began work as a research assistant to Professor Harry Waring, as well as helping PhD students working in the department. In 1960, she moved to the Australian National University in Canberra, where she was a temporary Lecturer in zoology. Pat also began her PhD program

there, working with Hugh Tyndale-Biscoe. She studied reproduction and other life-history characteristics of what is now recognized as the agile antechinus (*Antechinus agilis*). Whereas most research on marsupials had been on macropodids, she would continue working with dasyurids throughout her career. A major contribution from her doctoral research was her discovery of the unusual phenomenon of semelparity in male antechinus—in captivity, males died off or became sterile after their initial ("frantic") breeding season—now known to occur in the wild in several other species. After completing her PhD in 1966, she spent the bulk of her career, from 1967 until 2000, teaching and conducting research at La Trobe University in Melbourne, where she was the institution's first zoologist. Her work on penis morphology led to major revisions within *Antechinus*, with five species placed in three other genera. Throughout the 1980s and 1990s, Pat broadened her work to dasyurids in New Guinea, making numerous trips there and to the Aru Islands. Her research also includes morphology and reproduction in *Sminthopsis.* Pat began searching for the Julia Creek dunnart, *S. douglasi*—thought to be extinct—in 1991. She caught live animals a year later and began a breeding colony. Her work has inspired many other biologists working on marsupials and earned her recognition as an Honorary Life Member of the Australian Mammal Society in 1999, and Honorary Life Member of the American Society of Mammalogists in 2001. In 2000 Pat earned the Outstanding Achievement Award from the international Society of Women Geographers, and in 2003 she received the Ellis Troughton Memorial Award and Medal from the Australian Mammal Society. Woolley's pseudantechinus (*Pseudantechinus woolleyae*), described in 1988, is named in her honor.
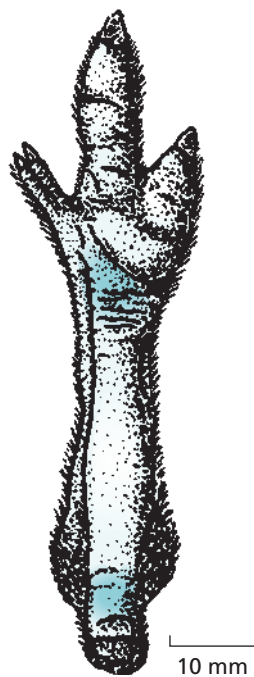
Figure 10.28 **Hind foot of a bilby.** The left hind foot of the greater bilby (*Macrotis lagotis*), showing the enlarged fourth digit and syndactylous second and third digits. *Adapted from Walton and Richardson (1989).*

(Figure 10.28). Bandicoots are unique among marsupials in having a well-developed patella (kneecap) and no clavicle (collar bone) (Jones 1968).

Dentition is polyprotodont, with 5 pairs of upper incisors and 48 total teeth (46 in some bilbies). The canines are well developed, and the molars are adapted for an omnivorous diet. The marsupium also is well developed and opens posteriorly. There are 8 teats, even though mean litter size usually is 4. This allows consecutive litters to be produced, as teats remain swollen after nursing the previous litter, and incoming neonates cannot attach to them.

Fossil History. The bandicoot fossil record of some 9 genera (mostly stem lineages to the living forms) dates from the late Oligocene. Molecular data suggest, however, that the order originated in the Paleocene (ca. 60 mya), with subsequent diversification of peramelids in the Miocene and early Pliocene (Kear et al. 2016; see also Travouillon and Phillips 2018). The precise timing of this diversification is contentious, particularly whether it preceded or was caused by the mid-Miocene drying of Australia.

Economics and Conservation. Valentine and coworkers (2013) showed that foraging (digging) by southern brown bandicoots (*Isoodon obesulus*) is a critical mechanism for soil turnover in Western Australia. Many species of peramelids have suffered significant population and range declines from presettlement times because of introduced predators and habitat loss to domestic livestock. Species of *Peroryctes* are hunted for food in New Guinea.

Peramelidae

The 6 genera and 20 species of living bandicoots (Figure 10.29) occur in a variety of habitats, primarily in Australia. Westerman and colleagues (2012) and Kear et al. (2016) confirm a basal phylogenetic division between the two Australian genera (Peramelinae) and 4 predominantly New Guinean (Peroryctinae, Echymiperinae) genera. Bandicoots range in size from the mouse bandicoot (*Microperoryctes murina*), with a maximum head and body length of 17 cm and tail of 11 cm, to the giant bandicoot (*Peroryctes broadbenti*), which reaches a total length of 90 cm and body mass of 5 kg. The 5 species of New Guinean spiny bandicoots (*Echymipera*) and the endangered Seram Island bandicoot (*Rhynchomeles prattorum*) lack the fifth upper incisor found in other peramelemorphs. All species are nocturnal, terrestrial, and solitary. They are insectivorous or omnivorous and occur in grassland, shrub, and rainforest habitats. Both groups exhibit sexual dimorphism, with males being larger than females. Bandicoots have short, coarse pelage, often with stiff, quill-like guard hairs and relatively small ears and tail.

In addition to the recently extinct desert bandicoot (*Perameles eremiana*), several peramelids are listed as endangered. *Echymipera davidi* is known from only a small area on the island of Kiriwina off the southeast coast of New Guinea, where human population growth and agricultural land conversion are driving habitat decline. *Peroryctes broadbenti* from southeastern New Guinea is threatened by hunting and habitat loss to oil palm plantations. *Rhynchomeles prattorum* is known only from seven specimens collected in the 1920s on the island of Seram; its forest habitat is being rapidly cleared and populated with introduced predators.

Thylacomyidae

There are two recognized species of bilbies. The threatened greater bilby (*Macrotis lagotis*) occurs in arid habitats of northwestern in Australia, much reduced from its historic range. The lesser bilby (*M. leucura*) probably became

Figure 10.29 **Northern brown bandicoot.** *Isoodon macrourus* and other bandicoots have shorter and coarser pelage than do bilbies.

Figure 10.30 **Greater bilby.** *Macrotis lagotis* is the last living member of Thylacomyidae.

Figure 10.31 **External features of a marsupial mole.** *Notoryctes typhlops* has large forefeet, reduced eyes, no pinnae, and a thick, leathery nasal shield. *Illustration from Nilsson et al. (2010).*

extinct in the 1960s. Gibson and Hume (2000) concluded that the digestive physiology of the greater bilby is flexible to accommodate both plants and animals in their diet, which allows them to survive in the arid regions to which they are now restricted (Gibson et al. 2002). Body mass of bilbies reaches 2.5 kg. Like peramelids, they have a chorioallantoic placenta and short gestation period. Bilbies have a long tail, 50%–60% of the head and body length, and longer, silkier pelage than bandicoots (Figure 10.30). Their long, rabbit-like ears reach beyond the tip of the snout and are folded over the eyes when individuals sleep. Bilbies are powerful burrowers; unlike bandicoots, they construct their own burrows. In the form of a deeply angled spiral that can be 2 m deep, burrows offer a refuge from desert heat during the day. Wild greater bilbies produce up to 4 litters per year, a much higher reproductive rate than in captive populations. However, longevity is much greater for captives (Southgate et al. 2000).

Notoryctemorphia

This order encompasses a single family, Notoryctidae, which includes the southern marsupial mole (*Notoryctes typhlops*), known by Aboriginal people as "itjaritjari," and the northern marsupial mole (*N. caurinus*), or "kakarratul" (Benshemesh and Aplin 2008, Benshemesh 2008). They represent the only completely fossorial marsupials. *Notoryctes* is widely distributed over much of northwestern and central Australia, occurring in shrub-desert areas and sandy bottomland soils. Their diet consists primarily of ants, termites, and beetle larvae (Pavey et al. 2012), which are taken as individuals burrow through soil. Although their morphological characteristics (noted below) are convergently similar to those of unrelated eutherian talpids and chrysochlorids (Benshemesh and Johnson 2003; Crumpton et al. 2015), marsupial moles have a different manner of burrowing. They essentially "swim" through the ground—substrate collapses behind them and they

leave no permanent tunnels (Benshemesh 2014). They also spend much more time foraging on the surface than eutherian moles and are active both day and night. Little is known of their reproductive biology.

Morphology. Like eutherian moles, the body of *Notoryctes* is **fusiform** (torpedo-shaped, compact, and tapered) and adapted for a fossorial existence. Maximum head and body length of adults is about 14 cm, with a stubby tail 2–3 cm long. Adults weigh about 60 g. The iridescent pelage is long and silky. Other fossorial adaptations include strong forelimbs with greatly enlarged, scoop-like claws on the third and fourth digits (Figure 10.31). There is a thick, keratinized nasal shield used to push dirt, and the cervical vertebrae are fused for added rigidity. There are no pinnae. Located under the skin, the vestigial eyes are 1 mm in diameter and have no lens; the optic nerve is greatly reduced.

Reduced epipubic bones occur in both sexes. Dentition is variable, with 40–44 teeth. The occlusal surface of the molars is **zalambdodont** (V-shaped), which is unusual among marsupials. During the breeding season, females have a well-developed marsupium that opens posteriorly. The testes are never scrotal but lie between the skin and the abdominal wall (Benshemesh 2008).

Fossil History. Notoryctids are known from the early Miocene of northwest Queensland. The extinct *Naraboryctes* appears to have achieved the same degree of fossorial adaptation as the extant *Notoryctes*, suggesting an even more ancient origin for moles' subterranean lifestyle (Beck et al. 2014). Duchêne and coworkers (2018) estimated a Paleocene divergence of noryctemorphians from bandicoots.

Economics and Conservation. Marsupial moles are eaten by Australian Aborigines, who follow distinctive trails left by the moles when traveling on the surface. Introduced foxes and cats also prey upon moles. Neither species of mole has any impact on grazing lands. Although both were formerly considered endangered, they are now considered of "least concern" by the IUCN.

Diprotodontia

This diverse order of 11 extant families includes the familiar kangaroos, koala, wombats, and numerous other primarily

herbivorous marsupials. As might be expected, given the approximately 155 species in this order, adaptive radiation has been extensive. Species feed on insects, nectar, leaves, or fruit, or they are omnivores. Many species are terrestrial, but some are arboreal. As noted above (Figure 10.17), 4 major clades are now recognized: (1) wombats and koala constitute Vombatiformes; (2) Macropodiformes encompasses Potoroidae (potoroos and bettongs), Macropodidae (kangaroos and wallabies), and Hypsiprymnodontidae (musky rat-kangaroo); (3) Phalangeroidea comprises Burramyidae (pygmy possums) and Phalangeridae (phalangers and cuscuses); and (4) Petauroidea includes Acrobatidae (feathertail possums), Tarsipedidae (honey possum), Pseudocheridae (ringtail possums), and Petauridae (gliders and relatives).

Morphology. All species are diprotodont with an enlarged and procumbent I_2 on each side; the second and third hind digits are syndactylous, convergently with bandicoots. In many arboreal diprotodonts, including the koala (Phascolarctidae), ringtail possums (Pseudocheiridae), and cuscuses (Phalangeridae), the first two digits of the forefeet oppose the other three digits (Figure 10.32)—that is, they are **schizodactylous**. On the hind feet, the big toe (**hallux**) is also opposable. This is not the case in terrestrial species, however. Dental adaptations include a large pair of lower incisors and three pairs of smaller upper incisors (although wombats have a single pair of upper and lower incisors). Upper canines are variable in size and shape; there are no lower canines.

Fossil History. The earliest fossil diprotodonts date from late Oligocene deposits of Australia, although molecular evidence points to earlier origins. The Pleistocene *Diprotodon* (Diprotodontidae) was the largest marsupial that ever lived (at ca. 2,800 kg).

Economics and Conservation. Many diprotodonts compete with domestic livestock on grazing lands. Other species have been (and still are) hunted for meat or hides. Some species of wallabies and kangaroos have been seriously reduced in density and distribution following European settlement, with several recent extinctions attributed to habitat loss or introduced predators.

Vombatiformes

Phascolarctidae

The familiar koala, with a superficial resemblance to a small bear (Figure 10.33), is the only extant species in this family. The family was once quite diverse, however, with seven fossil genera described. Black and colleagues (2012) discussed *Priscakoala lucyturnbullae* from Miocene deposits of northern Australia. Koalas occur in *Eucalyptus* woodlands throughout eastern and southeastern Australia. Both koalas and wombats (Vombatiformes) have a marsupium that opens posteriorly and vestigial tails (unusual in an arboreal species) and lack the first two premolars, among several other shared features. Unlike wombats, the koala
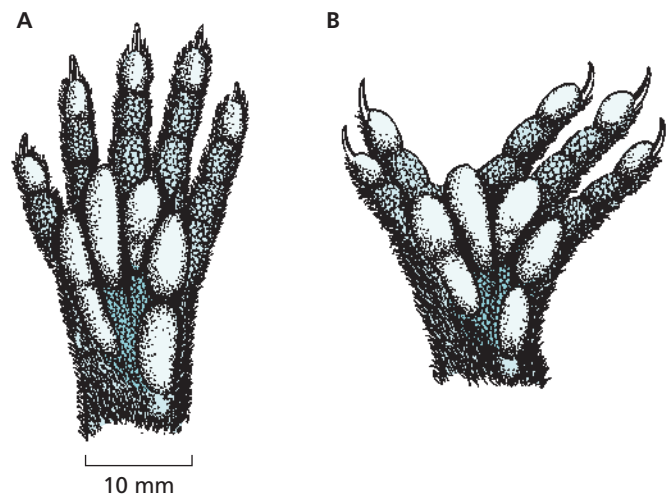
Figure 10.32 **Schizodactylous forefeet.** In many arboreal diprotodonts, including the koala, ringtail possums, and cuscuses, the forefoot is adapted for grasping. (**A**) Digits closed; (**B**) digits open. *Adapted from Walton and Richardson (1989).*

Figure 10.33 **Koala.** The koala (*Phascolarctos cinereus*) spends a large part of each day resting in a tree.

has three upper incisors, and the dentition is closed-rooted (i.e., not ever-growing). The angle of the dentary in koalas is not inflected, unlike in any other marsupial except the honey possum (see Table 10.2).

Koalas are sexually dimorphic, with males 50% larger than females. Both sexes produce low-frequency bellows during the breeding season (Ellis et al. 2011). Larger males have deeper bellows—a reliable index to body size—which translates to increased mating potential (Charlton et al. 2011; Ellis and Bercovitch 2011). Both sexes have a highly derived vocal anatomy in which the larynx is permanently descended and retractable, and novel vocal folds outside the larynx are present (Frey et al. 2018). Females produce distinct vocalizations ("rejection calls") when they refuse male copulation attemps (Charlton et al. 2017). With body mass ranging from 6.5 to 12.5 kg, koalas are among the largest arboreal browsers and are on the ground only while moving between trees. Koalas move between trees daily, both

day and night; daytime resting trees are not necessarily the same as nighttime feeding trees (Ellis et al. 2009). They do not build a nest but simply rest in the forks of trees. Briscoe and coworkers (2014) showed that koalas use trees to thermoregulate in hot weather, the cool trunks serving as a sink for conductive loss of body heat. Koalas are unusual among herbivores in their highly selective, specialized diet: leaves, stems, flowers, and even bark of numerous species of *Eucalyptus*. This is very poor-quality forage, but koalas have reduced energy requirements, moving slowly and remaining inactive up to 20 hours a day. Their alimentary tract has the largest cecum relative to body size of any mammal (see Chapter 7). Like bandicoots and bilbies, koalas have a chorioallantoic placenta; but because there are no chorionic villi, gestation is only about 35 days. Koalas can have young any month of the year, but Ellis and colleagues (2011) found that 60% of births occurred between December and March. As one of the most recognizable marsupials, koalas are important as a modern tourist attraction. Hundreds of thousands of koalas were harvested annually as part of the fur trade in Queensland from about 1906 through 1927 (Hrdina and Gordon 2004). The current conservation status of koalas is "vulnerable," mostly due to anthropogenic habitat degradation, disease, and introduced predators (McAlpine et al. 2015).

Vombatidae

The 2 genera and 3 species of wombats are short-limbed, plantigrade, powerful burrowers (Figure 10.34). Adult body mass is about 30 kg. The common wombat (*Vombatus ursinus*) is found in forested areas of southeastern Australia and Tasmania. The southern hairy-nosed wombat (*Lasiorhinus latifrons*) inhabits semiarid regions of southern Australia, and the critically endangered northern hairy-nosed wombat (*L. krefftii*) is now restricted to a 500-ha portion of Epping Forest National Park in central Queensland.

Although they share several characteristics with the koala, wombats have distinct features that reflect their terrestrial, grazing, semifossorial existence. Like rodents, they have a single pair of upper and lower incisors, no canines, and a reduced number of premolars (Figure 10.35). Dentition is open-rooted and continuously growing, which is unique among marsupials. Wombats are nocturnal and consume grasses and forbs; their broad skull, robust jaw musculature, and bilophodont cheek teeth are well adapted for chewing such tough, abrasive food (Sharp and Trusler 2015). Unlike the koala, they have a poorly developed cecum. During hot, dry days, *Lasiorhinus* wombats minimize time on the surface by remaining in deep, extensive, interconnected burrow systems. Benefits of burrows include protection from predators, fires, and harsh ambient conditions. Nonetheless, construction of burrows is energetically demanding, and wombats have a poor-quality diet. Their metabolic rate is extremely low, even for a marsupial (Evans et al. 2003). Most burrowing mammals are small; if large, they eat high-energy insects. Wombats are the largest bur-

Figure 10.34 **Southern hairy-nosed wombat.** Wombats such as this *Lasiorhinus latifrons* are the largest herbivorous mammals that burrow.
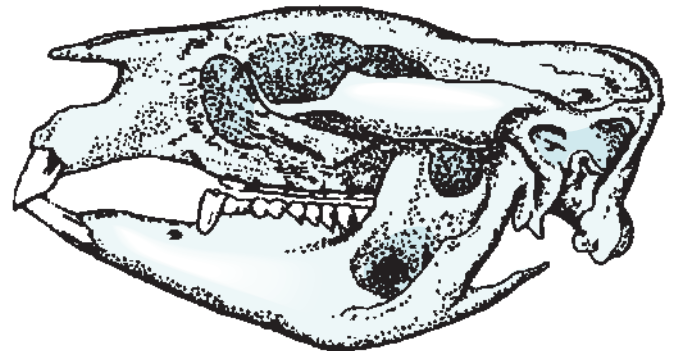
Figure 10.35 **Skull of a wombat.** The common wombat's (*Vombatus ursinus*) single pair of upper and lower incisors is unique among marsupials, though not among rodents and the aye-aye (a primate). *Adapted from DeBlase and Martin (1981).*

rowing herbivores (Finlayson et al. 2005) and yet have small home ranges throughout the year, given their body size (Evans 2008). They are seasonal breeders (Taggart et al. 2005). The well-developed marsupium, with 2 teats, opens posteriorly. A single offspring is born after gestation of 21 days and leaves the pouch permanently about 9 months after birth. Taggert and colleagues (2007) described growth and development in southern hairy-nosed wombats. The oldest fossil wombats, *Rhizophascolonus* and *Nimbavombatus* date from the early Miocene (Brewer et al. 2018).

Phalangeroidea

Burramyidae

There are 2 genera and 5 species of pygmy possums—the smallest of the possums. Mean body mass of adults ranges from 7 to 50 g, and head and body length is only 5–12 cm.

Figure 10.36 **Eastern pygmy possum *Cercartetus nanus*.** Members of *Cercartetus* are primarily insectivores, but *C. nanus* also consumes nectar.

The critically endangered mountain pygmy possum (*Burramys parvus*) is limited to terrestrial alpine areas above 1,300 m elevation in southeastern Australia (a habitat threatened by climate change). This species was known only from fossil remains until 1966, when a live animal was taken at Mount Higginbotham, Victoria (Mansergh and Broome 1994). Only 3 populations were thought to exist within an area of 10 km², more recently, additional populations have been located (Schulz et al. 2012). Unlike most endangered mammals, *B. parvus* appears to have high levels of genetic diversity within populations (Mitrovski et al. 2007). Shi and coworkers (2015) documented the importance of alpine boulder fields as thermal refuges for mountain pygmy possums. The remaining burramyids, all species of *Cercartetus*, are arboreal and occur in a variety of habitats in Australia and Tasmania (Figure 10.36). One species, the long-tailed pygmy possum (*C. caudatus*), also occurs in New Guinea. Tails are long and prehensile, the pouch opens anteriorly, and, like macropodids, females exhibit **embryonic diapause**.

Pygmy possums are nocturnal and omnivorous, consuming invertebrates, fruits, seeds, nectar, and pollen. They have long, extensible, "brushed" tongues with an extensive system of papillae, which are especially well developed in *Cercartetus*. Papillae may serve to increase the surface area for uptake of nectar and pollen. All burramyids enter torpor, but *B. parvus* is noteworthy because it enters prolonged periods of hibernation. Species of *Cercartetus* store fat at the base of the tail and may enter short bouts of hibernation. Both these adaptations probably contribute to the relatively long life spans of these small marsupials. Based on DNA sequence data from five nuclear genes, Meredith and colleagues (2009) suggested that the two genera of burramyids diverged from each other during the Eocene, somewhat older than the oldest (Oligocene) fossil evidence (Brammall and Archer 1999).

Phalangeridae

This family includes 4 species of brushtail possums (*Trichosurus*), the scaly-tailed possum (*Wyulda squamicaudata*), and 4 genera and 25 species of cuscuses (Burgin et al. 2018). Brushtail possums and the scaly-tailed possum occur only in Australia, whereas the cuscuses are widespread throughout Australia, New Guinea, and surrounding islands. The bear cuscus (*Ailurops ursinus*) is restricted to Sulawesi and nearby islands. All phalangerids occur in scrub or heavily forested areas. They are medium-sized, with large eyes, short snout, and soft, dense pelage (Figure 10.37). Adults range from 0.5 to 1.2 m total length and have a body mass of 1.1 to 4.5 kg. All are nocturnal, have long, prehensile tails, and are excellent climbers (Figure 10.38). Brush-tailed possums feed on leaves (they are **folivorous**), as well as flowers and nectar; *Phalanger* and *Wyulda* are omnivorous.

Figure 10.37 **Common brushtail possum *Trichorsurus vulpecula*.** This phalangerid is common in a wide variety of habitats, including suburbs, of northern, eastern, and southwestern Australia. It has become an invasive species in New Zealand.

A

B

C
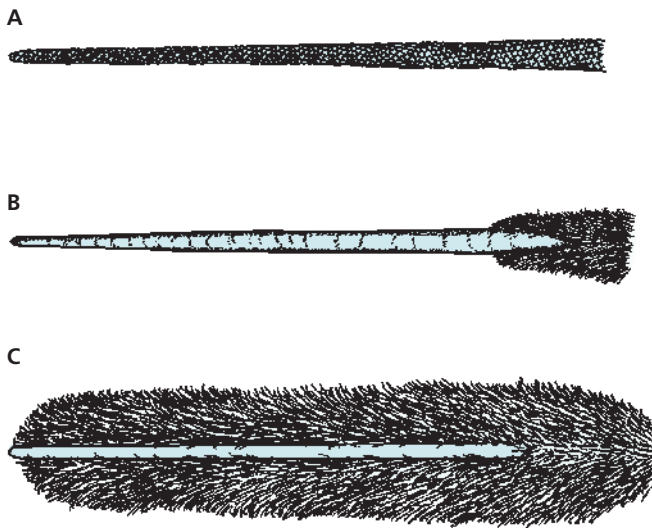
Figure 10.38 **Phalangerids vary in the amount of fur on the tail.** (**A**) Small, nonoverlapping conical scales cover the distal part of the tail in *Wyulda*; (**B**) strongly prehensile tail in *Phalanger* has fur at the base only; (**C**) well-furred tail in *Trichosurus* has a ventral friction pad. *Adapted from Walton and Richardson (1989).*

The marsupium opens anteriorly; litter size is 1 or 2. The gestation period is about 17 days, and young remain in the pouch for 4 to 7 months. Neonatal brushtail possums (*T. vulpecula*) enter the pouch about 2 minutes after birth and attach to a teat 10–15 minutes later (Veitch et al. 2000). Brushtail possums were introduced into New Zealand beginning in the 1800s to establish a fur trade, but have become an **invasive species**, causing serious damage to native forests and orchards and serving as primary hosts for bovine tuberculosis (Nugent et al. 2015). Possum control efforts are now a major conservation activity in New Zealand (Lohr et al. 2009; Beausoleil et al. 2016). The telefomin cuscus (*Phalanger matanim*), talaud bear cuscus (*Ailurops melanotis*), blue-eyed spotted cuscus (*W. wilsoni*), and black-spotted cuscus (*S. rufoniger*) are critically endangered; the gebe cuscus (*Phalanger alexandrae*) and woodlark cuscus (*P. lullulae*) are endangered. The most common threats to phalangerid populations are hunting and habitat loss to agriculture.

Fossil remains date from the late Oligocene. Based on nuclear DNA analyses, Meredith and coworkers (2009) date the origin of phalangerids to the Eocene, but with diversification of modern lineages delayed until the Miocene.

Petauroidea

Acrobatidae

This family includes only the feathertail glider (*Acrobates pygmaeus*), found in wooded habitats of eastern Australia, and the feather-tailed possum (*Distoechurus pennatus*),

which occurs in disturbed forests, gardens, and rainforests of New Guinea (Flannery 1995). They are named for the long, stiff, featherlike hairs on the side of the tail. The feathertail glider (Figure 10.39) is nocturnal and highly arboreal; at 10–14 g body mass, it is probably the world's smallest gliding mammal (Harris 2015). A furred **patagium** (gliding membrane) extends between the elbows and knees. The weakly prehensile tail aids both in climbing and as a rudder for gliding. The feather-tailed possum, however, is terrestrial and lacks a gliding membrane. Both species are primarily nectivorous and have long, brush-tipped tongues, similar to burramyids and tarsipedids, for taking nectar and pollen. Papillae on the tongue of *Acrobates* are longer and finer than those of *Distoechurus*. There is a general reduction in the size and number of teeth. Interestingly, although the species are **nectivorous**, their molars are **bunodont** for secondary feeding on insects. *Acrobates pygmaeus*, which may nest in groups of up to 20 individuals, has several litters per breeding season and exhibits embryonic diapause. Neither species is threatened or endangered. Acrobatids have no pre-Quaternary fossil record, but Meredith and colleagues (2009) estimated that the two genera diverged in the late Oligocene.

Pseudocheiridae

The 6 genera and 20 species of ringtail possums (Figure 10.40) in this family are closely related to the Petauridae. Pseudocheirids occur in Australia, New Guinea, and a few surrounding islands (Flannery 1995). Most are slow moving and inhabit forested areas; the rock ringtail possum (*Petropseudes dahli*) occurs on rocky slopes and outcrops. These arboreal, nocturnal species feed primarily on leaves, and many of their morphological features reflect this. For example, pseudocheirids have **selenodont** molars (cusps form crescent-shaped ridges for shearing tough plant tissue), a long alimentary tract, and a very large cecum. Greater gliders (*Petauroides volans*) selectively feed on *Eucalyptus* species that maximize their gain of nutritional nitrogen and minimize intake of toxic defense compounds (Jensen et al. 2015). The arboreal habits of pseudocheirids are aided by schizodactylous digits on the forefeet. The long, furred, prehensile tail is usually the same length as the head and body. A gliding membrane extends from the elbow to the ankle in *Petauroides*, not from the wrist as in *Petaurus*. The marsupium opens anteriorly and encloses either 2 or 4 teats.

The western ringtail possum (*Pseudocheirus occidentalis*), occurring in a small area of coastal southwestern Australia, is critically endangered due to drying climate, urban development, altered fire regimes, and predation by feral foxes and cats. Similar factors are driving the decline of several other species. Pseudocheirid fossils appear in the late Oligocene, just prior to the early Miocene diversification of living forms proposed by Meredith and coworkers (2010).

Petauridae

This family includes 4 species of trioks and the striped possum (*Dactylopsila*), Leadbeater's possum (*Gymnobelideus leadbeateri*), and 6 species of wrist-winged gliders (*Petaurus*; Burgin et al. 2018). The long-fingered triok is sometimes placed in its own genus as *Dactylonax palpator*. These arboreal gliders are named for the patagium that extends from the wrist to the ankle. Members of *Petaurus* are highly convergent on North American gliding squirrels (*Glaucomys*). All petaurids are medium-sized (0.1–2.0 kg), with some

Figure 10.39 **Feathertail glider (*Acrobates pygmaeus*).** This is the world's smallest gliding mammal. Note the gliding patagium (white margin from elbow to knee) and grasping toes.

Figure 10.40 **Lemuroid ringtail possum (*Hemibelideus lemuroides*).** This arboreal folivore is found only in two rainforest localities of northeastern Queensland.

type of dark dorsal stripe, long, well-furred, prehensile tails, and a well-developed marsupium that opens anteriorly (Figure 10.41). In some species, the pouch is partitioned into left and right compartments by a septum. Females usually give birth to a single young that remains in the pouch for 4 months. There are a total of 40 teeth; the diprotodont lower incisors are long and sharp, and the molars are bunodont.

Petaurids occur in forested areas of Australia, New Guinea, and surrounding islands. They are nocturnal and herbivorous or insectivorous. Arboreal locomotion is aided by the prehensile tail and opposable hallux. The northern glider (*Petaurus abidi*) is restricted to a small area of northwestern Papua New Guinea and is critically endangered due to deforestation and hunting. The critically endangered Leadbeater's possum was previously believed to be extinct, but populations were rediscovered in 1961 in Victoria, Australia. The mahogany glider (*P. gracilis*) is endangered because of habitat loss and fragmentation (Jackson et al. 2011). The poorly known Tate's triok (*Dactylopsila tatei*), restricted to Fergusson Island off Papua New Guinea, is also endangered. Petaurid fossils are known from the Oligocene; Meredith and colleagues (2010) estimated basal divergences among living forms in the early Miocene.

Figure 10.41 **Sugar glider (*Petaurus breviceps*).** This common and highly social petaurid has become a popular household pet.

Tarsipedidae

The unusual honey possum, or noolbenger (*Tarsipes rostratus*), is the sole member of this family. Average body mass of females is 12 g and males, about 9 g. The honey possum is the only non-volant mammal that feeds exclusively on nectar and pollen. Many of the adaptations of this tiny species are for its nectivorous diet. It has a long, pointed rostrum and a tubular mouth with an extensible, brush-tipped tongue (Figure 10.42). The 22 small, peg-like teeth are fewer in number than in any other marsupial. It also has a modified gut with a high passage rate and a high metabolic rate for a marsupial (Cooper and Cruz-Neto 2009; Bradshaw and Bradshaw 2012). The honey possum is crepuscular, arboreal, and occurs in shrubs and woodlands of southwestern Western Australia. The long tail is prehensile, and the hallux is opposable. Claws occur on only the 2 syndactylous digits of each hind foot; pads on the other digits are used to grip branches.

The marsupium is well developed. Honey possums exhibit embryonic diapause, and pouch young can occur throughout the year (Renfree et al. 1984). They are polyestrus; Oates and coworkers (2007) estimated gestation to be 23 days. Honey possums give birth to the smallest mammalian young; neonates weigh no more than 5 mg. In contrast, their sperm is about 0.3 mm long, the largest known among mammals. No pre-Quaternary fossils of tarsipedids have been discovered, though Meredith et al. (2009) estimate that the lineage diverged from petaurids and pseudocheirids in the Eocene.

Macropodiformes

In addition to three extant families, Macropodiformes includes the extinct clade Balbaridae, five genera of Oligo-Miocene kangaroos with well-developed canines (Butler et al. 2018). Some extinct macropodiforms, such as the Oligo-Miocene hypsiprymnodontid *Ekaltadeta*, were carnivores.

Hypsiprymnodontidae

This monotypic family includes only the musky rat-kangaroo (*Hypsiprymnodon moschatus*), which occurs in tropical forests of northeastern Queensland, Australia (Figure 10.43). Meredith and colleagues (2009) estimated that *Hypsiprymnodon* diverged from macropodids in the Oligocene; the earliest fossils are from the Miocene (Bates et al. 2014). Musky rat-kangaroos have a mean body weight of about 530 g. Unlike macropodids, they do not hop bipedally but bound using all 4 legs. Neither do they exhibit embryonic diapause. Lloyd and coworkers (2008) described unique aspects of spermatogenesis in the musky rat-kangaroo, including an acrosomal granule different from other marsupials. They are diurnal and generally terrestrial, foraging for fruits, seeds, and insects among leaf

Figure 10.42 Honey possum (*Tarsipes rostratus*). Honey possums feed strictly on nectar and pollen; they are important pollinators of *Banksia* (shown here) and other Protaceae and Myrtacae plants in southwestern Australia.

litter and downed logs on the forest floor. Populations appear to be stable with no significant threats.

Potoroidae

There are 4 genera and 12 extant species of potoroids, including potoroos (*Potorous*) and bettongs (*Bettongia* and *Aepyprymnus*). Potoroids are small, secretive, densely furred animals (Figure 10.44). The largest is the rufous bettong (*A. rufescens*) with mean body weight of about 3 kg. As in macropodids, hind limbs are larger than forelimbs, and the hind feet are large. The tail is weakly prehensile (bettongs carry nesting material with their tail); the upper canines are well developed, and there is a large, carnassial premolar. The **sacculated** stomach (several chambers) is not as well defined as in macropodids. Potoroids are opportunistic omnivores or herbivores. Most include underground fungi as a large part of their diet (Lee and Cockburn 1985). They

Figure 10.43 **Musky rat-kangaroo (*Hypsiprymnodon moschatus*).** This small macropodid is restricted to a small area of tropical rainforest in northeastern Queensland.

are generally solitary and nocturnal. In the northern bettong (*Bettongia tropica*), postpartum estrus occurs, followed by embryonic diapause. Pouch young permanently emerge at about 3.5 months of age and are weaned at 166–185 days old (Johnson and Delean 2001). Several extinct potoroid genera are recognized from Oligocene-Quaternary fossils, but Meredith and colleagues (2009) date the diversification of living forms to the mid-Miocene.

The conservation status of several species of potoroids is of serious concern, in part because of introduced house cats and red foxes (*Vulpes vulpes*), as well as loss of habitat. Gilbert's potoroo (*Potorous gilbertii*) may be the most critically endangered marsupial in Australia. There is a single population of 49 individuals in Two Peoples Bay National Park in southwestern Western Australia (Woinarski and Burbidge 2016). This population was discovered in 1994 after the species was presumed to be extinct for 120 years (Stead-Richardson et al. 2010). Gilbert's potoroo feeds predominantly (>90%) on fungi (Nguyen et al. 2005). The woylie, or brush-tailed bettong (*B. penicillata*), is also considered critically endangered by the IUCN, despite the initial success of conservation efforts in the 1990s. Marlow and coworkers (2015) showed that the decline of woylie populations at reserves in Western Australia after 2000 was driven by feral cat predation, even after successful control of feral foxes. Two species—the desert rat-kangaroo (*Caloprymnus campestris*) and the broad-faced potoroo (*P. platyops*)—are recently extinct. The Nullarbor dwarf bettong (*B. pusilla*) probably went extinct in the 1500s (McNamara 1997).

Macropodidae

This is the largest marsupial family, with 13 genera and 67 extant species. Body mass ranges from the 1-kg hare-wallabies (*Lagorchestes*) to 80-kg red kangaroos (*Macropus rufus*). Living macropodids are herbivores (but some extinct forms were carnivores) and occupy practically all terrestrial

Figure 10.44 **Long-nosed potoroo (*Potorous tridactylus*).** This species is widely distributed in southeastern Australia, but populations are declining.

habitats from deserts to rainforests throughout Australasia. The tree kangaroos (*Dendrolagus*) are semiarboreal.

Macropodid ecology and morphology parallels that of eutherian artiodactyls (deer, sheep, goats). Macropodids have a large, sacculate stomach in which microorganism-aided digestion occurs. As in some artiodactyls, food is regurgitated for additional chewing and then reswallowed. Macropodids are diprotodont, but, with the exception of the banded hare-wallaby (*Lagostrophus fasciatus*), the upper and lower incisors do not occlude. Canines are small or absent, and there is a **diastema** (gap anterior to the premolars) (Figure 10.45). The molars are **hypsodont** (high-crowned), and as in elephants and manatees, **mesial drift** occurs (forward movement of the cheekteeth in the jaw, as worn anterior teeth drop out). Among marsupials, this serial replacement of cheekteeth occurs only in macropodids and is most pronounced in *Macropus*. Only the pygmy rock wallaby (*Petrogale concinna*) has supernumerary molars (more than the usual four) that are shed throughout life.

Arman and Prideaux (2015) classified kangaroo diets into four types (fungivore/frugivore, browser, grazer, and mixed feeder). They also showed that most species characterized as browsers based on dentition are actually mixed feeders, and
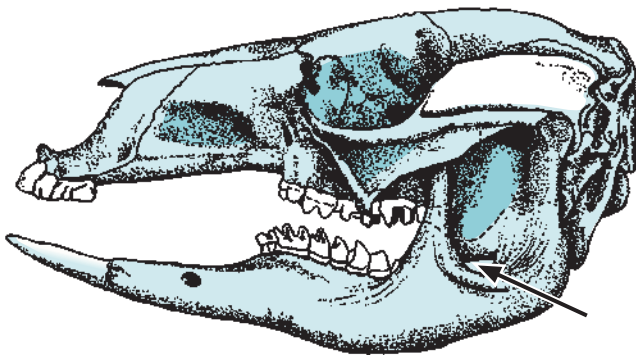
Figure 10.45 Wallaby skull. Skull of a wallaby shows the diprotodont dentition and diastema typical of herbivores. Note also the pronounced masseteric fossa of the mandible (*arrow*). *Adapted from DeBlaise and Martin (1981).*

that the proportion of dietary grass increases with body size (as in bovids). Mitchell and colleagues (2018) showed that facial length varies among kangaroo species as a function of diet and dental mechanics, rather than simple body size allometry. Species that chew tough plant tissue have shorter faces; those that chew softer foods or use neck muscles to crop forage have longer faces. Dietary adaptation has long been linked to the diversification of kangaroos. Couzens and Prideaux (2018) used crown height and microwear patterns in conjunction with phylogenetic analysis to argue that most of this diversification (represented by the Macropodini genera—*Lagorchestes, Macropus, Onychogalea, Setonix,* and *Wallabia*) took place rapidly in Pliocene, coincident with the spread of grasslands in Australia.

Strong, well-developed hind limbs (Figure 10.46) and large hind feet characterize macropodids ("big-footed"). Most species have a long, broad tail that acts as a balance during rapid (up to 50 km/h), bipedal hopping, and for support and propulsion during slower "pentapedal" locomotion (O'Connor et al. 2014). The tail serves as part of a "tripod" while the animal is sitting or foraging (Figure 10.47). The enlarged hindquarters give macropodids a low center of gravity in the pelvic area, which helps individuals maintain balance while hopping.

The marsupium is large and opens anteriorly. Mammary glands are complex, and the physiology of lactation is sophisticated, with pronounced differences in milk composition over time. Thus, a mother nursing both a developing pouch young and a young that has left the pouch but returns to nurse (a joey on foot) produces milk of different nutrient composition from different teats. Gestation in macropodids is long compared with that of other marsupials—close to the length of the estrous cycle. One young is produced at a time, and embryonic diapause (see Chapter 9) occurs in all species except the western gray kangaroo (*Macropus fuliginosus*). Gelin and coworkers (2015) describe how this complicated reproductive strategy allows flexible responsiveness to resource availability in eastern gray kangaroos (*Macropus giganteus*).

Figure 10.46 Eastern grey kangaroo (*Macropus giganteus*). Note the enlarged hind limbs and reduced forefeet typical of macropodids. In this stance, the tail serves as part of a tripod supporting the animal's weight.
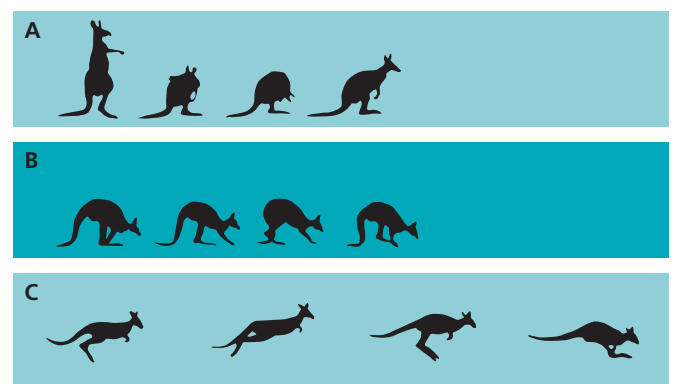
Figure 10.47 Tails in macropodids. Tails can serve a variety of functions in locomotion and foraging of macropodids. (**A**) Tail functions as a "tripod" during foraging. (**B**) Tail functions as a fifth limb in "pentapdedal" locomotion. (**C**) Tail serves as a counterbalance during rapid, bipedal hopping. *Adapted from Walton and Richardson (1989).*

European settlement has had little adverse effect on some of the larger species; in fact, livestock grazing has increased their numbers and distribution. Conversely, some large and many smaller macropodids are considered

endangered: Calaby's pademelon (*Thylogale calabyi*); mountain pademelon (*T. lanata*); dingiso (*Dendrolagus mbaiso*); Goodfellow's tree kangaroo (*D. goodfellowi*); Huon tree kangaroo (*D. matschiei*); ifola (*D. notatus*); narbalek (*Petrogale concinna*); and proserpine rock wallaby (*P. persephone*). The black dorcopsis (*Dorcopsis atrata*), golden-mantled tree kangaroo (*Dendrolagus pulcherrimus*), Wondiwoi tree kangaroo (*D. mayri*), and Scott's tree kangaroo (*D. scottae*) are critically endangered. Species that have gone extinct within the last 30 to 100 years include the toolache wallaby (*Macropus greyi*), central hare-wallaby (*Lagorchestes asomatus*), eastern hare-wallaby (*L. leporides*), and the crescent nailtail wallaby (*Onychogalea lunata*). The extinction of giant kangaroos, including *Procoptodon goliah* (the largest kangaroo that ever lived, with an estimated body weight of 232 kg; Helgen et al. 2006), occurred about 45,000 years ago, possibly due to a combination of human hunting (Prideaux et al. 2009) and environmental change.

SUMMARY

- Monotremes (Prototheria) include one living order (Monotremata), with two families—the duck-billed platypus and short- and long-beaked echidnas.

- Monotremes are oviparous (egg-laying). Other major characteristics include:
  - a cloaca (a single opening for the fecal, urinary, and reproductive tracts);
  - oviparity (egg-laying);
  - mammary glands but no teats;
  - a lower body temperature than most other mammals;
  - microchromosomes;
  - thread-like sperm;
  - uncoiled cochlea;
  - a pectoral girdle that retains coracoid, precoracoid, and interclavicle bones;
  - the platypus with ankle spur connected to a poison gland; and
  - a highly innervated bill, which responds to tactile and electrical stimuli.

- Marsupials (Theria: Metatheria) include 7 living orders and 19 living families.

- Major characteristics of marsupials are:
  - a marsupium (pouch) in many species;
  - a duplex uterus with lateral vaginae on either side of a medial vaginal canal;
  - a placenta but without villi;
  - a very short intrauterine gestation period and a prolonged lactation period;
  - a relatively small braincase compared to eutherians;
  - no corpus callosum;
  - reduced or absent auditory bullae;
  - palatal vacuities;
  - an articulation of the jugal bone (as well as squamosal) with the dentary;
  - an inflected angular process of the dentary;
  - epipubic bones;
  - different dental characteristics than eutherians;
  - a lower basal metabolic rate than eutherians; and
  - a smaller range in body sizes and narrower range of ecological niches than in placentals.

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DISCUSSION QUESTIONS

1. Compare the various "reptilian" features of monotremes with those of marsupials. What are the differences and similarities?

2. The platypus uses its bill for locating aquatic prey through electroreception. Why do you think this complex adaptation developed in place of simply searching visually for prey?

3. In species with an enclosed marsupium, pouch young spend prolonged periods breathing air with a very high carbon dioxide concentration. How do the developing neonates accommodate this "poisonous" environment during the lactation period?

4. What are the advantages in the marsupial mode of producing "expendable neonates" with a prolonged lactation period, compared with the eutherian mode of prolonged gestation with placental involvement? What are the disadvantages?

5. What is the evidence that the common ancestor of Marsupialia lived in North America? Does the phylogeny of living marsupials support a North American origin?

6. As noted in the text, the creation of the Panamanian land bridge about 3–5 mya allowed dispersal and interchange of South American metatherians and North American eutherians. Were the marsupials generally outcompeted? What evidence is needed to provide an answer? Is any of that evidence available?

CHAPTER 11

Orders: Macroscelidea, Afrosoricida, Tubulidentata

Macroscelidea

Macroscelididae

The elephant shrews or sengis comprise this family of 5 genera and 20 species (Schlitter 2005a; Dumbacher 2014; Wilson and Mittermeier 2018). Historically, they were sometimes included in the Order Insectivora together with the treeshrews (Family Tupaiidae). Evidence of skeletal, cranial, and dental features, as well as molecular analyses, supports the current ordinal placement (Dene et al. 1980; Yates 1984). Recent molecular methods applied to phylogenetic evidence indicates that elephant shrews are part of a monophyletic African clade of mammals (Superorder Afrotheria) that includes elephants, sea cows, hyraxes, aardvarks, and golden moles and tenrecs mentioned in Chapter 11 (Springer et al. 2004). Based on morphological and genetic characteristics, Dumbacher and colleagues (2014) described a new species, the Etendeka round-eared sengi (*Macroscelides micus*), which is endemic to northwestern Namibia. The new species appears to inhabit gravel plains and is sympatric with the Namib round-eared sengi (*M. flavicaudatus*), and allopatric with the Karoo round-eared sengi (*M. proboscideus*; Figure 11.1).

Elephant shrews are restricted to central and eastern Africa from about 15°N latitude southward. An exception is the North African elephant shrew (*Elephantulus rozeti*), which occurs from Morocco to western Libya. Macroscededids inhabit a diverse number of habitats, including desert, brushland, plains, forests, and rocky areas. Body mass of sengis ranges from 19 to 43 g (*Macroscelides*), 31 to 83 g (*Elephantulus* and *Petrosaltator*), 120 to 250 g (*Petrodromus*), and 320 to 750 g (*Rhynchocyon*). They are strictly terrestrial, highly cursorial, and generally diurnal, except during hot weather, when they become increasingly nocturnal (Lovegrove and Mowoe 2014). Lovegrove and colleagues (2001) studied heterothermy in the North African elephant shrew and the eastern rock elephant shrew (*E. myurus*). During bouts of torpor, which never exceeded 24-hour periods, body temperatures declined to about 5°C and oxygen consumption was only 2% of the basal metabolic rate. Elephant

Figure 11.1 **Body morphology of elephant shrews or sengis.** Note the long proboscis, enlarged hind limbs, and kangaroo-like appearance of this Karoo round-eared sengi (*Macroscelides proboscideus*). Convergence is evident in body form of sengis and several families of rodents, such as kangaroo rats (Rodentia: Heteromyidae), shown in figure 16.15A, or jerboas (Rodentia: Dipodidae), in figure 16.44.

shrews occurring in the southern African subregion (*Petrodromus tetradactylus*, *Elephantulus intufi*, and *E. brachyrhynchus*) reduce water and energy loss by avoiding extreme environmental temperatures; crepuscular activity and early morning sun-bathing supplement heat gain in cold (Downs and Perrin 1995). Recently, Boyles and coworkers (2012) and Oelkrug and colleagues (2012) measured body temperature and thermogenesis of free-ranging western rock elephant shrews (*Elephantulus rupestris*) and Cape rock elephant shrews (*E. edwardii*) during winter and in a winter-rainfall region of western South Africa. Although these syntopic species exhibit similar ecology and morphology, they unexpectedly displayed different body temperature patterns. As with other species of elephant shrews, western rock elephant shrews were heterothermic, with all individuals decreasing body temperature below 30°C on 34% of nights. In contrast, Cape rock elephant shrews rarely permitted their body temperature to decrease below 30°C. The nature of heterothermy in *E. edwardii* was qualitatively similar to that of other elephant shrews; however, torpor is deeper and longer in this species (Geiser and Mzilikazi 2011).

Sengis feed on insects and other animal and plant material. Although quadrupedal, they move bipedally in an erratic fashion when alarmed. Sengis are easily alarmed: they are nervous animals and constantly twitch their ears and nose while making squeaking, chirping sounds. Although monogamy is found in less than 10% of mammals, all four genera of sengis are socially monogamous. Pairs of rufous sengis (*Elephantulus rufescens*) will construct and maintain a complex system of trails through the leaf litter—the males spend about 40% of their active daylight hours trail-cleaning, compared to about 20% for female mates (Rathbun and Rathbun 2006). Scent-marking and sunbathing rolls are commonly performed on resting sites along

trails. Sengis do not construct or use shelters or burrows but may temporarily use burrows of other animals (Rathbun and Redford 1981). Young sengis are highly precocial at birth—they will forage one day after birth.

MORPHOLOGY

The common name of elephant shrews relates to their long, flexible, highly sensitive snout and large eyes and ears. The pelage is long and soft. The hind legs are longer than the forelegs, which gives rise to the ordinal and family name ("long limbs"). The kangaroo-like hind legs allow for hopping—a bipedal form of locomotion when moving rapidly. Forelimbs are pentadactyl, whereas hind limbs have either four or five toes. Size varies: head and body length and mass range from 95 mm and a maximum 50 g, respectively, in the short-eared elephant shrew (*Macroscelides proboscideus*) to 315 mm and about 400 g, respectively, in golden-rumped elephant shrews (Genus *Rhynchocyon*). Tail length is slightly shorter than head and body length. The skull has a complete zygomatic arch and auditory bullae, and the palate is noteworthy for its series of large openings (Figure 11.2). All genera have functional incisors except *Rhynchocyon*. The molars in elephant shrews are quadrituberculate (four-cusped), and the occlusal surfaces are dilambdodont. As in treeshrews, a cecum is present.

FOSSIL HISTORY

The sengis represent a monophyletic radiation endemic to Africa. Just as all extant elephant shrews are endemic to Africa, all known fossil representatives of the order are also from Africa. Tabuce and colleagues (2001) described an elephant shrew (*Nementchatherium senarhense*) from the Eocene epoch of Algeria. Other early elephant shrews include *Chambius kasserinensis* from the early to mid-Eocene of Tunisia and *Herodotius pattersoni* from the late Eocene of Egypt. Another Paleogene macroscelidean fossil is *Metoldobotes stromeri*, which dates from the Oligocene. Later fossil macroscelidids are quite variable structurally: Genus *Myohyrax* from the Miocene is similar to a hyrax (Hyracoidea: Procaviidae), and a Pliocene form (Genus *Mylomygale*) is similar to a rodent (Patterson 1965).

ECONOMICS AND CONSERVATION

The golden-rumped elephant shrew (*Rhynchocyon chrysopygus*) and the four-toed elephant shrew (*Petrodromus tetradactylus*) are harvested for meat in Kenya. The rufous elephant shrew (*Elephantulus rufescens*) is known to contract naturally occurring malaria and, along with other species in the genus, is used in medical research. Although an interesting group, elephant shrews are of little economic importance. Golden-rumped elephant shrews, the black-and-rufous
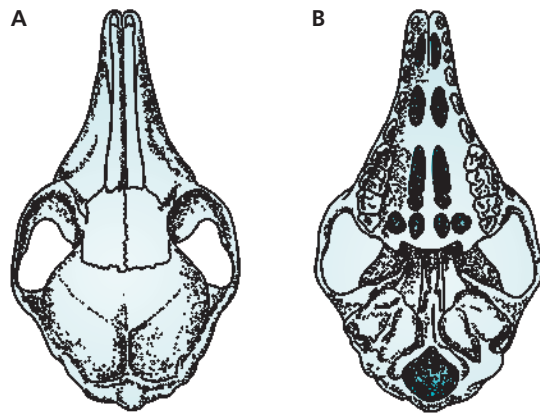
Figure 11.2 **Elephant shrew (sengi) skull characteristics.** (**A**) Dorsal and (**B**) ventral views of the North African elephant shrew, showing the complete zygomatic arch, large auditory bullae, and numerous perforations of the palate. *Adapted from DeBlase and Martin (1981).*

Figure 11.3 **Phylogenetic position of tenrecs based on 12 mtDNA genes.** Numbers are bootstrap support values (500 replicates). Note the basal position of hedgehogs for eutherian taxa as well as the position of moles (Talpidae), another "insectivore" family. *From Mouchaty et al. 2000a.*

elephant shrews (*R. petersi*), and Somali elephant shrews (*E. revoili*) are endangered.

Afrosoricida

Tenrecidae

There is a great diversity of form and function reflected in the 8 genera and 31 species of tenrecs and shrew tenrecs in this family (Bronner and Jenkins 2005; Wilson and Mittermeier 2018). All tenrecs are restricted to Madagascar: a single colonization from Africa originated from a common ancestor. Using complete sequences of three mitochondrial DNA (mtDNA) genes, Stanhope and colleagues (1998) suggested that tenrecids (and golden moles) be placed in a new order, Afrosoricida. Recent work applying molecular methods to phylogenetic analyses has indicated that the Family Tenrecidae is part of a monophyletic African clade of mammals that represents one of four early eutherian radiations. This clade, the Superorder Afrotheria, includes the elephants, sea cows, hyraxes, aardvarks, elephant shrews, and golden moles (Springer et al. 2004). Based on analyses of 12 mitochondrial genes, Mouchaty and coworkers (2000a) found that tenrecs were most closely related to the aardvark and African elephant (*Loxodonta africana*) (Figure 11.3).

The morphology of tenrecids defies a general description, as do their behavior and habitats. The family has a large range in body size from the very small pygmy shrew tenrec (*Microgale parvula*), which weighs 2–5 g, to the large web-footed tenrec (*Limnogale mergulus*), which weighs 60–110 g. Rice tenrecs (Genus *Oryzorictes*) look like moles, are fossorial, and occur in marshy areas. Long-tailed tenrecs (Genus *Microgale*) resemble shrews and occupy thick vegeta-

tion and ground litter in a variety of habitat types. The web-footed tenrec (*Limnogale mergulus*) is semi-aquatic and has a long, laterally flattened tail and webbed hind feet and looks like a small muskrat. It preys on fish, amphibians, and aquatic invertebrates in rivers, lakes, and marshes. This species is limited to stream habitat in eastern Madagascar and is active only at night (Benstead et al. 2001; Levesque et al. 2012; Levesque et al. 2013; Levesque and Lovegrove 2014). The lesser hedgehog tenrec (*Echinops telfairi*) is arboreal and has long slender digits that aid in grasping small branches and surfaces of bark. The greater hedgehog tenrec (*Setifer setosus*) and small Madagascar "hedgehogs" (*Echinops telfairi*) have sharp, barbed spines on the head, back, and sides, like erinaceids. Like hedgehogs, they have well-developed *panniculus carnosus* muscles and roll into a ball when threatened. Tenrecs have no auditory bullae and no jugal bone, and thus, they have an incomplete zygomatic arch (Cox 2006). Incisors and canines are usually small and unspecialized, and the upper molars are often zalambdodont.

Several species of tenrecs are heterothermic and enter torpor during the day or hibernate seasonally. Body temperatures are generally low, ranging from 30°C–35°C while individuals are active. The lowland streaked tenrec (*Hemicentetes semispinosus*; Figure 11.4) maintains a body temperature 1°C above ambient temperature while it hibernates during much of the winter (Stephenson and Racey 1994).

Additionally, several species, such as the streaked tenrec and the long-tailed tenrecs, which are equipped with quills located on the mid-dorsal region, produce vibrations that permit communication between mother and young

Figure 11.4 Lowland streaked tenrec (*Hemicentetes semispinosus*). Morphological diversity among the various species of tenrecs is pronounced.

Figure 11.5 **Giant otter shrew (*Potamogale velox*).** This semiaquatic potamogalid primarily occurs in west-central Africa.

(Eisenberg and Gould 1970; Kingdon et al. 2013). Sounds produced by quill vibration may contribute to sound communication and echolocation in adults and juveniles alike (Endo et al. 2010). The tailless or common tenrec (*Tenrec ecaudatus*) has the greatest number of mammae of all species of tenrecs—up to 12 pairs with a litter size averaging 32 young per litter (Eisenberg 1975; Wilson and Mittermeier 2018). As with many mammalian groups in Madagascar, several species of tenrecs are reduced in density and distribution as a result of habitat loss or other factors. The web-footed tenrec (*Limnogale mergulus*) is endangered, as are several other species of tenrecs.

Potamogalidae

The otter-shrews include 2 genera and 3 species and are found in west-central Africa (Bronner and Jenkins 2005; Wilson and Mittermeier 2018). Contrary to its name, the giant otter-shrew is not a true shrew (Soricidae); instead, it more closely resembles river otters (Carnivora: Mustelidae). Otter-shrews sport a dark brown or blackish coat marked with whitish or yellowish underparts; they possess a flattened muzzle housing many stiff white whiskers (Figure 11.5). Each whisker is innervated, and food is located by touch under water. The fur consists of a dense, short, soft protective coat of guard hairs, and frequent grooming, with two fused toes on each hind foot acting as combs, maintains its waterproof nature (Kingdon 2012). Otter-shrews have a sleek cylindrical body equipped with a laterally compressed tail that serves as their only means of propulsion in the water. Locomotion is a fish-like, side-to-side swimming motion. They possess small eyes and external ears covered by flaps that act as valves when the animal is submerged. Two fused toes on each hind foot act as combs for grooming to maintain their waterproof fur. Giant-otter shrews reside in a diversity of aquatic habitats but prefer
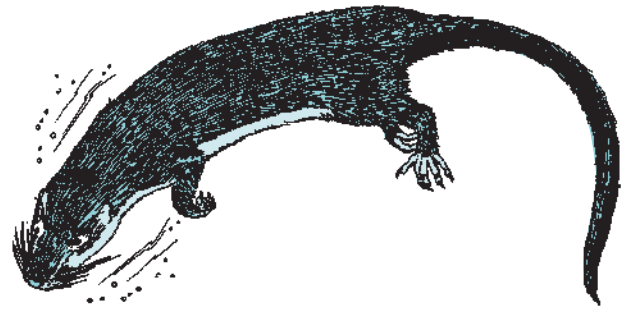
fast flowing rivers, streams, swamps, and coastal rivers from sea level to about 1,800 m elevation. They frequent small forest pools during the rainy season. Banks of rivers offer favorable habitats for breeding and nesting, and, like river otters, otter-shrews will excavate burrows in banks that are below water level. The giant otter shrew (*Potamogale velox*) is the largest living insectivore, with a total length up to 640 mm. They feed on freshwater crabs, fish, amphibians and mollusks. Otter-shrews are strictly nocturnal; they reside in burrows along streams and rivers during the day. Otter-shrews are hunted for their skin and also accidentally trapped in nets or fish traps. Local disappearances of otter-shrews are attributable to logging and habitat modification (Nicoll and Rathbun 1990). All species of otter- shrews are classified as endangered by the IUCN (2018).

Chrysochloridae

The golden moles encompass 10 genera and 21 species (Bronner and Jenkins 2005; Wilson and Mittermeier 2018). As noted in Chapter 11, chrysochlorids appear to be more closely related to the aardvark and elephant shrews than to other insectivore families (Springer et al. 1997a; Stanhope et al. 1998; Emerson et al. 1999). The smallest species of golden mole is Grant's golden mole (*Eremitalpa granti*) with a body mass of 15–30 g. The largest golden mole is the giant golden mole (*Chrysospalax trevelyani*), which weighs 410–500 g. Golden moles are distributed throughout central and southern Africa in forests, fields, and plains with soils suitable for burrowing (Figure 11.6). In these arid environments, free water is usually absent, and moles must exist without drinking water. Water requirements are greatly reduced by nocturnal foraging, torpidity, low metabolic rate, and very efficient kidney function (Seymour and Seely 1996; Fielden et al. 1990b). Physiologically, golden moles are unusual mammals in that they display daily and seasonal torpor (Kuyper 1985), and their body temperature is lower than expected for similar sized mammals. The Namib or Grant's golden mole (*E. granti*) exhibits a resting metabolic rate that is 20% of that expected for a small insectivorous mammal. Many of the same adaptations to enhance underground movement found in marsupial moles (Family

Figure 11.6 **Grant's golden mole (*Eremitalpa granti*).** Grant's golden mole is a leader among small mammals when it comes to monitoring seismic events.
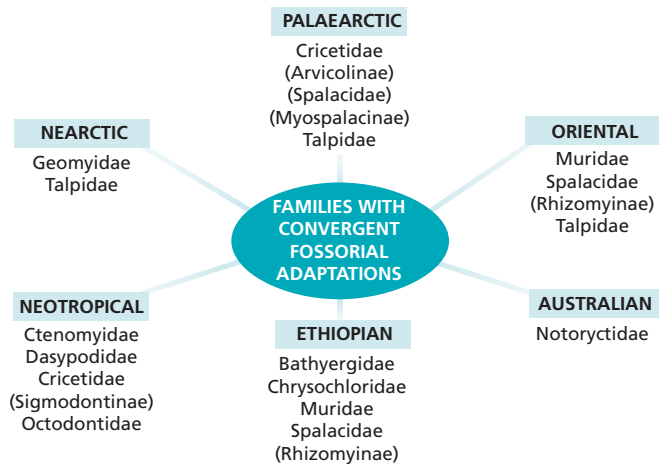
Figure 11.7 **Convergence in fossorial mammals.** Fossorial species from among several families occur in all faunal regions.

Notoryctidae) and true moles (Family Talpidae) are seen in chrysochlorids—a prime example of convergent evolution (Figure 11.7). Golden moles have no pinnae; they have poorly developed eyes with fused eyelids covered with skin. The pelage moves equally well in any direction. It is an iridescent red, yellow, green, or bronze, depending on the species. A smooth, leather-like pad covers the nose, which golden moles use for pushing soil. Grant's golden mole (*Eremitalpa granti*) lacks a permanent burrow system and forages for its prey on the dune surface at night; it literally "swims" though the loose sand that immediately collapses behind it. Unlike the forelimbs of talpids, those of golden moles are under the body and do not rotate outward. They dig by forward extension of the limbs and by scratching at the soil with large claws, especially those on the powerful third digit. For golden moles, as for talpids,

burrow depth and construction depends on local soil characteristics (Seymour et al. 1998; Merritt 2010).

The principal prey of *E. granti* are dune termites (Genus *Psammotermes*) and insect larvae that reside in clumps of dune grass and ostrich grass found on scattered islands throughout the vast xeric sands of the Namib Desert. The moles make remarkably straight paths between clumps of grasses in search of food—sometimes moles forage 5 or more kilometers per night in search of prey (Fielden et al. 1990a; Fielden 1991) without visual aid. Golden moles possess a hypertrophied malleus, adaptive for detection of low-frequency signals. *Eremitalpa* has been observed to occasionally dip its head and shoulders into the sand while foraging in an attempt to discern the position of prey from substrate vibrations. Such head-dipping behavior may be a means by which the mole may tightly couple its head to the substrate to localize seismic signals (Narins et al. 1997; Narins et al. 2016). Navigation is greatly enhanced in Grant's and Cape golden moles (*Chrysochloris asiatica*) by their disproportionately large auditory ossicles in their middle ear; these serve as adaptations for detecting ground vibrations (Narins et al. 1997; Mason and Narins 2002; Mason 2003; Lewis et al. 2006; Willi et al. 2006). The combined mass of the malleus and incus in *Eremitalpa* is approximately 0.1% of the animal's total body mass, compared to 0.00008% in humans. The giant golden mole (*Chrysospalax trevelyani*) is endangered, as are several other chrysochlorids. Recent molecular methods applied to phylogenetic evidence indicates that golden moles are part of a monophyletic African clade of mammals (Superorder Afrotheria), which includes elephants, sea cows, hyraxes, aardvarks, elephant shrews, and the tenrecs mentioned above (Springer et al. 2004).

Tubulidentata

Orycteropodidae

This is the only eutherian order with a single extant member. The only family in this order, Orycteropodidae, contains only one living species, the aardvark (*Orycteropus afer*). Aardvarks enjoy a wide distribution in Africa south of the Sahara Desert, occurring in habitats ranging from dry savanna to rainforests. Given their broad distribution, up to 18 subspecies have been described (Wible 2012), many of which are of questionable validity. As with pangolins, the aardvark is closely associated with the distribution of ant and termite mounds. An aardvark can excavate as many as 25 mounds a night (Taylor and Skinner 2000). The same mound may be visited repeatedly, with the aardvark foraging at previously excavated sites. Larvae, locusts, and even wild cucumbers (*Cucumis humifructus*) are also eaten. However, as with pangolins, the ant *Anoplolepis custodiens* is the most important prey species for aardvarks (Taylor et al.

2002), although numerous genera of ants and termites are taken depending on seasonal availability (Taylor 2011). Aardvarks are solitary, secretive, and elusive, making them difficult to observe. They are predominately nocturnal (rarely crepuscular) and travel as much as 30 km a night as they forage. The functional morphology of the tail of aardvarks is detailed by Endo and coworkers (2013). They locate prey with the aid of highly acute olfactory and auditory senses (Wible 2012). Their burrow system is extensive; several openings occur throughout a small area. Whittington-Jones and colleagues (2011) found that 27 other species of vertebrates used aardvark burrows, which buffer them from extremes of temperature and humidity and offer protection from predators. In the Kalahari Desert, survivorship of aardvarks may be threatened by climate change via direct and indirect effects of increasing heat and aridity (Rey et al. 2017). Microclimatic differences are crucial in the burrow dynamics and ecosystem engineering of aardvarks (Haussmann et al. 2018). Female aardvarks give birth to a single young after 7 months of gestation.

The aardvark is in Superorder Afrotheria, which includes elephants, manatees, dugong, hyraxes, tenrecs, golden moles, and elephant shrews (Murphy et al. 2007; Tabuce et al. 2008; Lehmann 2009). However, molecular, morphological, and fossil evidence has not resulted in a consensus as to the position of the aardvark relative to other mammalian orders.

MORPHOLOGY

The word "aardvark" is Afrikaans for "earth pig," and the species superficially resembles a pig (Figure 11.8A). It weighs up to 60 kg and is about 1.5 m in head and body length. The long, square snout is somewhat flexible, with tufts of hair that protect the nostrils during digging. The nasal septum has short, somewhat fleshy tentacles that probably serve an olfactory function. This supposition is further supported by the fact that the aardvark has more turbinate bones (scroll-like bones in the nasal passages) than any other mammal (Kingdon 1997). Aardvarks have small eyes and large, erect ears; the latter is unusual in myrmecophagous species. The yellowish brown hide is very tough, sparsely haired, and insensitive to ant and other insect bites. The forefeet have four toes, and the hind feet five, each with a heavy, strong, claw-like nail. The back is decidedly arched. Taylor (2011) gave a detailed review of other morphological aspects. Aardvarks can burrow rapidly
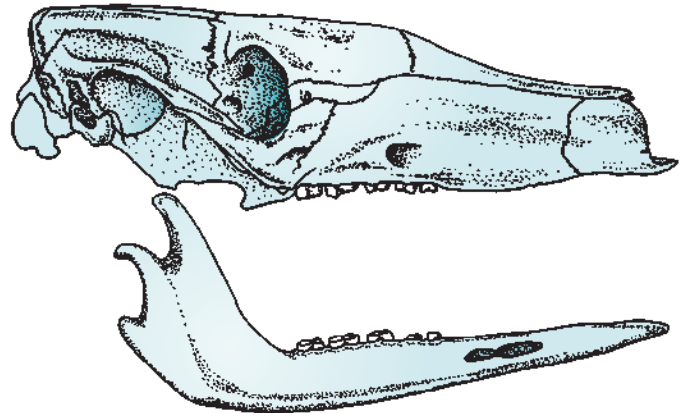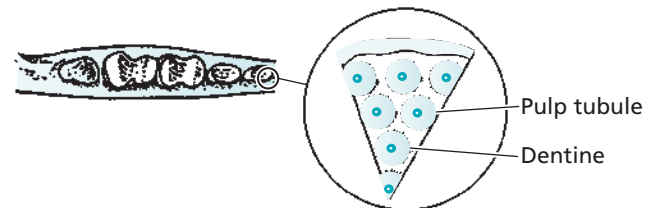
Figure 11.8 **Features of the aardvark.** (**A**) Pig-like snout, large ears, and heavy claws of an aardvark; (**B**) aardvark skull; (**C**) diagrammatic representation of the occlusal surface of the toothrow of an aardvark with a section of the pulp tubules and surrounding dentine. *Drawings adapted from DeBlase and Martin (1981) and K. Kowalski (1976).*

as well as break into ant and termite mounds (Louw et al. 2017). As in anteaters and pangolins, the aardvark's skull is elongated (Figure 11.8B), and it has a small tubular mouth with a long, sticky tongue. Aardvarks chew their food, however, and the dentition is fairly unusual. Incisors and canines are found only during the fetal stage, and adults typically have 20–22 cheekteeth. These teeth are composed of up to 1,500 pulp tubules surrounded by hexagonal prisms of dentine (Figure 11.8C) and account for the ordinal name ("tubule-toothed"). Teeth are open-rooted, without enamel, and are covered with cementum. Besides chewing with their teeth, aardvarks also grind ingested material in a muscular pyloric region of the stomach, similar to that of pangolins.

FOSSIL HISTORY

The fossil record of aardvarks is fragmentary. Although the sole living species is restricted to sub-Saharan Africa, fossil aardvarks are known from Europe and Asia. The earliest known tubulidentate (Genus *Myorycteropus*) is from early Miocene deposits of Kenya. The fossil Genus *Leptorycteropus* dates from the late Miocene of Kenya; many extinct species of *Orycteropus* are known from Pliocene and Pleistocene deposits in Africa. Lehmann (2009) transferred all fossil tubulidentates found in Europe and Asia, as well as two African species—extinct by the end of the Miocene or early Pliocene—to a new genus (*Amphiorycteropus*). Pleistocene remains are known from France, Greece, Turkey, India, and Madagascar (Lehmann et al. 2005; Lehmann 2009).

ECONOMICS AND CONSERVATION

Aardvarks are part of the bush-meat trade in central and east Africa and are eaten by natives. Their teeth are used as jewelry and good luck charms. Aardvarks are rarely seen. This is more a function of their behavior than actual rarity, and populations in most areas are believed to be stable.

SUMMARY

- The Macroscelidea, Afrosoricida, and Tubulidentata represent orders that are rich in diversity of form and function.
  - Historically, the Order Insectivora was a "wastebasket" taxon for families of uncertain affinities.
  - Insectivore species in these 3 orders retain many primitive eutherian characteristics, including their brain anatomy,

  dentition, cranial morphology, postcranial structures and cloaca.
  - The taxonomic history of these orders is complex and has been a mystery since the early 1800s and is one that is still being resolved today.

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DISCUSSION QUESTIONS

1. Sengis, sometimes called "elephant shrews," reside in Africa and are unique in that they are "socially monogamous." Please explain what "socially monogamous" means and elaborate on the role of trail maintenance in sengis. Can you think of the cost-benefit to sengis and adaptive value of maintaining trails in the natural environment? Approximately how many species of mammals are socially monogamous?

2. The common tenrec may have the largest litters of any mammalian species. Given its extremely large num-bers of young, what might you expect are its neonatal survival rate, dispersal of young from the natal area, and associated factors?

3. Aardvarks were once thought to be closely related to pangolins and xenarthrans. We now believe that their resemblance to members of those groups is a result of convergent adaptation for consuming ants (myrmecophagy). Can you name other groups of mammals that demonstrate convergence for myrmecophagy?

CHAPTER 12

Orders: Proboscidea, Hyracoidea, and Sirenia
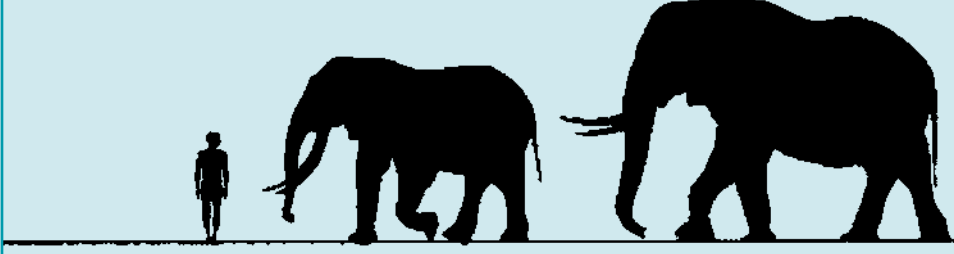
These three orders are often grouped together as **Paenungulata** ("near ungulates") based on their documented evolutionary relationships (Gheerbrant et al. 2005 provide an excellent summary). Molecular, anatomical, and karyotypic studies have strengthened support for the phylogenetic affinity of these orders (Madsen et al. 2001; Murphy et al. 2001b; Kellogg et al. 2007; Pardini et al. 2007; Tabuce et al. 2007). Along with the true ungulate Orders Perissodactyla and Cetartiodactyla (Chapter 19), the orders in this chapter derived from the primitive **Condylarthra**, a generalized ancestral order of land mammals that arose in the early Paleocene about 65 mya. The term "archaic ungulates" probably should be used in place of the commonly used "Condylarthra," however, because it is a wastebasket taxon (see Prothero 2017). By the early Eocene in Africa, about 54 mya, the three orders discussed in this chapter had evolved as well as numerous now-extinct taxa; classification of many of these fossil groups remains uncertain (Gheerbrant et al. 2005; Gheerbrant 2010). Although these orders began to diverge in the Eocene and appear very different today, they share certain anatomical characteristics. None has a clavicle, the digits have short nails (no nails in the Amazonian manatee, *Trichechus inunguis*), and there are four toes on the forefeet (five in Asian elephants). Females have two pectoral mammae between the forelegs (hyraxes have two inguinal pairs as well) and a **bicornuate** uterus. Males have abdominal testes with no external scrotum and no baculum. All are herbivorous, nonruminating, hindgut fermenters. The symbiotic **microfauna** (ciliated protozoans and bacteria) that break down vegetation occur in an enlarged cecum. Finally, the sirenians and elephants are unusual among mammals in their pattern of molariform tooth replacement, which is horizontal, not vertical as in other mammals. Proboscideans, sirenians, and hyraxes all flourished during the Oligocene and Miocene, but with only four extant families among them, they now are mere remnants of what were once very diverse and abundant groups. Because populations of elephants, manatees, and the dugong are declining throughout most of their range, their future is of concern to conservationists.

Table 12.1 Reproductive characteristics of African elephants. Age at first pregnancy and interval between pregnancies for forest and savanna elephants are markedly different. Reduced reproductive potential of forest elephants makes it difficult for populations impacted by poaching to recover.

NAME	FOREST ELEPHANT	SAVANNA ELEPHANT
	Loxodonta cyclotis	*Loxodonta africana*
LOCATION	West and central Africa	Eastern and southern Africa
HEIGHT	2.4–3 m	3–4 m
WEIGHT	2,000–5,000 Kg	4,000–7,000 Kg
FIRST PREGNANCY	23 years	12 years
TIME BETWEEN PREGNANCIES	5–6 years	3–4 years
POPULATION DOUBLING TIME	60 years	20 years

Data from Turkelo et al. 2017. J. Applied Ecol.

Proboscidea

Today, elephants are represented by a single family, the Elephantidae, with only three extant species. The Asian elephant (*Elephas maximus*) occurs south of the Himalayan Mountains in India (with 60% of all individuals), Sri Lanka, Indochina, and Indonesia and has been introduced to Borneo (although Fernando et al. 2003 considered them native). Authorities generally recognize 3 subspecies of Asian elephants: *Elephas maximus maximus* from Sri Lanka, *E. m. sumatrensis* from Sumatra, and *E. m. indicus* from mainland Asia (Shoshani 2005a), although questions remain about the validity of subspecies classification. Using DNA extracted from the dung of 118 Asian elephants from throughout their range, Fernando and colleagues (2000) found very low genetic diversity. Likewise, Vidya and colleagues (2005) found almost no mtDNA variation in Asian elephants throughout southern India, suggesting past gene flow was extensive. African elephants are distributed throughout Africa south of the Sahara Desert. Traditionally, 2 subspecies of the African elephant were recognized: the savanna (or bush) elephant (*Loxodonta africana africana*) in eastern, central, and southern Africa and the forest elephant (*L. a. cyclotis*) in central and western Africa. As the common names suggest, there are differences in habitat use as well as geographic distribution. Grubb and coworkers (2000) supported specific status for the forest elephant as *L. cyclotis* based on several morphological differences, as did Roca and colleagues (2001, 2005, 2007) based on molecular genetic differences. As noted by Roca and colleagues

(2015:159), "genetic evidence overwhelmingly indicates" that savanna and forest elephants are separate species. Most recently, Palkopoulou and coworkers (2018) undertook an extensive genomic survey of the 3 extant elephant species as well as 3 extinct species. They confirmed that savanna and forest elephants are separate species, having diverged 2 mya with no genetic interchange for about 500,000 years. Forest elephants are smaller than savanna elephants (Table 12.1), with more rounded ears and less massive tusks.

African and Asian elephants also exhibit several morphological differences, some of which are familiar to many people. Savanna elephants (Figure 12.1) are larger than

Figure 12.1 **Savanna elephant.** Note the large ears and concave back.
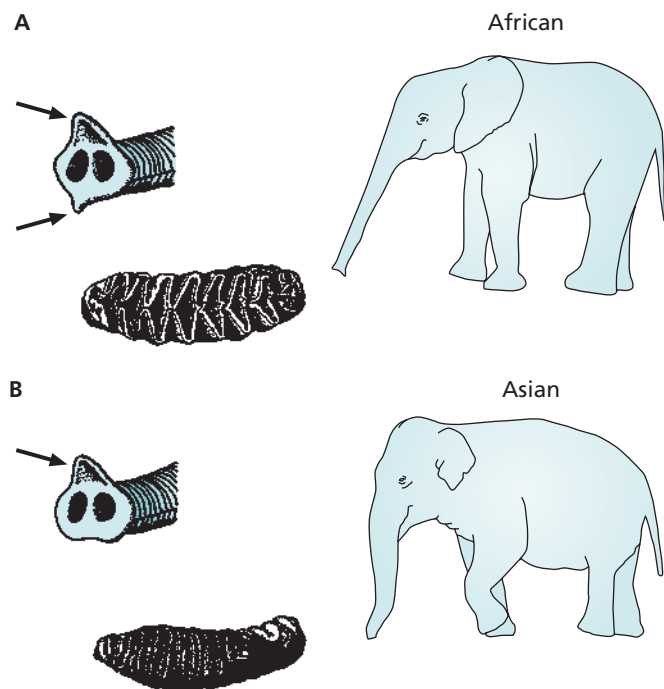
A   African

B   Asian

Figure 12.2 **Characteristics of elephants.** (**A**) An African elephant; (**B**) an Asian elephant. Note the different postures, with the shoulder above the head and a concave back in the African elephant. The Asian elephant has a larger, more bulbous skull, which is above the shoulder, and a convex back. The tip of the trunk has two lips (*arrows*) in African elephants and one lip in Asian elephants. The pattern of the laminar ridges on the occlusal surface of cheekteeth differs in African and Asian elephants. See text for other morphological differences. *Adapted from Eltringham (1982).*

Figure 12.3 **Importance of water.** As with most African wildlife, water is critical to elephants for drinking, washing, and cooling.

Asian elephants and have much larger ears and tusks; the back is concave with the shoulder higher than the head, and the tip of the trunk has 2 lips (Figure 12.2). African and Asian elephants have different occlusal surfaces on the cheekteeth (see Figure 12.2) and different numbers of nails on the hind feet: 4 in Asian and 3 in African elephants. There are 19 pairs of ribs in *Elephas*, 20 in *Loxodonta*. Chromosome complement, however, is $2N = 56$ in all species, with a high level of similarity in the structure of chromosomes (Houck et al. 2001).

Elephants occur in habitats from grasslands and shrublands to forests. Owen-Smith and Chafota (2012) found greater selectivity than expected in the vegetation consumed by savanna elephants. Regardless of habitat type, all elephants are closely tied to the availability of water (Figure 12.3). During the wet season, herbaceous vegetation and grasses are eaten. Shrubs, leaves, and tree bark are taken in the dry season, with flowers and fruits eaten when available. Fruit consumption and associated seed dispersal have been documented in *E. maximus* and *L. cyclotis* (Shumpei et al. 2007 and references therein). In agricultural regions, elephants can do extensive damage to cultivated crops. Large adults can consume up to 150 kg of vegetation a day, but because the digestive process is relatively in-

efficient compared with that of ruminants, half of this may pass through the gut undigested.

Large home ranges are needed to sustain groups of elephants because of the amount of food necessary to maintain an individual; the often dry, inhospitable habitat conditions; and the fact that aggregations of up to 50 individuals of mixed sex and various ages can form during portions of the year. As a result, home-range size can be 1,600 km² or more during seasons when resources are scarce. Elephants may move up to 30 km a day to reach better habitat conditions. Extent and distance moved depend on the quantity and quality of food and water available, as well as the degree of habitat fragmentation (Alfred et al. 2012). Elephant herds are capable of quickly degrading habitats and affecting the availability of resources to other herbivores. However, breaking, uprooting, or pushing trees over may actually improve their availability to small browsing herbivores (Kohi et al. 2011). Nonetheless, Hayward and Zawadzka (2010) found that savanna elephants have a greater impact on vegetation change than did limited rainfall.

Elephants are gregarious, with herds normally made up of family units of about 10 individuals. Females and their young, led by a matriarch, remain in these units (Vidya and Sukumar 2005). Different units made up of related individuals often join temporarily to form "bond groups." Depending on the time of year, males can be either solitary or in temporary all-male groups, with overlapping home ranges. Adult males join females when the latter enter estrus. Juvenile males leave herds when they become sexually mature, between 10 and 17 years of age.

Sexual maturity generally is reached in females between 9 and 12 years old, with peak fecundity from 25 to 45 years of age. Females 50 years and older rarely, if ever, breed. However, as shown in Table 12.1, the first pregnancy in forest elephants may not occur until 23 years of age. Reproduction is tied to the wet season and the availability of food and

water. Females are in estrus during the later part of the rainy season and first part of the dry season. Estrus is very brief, lasting only 2–4 days. The interval between estrous periods averages 4 years (Moss 1983) because of the long length of gestation and lactation. Following an average 22-month gestation, a single young is born (rarely twins) at the beginning of the wet season, when habitat conditions are optimal. Newborn savanna elephants weigh about 120 kg; newborn Asian elephants, 100 kg. They nurse for 3–4 years (with the mouth, not the trunk) and weigh 1,000 kg by 6 years of age. Lahdenperä and colleagues (2016), studying Asian elephants in Myanmar, found that when grandmothers were near, they increased both the reproductive success of their adult daughters and calf survival. Elephants grow throughout their lives, although growth rate decreases by age 15. Males exhibit a reproductive period called **musth** for 2–3 months each year, during which time hormone levels, sexual activity, and aggressive behavior increase. Although males are physiologically capable of breeding by 10–15 years of age, older males generally have greater success mating than do younger males (Hollister-Smith et al. 2007), and most successful matings are by mature males 30–50 years old.

Elephants make a variety of vocalizations audible to humans, including trumpeting, growling, roaring, and snorting. Langbauer (2000) discussed 31 different types of calls in African elephants. Vocalizations vary depending on the size and composition of the group and the reproductive status of individuals (Payne et al. 2003). Elephants also communicate with one another through high-amplitude, extremely low-frequency sound—as low as 14–35 Hz (cycles per second) (Payne et al. 1986; Langbauer et al. 1991)—which is well below the range of human hearing. Low-frequency sound allows groups or individuals up to 4 km apart to communicate and coordinate movements and helps males find females during their brief and unpredictable estrous periods. Low-frequency sound is used to communicate because it can travel over long distances and through obscuring vegetation much better than higher frequency sound. Also, large animals like elephants would physically have a difficult time producing high-frequency sound because of the length of their vocal cords. De Silva (2010) described 8 single and 5 combination calls in Asian elephants, with growls comprising nearly 66% of total vocalizations. Acoustic signals occurred in a variety of contexts with differences among sex and age classes. Nair and colleagues (2009) classified Asian elephant calls into 4 categories: trumpets, chirps, roars, and rumbles. Juveniles used all except chirp calls. Herler and Stoeger (2012) used the same 4 categories, but found Asian elephant calves used them all. In the vocal repertoire of savanna elephants rumbles were the most common and variable calls and were used for spatial cohesion of individuals and other social interactions (Soltis et al. 2008; Soltis 2010).

Elephants also use low-frequency **infrasounds** that have a seismic component and may complement communication between individuals in a herd (O'Connell-Rodwell et al. 2006; O'Connor-Rodwell 2007; Narins et al. 2016). It is believed that as these sounds travel through the ground, ele-phants can pick up the seismic signals—they are "listening" through their feet and trunks. Bouley and colleagues (2007) investigated the density, distribution, and structure of mechanoreceptors called "Pacinian corpuscles" in the feet of elephants and their role in seismic communication. In addition, the reptile-like cochlea of elephants may enhance sensitivity to the vibrations. Seismic signals can be picked up from hundreds of meters away, and possibly several kilometers. Communication can also occur through chemical signaling (Greenwood et al. 2005; Ghosal et al. 2012).

MORPHOLOGY

Elephants are the largest living terrestrial mammals. Aspects of anatomy, movement, dentition, and behavior relate to their size and associated long life span. The shoulder height of adult African savanna bull elephants can reach 4 m, with maximum body mass up to 7,000 kg. Sexual dimorphism is evident, with body mass smaller in females. As noted, African forest elephants are smaller than savanna elephants (see Table 12.1). Because they grow throughout life, the oldest elephant in a group often is the largest. Asian elephants are smaller than savanna elephants but generally heavier than forest elephants. Mean body mass of male Asian elephants is about 4,500 kg. The structure necessary to support such large mass gives rise to several modifications resulting in graviportal locomotion and a massive skeleton that makes up 15% of an individual's body mass, about twice that of most terrestrial mammals. The head is very large, in part to help support the trunk and ever-growing tusks. The bones surrounding the brain are thick but made less heavy by a series of air-filled pneumatic cavities, or sinuses (Figure 12.4). The feet are broad, with the phalanges embedded in a matrix of elastic tissue to help cushion the weight (Figure 12.5).

Throughout their evolutionary history, elephants may have benefited from increased body size in avoiding competition with the large herbivorous African perissodactyls that
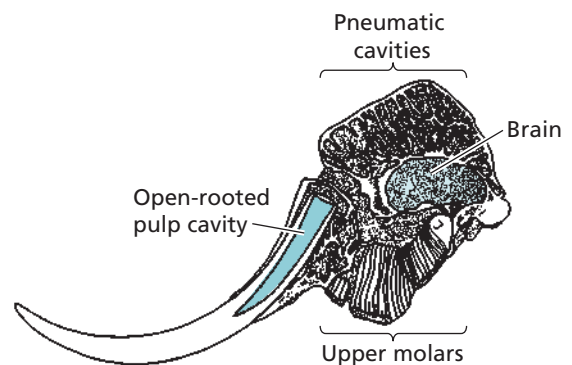
Figure 12.4 Elephant skull. Sagittal cross section of the skull of an African elephant, showing the extensive network of pneumatic cavities that help reduce the weight of the skull. Note the open-rooted pulp cavity of the tusk. The tusks grow throughout the life of the animal. *Adapted from Macdonald (1984).*
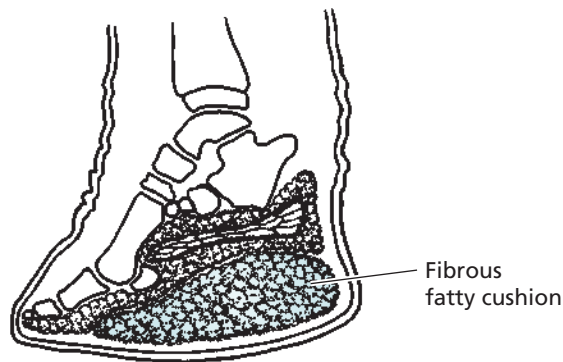
Figure 12.5 Forefoot of an African elephant. Although elephants are functionally plantigrade, they actually are digitigrade—walking on their toes. The bones of the feet, and the massive weight of the animal, are cushioned by fibrous, fatty connective tissue that uniformly distributes the weight over a broader area. *Adapted from Grzimek (1990).*

preceded them, as well as the cetartiodactyls that arose later. Large body size confers other benefits in addition to reduced competitive pressure. It allows elephants to move greater distances in response to habitat conditions with relatively less energy expenditure. It also reduces predation pressure; only humans threaten adult elephants. During the dry season African lions (*Panthera leo*) can take elephant calves (Loveridge et al. 2006). Along with benefits, large size also has its drawbacks. Elephants live in warm climates but have very few sweat or sebaceous glands. Heat dissipation without dehydration is a problem, especially in areas with limited water availability. Thus, elephants have very sparse body hair, a characteristic common to other large mammals in warm climates. Also, the wrinkled skin of elephants acts to hold water and facilitate its movement on the body surface, increasing the evaporative cooling effect (Lillywhite and Stein 1987). The large ears, especially of African elephants (see Figure 12.1), are highly vascularized, and when moved back and forth, they act as radiators or "thermal windows" (Weissenboeck et al. 2010) to dissipate heat. Behavioral characteristics such as seeking shade and reducing activity during the middle of the day also help reduce heat load.

The trunk is the most recognizable feature of elephants and gives rise to the ordinal name. It is an elongated, flexible, muscular upper lip and nose, with the nasal canal throughout its length. Trunks were well developed in 6 fetuses of African elephants that were only 97–117 days old

Elephants, Cancer, and Peto's Paradox

Cells are constantly dividing in mammals, as in any multicellular organism, and when they do, billions of base pairs of DNA must be copied. Invariably, mistakes occur in the process. Some of these "somatic mutations" affect biochemical pathways that would normally check the growth and proliferation of cancerous tumors. The occurrence of cancer in a species should be a function of lifespan (longer life means more cell divisions) and body size (large animals have more cells). So one would expect large, long-lived animals such as elephants to be at greater risk for cancer than small, short-lived species such as mice—a significant constraint on the evolution of large body size. But decades ago, Richard Peto and colleagues (1975) found that there is no relationship between risk of cancer and the body mass and lifespan of animals. This lack of correlation is known as "Peto's Paradox." Not only is there no relationship, but some species are relatively cancer resistant. Elephants, the largest terrestrial mammals, are an example, with mortality rates due to cancer of only 3% to 5% of individuals. In comparison, human mortality due to cancer is 11%–25% (Abegglen et al. 2015).

So what mechanisms might allow large animals like elephants to resist cancer? When cells incur DNA damage that can lead to cancer, they can either repair the damage or the cell can self-destruct (a process called "apoptosis"). One of the best-known genes for tumor suppression is known as TP53, which induces apoptosis in cells with damaged DNA. Whereas humans have a single copy of TP53, elephants have 20 copies (Abegglen et al. 2015; Sulak et al. 2016). Research has shown that damaged elephant cells are likely to self-destruct rather than incur carcinogenic mutations—which would be expected given their large number of TP53 genes. Vazquez and coworkers (2018) showed that TP53 in elephants actually triggers a "refunctionalized pseudogene"—LIF6—which induces apoptosis in damaged cells before they become cancerous. There are many large-bodied mammals, and as noted by Tollis and colleagues (2017), probably many cancer suppression pathways have evolved.

Interestingly, not all these pathways occur in large mammals. As noted in the section on naked mole-rats (Rodentia, Bathyergidae, *Heterocephalus glaber*) in Chapter 16, they are extremely long lived for a rodent and like elephants are resistant to cancer. However, they have a different tumor suppression system than elephants (Tian et al. 2013).

Peto's Paradox has led to discoveries of how evolutionary lineages deal with the relationships of body size, longevity, damaged cells, and resistance to cancer. These discoveries and continued research may aid in new therapies and approaches for cancers in humans as well.

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(Gaeth et al. 1999). The trunk has numerous uses. Because an elephant's head is so heavy, its neck is very short; thus, the animal cannot touch the ground with its mouth. The trunk is used to grasp food from the ground as well as from tall trees. It is extremely strong, yet the tip is sensitive enough to pick up small objects (such as peanuts in a zoo). Elephants drink by sucking up to 4 liters of water into their trunk at a time and squirting it into the mouth. Adults may drink 100 liters of water a day. Water is also sprayed from the trunk over the body to keep the animal cool (see Figure 12.3). Mud and dust also can be sucked into the trunk and sprayed on the body for this purpose, as well as to reduce insect infestations. Elephants also have an excellent sense of smell, and the trunk can be held upright in the air like a periscope to gain olfactory information from the surroundings.

The dental formula is 1/0, 0/0, 3/3, 3/3 = 26, and the teeth are highly specialized. The remaining upper incisor in extant elephants is the second (I2) and forms the characteristic tusk. The deciduous I2 is replaced by the permanent tooth between 6 and 12 months of age, when it is only about 5 cm long. Tusks (often collected by poachers as "ivory") are composed of dentine and calcium salts, with enamel only on the terminal portion. They are open-rooted (see Figure 12.4) and grow throughout life. Tusks are largest in African savanna bull elephants, reaching up to 3.5 m in length and 200 kg in weight in very old adults; 100–120 kg is more common. In female Asian elephants, the tusks are smaller and may not extend beyond the lower lip. Tusks are used in foraging, defense, and social displays.

The cheekteeth are large and hypsodont, with transverse **laminae** (ridges). These ridges are composed of dentine overlaid with enamel. Cementum occurs between the ridges. Posterior cheekteeth (equivalent to molars) are larger than those anterior (equivalent to premolars) and have a greater number of ridges. Asian elephants have more laminae than African elephants. Because the mandible is short and the cheekteeth long, only one upper and one lower molar (or parts of two) are active in each jaw at a time. Replacement of cheekteeth is horizontal from the back of the jaw—a process referred to as "mesial drift." The new tooth moves forward as the worn anterior tooth is pushed out. The third and final molars begin to come in by about 30 years of age and last for the remainder of an individual's life (Figure 12.6).

FOSSIL HISTORY

Although only three species of elephants survive today, this order was diverse and widespread throughout most of the Cenozoic era. Elephants occurred not only in Africa and Asia, but in Europe and North America throughout the Pleistocene and even reached South America at that time. The earliest fossil is *Eritherium azzouzorum* from the Paleocene of Morocco (Gheerbrant et al. 2012), which was similar to *Phosphatherium escuilliei* from the early Eocene of Morocco (Gheerbrant et al. 2005). The beginning of the Eocene likely saw rapid evolution of proboscideans; there are
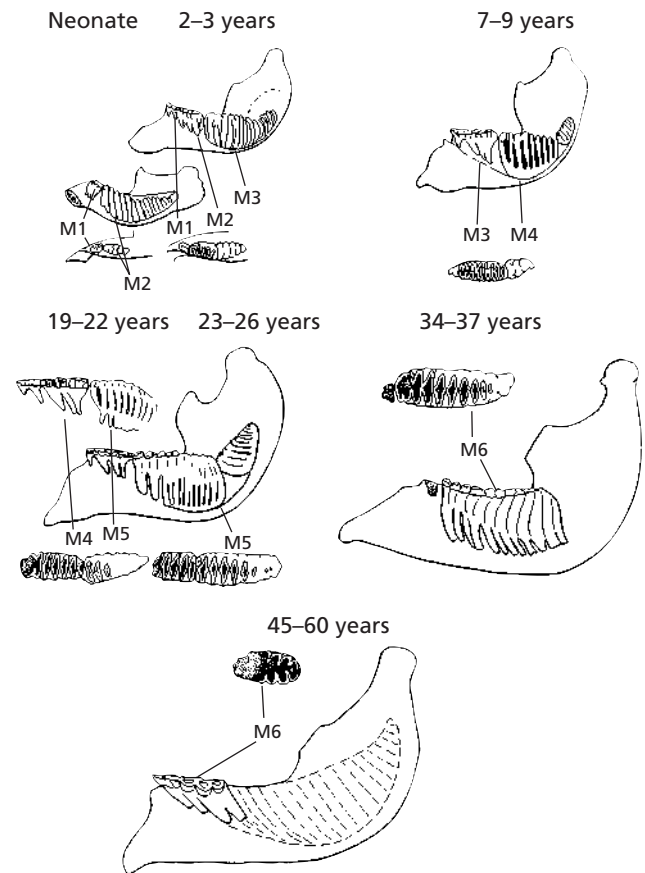
Figure 12.6 Proboscidean cheekteeth. Unlike the cheekteeth in most other species of mammals, those in elephants enter the jaw horizontally (called "mesial drift"). Because all the cheekteeth are deciduous in elephants, M1–M3 are equivalent to premolars, and M4–M6 are equivalent to molars in other mammals. Progression of teeth is shown for an African elephant, with ages approximated, especially after 30 years of age. *Data from Kingdon (1979).*

extensive fossil remains with several families recognized (Figure 12.7). Two of these extinct families, the Moeritheriidae and the Deinotheriidae, diverged early. The moeritheriids (Figure 12.8A), known from the Eocene and Oligocene of northern Africa, were only about a meter in height and probably amphibious. Deinotheriids occurred in Asia and Europe from the Miocene to Pliocene. Referred to as "hoe-tuskers," they were elephant-size with large, downward-curving tusks in the lower jaw (Figure 12.8B). Three other extinct families (included as Elephantiformes in Figure 12.7) have much closer affinities to today's elephants. The Family Gomphotheriidae, which was contemporary with moeritheriids and deinotheriids, Family Mammutidae (mastodons) from the early Miocene, and Family Stegodontidae from the mid-Miocene all had the large body size and many of the characteristic specializations of elephants today. Gomphotheriids had a pair of tusks in both the upper and lower jaws (Figure 12.8C). Mastodons probably survived until about 8,000 years ago. The North American mastodon (*Mammut americanum*) was contemporary with the arrival of humans on the continent. Skeletal material of mastodons

was first collected in North America from the Hudson River in 1705 (Sikes 1971). Although members of Family Stegodontidae survived until the late Pleistocene, only one proboscidean family remains extant.
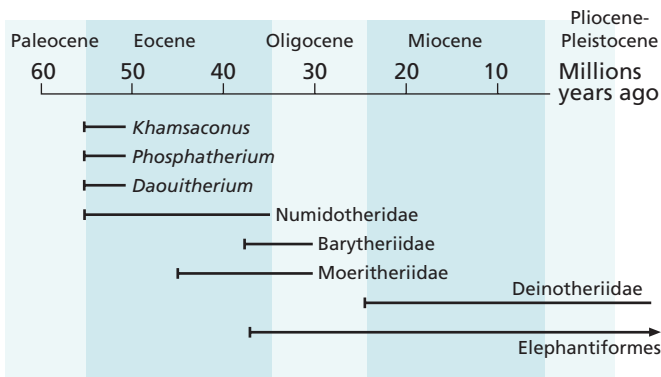
Figure 12.7 Representative lineages of proboscideans. The only extant family, the Elephantidae, is included here within the Elephantiformes, which also includes the extinct Families Stegodontidae, Gomphotheriidae, Amebelodontidae, Mammutidae, and the early Genera *Phiomia* and *Palaeomastodon*. Many other genera are recognized. *Modified and adapted from Gheerbrant et al. (2005) and Sanders et al. (2010).*

The family that survives today, the Elephantidae, is recognizable from the late Miocene Genus *Stegotetrabelodon*. The extinct Genus *Primelephas*, from the late Miocene to early Pliocene, gave rise to the 2 genera still extant today as well as the extinct Genus *Mammuthus*, the mammoths that were contemporary with early humans (Pitulko et al. 2016). The woolly mammoth (*M. primigenius*; Figure 12.8D) was often depicted in cave paintings and other artwork by Paleolithic humans (Figure 12.9A, B). This species went extinct less than 4,000 years ago (Palkopoulou et al. 2015). Complete specimens of woolly mammoths have been found frozen in Siberian ice. Recently, based on mitochondrial and nuclear genomes of the Pleistocene straight-tusked elephant *Palaeoloxodon antiquus*, Meyer and colleagues (2017) found that it was most closely related to the forest elephant, not the Asian elephant as previously believed. This result may likely necessitate significant revision of the Genus *Loxodonta*.

ECONOMICS AND CONSERVATION

The involvement of elephants in human culture, religious tradition, and history is extensive. Humans hunted mammoths as long as 70,000 years ago (Owen-Smith 1988). We
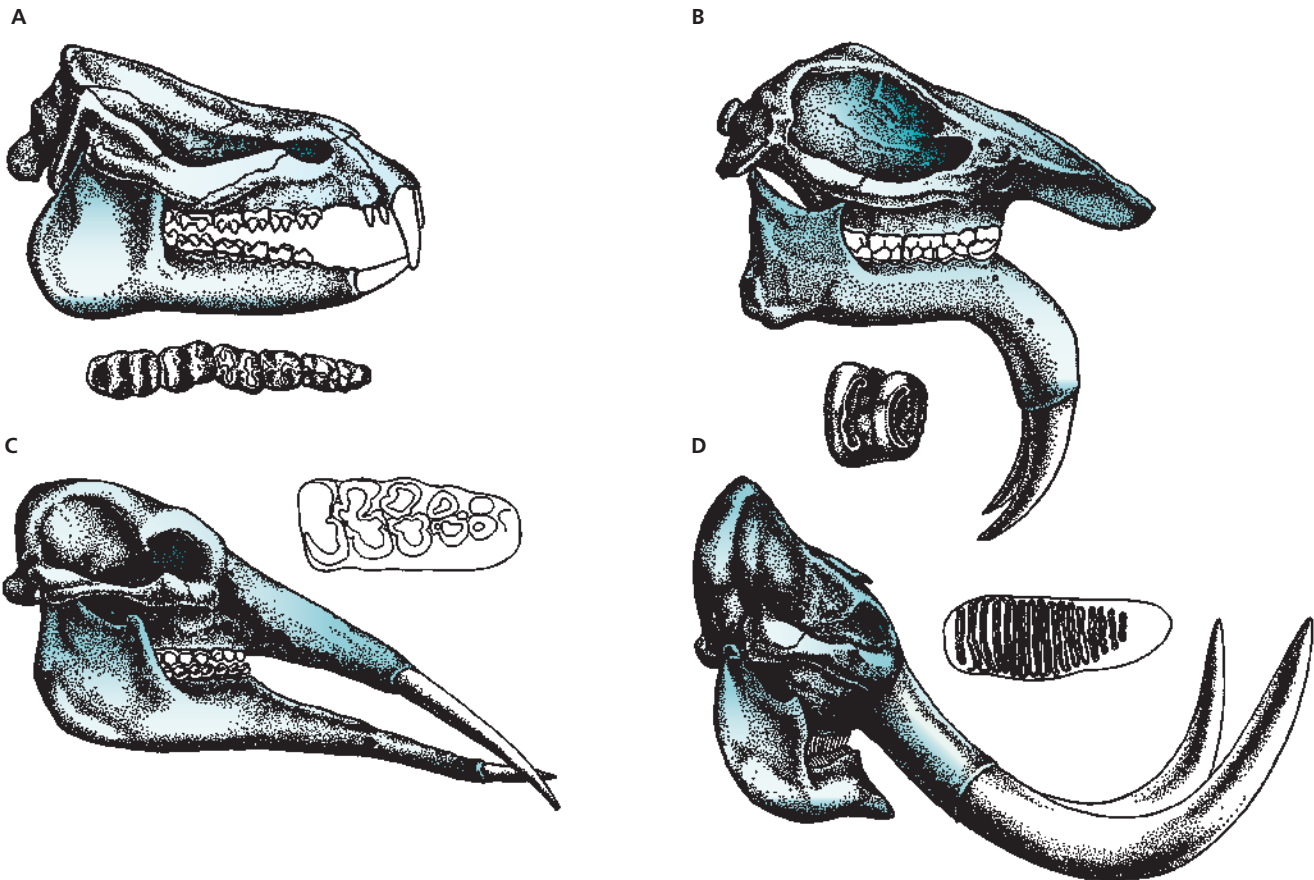
Figure 12.8 Fossil skulls of early proboscideans. (A) The late Eocene Genus *Moeritherium*, actual length about 33 cm. **(B)** The Miocene Genus *Deinotherium*, actual length about 1.2 m. **(C)** Genus *Gomphotherium*, actual length about 1 m, occurred in the Miocene. **(D)** The actual length of the woolly mammoth skull is about 2.7 m. Note the changes in the molar cusp patterns of the early proboscideans, with the occlusal surface of mammoths being very similar to modern elephants. *Adapted from Carroll (1988).*

A

B
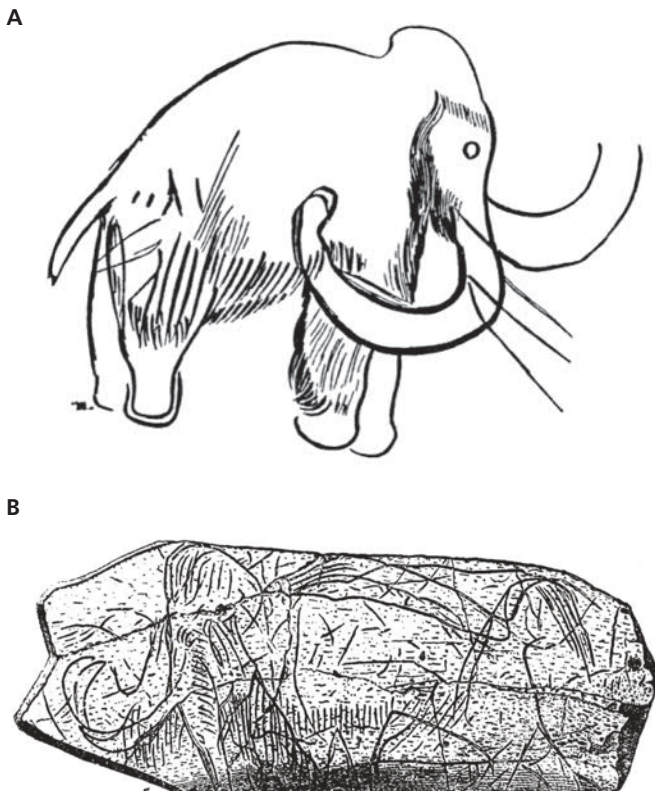
Figure 12.9 Paleolithic art of the woolly mammoth.
(**A**) This drawing of a woolly mammoth is from the cave wall of Les Combarelles aux Eyzies, France. (**B**) Image of a mammoth carved on a piece of ivory from the Abri de la Madeleine cave in Dordogne, France. Not actual sizes.

are all aware of the central importance of elephants in circuses and as zoo animals since ancient times and of their role in the famous march of Hannibal over the Alps in 218 BCE. Asian elephants have been important as draft animals throughout many parts of Asia for over 5,000 years, although they can be considered "exploited captives" as opposed to domesticated species. Elephants remain important in terms of conservation efforts throughout their ranges. Population declines have been attributed to drought, loss of habitat associated with increased human population growth and desertification, and poaching for meat and ivory. Poaching escalated when prices for ivory increased significantly during the 1970s and 1980s, and it continues to be a serious problem (Breuer et al. 2016; Turkalo et al. 2017). As noted by Archie and Chiyo (2011), poaching not only kills an individual, but can also have broader negative effects on the behavior, genetic structure, reproduction, and health of elephant herds. Conversely, however, several African countries must cull elephants from areas where their population densities are too high relative to limited forage resources. The animals can destroy crops (Pant et al. 2016), increase soil erosion, kill overstory trees through chronic herbivory (Rutina and Moe 2014; Morrison et al. 2016), and depress the resource base for other species. Countries that cull elephants may depend on the legal harvest and sale of ivory to fund their wildlife management programs. Problems arise because legally harvested ivory cannot be distinguished from poached ivory, and the legal trade promotes more illegal poaching by providing a market (Wasser et al. 2010). Future developments in molecular genetics and x-ray or stable isotope techniques may allow investigators to pinpoint the source population of ivory and help alleviate this problem (Ishida et al. 2013). Currently, assays are available to identify the species of elephant that illegal ivory is from (Kitpipit et al. 2016, 2017); geographic locales of illegal ivory can be determined using mtDNA methods (Ishida et al. 2013). Wasser and colleagues (2015) sampled elephant DNA from 1,500 dung piles throughout the ranges of savanna and forest elephants and matched results to poached ivory. They found poaching was concentrated in two areas: Tanzania and Mozambique for savanna elephants, and the Tridom area, which includes parts of Gabon, Cameroon, and the Republic of Congo, for forest elephants. The Asian elephant is endangered because of declining populations and fragmented, degraded habitat. The African elephants are considered threatened in some areas of their range, with *L. cyclotis* numbers dramatically reduced because of poaching and habitat loss. Given their slow growth rate (see Table 12.1) recovery of these populations will take many decades (Turkalo et al. 2017) even without poaching loss.

Hyracoidea

Referred to in several places in the Old Testament as "rock badgers" or "conies," hyraxes comprise a single family, Procaviidae, with 3 genera and 5 species (Shoshani 2005b). Past taxonomic confusion surrounding hyraxes is reflected in the many misnomers associated with them. For example, they are sometimes called "rock rabbits." Because of their superficial resemblance to rodents (Figure 12.10), taxonomists initially grouped hyraxes with the guinea pigs. The family name means "before the caviids"—caviids are guinea pigs. Even the common name "hyrax" is a misnomer because it means "shrew mouse." None of these associations is accurate, because based on fossil and molecular evidence, hyracoids are most closely related to the other "subungulates," elephants and manatees.

Hyraxes are distributed in central and southern Africa, Algeria, Libya, Egypt, and parts of the Middle East, including Israel, Syria, and southern Saudi Arabia. The rock hyrax (*Procavia capensis*) is the most widely distributed geographically and elevationally. They occur in rocky outcrops from sea level to 4,200-m elevation in Africa and the Middle East. The yellow-spotted rock hyrax, or bush hyrax (*Heterohyrax brucei*), is found in similar rocky habitats in northeast to southern Africa. There may be several additional species among the 24 recognized subspecies of bush hyrax (Hoeck 2011). The 2 species of

Figure 12.10 **Hyrax characteristics.** Hyraxes, like this pair of rock hyraxes (*Procavia capensis*), superficially resemble rodents but are not closely related to them. Note the prominent white fur surrounding the middorsal gland.

Figure 12.11 **Unusual alimentary tract.** The alimentary tract of a hyrax includes the stomach (*s*), a large cecum (*c1*) at the beginning of the large intestine, and a second, paired cecum (*c2*) at the end of the large intestine. *Adapted from Grzimek (1990).*

arboreal tree hyraxes (Genus *Dendrohyrax*) inhabit forested areas of Africa up to 3,600-m elevation. The terrestrial species are diurnal or crepuscular and form large colonies. Conversely, tree hyraxes are nocturnal and solitary.

All hyraxes are herbivorous and feed on a variety of vegetation. Grasses make up a large part of the diet of the rock hyrax; the hypsodont dentition grinds this abrasive material. The other hyraxes have more brachyodont dentition because they consume less abrasive vegetation. Although they do not ruminate, hyraxes have a unique digestive system involving one large cecum and a pair of ceca on the ascending colon (Figure 12.11).

Colony size varies according to species, with the rock hyrax maintaining group sizes up to about 25 and the yellow-spotted hyrax up to 35. Larger group size allows for decreased individual vigilance toward potential predators (Fansom et al. 2011). Mbise and colleagues (2017) found larger populations of the rock hyrax and bush hyrax where there was higher human presence, possibly because of fewer natural predators and more food availability. Fluctuations in abundance of these species were synchronous over a 13-year period in Zimbabwe (Barry et al. 2015). Hyraxes are poor thermoregulators. Individuals in a colony may huddle together to help conserve heat and maintain body temperature (Figure 12.12). Rock hyraxes bask in the sun to help warm up during winter, or simply to maintain body temperature on cold days (Brown and Downs 2007), but during the summer they seek cool refuges in the rocks to escape lethal high temperatures and

to reduce water loss (Brown and Downs 2005, 2006). As might be expected in colonial species, hyraxes are very vocal and make a variety of different types of sounds, including whistles, screams, croaks, and chatter. A population of the western tree hyrax (*Dendrohyrax dorsalis*) in Benin vocalized primarily from dusk to midnight, and again in the very early morning (Djossa et al. 2012). Koren and Geffen (2009, 2011) showed that complex vocalizations ("singing") served to identify individual rock hyraxes, as well as attributes such as body weight, reproductive condition, and social status. Demartsev and colleagues (2016) discussed the dynamics of singing and counter-singing in male rock hyraxes.

Reproductive maturity in both sexes occurs at about 16 months of age. Females come into estrus once a year. Gestation is a relatively long 8 months, with litter size ranging from 1 to 4. Neonates are precocial, with most births occurring during the wet season. Young males disperse from their natal area between the ages of 16 and 30 months and try to establish their own breeding territories.

MORPHOLOGY

Hyraxes are short, with compact bodies and very short tails. Pelage color is brown, gray, or brownish yellow. Total length varies from 32 to 60 cm and body mass from 1 to 5 kg. There is no sexual dimorphism. Hyraxes from warm, arid regions have shorter, less dense pelage than tree hyraxes and those from high-elevation alpine areas. Hyraxes have a prominent middorsal gland about 15 mm

Figure 12.12 **Group of rock hyraxes.** As noted, colony sizes may reach 25 individuals.

long surrounded by lighter colored hair (see Figure 12.10). The gland varies in size among species, being most noticeable in the western tree hyrax and least so in the rock hyrax. Highly odiferous, the gland functions in courtship, mating, and kin recognition.

Because hyraxes inhabit rocky cliffs or move through trees, good traction for climbing and jumping has obvious adaptive value. This is achieved through specialized elastic, rubbery pads on the soles of the feet. These pads are kept moist by secretory glands that make the feet similar to suction cups. The toes have short, hoof-like nails except for the second digit on the hind feet, which has a claw used for grooming (Figure 12.13).

Unlike that of elephants and sirenians, the molariform dentition in hyraxes is not replaced horizontally. The dental formula for the permanent dentition is 1/2, 0/0, 4/4, 3/3 = 34. Deciduous canines may be retained in rare cases, but there is usually a diastema between the incisors and cheekteeth (Figure 12.14A). The upper incisors are long, pointed, and triangular in cross-section and have a gap between them. They are ever-growing and stay sharp because the posterior sides do not have enamel. Gheerbrant and colleagues (2005; see their table 7.4) discuss other primitive and derived features of hyracoids.

FOSSIL HISTORY

Hyracoids first appear in the early Eocene of Africa and were abundant and diversified. They were the most common herbivorous mammals in early Tertiary African communities and ranged in size from 3 kg to 1,400 kg. Rasmussen and Gutiérrez (2010) recognized 4 families

Figure 12.13 **Hyracoid digits.** The first and fifth toes are absent on the hind feet of a hyrax. The toes of the hyrax have hoof-like nails, except for the second digit on the hind feet (pes). These have a claw that is used for grooming the fur. The soles have glandular pads that make them moist and increase adhesion to steep, rocky inclines.

A

B
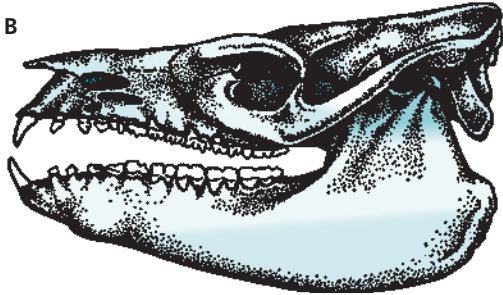
Figure 12.14 **Hyracoid skulls.** (**A**) The skull of a modern tree hyrax, with a well-defined diastema; actual length about 12 cm. This can be contrasted with (**B**) an early Oligocene hyracoid Genus *Megalohyrax*; actual length about 30 cm. *Adapted from Romer (1966).*

(Pliohyracidae, Geniohyidae, Saghatheriidae, and Titanohyracidae) and 17 genera of extinct hyracoids. The earliest, most basal fossil hyracoid is the geniohyid *Seggeurius amourensis*. Euasian pliohyracids from the late Miocene, including the Genera *Pliohyrax*, *Hengduanshanhyrax*, *Kvabebihyrax*, and *Postschizotherium*, exhibited gigantism with body masses from 800 to 1,400 kg. Likewise, saghatheriids such as *Megalohyrax eocaenus* (Figure 12.14B; Thewissen and Simons 2001) and titanohyracids such as *Titanohyrax mongereaui* weighed about 1,000 kg. The first specimens attributable to modern procaviids are from the late Miocene of Namibia (Rasmussen et al. 1996). By this time, only smaller forms of hyraxes survived. Larger species may have died out because they could not compete with perissodactyls and cetartiodactyls. Tabuce and colleagues (2017) provide an excellent summary of fossil hyracoids.

ECONOMICS AND CONSERVATION

Tree hyraxes are hunted for their meat, as well as for fur for blankets—and for clothing at one time. All tree hyraxes are affected by the loss of forest habitat, although no species of hyrax is currently threatened or endangered. Because hyraxes in a colony defecate and urinate in a traditional place, massive caked deposits form on the rocks. This material has been used by natives as a decorative dye and by Europeans as a fixative in perfumes (Kowalski 1976).

Sirenia

This order includes only 2 extant families. The Family Dugongidae has 1 living species, the dugong (*Dugong dugon*), as well as the recently extinct Stellar's sea cow (*Hydrodamalis gigas*). The Family Trichechidae has 3 extant species of manatees in Genus *Trichechus*. The ordinal name is derived from the sirens, or sea nymphs, of mythology; dugongs and manatees may have been the basis for the myth of mermaids. Like whales, sirenians never leave the water. Unlike whales, however, they are strictly herbivorous and represent the only mammalian marine herbivores. They inhabit coastal areas, estuaries, bays, and inland river systems in tropical regions, where they feed on submerged and emergent vegetation. Sirenian distribution is restricted to (1) relatively shallow coastal areas because the plants they depend on require sunlight and (2) tropical and subtropical regions with water temperatures near 20°C because of their low metabolic rates and poor thermoregulatory abilities. In contrast to terrestrial herbivores, sirenians have limited competition from other mammals within their feeding niche of shallow-water vegetation. The 4 extant species represent vestiges of an order that was abundant and very diverse during the Tertiary period, with fossil remains of about 20 known genera.

MORPHOLOGY

Sirenians exhibit many of the same adaptations for life in the water as do whales. They are large, with a fusiform body shape (Figure 12.15), and are devoid of fur except for very short, stiff bristles around the snout. There is no external ear (pinnae), the nostrils are valvular and located on the top of the rostrum, the lips and snout are very flexible, with whiskers that enhance tactile acuity, and the tail is horizontally flattened. The forelimbs are paddle-like, and there are no external hind limbs. Only small, paired vestigial bones, suspended in muscle, represent the remains of the pelvis. The rostrum and lower jaw are deflected downward, especially in the dugong (Figure 12.16), to facilitate bottom feeding. The skeletal bones are very dense and massive (**pachyostotic**), an adaptation to increase body mass and overcome the buoyant effects of living in shallow, saltwater habitats. The lungs are long and thin, extending for much of the length of the body cavity (Figure 12.17). This helps to evenly distribute the buoyant effects of the air as an animal breathes. Unlike many whales, sirenians have no dorsal fin, nor do they echolocate.

FOSSIL HISTORY

In addition to the two extant sirenian families, there are two well-represented extinct families (Figure 12.18): the Prorastomidae and the Protosirenidae (Gheerbrant et al.
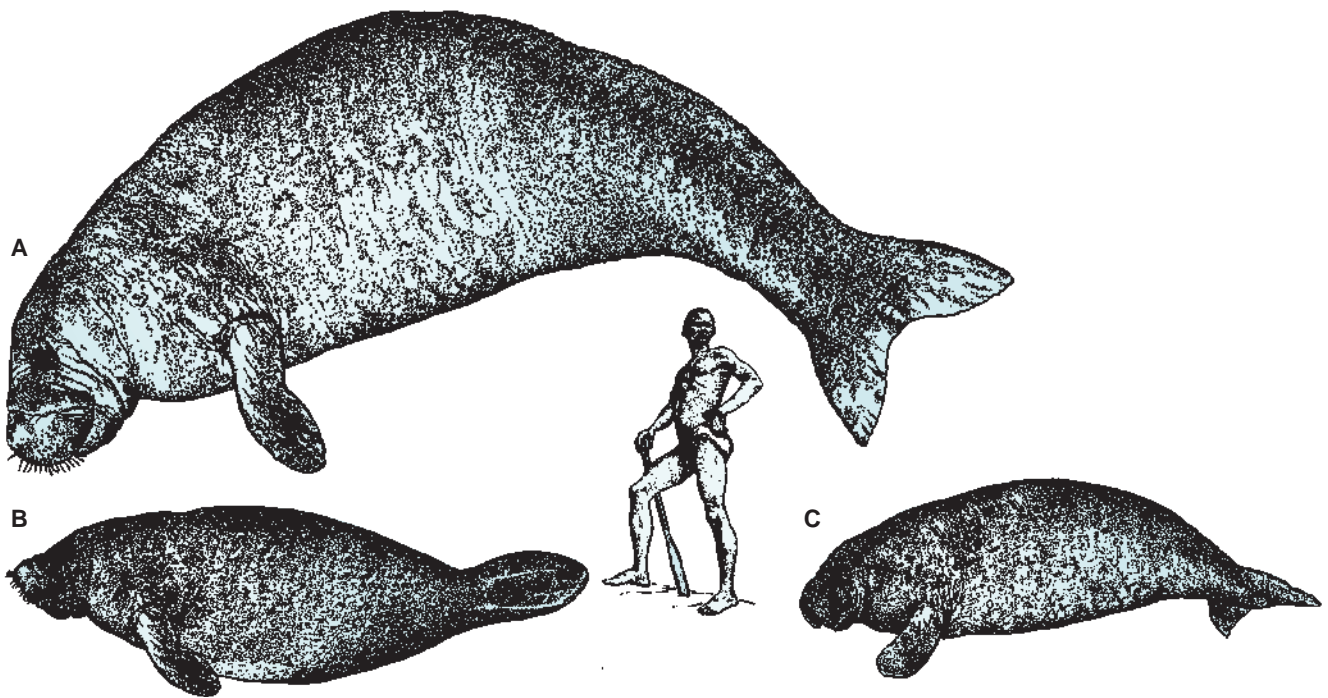
Figure 12.15 Sirenian sizes. The relative sizes of (**A**) a recently extinct Steller's sea cow, (**B**) a manatee, and (**C**) a dugong are shown in relation to a 6-foot-tall (2 m) person. Sirenians have a fusiform body shape, forelimbs modified into flippers, and no external hind limbs. The most noticeable external differences between manatees and the dugong are in the shape of the tail and the extreme downward deflection of the rostrum in dugongs (see Figure 12.16).
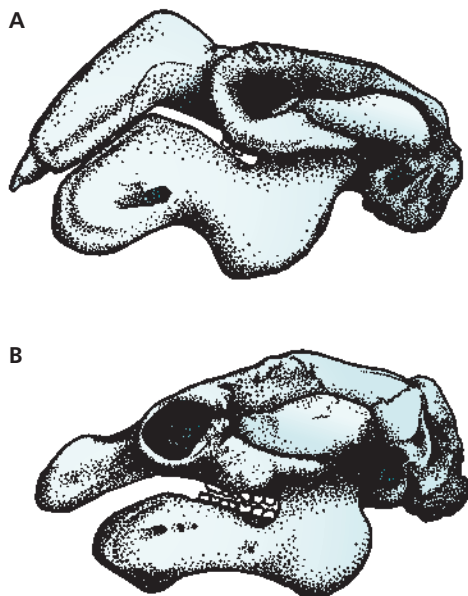
Figure 12.16 Sirenian skulls. Skull of a (**A**) dugong, showing the reduced dentition and strongly deflected rostrum, which is a greatly enlarged premaxilla bone. Note also that the anterior portion of the lower jaw (mandibular symphysis) is strongly deflected downward. Both are adaptations for bottom feeding. (**B**) A West African manatee skull shows the greater number of cheekteeth than in dugongs. Teeth are replaced from the back of the jaws as they slowly move forward (mesial drift) and as anterior teeth are worn out and lost. *Adapted from DeBlase and Martin (1981).*

2005; Domning et al. 2010; Berta 2017). Springer and colleagues (2015) noted evolutionary transitions from prorastomids to protosirenids. The first fossils recognizable as sirenians, the Genus *Prorastomus*, are from the mid-Eocene. Prorastomids, including *Pezosiren portelli*, were amphibious quadrupeds. They spent most of their time in the water, had four well-developed legs, and were capable of terrestrial locomotion (Figure 12.19). Protosirenids from the middle and late Eocene, including Genera *Protosiren* and *Ashokia*, were more derived aquatic quadrupeds and had shorter hind legs and spent less time on land. The oldest and smallest fossil from the genus—*P. eothene*—was from mid-Eocene deposits in Pakistan (Zalmout et al. 2003). The largest protosirenid known is the recently discovered *Libysiren sickenbergi* from the mid-Eocene of Libya (Domning et al. 2017). Thus, the fossil record documents "important macroevolutionary changes leading from terrestrial prorastomids to semiaquatic protosirenids to fully aquatic sirenians" (Berta 2017:31). Eocene fossil remains of sirenians also are noteworthy in the retention of a fifth premolar. This is unique among Tertiary eutherian mammals, as sirenians were the last eutherians to retain five premolars (Domning et al. 1982; Gheerbrant et al. 2005).

Better fossil evidence exists for the dugongids than for the trichechids, including many mid-Eocene to Recent taxa from Africa (Domning et al. 2010); no fossil manatees have been found in Africa. Although dugongids are represented

as early as the mid-Eocene by Genera *Eotheroides*, *Eosiren*, and many other "halitheriin" genera (Berta et al. 2015), there is no direct fossil evidence for Genus *Dugong*. Velez-Juarbe and Domning (2015) described a new genus and species of late Oligocene dugongid, *Callistosiren boriquensis*, from the Caribbean. The early Miocene Genus *Dusisiren* (Figure 12.20) is the earliest known ancestor of the recently extinct sea cow, Genus *Hydrodamalis* (see the section later in this chapter on Dugongidae). Fossil remains of trichechids date from the middle to late Miocene Genus *Potamosiren*, including *P. magdalensis* from Colombia. As mentioned, Miocene sirenians were abundant, diverse, and widespread. Whereas the geographic distributions of the four living sirenian species generally do not overlap, multispecies communities are evident in the fossil record (Velez-Juarbe et al. 2012).
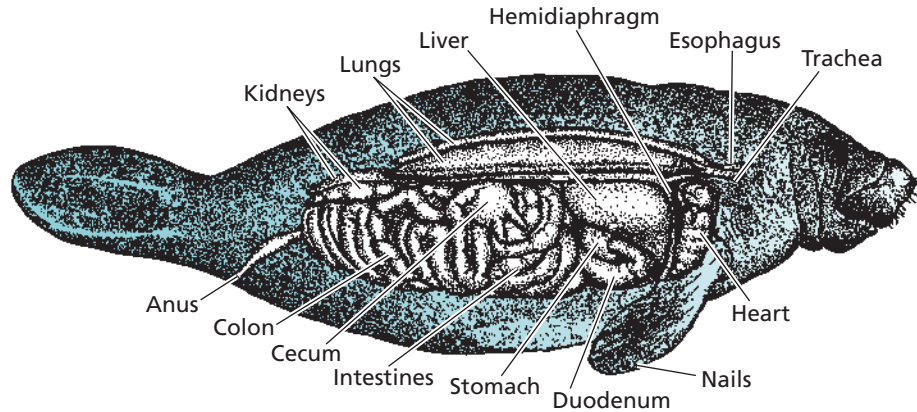
Figure 12.17 **Internal anatomy of a manatee.** Note the lungs lying in a horizontal position along the back. *Adapted from O'Shea (1994).*
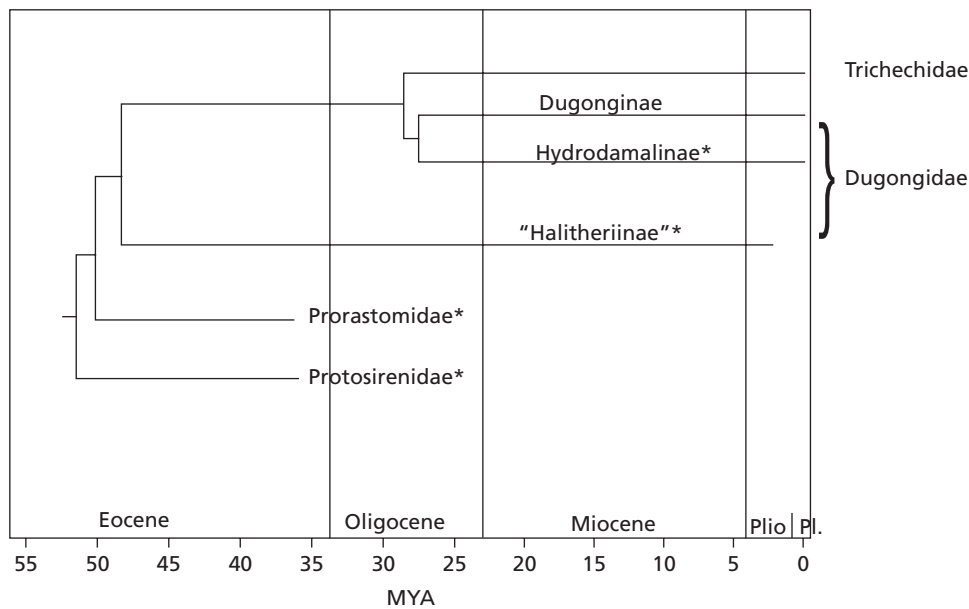
Figure 12.18 **Extant and extinct lineages of sirenians and their geological ranges.** Extinct lineages are denoted by (*). The extinct subfamily Halitheriinae is considered to be paraphyletic. *Modified and adapted from Berta et al. (2015).*
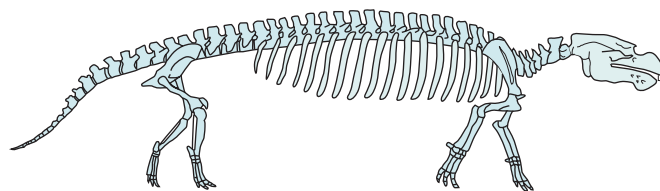
Figure 12.19 **Skeleton of *Pezosiren portelli*.** Unlike modern sirenians, this sirenian from the middle Eocene was capable of terrestrial locomotion.
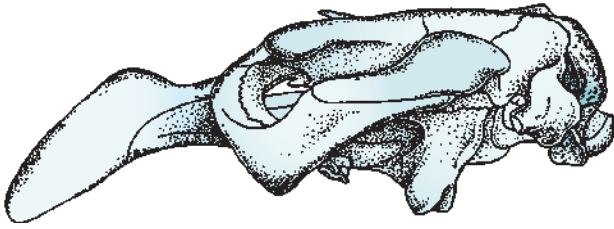
Figure 12.20 Sea cow ancestor. Lateral view of the cranium of *Dusisiren*, an early Miocene ancestor of the recently extinct sea cow. Note the strongly deflected rostrum, characteristic of dugongs today. *Adapted from Carroll (1988).*

ECONOMICS AND CONSERVATION

There is reason for concern today among conservationists about the immediate future of dugongs and manatees. Historically, hunting for meat, bones, hides, and fat caused severe population reductions. Such reductions are not easily overcome by the very slow reproductive rate of this group. Nonetheless, Marsh and colleagues (2015) concluded that the "substantial" harvest of dugongs by indigenous people in the Torres Strait between Australia and Papua New Guinea was sustainable. Hines and coworkers (2005) found the greatest threat to dugongs was mortality caused by incidental catch in fishing nets. All four species of sirenians are considered threatened by the IUCN. In the United States, the West Indian manatee (*Trichechus manatus*) is protected by the Marine Mammal and the Endangered Species Acts. The species has been protected by the state of Florida since 1893. But animals are still lost because of poaching or being pinned by flood-control gates and drowning; in addition, being struck accidentally by boat propellers (Figure 12.21) accounts for a significant proportion of manatee deaths in Florida (Jett and Thapa 2010). Manatees may be unable to detect and avoid oncoming boats because of poor hearing sensitivity at low frequencies (Gerstein et al. 1999), boat speed, water depth, or other factors (Edwards et al. 2016; Martin et al. 2016). Entanglement in fishing gear and ingestion of marine debris also contribute to death of manatees (Reinert et al. 2017). Loss of habitat to development presents a continuing threat to populations, as do destruction of submerged vegetation and reduced water quality. Commercial fishing, seismic surveys, and drilling for gas and oil also negatively affect populations.

FAMILIES

Dugongidae

Dugongs are found in coastal areas of the Pacific Ocean to latitudes about 27° north and south of the equator throughout Micronesia, New Guinea and northern Australia, the Philippines, and Indonesia northward to Vietnam. In the Indian Ocean, they occur around Sri Lanka and India, and

Figure 12.21 Boat propeller wounds. Contact with boat propellers is a primary mortality factor affecting manatee populations in Florida. Most manatees show evidence of scarring from propellers, with wounds such as these most often being fatal.

from the Red Sea south along the east coast of Africa to Mozambique. They attain a maximum body length of 4 m. Average mass is 420 kg, with a maximum of about 900 kg. Unlike in manatees, in dugongs the tail fluke is notched (see Figure 12.15), and the rostrum is much more strongly deflected downward (see Figure 12.16).

Although technically the adult dental formula is 2/3, 0/1, 3/3, 3/3, the anterior pair of upper incisors, all the lower incisors, and the canine are represented only by vestigial (remnant) alveoli. Thus, the dentition actually seen is 1/0, 0/0, 3/3, 3/3. The upper incisor in males forms a short, thick tusk, but in females it does not erupt. The molars are cylindrical and cement-covered and move in horizontally from the back of the jaw as anterior teeth are worn away. In old adults, only one or two remain. These are open-rooted and grow throughout the life of the individual. Relative to their body size, the occlusal surface area of the cheekteeth of dugongs is very small compared to that of other herbivores. Lanyon and Sanson (2006:150) suggested that "there may

not have been great selection pressure acting on mainte-nance of an effective dentition in the dugong." Horny pads in the mouth may have a primary role in chewing. In this regard, the dugong appears to be intermediate between manatees, with numerous complex and durable cheekteeth, and the closely related Steller's sea cow, which was edentate.

Dugongs avoid freshwater much more than manatees. They generally are solitary or live in small groups, although the only cohesive social unit appears to be a mother and her young. They forage by using their forelimbs to "walk" along the bottom, feeding on softer, less abrasive vegetation in the Families Hydrocharitaceae and Potamogetonaceae, which have less silica content than true grasses (Family Gramineae) (Figure 12.22). Dives usually are <3 minutes dura-tion and <5 m depth (Chilvers et al. 2004). Wirsing and col-leagues (2007) found that although food was more abundant in shallow water, dugongs preferred deeper water when tiger sharks (*Galeocerdo cuvier*) were present; dugongs chose safety over food. Loss of plant biomass from dugong grazing activ-ity in sea-grass beds can exceed 50% of plant productivity (Masini et al. 2001). Conversely, feeding by dugongs can benefit sea-grasses by spreading large numbers of their seeds in fecal matter (Tol et al. 2017). Sexual maturity is attained by both sexes between 7 and 14 years of age. A single young is born following a 12-month gestation. For a population in Moreton Bay, Australia, Burgess and colleagues (2012) found puberty occurred when individuals reached a body length of about 2.5 m, although "social maturity" depended on development of tusks and body length > 2.6 m.

Based on molecular and morphological data, Springer and colleagues (2015) found a close association between Steller's sea cow, the dugong, and fossil dugongids. The re-cently extinct Steller's sea cow was much larger than the dugong or manatees (see Figure 12.15). Total length was about 7.5 m, greatest circumference was over 6 m, and body mass was about 5,000 kg, which was 5 to 6 times greater than that of sirenians today. This great size was an adapta-tion for the cold North Pacific waters they inhabited around the Commander Islands and Bering Island, where the spe-cies was first discovered in 1741. By then, its range had been greatly reduced, with a remnant population of 1,000–2,000. Sea cows had no teeth, but instead used rough plates in the mouth to forage on kelp. Slow moving in shallow water and with few natural predators, they were easy prey for sailors seeking fresh meat and hides. Relentless slaughter followed their discovery, and Steller's sea cow was extinct by about 1768—only 27 years after its discovery. Estes and col-leagues (2016) suggested that loss of sea otters (*Enhydra lutris*) and associated kelp would have doomed the sea cow regardless. Marsh and colleagues (2002, 2011) and Marsh (2014) extensively reviewed biology, distribution, threats, and conservation initiatives for the dugong.

Trichechidae

The West Indian manatee (Figure 12.23) occurs from Flor-ida south through the Caribbean Sea to northeast Brazil. Individuals have been reported as far north as Rhode Is-land (Odell 2003). Hunter and colleagues (2012) found that populations in Florida (*T. m. latirostris*) and Puerto Rico (*T. m. manatus*), now considered as subspecies, were genet-ically distinct. The Amazonian manatee is found through-out the Amazon River Basin of South America, but it does not tolerate saltwater. The West African manatee (*Tri-chechus senegalensis*) is distributed in fresh- or salt-water riv-ers and estuaries, and along the west coast of Africa from Senegal to Angola. Cool winters, deep water, and strong

Figure 12.22 Dugong feeding in shallow water substrate. Feeding is enhanced by the pronounced deflection of the rostrum.

Figure 12.23 A West Indian manatee (*Trichechus manatus*). Manatees often swim close to the surface, which makes them more susceptible to being struck by boat propellers.

currents are significant ecological barriers to dispersal of manatees (Domning 2005). Average body length is from 2.5 to 4 m, with body mass typically between 150 and 360 kg. Maximum body mass can approach 1,600 kg.

Unlike dugongs, manatees have a rounded, spatulate tail (see Figure 12.15). Manatees have small nasal bones, unlike dugongs. They are also unusual among mammals in having six cervical vertebrae instead of seven (Buchholtz et al. 2007). Adult dentition includes only cheekteeth; as in elephants, these are replaced consecutively from the rear of the jaw (mesial drift) as anterior molars are worn down and lost. Interestingly, mesial drift also occurs in a curious assemblage of other species, including wallabies (Diprotodontia: Macropodidae), the silvery mole-rat (Rodentia: Bathyergidae, *Heliophobius argenteocinereus*), and gundis (Rodentia: Ctenodactylidae). Molars of manatees are brachyodont, bunodont, close-rooted, and have enamel. Unlike elephants, manatees have 4 or 5 teeth in place at a time on each side of the jaws. Again in contrast to elephants, manatees have an indefinite number of molars (between 10 and 30). Teeth move forward as the bony interalveolar septa between them are constantly resorbed and redeposited (Beatty et al. 2012). This "functional polyphyodonty" is an adaptation to the aquatic grasses and other abrasive, coarse, submerged vascular plants, often found in sand and mud, that manatees consume and that quickly wear down their teeth.

Manatees are usually seen as solitary individuals, paired, or in small groups. Hartman (1979) and Odell (2003) discussed their social ecology and behavior. In Florida, groups of several hundred may form in the winter as the animals congregate around warm-water discharge sites, but the primary social unit is a cow and her calf. Wind, water depth, abundance of food, water quality, and surrounding habitats are all factors that influence spatial distribution of West Indian manatees (Jimenez 2005). Seasonal movements and migratory behavior of *T. manatus* were described by Deutsch and colleagues (2003), and for Amazonian manatees by Arraut and coworkers (2010). The average one-way seasonal migration between northern warm-season ranges and southern winter ranges was 280 km. Manatees tended to migrate when water temperatures fell below 20°C. Mean daily travel distance was only about 2.5 km, with males tending to move more than females.

Manatees vocalize for communication rather than navigation, mainly to maintain contact with group members. Communication between a cow and her calf is especially critical at night or in turbid waters (Sousa-Lima et al. 2002). Vocalizations are complex, and involve multiple harmonics, frequency modulations, overtones, and other acoustic elements that likely result in individual recognition (O'Shea et al. 2006). Manatees are sexually mature between 3 and 4 years of age. A single calf is born after a gestation of about 13 months and is weaned at 12 to 18 months of age. Thus, the reproductive potential of populations is limited (Koelsch 2001), and losses to boats and other causes may not be easily overcome. All 3 species of manatees are considered threatened (IUCN 2018). O'Shea (2014) provided a comprehensive review of the family.

SUMMARY

- The three seemingly disparate Orders Proboscidea, Hyracoidea, and Sirenia arose from a common terrestrial ancestor and began to diverge by the early Eocene.

- Elephants, hyraxes, manatees, and the dugong share several skeletal and anatomical features.
  - All have a large cecum where vegetation is broken down by symbiotic microorganisms.
  - All are hindgut fermenters with moderate digestive efficiency.
  - Replacement patterns of the cheekteeth in the elephants and the sirenians exhibit mesial drift, in which teeth are replaced horizontally from the back of the jaw.

- Dugongs have a reduced number of functional cheekteeth and are restricted to less abrasive forage than are manatees.

- In addition to the Asian elephant, two species of African elephants are now recognized, the savanna (bush) elephant (*Loxodonta africana*) and the forest elephant (*L. cyclotis*).

- All three orders were much more diverse and widespread throughout the Tertiary than they are today, with numerous known fossil genera recognized.
  - Survival of extant elephants and sirenians is a concern as populations continue to decline in most areas.

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DISCUSSION QUESTIONS

1. Why do elephants use very low-frequency sound, whereas bats use very high-frequency sound? How might body size and habitats be factors?

2. Savanna elephants are the heaviest terrestrial mammals. What are the ultimate constraints on the upper limit of body weight in terrestrial mammals? Why can whales get so much larger?

3. What factors contribute to the low reproductive rate of both proboscideans and sirenians? How does this affect conservation efforts?

4. If you were studying vocalizations in elephants, what variables might you consider that could influence what you recorded?

5. Contrast the differences in the dentition of dugongs and manatees. What do these differences in families within the same order suggest about the evolutionary process in general?

6. If today's environmental ethic and concern for endangered species were in vogue 250 years ago, do you think the Steller's sea cow would have gone extinct? Should we be concerned today for species with only remnant populations that may be "on their way out" anyway from an evolutionary standpoint?

Orders: Pilosa and Cingulata

Superorder Xenarthra
Order Pilosa
Order Cingulata

Superorder Xenarthra

This taxon, found only in the Western Hemisphere and formerly referred to as Order Edentata (meaning "without teeth"), now encompasses armadillos (Order Cingulata) and the anteaters and tree sloths (Order Pilosa). Xenarthrans are a morphologically diverse group and form one of the basal clades of mammals. Molecular evidence suggests they arose about 100 mya (Delsuc et al. 2004). The "few living and numerous fossil representatives are characterized by quite disparate and highly derived (indeed, often bizarre) anatomical and ecological specializations" (Gaudin et al. 1996:32). The name "Xenarthra" refers to the presence of at least two accessory, or supplemental, "xenarthrous" intervertebral articulations, or xenarthrales ("strange joints"), located primarily on the lumbar and some posterior thoracic vertebrae (Figure 13.1). These give added rigidity and mobility to the axial skeleton (Gaudin 1999a; Oliver et al. 2016). Additional characteristics shared by xenarthrans include loss of incisors and canines, as well as cheekteeth (if present) that grow continuously and are without enamel (Green and Kalthoff 2015). In terrestrial species, the acromion and coracoid processes of the scapula are separate and well developed to enhance muscle attachment for digging. These are rudimentary, fused processes in most therian mammals. Also, the transverse processes of the anterior caudal vertebrae and the ischia are fused in all xenarthrans, except the silky anteater (*Cyclopes didactylus*). Several other features of the skeleton and musculature define these two orders, including dermal ossicles in the skin, position of the infraorbital canal, and a secondary scapular spine (see appendix in Gaudin 2008).

All xenarthrans have low metabolic rates (Figure 13.2) and low body temperatures, which average about 34°C, compared with 36°C–38°C in other mammals. Because of their low basal metabolic rates and poor thermoregulatory abilities, xenarthrans generally are geographically limited to tropical and semitropical habitats from Mexico southward throughout South America; only the nine-banded armadillo (*Dasypus novemcinctus*) occurs as far north as the United States.
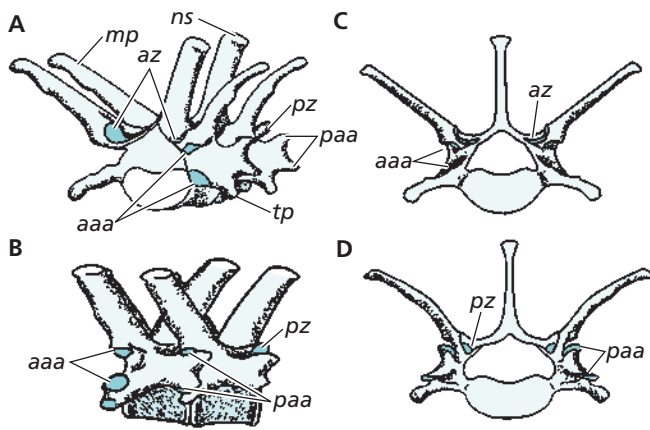
Figure 13.1 **Vertebrae of xenarthrans.** Third and fourth lumbar vertebrae in the nine-banded armadillo show the extra articular surfaces (*shaded throughout*): (**A**) anterior three-quarters view; (**B**) lateral view (anterior to the left); (**C**) anterior view; (**D**) posterior view. *Abbreviations*: az = anterior zygapophysis; mp = metapophysis; ns = neural spine; pz = posterior zygapophysis; tp = transverse process; aaa = anterior accessory intervertebral facets; paa = posterior accessory intervertebral facets. *Adapted from Gaudin and Biewener (1992).*
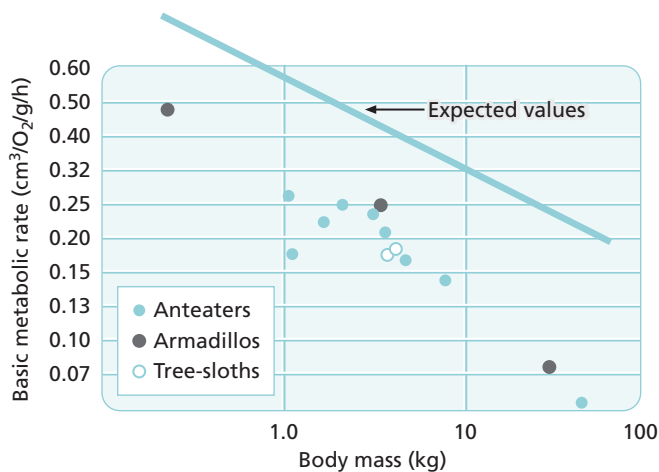
Figure 13.2 **Lower metabolic rates in xenarthrans.** The expected relationship of mass-specific basal metabolic rate of mammals (*line*), calculated as basal metabolic rate = constant (body mass$^{-0.25}$), is much greater than the metabolic rates that occur in xenarthrans. *Data from McNab (1985).*

Extant and extinct xenarthrans are represented by two orders (Gaudin 2003; Gardner 2005). Order Cingulata includes the living long-nosed armadillos (Family Dasypodidae), a variety of other armadillo species in the newly recognized family Chlamyphoridae (Gibb et al. 2016), as well as three extinct families. Order Pilosa includes the two-toed tree sloths (Family Megalonychidae) and the three-toed tree sloths (Family Bradypodidae) in a clade (the Folivora) with four extinct families. A second clade (the Vermilingua) includes the true anteaters (Family Myrmecophagidae) and the silky anteater in its own monotypic family (Cyclopedidae) (Figure 13.3).

Anteaters and armadillos share several characteristics related to a **myrmecophagous** mode of feeding, with diets composed predominantly of ants and termites (sloths are folivores; they eat mainly leaves). Because ants and termites form large colonies and are common in tropical and semitropical areas throughout the world, they offer an excellent potential energy source to various mammalian groups, including echidnas (Order Monotremata), the marsupial numbat (*Myrmecobius fasciatus*; Order Dasyuromorphia), rabbit-eared bandicoots (Order Peramelemorphia), pangolins (or scaly anteaters; Order Pholidota), the aardvark (*Orycteropus afer*; Order Tubulidentata), and even some carnivores such as the aardwolf (*Proteles cristatus*) and the sloth bear (*Melursus ursinus*). Myrmecophagy among these diverse lineages is a good example of phylogenetic convergence (Delsuc et al. 2014).

Morphological features for myrmecophagy include long snouts and long, powerful, sticky tongues. Dentition is reduced or absent, and the coronoid process of the mandible is reduced, whereas the hyoid elements (bones and muscles of the tongue) are enlarged (Naples 1999). Strong, heavily clawed forepaws are used to dig into anthills and termite mounds. Small pinnae and valvular nostrils reduce susceptibility to biting from their prey. The integument also offers protection. Armadillos have an armored carapace, whereas the anteaters are heavily furred. Stomachs are generally simple with thickened, muscular, often **keratinized** (characterized by a tough, fibrous protein) pyloric regions to aid in digestion and protect against the formic acid contained in many ant species. Xenarthrans usually have low reproductive capacities and a strategy of small litter size and extended parental care.

ORDER PILOSA

Fossil History

The 14 genera and 30 species of xenarthrans living today represent less than 10% of the known number of extinct genera; over 200 have been described (Superina and Loughry 2015), with numerous species of fossil sloths (Pujos et al. 2017; Toledo et al. 2017). The oldest fossil sloth is *Pseudoglyptodon* from the late Eocene. Four families of fossil sloths have been described: the Nothrotheriidae, Megatheriidae, Mylodontidae, and Scelidotheriidae (Gaudin 2004; Gaudin and Croft 2015; see Figure 13.3). The oldest mylodontid and megatheriid fossils date from the late Oligocene. The oldest fossil anteater is *Protamandua* from the mid-Miocene (Gaudin and Croft 2015).

The two extant genera of sloths diverged about 40 mya (late Eocene), and their arboreal (suspensory) locomotion is a remarkable example of convergence (Gaudin 2004; Nyakatura 2012). Whereas living sloths weigh from 4 to 6 kg., no fossil sloths are known to have been arboreal. Many of these ground sloths were massive—for example, *Propalaehoplophorus* (Figure 13.4); the giant ground sloth
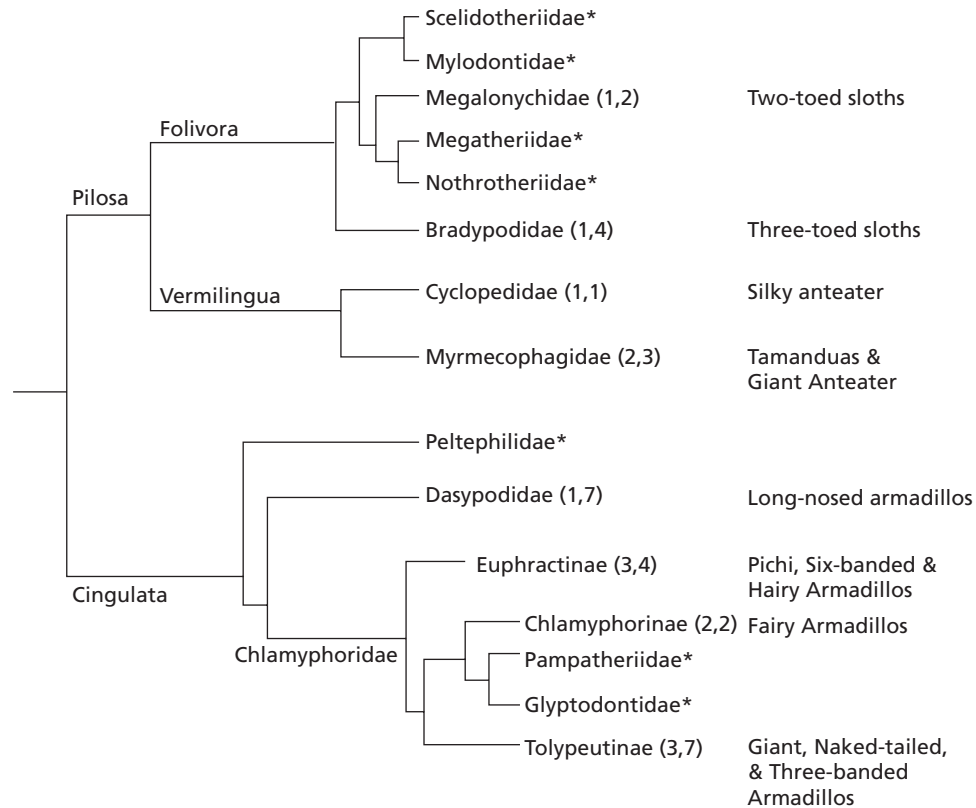
Figure 13.3 Phylogeny of xenarthrans. The superorder Xenarthra consists of two orders and six extant families. Seven extinct families are indicated by (*); the number of genera and species in the extant families is in parentheses. *Compiled and redrawn from Rose et al. (2005), Gaudin and Croft (2015), and Gibb et al. (2016).*
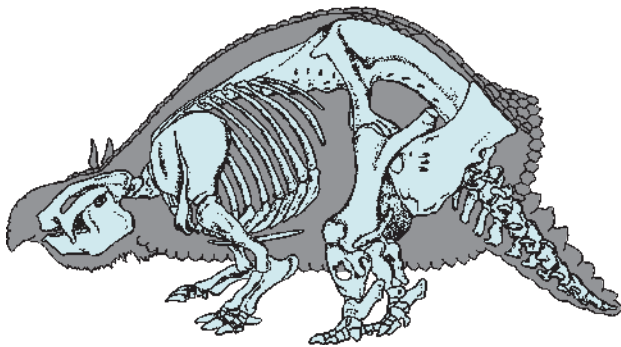
Figure 13.4 An extinct glyptodont. The extent of the armored carapace of this early Miocene xenarthran (*Propalaeohoplophorus*) is shown in outline, with a portion of the scute (scale-like) pattern shown. Note the massive nature of the limbs and heavy, inflexible vertebrae, necessary to support the carapace, which made up 20% of the body mass. *Adapted from Gregory (1951).*

(*Megatherium americanum*) weighed over 2,700 kg. Several species of sloth became extinct recently, eliminated by humans only a few hundred years ago. These include the ground sloth (*Mylodon listai*), whose bones, hide, and reddish hair were found with human artifacts in a cave in southern Argentina. The Puerto Rican ground sloth (*Acratocnus odontrigonus*) and the Lesser Haitian ground sloth (*Synocnus comes*) also survived until 400–500 years ago.

Families

Megalonychidae

This family includes one genus and two extant species of arboreal two-toed sloths—once included with the three-toed sloths in Family Bradypodidae. Based on a number of cranial characteristics (Figure 13.5), as well as molecular analyses (Greenwood et al. 2001), two-toed sloths are now considered the only living members of Family Megalonychidae (Webb 1985a; Wetzel 1985). Hoffmann's two-toed sloth (*Choloepus hoffmanni*) occurs from Nicaragua southward through Peru and central Brazil. Linné's two-toed sloth (*C. didactylus*) is found east of the Andes Mountains in northern South America.

As with all xenarthrans, members of this family have no incisors or canines; the cheekteeth are usually 5/4. The anterior upper premolar is **caniniform** (shaped like a canine tooth; see Figure 13.5) and separated from the rest of the
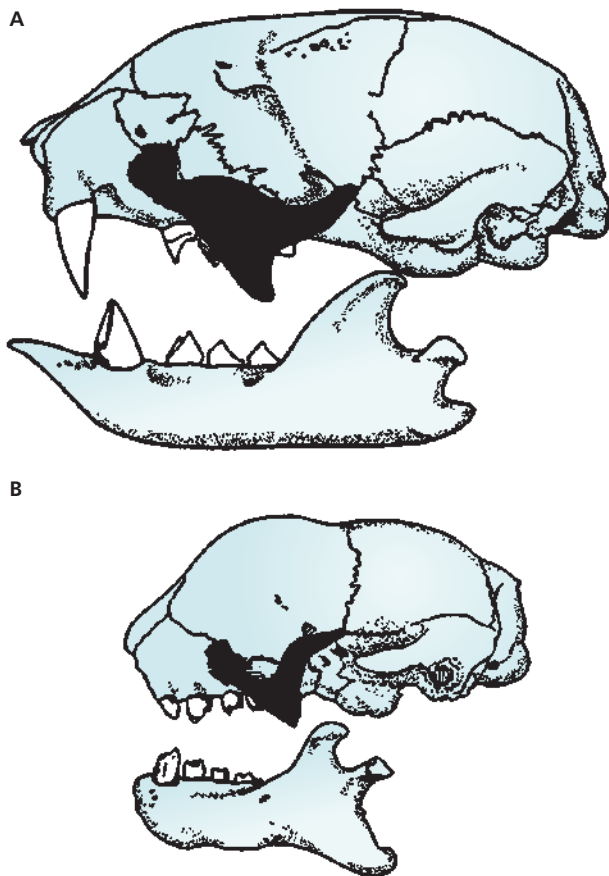
Figure 13.5 **Features of sloth skulls.** Skulls of (**A**) a two-toed sloth and (**B**) a three-toed sloth. Note the distinctive anterior caniniform premolar (a premolar that looks like a canine tooth) in the two-toed sloth. Both skulls have an incomplete zygomatic arch with the jugal bone (*black*), a flattened plate with upper and lower processes on the posterior edge. Also note the difference in the shape of the mandibles. (Both skulls are not to scale). *Adapted from Hall and Kelson (1959).*

Figure 13.6 **Large recurved claws in sloths and anteaters.** Right front foot of several species showing similarity of the claws in each family. (**A**) Lateral view and (**B**) ventral view with toes spread of a three-toed sloth; (**C**) ventral view of a two-toed sloth; (**D**) lateral view of a giant anteater; (**E**) ventral view of a southern tamandua, showing the large central digit. (Not to relative scale.) *Adapted from R. I. Pocock (1924).*

molariform dentition by a diastema. These teeth are sharp because of unique occlusion of the anterior surface of the lower caniniform premolar with the posterior surface of the upper one.

Two-toed sloths have 2 toes on the forefeet, each with a long (80–100 mm), sharp claw, and 3 toes on the hind feet. They differ from three-toed sloths not only in the number of digits on the forefeet (Figure 13.6), but also in being somewhat larger and heavier. Their total length ranges up to 740 mm, and body mass reaches 8.5 kg. Unlike most mammals, which have 7 cervical vertebrae, two-toed sloths may have 5, 6, or occasionally 8.

Two-toed sloths are more active than three-toed sloths, although both expend very little energy (Pauli et al. 2016). Nyakatura and colleagues (2010) described the mechanics of locomotion of *C. didactylus*. Two-toed sloths move to a different tree each day, and they have a broader range of feeding habits than three-toed sloths, which correlates with a more diverse gut microbiota (bacteria) for digestion (Dill-

McFarland et al. 2016). They are almost entirely arboreal and folivorous and spend most of their adult life hanging upside down from tree branches. They do, however, descend to the ground to defecate (at intervals of about four days in captivity) and apparently are capable swimmers. Their long, brownish gray pelage often has a greenish color because of green algae growing on it (see box).

Two-toed sloths give birth to a single young; females do not reach sexual maturity until 3 years of age, males not until they are 4 or 5 years old. Gestation is 10 months

Green Fur and Symbiosis in Sloths

In addition to insulation, mammalian pelage provides a variety of benefits—one of which is camouflage provided by stripes, spots, or cryptic coloration of the fur. Common names such as "green ringtail possum" (*Pseudochirops archeri*) and "green monkey" (*Chlorocebus sabaeus*) are misnomers—there are no green mammals. The closest green-colored mammals are sloths, most of which have a distinct greenish tint to their fur. This color is not from a pigment or structural characteristics of the fur, but is caused by algae. In two-toed sloths algae grow in the deep grooves that run the length of each hair, and in three-toed sloths in the irregular edges of the cuticular scales on each hair shaft.

Algae on sloths has been noted by several investigators with the general assumption that it forms a symbiotic relationship—the alga get a warm, wet place to live, and the relatively defenseless sloths benefit from the green camouflage as they move slowly through their treetop habitats. This interesting relationship has been studied for over 130 years with the primary algal species identified as *Trichophilus welckeri* (Chlorophyta, Ulvophyceae). Suutari and colleagues (2010) expanded on the diversity of known algal species—as well as the "small-scale ecosystem" of cyanobacteria, fungi, diatoms, moths, beetles, cockroaches, and round-worms—in the fur of sloths. It is likely that *T. welckeri*, which thrives in wet, warm conditions, is host-specific to sloths (as are two other *Trichophilus* species). That is, *Trichophilus* coevolved with sloths and do not otherwise occur in the environment. Fountain and colleagues (2017) found support for co-evolution between algae and three-toed sloths, with subsequent host switching to two-toed sloths. Moths in the fur increase nitrogen levels, which aids algal growth; sloths also eat the algae (Pauli et al. 2014). This mutualistic relationship benefits the algae and allows "green" sloths to blend in nicely with their forested habitats.

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for both species of *Choloepus* (Taube et al. 2001) with a 15- to 16-month interval between births. There is little seasonality to reproduction, probably because of the more generalist diet of two-toed sloths compared to *Bradypus*. Peery and Pauli (2012) discussed the mating system in *C. hoffmanni*. About 50% of females switch mates annually (Garces-Restrepo et al. 2017). Two-toed sloths are very long-lived; captive individuals reach over 31 years of age.

Both two-toed and three-toed sloths are poor thermoregulators. Their body temperature tracks the ambient temperature to a much greater extent than is the case in other mammals. This is especially evident in two-toed sloths, whose body temperature varies between 24° and 33°C, a factor that limits their geographic distribution to warm, tropical regions. Neither species is endangered or threatened.

Bradypodidae

The 4 species of three-toed sloths, all in Genus *Bradypus*, are arboreal folivores distributed from Honduras south through northern Brazil. Although they can be active day and night, they are truly "slothful." Fernandez Gine and colleagues (2015) found maned sloths (*B. torquatus*) rested 18.5 h during a 24-h period. Pauli and colleagues (2016) found the field metabolic rate of a brown-throated sloth (*B. variegatus*) was the lowest ever recorded for a nonhibernating mammal. They have more narrowly restricted movement (Falconi et al. 2015) and feeding habits than two-toed sloths. The teeth of three-toed sloths have no enamel. They are cylindrical, with a central core of soft dentine, surrounded by harder dentine and then cementum. The stomach has several compartments and cellulose digestion is aided by microfauna. Passage of digesta is slow because of the low metabolic rate and slow fermentation. Three-toed sloths (Figure 13.7) are smaller and generally more common than *Choloepus* in areas of sympatry. The heaviest bradypodids are maned sloths, in which females are significantly larger than males (Lara-Ruiz and Chiarello 2005). Like the two-toed sloths, three-toed sloths usually have a greenish tint to their thick pelage because of a commensal relationship with algae living there (see box). Bradypodids have three well-clawed toes on the forefeet (see Figure 13.6). Unlike most mammals, they have 8 or 9 cervical vertebrae, which allows for greater flexibility in the neck; they can rotate their heads in a 270° arc.

Litter size is 1, and gestation is only 5–6 months (compared with about 10 months in *Choloepus*). Reproduction in *Bradypus* is clearly seasonal. In the maned sloth, breeding occurs August–October, with births from February to April (Dias et al. 2009). This may be related to the seasonal variation in food of the more specialized diet of three-toed sloths compared to two-toed sloths (Taube et al. 2001).

Anderson and Handley (2001) first described the pygmy three-toed sloth (*B. pygmaeus*). This species is endemic to Isla Escudo de Veraguas, an island 4.3 km^2 in size 17.6 km off the Caribbean coast of Panama, and is critically endangered because of habitat loss, development, and collecting (Voirin 2015). The maned sloth is threatened because of forest fragmentation and loss (Lara-Ruiz et al. 2008).

Myrmecophagidae

The 2 genera and 3 species in this family are edentate and highly specialized for myrmecophagy, as suggested by the family name. Anteaters occur in forested or savanna habitats from southern Mexico south into South America, east of the Andes Mountains as far south as Paraguay. They have long, tapered skulls (Figure 13.8), with an elongated rostrum, especially in the giant anteater (*Myrmecophaga tridactyla*), long tongues, and very small mouths. The tongue of the giant anteater has a maximum width of only 13 mm but can be extended up to 600 mm, a distance equal to the length of the skull (Naples 1999). It is anchored on the sternum and is covered with a viscous secretion produced in the submaxillary glands. The tongue also has tiny, barblike spines (papillae) directed posteriorly. Casali and colleagues (2017) described the tongue morphology of the Vermilingua. Both the spines and the secretion aid in trapping ants. The giant anteater has coarse, shaggy gray hair with a dark diagonal stripe on the shoulders, and a bushy tail (Figure 13.9A). Total length averages about 2 m, and they may weigh as much as 40 kg. They are entirely terrestrial and active throughout the day or night. Andrea Quiroga and colleagues (2016) found abundance of giant anteaters was lower in areas with high human disturbance, whereas abundance was higher in areas without jaguars (*Panthera onca*).

The 2 species of lesser anteaters, or tamanduas, are intermediate in size, active day or night, and forage on the ground and in trees. They have coarse tan or brown pelage. In the northern tamandua (*Tamandua mexicana*) and in southern specimens of the southern tamandua (*T. tetradactyla*) black fur forms a "vest" (Figure 13.9B). Tamanduas have a prehensile tail that aids in climbing. All species have long, sharp, powerful claws for foraging, with the middle claw often enlarged (see Figure 13.6D, E). Stomachs are simple with the pyloric portion strengthened for digesting insects. Litter size in anteaters is generally only 1. Pereira and coworkers (2004) reported karyotypes of 2n = 60 in the giant anteater, and 2n = 54–56 in the southern tamandua. The giant anteater is considered threatened because of habitat loss, hunting, illegal trade, and fires.

Cyclopedidae

This family is monotypic, with a single genus and species—the silky or pygmy anteater. According to molecular analyses, cyclopedids diverged from myrmecophagids about 41 mya and exhibit a great deal of genetic diversity (Coimbra et al. 2017). Based on extensive morphological and molecular data from specimens throughout their range, Miranda and colleagues (2018) suggested 7 species of *Cyclopes* should be recognized. The silky anteater is widespread and occurs in rainforests from southern Mexico to Brazil and Bolivia at elevations from sea level to 1,500 m. The common name derives from the fine, soft pelage that is gray to yellowish in color with a darker dorsal band. This is the smallest anteater—about 55 cm in total length and only 300 g or less in body mass. They are nocturnal, and almost entirely arboreal, feeding primarily on ants. They shelter during the day curled up in a ball in the tree canopy. Like tamanduas, the silky anteater has a prehensile tail, which is naked on the ventral surface. Females have one young yearly. The chromosome number, 2n = 64, is the highest among anteaters (Pereira et al. 2004). Populations are widespread and appear to be stable.

Figure 13.7 **Pale-throated sloth (*Bradypus tridactylus*).** Long forelimbs and coarse pelage are characteristic of sloths. Note the youngster clinging to the back.

Figure 13.8 **Giant anteater skull.** The elongated rostrum and tapered skull of a giant anteater (*M. tridactyla*).

A

B
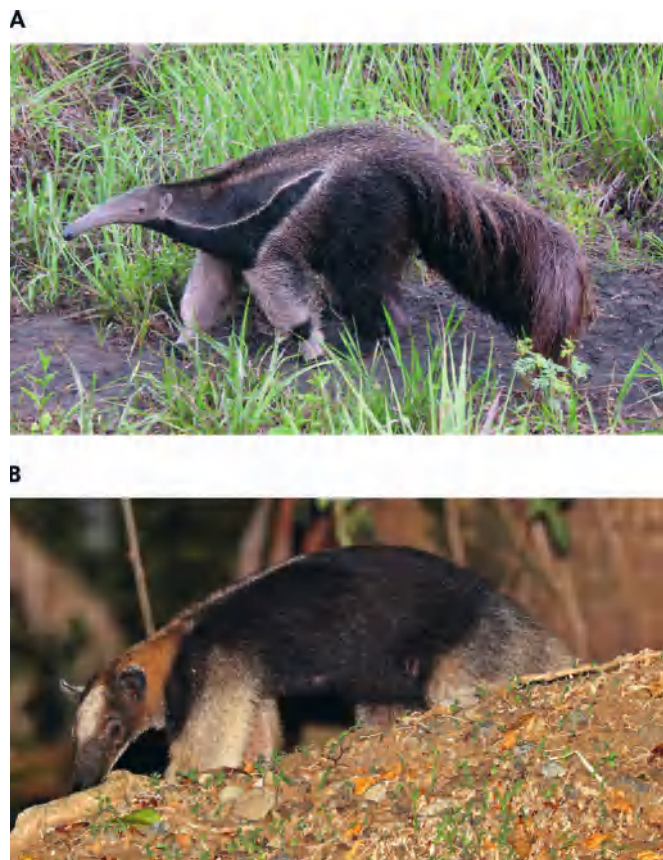
Figure 13.9 **Features of anteaters.** (**A**) Coarse hair, diagonal shoulder stripe, and long, tapered skull of the giant anteater (*Myrmecophaga tridactyla*); (**B**) distinctive "vest" of the northern tamandua (*Tamandua mexicana*), a smaller, semiarboreal anteater.

ORDER CINGULATA

Fossil History

The fossil history of cingulates is rich and diverse, with over 200 described genera (Gaudin 2003; Moeller-Krull et al. 2007). The earliest known fossil cingulates are from the middle Eocene of South America (Gaudin and Croft 2015), although they probably date from even earlier times. Three extinct families of cingulates are recognized: the Peltephilidae, the huge, herbivorous Pampatheriidae, and the closely related, highly diverse Glyptodontidae. The oldest pampatheriid dates from the mid-Miocene, whereas the oldest glyptodontids are from the mid- to late Eocene. Herrera and colleagues (2017) described a new genus and species of cingulate, *Lumbreratherium oblitum*, from the middle Eocene of Argentina. Billet and coworkers (2011) described the cranial remains of *Kuntinaru boliviensis*, a late Oligocene cingulate from Bolivia. However, the best-known fossils are the giant glyptodonts that were an abundant and diverse part of the South American fauna until they went extinct at the end of the Pleistocene (Mitchell et al. 2016). Glyptodonts were over 3 m long, and had a heavily armored head, back, and tail. Some weighed as much as 2,400 kg. Despite their massive size, recent molecular analyses (Gibb et al. 2016; Mitchell et al. 2016) show that glyptodonts are closely related to living fairy armadillos, which are <1 kg.

Families

There are certainly unresolved taxonomic issues with the cingulates regarding the relationships between extant and extinct lineages. Traditionally, living armadillos have been placed in a single family, Dasypodidae, with 3 subfamilies: the long-nosed armadillos (Dasypodinae; *Dasypus*); fairy armadillos, hairy armadillos, the six-banded armadillo (*Euphractus sexcinctus*), and the pichi (*Zaedyus pichiy*) (Euphractinae); and the naked-tail armadillos, three-banded armadillos, and the giant armadillo (*Priodontes maximus*) (Tolypeutinae). Molecular work by Gibb and colleagues (2016) suggested splitting armadillos into two families: Dasypodidae with 7 species of long-nosed armadillos in the Genus *Dasypus*, and the remaining 8 genera and 13 species placed in a new Family Chlamyphoridae (see Figure 13.3). Alternatively, Gaudin and Lyon (2017:64) advocated raising the 3 subfamilies of chlamyphorids to family status to better reflect "the age, morphological disparity, and taxonomic diversity encompassed by cingulates in general and the Chlamyphoridae in particular."

Armadillos feed opportunistically on a variety of invertebrates and also consume various amounts of vegetation and carrion. They share the usual xenarthran reduction in dentition, having only peg-like molariform teeth, which are small, open-rooted, homodont, and without enamel. The giant armadillo is exceptional among terrestrial mammals in having up to 100 small, somewhat vestigial cheek-teeth. Although incisors form in embryonic *D. novemcinctus*, they degenerate and rarely persist by the time of birth.

Armadillos have several unique morphological characteristics, the best known of which is the hard, armor-like carapace (Figures 13.10 and 13.11) that gives the group its common name. Plates of ossified dermal "scutes" cover the head, back and sides, as well as the tail in most species (Vickaryous and Hall 2006; Krmpotic et al. 2015). Non-overlapping, keratinized epidermal scales cover the scutes. The bands of armor are connected by flexible skin. The outside of the legs also has some armored protection, but not the inside of the legs or the ventral surface. The tough skin in these areas is covered by coarse hair. The carapice "has been a major determinant of the lifestyle of armadillos" (Superina and Loughry 2012:217) and impacts respiration, thermoregulation, reproduction, and locomotion. Chen and colleagues (2011) discussed aspects of the microstructure and mechanical strength of the carapice. The vertebrae in armadillos are modified for attachment of the carapace, which actually articulates with the metapophyses of the lumbar vertebrae (see Figure 13.11).
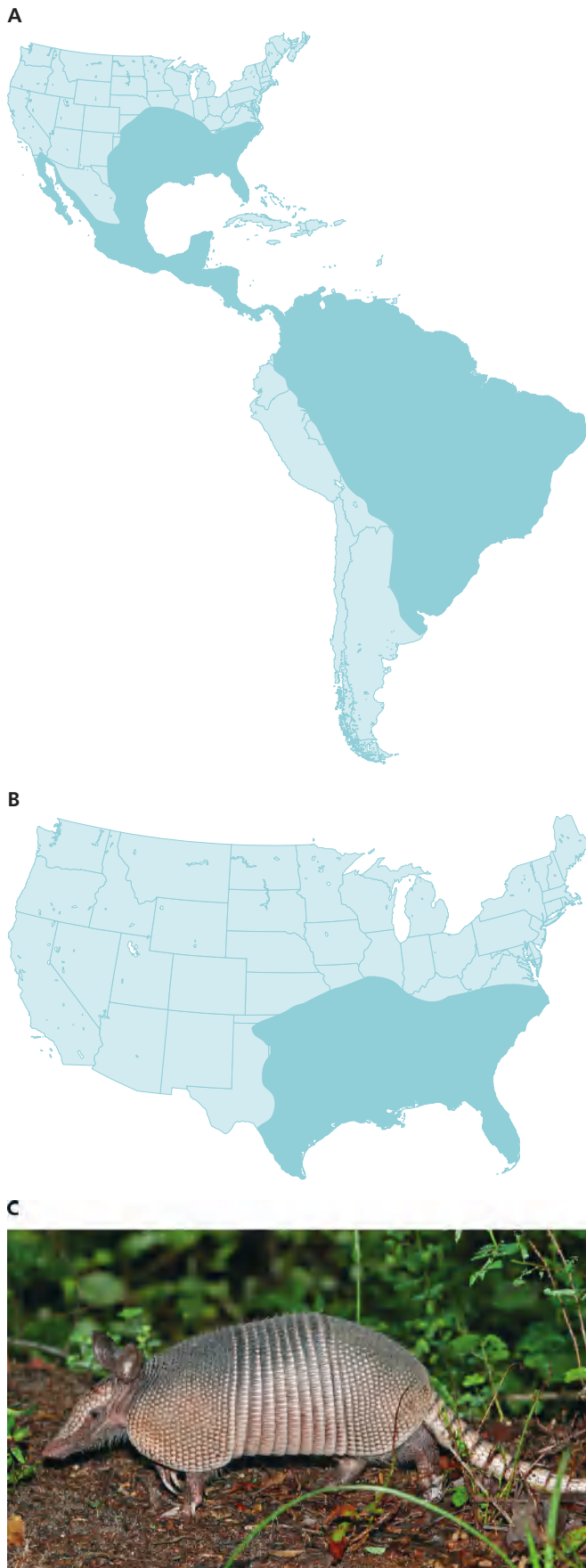
Dasypodidae

The 7 species of long-nosed armadillos in the Genus *Dasypus* occur in a variety of habitats from the United States through Central America south to central Argentina. The nine-banded armadillo is the only xenarthran in North America (see Figure 13.10). It has extended its distribution significantly since the late 1800s through natural dispersal as well as by introduction to Florida (Layne 2003); it is the most widely distributed of any armadillo. Cold ambient temperatures probably limit distribution northward, as does their high thermal conductance, their inability to enter torpor, and the lack of food in winter (McNab 1985). Nonetheless, they have advanced as far north as central Kansas (Taulman and Robbins 2014), where the mean minimum temperature in January is –8° C. Nine-banded armadillos in North America exhibit reduced genetic variability compared to those in Mexico (Arteaga et al. 2012) and South America (Huchon et al. 1999). In the United States, *D. novemcinctus* is commonly called the "nine-banded armadillo" because its carapace usually has nine movable bands (see Figures 13.10 and 13.11), although band number varies throughout its geographic range.

Reproduction in *Dasypus* is noteworthy. Delayed implantation occurs, as does **monozygotic polyembryony** (several embryos from a single zygote) in some species (Loughry et al. 1998.). In *D. novemcinctus*, four young of the same sex are produced after division of a single fertilized ovum; in the southern long-nosed armadillo (*D. hybridus*), eight young normally are produced. From a common placenta, each embryo develops its own placenta, with no mixing of blood or nutrient material between embryos (Talmadge and Buchanan 1954). Eisenberg (1981:55) considered this a "novel way of increasing the reproductive capacity" of *Dasypus*. Other aspects of obligate polyembryony were noted by Loughry and coworkers (2005).

Because *D. novemcinctus* contracts naturally occurring leprosy (*Mycobacterium leprae* is the causative agent), it is a valuable model for a wide range of biomedical research projects. Williams and Loughry (2012) found annual infection rates of a population of nine-banded armadillos in Mississippi was 4.5%–15%, primarily in older animals. Morgan and Loughry (2009) found no behavioral differences in armadillos with and without leprosy; Oli and colleagues (2017) discussed the impact of leprosy on the dynamics of a nine-banded armadillo population. No dasypodids are considered endangered or threatened.

Figure 13.10 **The nine-banded armadillo.** (**A**) Range within the Western Hemisphere; (**B**) recent range in the contiguous U.S., which expands north during mild winters and receeds south during harsh winters; (**C**) the nine bands are evident in this individual from central Florida. (**A**) *From McNab (1985).*
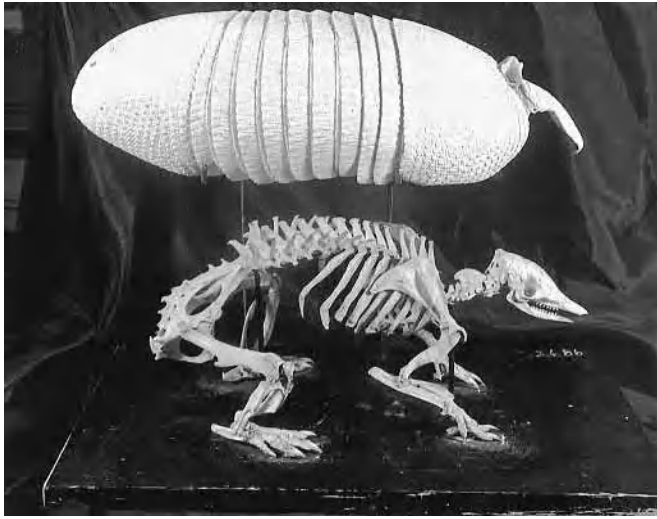
Figure 13.11 Carapace and articulated skeleton of a nine-banded armadillo. The metapophyses of the lumbar vertebrae support the carapace.

Figure 13.12 **Size comparison.** Approximate relative sizes of (**A**) the giant armadillo (*Priodontes maximus*) and (**B**) the nine-banded armadillo (*Dasypus novemcinctus*). *Adapted from Eisenberg (1989).*

Chlamyphoridae

The systematics of this family vary among authorities. The 8 genera and 13 species of chlamyphorids are generally placed in 3 subfamilies: the previously noted Euphractinae and Tolypeutinae, as well as the Chlamyphorinae, which includes the pink fairy armadillo (*Chlamyphorus truncatus*) and the greater fairy armadillo (*Calyptophractus retusus*). Alternatively, Gaudin and Lyon (2017) recognized 4 extant cingulate families: Dasypodidae, Chlamyphoridae, Euphractidae, and Tolypeutidae, as well as the extinct families Peltephilidae, Pampatheriidae, and Glyptodontidae. Species of chlamyphorids vary in size from the tiny (100 g or less) pink fairy armadillo to the rare giant armadillo (*Priodontes maximus*) (Figure 13.12), which weighs up to 60 kg.

Like the long-nosed armadillos, most chlamyphorids burrow extensively. The large hairy armadillo (*Chaetophractus villosus*) in Argentina makes short, simple burrows while searching for food or temporary shelter, whereas permanent home burrows are longer, deeper, and more complex (Abba et al. 2005). Three-banded armadil-los were considered to be nondiggers, simply using burrows excavated by other species. However, Attias and colleagues (2016) found that both the southern three-banded armadillo (*Tolypeutes matacus*) and Brazilian three-banded armadillo (*T. tricinctus*) dig their own small, shallow burrows. Aya-Cuero and colleagues (2017) described burrow openings of the giant armadillo; they also estimated population density was 5.8/100 km^2 on their study area in savannas and forests of Colombia. Average life span of sexually mature screaming hairy armadillos (*Chaetophractus vellerosus*) in a population in Argentina was <2 years (Abba et al. 2017).

Actis and colleagues (2017) tested bone mineral density (BMD) in lactating pichis (*Zaedyus pichiy*), a small species that occurs farther south than any other armadillo. Like other armadillos, the pichi eats primarily insects, ants, and other invertebrates—poor sources of minerals for a developing carapace in young. Nonetheless, BMD in lactating females was similar to that of males. Whether high BMD is necessary for reproduction in other species of armadillos is unknown.

Two species of dasypodids are considered threatened because of hunting pressure and habitat loss: the giant armadillo and the three-banded armadillo.

SUMMARY

- Xenarthrans have accessory vertebral articulations (xenarthrales) that give added rigidity and flexibility to the axial skeleton.
  - They occur only in the New World; the nine-banded armadillo is the only xenarthran in the United States.

- They are restricted to warm regions because of their poor thermoregulatory abilities.

- Anteaters (Pilosa; Vermilingua) have a number of characteristics related to their myrmecophagous diets, including
  - long rostrums (snouts) with long, sticky tongues,

○ lack of dentition (edentate),
○ large claws on forefeet, and
○ tough hide or scales, which offer protection from biting ants and termites.

• Sloths (Pilosa; Folivora) include two species of two-toed sloths and four species of three-toed sloths.
○ All have low metabolic rates and are arboreal, spending much of their life hanging upside down in trees.
○ Sloth fur has a greenish tint because of algae growing on it.

• Armadillos (Cingulata) are characterized by a hard carapace.
○ In most species, ossified dermal "scutes" cover the head, body, and tail.
○ Some long-nosed armadillos (*Dasypus* sp.) exhibit monozygotic polyembryony.
○ The nine-banded armadillo contracts naturally occurring leprosy and is a valuable model in medical research.

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DISCUSSION QUESTIONS

1. We noted the symbiotic relationship between sloths and the algae that grow on their pelage, and the benefits to both groups. Are there any negative consequences?

2. What were the positive benefits of gigantism and heavy body armor in glyptodonts? What were possible drawbacks?

3. Discuss the relationships among low metabolic rates, poor thermoregulatory abilities, geographic distributions, and small litter sizes in xenarthrans.

4. Why might you expect to find "altruistic" behavior among populations of the nine-banded armadillo rather than in some of the other species of mammals?

Orders: Scandentia and Dermoptera

Scandentia

This order is represented by two families, Ptilocericidae and Tupaiidae, collectively referred to as treeshrews. The order contains 4 genera and 23 species (Helgen 2005; Olsen et al. 2005; Wilson and Mittermeier 2018) (Figure 14.1). The common name is unfortunate because ptilocercids and tupaiids are certainly not shrews. Historically, treeshrews have been considered basal members of the order Primates or placed within the Family Macroscelididae in the insectivoran clade Menotyphla. Because they have long been considered the most primitive living primates, treeshrews have generated debate and controversy out of proportion to their size as a group. As such, they probably have a richer and more confused taxonomic history than any other mammalian family. Campbell (1974) provided an excellent review summarizing dental, skeletal, and anatomical evidence against considering treeshrews as primates. Anatomy and related systematics of the group are discussed in detail by Luckett (1980a). Treeshrews show a close relationship with primates (Sargis 2002c; 2004) and demonstrate unique behavioral traits of absentee maternal care and social monogamy (Emmons 2000). Most authorities, however, consider treeshrews to be a distinct lineage separate from either the primates or insectivores and place them in their own order as we have done; however, there is strong disagreement about the phylogenetic relationships of treeshrews (Murphy et al. 2001b; Silcox et al. 2005).

Ptilocercidae

Pen-tailed treeshrews comprise a single family with 1 genus and 1 species (Helgen 2015; Wilson and Mittermeier 2018) inhabiting Indonesia, Malaysia, and Thailand. Pen-tailed or feather-tailed treeshrews (*Ptilocercus lowii*) are 100–140 mm in head and body length, with a tail length of 90–130 mm, and they weigh 25–60 g. The common name, "pen-tailed," is derived from its naked tail, which has bushy white hairs at the tip, resembling an old fashioned quill pen or bottle brush. Their

fur is soft and grayish brown except for the underside with is grayish yellow. Unlike the small thick ears of *Tupaia*, the ears of *Ptilocercus* are rather large and thin. The eyes of pen-tailed treeshrews are larger than those of treeshrews possessing a well-developed *tapedum lucidum* and white eyeshine enhancing night vision. Pen-tailed treeshrews are nocturnal and arboreal, rarely descending to the ground; they make simple nests of dried leaves, twigs, and plant fibers within hollow trees or on branches. The lower incisors are procumbent and used for grooming. The functional morphology of 12 species of tupaiids was analyzed and compared to other members of the Order Scandentia (Sargis 2002a; 2002b). The forelimb of *P. lowii*, the only ptilocercine, was found to be better adapted for arboreal locomotion, while that of tupaiines was better adapted for scansorial (terrestrial) locomotion. Sargis (2001) discussed differences in the axial skeleton of the pen-tailed treeshrew compared to other tupaiids, and felt *P. lowii* was primitive to the more derived tupaiines. Pen-tailed treeshrews inhabit primary or secondary forests from sea level to 1,000 m; their diet is notably omnivorous and includes worms, insects, mice, small birds, lizards, and fruits; they are certainly unique as they are the only known wild mammal that chronically consumes alcohol (Wiens et al. 2008). Treeshrews radio-collared in a West Malaysian rainforest were reported to consume alcoholic nectar daily from flower buds of the bertam palm (*Eugeissona tristis*), which they pollinate. Nectar high in alcohol is produced by specialized flower buds that harbor a community of fermenting yeast. From this source pen-tailed treeshrews regularly consumed doses of alcohol that would inebriate humans; however, treeshrews showed no signs of intoxication. Measurements of a biomarker of ethanol breakdown indicated that treeshrews could be metabolizing alcohol by a pathway of alcohol detoxification that is not used as commonly by humans. The benefit of ingested alcohol for treeshrews is unclear; we do not know how they mitigate the risk of continuous high blood alcohol concentrations (Wiens et al. 2008).

Tupaiidae

The treeshrews comprise 3 genera and about 22 species (Wilson and Mittermeier 2018). They resemble long-snouted squirrels. They have a slender body and adults weigh less than 400 grams with head and body length of about 100–220 mm and tail length of 90–225 mm. The pelage consists of long, straight guard hairs with shorter, softer wooly underfur (see Figure 14.1). Treeshrews are restricted to the Oriental faunal region, ranging from India, southern China, and the Philippines southward through Borneo and the Indonesian islands (Sargis et al. 2014a, 2014b; Sargis et al. 2017). Throughout their range, treeshrews occur in forested habitats up to an elevation of 2,400 m. Like tree squirrels (*Sciurus*), they are diurnal and arboreal, and their senses of hearing and smell are keen. Treeshrews feed primarily on insects and fruits. Species of

Figure 14.1 A typical tupaiid. This common treeshrew (*Tupaia glis*) superficially resembles a squirrel. Tupaiids have had a confused taxonomic history—at various times being placed in the Orders Primates and Insectivora and currently within their own order, Scandentia. *Adapted from Cabrera (1925).*

treeshrews studied in Malaysia were primarily frugivorous and concentrated on small, soft, avian-dispersed fruits. Although chiefly insectivorous, treeshrews may consume fruit to add extra calories or nutrients such as calcium to their high-protein diet (Emmons 1991). Treeshrews are highly vocal and live as monogamous pairs in dense tropical forest regions of Southeast Asia (Emmons 2002). Each species can be identified by its distinctive call emitted during aggression, defense, or alarm situations or due to disturbance (Binz and Zimmermann 1989; Schehka et al. 2007). Comparative bioacoustics were employed to discriminate among 3 cryptic species of diurnal *Tupaia*—namely *T. glis*, *T. belangeri* and *T. chinensis* (Esser et al. 2008). All species scent-mark extensively, using special scent glands, urine and even feces for marking territories. Also, the larger species such as the Mindanao treeshrew (*Urogale everetti*), confined to the island of Mindanao, and the large treeshrew (*Tupaia tana*), of Borneo and Sumatra, spend most of their time on the ground.

Treeshrews are similar to sengis (Family Macroscelididae) in that they both have a maternal absentee system of neonatal care; however, treeshrews are more extreme and

unique. Research has confirmed that at least 3 species of treeshrews (pygmy, northern, and large) exhibit absentee maternal care coupled with social monogamy (Emmons 2000; Sargis 2004; Munshi-South 2007). Treeshrews build nests of dried leaves in hollow trees or in root systems. Two nests are constructed—one for the parents and one for the young. The "natal" nest is made by the male—a departure from the usual mammalian scheme. Following a gestation period of 45–50 days, 1 to 3 young are born without fur and closed ears and eyes. These altricial young are born in a separate nest from the parents. Another unconventional aspect of parental care in treeshrews pertains to the minimal amount of time the mother actually spends with her young. The mother visits her young only once every 48 hours to nurse them for 10 to 15 minutes; however, during this short visit, she is able to provide from 5–15 g of milk to the rapidly growing young. This milk is high in protein (10%) to encourage rapid growth and has a very high fat concentration (25%) so young can maintain a high body temperature close to 37°C despite the absence of the mother in the nest. The milk contains a small proportion of carbohydrate (2%) necessary to satisfy the immediate energy needs of the sedentary pups. About 1 month following birth, the pups disperse from their "natal" nest and join the parents in the "parental" nest. All in all, the mother spends only 1.5 hours with the infants during the nursing phase and shows no toilet care during this period. Young reach sexual maturity in about 4 months.

MORPHOLOGY

As mentioned earlier, treeshrews superficially resemble squirrels, although they have a more slender snout. Emmons (2000:17) noted that "the diurnal treeshrews have virtually no salient facial vibrissae, while the nocturnal *P. lowii* has a large spray of them." The limbs are equal in length, pentadactyl, and have long claws. Maximum total length is about 450 mm, one-half of which is the tail. Some primate-like characteristics of treeshrews include relatively large braincase, resemblance of the carotid subclavian arteries to those of humans, the permanent sac, or scrotum, for the testes in males, and orbits completely encircled in bone. Treeshrews also possess a toothcomb consisting of the middle 4 lower incisors; however, unlike lemurs, which also possess a tooth comb, the tooth comb of treeshrews does not include the canines. Unlike elephant shrews or sengis, with which they are sometimes grouped, treeshrews have tribosphenic molars and an unperforated palate. Like elephant shrews and several families of "insectivores," the occlusal surface of the upper molars is dilambdodont. The dental formula is 2/3, 1/1, 3/3, 3/3 = 38. The distinctiveness of hand bones (manus) proportions among 4 species of treeshrews was assessed by Sargis and colleagues (2013). Their analysis supported separation of the 4 species and demonstrated the value of assessing hand proportions in distinguishing closely related species of treeshrews.

FOSSIL HISTORY

The only definite fossil treeshrew (*Palaeotupaia sivalicus*) was described from mid-Miocene deposits in India (Chopra and Vasishat 1979). None of the previous reports of fossils referable to treeshrews, summarized by Jacobs (1980), provides unequivocal association with the family, however. Although not suggesting any phylogenetic relationship, Emmons (2000) noted the striking resemblance of treeshrews to Genus *Crusafontia*, a Jurassic-period pantothere.

ECONOMICS AND CONSERVATION

Because of the continued loss of forest habitat throughout their range, six species are considered endangered or threatened. They do little damage to crops or plantations and are of no economic significance, although they may play a role in seed dispersal (Shanahan and Compton 2000).

Dermoptera

Cynocephalidae

This order has a single family, which contains two genera and two species (Stafford 2005; Wilson and Mittermeier 2018). Dermopterans (literally, "skin-winged") are commonly called "flying lemurs," or colugos (Figure 14.2). The latter name certainly is preferable, however, because dermopterans do not fly and are not lemurs. Instead, they glide (they are **glissant**). Like the treeshrews, this order also has a confusing taxonomic history. Historically, colugos have been grouped taxonomically with the bats, "insectivores," or primates. McKenna and Bell (1997) considered dermopterans a suborder of the primates. As noted, this order now contains a single family with two genera (*Cynocephalus*

Figure 14.2 Characteristic external features of colugos. The extent of the patagium is evident in this colugo.

and *Galeopterus*), each with one species. Using dental morphology, Stafford and Szalay (2000) argued that two genera should be recognized—the Philippine colugo (*C. volans*) and Sunda colugo (*G. variegatus*).

The Philippine colugo is found in the southern Philippines, whereas the Sunda colugo occurs in Indochina, Malaya, Sumatra, Java, Borneo, and small islands nearby. These parapatric species are completely arboreal and inhabit lowland and upland forests and plantations. Colugos are primarily nocturnal, foraging on flowers, leaves, and fruits. Wischusen and Richmond (1998) reported that the mean duration of foraging bouts in *C. volans* was 9.4 minutes with 12 bouts per night being typical. Unlike other arboreal folivores—such as the koala (*Phascolarctos cinereus*) or three-toed sloth (*Bradypus variegatus*)—*C. volans* is a generalized forager, feeding on young leaves from many different tree species. Colugos are solitary in their roosting, foraging, and gliding habits. Reproductive females are reportedly observed with infants tucked into their patagium. Colugos den in tree cavities or hang upside down from branches during the day (with their head remaining upright, unlike bats). They move among trees very efficiently; colugos are the premier gliding mammals, and their morphological adaptations for this means of locomotion are pronounced. Breeding occurs throughout the year. The length of gestation ranges widely from 60 to 150 days for the Philippine colugo and up to 180 days for the Sunda colugo. Females give birth to a single young weighing about 36 g. The offspring are altricial and reside with the mother continually for about 6 months. Juvenile colugos are weaned at about 6 months of age but young do not reach adult size until 3 years of age (Lim et al. 2013; Stalder et al. 2010).

MORPHOLOGY

The patagium of colugos is more extensive than in any of the gliding marsupials or rodents. It extends from the neck to the digits of the forelimbs, along the sides of the body and hind limbs, and encloses the tail (see Figure 14.2). Colugos weigh between 1 and 2 kg, with head and body length of 340–400 mm and tail length of 170–270 mm. *Galeopterus variegatus* is the larger species. Despite the colugos' size, glide distances of over 100 m are common, with very shallow glide angles (Kawashima et al. 2018). Thus, while gliding 100 m, a colugo loses less than 10 m in elevation. Colugos are helpless on the ground but adept at climbing high into trees, aided by long, curved claws. Their brownish-gray and white, mottled pelage camouflages them against tree trunks. Colugos have a keeled sternum, as do bats and other gliding species.
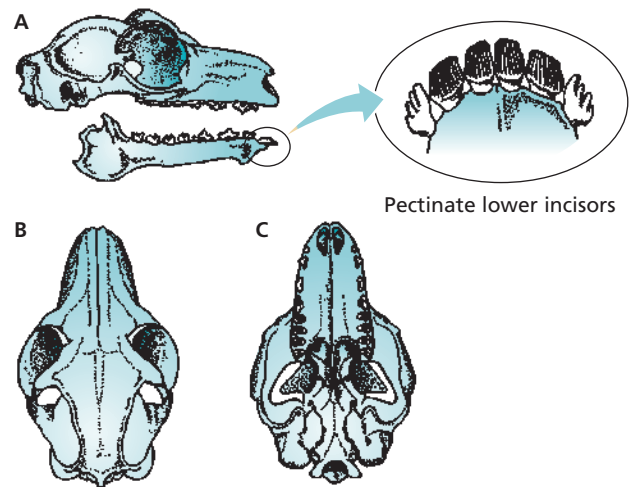
Figure 14.3 **Colugo skull features.** (**A**) Lateral, (**B**) dorsal, and (**C**) ventral views of the skull of a colugo with evident post-orbital processes and temporal ridges. (*Inset*) Pectinate lower incisors are a characteristic feature of the two species in this unusual order. *Adapted from Lawlor (1979).*

The dental formula is 2/3, 1/1, 2/2, 3/3 = 34. The first two lower incisors are procumbent and **pectinate** ("comb-like," with 5–20 distinct prongs from a single root), a feature unique to dermopterans. These lower incisors are used to grate food and groom the fur. The upper incisors are small, with distinct spaces between them, and the postorbital processes and temporal ridges are well developed (Figure 14.3). Stafford and Szalay (2000) provided a detailed analysis of the craniodental morphology of the two species.

FOSSIL HISTORY

The extinct Family Plagiomenidae is placed in the Order Dermoptera and dates from the late Paleocene epoch in North America and early Eocene epoch in Europe. Marivaux and coworkers (2006) described newly discovered fossil dermopterans from different regions of South Asia (Thailand, Myanmar, and Pakistan) ranging from the late middle Eocene to the late Oligocene.

ECONOMICS AND CONSERVATION

Colugos are hunted for their fur and for food, but habitat loss to logging and farming is a greater threat to populations. *C. volans* is presently considered threatened.

SUMMARY

• Order Scandentia is represented by 2 families, Ptilocercidae and Tupaiidae, collectively referred to as "treeshrews," and contains 4 genera and 23 species. They probably have a richer and more confused taxonomic history than any other mammalian family.

• The Dermoptera is represented by a single family, which contains two genera and two species (Stafford 2005). Order Dermopterans (literally, "skin-winged") commonly are called "flying lemurs" or colugos (Figure 14.2). Today, they are now considered to be the closest living relatives of primates.

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DISCUSSION QUESTIONS

1. Research has confirmed that three species of tree-shrews exhibit absentee maternal care coupled with social monogamy. Please define and elaborate on this unique arrangement.

2. Can you list five morphological characteristics of treeshrews that are analogous to members of Order Primates?

3. Can you name a group of primates that possess incisor teeth similar to those of colugos?

Order: Primates

The name "primates" means "the first animals," a definition that reflects an early, incorrect, and anthropocentric bias, which gives special importance to the order that contains humans. Primates may have originated as early as the Cretaceous, although the fossil record begins in the early Paleocene with representatives of the extinct Infraorder Plesiadapiformes (*Plesiadapis*). Two other early Eocene primate genera were *Archicebus* and *Teilhardina*, both small with estimated body weight similar to modern mouse lemurs (Gebo et al. 2015; Dagosto et al. 2018). Following radiations in the Paleocene and Eocene, primates dispersed into tropical areas of all continents except Australia by the mid-Tertiary. These radiations resulted in the two recognized suborders of living primates (Kay et al. 1997). Suborder Strepsirrhini consists of seven living families—Lemuridae, Lepilemuridae, Indriidae, Galagidae, Daubentoniidae, Cheirogaleidae, and Lorisidae (Table 15.1)—and three extinct ones—Megaladapidae, Archaeolemuridae, and Palaeopropithecidae (Szalay and Delson 1979; Fleagle 1988; Groves 2001, 2005). Suborder Haplorrhini has nine living families—Tarsiidae, Cebidae, Callitrichidae, Aotidae, Pitheciidae, Atelidae, Cercopithecidae, Hylobatidae, and Hominidae (Table 15.1).—and four extinct ones—Omomyidae, Parapithecidae, Oreopithecidae, and Pliopithecidae. Strepsirrhines and haplorrhines are believed to have diverged by the early Eocene (Kay et al. 1997; Ni et al. 2013; Dunn et al. 2016). Whereas the Eocene climate was warm, the Oligocene was much cooler (the Eocene-Oligocene Transition) with resultant environmental and faunal changes. During the Oligocene, Asian primates were dominated by strepsirrhines, whereas haplorrhine radiation increased in Africa, including the distant ancestors of humans (Ni et al. 2016). A phylogeny of extant primates is shown in Figure 15.1.

Table 15.1   Living primates*

	Number of Living Genera, Species	Distribution
Suborder Strepsirrhini		
Family Lemuridae	5, 21	Madagascar, Comoros Islands
Family Cheirogaleidae	5, 31–32	Madagascar
Family Lepilemuridae	1, 26	Madagascar
Family Indriidae	3, 19	Madagascar
Family Daubentoniidae	1, 1	Madagascar
Family Lorisidae	4, 12	Central Africa, Southeast Asia, Sri Lanka
Family Galagidae	5, 17–18	Africa
Suborder Haplorrhini		
Family Tarsiidae	1–3, 10–11	Indonesia, Philippines
Family Cebidae	3, 21–29	Central and South America
Family Aotidae	1, 11	Central and South America
Family Callitrichidae	6–7, 41–47	Central and South America
Family Pitheciidae	4–5, 43–44	Central and South America
Family Atelidae	5, 25	Central and South America
Family Cercopithecidae	23, 134–159	Africa, Asia, Indonesia
Family Hylobatidae	4, 18–19	Southeast Asia, China, Indonesia
Family Hominidae	3–4, 6–8	Worldwide

Data from Mittermeier et al. (2013a); IUCN (2018). Burgin et al. (2018) combined Aotidae and Callitrichidae with Cebidae.

*Living primates are divided into 2 suborders and 16 currently recognized families, 52–53 genera, and between 439 species (IUCN 2017) and 479 species (Mittermeier et al. 2013). Burgin et al. (2018) have proposed as many as 84 genera and 518 species.
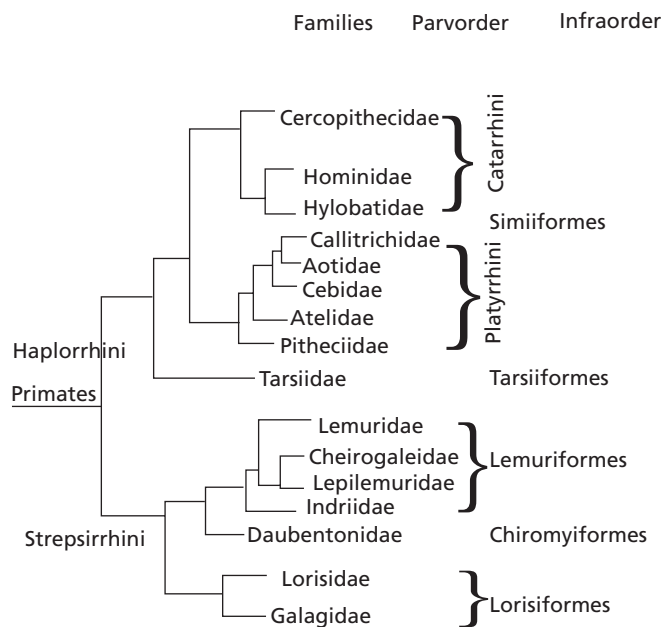
Figure 15.1 Primate phylogeny. This cladogram shows currently recognized suborders, families, infraorders, and parvorders of primates. *Modified and adapted from Perelman et al. (2011); alternate phylogenies are in Schneider and Sampaio (2015); Garbino and Martins-Junior (2018).*

Ordinal and Morphological Characteristics

Several morphological features characterize primates, although many species are quite generalized. Primates range in size from the endangered Berthe's mouse lemur (*Microcebus berthae*), with head and body length of only about 9 cm and weight of about 30 g, to gorillas (*Gorilla gorilla*) at 2 m height and 275 kg body weight. Primates are distributed in the warmer areas of Africa, Asia, and the Western Hemisphere, about 30° north and south of the equator (an exception is the Japanese macaque [*Macaca fuscata*], which lives in areas that have considerable snow); humans are everywhere. Females exhibit a menstrual cycle and males have scrotal testes and a pendulous penis with a baculum; there is no baculum in tarsiers, four species of New World monkeys (Cebidae), and humans. General characteristics include

- opposable thumb (pollex) and big toe (hallux; except in humans);
- digits with nails or sometimes claws (**unguiculate**);
- plantigrade and usually pentadactyl;
- a clavicle (**claviculate**);
- digits with fleshy pads and friction ridges (our "fingerprints");
- reduced rostrum with eyes directed forward for stereoscopic (binocular) vision;
- reduced olfactory acuity;
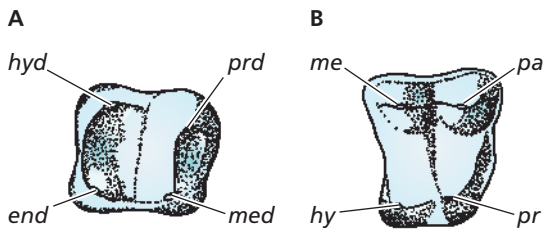
Figure 15.2 Primate teeth. The basic four-cusped crown pattern of primates: (**A**) lower left molar; (**B**) the upper right molar. *Abbreviations*: end = entoconid; hy = hypocone; hyd = hypoconid; me = metacone; med = metaconid; pa = paracone; pr = protocone; prd = protoconid. *Adapted from Vaughan (1986).*

- large brain relative to body size; brain with **calcarine fissure**;
- molars quadrituberculate, bunodont, and brachyodont (Figure 15.2);
- tail on monkeys (prehensile only in a few cebids); none on apes; and
- at least partially arboreal, except for humans.

Various investigators have extended this characterization by discussing the evolutionary trends that help to define the primates (Macdonald 1984; Groves 2001).

1. The hands and digits have become refined, with increased mobility of the digits. There are sensitive pads on the digits, and as noted, they have friction ridges for grasping—important in arboreal species.
2. Both the absolute and relative brain sizes have increased, with elaboration of more **cerebral cortex.** A trade-off has occurred between increased dependence on sight, which is correlated with enlarged brain areas that are associated with vision, and decreases in brain areas associated with olfaction.
3. The shortened rostrum is associated with a decline in the use of smell and a concomitant shift to binocular, stereoscopic vision.
4. Reproduction occurs at a slower rate, sexual maturity is delayed, and life spans are longer.
5. The diet has progressively shifted to greater reliance on fruits, seeds, and foliage, with a decline in the amount of animal matter consumed.
6. Social and mating systems include a diverse array of complex sociospatial and breeding patterns.

The skull of all modern strepsirrhine primates has a bony postorbital bar (Figure 15.3), whereas haplorrhines have a postorbital plate (Figure 15.4). The braincase surrounding the proportionately large brain is expanded. All primates have a petrosal-covered **auditory bulla**, the tympanic floor of which is derived from only the petrosal plate and ectotympanic bone. The jaw symphysis became progressively more ossified in more derived primates.
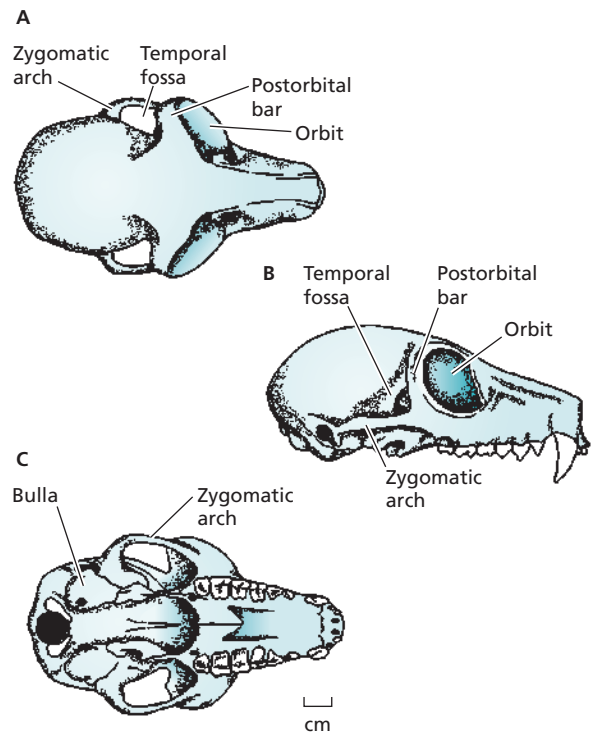
Figure 15.3 Strepsirrhine skull. (**A**) dorsal, (**B**) lateral, and (**C**) ventral of the skull of a strepsirrhine—the ruffed lemur (*Varecia variegata*). Key characteristics include the forward-facing eyes and the lateral postorbital bar. Strepsirrhine primates have an orbital cavity confluent with the temporal fossa, in contrast to haplorrhines, whose postorbital plate demarcates the rear of the orbit. *Adapted from Martin (1990).*
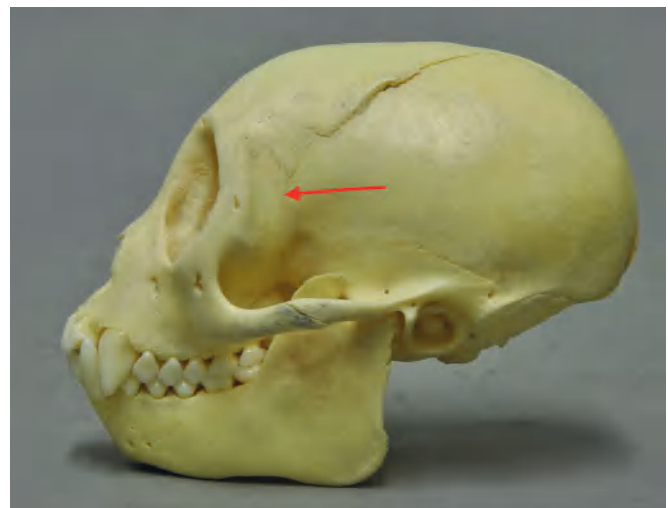
Figure 15.4 Haplorrhine skull. Note the postorbital plate (*arrow*) in this skull of a tufted capuchin (*Cebus apella*), which separates the eye orbit and the temporal fossa, unlike in strepsirrine skulls (Figure 15.3).

Both the tree shrews (Order Scandentia) and the colugos (Order Dermoptera) were once included in the same order with the primates. In older classifications (Luckett and Szalay 1975; Fleagle 1988; Martin 1990), the primates

were divided into prosimians and anthropoids. Research to refine the evolutionary tree for primate lineages has included the use of both nuclear DNA (Perelman et al. 2011) and mitochondrial DNA (mtDNA) (Weinreich 2001; Pastorini et al. 2002). The number of recognized species has increased dramatically in the past several decades, largely due to new techniques for distinguishing cryptic species. The number of recognized species varies from about 439 (IUCN 2018) to as many as 518 (Burgin 2018).

Fossil History

The earliest primates in Europe and North America during the Paleocene and Eocene epochs produced a number of forms grouped together in the Plesiadapiformes (Figure 15.5; Kay et al. 1997; Silcox et al. 2005). These small, squirrel-like mammals had elongated skulls with the eye orbits and temporal region of the skull not separated by a bony plate or bar. The radius and ulna in the forelimb and tibia and fibula of the hind limb were separate, permitting rotation of the feet. The digits of the hands and feet were long enough to grasp the limbs and branches of trees. The terminal digits still had claws.

The Adapiformes, extinct relatives of today's lemurs, evolved during the early Eocene (Gebo et al. 2001). They ranged through the tropical and subtropical forests that then covered North America and Eurasia. Two genera, *Smilodectes* and *Notharctus*, had a bony postorbital bar completely enclosing the orbit. No diastema occurred between the incisors and canines, resulting in a continuous tooth row. *Smilodectes* had eyes that were directed forward, for binocular, stereoscopic vision. The first digit of each foot was set apart from the others, suggesting a degree of opposability. These small primates were capable climbers, grasping branches as they moved through trees (Gingerich 2012). Other features associated with arboreal activity were their flexible back and long tail, useful for climbing and balance.

An early haplorrhine group, the Omomyidae, arose during the Eocene, and included *Tetonius* from North America and *Necrolemur* from Europe. They had large orbits located in a short, flat face; the large eyes suggest they were nocturnal. Short jaws contained large canines and rather primitive molars. Fossil evidence indicates that lemur-like primates (Lemuriformes) diversified in Asia, particularly on the Indian subcontinent (Marivaux et al. 2001). Fossils of one genus (*Afrotarsius*) from the Oligocene epoch are nearly identical to modern tarsiers in leg specializations that provide for the unique locomotion of members of this family of primates (Rasmussen et al. 1998).

Fossil remains of modern New World monkeys are rare, making an assessment of platyrrhine origins difficult. However, they evolved from African ancestors that migrated to South America in the Oligocene (de Oliviera 2009). Fossil evidence for the catarrhine primates of Asia and Africa (Old World primates) is more complete, extending from the Eocene to the Recent epochs (Fleagle 1988; Martin 1990). The fossil evidence from North Africa for one genus (*Parapithecus*) is relatively complete. This taxon was characterized by a jaw that was only 5 cm in length but was deep, with a **condyle** located high on an **ascending ramus** to articulate with the skull. This latter trait is characteristic of modern cercopithecid primates.

Paleontologists previously believed that the earliest primates likely diverged from a common ancestor approximately 65 mya. In contrast, the evidence from DNA-based studies suggested a divergence at about 90 mya. Tavare and colleagues (2002; but see Bower 2002) used a mathematical analysis of the fossil record to estimate an age of 81.5 mya for the most recent common ancestor of living primates.

The most widely accepted proposal for the development of traits that characterize primates is the arboreal theory (Martin 1979; but see Cartmill 1972). An arboreal ancestry explains the adaptations of the visual system, including the forward-facing eyes and enlarged visual cortex of the brain for stereoscopic vision. These factors produce depth of field—the range of distance along the line-of-sight with a clear image. It also explains many of the skeletal adaptations of the limbs and digits, which permit easy and safe movement in trees. The theory also accounts for hands with opposable thumb gradually replacing the mouth for gathering and handling food.

2 cm

Figure 15.5 **Ancestral primate.** One of the earliest ancestors of the primate lineage was *Plesiadapsis tricuspidens*, from the early Eocene. Note in particular the flexible spine and long tail. Skeletal portions shown with dark lines are known from fossils; portions shown in blue are reconstructed. Probably weighing about 2 kg, this animal was about the size of a squirrel. *Adapted from Tattersall (1970).*

Economics and Conservation

In some cultures, primates are considered sacred and are protected, whereas in other cultures, they are hunted for food. Overhunting has reduced or eliminated many species—for example, the critically endangered western red

colobus monkey (*Piliocolobus badius*; Oates et al. 2000). Other primate species have been and continue to be important for medical research, such as the rhesus macaque (*Macaca mulatta*), chimpanzee (*Pan troglodytes*), and northern night monkey (*Aotus trivirgatus*). In February 2018, the IUCN recognized 439 primate species of which 123 (28%) were endangered and 64 (14.6%) were critically endangered.

The most significant threat to the continued existence of many primate populations—75% have declining populations—comes from habitat destruction and other negative anthropogenic impacts. According to Estrada and coworkers (2017:1), these threats include "global and local market demands, leading to extensive habitat loss through the expansion of industrial agriculture, large-scale cattle ranching, logging, oil and gas drilling, mining, dam building, and the construction of new road networks in primate range regions. Other important drivers are increased bushmeat hunting and the illegal trade of primates as pets and body parts, along with emerging threats such as climate change and anthropogenic diseases."

One mining threat involves coltan, a mineral known industrially as tantalite. Tantalite is used for coating components in a variety of modern electronic devices, including cell phones and computer parts. The demand for tantalum is very high, and the area where coltan is most readily mined is in the eastern Congo—with severe negative impacts on gorillas and other primates. In addition to anthropogenic impacts, Ebola virus has decimated some populations of gorillas and chimpanzees in the Congo River basin, and orangutans also show signs of Ebola virus infections.

Conservation efforts for primates include establishing reserves where habitat should be left undisturbed. This has been done with some positive effect in Sulawesi, Indonesia, for example. Reserves are designed to protect primate diversity, including the spectral tarsier (*Tarsius tarsier*), the critically endangered Celebes crested macaque (*Macaca nigra*),

the Tonkean macaque (*M. tonkeana*), and several other species. For a limited number of endangered species, captive breeding stocks have been established for reintroduction into native habitat, as has been done with the golden lion tamarin (*Leontopithecus rosalia*) in Brazil (Mittermeir and Cheney 1986). Several locales now have successfully reproducing, viable populations. The outcome of conservation measures will be known only several decades from now as researchers continue to monitor the diminishing population levels of a large percentage of primate species.

Suborder Strepsirrhini

The strepsirrhines include 7 families of lemurs, lorises, galagos, and the aye-aye (see Figure 15.1). These families are concentrated on Madagascar—where there are 4 endemic families—but also include species that live in mainland Africa, Southeast Asia, and the Malay Archipelago. Besides a postorbital bar versus a postorbital plate, several traits distinguish strepsirrhine from haplorrhine primates. The **rhinarium** of strepsirrhines is an area of moist, hairless skin surrounding the nostrils (Figure 15.6); they are sometimes called "wet-nosed primates." The maximum dental formula for lemurs and lorises is 2/2, 1/1, 3/3, 3/3 = 36 teeth. The 2 lower incisors and the incisiform lower canine form a distinctive toothcomb used for grooming. Strepsirrhines have a **bicornuate** uterus, which contrasts with the fused simplex uterus of the haplorrhines. The **epitheliochorial placenta** in lemurs and lorises is distinct from the haplorrhines. In general, strepsirrhines produce neonates that are smaller relative to the mother's body weight than those of haplorrhines (Leutenegger 1973). The strepsirrhines and haplorrhines are monophyletic groups that diverged about 63 mya (Perelman et al. 2011). Masters and colleagues (2013) conducted the most recent systematic analysis of the
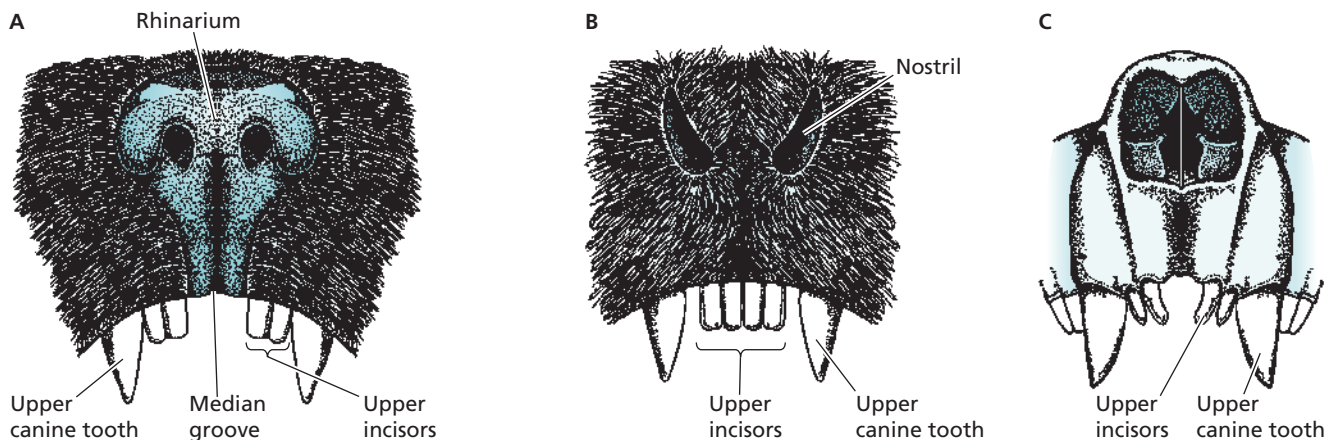
Figure 15.6 Snout variation. Snout of (**A**) a strepsirrhine compared to that of (**B**) a haplorrhine. Strepsirrhines retain the ancestral rhinarium surrounding the nostrils. Hair obliterates the rhinarium in haplorrhines. (**C**) Anterior view of the skull of a strepsirrhine. *Adapted from Martin (1990).*

strepsirrhines. All families on Madagascar face extremely serious conservation crises because of habitat loss and other factors (Schwitzer et al. 2014).

INFRAORDER LEMURIFORMES

Cheirogaleidae

There are 5 genera and as many as 40 species of cheirogaleids (Burgin et al. 2018), most of them recognized in the past few decades, and all in Madagascar. In the Genus *Cheirogaleus* there are 5 species of dwarf lemurs—although several new species have been proposed (Frasier et al. 2016; McLain et al. 2017). The hairy-eared dwarf lemur (*Allocebus trichotis*) is in its own monotypic genus, whereas the Genus *Microcebus* has 20 species of mouse lemurs, many of them recently recognized (Radespiel et al. 2008; Louis et al. 2008), including the Marohita mouse lemur (*M. marohita*; Rasoloarison et al. 2013). There are 2 species of giant mouse lemur (Genus *Mirza*) and 4 species of fork-marked lemurs (Genus *Phaner*). Schwitzer and coworkers (2013a) extensively reviewed the cheirogaleids.

Fossil evidence indicates that members of this family were once more widespread, occurring eastward into areas of what is now Pakistan in south-central Asia (Marivaux et al. 2001). The molecular phylogeny of cheirogaleids has been examined using mtDNA (Pastorini et al. 2001), with support for generic status of the giant mouse lemurs as distinct from Genus *Microcebus*.

As the common names imply, all cheirogaleids are small. Dwarf lemurs are 19–30 cm in head and body length, with tails about the same length. They weigh from 300 g to slightly less than 1 kg. Mouse lemurs are even smaller, with head and body length of 13–17 cm, tail length of 17–28 cm, and body weight up to about 60 g; the smallest is Madam Berthe's mouse lemur, which weighs only 30 g. The dental formula, similar to other lemurs, is 2/2, 1/1, 3/3, 3/3 = 36.

Cheirogaleids inhabit dry forests in western Madagascar. Their fur is dense and woolly, varying from gray to reddish brown to cinnamon, with lighter underparts. Fork-marked lemurs (Figure 15.7) are characterized by a well-defined spinal stripe that bifurcates on the crown, where it joins dark eye rings. All species are arboreal and nocturnal and have large eyes. These small, agile primates scurry in short runs and dart squirrel-like from place to place. Dwarf lemurs are primarily frugivorous, mouse lemurs are primarily insectivorous, and fork-crowned lemurs consume insects, tree gum, and fruits.

Cheirogaleids are solitary or found in pairs. Females give birth to 1–3 young per pregnancy and nurse them with two pairs of mammae, one inguinal and one pectoral. Communication apparently involves less scent-marking than in most other strepsirrhines. They also communicate through vocalizations, facial expressions, and body postures. Because of forest destruction throughout Madagascar, densities of many species are declining and the num-

Figure 15.7 **Fork-marked lemur.** A Masoala fork-marked lemur (*Phaner furcifer*). *From an 1868 print by P. W. M. Trap.*

ber of listed species has risen dramatically. There are now 16 cheirogaleids listed as endangered, and 4 other species are considered critically endangered.

Lepilemuridae

The sportive lemurs (Genus *Lepilemur*) were included in the Family Lemuridae but are now in their own family. Work by several investigators (Andriaholinirina et al. 2006; Louis et al. 2006) has greatly increased the number of recognized species in this family to 26 (Schwitzer et al. 2013b). Lei and coworkers (2017) discussed the phylogeny of lepilemurids based on mitochondrial genomes from all species. Sportive lemurs (Figure 15.8) are restricted to Madagascar, where they inhabit both dry deciduous forests and tropical rainforests. All are nocturnal and arboreal. They have dense, woolly fur that is usually shades of red, mixed with brown or gray. The undersides are pale gray or yellowish white. Some species have a lengthy spinal stripe from the head to the base of the tail. They are medium-sized, with head and body length of 28–35 cm, tail ranging from 25–28 cm, and body weight of 0.5–1.2 kg. The diet of sportive lemurs is primarily leaves, but they also eat bark, fruits, and flowers.

Lepilemurids exhibit vertical clinging and leaping, moving from one tree trunk to the next with occasional hops

Figure 15.8 **Lepilemuridae.** Sportive lemurs, such as the Milne-Edwards sportive lemur (*Lepilemur edwardsi*), live in the deciduous and humid forests of Madagascar. They sleep during the day in tree hollows and feed at night on leaves supplemented with fruit, flowers, and bark.

on the ground. The hind limbs are considerably longer than the forelimbs. They also have a prehensile thumb, which is pseudo-opposable and capable of strong grips on vertical branches.

Socially, sportive lemurs live solitary lives except for mothers with their infants. Some marking occurs with urine and the glands in the anal region. The primary means of communication is a relatively extensive vocal repertoire. Mothers give birth to single young and carry them in their mouths as they move. Population densities of most lepilemurids are declining, again primarily due to forest habitat destruction on Madagascar. Of the 26 species currently recognized, 15 are endangered, and 5 others are critically endangered.

Indriidae

This family consists of 9 species of woolly lemurs (Genus *Avahi*), the indri (*Indri indri*), and 9 species of sifakas (Genus *Propithecus*), all of which occur only on Madagascar. Much of the revision of this family, greatly expanding the number of species, was done by Groves (2001), with more recent work summarized by Mittermeier and colleagues (2013b). All indriids are arboreal and nocturnal. Woolly lemurs are the smallest, with head and body length of 26–30 cm, tail length of 55–70 cm, and a weight of about 1 kg. Sifakas are intermediate in size, with head and body length of 40–60 cm, tail length of 45–60 cm, and body weight of 3.5–8.0 kg. The indri is the largest strepsirrhine primate. It is 53–70 cm in head and body length, with a very short tail, and weighs 7–10 kg. The diet of all indriids consists of leaves, fruits, flowers, and bark. Species differ in their general habitat preferences and activity patterns (Mittermeier et al. 2013b).

Locomotion involves vertical clinging and leaping between tree trunks and shrubs. In conjunction with this pattern of movement, the hind limbs are considerably more developed than the forelimbs. The hand is prehensile, with the thumb being pseudo-opposable. The lower incisors are arranged in a comb-like configuration for grooming. Indriids have moderate sized eyes and a distinct but modest muzzle. The thick fur varies in color, depending on the species, from white and black to brown, maroon, reddish, and orange. There are no distinct sexual differences in either body size or color patterns within different species of indriids. However, Gordon and colleagues (2013) found changes in ecological variables impacted female body weight of sifakas more than males.

Indriids live in small social groups of 3 to 6 individuals, containing adults of both sexes and young. Most births are of single young, and mothers nurse their infants with a single pair of pectoral mammae. Young are generally carried crosswise to the body axis and under the abdomen as small infants; after a few weeks, they switch to riding on the backs of their mothers. Indriids, particularly sifakas, have distinct home ranges, which they defend against intruders. Communication is via scent-marking, vocalizations, and visual expressions and postures. Almost all species are of conservation concern. The indri is critically endangered, 6 of the 9 species of woolly lemurs are endangered, and all 9 species of sifakas are either critically endangered (4) or endangered (5).

Lemuridae

The "true" lemurs include 5 living genera: *Eulemur* (12 species), *Hapalemur* (5 species of bamboo lemurs), the ring-tailed lemur (*Lemur catta*), the greater bamboo lemur (*Prolemur simus*), and 2 species of ruffed lemurs—the red ruffed lemur (*Varecia rubra*) and the black-and-white ruffed lemur (*V. variegata*; Figure 15.9). Lemurids occur only on Madagascar. They are diurnal or crepuscular and generally arboreal, but some species—the ring-tailed lemur for
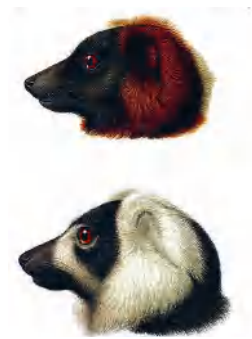
Figure 15.9 **Ruffed lemurs.** (*Top*) The red ruffed lemur (*Varecia rubra*) and (*bottom*) black-and-white ruffed lemur (*V. variegata*) both exhibit the elongated muzzle and characteristic "ruff" of fur around the neck. *Photo of an 1890 print by John Gerrard Keulemans.*

example—spend considerable time on the ground. Lemurids are medium-sized, ranging from 26–45 cm in head and body length, with tails of 25–56 cm, and body weight of 2–4 kg. Schwitzer and colleagues (2013c) discussed their systematics and taxonomic history.

Given their daytime activity, unique among strepsirrhines, the eyes of lemurs are smaller than those of their close relatives. They also have a more prominent muzzle than most strepsirrhines. The diets of the ring-tailed lemur, *Eulemur*, and *Varecia* consist of fruits, flowers, and some vegetation, primarily leaves. The diet of *Hapalemur* consists of bamboo shoots and reeds.

This is the most colorful of the strepsirrhine families, with pelage ranging from gray and greenish gray to brown and reds of various hues. Almost all species have a distinct ruff of fur around the neck, which differs in color from that of the main body pelage. All species possess ear tufts. Some species, such as the black lemur (*Eulemur macaco*) exhibit **sexual dichromatism**—that is, males and females have distinctly different pelage colors. All members of the family move by clinging and leaping, except ring-tailed lemurs, which extensively use quadrupedal walking and climbing. Lemurids have hind limbs that are considerably longer and more developed than the forelimbs. They use their long tails for balance during their bounding movements and as they climb among tree limbs.

Socially, lemurids are more gregarious than other strepsirrhines; the eastern lesser bamboo lemur (*H. griseus*) lives in groups of 3 to 6. Several species of *Eulemur* live in groups of 20 or more, including several adults of both sexes. Single births are most common, but twins occur occasionally. The red ruffed lemur and black-and-white ruffed lemur have litters of up to 6 young. Females nurse their young with a single pair of pectoral mammae. Female *Eulemur*, *Varecia*, and the ring-tailed lemur carry their infants on their abdomen at right angles to the main body axis, similar to the indriids. When they are somewhat older, young ride on their mother's back. Lemurid communication includes considerable scent-marking of branches and tree trunks, using urine, anal glands, and specialized sternal glands. The ring-tailed lemur possesses cutaneous arm glands, which are used to mark objects. DelBarco-Trillo and colleagues (2012) examined scent communication related to social complexity in 8 species of *Eulemur*. Lemurids also have a modest vocal repertoire and use both facial expressions and body postures for visual communication.

Human population and activities have severely impacted most lemurids—13 of the 21 species are either critically endangered (8) or endangered (5). The greater bamboo lemur, which inhabits only 1%–4% of its historical range, is critically endangered and in immediate danger of extinction. Other critically endangered lemurids are the blue-eyed black lemur (*Eulemur flavifrons*), the white-collared lemur (*E. cinereiceps*), the mongoose lemur (*E. mongoz*), the Alaotra reed lemur (*Hapalemur alaotrensis*), the golden bamboo lemur (*H. aureus*), the black-and-white ruffed lemur, and the red ruffed lemur. The 5 species of endangered lemurs are the collared brown lemur (*E. collaris*), Sanford's brown lemur (*E. sanfordi*), the crowned lemur (*E. coronatus*), the white-fronted lemur (*E. albifrons*), and the ring-tailed lemur.

INFRAORDER CHIROMYIFORMES

Daubentoniidae

The sole surviving species in this family is the endangered aye-aye (*Daubentonia madagascariensis*; Figure 15.10), endemic to Madagascar. Aye-ayes have a head and body length of about 40 cm and longer, bushy tails (ca. 60 cm). They have coarse dark brown or black fur, and the face is short and broad with a tapered muzzle. The dental formula is 1/1, 0/0, 1/0, 3/3 = 18, with enlarged, continuously growing, protruding incisors that self-sharpen like rodent incisors and are used for chewing and gnawing. Given their unusual appearance, they have a very confused taxonomic history

Aye-ayes have the largest distribution of any extant lemur and are adapted to a variety of habitats and elevations. They were introduced to Nosy Mangabe Island off the northeast coast of Madagascar in 1966 and 1967, and the population still survives there. They are generally solitary, except for mothers with young. Home ranges are approximately 5 ha (Petter 1972). Females nurse their young with a single pair of inguinal mammae. Aye-ayes are nocturnal insectivores. Their hands have long fingers, and the middle finger has a long, wire-like claw used for extracting larval insects from wood (Thompson et al. 2016) and to remove the pulp from fruits such as mangos and coconuts. Perry and colleagues (2013) analyzed population genomics of aye-ayes from northern, eastern, and western portions of their range. They found strong differentiation in the northern population, suggestive of a barrier to gene flow. At one time, aye-ayes were protected by local custom because the people believed that anyone who harmed one would die. Conversely, aye-ayes were often killed if found because they were thought to be evil and bring bad luck. The primary reason
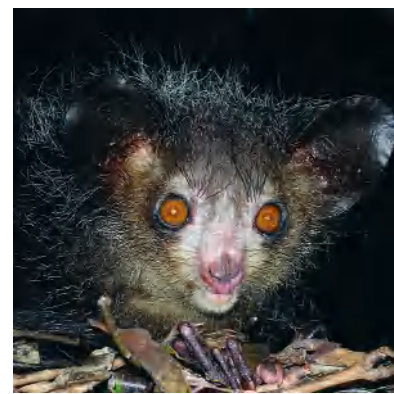
Figure 15.10 Daubentoniidae. The aye-aye (*Daubentonia madagascariensis*) uses its specially adapted middle digit to probe for insects.

for the demise of the aye-aye, however, has been destruction of its forest habitat through cutting and burning to use the land for agriculture and to plant imported tree species for managed forests. As noted, the aye-aye is endangered, and populations throughout their extensive range are low. The large aye-aye (*Daubentonia robustus*) was driven to extinction within the last 1,000 years.

INFRAORDER LORISIFORMES

Lorisidae

There are 4 genera and 12–15 species of lorises, angwantibos, and pottos (Munds et al. 2013; Burgin et al. 2018). Two subfamilies are often recognized: Perodicticinae for the pottos and angwantibos and Lorisinae for the lorises. They are distributed from sub-Saharan Africa to India, Southeast Asia, Indonesia, and the Philippines. The golden angwantibo (*Arctocebus aureus*) and the Calabar angwantibo (*A. calabarensis*) are the only species in this genus and occur in West Africa. The 2 species of slender loris—the gray slender loris (*Loris lydekkerianus*) and the red slender loris (*L. tardigradus*; Figure 15.11)—are found in southern India and Sri Lanka. The 5 species of slow lorises (Genus *Nycticebus*) live in much of Southeast Asia and on neighboring islands. Historically, a single species of potto—the West African potto (*Perodicticus potto*)—was recognized. More recent work based on molecular and morphological analyses (Munds et al. 2013; Pozzi et al. 2015) elevated two former subspecies to species status, the East African potto (*P. ibeanus*) and Milne-Edwards's potto (*P. edwardsi*). The false potto was considered a distinct genus and species (*Pseudopotto martini*) based on 2 skulls and a skeleton, but is now considered to be synonymous with *P. edwardsi*.

The smallest members of this family are the angwantibos and slender lorises, which are only 18–25 cm in head and body length and 85–500 g body weight. The slow lorises and pottos are larger, ranging from 200–400 mm in head and body length and weighing 1.0–1.4 kg. Tails are very short or absent in lorisids, except for pottos, which have a tail about 65 mm in length. All lorisids have thick, dark, woolly fur ranging from brown to gray and black with light underparts. They have relatively large eyes, with generally flattened faces, although some species have distinct muzzles that may be either pointed or short and rounded. Like that of the galagos and lemurs, the dental formula of lorisids is 2/2, 1/1, 3/3, 3/3 = 36.

Most lorisids are nocturnal, and all are arboreal. Their habitat varies, depending on the species, from bamboo and evergreen forests to tropical rainforest; some species use logged areas and shrublands. They are slow but sure climbers, using a strong grip made possible by prehensile hands and feet that have the thumb (pollex) set at nearly a 180° angle from the remaining digits; it is thus termed "pseudo-opposable." Many members of the family can climb well in a suspended position, below limbs or moving on top of

Figure 15.11 Lorisidae. The red slender loris (*Loris tardigradus*) is native to India and Sri Lanka.

them. The index finger (second digit) is reduced in most species to a tubercle (knob), and the second toe is modified as a toilet or grooming claw in lorises, slow lorises, and pottos. Lorisids are insectivorous, frugivorous, or both. Interestingly, slow lorises are one of the few groups of mammals known to use venom as part of their life history (see box) which may serve several functions (Ligabue-Braun et al. 2012; Nekaris et al. 2013).

Lorisids live alone or in pairs. They generally have single births, though twinning occurs occasionally for all but pottos. Species engage in marking behavior, using urine or anal glands. They also communicate using vocalizations and limited facial expressions. The Javan slow loris (*N. javanicus*) is critically endangered because of habitat loss and use in the pet trade; the red slender loris is endangered. Nekaris (2013) provides an excellent summary of the family.

Galagidae

As noted, the galagids were formerly a subfamily within the Lorisidae but are now considered a distinct family. The taxonomy of galagids has undergone considerable revision (Jenkins 1987; Nash et al. 1989; Groves 1989, 2001). What was 1 genus was split into 3 genera and 19 species (Groves 2005). More recently, the IUCN (2018) recognized 5 genera and 17 species, including the northern needle-clawed galago (*Euoticus pallidus*) and southern needle-clawed galago (*E. elagantulus*); 4 species of lesser galagos (Genus *Galago*); 7 species of dwarf galagos (Genus *Galagoides*); the thick-tailed galago (*Otolemur crassicaudatus*) and Garnett's greater galago (*O. garnettii*; Figure 15.12), as well as 2 spe-

Loris Venom

Although venom is a common part of the life-history strategies of many animals, very few venomous mammals are known. These include the male duck-billed platypus (*Ornithorhynchus anatinus*; see Figure 10.7), which have a spur on the ankle that is used against other males during the mating season. The European water shrew (*Neomys fodiens*) and Mediterranean water shrew (*N. anomalus*), as well as the northern short-tailed shrew (*Blarina brevicauda*) use toxins in their saliva to incapacitate or kill prey, often species larger than themselves. The Haitian solenodon (*Solenodon paradoxus*) and Cuban solenodon (*S. cubanus*) also have toxic saliva, possibly for prey capture or intraspecific interactions. The three species of vampire bats also have a toxin in their saliva to facilitate anticoagulation. The only venomous primates known are slow lorises (Genus *Nycticebus*)—five species are currently recognized and presumably all use a toxin (Nekaris et al. 2013; Rode-Margono and Nekaris 2015). When threatened, a loris raises its arms above its head and mixes saliva with the "brachial" gland fluid on the inside of the elbow. Mixing the saliva apparently activates the toxin in the brachial exudate. What happens next depends on the threat: the mixture is kept in the mouth if the loris is about to bite or spread on the top of the head as a defensive move to deter a potential predator. Besides vegetation, slow lorises consume animal prey, and the venom can be lethal. The bite is painful to humans and in rare cases can lead to death. Both field and lab observations suggest that the loris venom is an effective predator deterrent. Additionally, spreading the toxin on their fur appears to reduce both prevalence and intensity of **ectoparasite** infestation. Finally, loris toxin, like that of the platypus, may be used against conspecifics during the breeding season. Other mammalian species may also use toxins, and continued research will further elucidate the fascinating mosaic of ecological and evolutionary interactions that contribute to this life-history strategy in lorises and other mammals.

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Figure 15.12 Galagidae. Garnett's greater galago (*Otolemus garnetti*) is a fairly common species, ranging from southern Somalia to Tanzania and Kenya.

cies in the Genus *Sciurocheirus*—Allen's galago (*S. alleni*) and the Gabon squirrel galago (*S. gabonensis*). Burgin and colleagues (2018) listed 6 genera and 20 species. Masters and coworkers (2017) suggested that the Genus *Galagoides* is not monophyletic and that 5 species should be placed in their own genus (*Paragalago*). Continued research will likely lead to additional new species (Svensson et al. 2017) and taxonomic changes in this family.

All galagids live in sub-Saharan Africa; they inhabit rainforest in West Africa and woodland savanna from Senegal to East Africa down to southern Africa. Galagids are arboreal, leaping and bounding from branch to branch and between tree trunks. Two adaptations, well-developed hind limbs and a long tail used for balance, aid in arboreal locomotion. Galagos are nocturnal and have large eyes that allow them to see well at night. They range in size from the diminutive dwarf galago (*Galago demidoff*), which has a head and body length of only 12 cm, tail of 17 cm, and weighs only 60 g, to the much larger thick-tailed greater galago with a head and body length of 32 cm, tail length of 47 cm, and weight of 1.2 kg. Galagids are pentadactyl, with the second toe modified as a toilet claw. Their diet varies from primarily insectivorous to omnivorous, including fruits, grains, and even small mammals. They have soft, woolly fur, ranging in color from gray to brown and russet brown, with lighter undersides. Galagids apparently live in groups of up to 7–9 individuals. For some species, mothers and infants may nest separately. They build well-concealed nests in trees or use tree cavities. Single births or twins occur for all species studied. Mothers nurse their young with 2 to 3 pairs of mammae. Early in their infants' development, mothers carry their young by gripping them by the scruff of the neck. Galagos communicate via urine marking and vocalizations, notably the cry-like sound made by young. This characteristic gave rise to the common name "bushbabies." They also communicate visually with facial expressions and body postures. The Rhondo dwarf galago (*Galagoides rondoensis*), limited to a small area of coastal forest in Tanzania, is critically endangered.

Suborder Haplorrhini

The living primates within this suborder include 9 families (see Table 15.1), which live in Africa, Asia, and Central and South America. In addition to the previously mentioned characteristics that distinguish haplorrhines from strepsirrhines, haplorrhines have a **hemochorial placenta**, a postorbital plate, and spatulate incisors. The maximum dental formula is 2/2, 1/1, 2/2, 3/3 = 32 teeth in catarrhine (Old World primates) from Asia and Africa and 2/2, 1/1, 3/3, 3/3 = 36 teeth in those from Central and South America (New World platyrrine primates). Distinctive differences in the visual and olfactory systems of haplorrhines also separate them from strepsirrhines.

INFRAORDER TARSIIFORMES

Tarsiidae

Traditionally, all species of tarsiers were included in Genus *Tarsius* (Figure 15.13). The IUCN (2018) recognized 10 species, all within *Tarsius*. Shekelle and colleagues (2013) recognized 9 species of *Tarsius* and 2 additional genera—*Carlito syrichta* (the Philippine tarsier) and *Cephalopachus bancanus* (the Western tarsier) from Brunei, Indonesia, and Malaysia. Shekelle and coworkers (2017) named two new tarsier species from Sulawesi, Indonesia. Burgin and colleagues (2018) listed 3 genera and 13 species.

All modern tarsiers inhabit the islands of Indonesia, the Malay Archipelago, and the Philippines. Inclusion of *Tarsius* in the Haplorrhini, within their own infraorder, is based on fossil evidence, molecular data, and morphology, but the systematic position of tarsiers—often referred to as "living fossils"—among other primates remains debatable. Numerous fossil taxa have been described from Eocene, Oligocene, and Miocene deposits from Europe, North America, and Asia, and three clades of tarsiers may have split as early as the Oligocene. Ni and coworkers (2013) described one of the earliest known primate fossils (*Archicebus achilles*), which are considered the most basal tarsiiform, from an early Eocene deposit in China. Shekelle and colleagues (2013) provided an excellent summary of the fossil history of tarsiers.

Head and body length ranges from 10 to 14 cm, with tail from 20 to 26 cm, and body weight of 100–130 g. The pelage is gray to gray-brown, with the face more ochre-colored in some species. A distinct tuft of fur occurs on the distal third of the tail.

All species are crepuscular and nocturnal. They have very large eyes and a short snout (see Figure 15.13). The hind limbs, associated with their vertical clinging and leaping mode of locomotion, are considerably more developed than the forelimbs. Tarsiers bound rapidly from one tree trunk to another, sometimes jumping 2 m in one leap. They can also hop on the ground. Tarsiers inhabit primary and secondary rainforest, with some species also found in shrub

Figure 15.13 **Tarsiidae (*Tarsius* sp.).** Tarsiers have very large eyes and short snouts. They inhabit rainforests, shrub areas, and plantations, where they consume insects and some vertebrates.

habitats. They are primarily carnivores, consuming insects, lizards, and spiders.

Tarsiers are territorial, defending **core areas** within their overlapping home ranges. They spend considerable time patrolling and marking territory boundaries. Ramsier and colleagues (2012) found that the Philippine tarsier vocalized at extremely high frequencies—among the highest of any terrestrial mammal. This ultrasonic communication, from 70 to 90 kHz, may function to avoid background noise and detection by predators. Tarsiers live in pairs, although sometimes females with young are found alone. They give birth to single, precocial young, capable of movement through the trees. Youngsters ride on the mother's back and can also be carried in her mouth. The Siau Island tarsier (*Tarsius tumpara*) is critically endangered; the Peleng tarsier (*T. pelengensis*) and Sangihe tarsier (*T. sangirensis*) are listed as endangered.

INFRAORDER SIMIIFORMES

PARVORDER PLATYRRHINI

The number of families included within the platyrrhines has had a very confused taxonomic history (Groves 2005; Mittermeier et al. 2013a), ranging from inclusion of 2 to 6 families. Some authorities have placed the marmosets and tamarins (Family Callitrichidae) and the night monkeys (Family Aotidae) within the Cebidae. According to molecu-

lar phylogenies, the callitrichids clearly have a close affinity with the cebid Genera *Cebus* and *Saimiri*; however, we follow Mitteremeir and colleagues (2013a) and the IUCN (2018) in recognizing 5 families within the parvorder Platyrrhini: Family Cebidae, the squirrel monkeys and capuchins; Family Atelidae, the howler, spider, and woolly monkeys, as well as muriquis; Family Pitheciidae, the titis, uacaris, and sakis; and the callitrichids and aotids as separate families. New World (neotropical) primates diverged about 40 mya near the Eocene/Oligocene transition.

Cebidae

Until recently, cebids included 10 or 11 genera and from 67 to 77 recognized species. The family currently consists of 3 genera and from 21 species (IUCN 2017) to 29 species (Rylands and Mittermeier 2013a), including in the Subfamily Cebinae, 16 to 22 species of capuchin monkeys in the Genera *Cebus* and *Sapajus*, as well as 5 to 7 species of squirrel monkeys (Genus *Saimiri*) in the Subfamily Saimirinae. Burgin and colleagues (2018) grouped the callitrichids and aotids as cebids, and recognized 11 genera and 89 species. Rylands and Mittermeier (2013a) provided an extensive review of the systematics of cebids, as did Garbino and Martins-Junior (2018); taxonomic revisions are likely to continue.

The two subfamilies diverged about 14 to 15 mya. Capuchins live in a variety of habitats with a wide geographic distribution from Honduras to the Amazon Basin and Paraguay. Pelages are generally brown with white chest and head (Figure 15.14) and a black cap. Head and body length is 30–55 cm, with tails the same length and maximum body

Figure 15.14 **White-headed capuchin (*Cebus capucinus*).** This intelligent cebid is the "organ grinders" monkey.

Figure 15.15 **Bolivian (or Peruvian) squirrel monkey (*Saimiri boliviensis*).** They occur from Bolivia and Brazil north to Costa Rica.

weight of 5 kg. The diet is omnivorous. Capuchins live in groups of 5–40 or more individuals consisting of related females, their progeny, and several males, one of which is dominant. They have single births, and males do not participate in caring for the young. They use urine to mark territories, the boundaries of which are defended.

Squirrel monkeys (Figure 15.15) occur in tropical rainforests from Costa Rica south to central Brazil and Bolivia. The pelage is olive, yellow-orange, white, and black. The head and body is 25–35 cm in length, with tails of 35–42 cm and body weight of 750 g to 1 kg. They use their relatively long, prehensile tails for balance. Squirrel monkeys are omnivores, consuming fruits, insects, bird eggs, nuts, and small vertebrates. They live in large social groups of up to 500 individuals, splitting up into smaller groups for daily foraging. They are more vocal than other cebids, using sounds as the primary means of communication. They mark their tails and fur by rubbing them with urine. Squirrel monkeys are polygynous, and females are the only caregivers for the young. Paim and coworkers (2013) investigated distribution, diversity, and conservation of squirrel monkeys in the central Brazilian Amazon.

Four species of cebids are critically endangered: the Ecuadorian white-fronted capuchin (*Cebus aequatorialis*), the blond capuchin (*C. flavius*), the Ka'apor capuchin (*C. kaapori*), and the buff-headed capuchin (*C. xanthosternos*). Three others are endangered: the Santa Marta white-fronted capuchin (*C. malitiosus*), the varied white-fronted capuchin (*C. versicolor*), and the crested capuchin (*Sapajus robustus*).

Callitrichidae

Formerly a subfamily within the Cebidae, callitrichids encompass 6 or 7 genera and 41 to 47 species, including
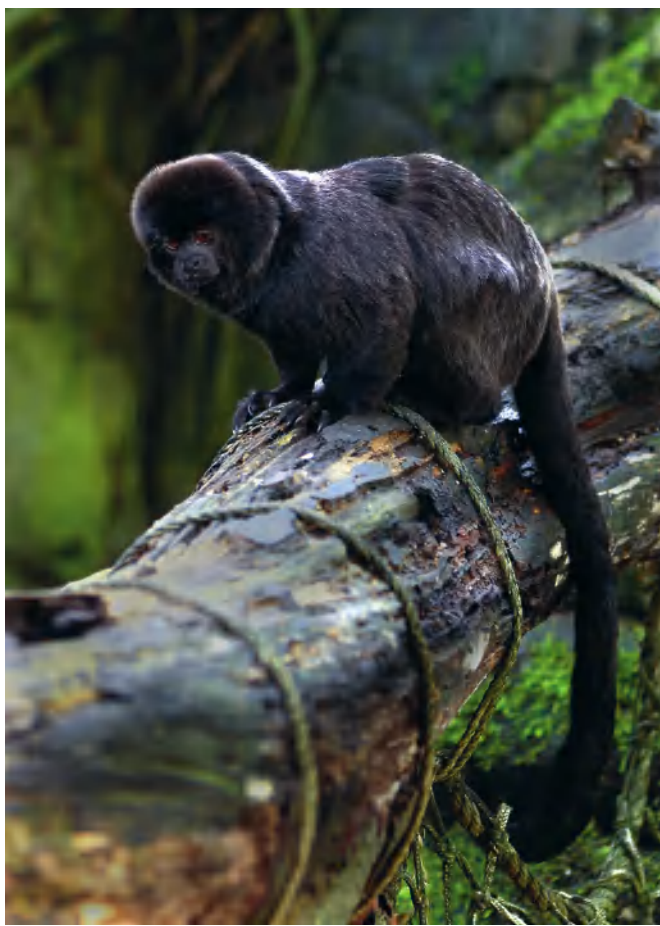
Figure 15.16 **Goeldi's monkey (*Callimico goeldii*).** This species, found in the western Amazonian basin, is named after Swiss naturalist Emil August Goeldi—as is Goeldi's spiny rat (*Proechinys goeldii*), a bird, frog, and 17 species of South American ants.

Figure 15.17 **Pygmy marmoset (*Cebuella pygmaea*)**. One of the world's smallest primates, this animal weighs only about 100 g.

Goeldi's monkey (*Callimico goeldii*; Figure 15.16), the pygmy marmoset (*Cebuella pygmaea*; Figure 15.17), other marmosets in the Genera *Callithrix* (6 species) and *Mico* (13 to 14 species), 4 species of lion tamarins (Genus *Leontopithecus*), and 15 to 20 species of tamarins (Genus *Saguinus*). Some authorities have argued for splitting *Saguinus* into two genera (small versus large tamarins) to include a new Genus *Leontocebus* (Buckner et al. 2015; Rylands et al. 2016). Rylands and Mittermeier (2013b) considered the black-crowned dwarf marmoset a separate genus (*Callibella humilis*).

The 3 genera of marmosets live in areas from mid–Central America southward to roughly the middle of South America. Marmosets are among the smallest primates, with a head and body length of 20 cm, tails somewhat shorter than the body, and body weight of <700 g—all smaller than the smallest cebid. They inhabit the upper tree canopy where they feed on fruit and small animals. They have claw-shaped nails (tegulae) on the ends of their digits. They live in family groups of 3–15 individuals, generally with a single male, several females, and the progeny. Marmosets exhibit both monogamy and polygyny. Infant care is shared among all members of the group. They scent-mark with urine around their home range. Facial expression can play a significant role in conspecific communication (Kemp and Kaplan 2013).

Tamarins live in tropical rainforests and open forests from Central America to the Amazon basin. Head and body lengths are from 18 to 30 cm, with tails 25–44 cm long, and body weight of 200–900 g. Pelage colors vary from black, white, and brown mixes to all black. Many taxa have some form of moustache around the mouth. The lower canine teeth are longer than the incisors—a feature that differentiates them from marmosets. They are omnivores, consuming plants, insects, fruits, and small invertebrates. Tamarins can live in social groups of up to 40 individuals comprised of several family units, although more often they occur in single-family units of 3–9 individuals. Tamarins are generally monogamous, occasionally polygynous. They give birth to twins, and the father is the primary caregiver.

Lion tamarins have red, gold, and yellow pelage. They are up to 30 cm head and body length and weigh up to 1 kg. They are arboreal and live in the rainforests of eastern Brazil. The diet consists primarily of insects obtained from under tree bark. They also consume small lizards and a variety of fruits. They live in small family groups, and parental care is shared.

Critically endangered callittrichids are the black-faced lion tamarin (*Leontopithecus caissara*) and the cotton-headed tamarin (*Saguinus oedipus*; Figure 15.18). Endangered species are the buffy-headed marmoset (*Callithrix flaviceps*), the golden lion tamarin (*L. rosalia*), the golden-headed lion tamarin (*L. chrysomelas*), the golden-rumped lion tamarin (*L. chrysopygus*), the Brazilian bare-faced tamarin (*Saguinus bicolor*), and the silvery-brown tamarin (*S. leucopus*).

Figure 15.18 **Cotton-headed tamarin (*Saguinus oedipus*).** These highly-social callitrichids are critically endangered because of habitat loss. Populations were greatly reduced in the 1970s, when animals were taken for medical research.

Aotidae

The night monkeys include 11 species within the Genus *Aotis*, previously considered a subfamily within the Cebidae. Night monkeys are totally arboreal and live in a variety of forest types from Panama south to northern Argentina and Paraguay. They are the only haplorrhines active primarily at night, and several individuals will sleep together in a tree during the day. Their eyes are large, capturing more light and enhancing vision; they lack color vision. Night monkeys range in size from 29 to 45 cm head and body length, with tails about the same, and weigh between 450 g and 1.3 kg. Night monkeys typically live at moderate elevations and have thicker fur than other New World monkeys. They use a great deal of vocal communication. They form pair bonds and are monogamous, living in small family groups of parents and their progeny. The diet consists primarily of fruit, but they will also eat leaves, insects, fungi, and flowers. Fernandez-Duque and colleagues (2013) reviewed the family.

Atelidae

The atelids, also a former subfamily within the Cebidae, were elevated to family status by Groves (2005). The 5 genera and 25 species include 12 species of howler monkeys (Genus *Alouatta*) in the Subfamily Alouattinae; and 7 species of spider monkeys (Genus *Ateles*), 2 species of muriquis (Genus *Brachyteles*), 4 species of woolly monkeys (Genus *Lagothrix*), and the Peruvian yellow-tailed woolly monkey (*Oreonax flavicauda*) in the Subfamily Atelinae. Rylands and Mittermeier (2013c) provided a comprehensive review of atelids. They all have prehensile tails that are longer than their bodies and serve as a fifth hand. Considered **semi-brachiators**, they swing by their arms from branch to branch and use the tail to grab tree limbs as they move through forest canopy. On the ground, they are capable of upright walking. Atelids are generally frugivores or folivores.

Howler monkeys are highly ubiquitous and inhabit the forests of Central and South America, feeding high in the canopy. They attain head and body lengths of 55–93 cm, with tails of about equal length. They can weigh up to several kilograms. They are folivores, consuming leaves and occasionally other plant parts (Espinosa-Gomez et al. 2013). Their howling behavior (Figure 15.19), facilitated by an enlarged hyoid bone, which enables the expansion of a vocal sac, is among the loudest of any land mammal. Howler monkeys live in social groups with multiple males and females. Their loud calls can function in spacing of social groups (Hopkins 2013) as well as mate defense (Holzmann et al. 2012). Ruiz-Garcia and colleagues (2017) analyzed the phylogeny of howler monkeys.

Spider monkeys occur in evergreen or deciduous dryland forests from southern Mexico to central Brazil. They have head and body length of about 60 cm, with tails of 89 cm, and body weights up to 6.5 kg. The pelage colors include gold, black, and brown. They live in groups of 15–25 individuals, but often split up into smaller subgroups for daily foraging. Spider monkeys are polygynous, and females provide most of the infant care. Ramos-Fernandez and colleagues (2013) investigated long-term site fidelity of Geoffroy's spider monkey (*Ateles geoffroyi*).

Muriquis (also called "woolly spider monkeys") live only in coastal Atlantic rainforests in southeastern Brazil. As their name implies, they are closely related to both the spider and woolly monkeys. Muriquis have a head and body length of 40–60 cm, with a longer tail, and weigh up to 12 kg, the largest of the New World monkeys. They are folivores, but they also consume some fruits and flowers. They live in groups of about 8–40 individuals, are

Figure 15.19 **Mantled howler monkey (*Alouatta palliata*).** Howler monkeys are arboreal and diurnal. They eat both fruit and leafy materials and often live in groups of up to 25 individuals.

Figure 15.20 **Brown woolly monkey (*Lagothrix lagotricha*).** Note the prehensile tail. Considered threatened, populations continue to decline because of habitat lost to agriculture.

Figure 15.21 **White-faced saki (*Pithecia pithecia*).** They inhabit forests of northeastern South America, where they brachiate to forage, but can also search for food on the ground.

polygynous, and do not defend territories. Coles and co-workers (2012) investigated the social dynamics of the endangered southern muriquis (*B. arachnoides*).

The woolly monkeys (Figure 15.20) are very similar to the spider monkeys and muriquis with respect to size, diet, and social behavior. They inhabit forested regions of the Amazon basin, the Orinoco River region, and the eastern slopes of the Andes Mountains. The pelage is pale gray and brown. They are 60–75 cm in head and body length, with slightly longer tails, and body weights up to 6 kg. They are found primarily in the canopy and eat fruits and leaves. Woolly monkeys live in social groups of up to 100 individuals, but split into smaller troops for foraging.

Many species of atelids are either endangered or critically endangered primarily due to habitat destruction as human population increases and there is greater demand for agricultural lands. Endangered species include the Yucatán black howler monkey (*Alouatta pigra*), the Maranhão red-handed howler monkey (*A. ululata*), Geoffroy's spider monkey (*Ateles geoffroyi*), the white-bellied spider monkey (*A. belzebuth*), the black-faced spider monkey (*A. chamek*), the white-cheeked spider monkey (*A. marginatus*), the southern muriquis, and the Peruvian woolly monkey (*Lagothrix cana*). Critically endangered atelids are the brown-headed spider monkey (*Ateles fusciceps*) and variegated spider monkey (*A. hybridus*), the northern muriqui (*B. hypoxanthus*), the Colombian woolly monkey (*L. lugens*), and the Peruvian yellow-tailed woolly monkey.

Pitheciidae

There are 4 genera and 43 species (IUCN 2018) or 44 species (Ferrari et al. 2013) in this family. The Subfamily Pithecinae includes 5–6 species of saki monkeys (Genus *Pithecia*), 4–5 species of bearded sakis (Genus *Chiropotes*), and 2–3 species of uacaris (Genus *Cacajao*) (see Boubli et al. 2008). The Subfamily Callicebinae contains 30–31 species of titi monkeys (Genus *Callicebus*). As with many primate families, taxonomy of pitheciids is in flux; Burgin and colleagues (2018) reported 7 genera and 58 species.

All pitheciids are highly arboreal with very little terrestrial activity (Barnett et al. 2012). Sakis (Figure 15.21) inhabit rainforests in northern and central South America. They attain a head and body length of 30–50 cm and have long bushy tails. Body weight can reach 2 kg. The pelage is brown, reddish brown, or gray. Some species lack fur on the face. Sakis are omnivores, consuming leaves, flowers, fruits, and small rodents. They use a varying series of vocal communications for contacting one another or warning of predators. They are polygynous and live in mixed-sex groups of up to 30 individuals.

The closely related bearded sakis live in northeastern South America, southward into northern Brazil. Head and body length is similar to that of sakis, with long hairy tails and body weight from 2 to 4 kg. Bearded sakis are primarily frugivores but also consume a variety of plants (Shaffer 2013). They are polygynous and live in groups of 18–20 individuals of mixed sexes.

Titi monkeys are among the most diverse primate groups. Many new species have been described in the past several decades. Using nuclear and mitochondrial loci, Byrne and colleagues (2016) identified four clades of *Callicebus*, with divergence times in the Miocene. Carneiro and colleagues (2016) and Hoyos and coworkers (2016) investigated the molecular phylogenetics of different clades of titi

monkeys. Body sizes, tail lengths, and body weights are quite diverse in this group, ranging from the tiny, 480-g Stephen Nash's titi (*Callicebus stephennashi*) to the 4.5 kg black-headed uacari (*Cacajao hosomi*). Titis inhabit forests ranging from Colombia southward through Brazil to northern Paraguay. Pelage is brown, black, or shades of reddish brown. Some species have distinct markings or stripes on the head, probably for visual communication or perhaps as camouflage from aerial predators. They also communicate vocally, defending a territory by using cries. Bezerra and colleagues (2017) reviewed vocal communication in pitheciids. Titis live in small family groups, are monogamous, and males are the primary caregivers for infants and young.

The bald-headed uacari (*C. calvus*) and black-headed uacari live only in forests of the upper Amazon Basin. They range from 40 to 45 cm in head and body length and have tails that are much shorter, ranging from 15 to 18 cm. They have long, coarse hairs on their body, and heads without fur (Figure 15.22). They occur in groups of up to

Figure 15.22 **Bald-headed uakari (*Cacajao calvus*).** This threatened pitheciid occurs in Peru and Brazil, where populations are declining.

100 individuals but are also found in smaller, family-sized groups. They subsist primarily on seeds and fruit, though take arthropods seasonally (Barnett at al. 2013), as well.

Critically endangered pitheciids include the blond titi (*Callicebus barbarabrownae*), the Caquetá titi (*C. caquetensis*), the San Martin titi (*C. oenanthe*), and the black-bearded saki (*Chiropotes satanas*). Endangered species in this family are Coimbra-Filho's titi (*Callicebus coimbrai*), the Beni titi (*C. modestus*), the Olalla Brother's titi (*C. olallae*), the white-nosed saki (*Chiropotes albinasus*), and Uta Hick's bearded saki (*C. utahickae*).

PARVORDER CATARRHINI

Cercopithecidae

Called "typical" or Old World monkeys, the 23 genera and 134 species (IUCN 2018) to 159 species (Zinner et al. 2013) of cercopithecids represent close to 33% of known extant primates. They are distributed throughout much of Africa and southern Asia, including the Malay Archipelago. Cercopithecids live as far north as northern Japan and as far south as southern Africa. Males of all genera have large canines (Figure 15.23). Old World monkeys have powerful muscles to provide good grinding action for the teeth; sexually receptive females have **perineal swelling.**

The family is divided into 2 subfamilies. The Subfamily Cercopithecinae, consists of 13 genera and about 81 species occurring predominantly in Africa, although some species occur in Asia. The Subfamily Colobinae has 10 genera and about 78 species. Analyses using mtDNA (Zhang and Ryder 1998) and a combination of molecular, fossil, and biogeographic information (Stewart and Disotell 1998) revealed that the common ancestor of colobines and cercopithecines lived in Africa. The ancestors of today's Asian colobine groups migrated from Africa during the late Pliocene or early Pleistocene epoch. At about the same time, the ancestors of the macaques also spread from Africa to Asia, where considerable diversification occurred. Genus *Macaca* is the most widespread of any nonhuman primate, extending from the Barbary macaque (*M. sylvanus*) in North Africa to the Japanese macaque in Japan (*M. fuscata*). Zinner and co-workers (2013) extensively reviewed the systematics of cercopithecids.

Cercopithecines live in a range of terrestrial habitats. The subfamily ranges in size from the small Angolan talapoin monkey (*Miopithecus talapoin*) and Gabon talapoin (*M. ogouensis*), with body weights up to 1.4 kg, to the largest members of the group, the drills and mandrills (Genus *Mandrillus*), with body weights of 12.0–25.0 kg. Sexual dimorphism is pronounced in genera such as *Mandrillus*, intermediate in others like the macaques, and essentially absent in *Miopithecus* and other genera.

Coat colors include shades of brown, gray, and red, as well as black and white. Some genera such as *Mandrillus*

and *Cercopithecus* (guenons, cercopithecus monkeys) and some macaques have brightly colored patches of skin on the nose and face, the scrotum, or the rump. They can also have browridges or other patterns of hair in the head

Figure 15.23 **Enlarged canine teeth in male cercopithecids.** (**A**) Olive baboon (*Papio anubis*); (**B**) mandrill (*Mandrillus sphinx*).

region, which accentuate facial expressions or eye movements. Cercopithecines such as baboons (Genus *Papio*) are better adapted for terrestrial locomotion because they have relatively longer front limbs and "knuckle walk" quadrupedally using their hands. Others, such as the mangabeys (Genus *Cercocebus*), which are primarily arboreal, have larger, more developed hind limbs. The guenons and mangabeys, as well as some less well-known genera such as Allen's swamp monkey (*Allenopithecus nigroviridis*) and the gray-cheeked mangabey (*Lophocebus albigena*; Figure 15.24), have a diet consisting primarily of leaves. Other genera, such as *Macaca* and *Papio*, eat more fruits and seeds and may, on occasion, catch and consume other animals.

Social organization and other traits of cercopithecine monkeys vary greatly. The various forms of social organization in this taxon reflect a combination of evolutionary selection pressures related to finding resources, such as food and shelter, and the threat of predation. Permanent large groups occur in some species; Devreese and colleagues (2013) found a stable group size was about 135 in agile mangabeys. Vocal and visual communication of cercopithecines has been the subject of considerable research (see Gustison et al. 2012; Ghazanfar and Takahashi 2014).

The second subfamily of cercopithecids, the colobines, occurs predominantly in Asia, although some, notably black colobus monkeys (Genus *Colobus*), red colobus monkeys (*Piliocolobus*; Figure 15.25), and olive colobus monkey (*Procolobus*), occur in Africa. Colobines are characterized by the absence of cheek pouches and the presence of large salivary glands and a sacculated stomach. The upper portion of the stomach has a nearly neutral pH with bacteria that aid in fermentation and breakdown of leafy vegetation.

Figure 15.24 **Grey-cheeked mangabey (*Lophocebus albigena*).** This common and widespread species is found throughout central Africa, primarily in lowland forests.

Figure 15.25 **Ashy red colobus (*Piliocolobus tephros-celes*).** This species is one of numerous endangered cercopithe-cids. Besides habitat loss, another factor is that chimpanzees prey upon the ashy red colobus.

Colobines are generally more slender than cercopithecines. Differences in dentition and the more specialized stomach are related to the diet of colobines, which for many genera consists of leafy vegetation. Not all colobines, however, are folivores. Many include fruits, seeds, flowers, and other materials in their diets (Hanya and Bernard 2012).

Colobines live in a variety of forest types, but they also occur in cultivated fields, rural and urban areas, and dry scrublands. Their coat colors are as varied as those of cercopithecines. Some of the common names for particular species exemplify the special pelage patterns that characterize many of them, including the golden snub-nosed monkey (*Rhinopithecus roxellana*), the white-rumped black leaf monkey (*Trachypithecus francoisi*), and the white-fronted sureli (*Presbytis frontata*). Most colobines are arboreal, although some, such as the northern plains gray langur (*Semnopithecus entellus*), spend most of their time on the ground. Colobines can walk bipedally along branches, supporting themselves by grasping other branches with their forelimbs, and they often leap between trees.

Colobines live in social groups ranging in size to >100. Average group size may be smallest in the Mentawi Islands sureli (*Presbytis potenziani*), with groups of only 3 to 4 individuals. These monkeys are uniquely monogamous among colobines. Most other colobines live in groups that average 10–20 individuals with 2 or more adult males and adult females with a polygynous mating system. There are 15 species of critically endangered Old World monkeys and another 35 species that are endangered (IUCN 2018).

Hylobatidae

The hylobatids include 4 genera and 18–20 species. There are 3 genera of gibbons: *Hylobates* (7 species), *Hoolock* (2 species; formerly considered Genus *Bunopithecus*; see Mootnick and Groves 2005), and *Nomascus* (7 species). The siamang (*Symphalangus syndactylus*) comprises a monotypic genus. Phylogenetic analyses of this family include those of Chan and coworkers (2010, 2013), Matsudaira and Ishida (2010), and Thinh and coworkers (2010). Chivers (2013) reviewed the systematics of hylobatids. Fan and colleagues (2017) proposed a third species of *Hoolock* from eastern Myanmar and southwest China based on morphological and genetic data, the Gaoligong (or skywalker) hoolock gibbon (*H. tianxing*).

Hylobatids inhabit evergreen rainforests and monsoon deciduous forests of Southeast Asia and portions of the Malay Archipelago. Species range from 45 to 90 cm in head and body length with body weights of 5–12 kg. Like other apes, hylobatids do not have tails. Their fur is dense and shaggy (Figure 15.26), and pelage color ranges from white and gray to red, black, and brown. Distinct facial rings often differentiate the eyes, nose, or mouth, and some have tufts on the crown of the head.

One of the most distinguishing traits of hylobatids is true brachiation with associated muscular/skeletal adaptations of the shoulder (Chivers 2013). They also climb quadrupedally and walk bipedally on branches. The arms are considerably longer than their legs. Hands are prehensile with a fully opposable thumb used to grasp branches as they brachiate. About two thirds of the diet of gibbons is fruit pulp, and much of the remainder is leaves. The diet of the siamang is about half leaves and half fruit.

Hylobatids live in family groups with a monogamous adult pair and several juveniles. A single young is produced every 2–3 years. Male siamangs provide considerable parental care. All species are highly territorial. Most hylobatids engage in daily bouts of singing, which includes duets of "great calls" involving the adult male and female (Terleph et al. 2018). These appear to serve at least two functions: (1) advertising their presence and territorial defense and (2) establishing and maintaining pair bonds. With the exception of the eastern hoolock gibbon (*H. leuconedys*), every species of hylobatid is either critically endangered (4 species) or endangered (13 species).

Figure 15.26 **White-handed gibbon (*Hylobates lar*).** Although fairly widely distributed in forested areas of Indonesia, Malaysia, Myanmar, and Thailand, white-handed gibbons are endangered because of population declines caused by habitat loss and hunting.

Hominidae

The phylogeny of hominids has been revised several times in recent decades (Fleagle 1988; Groves 1989; Groves 2005). Currently, the family consists of 4 genera and 8 extant species: two species of gorillas, the eastern gorilla (*Gorilla beringei*) and the western gorilla (*G. gorilla*); the common chimpanzee (*Pan troglodytes*) and the pygmy chimpanzee, or bonobo (*P. paniscus*); the Bornean orangutan (*Pongo pygmaeus*), the Sumatran orangutan (*P. abelii*), and the recently described Tapanuli orangutan (*P. tapanuliensis*; Nater et al. 2017); and humans (*Homo sapiens*). Prado-Martinez and colleagues (2013) conducted an extensive analysis of genetic diversity in great apes, the largest primates. Most births are single young, which have the longest developmental periods of any primate—usually 2–3 years until weaning and several more years to attain sexual maturity. All species of hominids exhibit sexual dimorphism, with males larger than females. Other than humans, all hominids are critically endangered (the 2 species of gorillas and 3 species of orangutans) or endangered (chimp and bonobo).

Orangutans (Figure 15.27A) occur in lowland and hilly tropical rainforests of Borneo and northern Sumatra. Males have head and body lengths of about 97 cm and weigh 60 to 90 kg. Females have a head and body length of 78 cm and weigh 40 to 50 kg. They are covered by coarse, sparse, long hair that varies in color from reddish to orange, chocolate, or maroon. Orangs spend most of their lives in trees, where they move by brachiation. Their diet is about 60% fruit augmented by leaves and shoots. They also consume insects, tree bark, eggs from bird nests, and small mammals. Orangs live primarily solitary lives, except for mating and mothers with infants. Males have large home ranges that overlap the ranges of as many females as possible. Although most information on tool use pertains to chimpanzees, orangutans also use sticks as tools to extract termites, ants, and bees from trees (Mulcahy and Call 2006; Williamson et al. 2013). The most common vocalization is the long call of the male, usually given early in the morning. The call may function to attract mates, signal ownership of a particular area, or simply alert other orangutans of the male's location.

The two species of chimpanzee (Figure 15.27B) live in central Africa in a variety of habitats, ranging from woodland savanna to deciduous and humid forests. Common chimpanzees have a head and body length of 77 to 92 cm for males and 70 to 85 cm for females; males weigh about 40 kg and females about 30 kg. Pygmy chimpanzees, despite their name, are only slightly smaller than common chimpanzees. Morphological and molecular data reveal that the two *Pan* species group together in a clade and that they are most closely related to Genus *Homo* (Barriel 1997; Duda and Zrzavy 2013; Perelman et al. 2013). Both species have long, coarse, sparse hair that is generally black but can turn gray in older animals. Their diet consists primarily of fruits supplemented with leaves, seeds, flowers, and several other plant foods. In addition, common chimpanzees, but not bonobos, consume meat, sometimes caught through cooperative hunting (Goodall 1986).

They live in complex communities with approximately 12–100 individuals, splitting into smaller parties of 3–6 (common chimpanzees) or 6–15 (bonobos), which frequently change composition. Chimpanzees use tools several ways, such as to obtain food and water, as they cope with seasonal changes in resources (Sanz and Morgan 2013). They use stone tools (Mercador et al. 2002), save tools for future use (Mulcahy and Call 2006), and can be selective in terms of recruiting partners when collaboration is necessary, for example, to obtain food (Melis et al. 2006). Chimpanzees communicate through a full range of vocalizations (Fedurek et al. 2013) and facial expressions, as well as demonstrative behavior, including throwing branches and rocks.

The gorillas (Figure 15.27C) are the largest primates, with males having a head and body length of 160 to 180 cm and weight of 140 to 180 kg, and females with head and body length of 140 to 155 cm and weight of 80 to 95 kg. They live in tropical rainforests in widely separated populations in East and West Africa. The relatively dense fur is black to gray-brown. Older adult males have silver hairs on

A

B

C
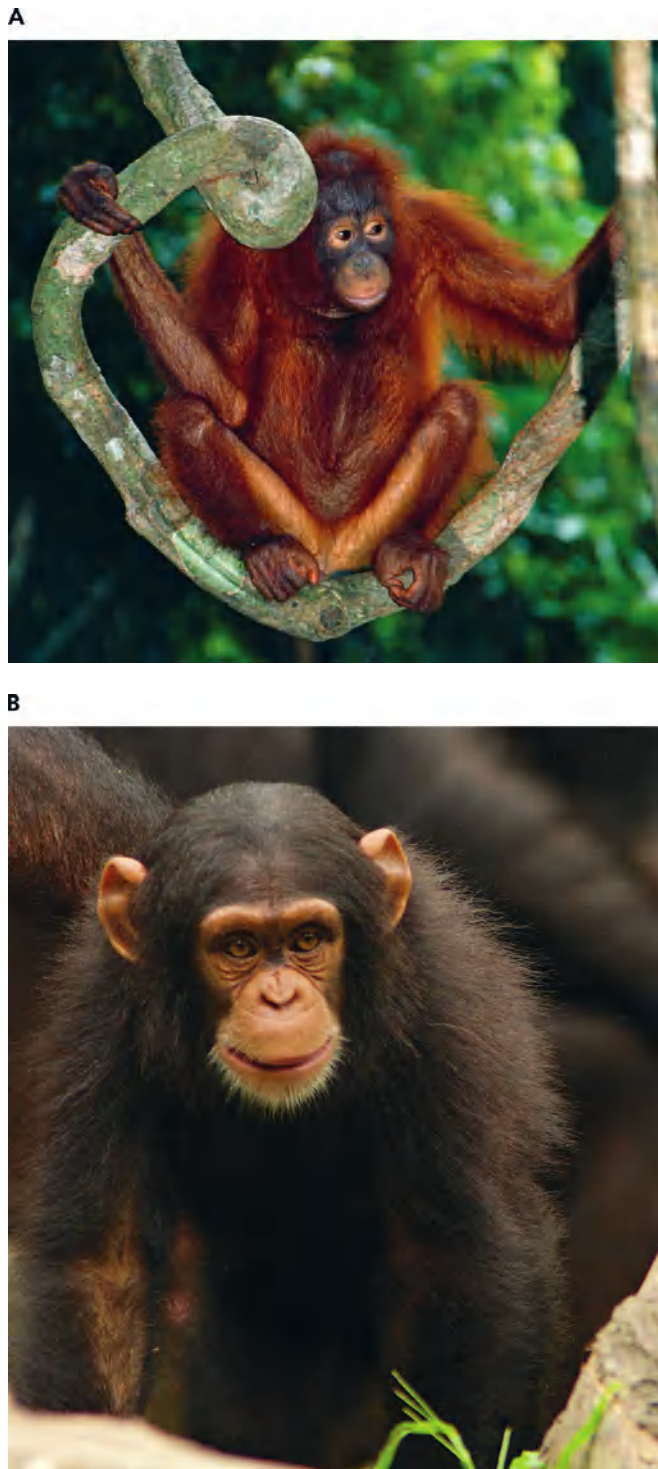
Figure 15.27 Hominidae. The great apes include (**A**) orangutans (*Pongo pygmaeus*), (**B**) common chimpanzees (*Pan troglodytes*), and (**C**) western gorillas (*Gorilla gorilla*).

their backs. The diet of gorillas in East Africa is almost entirely folivorous, consisting of leaves and stems, whereas West African gorillas eat more fruit. They live in relatively stable social groups of 5–30 individuals in East Africa, usually with 1 silver-backed male, several black-backed males, females, adolescents, and younger gorillas. Groups in West Africa are smaller, averaging about 5 individuals. Gorillas are primarily terrestrial, moving quadrupedally, often using the knuckles of the hand. They can climb trees, al-

though this activity is more prevalent in younger animals. Some gorillas nest in trees at night. Males stand bipedally to perform a chest-beating display. They communicate by facial expressions and a series of barks, grunts, and other sounds (Salmi et al. 2013). Schaller (1963) and Fossey (1983) did much of the early work on their social behavior.

Humans are characterized by erect bipedalism; reduced sexual dimorphism relative to other hominids; a large brain, averaging about 1,300 cm³, contained in a large

vaulted cranium; and a skeleton that is less robust and more gracile than those found in recent hominid ancestors. Human social organization is varied, including monogamy, polygyny, and in a few instances, polyandry. Young are born in a relatively altricial state, and there is an extended period of physical and behavioral development.

Humans evolved from an ancestral African ape stock beginning at least 7 mya (Figure 15.28). New fossil finds continually alter and refine perspectives on the evolution of human ancestors, although many of the fossils are fragmentary, and new genera and species await description. It is important to realize that the lineage from archaic to modern humans (*Homo sapiens*), as with all species, was not linear and ladder-like but contained many branches of different species that often lived simultaneously in different regions and eventually went extinct. As noted by VanSickle (2016:354), the "roadmap" of human evolution looks like "the roadways of a complex city, complete with dead ends, detours, roundabouts, and side roads representing both the fossils we know and the hominin species we haven't discovered yet." Currently, the earliest known hominin fossils are *Sahelanthropus tchadensis* from northern Chad, Africa, from the

late Miocene, approximately 7 my old (Brunet et al. 2002; Lebatard et al 2008). Another early hominin was *Orrorin tugensis* from 6-my-old deposits from East Africa (Kenya). Morphologically intermediate to Miocene apes and later *Australopithecus* (Almecija et al. 2013), *O. tugensis* was, like all early hominins, small—just over 1 m in height and perhaps 50 kg body weight—and showed the first evidence of archaic bipedalism (Galik et al. 2004; Richmond and Jungers 2008). It should be noted that there is debate as to whether or not *S. tchadensis* and *O. tugensis* are actually hominins—that is, where they fall on the ape-hominin continuum.

Ardipithecus ramidus, found in Central Ethiopia, dates to 4.5 mya or earlier. Based on postcranial bones, *Ar. ramidus* was about the size of a modern chimp and weighed approximately 50 kg. Morphology of femur and pelvis indicate adaptations toward regular bipedalism (although more primitive than later *Australopithicus*) as well as movement in trees (White et al. 2009).

Several species of *Australopithicus* lived from 4 mya up until about 1.5 mya and are known from many sites in east, central, and southern Africa. They were habitually bipedal, but may have returned to trees for sleeping, predator avoid-
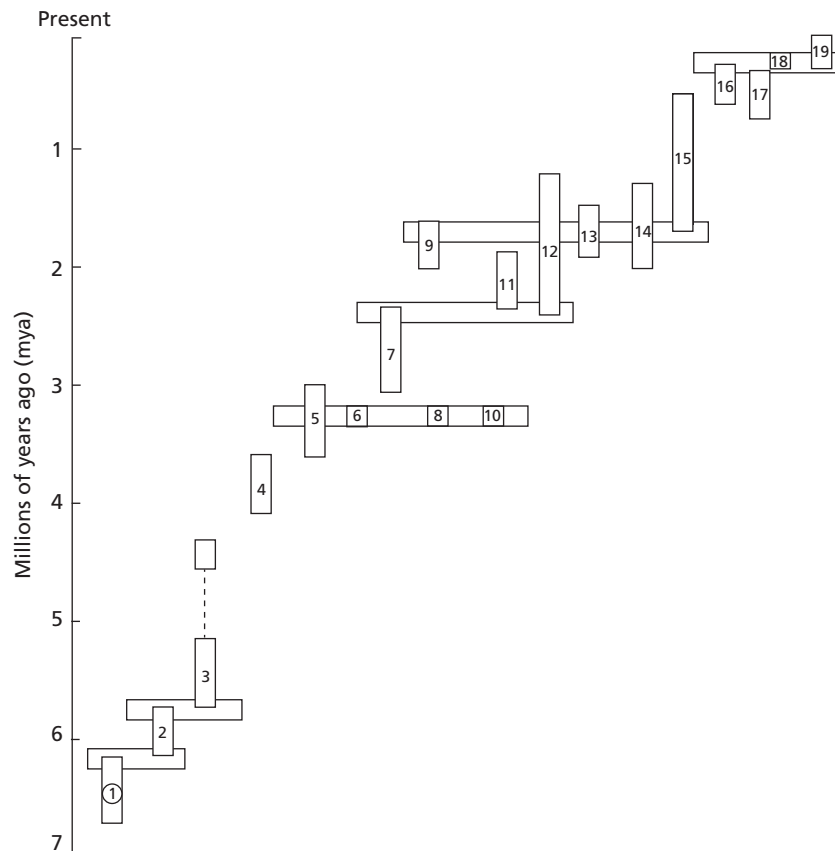
Figure 15.28 Human evolution. Numbered vertical rectangles indicate taxa and approximate temporal distribution. Horizontal rectangles include concurrent taxa. During the course of human evolution several taxa coexisted; all but one species have gone extinct during the evolution of our lineage. Numbered taxa are: 1. *Sahelanthropus tchadensis*; 2. *Orrorin tugensis*; 3. *Ardipithecus ramidus*; 4. *Australopithicus anamensis*; 5. *A. afarensis*; 6. *A. bahrelghazali*; 7. *A. africanus*; 8. *A. deyiremeda*; 9. *A. sebida*; 10. *Kenyanthropus platyops*; 11. *Paranthropus aethiopicus*; 12. *P. boisei*; 13. *P. robustus*, 14. *Homo habilis*; 15. *H. erectus*; 16. *H. neanderthalensis*; 17. *H. heidelbergensis*; 18. *H. floriensis*; 19. *H. sapiens. Modified and adapted from Haile-Selassie at al. 2016; VanSickle 2016; and others.*

ance, and feeding. The oldest described species is *A. anamensis*, which lived in east Africa about 4 mya, followed closely by *A. afarensis* 3–3.5 mya (including the most complete skeleton ever found—the famous "Lucy") and *A. bahrelghazali*. *A. africanus* lived 2 to 3 mya in southern Africa, and with its human-like hands, likely used tools (Skinner et al. 2015); this species, along with *A. sebida* (Berger 2013), which lived 1.5–2 mya, was smaller than its older relatives. The phylogenetic relationships between the archaic Genus *Australopithecus* and *Homo* remain uncertain, although most authorities believe at least one species of *Australopithecus* was ancestral to *Homo*.

Hominin diversity in the mid-Pliocene is apparent with the discovery of *Kenyanthropus platyops*, from 3.5-my-old deposits in Kenya. Contemporary with *A. africanus* and possibly a second species, *A. deyiremeda* (Spoor et al. 2010, 2016; Haile-Selassie et al. 2015, 2016), several early hominins coexisted during this period. Taxon diversity of hominins is evident from 4 mya to about 40,000 years ago (Wood and Boyle 2016), and included several species of *Paranthropus*. Considered a subgenus by some authorities, the stout *Paranthropus* includes *P. aethiopicus* from 2–2.5 mya and *P. robustus* from about 1.5 mya. *Paranthropus boisei* lived from about 1.2 to 2.5 mya and was concurrent with *A. africanus* and the later *A. sebida* Craniofacial and dental structure varied markedly among these taxa.

The oldest described species of *Homo* is *H. habilis*, from about 2 mya. This tool-user was concurrent in eastern and southern Africa with species of *Paranthropus* (which likely used crude tools as well), and possibly contemporaneous *Homo rudolfensis* in east Africa. These crude "Acheulean" mode tools were palm-sized hand axes used for rudimentary cutting and scraping. More sophisticated tools were produced by *H. erectus*, known from fossils in east Africa dating to 1.8 mya; *H. erectus* migrated out of east Africa into western Africa, Europe, and Asia. Many specimens of *H. heidel-*

bergensis, which range from 300,000 to 1 million years old and share characteristics of both *H. erectus* and early humans, have been found in European deposits. Also, by approximately 320,000 years ago, and concurrent with major shifts in environmental conditions, tool makers had transitioned to more sophisticated, smaller, more precise tools—marking the appearance of the Middle Stone Age (Brooks et al. 2018; Deino et al. 2018; Potts et al. 2018).

Homo naledi was described from South African Middle Pleistocene deposits between 236,000 and 335,000 years old. They had a mix of ancestral and derived morphological characteristics (long lower limbs, reduced sexual dimorphism seen in modern humans) but with smaller bodies and braincase (Berger et al. 2015, 2017; Dirks et al. 2017; Garvin et al. 2017; Schroeder et al. 2017), unlike contemporary large-brained *Homo*. Modern humans (*H. sapiens*) arose in east Africa about 200,000 years ago (Richter et al. 2017), and some eventually migrated to Europe and Asia, as well as Australia and eventually the Americas. All people today are descended from this migration. Bae and colleagues (2017) reviewed the dispersal routes of early modern humans out of Africa based on evidence from genetics, paleontology, and paleoclimatology. Concurrent with early *H. sapiens*, other archaic humans include the familiar Neanderthals (*H. neanderthalensis*) in Europe and western Asia from about 150,000 to 28,000 years ago. Interbreeding occurred, and data suggests we all have 1%–3% Neanderthal DNA (Fu et al. 2015; Kuhlwilm et al. 2016); admixture of another archaic group from this period, the Denisovans, is evident in modern Asians as well (Sankararaman et al. 2016; Vernot et al. 2016; Browning et al. 2018). An intriguing offshoot of *Homo* phylogeny are the "Hobbit" fossils (*H. floresiensis*) confined to Flores Island, Indonesia (Babb et al. 2012). Probably descended from *H. erectus*, these tiny individuals were 1 m tall, weighed only 25 kg, and had very small brains. They lived until 12,000 years ago.

SUMMARY

- Primates is a large order comprising 16 living families, from 52 to possibly as many as 84 genera, and from 459 to 518 species, including humans.
  - Considerable taxonomic revision of the order occurred during the past several decades, resulting in more recognized species and genera.

- Primates are largely tropical and subtropical in distribution, ranging through Africa, Madagascar, Asia, South and Central America, the Malay Archipelago, and Japan.

- Major characteristics of the group include
  - refined hands and digits with nails replacing claws,
  - binocular stereoscopic vision,

  - a complete postorbital bar or plate,
  - a reduced muzzle,
  - bunodont and brachydont cheekteeth,
  - slower rates of reproduction with increased developmental time, and
  - a progression of sociospatial systems ranging from overlapping home ranges to a diverse array of social and mating systems.

- The first primates appeared about 70 mya and are grouped together as plesiadapids.
  - Adapids probably evolved from the plesiadapids and are ancestral to modern lemurs.

○ Another fossil group, Omomyidae, is ancestral to the tarsiers.

○ *Parapithecus*, a fossil genus from Africa and Asia, is ancestral to today's cercopithecoid primates.

• The arboreal theory is the most accepted concerning the evolution of traits that characterize primates.

• Living primates are divided into the Subfamilies Strepsirrhini and Haplorrhini.

• The 7 families of strepsirrhines are characterized by a bicornuate uterus, epitheliochorial placentation, relatively small neonates, and a maximum dental formula of 2/2, 1/1, 3/3, 3/3 = 36.

○ Although the majority of strepsirrhines are concentrated on Madagascar, some groups live in Africa and Asia, including the Malay Archipelago. Many of the Madagascar species are endangered due to habitat destruction.

• The 9 families of haplorrhines are characterized by a fused simplex uterus, hemochorial placentation, neonates that are larger relative to the mother's size, differences in the rhinarium compared with stepsirrhines, and maximum dental formulae of 2/2, 1/1, 3/3, 3/3 = 36 in New World species or 2/2, 1/1, 2/2, 3/3 = 34 in Old World species.

○ Haplorrhines are distributed throughout Africa, Asia, the Malay Archipelago, and Latin America; humans are in all habitable regions.

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DISCUSSION QUESTIONS

1. What relationships would you expect between the physical size of different primates and their (a) diet, (b) habitat, and (c) social system?

2. One of the critical issues presented throughout this chapter concerns the large number of endangered or critically endangered primates. What are key human dimensions that should be considered in conservation efforts?

3. More and more, scientists are relying primarily on DNA-based molecular information for making decisions about taxonomy. This has resulted in the recognition of many more "new" species of primates. Are more traditional approaches (anatomy, behavior, morphology) to taxonomic decisions still useful, or should we rely solely on DNA-based evidence? Why?

Orders: Rodentia and Lagomorpha

This chapter includes two structurally and functionally similar orders—the Rodentia (rodents) and Lagomorpha (pikas, rabbits, and hares). All rodents have a single pair of continuously growing, chisel-like upper and lower incisors. Rabbits, hares, and pikas are characterized by a second pair of small, round peg teeth posterior to the upper incisors. The enlarged incisors in both these orders are adapted for gnawing, and both have a diastema without canines between the incisors and the cheekteeth. Given the morphology, paleontology, and molecular genetics of these two orders, they are grouped together in the clade Glires (Lacher et al. 2016). We include rodents and lagomorphs in a single chapter because of their similarities in feeding and associated structural characteristics, as well as their clear phylogenetic relationship (Carleton and Musser 2005; Asher and Helgen 2010; Meredith et al. 2011).

Rodentia

Rodents constitute the largest mammalian order. They exhibit an array of structural and functional adaptations, with 5 generally recognized suborders (Figure 16.1). The estimated number of species ranges from 2,285 (IUCN 2018) to 2,552 (Burgin et al. 2018). The number of species is difficult to pinpoint because new morphological and molecular techniques (see Chapter 2) are used to continually describe new species, uncover closely related cryptic species, or combine previously recognized species. This state of flux extends to the family level as well. Wilson and colleagues (2016, 2017) in their two superb volumes on rodents recognized 34 families, whereas Burgin and coworkers (2018) list 36. Authorities also differ as to the status of certain families relative to subfamilies. For example, the naked mole-rat (*Heterocephalus glaber*) was placed in a monotypic Family Heterocephalidae by Patterson (2016) and Burgin and colleagues (2018), but was grouped with the African mole-rats (Bathyergidae) by the IUCN (2018). The monotypic
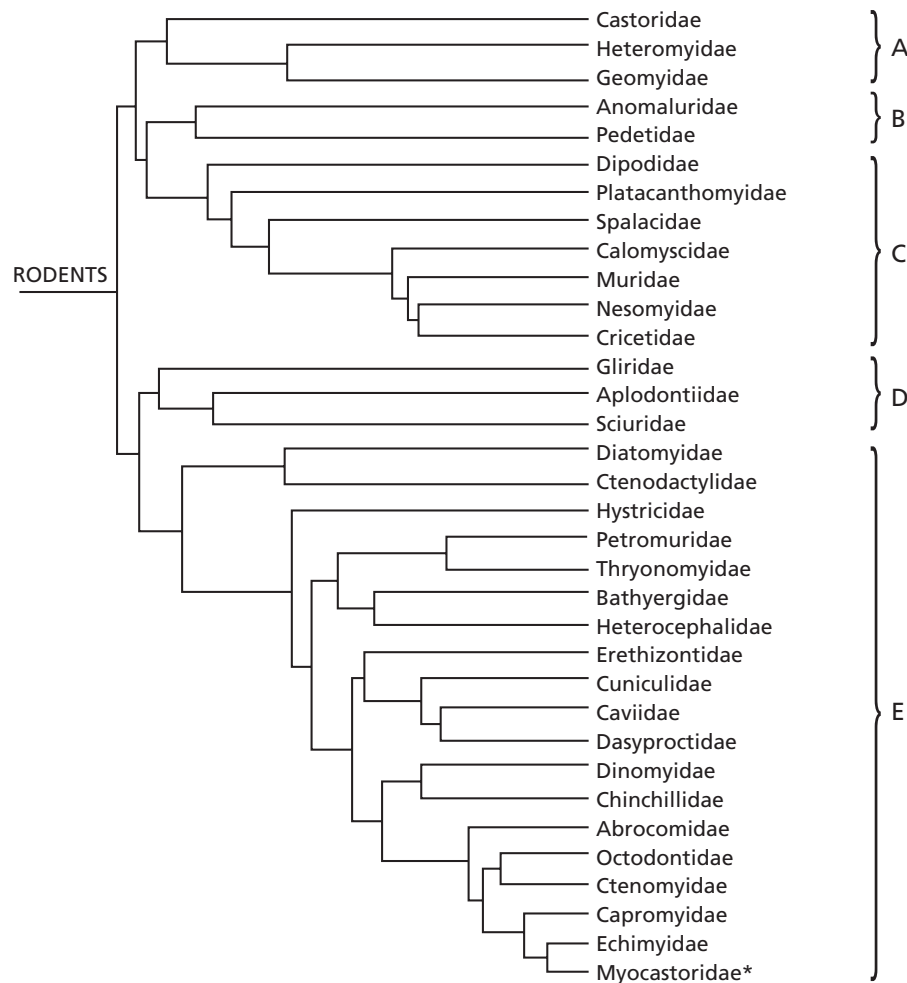
Figure 16.1 Phylogeny of rodent families and suborders. Suborders are (**A**) Castorimorpha, (**B**) Anomaluromorpha, (**C**) Myomorpha, (**D**) Sciuromorpha, and (**E**) Hystricomorpha. Given the complexity of the Order Rodentia, changes at the family level can be expected with future research and new techniques. * now included in Family Echimyidae

Family Myocastoridae (the nutria, *Myocastor coypus*) was recognized by the IUCN (2018) but not by Wilson and coworkers (2016) or Burgin and coworkers (2018). Both the IUCN (2018) and Burgin and colleagues (2018) retained the Capromyidae (hutias) as a family, whereas Wilson and colleagues (2016) did not. Given the large number of rodent species, their degree of diversity and adaptability, and convergent evolutionary trends, it is not surprising that the systematic relationships are complex and result in an array of suborders, superfamilies, and subfamilies. Regardless of taxonomic uncertainties, about 44% of living mammalian species are rodents and they have a **cosmopolitan** (worldwide) distribution. They are native everywhere except Antarctica, New Zealand, and a few oceanic islands. Rodents have adapted very successfully to a wide range of habitats and are found in all biomes, often as **commensals** with humans. They also exhibit a diverse array of locomotor adaptations, including plantigrade, cursorial, swimming, fossorial, jumping, and gliding. Most rodents are small (20–100 g), although the largest, the greater capybara (*Hydrochoerus hydrochaeris*), can reach 50 kg (Figure 16.2).

MORPHOLOGY

Despite the large number of species and their widespread distribution and diversity, rodents are surprisingly uniform in several general morphological characteristics. As noted, the diagnostic characteristic that defines all rodents is a single pair of upper and lower incisors (Figure 16.3). Their large incisors are open-rooted and ever-growing and are used for gnawing (the name *Rodentia* is derived from the Latin *rodere*, to gnaw and *dentis*, tooth). As gnawing quickly wears down the tips of the incisors, a chisel-like edge forms because the anterior side of each incisor is covered with enamel and wears more slowly than the posterior side, which lacks enamel. In many species, the mouth can close behind the incisors, and the animal can have either internal or external cheek pouches for transporting food. Rodents also have a diastema, which is a gap between the incisors and cheekteeth that allows for maximum use of the incisors in manipulating food. Canine teeth are absent, and the number of molariform teeth is reduced. Molariform dentition may or may not be ever-growing, and many

Figure 16.2 **Greater capybara (*Hydrochoerus hydro-chaeris*).** This is the largest living rodent. Native to South America, it can reach 50 kg in body weight. Formerly in its own family (Hydrochoeridae), it is now included in Family Caviidae.
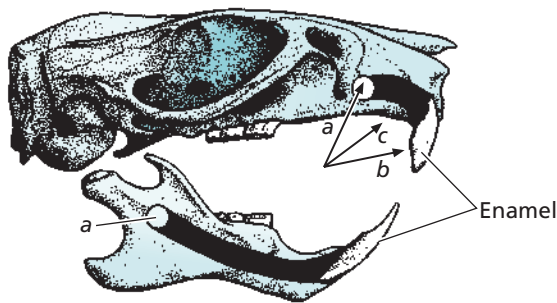
Figure 16.3 **Skull of a rodent.** Note the characteristic features of rodents, including a single pair of upper and lower incisors, which are open-rooted (*a*) and grow throughout an individual's life; the incisors' beveled edges (*b*); and the diastema (*c*) between incisors and cheekteeth. *Adapted from Lawlor (1979).*

Figure 16.4 **Rodent molariform occlusal surfaces.** Many different patterns occur in the occlusal surfaces of molariform teeth of rodents. (**A**) Ring of enamel in a mole-rat; (**B**) prismatic in murids, voles, and lemmings; (**C**) flat with lakes of dentine surrounded by enamel in Old World porcupines; (**D**) transverse ridges in a chinchilla; (**E**) cuspidate pattern in many species; (**F**) folded enamel in a murid. *Adapted from Lawlor (1979).*

different cusp patterns occur (Figure 16.4) on the occlusal (chewing) surface.

Rodents have dental formulae greatly reduced from the primitive eutherian number. A typical dental formula is 1/1, 0/0, 0/0, 3/3 = 16. Rodents never have more than two pairs of premolars, and no species has more than 22 teeth, except the silvery mole-rat (*Heliophobius argenteocinereus*), with 1/1, 0/0, 3/3, 3/3 = 28. Even then, not all the premolars are in place at the same time. Rodents generally are herbivorous or omnivorous, depending on the season and availability of food items. Coprophagy (reingestion of their own fecal pellets taken directly from the anus) has been reported in 11 families of rodents (Hirakawa 2001). Females have a duplex uterus, males have a baculum, and the testes may be scrotal only during the breeding season. The jaw musculature and skull structure associated with the dentition serve as important criteria for grouping rodents.

Mammalogists have sought consensus regarding family relationships of rodents since the 1850s. Simpson (1945:197) noted that these relationships involve "an intricate web of convergence, divergence, parallelism, and other taxonomic pitfalls." Despite the previously noted lack of consensus in rodent classification, three groupings for rodents, first suggested by Simpson (1945), have been accepted: **sciuromorph** (squirrel-shaped), **myomorph** (mouse-shaped), and **hystricomorph** (porcupine-shaped). Each group is distinguished by skull structure and jaw musculature, specifically the origin of the masseter muscles (Figure 16.5).
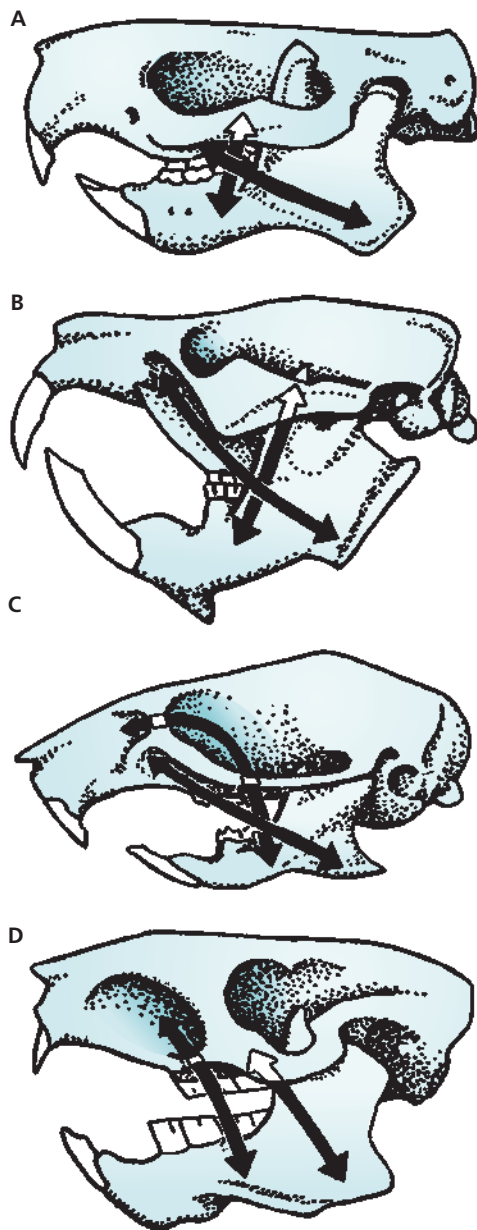
Figure 16.5 **Masseter muscle complex in rodents.**
Diagrammatic representation of the origin and insertion of the masseter muscles in (**A**) an aplodontid-like, primitive protrogomorph form with the origin of the masseter muscle entirely on the zygomatic arch and not anterior on the rostrum. (**B**) Sciuromorphs have a small infraorbital foramen through which no masseter muscles pass. Origin of the middle muscle is anterior to the eye, and the deep muscle is beneath the zygomatic arch. (**C**) A slightly larger infraorbital foramen is found in myomorphs, with the deep portion of the masseter muscle passing through it and originating on the rostrum, whereas the middle masseter is anterior to the eye, as in sciuromorphs. (**D**) In hystricomorphs, the infraorbital foramen is very large; the deep masseter muscle passes through it and attaches anterior to the eye, and the middle masseter originates on the zygomatic arch. Sciuromorpha, Myomorpha, and Hystricomorpha have traditionally been considered rodent suborders. Two additional suborders are now generally recognized: Anomaluromorpha and Castorimorpha (see Table 16.1 and Figure 16.1). *Adapted from Romer (1966).*

These three groups are considered suborders; however, not all families readily fit into one of the groups. More recent molecular genetic work has helped clarify relationships of these clades and reduce inconsistencies, and two additional suborders have emerged: the **anomaluromorphs** and the **castorimorphs** (Table 16.1; also see Figure 16.1).

Besides the characteristics of the infraorbital foramen and jaw musculature, all rodents, whether living or extinct, have one of only two types of lower jaw, depending on the insertion of the masseter muscle. They are either **sciurognathous**, with a relatively simple mandible that has insertion directly ventral to the molariform dentition, or **hystricognathous**, with a strongly deflected angular process and flange-like, or ridged, mandible for masseter insertion ventral and posterior to the teeth (Figure 16.6). Numerous studies have examined the Order Rodentia for answers to questions of monophyly, the radiation of major lineages, and relationships among families. Although these questions will certainly continue to be examined, the large amount of recent molecular and morphological research "has made the case for rodent monophyly vastly more secure" (Carleton and Musser 2005:745).

FOSSIL HISTORY

As might be anticipated from such a large group, the fossil history of rodents is complex. Modern rodents appeared early in the fossil record—all with reduced dentition, enlarged incisors, and diastema. Rodent-like reptiles with these characteristics, the **Tritylodonts** (Figure 16.7A), had developed by the late Triassic period with as many as 17 described genera, concurrent with the appearance of seed-bearing vegetation. Tritylodonts were succeeded by the multituberculates about 50 my later, in the mid-Jurassic period. These highly successful, early rodent-like mammals also had enlarged incisors, no canines, and cheekteeth with multiple cusps (Figure 16.7B). With over 200 known species, they survived for 160 my. Neither tritylodonts nor multituberculates evolved into rodents, however, although the latter were concurrent with early rodents and likely were replaced by them (Lacher et al. 2016). The oldest known members of Order Rodentia date from the late Paleocene in North America and Eurasia. They include the families Alagomyidae (possibly the most basal forms), Ischyromyidae, and Paramyidae (Figure 16.7C). The paramyids were ancestral to several rodent families, and their closest living descendant, based on jaw and muscle structure and dentition, is the mountain beaver (Aplodontiidae: *Aplodontia rufa*). Remarkable adaptive radiation of rodents occurred throughout the Cenozoic (Fabre et al. 2012), with many families established by the late Eocene or early Oligocene (Lacher et al. 2016), driven in part by their small size, short gestation, and rapid population turnover rates (Churakov et al. 2010).

Table 16.1 Currently recognized suborders and families of Order Rodentia

Taxon*	Common name(s)	Distribution§
Suborder Sciuromorpha		
Aplodontiidae (1, 1)	Mountain beaver	Nea
Sciuridae (60–62, 292–298)	Squirrels	Nea, Neo, Pal, Eth, Ori
Gliridae (9, 28–29)	Dormice	Pal, Eth, Ori
Suborder Castorimorpha		
Castoridae (1, 2)	Beavers	Nea, Pal
Heteromyidae (5, 66)	Kangaroo rats and mice; pocket mice	Nea, Neo
Geomyidae (7, 41)	Pocket gophers	Nea, Neo
Suborder Anomaluromorpha		
Anomaluridae (2–3, 6–7)	Scaly-tailed flying squirrels	Eth
Pedetidae (1, 2)	Springhares	Eth
Suborder Hystricomorpha		
Infraorder Ctenodactylomorphi		
Ctenodactylidae (4, 5)	Gundis	Eth
Diatomyidae (1, 1)	Laotian rock rat	Ori
Infraorder Hystricognathi		
Hystricidae (3, 11)	Old World porcupines	Eth, Pal, Ori
Thryonomyidae (1, 2)	Cane rats	Eth
Petromuridae (1, 1)	Dassie rat	Eth
Heterocephalide (1, 1)†	Naked mole-rat	Eth
Bathyergidae (5, 16–21)	Mole-rats	Eth
Erethizontidae (3, 17)	New World porcupines	Nea, Neo
Cuniculidae (1, 2)	Pacas	Neo
Caviidae (6, 20–21)	Guinea pigs, cavies, Patagonian hares	Neo
Dasyproctidae (2, 15)	Agoutis, acouchis	Neo
Chinchillidae (3, 6–7)	Viscachas, chinchillas	Neo
Dinomyidae (1, 1)	Pacarana	Neo
Abrocomidae (2, 10)	Chinchilla rats, Inca rats	Neo
Ctenomyidae (1, 69)	Tuco-tucos	Neo
Octodontidae (8, 14)	Degus, rock rats, viscacha rats	Neo
Echimyidae (25–27, 93–99)	Spiny rats	Neo
Suborder Myomorpha		
Superfamily Dipodoidea		
Sminthidae (1, 14)‡	Birch mice	Pal
Zapodidae (3, 5–12)	Jumping mice	Nea, Pal
Dipodidae (12–13, 33–37)	Jerboas	Eth, Pal
Superfamily Muroidea		
Platacanthomyidae (2, 2–5)	Tree mice	Pal, Ori
Spalacidae (7, 26–28)	Bamboo rats, zokors, blind mole-rats	Pal, Eth, Ori
Calomyscidae (1, 8)	Brush-tailed mice	Pal
Nesomyidae (21, 67–68)	Pouched rats and mice, climbing rats and mice, tufted-tailed rats	Eth
Cricetidae (144–145, 748–792)	New World rats and mice	Nea, Neo
Muridae (157–159, 834)	Old World rats and mice	Worldwide

Adapted from Lacher et al. (2016) and Burgin et al. (2018). Note that the IUCN (2018) often recognizes fewer taxa, and other authorities may vary somewhat in the number of genera and species for several families.

*Approximate number or range of genera and species in parentheses.
§Faunal regions: Nea = Nearctic; Neo = Neotropical; Pal = Palearctic; Eth = Ethiopian; Ori = Oriental.
†Split from Bathyergidae. Recognized by Lacher et al. (2016) and Burgin et al. (2018). Merged with Batyergidae by IUCN (2018).
‡Formerly called Sicistidae. Merged with Dipodidae by IUCN (2018).

ECONOMICS AND CONSERVATION

Rodents had and continue to have both positive and negative effects on humans. Several species are of economic importance as food for humans, and the fur of other rodents is valuable in the garment industry. North American rodents important as furbearers include the muskrat (*Ondatra zibethicus*) and beaver (*Castor canadensis*), as well as the introduced nutria or coypu (Baker and Hill 2003; Bounds et al. 2003; Erb and Perry 2003). The South American chinchilla (*Chinchilla lanigera*) is another important furbearer, with countless individuals bred in captivity
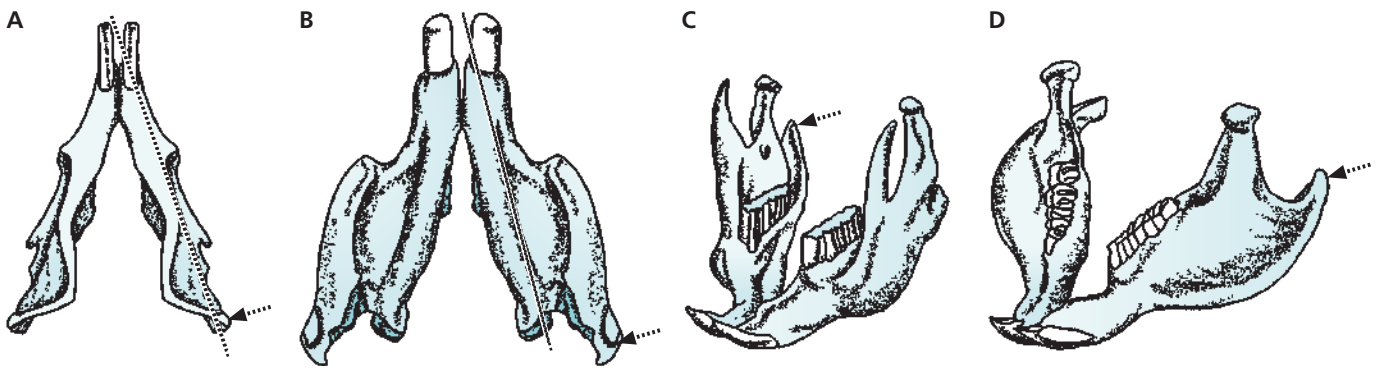
Figure 16.6 Sciurognath versus hystricognath lower jaws. Ventral view of the mandible of (**A**) a sciurognathus rodent and (**B**) a hystricognathus rodent showing the relationship of the very long incisors (*dotted lines*) to the angular process (*arrows*). (**C**) In the dorsolateral view of the sciurognath, note the large coronoid process and surface directly below teeth for insertion of the masseter muscles. (**D**) In the hystricognath, the coronoid process is greatly reduced, and insertion of the masseter is on the large, bony flange of the angular process. *Adapted from Savage and Long (1986).*
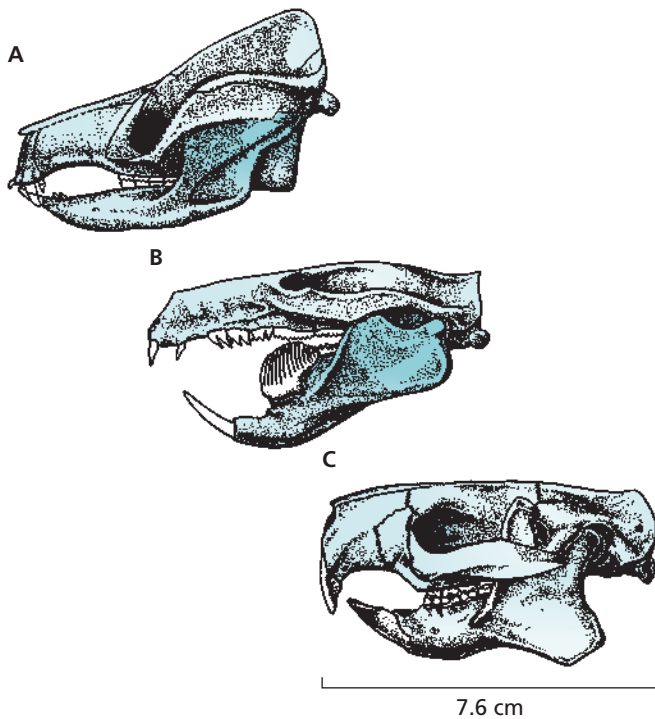
Figure 16.7 Rodent-like fossils. A mammal-like reptile (**A**) *Oligokyphus* (actual length about 7.6 cm), from the Jurassic period, with a diastema and enlarged incisors. These characteristics are also evident in a multituberculate mammal (**B**) *Ptilodus* (7.6 cm in length) from the Paleocene epoch. Compare with (**C**) *Paramys* (7.6 cm in length), from the oldest known rodent family, the Paramyidae. *Adapted from Romer (1966).*

tem engineers that impact landscapes far out of proportion to their population densities. Today, rodent populations are important for scientific purposes as well. Much of the work in population dynamics, animal behavior, physiology, and psychology has relied heavily on rodents as experimental animals. Researchers often use them in field or laboratory studies because of their rapid turnover rates, short gestation periods, large litter sizes, rapid sexual maturity, and easy handling. Many species of voles (Genus *Microtus*) or lemmings (Genus *Lemmus*) show predictable, three- to four-year population cycles throughout large geographic areas. Factors that cause these cycles, and how they operate, are still being studied to determine how biotic and abiotic factors interact to affect population dynamics. Rodents such as guinea pigs (Genus *Cavia*), the house mouse (*Mus musculus*), and the brown rat (*Rattus norvegicus*) are important research animals in biological laboratories throughout the world.

On the negative side, numerous rodent species worldwide severely damage crops and grain stores. Rodents consume an average $30 billion worth of cash crops and cereal grains each year. Historically, rodents, specifically European rats (*Rattus* spp.), were vectors for epidemics of bubonic plague that ravaged human populations periodically throughout the late Middle Ages, killing millions of people. Bubonic plague remains a problem throughout many less-developed areas of the world. Rodents are vectors or reservoir hosts for a variety of other viral, bacterial, fungal, and protozoan infectious diseases, including murine typhus, leptospirosis, listerosis, rickettsial diseases, rabies, Lassa fever, Q fever, histoplasmosis, Lyme disease, and hantaviruses (see Chapter 27). Nonetheless, in the Hindu Karni Mata Temple in India, as many as 25,000 black rats (*R. rattus*) are considered to be holy and are venerated and cared for.

throughout the world. Ecologically, rodents are the primary prey for numerous avian and terrestrial predators in a variety of habitats around the world. Without them, all trophic food webs would be dramatically altered. Additionally, beavers and prairie dogs (Genus *Cynomys*) are ecosys-

SUBORDER SCIUROMORPHA

The three families (Aplodontiidae, Sciuridae, and Gliridae) in this suborder have a small infraorbital foramen with no passage of any part of the masseter muscle through it. They are generally considered to represent a basal position in rodent evolution. The sciurids and glirids are very closely related (Montgelard et al. 2008 and references therein).

Aplodontiidae

This is a monotypic family of one extant genus and species. The mountain beaver (also called a "boomer" or "sewellel") is endemic to the Pacific Northwest from British Columbia to northern California. The species is of special interest because it is the most primitive living rodent. Mountain beavers (which are not limited to mountains and definitely are not beavers) occur in humid forested areas with a dense understory associated with heavy rainfall. They are restricted to wet areas, usually at lower elevations, in part because their primitive kidneys cannot produce concentrated urine, and they need to drink large amounts of water. Although *Aplodontia* is considered here as a sciuromorph, the masseter muscles originate entirely on the zygomatic arch (see Figure 16.5A); as such, mountain beavers can be considered the only living "protrogomorph" rodent (Wood 1965) and do not generate as great a bite force as sciurids (Druzinsky 2010) or most other rodents. They are stocky, have a very short external tail (<50 mm), and weigh up to 1.5 kg. Females are about 10% smaller than males. Pelage is dark brown with a slightly lighter belly. The pinnae are small with a white spot at the base. There are numerous long vibrissae on the snout. The dorsoventrally flattened skull is distinctive, appearing triangular from above, with flask-shaped auditory bullae and cheekteeth that have unique projections (Figure 16.8). Projections of cheekteeth in the mandible point inward (lingual),
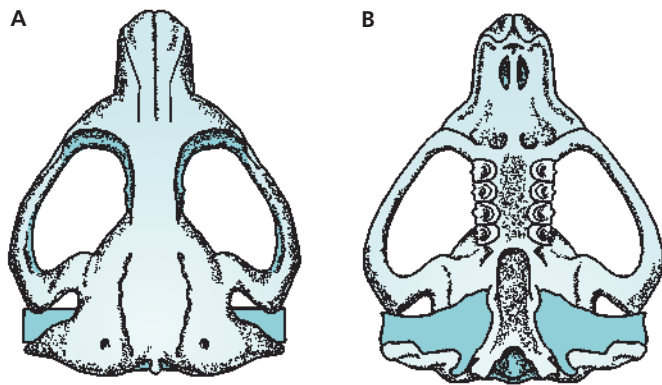
whereas those on the maxilla are buccal (outward toward the cheek). Incisors and cheekteeth are open-rooted and grow continuously. The dental formula is 1/1, 0/0, 2/1, 3/3 = 22. Mountain beavers are found in small colonies but are not particularly social. They burrow extensively, often near streams or in moist ground. Burrows can be fairly complex and can extend for 300 m. Mountain beavers are primarily folivorous and can climb as part of their foraging; ferns are a preferred food. Piaggio and colleagues (2013) discussed molecular phylogeny of the mountain beaver and the 7 recognized subspecies. Mountain beavers can cause severe problems by damaging or consuming seedlings planted as part of forest regeneration programs (Feldhamer et al. 2003a). Fossil aplodontids date to the Eocene. They were very diverse with >100 species in the Oligocene, but then declined in the Miocene (Hopkins 2007, 2016; Maridet et al. 2017).

Sciuridae

The squirrels are a large and diverse family with 60 to 62 genera, and close to 300 species distributed worldwide except for Australia, Madagascar, southern South America, and some desert regions. Koprowski and colleagues (2016) provided a thorough overview of the systematics, life history, and diversification of sciurids. Traditionally, this family was divided into 2 subfamilies that reflected the diversity of habitats and behavioral characteristics of this large family: the tree squirrels and ground squirrels (Sciurinae) and the "flying" (gliding) squirrels (Petauristinae). However, based on molecular studies, Thorington and Hoffmann (2005) recognized 5 subfamilies. The validity of these subfamilies has been reinforced with both morphological and molecular data. The Subfamily Sciurillinae includes a single living species—the neotropical pygmy squirrel (*Sciurillus pusillus*). This small, vocal, highly arboreal squirrel is distributed in northern South America. In contrast to this small squirrel are the 4 extant species of giant tree squirrels (Genus *Ratufa*; Figure 16.9) that comprise the Subfamily Ratufinae. They occur throughout Southeast Asia, India, and Sri Lanka in closed canopy forests. These 2 suborders represent older lineages that diverged prior to the remaining 3 subfamilies, which have numerous genera and species. The Subfamily Callosciurinae includes approximately 14 genera and 67 species of tree and striped squirrels found throughout Southeast Asia. This diverse group has both terrestrial and arboreal members. There are about 20 genera and 89 species of tree and flying squirrels in the Subfamily Sciurinae. They are widely distributed in North and South America, Northern Eurasia, and Southeast Asia. The final subfamily is the Xerinae, which includes 24 genera and 131 species of ground squirrels in North America, Africa, and Eurasia.

Tree squirrels, including the well-known gray squirrel (*Sciurus carolinensis*) and the fox squirrel (*S. niger*), den in tree cavities or build nests among tree limbs. They gener-

Figure 16.8 **Mountain beaver skull.** (**A**) Dorsal and (**B**) ventral views of a mountain beaver skull showing the triangular skull shape, flask-shaped auditory bullae (*shaded*), and labial projections on upper cheekteeth. Lingual projections occur on the lower cheekteeth. *Adapted from Lawlor (1979).*

Figure 16.9 **Malabar giant squirrel (*Ratufa indica*).** The four species of giant squirrels in this genus occur in India and Southeast Asia.

Figure 16.10 **Yellow-bellied marmot (*Marmota flaviventris*).** An unusual pose atop Mt. Dana, Yosemite, California. There are 14 species of marmots worldwide.

Figure 16.11 **Gliding adaptations.** The patagium and flattened tail, essential for maneuverability and extending time in the air, are clearly seen in this ventral view of a southern flying squirrel (*Glaucomys volans*).

ally are diurnal and arboreal. In boreal and cool temperate areas, most species hibernate. Ground squirrels and marmots (Figure 16.10) are terrestrial and burrow, and many species both hibernate and estivate. Helgen and colleagues (2009) revised the ground squirrel Genus *Spermophilus*, with about 38 species throughout Eurasia and North America. Based on morphological and genetic characters, they recognized 7 former genera as best representing the taxonomy, ecomorphology, and biogeography of North American ground squirrels.

Approximately 50 species of flying squirrels (Subfamily Sciurinae) occur in both the Eastern and Western Hemispheres. They are distinguished by a furred patagium between the front and hind limbs, which in some species also includes the neck and tail. The patagium increases the surface area for extended gliding locomotion (Figure 16.11) and enhances maneuverability. Members of the Asian Genus *Petaurista*, for example, glide for distances up to 450 m and can turn 90° in midair. In North America, the best-known flying squirrels are in the Genus *Glaucomys*. The scaly-tailed flying squirrels (Family Anomaluridae in this chapter) have filled the gliding niche in Africa. In Australia, several species of marsupial phalangers (Family Phalangeridae) are also gliders. These cases of similar morphological adaptations and behaviors in similar habitats are good examples of evolutionary convergence.

Sciurids can be serious crop pests in many agricultural areas throughout the world. In North America, the conservation and management of the 5 species of prairie dogs—all of which have declining populations—often are controversial and present challenges for resource agencies (Hoogland 2003). Worldwide, 3 species of sciurids are critically endangered, and another 12 species are endangered (IUCN 2018)—although data are lacking on many other species. The oldest fossil squirrel, *Hesperopetes thoringtoni*,

dates from the late Eocene. Other early fossil sciurids include *Protosciurus* from the Oligocene, and *Miosciurus* from the early Miocene.

Gliridae

This family (formerly called Myoxidae) includes 9 genera and 28 to 29 species of dormice within 3 subfamilies. The Subfamily Graphiurinae includes 15 species of African dormice, all in the Genus *Graphinus*. There are 6 genera and 12 species of Palearctic dormice in the Subfamily Leithiinae. The Subfamily Glirinae includes only the fat dormouse (*Glis glis*)—the largest member of the family at up to 200 g body weight—and the Japanese dormouse (*Glirulus japonicus*), one of the smallest glirids with a body weight <45 g. Nunome and colleagues (2007) examined phylogenetic relationships among the glirids, as have others (Fabre et al. 2015; Moska et al. 2018). Dormice occur in Europe and eastward to central and southern Asia, in Africa, and in southern Japan. They were accidentally introduced into England in the early 1900s. They are small to medium in size, with head and body length 60–190 mm and tail length 40–165 mm. They are nocturnal, semiarboreal, and occupy forests, shrublands, residential areas, and rocky outcrops, where they forage for mast (nuts), fruits, spiders, and insects. Glirids have a simple stomach without a cecum, suggesting a diet low in cellulose. Species may nest in tree cavities, attics, or burrows. Several species nest communally (Vinals et al. 2017). Dormice put on weight in the fall and enter extended periods of hibernation (up to 7 months) or dormancy until spring. Fat dormice may not reproduce in years with poor mast crops and reduced resources (Bieber et al. 2017; Langer et al. 2018). Many species are associated with residential areas, where they can become pests in gardens, orchards, or houses. In Europe the fat, or edible, dormouse (Figure 16.12) has been considered a delicacy since ancient Roman times. It is still trapped for its fat and for use as food. Glirids are an ancient lineage, with a fossil record dating from the early Eocene (Holden-Musser et al. 2016).

SUBORDER CASTORIMORPHA

The three families (Castoridae, Heteromyidae, and Geomyidae) in this suborder have few morphological similarities, but this grouping is supported by molecular data.

Castoridae

This family contains only 2 extant species, both restricted to the Northern Hemisphere. The Canadian beaver (*Castor canadensis*) occurs in Alaska, Canada, and throughout much of the United States, and the European beaver (*C. fiber*) occurs throughout northern Eurasia. The

Figure 16.12 Fat dormouse. Also called the "edible dormouse," *Glis glis* can weigh up to 200 g. It is still trapped in parts of Europe and eaten as a delicacy.

family name comes from the two pairs of castor glands and a pair of anal glands in both males and females. These glands produce material with strong pheromones and is deposited on logs and mud piles to demarcate territories. Beavers mate only once a year in the winter. Gestation is about 3.5 months. Litter size is usually 2 to 4, with young born in the spring. Beavers are generally considered to be monogamous; however, Crawford and coworkers (2008) found multiple paternity in 5 of 9 litters they examined.

The two species are morphologically very similar and well adapted to aquatic habitats. They are large, with head and body length up to 0.9 m and maximum weight of 40 kg. With long, heavy guard hairs overlaying fine, insulating underfur, both body size and pelage enhance their heat retention capabilities to allow prolonged periods in icy water. The familiar spatulate (flattened) tail is used in swimming, construction of dams and lodges, and behaviors such as tail slapping to warn other beavers of perceived danger. Additional aquatic adaptations include a **nictating membrane** (a thin membrane that can be drawn over the eyeball), valvular nostrils and ears that close while under water, and fully webbed hind feet. Mott and colleagues (2011), who recorded within-lodge behavior of *C. canadensis*, found that beavers spent 95% of their time in lodges feeding, sleeping, or grooming. They do not hibernate during winter, however. Graf and coworkers (2018) found that European beavers in southeast Norway spent only 2.8% of their active time diving. Dives were shallow (<1 m) and of short duration (<30 sec). Beavers cut (Figure 16.13) and feed on a variety of trees. They eat the cambium, bark, leaves, and roots and store sections of trees and twigs underwater for food during the winter. Beavers can swim partially underwater with their mouths open, carrying cut branches, without water entering the lungs. They breathe through the nose, not the mouth. The epiglottis is above the soft palate, so as they breathe, air moves through the nostrils to the trachea and lungs. Also, the posterior part of the tongue is convex and blocks the pharynx, except when the animal swallows (Coles 1970).

Beavers have a tremendous influence on ecosystem structure and function through construction of dams (Figure 16.14), and they also have positive and negative economic effects (Baker and Hill 2003; Busher 2016). Dams are often very large and complex and can reach 600 m in length, although 25 m is about average. The depth and width of a watercourse influences dam-building behavior (Hartman and Tornlov 2006). Beavers impound large areas, creating ponds of still, often deep water. These ponds deter terrestrial predators from reaching the lodge and make it easier for the beavers to float food and building material to the lodge.

Figure 16.13 **Beaver tree-cutting.** Beavers are ecosystem engineers and impact habitats more than any animal other than humans.

In the early 1800s, the quest for beaver pelts for the European market was a prime motivating factor in the early exploration of western North America by trappers. Beaver populations were overexploited and extirpated throughout most of their range. European beavers were also reduced throughout their range. Although populations have recovered, genetic diversity remains low (Horn et al. 2014). Many current populations are the result of reintroductions to a former range. Canadian beavers have been introduced to southern South America (Anderson et al. 2009) as well as several European countries (Dewas et al. 2012), often with negative results for native fauna.

The fossil record of castorids dates to the Eocene, and possibly to the Paleocene. Numerous fossils are known from North America, Europe, and Asia. Fossils have been grouped into four subfamilies based on cranial and dental characteristics: Agnotocastorinae, Paleocastorinae, Castoroidinae (which includes the giant beavers, Genus *Trogontherium*, in Europe, and the North American Genus *Casteroides*), and Castorinae. The latter subfamily led to modern beavers, with *Castor* appearing about 8 mya (Busher 2016).

Heteromyidae

The kangaroo rats, kangaroo mice, and pocket mice include 66 species in 5 genera. Phylogenetically, they are closely related to the geomyids (pocket gophers). Three subfamilies are traditionally recognized (Patton 2005; D. Hafner 2016): Heteromyinae (16 species of spiny pocket mice Genus *Heteromys*, which includes the subsumed

Figure 16.14 **Dam-building by beavers.** Dams across small creeks in Lamoille Canyon, Nevada.

Genus *Liomys*); Perognathinae (9 species of silky pocket mice Genus *Perognathus* and about 18 species of coarse-haired pocket mice Genus *Chaetodipus*); and Dipodomyinae (2 species of kangaroo mice Genus *Microdipodops* and about 19 species of kangaroo rats Genus *Dipodomys*). Heteromyids are distributed from southwestern Canada through the western United States and Central America to northwestern South America. Kangaroo rats and kangaroo mice take their name from their superficial similarity to marsupial kangaroos (Figure 16.15A). Pocket mice and spiny pocket mice are most often quadrupedal. The forefeet of heteromyids are small, whereas the longer, stronger hindlimbs allow for rapid, erratic, bipedal hopping. Body sizes of most heteromyids—including *Microdipodops*, *Perognathus*, *Chaetodipus*, and *Heteromys*—are small (<30 g). Kangaroo rats are larger, with body weights generally from 50 to 75 g, although the desert (*D. deserti*), banner-tailed (*D. spectabilis*), and Nelson's (*D. nelsoni*) kangaroo-rats can all reach >100 g body weight. The largest is the giant kangaroo rat (*D. ingens*), with maximum male body weight of 195 g. Like the pocket gophers, all

A

B

C

Figure 16.15 **Kangaroo rat.** (**A**) Long, tufted tail, elongated hind limbs, and kangaroo-like bipedal body shape of Merriam's kangaroo rat (*Dipodomys merriami*); (**B**) lateral view of the cranium of *Dipodomys* showing the thread-like zygomatic arch and infraorbital foramen that pierces the rostrum (*arrow*); (**C**) dorsal view showing very large, inflated auditory bullae (*shaded*).

heteromyids have externally opening, furred cheek pouches, which they use to carry seeds back to their burrows for long-term storage. They may consume more perishable food items as they forage.

Heteromyid skulls are often quite distinctive. A characteristic feature of the family is that the infraorbital foramen pierces the **rostrum** (the anterior region of the cranium—Figure 16.15B), and several genera have greatly inflated auditory bullae (Figure 16.15C). Large auditory bullae increase auditory acuity, which is of value in detecting potential nocturnal predators. They also aid in maintaining balance while kangaroo rats and mice hop to elude those predators. Their long tail aids in balance and allows them to change direction in mid-air. Kangaroo rats also avoid predators by foraging less on bright moonlit nights during summer; pocket mice and kangaroo mice do not reduce foraging on moonlit nights, however (Upham and Hafner 2013).

Heteromyids are often found in arid regions in the western United States; they are the rodents best adapted to dry, desert conditions. Kangaroo rats and pocket mice can exist for prolonged periods without free water. They survive on the moisture in food (mostly seeds) as well as metabolic water production. They also conserve water by producing highly concentrated urine, being nocturnal, and remaining inactive in relatively humid, cooler burrows throughout the day. Spiny pocket mice occur in wetter, tropical habitats of Central and South America. The San Quintin kangaroo rat (*D. gravipes*) from northwest Baja California is considered critically endangered. It has not been found since 1986 and likely is extinct. Also, the San Jose Island kangaroo rat (*Heteromys insularis*) is critically endangered. Several other species of heteromyids are endangered: the Jaliscan spiny pocket mouse (*H. spectabilis*), Nelson's pocket mouse (*H. nelsoni*), the giant kangaroo rat (*D. ingens*—see Blackhawk et al. 2016), and Stephen's kangaroo rat (*D. stephensi*).

The earliest known fossil heteromyid is *Proheteromys*, from the Oligocene to the mid-Miocene of North America. From the late Miocene until the early Pliocene there were about nine extinct genera of heteromyids with many described species; *Prodipodomys* lasted until the early Pleistocene. D. Hafner (2016) provided an excellent review of molecular phylogenetic studies of heteromyids as well as all aspects of their natural history.

Geomyidae

The 7 genera and approximately 41 species of pocket gophers are restricted to the Western Hemisphere from southern Canada through Mexico to extreme northern Colombia. There is 1 subfamily (Geomyinae) with 2 tribes: the Thomomyini encompasses 12 species of smooth-toothed pocket gophers in the Genus *Thomomys*; the Geomyini include 6 genera and 29 species of groove-toothed pocket gophers. Spradling and colleagues (2016) provided
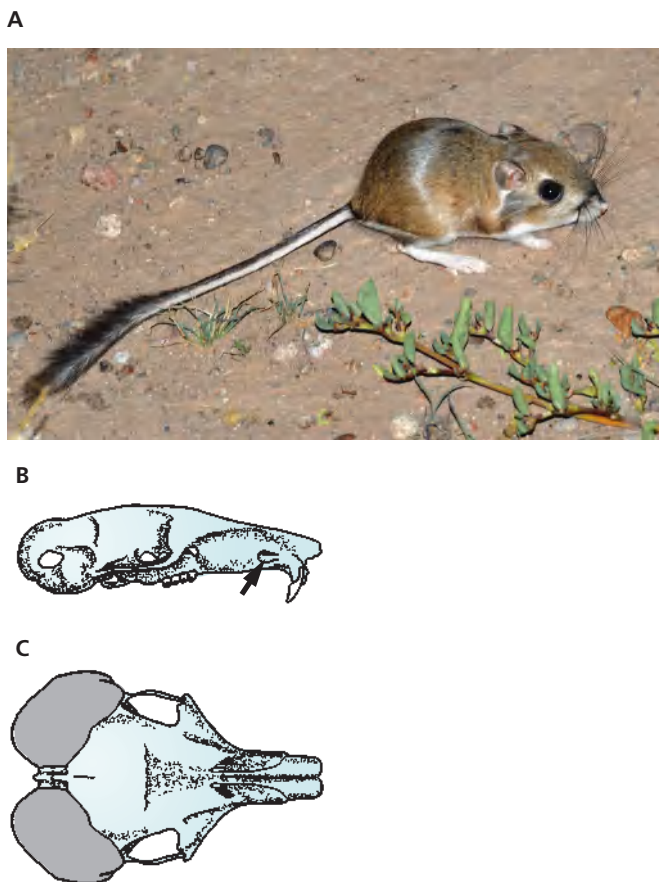
a systematic revision of the Genus *Orthogeomys*. Pocket gophers occur in a variety of habitats with soil conducive to burrowing. Geomyids are generally small (<200 g body weight), 120–440 mm in total length, including a tail 40–140 mm long. There are significant size differences among species, however. The maximum body weight ranges from 70 g in Baird's pocket gopher (*Geomys breviceps*) and the Wyoming pocket gopher (*T. clusius*) to over 1 kg in the smoky pocket gopher (*Cratogeomys fumosus*) in Mexico (J. Hafner 2016). Despite size differences, all pocket gophers have the same fusiform body shape that reflects their fossorial mode of existence. Visual and auditory acuity is reduced in favor of enhanced tactile and olfactory sensitivity. They have thickset, chunky bodies with small eyes and pinnae (Figure 16.16). There are claws on the forefeet and hind feet for digging; those on the forefeet are larger. All teeth are ever-growing, and the dental formula is 1/1, 0/0, 1/1, 3/3 = 20. The incisors extend anteriorly (that is, they are procumbent) so the lips can be closed behind them to keep dirt out of the mouth when the animal is digging. The pectoral girdle is highly developed for digging, with a short, powerful humerus and a keeled sternum for enhanced muscle attachment, similar to that in the 3 families of moles. The pelvic girdle is small and relatively undeveloped. Pelage is short (causing less resistance as they move through tunnels), brownish to gray on the dorsum and slightly lighter on the venter. Because the diameter of a burrow tunnel is not much larger than a pocket gopher's head, the loose skin allows individuals to reverse direction in a tunnel by "somersaulting" between the forelegs. Coloration generally parallels the soil color in which they live (Rios and Alvarez-Castaneda 2012).

Gophers feed on subterranean parts of plants, primarily roots and tubers, although occasionally they leave their tunnels and forage aboveground. Food is brought back to storage chambers in large, externally opening, furred cheek pouches that extend from the mouth to the shoulder (thus, the common name "pocket" gopher). Tunnels, which are very energetically demanding to construct, can be quite extensive and include chambers for shelter, nesting, food storage, and fecal deposits. Tunnels are most easily noted by a series of aboveground mounds. Pocket gopher mounds

Figure 16.16 **Fossorial adaptations.** This lateral view of a Botta's pocket gopher (*Thomomys bottae*) shows the fusiform body shape of these fossorial species.

are differentiated from those of moles by having a fan rather than a conical shape and by the entrance hole not being in the center of the mound. Tunnels are defended against conspecifics except during the mating season when a male will enter a female's tunnel. Gestation is about 3 weeks in smaller species and a month or more in larger species. Litter size is also related to body size, with smaller species having larger numbers of young.

Gophers can damage croplands, gardens, seedlings, and fields with their digging, and there are numerous types of traps and other methods used in efforts to eradicate them. However, on the positive side, they also aerate soil, increase water penetration into the soil, promote early successional plants, and enhance plant diversity and community structure (Sherrod et al. 2005).

The big pocket gopher (*Heterogeomys lanius*) is considered critically endangered by the IUCN (2018). The Michoacan (*Zygogeomys trichopus*) and tropical pocket gophers are endangered. Pocket gophers likely diverged from the closely related heteromyids in the Eocene, and the earliest fossil (*Gregorymys veloxikua*) is from the late Eocene of Mexico (Jimenez-Hidalgo et al. 2018). J. Hafner (2016) provided a superb review of geomyid systematics and life history characteristics.

SUBORDER ANOMALUROMORPHA

This suborder includes the scaly-tailed squirrels (Family Anomaluridae) and the springhares (Family Pedetidae). Skulls have very large infraorbital foramina—characteristic of hystricomorphs—for passage of much of the masseter muscle. Both families have typical sciurognath structure of the lower jaw, however. Thus, these two families can be considered "hystricomorphous sciurognaths." Their association is strongly supported by molecular data.

Anomaluridae

The scaly-tailed flying squirrels (also called "anomalures") are restricted to West and Central Africa, where they inhabit tropical rainforests. There are 7 extant species in 3 genera, and 2 subfamilies are recognized: the Anomalurinae includes 4 species in the Genus *Anomalurus*; the Zenkerellinae includes 2 species in Genus *Indurus* as well as the Cameroon scaly-tailed squirrel (*Zenkerella insignis*). With the one exception of *Z. insignis*, all have a well-formed patagium that encloses the forelimbs, hind limbs, and tail. The Cameroon scaly-tailed squirrel is the sister group to the two other genera (Heritage et al. 2016; Marivaux et al. 2017; Fabre et al. 2018), with the divergence dating to the Eocene. It is likely that *Zenkerella* merits inclusion in its own Family Zenkerellidae. The resemblance of anomalurids to sciurid flying squirrels is due to convergence, not to phylogenetic relationship. The color of the silky fur is variable among the species. The common name is derived

Figure 16.17 **Convergence in gliding.** The hairless, overlapping scales at the base of the tail are apparent in this scaly-tailed flying squirrel. Note the similarity in patagium and body form between this African anomalurid and the North American flying squirrel in Figure 16.11; together they form a good example of phylogenetic convergence. *Adapted from Macdonald (1984).*

from 6 to 9 keeled scales found at the ventral base of the tail (Figure 16.17). In addition to their claws, these scales probably help with traction while climbing or landing on a tree trunk after a glide. Maximum body weights range from 17 g in Zenker's pygmy scaly-tailed squirrel (*Idiurus zenkeri*) to almost 2 kg in Pel's scaly-tailed squirrel (*Anomalurus pelii*). The dental formula is 1/1, 0/0, 1/1, 3/3 = 20. Anomalurids are arboreal and den in tree cavities up to 35 m above ground. They are primarily nocturnal and herbivorous, feeding on leaves, fruits, nuts, and sap. They may form colonies of up to 100 individuals. The fossil anomalurid Genera *Paranomalurus*, *Prozenkerella*, and *Downsimys* date from the Oligocene (Jackson 2016) whereas the oldest, *Pondaungimys* is from the mid-Eocene of Myanmar (Coster et al. 2015).

Pedetidae

Two morphologically similar species are now recognized in this family, the South African springhare (*Pedetes capensis*; Figure 16.18) and the East African springhare (*P. surdaster*), once considered a synonym of *P. capensis*. Springhares occur in sandy soils or cultivated areas throughout semiarid regions of southern and east-central Africa. Total length reaches 900 mm, including a tufted tail up to 500 mm, and body mass ranges from 3 to 4 kg. The skull is heavy with long nasal bones that extend beyond the premaxillary bones, and there is a large infraorbital foramen.

Figure 16.18 **South African springhare (*Pedetes capensis*).** They occur in semiarid regions of southern and east-central Africa.

The dental formula is 1/1, 0/0, 1/1, 3/3 = 20. As noted, pedetids can be considered "hystricomorphous sciurognaths" based on their infraorbital structure and historically their phylogenetic position has been uncertain. Their sister relationship with the Anomaluridae, within Suborder Anomaluromorpha, is established by both morphological and molecular data.

Like North American kangaroo rats, springhares have large hind feet and muscular hind limbs modified for bipedal, jumping locomotion (Figure 16.19). They exhibit erratic hopping when frightened or escaping predators. Springhares burrow and tunnel extensively, and if they sense danger as they are about to leave their burrow, they "spring" immediately into the air from one of multiple exits, a behavior that gave rise to the common name. Individuals use numerous different burrows and change them frequently (Peinke and Brown 2005). They breed throughout the year, gestation is 2.5 months—long for a rodent—and litter size is usually 1. Females produce 3 to 4 litters annually. Springhares are nocturnal and herbivorous, feeding on a variety of grasses, leaves, stems, and cultivated crops. When foraging, they move slowly in a quadrupedal manner. They are hunted both because of the damage they do to crops and as a source of food by the Xhoisan people of South Africa. Five extinct genera of pedetids—*Megapedetes*, *Oldrichpedetes*, *Parapedetes*, *Propedetes*, and *Rusingapedetes*—all from the early to late Miocene are known from Africa, Greece, Turkey, and the Arabian Peninsula (Pickford and Mein 2011; López-Antoñanzas 2016a).

SUBORDER HYSTRICOMORPHA

This is the largest suborder within the Rodentia, and includes 18 extant families within 2 infraorders: the Ctenodactylomorphi with 2 families and the Hystricognathi with 16 families.

Figure 16.19 **Springhare morphology and jumping locomotion.** The reduced forelimbs, long, powerful hind legs, and long tail evident in these various postures of the springhare resemble those of the smaller kangaroo rat (heteromyid) and larger kangaroo (macropodid). *Adapted from Macdonald (1984).*

Infraorder Ctenodactylomorphi

Ctenodactylidae

The 4 genera and 5 species of gundis are found in sparsely vegetated, rocky, semiarid regions of northern Africa from Morocco east through Somalia. Species distributions overlap very little. Morphologically, gundis (Figure 16.20) are very similar to pikas (Order Lagomorpha: Ochotonidae), which are discussed later in this chapter. Gundi skulls have a large infraorbital foramen (Figure 16.21). They are unusual in that the paroccipital processes are very long and curve under and contact the auditory bullae. Three of the 4 genera of gundis (*Massoutiera*, *Felovia*, and *Ctenodactylus*) are also unusual among rodents because premolars of adults are lost due to mesial drift (Gomes Rodrigues et al. 2012)—a condition also found in elephants, manatees, and some wallabies (Lentle and Hume 2010). Gundis are about the size of guinea pigs (*Cavia porcellus*). The desert gundi (*C. vali*) is the smallest, with a body weight of 185 g; the common gundi (*C. gundi*) is the largest, at up to 400 g (López-Antoñanzas 2016b). They have extremely dense pelage, which is groomed with the comb-like hind toes (the family name means "comb-toes"). Females have an unusual lateral pair of cervical mammae at the base of the forelimb, as well as a pair on the anterior part of the thorax. Gundis are opportunistic herbivores and are able to exist on only the water obtained in vegetation. They are diurnal, which is unusual in a desert rodent, and live in small colonies or family groups. Colonies vary in size, depending on habitat and associated food availability, and represent fairly distinct breeding units (Nutt 2007). Breeding begins when animals are <1 year old. Gestation is about 2 months, and under good conditions, 2 litters a year are produced. Gundis do not burrow but seek shelter among rocks during the hottest part of the day. When threatened or alarmed, they "play possum," a fear response in which they can remain motionless for up to 12 hours. Ctenodactylids date from

Figure 16.20 **Common gundi (*Ctenodactylus gundi*).** Note the remarkable resemblance of a gundi, a rodent, to a pika shown in Figure 16.58, which is a lagomorph.
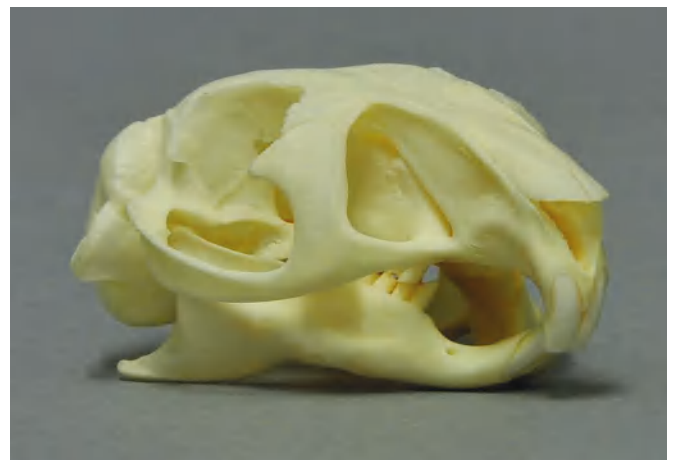
Figure 16.21 **Skull of a common gundi.** Note large infraorbital foramen (hystricomorphous) but with a sciurognathous mandible.

the early Oligocene with 16 genera and at least 27 described fossil species (López-Antoñanzas 2016b). No extant ctenodactylid is considered threatened or endangered (IUCN 2018).

Diatomyidae

The Laotian rock rat (*Laonastes aenigmamus*), or kha-nyou, described by Jenkins and colleagues (2005) is currently the only recognized extant member of this family, although based on karyotypic diversity, Richard and colleagues (2016) suggested it is a multispecies genus. They originally placed the rock rat in a new family (Laonastidae), but this squirrel-like rodent, often described as "enigmatic," is generally considered to be the only surviving diatomyid (Dawson et al. 2006; Huchon et al. 2007; Jenkins 2018)—a family thought to be extinct for the past 11 my.

Often described as a "living fossil" or "relict species," the Laotian rock rat has a pointed rostrum, long vibrissae, and a bushy tail. Head and body length reaches 30 cm with a tail about 16 cm long. Body weight is about 400 g. The pelage is soft and gray to black on the dorsum and somewhat lighter on the venter. The species has a large, hystricomorphous infraorbital foramen, bilophodont cheekteeth (like the extinct Genus *Diatomys*), and lacks a coronoid process on the mandible. The mandible is generally described as sciurognathus (see Flynn 2007), although Hautier and co-workers (2011) considered it neither sciurognathus nor hystricognathus. Likewise, the placentation is structurally unusual (Carter et al. 2013). Laotian rock rats are primarily herbivorous, taking leaves, fruits, and seeds, but also feed on insects. It is again unusual for a rodent in having an enlarged forestomach. The species is known to occur only in rocky, forested areas of Laos and Vietnam. Four fossil genera of diatomyids have been described—*Fallomus* from the early Oligocene is the oldest—as well as *Diatomys*, *Marymus*, and *Willmus* (Jenkins 2018). Populations of the Laotian rock rat are decreasing due to habitat loss and fragmentation as well as trapping for food. The species was considered endangered when first rediscovered but has since been delisted (IUCN 2018).

Infraorder Hystricognathi

Hystricidae

The 3 genera and 11 species of Old World porcupines occur throughout southern Africa, coastal North Africa, the Middle East, India, and Asia, including Indonesia, Borneo, and the Philippines. The crested porcupine (*Hystrix cristata*; Figure 16.22) is also found in Italy, where it was probably introduced thousands of years ago from Tunisia (Trucchi and Sbordoni 2009). Hystricids inhabit a variety of habitat types, including deserts, forests, and steppes from sea level to 3,500 m. Pelage is variable among the 3 genera.

Figure 16.22 **A crested porcupine (*Hystrix cristata*).** The quills of hystricids do not have barbs.

The long-tailed porcupine (*Trichys fasciculata*) of Indonesia and Borneo has weak spines, or bristles, without quills, and a long tail. The African (*Atherurus africanus*) and Asiatic brush-tailed porcupine (*A. macrourus*) have short, soft spines on the head, legs, and ventral surface. Very long, flat, grooved spines are on the back. The 8 species of crested porcupines have a short tail and long, hollow quills. These are grouped in clusters of 5 to 6 over the posterior two-thirds of the body and produce a rattling sound as they move. Their head and shoulders are covered with long, stiff bristles. The tips of hystricid quills do not have barbs, unlike those of New World porcupines, which are not closely related. Old World porcupines are terrestrial, generally nocturnal, and herbivorous. They feed on grasses, roots, tubers, fruits, and seeds, as well as insects and carrion. They are considered pests in portions of their range because of the damage they do to plantations. They also are hunted throughout much of their range or raised for food in many areas. Gestation is 3 to 4 months in crested, cape (*H. africaeaustralis*), and Indian crested porcupines (*H. indica*), with litter size ranging from 1 to 3. Fossil hystricids from the late Miocene are known from southern Asia, southeastern Europe, and North Africa (Winkler et al. 2010; Barthelmess 2016a). No Old World porcupines are considered endangered, although the Philippine porcupine (*H. pumila*) is threatened (IUCN 2018).

Thryonomyidae

The 2 species of cane rats, or "grasscutters," occur throughout Africa south of the Sahara Desert. The greater cane rat (*Thryonomys swinderianus*) is a semiaquatic inhabitant of marshy areas and savannas, whereas the lesser cane rat (*T. gregorianus*) is found in drier upland areas. Neither species inhabits forested or shrub areas. Cane rats have the typical chunky body shape of hystricomorphs (Figure 16.23), with a male greater cane rat reaching a body mass of 9 kg; lesser cane rats are smaller (2.5 kg). Males are

Figure 16.23 Greater cane rat (*Thryonomys swinderianus*). This is one of the largest rodents in Africa.

Figure 16.24 Dassie rat, or noki (*Petromus typicus*). This species occupies rocky outcrops; the genus name means "rock mouse."

larger than females. After the cape porcupine and crested porcupine, cane rats are the largest rodents in Africa. Their skulls are heavy, with a very large infraorbital foramen, and there are 3 grooves on the anterior surface of each upper incisor. Pelage is coarse and bristle-like. Thryonomyids are monogastric and highly specialized for feeding on grasses (as the common names suggest). Data on reproduction in the greater cane rat have come mostly from captive individuals. They can breed at 5 months of age (presumably the lesser cane rat as well). Gestation is also about 5 months long. Two litters can be produced yearly with 2 to 6 young per litter (López-Antoñanzas 2016c). Both species can reach very high population densities and cause significant damage to cultivated crops and plantations. Cane rats also are an important food source for native people (Adenyo et al. 2017); they are hunted or farmed, and large quantities of the meat are sold in markets. Several fossil genera and species of thryonomyids are known, the oldest being from the early Miocene of Africa (*Paraphiomys*). They spread northeast as far as Pakistan by the mid-Miocene (*Paraulacodus* and *Kochalia*); *Protohummus dango* is known from the late Miocene of the United Arab Emirates (López-Antoñanzas 2016c).

Petromuridae

The monotypic dassie rat (*Petromus typicus*) is restricted to southern Angola, Namibia, and northwest South Africa. It occurs in desert habitats with large, rocky outcrops, where it lives in small family groups. Because it is neither a dassie (common name sometimes applied to a hyrax, Family Procaviidae) nor a true rat, the African name "noki" may be more appropriate. The noki is fairly small and squirrel-like (Figure 16.24), with a body weight of about 200 g. It has soft, yellow-orange to brown pelage, and no underfur. The skull is rather flat and the ribs flexible, which allows the noki to squeeze through rocky crevices. Nokis are diurnal, but may avoid extreme midday temperatures. They feed on grasses, flowers, shrubs, and other plant material and are coprophagous. The crowns of the cheekteeth are unusual: the labial

side of the lower teeth and the lingual side of the upper teeth are raised above the rest of the occlusal surface. The name "Petromyidae" occurs in earlier literature for this family, which is most closely related to the cane rats (Family Thryonomyidae; see Figure 16.1). Fossil evidence shows a wider geographic distribution, specifically for *P. antiquus* from the late Miocene of Kenya (López-Antoñanzas 2016d).

Heterocephalidae

This monotypic family currently includes only 1 species, the naked mole-rat (*Heterocephalus glaber*), although genetic, morphological, and karyotypic differences within its geographic distribution may lead to future species differentiation (Patterson 2016). Historically, the naked mole-rat was included within the Family Bathyergidae (following section). Molecular evidence convincingly shows that *H. glaber* diverged from the bathyergids during the early Oligocene and since then has accrued many distinctive characteristics. There are many derived morphological features of the naked mole-rat as well as many that are shared with the bathyergids (Patterson and Upham 2014; Patterson 2016). Naked mole-rats are fossorial and occur throughout the Horn of Africa region in arid, semi-desert scrub. They

are fairly small, generally 30–35 g body weight. They feed while in the burrow system, taking bulbs, tubers, and roots; they get the water they need from their food. A marked feature is their highly protruding incisors.

The common name reflects the almost complete lack of fur; instead, they have bare, wrinkled skin with only a few tactile hairs present (Figure 16.25), unlike bathyergid mole-rats which are fully furred. Along with their reduced metabolic rate, their lack of fur allows for easier dissipation of body heat while underground. Naked mole-rats have the most highly developed eusocial system known among mammals (see Chapter 23); it is a colonial system similar to that of certain insects (Jarvis 1981; Honeycutt 1992). They cooperate in tunnel digging, predator defense, and reproduction. Individuals vary greatly in body size depending on their function in the colony—smaller workers versus larger nonworkers. The one reproductively active female (the "queen") is the largest individual and mates with one of very few reproductively active males in the colony. Gestation is 9 to 10 weeks, with litter size up to 28 young. Given 4 to 5 litters per year, a queen can have a very high reproductive potential. Breeders appear to live longer than nonbreeders (Dammann et al. 2011). Other adults do not breed but take part in foraging, caring for young, and other cooperative functions. Nonbreeders are not sterile, however, and may disperse to establish new colonies or replace breeders that die. Individuals in a colony are very inbred (Reeve et al. 1990). In addition to the interest shown in their social structure, mole-rats are becoming very popular for use in research labs because of several other intriguing characteristics. Their life spans can exceed 30 years—remarkable for a rodent (Perez et al. 2009). They are also resistant to pain (Smith et al. 2011), insensitive to low levels of oxygen (Avivi et al. 2010), and resistant to cancer

(Kim et al. 2011; Gorbunova et al. 2012; Xiao et al. 2013) as well as heart disease (Grimes et al. 2012). Like that of bathyergids, the fossil record of the naked mole-rat extends to the Miocene of East Africa. Patterson (2016) provided an excellent review of the systematics and life-history characteristics of the naked mole-rat.

Bathyergidae

There are 5 genera and 16 to 21 species of African mole-rats; the number of species varies among authorities. African mole-rats are strictly fossorial and occur in a variety of habitats in the hot, dry regions of Africa south of the Sahara Desert. Of the 5 genera, *Bathyergus* and *Georychus* are in southern Africa, whereas *Cryptomys*, *Fukomys*, and *Heliophobius* occur farther north in east, central, and western Africa. Bathyergids range in size from the Zambian mole-rat (*F. amatus*), with males having a maximum head and body length of about 105 mm and body weight of 70 g, to the Cape Dune mole-rat (*B. suillus*), with head and body length of 350 mm and body weight of 1.3 kg. As with other fossorial rodents, bathyergids have a fusiform body shape (Figure 16.26), short legs and tail, large claws on the forefeet, no pinnae, and small eyes. The pelage is short and soft. Like the naked mole-rat, they have large, procumbent incisors. Although the infraorbital foramen is small, with little passage of masseter muscle, jaws of African mole-rats (as well as the naked mole-rat) are hystricognathous with a strongly deflected angular process. This group also has an unusual crown pattern on the molars (see Figure 16.4A). All species burrow extensively, with tunnel length of the African mole-rat (*Cryptomys hottentotus*) reaching over 300 m, and that of Mechow's mole-rat (*Fukomys mechowii*) over 2,200 m (Sumbera et al. 2012). Tunnels are complex with numerous secondary branches and chambers for nesting, feeding, and defecation. African mole-rats act as ecosystem engineers because their tunneling activity changes soil and vegetation characteristics (Hagenah and Bennett 2013). They feed pri-

Figure 16.25 Naked mole-rats. Many morphological adaptations of these naked mole-rats are similar to those found in other fossorial species such as pocket gophers, but the wrinkled and nearly hairless skin is unique among terrestrial species.

Figure 16.26 Cape mole-rat (*Georychus capensis*). The fusiform body shape typical of bathyergids and other fossorial taxa is evident.

marily on underground bulbs and tubers of perennial plants, and are coprophagous. Several species of bathyergids are solitary, including the Namaqua dune mole-rat (*B. janetta*) and the cape mole-rat (*Georychus capensis*; Visser et al. 2017). Other species are found in pairs or small groups, including the Togo mole-rat (*C. zechi*), whereas some species form very large colonies of 80 or more individuals. Parag and colleagues (2006) related the degree of sociality and breeding patterns to baculum size and penile morphology in bathyergids. Reproduction is also variable depending on the species. Gestation is about 46 days in the cape mole-rat and up to 4 months in Mechow's mole-rat. Most species have several litters per year with 2 to 4 young per litter.

The earliest bathyergids are from early Miocene deposits in southern and eastern Africa (Winkler et al. 2010). No African mole-rats are considered endangered, although the Kafue mole-rat is threatened. Honeycutt (2016) provided a thorough review of the family.

Erethizontidae

New World porcupines encompass 3 genera and about 17 species. The bristle-spined porcupine (*Chaetomys subspinosus*) of southeast Brazil is so different from other erethizontids that it is placed in its own subfamily (*Chaetomyinae*). All other New World porcupines are in Subfamily Erethizontinae, which includes two genera. The North American porcupine (*Erethizon dorsatum*) occurs throughout much of Alaska, Canada, the United States except for the southeastern portion, and into northern Mexico. The remaining erethizontids are in Genus *Coendou* and occur from northern Mexico south to central South America. They are found in mixed coniferous forests, tropical forests, grasslands, and deserts. Despite their generally chunky, heavyset bodies, erethizontids are more arboreal (Figure 16.27) than most of the Old World porcupines. The North American porcupine is both terrestrial and semiarboreal, whereas South American species have prehensile tails (Figure 16.28A) and spend most of their time off the ground. Heavy spines up to 10 cm long with a barbed tip (Figure 16.28B), embedded singly and not in clusters as they are in Old World porcupines, occur over much of the dorsum and sides of the body. The ventral surface has coarse, long hair and no spines. Contrary to popular belief, porcupines do not intentionally sling their quills at attackers. The quills are loosely rooted, however, especially in the tail, and can easily become embedded in predators (Roze and Ilse 2003). Because of the barbed tip, the quill works continuously deeper into the wound and can even cause death. The bristle-spined porcupine is unique among rodents in having quills that do not have hard, sharp tips but are stiff and dry, similar to the strands in an old-fashioned broom—another common name for them is the broomstraw-spined porcupine. Body weights range from about 0.6 kg in Roosmalen's porcupine (*C. roosmalenorum*) to 12 kg in *E. dorsatum*. Tails lengths vary from short to long depending on the species. New World

Figure 16.27 North American porpcupines (*Erethizon dorsatum*). New World porcupines are more arboreal than are their Old World counterparts.

porcupines are not closely related to those in the Old World (Family Hystricidae).

Porcupines are herbivorous with diets dependent on seasons and location. The North American porcupine eats leaves, stems, berries, grasses, and forbs. It does not hibernate and gains up to 40% of its body weight to survive winter, when it feeds on tree bark and cambium. In *E. dorsatum*, with which most work on porcupines has been done, a single young (called a "porcupette") is born following a gestation of about 7 months. Young are precocial, fully furred, and active, with soft spines that harden after a few hours. Despite the defense provided by spines, porcupines have a variety of potential predators, with the fisher (*Martes pennanti*) being the most adept at flipping them over and attacking the unprotected ventral area. The bristle-spined porcupine, which has a limited geographic distribution and very small home ranges (Oliveira et al. 2012), is threatened; no erethizontids are endangered (IUCN 2018). Fossils date to the Oligocene. Barthelmess (2016b) provided an excellent review of the systematics and life history of the family.

Cuniculidae

There are 2 species in this family. The lowland, or spotted, paca (*Cuniculus paca*) occurs in forested areas from lowlands to higher elevations in central Mexico south to Paraguay and Argentina, usually near rivers or streams. The mountain paca (*C. taczanowskii*) occurs in dense forest in the Andes Mountains of northwestern South America from Venezuela to Bolivia, at elevations up to 4,000 m (Samudio 2016). Formerly placed in the Genus *Agouti*, in the now defunct Family Agoutidae, pacas have the typical robust hystricomorph form and weigh up to about 10 kg. Their coarse pelage is reddish-brown dorsally, with a paler venter and 4 rows of white spots on each side of the body

A

B
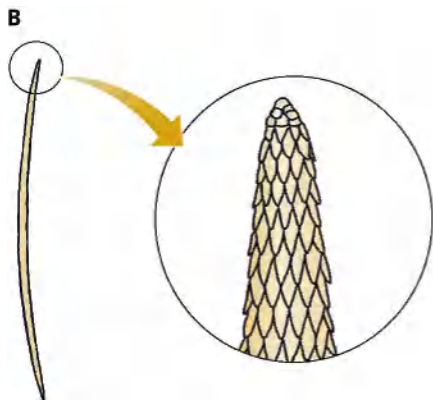
Figure 16.28 Porcupine quills. (**A**) The familiar pelage of erethizontids with guard hairs modified as quills is seen in the Brazilian porcupine (*Coendou prehensilis*); note the prehensile tail wrapped around a limb. (**B**) A diagrammatic enlargement of the overlapping barbs on the tip of a quill. *Diagram from Feldhamer et al. (2003b).*

(Figure 16.29). The skull is unique in that a portion of the zygomatic arch is enlarged and contains a large sinus (Figure 16.30), possibly for amplification of vocalizations or tooth-grinding sounds. Lima and colleagues (2018) investigated the vocal repertoire of *C. paca* in relation to group size. The dental formula is 1/1, 0/0, 1/1, 3/3 = 20. Females give birth once or twice a year, usually to a single young. Gestation is about 4 months. Pacas are primarily nocturnal (Michalski and Norris 2011), terrestrial, burrowing herbivores that eat a variety of plants, leaves, seeds, and fruits. They also exhibit coprophagy (Aldrigui et al. 2018). Pacas can be serious pests on crops, gardens, and plantations and sometimes are killed for this reason. More often, however, pacas are harvested for their excellent meat (Gallina et al. 2012). They are considered to be the best-tasting, most edible South American rodent, and since the 1980s there have been efforts in many South American countries to domesticate lowland pacas for

Figure 16.29 A lowland or spotted paca. Because of their excellent meat, pacas are hunted as well as raised domestically.

20 mm
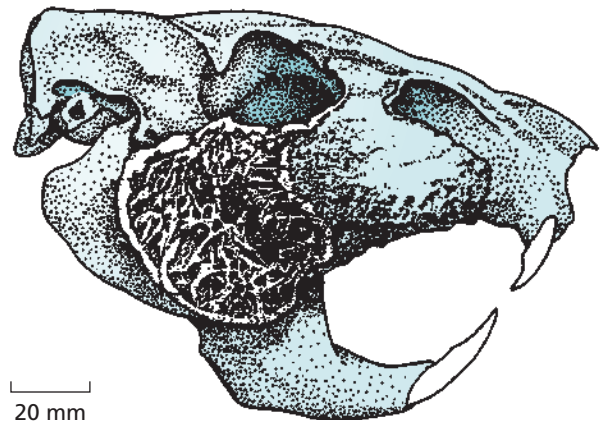
Figure 16.30 Skull of the paca. The large, distinctive zygomatic arch of the lowland paca (*Cuniculus paca*) is evident. *Adapted from Eisenberg (1989).*

commercial production. Hunting and habitat loss have greatly reduced population numbers in large parts of their range, although neither species is considered endangered (IUCN 2018). Although pacas diverged from other hystricomorphs in the early Miocene, the oldest fossils are only from the late Pleistocene (Samudio 2016).

Caviidae

The guinea pigs, cavies, and Patagonian "hares," or maras, encompass 6 genera and 20 species. They occur throughout South America, except for the Amazon basin. Three subfamilies are currently recognized. The Subfamily Caviinae includes 14 species of guinea pigs (Genus *Cavia*), cavies (Genus *Galea*), and mountain cavies (Genus *Microcavia*). The Subfamily Dolichotinae includes 2 species of Patagonian hares or maras—the Patagonian mara (*Dolichotis patagonum*) and the Chacoan mara (*D. salinicola*). The Subfamily Hydrochoerinae includes 2 species of capybaras (Genus *Hydrochoerus*) and 2 species of rock cavies (Genus *Kerodon*). Caviids share a robust body form with relatively short limbs and ears and a vestigial tail. The maras are exceptions (Figure 16.31). They have longer ears and are adapted for cursorial locomotion by having long hind legs, a reduced clavicle, and reduced number of digits. The dentary bones of caviids have a prominent lateral groove. The upper cheekteeth converge anteriorly; thus, the toothrows form a V-shape. Cavies are probably the most abundant and widespread rodents in South America (Figure 16.32). Caviids occur in numerous habitat types and exhibit a variety of social systems related to differences in resources, predation risk, and climate (Adrian and Sachser 2011; Lacher 2016). The origin of the domestic guinea pig (*Cavia porcellus*) is uncertain, although it has been raised for consumption for thousands of years.

In the past, the greater capybara (*H. hydrochaeris*; see Figure 16.2) and lesser capybara (*H. isthmius*), as well as the rock cavies (Figure 16.33), were in their own family. The

Figure 16.32 **Spix's yellow-toothed cavy (*Galea spixii*).** There are 5 species in Genus *Galea*, all with yellow-pigmented incisors, which set them apart from other caviids.

Figure 16.33 **Rock cavies.** Rock cavies (*Kerodon rupestris*), also called mocó, occur in rocky habitats of eastern Brazil. *Photo by B. Gratwicke.*

Figure 16.31 **Patagonian "hares," or maras (*Dolichotis patagonum*), in Valdes Peninsula, Patagonia.** Maras are morphologically distinctive and unusual caviids.

subfamily name means "water pig" and suggests both the habitat affinity and general body form of capybaras. They are semiaquatic, have partially webbed feet, and are closely associated with water throughout their range, which extends from Panama south to Argentina east of the Andes Mountains. They swim and dive with agility and feed on aquatic plants. In contrast, as suggested by their name, rock cavies are found in rocky outcrops in semiarid habitats. They have a head and body length of 30 to 40 cm and weigh about 1 kg, whereas capybaras are the largest living rodents with a large head, small eyes, and ears placed high on the head. Their pelage is short, coarse, and fairly sparse. Head and body length is about 1.3 m, and mean body mass is 28 kg, although individuals can reach 65 kg or more. The skull is distinctive, with a very long paroccipital process, grooved dentary bones, and an upper third molar that is

longer than the combined length of the other 3 cheekteeth. Capybaras are gregarious, living in groups of 20 or more, including adults and their offspring (Herrera et al. 2011). As expected in a social species, capybaras have a range of vocalizations (Barros et al. 2011). They are hunted either for food or to reduce agricultural damage. In Venezuela, Colombia, and Argentina, capybaras are ranched for meat and leather.

Salvador and Fernandez (2008) studied reproduction and growth of Santa Caterina's guinea pig (*Cavia intermedia*). With only about 40 living individuals, it is considered critically endangered and is known only from a 4-ha area on Moleques Island do Sul in Brazil, which may be the smallest geographic range of any mammalian species. No other caviids are endangered. The oldest fossil caviids date from the late Miocene.

Dasyproctidae

This family is made up of about 13 species of agoutis (Genus *Dasyprocta*) and 2 species of acouchys (Genus *Myoprocta*). Dasyproctids were sometimes included in the Family Cuniculidae (pacas). They occur from southern Mexico south to central South America east of the Andes Mountains. Agoutis were introduced into Cuba and several other Caribbean islands. Dasyproctids are generally diurnal but avoid high temperatures (Cid et al. 2015). They are burrowing herbivores, which form small family groups. They inhabit forests, brushlands, and grasslands, always in association with water. Agoutis also frequent agricultural areas and gardens; acouchys are less adaptable to human disturbance, preferring lowland rainforests of the Amazon basin. As the only rodents in neotropical forests that bury seeds, dasyproctids fill a very important ecological role as dispersers of plants (Galetti et al. 2010; Gilbert and Lacher 2016). Population density and home range of red-rumped agoutis (*D. leporina*) are related to the spatial distribution of Brazil nut trees (*Bertholletia excelsa*) (Jorge and Peres 2005). Both genera are similar in appearance, with a coarse, glossy, orange-brown to black pelage. The pelage is long, thick, and often of a contrasting color in the posterior area (the family name means "hairy-rumped"). Hair on the rump is flared when an individual is threatened or alarmed. Agoutis range in size from 3 kg body weight in the orange agouti (*D. croconota*) to 6 kg in the black agouti (*D. fuliginosa*; Figure 16.34). Acouchys are about 1.5 kg body weight with longer, white-tipped tails. Gestation in agoutis is up to 4 months, with litter sizes of 1 to 3 precocial young; gestation in the smaller acouchys is about 3 months.

Humans hunt them for food, and populations of many species have declined in some areas, often because of forest fragmentation (Jorge 2008). The Ruatan Island agouti (*D. ruatanica*) is endangered; the Mexican agouti (*D. mexicana*) has lost 90% of its habitat in the past 50 years and is critically endangered. Fossil dasyproctids may extend to the early Eocene, but specimens clearly related to the extant genera are from the late Miocene,

which is when *Dasyprocta* and *Myoprocta* diverged (Gilbert and Lacher 2016).

Chinchillidae

The 3 fairly diverse genera and 6 living species in this family are distributed in South America from the Andes Mountains of Peru south to southern Argentina. Two subfamilies usually are recognized: the monotypic Lagostominae includes only the Argentine plains viscacha (*Lagostomus maximus*); the Chinchillinae has 3 species of mountain viscachas (Genus *Lagidium*) and 2 species of chinchillas (Genus *Chinchilla*) (Spotorno and Valladares Faúndez 2016). All have a large head with large eyes and ears and very dense, soft pelage. The plains viscacha (Figure 16.35) lives in large colonies in semiarid scrub

Figure 16.34 **Black agouti (*Dasyprocta fuliginosa*).** This large agouti is distributed in forest and savanna habitats of northern South America.

Figure 16.35 **Plains viscacha (*Lagostomus maximus*).** Males have more pronounced black facial bands than do females.

and grassland areas of Argentina, Paraguay, and Bolivia, where it creates extensive burrow systems. Its burrowing has significant ecosystem effects both above and below ground (Villarreal et al. 2008). The 2 species of chinchillas form colonies in dry, steep, rocky, rather barren areas. The 3 species of mountain viscachas, which look like rabbits with long, strongly curved tails, also form colonies in these types of habitat at elevations up to 4,800 m. Size dimorphism is evident in the plains viscacha, with the maximum body weight of males (almost 9 kg) nearly twice that of females (5 kg). In wild chinchillas, males (maximum 490 g body weight) are only about 10% heavier than females. Like all rodents, chinchillids are herbivores. The plains viscacha eats primarily grasses, shrubs, seeds, and fruits. Chinchillas also feed on grasses, shrubs, ferns, and cacti. Mountain viscachas take a variety of leaves, flowers, fruits, seeds, and roots.

Populations of plains viscacha are greatly reduced because they are pests on crops and compete for rangeland forage with domestic livestock. They are also taken for their fur and meat. Likewise, population densities of mountain viscacha have declined because they are hunted for their meat and fur. Chinchilla fur has been highly prized for centuries and is one of the most valuable of any mammal in the world. Both the short-tailed chinchilla (*C. chinchilla*) and the long-tailed, or Chilean, chinchilla (*C. lanigera*) are extirpated throughout much of their original ranges, and both are endangered (Valladares et al. 2014; IUCN 2018). The Peruvian plains viscacha (*L. crassus*) is recently extinct. The chinchillids first appear in the fossil record from the late Oligocene. Rasia and Candela (2017) described *L. telenkechanum* from the late Miocene of Argentina. For extant taxa, fossil evidence is known only for the plains viscacha, from the late Pleistocene (Spotorno and Valladares Faúndez 2016).

Dinomyidae

The monotypic pacarana (*Dinomys branickii*) is a rare inhabitant of humid, tropical forests at elevations from 200 to 3,400 m in the Andes Mountains from Colombia and Venezuela south to Bolivia. The pacarana looks like a huge guinea pig (Figure 16.36). The body is heavyset (about 15 kg) with coarse, brownish-black pelage and 4 lines of white spots on each side from the shoulders to the rump. Pacaranas are slow, lumbering, nocturnal, generalist herbivores that forage on a variety of vegetation including agricultural crops. Their population levels apparently have never been high. Saavedra-Rodriguez and colleagues (2012) investigated factors limiting distribution and abundance of the pacarana, the most critical of which was availability of dens. Information on reproduction is based on captive individuals. They breed throughout the year, gestation is about 8 months, and litters range from 1 to 4 young. The fossil record extends to at least the Oligocene (Rinderknecht et al. 2011). Although there is a single extant species today, there was a noteworthy radiation in the Miocene with 22

Figure 16.36 A pacarana (*Dinomys branickii*). This rare rodent occurs in northern South America.

fossil genera and at least 50 described fossil species that occupied various ecological niches throughout South America (Mares and Braun 2016). Among these species was *Josephoartigasia monesi* from the Pliocene-Pleistocene of Uruguay; it is estimated to have weighed 1,000 kg—probably the largest rodent that ever lived (Rinderknecht and Blanco 2008).

Abrocomidae

Abrocomids have been included as a subfamily within either the large Families Octodontidae or Echimyidae; they have the same geographic distribution as the octodontids. There are 8 extant species of chinchilla rats (Genus *Abrocoma*) and 2 species of Inca rats (Genus *Cuscomys*). The chinchilla rats are considered to comprise 3 groups. The Bolivian chinchilla rat (*A. boliviensis*) is known from only 2 specimens from Santa Cruz, Bolivia. Likewise, Bennett's chinchilla rat (*A. bennettii*) occurs only in Chile. The remaining 6 species form the "ashy chinchilla rat" group. Five of these species are known only from the type locality and were considered subspecies of the ashy chinchilla rat (*A. cinerea*), but have now been raised to species status. They are Budin's chinchilla rat (*A. budini*); the Famatina chinchilla rat (*A. famatina*); the Mendozan chinchilla rat (*A. vaccarum*); the Sierra del Tontal chinchilla rat (*A. schistacea*); and the Uspallata chinchilla rat (*A. uspallata*) (Patton and Emmons 2015; Emmons 2016). Likewise, the Inca rats are both limited to a few specimens from the type localities. The Ashaninka Inca rat (*C. ashaninka*) is found only near Junín, Peru. The Machu Picchu Inca rat (*C. oblativus*) was first described from skeletal remains of 2 individuals found in Inca burial sites. The species was believed to be extinct for 500 years until 2009, when one was photographed near the Machu Picchu ruins (Patton and Emmons 2015; Emmons 2016).

Figure 16.37 Bennett's chinchilla rat (*Abrocoma bennettii*). (*Inset*) Note the small dermal tubercules on the soles of the feet typical of abrocomids. *From an 1836 drawing from Darwin's* The zoology of the voyage of H. M. S. Beagle.

Abrocomids are rat-like in appearance, with somewhat pointed snouts and long tails (Figure 16.37). They have long, soft, thick pelage—similar to but not of the same quality as true chinchilla fur. All live in rocky, semiarid shrublands of the Andes Mountains, at elevations up to 5,000 m, where they burrow among crevices. Abrocomids feed on leaves, seeds, and fruits. Litter sizes are small, an average of about 2 young; gestation is lengthy at close to 4 months. The Bolivian chinchilla rat, with a very limited range, is considered critically endangered. All other members of the family, with the exception of Bennett's chinchilla rat, have extremely limited ranges but are currently listed as "data deficient" (IUCN 2018). The fossil record extends to the Miocene.

Ctenomyidae

This family, closely related to the Family Octodontidae, is composed of about 69 species of tuco-tucos in the single Genus *Ctenomys*. Because their fossorial habits have resulted in relative isolation and disjunct distributions of species, *Ctenomys* is a diverse, rapidly evolving, polytypic taxon (Castillo et al. 2005). Parada and coworkers (2011) and Mora and colleagues (2013) examined the phylogenetic relationships of tuco-tucos. They are distributed from central South America south to Tierra del Fuego and occur from sand dune to forest habitats and soil types suitable for burrowing, from sea level to 4,000 m elevation. Freitas (2016) discussed 8 phylogeographic species groups that encompass 43 tuco-tuco species; the remaining 26 species cannot be assigned to any of these groups. These fossorial rodents are morphologically similar to North American pocket gophers (Family Geomyidae). Like geomyids, tuco-tucos have broad, thick incisors, small eyes, short, thick pelage, and enlarged claws. Unlike geomyids, however, they lack external cheek pouches. The genus name

Figure 16.38 Long-tailed tuco-tuco (*Ctenomys fulvus*). This individual is emerging from a burrow.

("comb mouse") is derived from the stiff fringe of hairs around the soles of the hind feet and toes, which is used to groom dirt from the fur. The burrow systems vary in size and shape and can be very extensive (Figure 16.38). Population densities can reach 200 per ha. As might be expected, there is a direct relationship between the metabolic cost of digging and soil hardness. There are also skull, dental, and forelimb adaptations related to digging (Borges et al. 2017; Morgan et al. 2017). Ctenomyids use high-intensity, low-frequency vocalizations to communicate among tunnel systems (Amaya and Areta 2018). The "tloc-tloc" alarm call, which gave rise to the common name, can be heard when the animals are underground. They are diet generalists and consume a high proportion of the plant species available. Reingestion of fecal pellets (coprophagy) occurs while the animals are resting or between feeding bouts. Colonies can become serious pests in plantations because they destroy roots and girdle trees. Although long-lived for a rodent (2 to 3 years), tuco-tucos are not sexually active until 6 to 8 months of age. Gestation is prolonged (about 100 days), and litters are small (1 to 4 young). Most species probably have a single litter each year.

Three species are critically endangered: Reig's tuco-tuco (*C. osvaldoreigi*), Roig's tuco-tuco (*C. roigi*), and the social tuco-tuco (*C. sociabilis*). Six other species are endangered: Bonetto's tuco-tuco (*C. bonettoi*), Flamarion's tuco-tuco (*C. flamarioni*), the furtive tuco-tuco (*C. occultus*), the Pilar tuco-tuco (*C. pilarensis*), the Rio Negro tuco-tuco (*C. rionegrensis*), and the southern tuco-tuco (*C. australis*).

The oldest fossil genera date from the late Miocene, whereas the oldest material from *Ctenomys* is early Pliocene (Verzi 2008; Verzi et al. 2010). Bidau (2015) and Freitas (2016) reviewed the systematics and life history characteristics of ctenomyids.

Octodontidae

The 8 genera (Ojeda 2016, although see Verzi et al. 2015 and below) and 14 species of octodontids occur in the Andean region of Peru, Bolivia, Chile, and Argentina. There are 4 presumptive genera of viscachas—the red viscacha rat (*Tympanoctomys barrerae*), Kirchner's viscacha rat (*T. kirchnerorum*)—and 3 species in monotypic genera—the common viscacha rat (*Octomys mimax*), the golden viscacha rat (*Pipanacoctomys aureus*) and the Chalchalero viscacha rat (*Salinoctomys loschalchalerosorum*). The mountain degu (*Octodontomys gliroides*) is also in a monotypic genus, whereas the Genus *Octodon* includes 4 other degu species. Octodontids also include 3 species of rock rats (*Aconaemys*) as well as the coruro (*Spalacopus cyanus*). Suarez-Villota and colleagues (2016) discussed phylogenetic and biogeographic relationships of octodontids. They are morphologically and ecologically very diverse and occur in several habitat types from sea level to high elevation. Octodontids are small to medium size, with body weights ranging from 80 g in Kirchner's viscacha rat to 300 g in the common degu (*Octodon degus*). Species in the family have thick, silky pelage (Figure 16.39) and often have tufted tail tips. Unlike those of many other rodent families, the occlusal surfaces of the molars usually are simple, with a single lingual and labial fold forming a figure-8 pattern in most species. This pattern gives rise to the family name.

Habitats, life history, and feeding habits vary among species. Viscacha rats inhabit arid areas including sand

Figure 16.40 **Coruro (*Spalacopus cyanus*).** Tunnels may reach 600 m in length.

dunes and salt basins of Argentina. The degus, rock rats, and the coruro occupy grasslands, forests, and semiarid areas with rocky slopes. The mountain degu and common viscacha rat are primarily surface-dwelling generalists. Degus, rock rats, and the red viscacha rat are semifossorial. The common degu nests communally. Although adult females can recognize their own pups, they do not discriminate between related and unrelated pups during nursing (Ebensperger et al. 2006), and sociality is not necessarily kin-based (Davis et al. 2016). Frequency of dispersal increases with more degus using a burrow system (Quirici et al. 2011). The coruro (Figure 16.40) is completely subterranean. This social octodontid digs tunnel systems up to 600 m long in which it stores large amounts of food (Begall and Gallardo 2000). Coruros maintain nomadic colonies of up to 26 individuals that move to a new area after depleting food resources at a site. Feeding habits are also diverse. Viscacha rats eat halophytic (high salt content) vegetation after removing as much salt as they can. The mountain degu feeds on cacti. Rock rats and coruros take underground roots, bulbs, and tubers. Gestation ranges from 2 to 3 months depending on the species, and litter sizes vary as well.

Octodontids are of special interest because they exhibit the greatest span of chromosomal number ($2N = 38–102$) of any mammalian family. This exceptional range is because the red viscacha rat is the only known mammalian tetraploid, with a chromosome complement of $4N = 102$. As a result, sperm in this species have a very large head with close to twice the nuclear DNA content of other mammalian species (Gallardo et al. 1999; Kohler et al. 2000). Teta and coworkers (2014) described a new species of *Tympanoctomys*. Both the golden viscacha rat and the Chalchalero viscacha rat (subsumed under the Genus *Tympanoctomys* by Verzi et al. 2015 and the IUCN 2018) are considered critically endangered, as is the Pacific degu (*Octodon pacificus*), found only on Mocha Island off the coast of central Chile (Vianna et al. 2017). Octodontids likely originated in the

Figure 16.39 **Degu (*Octodon degus*).** These octodontids often nest communally. They are the heaviest of the octodontids.

Oligocene with divergence of the various taxa during the Miocene (Verzi et al. 2015).

Echimyidae

The echimyids are a large, diverse family of approximately 27 genera and 99 extant species of South American spiny-rats, hutias, and coypus grouped into 4 subfamilies (Fabre and colleagues 2016; see Emmons et al. 2015 and Fabre et al. 2017 for alternate arrangements). The largest subfamily is the Echimyinae, with 5 genera and about 30 species of terrestrial spiny-rats as well as the coypu in the Tribe Myocastorini, and an additional 13 genera and 46 species of brush-tailed and tree-rats (Tribe Echimyini). The Subfamily Euryzgomatomyinae encompasses 3 genera and 12 species of Atlantic forest terrestrial spiny-rats. The Subfamily Capromyinae includes 4 genera and 9 species of Cuban, Bahamian, and Jamaican hutias (Tribe Capromyini), as well as the Hispaniola hutia (Tribe Plagiodontini, *Plagiodontia aedium*). A final, unnamed subfamily includes the enigmatic groove-toothed spiny-rat (*Carterodon sulcidens*). It occurs from Honduras south to central South America; hutias occur throughout the West Indies. The hutias were recently considered to represent their own family (Capromyidae). Likewise, the coypu (or nutria, *Myocastor coypu*) was also placed in its own family (Myocastoridae) (see below).

Almost all echimyids have spiny, sharp, stiff, bristle-like pelage. The spiny-rats and tree-rats have the typical rat-like pointed rostrum. Habitat preferences vary but are closely tied to availability of water. Some genera are semi-fossorial burrowers, others are terrestrial, and many are arboreal. They live in habitats as varied as seasonally flooded bottomlands to upland forests. Most echimyids are nocturnal; exceptions are the hutia and the coypu. Many species include fruits in their diet, although a wide range of vegetation, seeds, and arthropods are taken depending on the species. Spiny-rats in the Genus *Proechimys* (Figure 16.41), which encompasses about 22 species, have karyotypes ranging from $2N = 14$ to $2N = 62$ (Machado et al. 2005; Amaral et al. 2013). Several species of spiny rats in the Genera *Boromys*, *Brotomys*, and *Heteropsomys* from Cuba, Puerto Rico, and the Dominican Republic have been described from remains found with human artifacts and are very re-

cently extinct (Guarch-Delmonte 1984). The red-crested tree-rat (*Santamartamys rufodorsalis*), not found since 1898, was rediscovered in 2011 in El Dorado Nature Reserve in northern Colombia. It is now listed by the IUCN (2018) as critically endangered. Other critically endangered echimyids are the unicolored tree-rat (*Phyllomys unicolor*)—with only a single specimen found recently—and the Mantiqueira Atlantic tree-rat (*P. mantiqueirensis*). Six other species are considered endangered.

As noted, the coypu has previously been placed in its own family based on morphology and serology. It is native to South America from Chile and Argentina north to Bolivia and Brazil. Coypus are large (up to 10- kg body mass) and heavy-bodied, with rather coarse pelage and a long, round, sparsely furred tail. Their webbed hind feet adapt them to aquatic habitats in and around fresh or brackish marshes or slow-moving streams. They make floating platforms, which they use as feeding stations for consuming aquatic vegetation. They form kin groups and can have a polygynous mating system (Tunez et al. 2009). Coypus have been widely introduced into Europe, Asia, Africa, and North America. In the United States, most were introduced in the early to mid-1900s for fur farming. They escaped, or were released, and now occur in the Gulf Coast states and along the West Coast to Washington and the East Coast to Maryland. Populations are also established in several parts of southern Canada. The fur is of major economic importance in South America, and in the United States, millions of pelts were harvested annually (Bounds et al. 2003) until the decline of the fur industry. In many areas where they have been introduced, they are serious pests because they overgraze and degrade wetlands (Klima and Travis 2012).

The 5 genera and about 10 extant species of hutias occur in remote forested or rocky valleys and small islands in the West Indies. Hutias are chunky, with short legs, a large head, and small eyes and ears. They range in body weight from 450 g in the dwarf hutia (*Mesocapromys nanus*) to 8 kg in Demarest's hutia (*Capromys pilorides*; Figure 16.42). The coarse pelage varies from yellowish

Figure 16.41 Long-tailed spiny-rat (*Proechimys longicaudatus*). Found in dry forests, savannas, and shrublands, the species is distributed in Brazil, Bolivia, and Paraguay.

Figure 16.42 Demarest's hutia (*Capromys pilorides*). Found throughout Cuba in a variety of habitats, this is the heaviest hutia.

gray to black on the dorsum and is paler on the venter. Desmarest's hutia is an arboreal folivore and unlike almost all other hutias, is fairly common (Witmer and Lowney 2007). The Jamaican hutia (*Geocapromys brownii*) feeds on terrestrial plants. Hutias also consume small lizards. Six species of hutias have become extinct during the last few hundred years in Cuba, Haiti, Puerto Rico, the Virgin Islands, and the Dominican Republic. Of the 10 extant species, 4 are considered endangered, and 2 are critically endangered—the dwarf hutia and the little earth hutia (*Mesocapromys sanfelipensis*; see Lopez et al. 2018). Habitat loss and overharvesting for food, as well as the introduction of the small Asian mongoose (*Herpestes javanicus*) and feral house cats (*Felis catus*) have caused the severe population declines.

Echimyids originated in the late Oligocene-early Miocene. The oldest stem fossil genus, *Xylechimys*, is from the late Oligocene. Emmons and colleagues (2015) and Fabre and coworkers (2016) provided exhaustive reviews of the family.

SUBORDER MYOMORPHA

The affinities of these families are well established.

Superfamily Dipodoidea

Sminthidae

Although currently placed within the Dipodidae by the IUCN, most authorities (Cserkesz et al. 2016; Holden et al. 2017; Burgin et al. 2018) place the single genus (*Sicista*) and 14 presumptive species of birch mice in their own Family Sminthidae (which was previously referred to as "Sicistidae"). Unlike dipodids, birch mice have a simple, unmodified hind foot and are terrestrial or semiarboreal. These small mice (from 4 to 19 g body weight) have an extensive geographic distribution from Eastern Europe through central Asia, where they inhabit a variety of grassland, steppe, forest, meadow, and semi-arid habitats. They have prehensile tails and are excellent climbers, but do not have large, specialized hind limbs like dipodids. The dorsal pelage is used to separate birch mice into 2 groups: the smaller, lowland striped birch mice have 1 to 3 dark, mid-dorsal stripes, and the larger, unicolored montane species, which have no stripe (Holden et al. 2017). The 5 species of striped birch mice are the northern birch mouse (*S. betulina*), southern birch mouse (*S. subtilis*; Figure 16.43), Hungarian birch mouse (*S. trizona*), Strand's birch mouse (*S. strandi*), and Nordmann's birch mouse (*S. loriger*).

Birch mice are generally nocturnal omnivores, consuming a variety of insects, flowers, seeds, leaves, fruit, and underground bulbs, depending on species. Average litter size varies from 2 to 8, again depending on the species, and gestation is from 3 to 4 weeks. The Armenian birch mouse

Figure 16.43 Southern birch mouse (*Sicista subtilis*). Note the dark, mid-dorsal stripe.

(*S. armenica*) and the Kazbeg birch mouse (*S. kazbegica*) are endangered. The fossil record of the family extends to the late Eocene of Asia with the appearance of *Allosminthus*. The family radiated extensively throughout the Oligocene and Miocene. As many as 13 extinct genera (as well as the extant *Sicista*) are known from Europe, Asia, and North America (Holden et al. 2017).

Zapodidae

The 3 genera and 5 species (Malaney et al. 2017 recognized 4 species) of jumping mice were formerly in their own family, then included as a subfamily of Dipodidae, and are once again placed in a family of their own. Four of the 5 living species occur in North America. The meadow jumping mouse (*Zapus hudsonius*) enjoys the broadest distribution occurring from Alaska and south throughout southern Canada, as well as much of the Midwest and eastern contiguous United States. The Pacific jumping mouse (*Z. trinotatus*) occurs in coastal northern California to southwestern British Columbia. The western jumping mouse (*Z. princeps*) extends from northwest Canada to the northwestern United States, south to Utah and east to the Dakotas. The woodland jumping mouse (*Napeozapus insignis*) is found throughout the northeast United States into southeast Canada. The Chinese jumping mouse (*Eozapus setchuanus*) is the sole extant Old World zapodid and occurs in central China.

Jumping mice inhabit brushy fields and forests, often associated with wet areas, where they feed on seeds, fruits, fungi, and insects. Zapodids have elongated hind limbs and feet used in jumping locomotion and a very long tail, which

is about 1.5 times the head and body length. The woodland jumping mouse can leap up to 2 m when alarmed—noteworthy given its head and body length is only about 90 mm. Pelage is brown on the dorsum, golden on the sides, and white on the venter. Gestation is about 3 weeks, litter size averages 4 to 6 young, and a female has 1 to 2 litters annually. No jumping mice are currently considered threatened or endangered. The fossil record of the family extends to the early Miocene in Asia; several extinct genera have been described from North America. Whitaker (2017) reviewed the systematics and life history characteristics of the family.

Dipodidae

This family includes 13 genera and approximately 35 species of jerboas among 4 subfamilies (Michaux and Shenbrot 2017): Subfamily Cardiocraniinae, which includes 7 species of pygmy jerboas in the Genera *Cardiocranius* and *Salpingotus*; the monotypic Subfamily Euchoreutinae with only the long-eared jerboa (*Euchoreutes naso*); Subfamily Allactaginae, which includes 5 genera and 16 species of 5-toed jerboas; and Subfamily Dipodinae, with 5 genera and 11 species of 3-toed jerboas. There is little consensus on the number of species in the family despite new advances in morphometric and molecular markers. Jerboas are distributed from the Sahara Desert east across southwestern and central Asia to the Gobi Desert; they inhabit arid, semidesert, and steppe regions, where they burrow in sandy or loamy soils. A vertical process on the jugal bone protects the eye when the head is used in digging, and a fold of skin closes the nostrils. Many of the same adaptations found in the heteromyids (kangaroo rats and kangaroo mice) to conserve water also occur in jerboas. They are small to medium-sized, bipedal rodents (Figure 16.44), with light, sandy-colored pelage, and head and body length ranging from about 35 to 260 mm. They have large eyes and long ears in the 5-toed and long-eared jerboas (the latter species, with a head and body length of about 100 mm, has ears

Figure 16.45 **Lesser Egyptian jerboa (*Jaculus jaculus*).** This small dipodid is found throughout North Africa and the Arabian peninsula. Note the length of the hind feet in relation to head and body length; also see Figure 16.44.

up to 50 mm long). Long ears enhance hearing as well as help to dissipate body heat. Jerboas are strongly bipedal and highly adapted for jumping, with the long, tufted tail used for balance and to aid in rapidly changing direction. In most species, the 3 central metatarsals of the hind foot are fused, forming a cannon bone, and the first and fifth toes are lost. The strong hind legs are 4 times longer than the front legs. Hind foot length in these species is often half the head and body length (Figure 16.45). They are very fast and can leap several meters.

Jerboas are omnivorous, with diets dependent on the species, but generally they take insects, seeds, fruits, leaves, and fungi. The long-eared jerboa listens for flying insects and jumps to snatch them out of the air. Some species breed only once a year, others 3 times annually. Gestation ranges from 2.5 weeks to 6 weeks and litter size varies from 2 to 9 young per litter. Dipodids are either obligate or facultative hibernators in burrows; winter hibernation may last as long as 9 months in some species, depending on latitude. Likewise, jerboas may enter torpor in the summer during particularly hot, dry periods. No dipodids are currently endangered (IUCN 2018). Jerboas are believed to have diverged from zapodids during the Eocene-Oligocene transition when global temperatures decreased.

Superfamily Muroidea

This group includes the Families Platacanthomyidae, Spalacidae, Calomyscidae, and Nesomyidae, as well as the highly speciose Cricetidae and Muridae. Schenk and colleagues (2013) presented an extensive phylogeny of the muroids. They identified Eurasia as the likely origin of the group, with subsequent colonizations of Africa, North America, Southeast Asia, Australia and surrounding islands, South America, and Madagascar.

Figure 16.44 **Convergence in desert rodents.** Long hind feet and tail and reduced forelegs of the great jerboa (*Allactaga major*) are similar to the pattern seen in desert rodents such as the kangaroo rats (Figure 16.15) and the springhare (Figure 16.18). *An 1822 print from Deutsche Akademie der Wissenschaften zu Berlin.*

Figure 16.46 Soft-furred tree mouse (*Typhlomys cinereus*). Tree mice in this genus have poor vision (note the small eyes) and likely move through the branches using echolocation, much as bats do.

Platacanthomyidae

Formerly considered a tribe or subfamily within the Family Muridae, the 2 genera and 5 living species of tree mice currently enjoy family status. The Malabar spiny tree mouse (*Platacanthomys lasiurus*) occurs in southwest India. The Chapas tree mouse (*Typhlomys chapensis*) occurs in southwest China and northwest Vietnam. The soft-furred tree mouse (*T. cinereus*; Figure 16.46), the Dalou Mountains tree mouse (*T. daloushanensis*), and the dwarf tree mouse (*T. nanus*) all have fairly restricted ranges in China (Giarla 2017). Cheng and colleagues (2017) revised the Genus *Typhlomys*. All species occur in tropical evergreen and deciduous forest habitats. Tree mice are small, 70 to 140 mm head and body length, with a tail the same length or longer. The long tail ends in extended brush-like hairs. Maximum body weight ranges from 13 g in the dwarf tree mouse to 30 g in soft-furred and Dalou Mountains tree mice. The Malabar spiny tree mouse has sharp spines throughout the dorsal fur with fewer, smaller spines on the ventral surface. In contrast, species of *Typhlomys* have soft, dark dorsal pelage without spines. They also have tiny eyes and, despite being arboreal, have poor vision (*Typhlomys* means "blind mouse"). The Chapa tree mouse uses high-frequency echolocation to navigate among the branches (Panyutina et al. 2017); the other *Typhlomys* species might as well. All platacanthomyids are nocturnal. The spiny tree mouse feeds on seeds, fruits, and a variety of wild plants and cultivated crops. Feeding habits of *Typhlomys* are less well known but likely involve seeds, fruits, and vegetation. In some areas, populations of tree mice can reach high enough densities to become pests. The oldest fossil attributed to the family is *Neocometes* from the early Miocene, which has been found throughout Eurasia.

Spalacidae

Another family formerly included as a subfamily among murids, the spalacids currently encompass 7 genera and 28 species in 3 subfamilies (Norris 2017). The Subfamily Myospalacinae includes 2 genera (*Eospalax* and *Myospalax*) and 11 species of zokors. They are distributed in East Asia, Russia, China, and Mongolia. The Subfamily Spalacinae has 2 genera (*Spalax* and *Nannospalax*) and 11 species of blind mole-rats. These are unrelated to the naked mole-rat (Family Heterocephalidae) or the African mole-rats (Family Bathyergidae). Blind mole-rats occur in Eastern Europe, the Balkan countries, Anatolia, and the Middle East. The Subfamily Rhizomyinae is divided into 2 tribes—Tachyoryctini includes 2 species of root rats (Genus *Tachyoryctes*; see Sumbera et al. 2018), which have a disjunct distribution in East Africa. The Tribe Rhizomyni has 2 genera (*Rhizomys* and *Cannomys*) and 4 species of bamboo rats that occur in south-central and southeastern Asia. In the past, bamboo rats (Genus *Rhizomys*), the lesser bamboo rat (*Cannomys badius*), and African mole-rats (Genus *Tachyoryctes*) were in their own family, the Rhizomyidae. These three subfamilies represent fairly distinct lineages that likely diverged in the late Oligocene to early Miocene.

All spalacids are fossorial or semi-fossorial, with a mole-like or gopher-like appearance. They range in size from a body weight of about 150 g in the Middle East blind mole-rat (*Nannospalax ehrenbergi*) to the 4 kg Indomalayan bamboo rat (*Rhizomys sumatrensis*). Spalacids occur in a variety of habitat types including semi-arid areas, grasslands, forests, bamboo stands, and cropland where soils are conducive to digging. Zokors are powerful diggers, constructing extensive burrow systems 2 m below the ground and reaching up to 100 m long. Nonetheless, at night they may occasionally forage above ground. Zhou and Zhou (2008) and Tsvirka and colleagues (2011) investigated genetic diversity and phylogeny of zokors. Blind mole-rats are mole-like in general body form except that they do not have large, spatulate forefeet. They have small eyes, but these are beneath the skin with no external openings. With little or no visual acuity, blind mole-rats have a line of short bristles on each side of the rounded snout that enhance tactile sensitivity (Figure 16.47). Extensive karyotypic variation occurs in both *Spalax* and *Nannospalax* (Arslan et al. 2016). Fossils date from the early Miocene (Winkler et al. 2010; Lopez-Antoanzas and Wesselman 2013). The sandy mole-rat (*Spalax arenarius*), endemic to southern Ukraine, and the giant mole-rat (*Tachyoryctes macrocephalus*; see Vlasata et al. 2017) of Ethiopia are endangered.

Calomyscidae

This family of a single genus (*Calomyscus*) includes 8 species of brush-tailed mice (Kilpatrick 2017). The genus name means "beautiful mouse." In size, pelage, and general morphology, they are very similar to the Genus *Peromyscus* (Family Cricetidae), where they were once included

Figure 16.47 Blind mole-rat (*Nannospalax leucodon*). Note the procumbent incisors and extensive vibrissae.

Figure 16.48 Giant African pouched rat (*Cricetomys gambianus*). Found throughout sub-Saharan Africa, these animals can be trained to detect landmines.

as "mouse-like hamsters." Dorsal pelage is a buffy-brown, orange tinged, or gray with a lighter belly. The ears are large, about as long as the hind feet. Body weights range from about 20 g to nearly 40 g. Species of brush-tailed mice look so similar that only one was recognized prior to the advent of molecular and karyotypic methods. They occupy a variety of habitats from forests to barren, arid, rocky hills up to 3,500 m elevation throughout the Middle East. Calomyscids can be active day and night during winter and are nocturnal during the summer. They feed primarily on seeds, with occasional fruit and leaves. Reproductive data are limited; gestation is about 30 days with average litter size of 3 young. The fossil record dates to the late Miocene *Calomyscus delicates* from Spain. No calomyscids are endangered or threatened (IUCN 2018).

Nesomyidae

This is a large family of 21 genera and currently about 68 species found within 6 subfamilies (Goodman and Monadjen 2017) occurring in sub-Saharan Africa and Madagascar. The Subfamily Cricetomyinae includes 3 genera and 9 species of pouched rats (Figure 16.48) and mice, named for the cheek pouches where they transport seeds, grains, and other materials back to burrows and nests. One species, the giant African pouched rat (*Cricetomys gambianus*), is trained to find landmines so they can be removed (see box). The monotypic Subfamily Delanymyinae includes only the threatened Delany's swamp mouse (*Delanymys brooksi*), a tiny (about 6 g) climbing mouse found in swamps and marshes in higher elevation forests. There are 6 genera and 26 species of climbing mice and fat mice in Subfamily Dendromurinae. Species include several climbing or tree mice (Genus *Dendromus*), with very long, semi-prehensile tails, and several species of fat mice (Genus *Steatomys*)—so named

because they accumulate a great deal of fat that allows them to estivate during times with reduced food availability. The monotypic Subfamily Mystromyinae includes only the enigmatic African white-tailed rat (*Mystromys albicaudatus*). There are 9 genera and 27 species of tufted-tail rats in Subfamily Nesomyinae, all endemic to Madagascar, including 11 species of Genus *Eliurus* found in forested areas. The Subfamily Petromyscinae contains 4 species of pygmy rock mice in Genus *Petromyscus*. The taxonomy of the family has historically been fairly confused because of the morphological diversity among species. Many taxa have been placed within the Families Cricetidae and Muridae in the past (Goodman and Monadjen 2017). Molecular genetic analyses have clarified the monophyly of nesomyids, but many issues remain unresolved.

Body form and function in the family are variable, as are dental formulae and means of locomotion. The smallest nesomyid is the South African pouched mouse (*Saccostomus campestris*), with a maximum body weight of 50 g; the largest is the southern giant pouched rat (*Cricetomys ansorgei*), with males close to 3 kg. As might be expected given their morphological diversity, members of the family are found in a variety of habitats, including forests, deserts, grasslands, wetlands, and savannas. Most species are nocturnal and nest in burrows or rock crevices. Feeding habits are diverse but likely include seeds, leaves, and fruits.

The Mount Kahuzi African climbing mouse (*Dendromus kahuziensis*) is critically endangered. The white-tipped tuft-tailed rat (*Eliurus penicillatus*), the Malagasy giant jumping rat (*Hypogeomys antimena*), the long-tailed big-footed mouse (*Macrotarsomys ingens*), the white-tailed mouse (*Mystromys albicaudatus*), the lowland Red Forest rat (*Nesomys lambertoni*), and the eastern voalavo (*Voalavo antsahabensis*) are endangered. Fossils of this family date from the early Miocene deposits throughout much of Africa (Winkler et al. 2010).

Cricetidae

The Cricetidae encompasses the New World rats and mice. With 5 subfamilies (Table 16.2), 145 genera, and about 792 species, the cricetids are second only to the murids in total

African Giant Pouched Rats Detect Landmines

The occurrence of anti-personnel landmines and other unexploded ordnance is a major problem in many regions of the world. There are countless landmines and other unexploded ordnance, some dating back to World War II, which pose a risk of detonation throughout 61 countries. Annually, landmines and explosive remnants of war kill over 2,000 people, 42% of them children. Countless other victims are maimed for life. The scope of the problem is further evident in the fact that the United Nations has 14 different agencies, programs, and departments working on de-mining activities. Dogs, with their very acute olfactory abilities, have always been the primary means of detecting explosives by odor. During the past 20 years, however, another mammalian species—the African giant pouched rat (*Cricetomys gambianus ansorgei*)—has also been used for this purpose.

Historically considered to be crop depredators and sometimes hunted and eaten, African giant pouched rats are used for landmine detection because of their acute sense of smell, fairly long life-span, and ability to work on a lead. Also, unlike dogs, pouched rats are relatively inexpensive and easy to maintain, and their low body weight does not activate landmines. Because they do not bond with their handler in the same way that a dog would, they can work with any trained person and often change handlers when they finish their training. Each pouched rat must become accredited under International Mine Action standards. Training is conducted by APOPO, an acronym for Anti-Personnel Landmines Detection Product Development, which is a global nonprofit organization with Belgian roots and is based in Morogoro, Tanzania. Trained pouched rats are used successfully in a number of countries to remove landmines and other explosive remnants of war, and they serve a novel and little-known humanitarian purpose, certainly earning their nickname—HeroRATs.

But APOPO is also carrying out ongoing research and development into using rats as a diagnostic tool for tuberculosis detection. Human sputum samples are collected from over 100 partner clinics and are transported to one of APOPO's centralized facilities, where they are heat inactivated, sorted, and placed under a specialized chamber for inspection by a rat. APOPO's lab confirms the samples for tuberculosis before getting results back to the clinics, which then alert the patients before they leave and thus prevent them from unknowingly passing the disease on to family, friends and colleagues.

Research is also underway to determine if the rats can be a tenable option for detecting people trapped under rubble, as well as to examine the abilities of the rats to detect pangolins—the world's most widely trafficked mammals—as well as African blackwood, an illegally logged and trafficked timber. Check the APOPO website (http://www.apopo.org) for more information. To help support their efforts it is possible to donate to the charity or "adopt" a HeroRAT.

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A HeroRAT receives a reward during training.

number of species among mammals. The systematics of the family in relation to murids have been difficult to untangle for 150 years, as have subfamily designations because the size and heterogeneity of this group make generalizations on form and function difficult. Molecular genetic analyses have greatly aided in resolution but many questions remain. The Subfamily Arvicolinae is widespread throughout the Northern Hemisphere in both the Old and New World (Nearctic faunal region), and includes a variety of voles (Figure 16.49) and relatives. Subfamily Neotominae (Figure 16.50) also is found in the Nearctic, Subfamily Tylomyinae is primarily in Central America, and the largest subfamily (Sigmodontinae) occurs throughout South America (Neotropical faunal region). Subfamily Cricetinae (Figure 16.51) is widely distributed in the Palearctic faunal region. Generally, cricetids are small (body weight <100 g), although muskrats (*Ondatra zibethicus*) can weigh 2 kg. Head and body length is about equal to tail length. Dorsal pelage is often brownish with a lighter venter (Pardiñas et al. 2017). The dental formula is 1/1, 0/0, 0/0, 3/3 = 16.

Habitats, feeding habits, reproduction, and activity periods of cricetids are as varied and diverse as those of the murids. Given the extremely wide geographic distribution of this family, they occupy diverse habitats (numerous types of

Figure 16.49 California vole (*Microtus californicus*). One of many species in the large Genus *Microtus*, one of 29 genera within Subfamily Arvicolinae.

Figure 16.50 Key Largo woodrat (*Neotoma floridina smalli*). This endangered subspecies of eastern woodrat, one of 27 species of woodrats in Subfamily Neotominae, is restricted to the northern part of Key Largo, Florida.

deciduous and coniferous forests, deserts, grasslands, steppes, wetlands, shrublands) and are an important part of the small mammal fauna throughout various ecosystems. Feeding habits are equally diverse and include herbivores, opportunistic omnivores, insectivores, granivores, and others. Breeding is generally seasonal but may occur throughout the year in the tropics. Gestation varies by body size but is about 3 weeks, with 5 to 6 per litter. The earliest fossil cricetids are from the late Eocene of Asia and North America (Rodrigues et al. 2010). Thirty-two species are endangered, and another 20 are critically endangered (IUCN 2018). Pardiñas and colleagues (2017) provided an exhaustive account of the systematics and life history of the cricetids.

Muridae

Murids have more species than any other mammalian family as well as a very confusing taxonomic history. They illustrate the dynamic nature of systematics as new, more sophisticated molecular techniques allow for more informed analyses of relationships. The Family Muridae was once considered to include 17 subfamilies. Numerous molecular studies have elevated several of these subfamilies back to family status, including the Platacanthomyidae, Spalacidae, Calomyscidae, Nesomyidae, and Cricetidae. With the murids, these families now constitute the Superfamily Muroidea (see Table 16.1). Murids now include 5 subfamilies, 19 tribes, 157 to 159 genera, and well over 800 species (Denys et al. 2017). As shown in Table 16.3, the Subfamilies Leimacomyinae and Lophiomyinae are monotypic, each with a single genus and species. Subfamily Deomyinae has 57 species and Gerbillinae 101 species. Subfamily Murinae encompasses 656 species, or about 80% of the family.

With the exception of Antarctica and some oceanic islands, murids are distributed worldwide, either naturally or through introduction, especially onto many formerly unoccupied islands. Like cricetids, murids are generally small, with thin, scaly tails equal to or longer than the head and body length. Body weights are usually <100 g; extremes are as low as 3 g in African pygmy mice (*Mus minutoides*) and up to 1 kg in the maned rat (*Lophiomys imhausi*). As might be expected of a family that includes almost 13% of all living mammalian species, murids are found in a diverse array of habitats including deserts, rocky slopes, steppes, grasslands, wetlands, and numerous types of forests. The usual dental formula is 1/1, 0/0, 0/0, 3/3 = 16. Molar structure within subfamilies and genera is quite variable. Molars can be rooted or rootless, cuspidate or prismatic (see Figure 16.4). Tooth structure reflects the plant materials, invertebrates, or small vertebrates consumed. The edentate Sulawesi shrew-rat (*Paucidentomys vermidax*) from south-central Sulawesi Island, Indonesia (Esselstyn et al. 2012), is unique among rodents in having no cheekteeth, and it feeds on earthworms. Gestation varies but ranges from 3 to 6 weeks. Females may produce many litters annually, often with large litter sizes—up to 15 young in soft-furred mice (*Praomys*) and 14–18 in bandicoot rats (*Bandicota*).

Originally found throughout most of the Eastern Hemisphere, two of the largest genera (*Rattus*, with about 66 species, and *Mus*, with about 38 species) have been inadvertently introduced by humans throughout most of the world. These 2 genera include the ubiquitous brown (Norway) rat (*R. norvegicus*) and the house mouse (*M. musculus*), two species commensal with humans almost everywhere. Most murids are nocturnal, but some genera, such as the striped grass mice (Genus *Lemniscomys*; Figure 16.52), are diurnal. Still others, such as the African grass rats (Genus *Arvicanthis*), water rats (Genus *Hydromys*), groove-toothed swamp rats (Genus *Pelomys*), and brush-furred mice (Genus *Lophuromys*), are active both day and night. There are 15 critically endangered murid species and another 52 endangered species (IUCN 2018).

Table 16.2   Currently recognized subfamilies, tribes, and common names within Family Cricetidae

Subfamily	Tribe	Common names*
Arvicolinae	Arvicolini	True voles (9, 95)
	Dicrostonychini	Collared lemmings (1, 7)
	Ellobiusini	Mole voles (1, 5)
	Lagurini	Steppe voles & steppe lemmings (2, 3)
	Lemmini	Lemmings (3, 7)
	Myodini	Red-backed & mountain voles (7, 36)
	Ondatrini	Muskrats (2, 2)
	Phenacomyini	Heather & tree voles (2, 5)
	Pliomyini	Balkan snow vole (1, 1)
	Prometheomyini	Long-clawed mole vole (1, 1)
Cricetinae		Hamsters (7, 18)
Neotominae	Baiomyini	Pygmy & singing mice (2, 4)
	Neotomini	Woodrats (4, 27)
	Ochrotomyini	Golden mouse (1, 1)
	Reithrodontomyini	Harvest mice & deer mice (9, 108)
Sigmodontinae	Abrotrichini	Long-clawed & soft-haired mice (5, 17)
	Akodontini	Akodonts, grass mice & relatives (16, 83)
	Andinomyini	Puna & Andean mice (2, 3)
	Euneomyini	Chinchilla rats & relatives (3, 6)
	Ichthyomyini	Water mice & fish-eating rats (5, 18)
	Oryzomyini	Rice rats & relatives (29, 141)
	Phyllotini	Vesper, gerbil, & leaf-eared mice (11, 59)
	Reithrodontini	Conyrats (1, 3)
	Sigmodontini	Cotton rats (1, 14)
	Thomasomyini	Climbing & oldfield mice (5, 74)
	Wiedomyini	Red-nosed mice & relatives (3, 4)
	Incertae sedis	Sigmodontines (5, 12)
Tylomyinae	Nyctomyini	Vesper rats (2, 2)
	Tylomyini	Climbing rats (2, 8)

Adapted from Wilson et al. (2017).

*Numbers of genera and species are in parentheses.

Figure 16.51   Common hamster (*Cricetus cricetus*). There are 18 species of hamsters in the Subfamily Cricetinae.

Fossil murids date from the early Miocene in Africa and Asia. What followed was a remarkable, highly successful adaptive radiation. Denys and colleagues (2017) provided a comprehensive review of the history of taxonomic research and systematics, as well as life-history characteristics of this family.

Lagomorpha

Lagomorphs (meaning "hare-shaped") include 11 genera and about 63 species of rabbits (10 genera) and hares (Genus *Lepus*) in Family Leporidae, as well as 1 genus (*Ochotona*) of 29 species of pikas in Family Ochotonidae (Lissovsky 2014; Smith et al. 2018). Systematic treatments (Figure 16.53) are often controversial because of rapid radiation, hybridization, and local adaptations to a variety of habitats (Melo-Ferreira et al. 2012; Melo-Ferreira and Alves 2018). Lagomorphs occur worldwide except for the southern portions of South America, Australia, and New Zealand, and islands such as Madagascar, the Philippines, and those in the Caribbean. A few species of leporids have, however, been introduced into some of these places. For example, the European wild rabbit (*Oryctolagus cuniculus*), which is native to Spain, has been introduced throughout Europe, the British Isles, numerous Mediterranean, Caribbean, and oceanic islands, North and South America, Australia, and New Zealand. This species (Figure 16.54) is a prime example of the potential pitfalls of introducing an **exotic**, as species can become invasive and cause habitat degradation, competition with native species, and altered community structure and function. Of about 12

Table 16.3 Currently recognized subfamilies, tribes, and common names within Family Muridae

Subfamily	Tribe	Common names*
Deomyinae		Spiny mice & brush-furred rats (4, 57)
Gerbillinae	Ammodillini	Ammodile (1, 1)
	Gerbillini	Gerbils & jirds (9, 72)
	Taterillini	Taterils (4, 28)
Leimacomyinae		Buttner's African forest mouse (1, 1)
Lophiomyinae		Maned rat (1, 1)
Murinae	Apodemini	Field mice (2, 23)
	Arvicanthini	Grass rats & relatives (18, 92)
	Chiropodomyini	Pencil-tailed tree mice (1, 6)
	Hapalomyini	Marmoset rats (1, 3)
	Hydromyini	Australasian semiaquatic rats & mice (42, 181)
	Malacomyini	African swamp rats (1, 3)
	Micromyini	Eurasian harvest mouse (1, 1)
	Millardiini	Indian rats (4, 8)
	Murini	True mice (1, 41)
	Otomyini	Vlei rats (2, 31)
	Phloeomyini	Philippine cloud rats (5, 18)
	Pithecheirini	Southeast Asia tree rats (2, 3)
	Praomyini	African soft-furred mice (8, 54)
	Rattini	True rats (43, 185)
	Vandeleurini	Long-tailed climbing mice (1, 3)
	Incertae sedis	Ethiopian amphibious rat & others (3, 4)

Data modified from Wilson et al. (2017).

*Numbers of genera and species are in parentheses.

Figure 16.52 Striped grass mouse (*Lemniscomys striatus*). Usually found in grassy habitats, they are also called zebra mice.

species of leporids introduced to various regions of the world, 3 are considered invasive: the European wild rabbit, the European hare (*Lepus europaeus*), and the eastern cottontail rabbit (*Sylvilagus floridanus*) (Cooke et al. 2018).

MORPHOLOGY

All lagomorphs are small to medium-sized terrestrial herbivores. The diagnostic feature of the order is the occur-
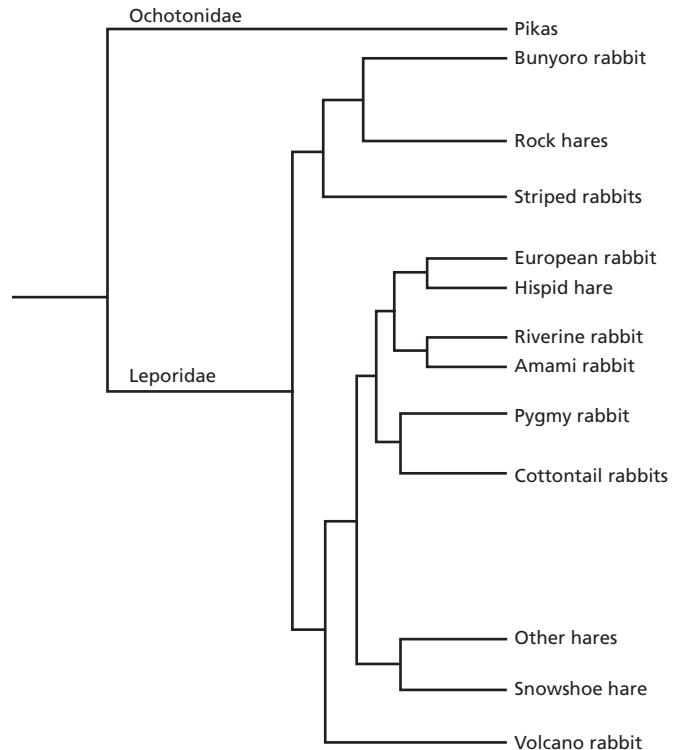
Figure 16.53 Phylogenetic relationships of lagomorphs. *Modified from Robinson and Matthee (2005); Melo-Ferreira et al. (2012) give an expanded analysis of "other hares."*

Figure 16.54 **European wild rabbit (*Oryctolagus cuniculus*).** Introduced into many countries around the world, this invasive species can cause significant damage to native communities.

Figure 16.55 **Peg teeth.** Lateral view of the (**A**) cranium and (**B**) mandible of a leporid, the arctic hare. Although superficially rodent-like, note the peg teeth (*arrows*) and fenestrated rostrum, especially evident in the enlarged view (**C**). *Adapted from DeBlase and Martin (1981).*

Figure 16.56 **Lagomorph upper incisors.** (**A**) Anterior view of the upper incisors of an ochotonid showing the characteristic notch on the cutting surface. (**B**) The upper incisors of a leporid do not have a notch. *Adapted from DeBlase and Martin (1981).*

rence of peg teeth, a second pair of small incisors without a cutting edge, immediately behind the larger, rodent-like first incisors (Figure 16.55). A third pair of lateral incisors is lost before birth or immediately thereafter. The cutting edge of the primary incisors is notched in pikas but not in rabbits and hares (Figure 16.56). The dental formula is 2/1, 0/0, 3/2, 2–3/3 = 26–28. The cheekteeth are hypsodont with 2 transverse enamel ridges, whereas rodents usually have several transverse ridges. The cheekteeth and incisors are open-rooted and ever-growing. In leporids, but not ochotonids, the rostral portion of the maxilla is **fenestrated** (having small, lattice-like perforations in the bone; see Figure 16.55), and the frontal bone has a supraorbital process. Rabbits and hares generally have large ears and elongated hind limbs to accommodate their saltatorial locomotion. Rabbits have a well-known "cotton-ball" tail, but the tail in hares is longer. Pikas are rodent-like in appearance and have short limbs, small ears, and no external tail. Although agile, they do not have the running ability of leporids. Unlike rodent feet, the feet of lagomorphs are fully furred. They are herbivorous, with a cecum housing microfauna for cellulose digestion, and gain enhanced energy efficiency through reingestion of fecal pellets (coprophagy). A cloaca is present, the uterus is duplex, and there is no baculum. Females of most species are larger than males—an uncommon feature

among mammals. Davis and Roth (2008) found little evidence that this female-biased size dimorphism was related to fecundity or other reproductive factors.

FOSSIL HISTORY

Rose and coworkers (2008) reported on the earliest fossil evidence of a lagomorph, found in early Eocene strata from India. They suggested that leporids and ochotonids might have diverged about that time—a finding in agreement with molecular evidence (Springer et al. 2003). Both Old and New World fossil leporids are known from the late Eocene, whereas fossil ochotonids are known from the

mid-Oligocene in Asia. Both families were much more diverse in the Tertiary period than they are today, with 21 fossil genera of leporids and 23 fossil genera of ochotonids recognized (Smith et al. 2018).

ECONOMICS AND CONSERVATION

Pikas are of limited economic importance, with a few Asian species considered to be agricultural pests. Rabbits and hares are often important as game species. Most species of cottontail rabbits (Genus *Sylvilagus*) are hunted; the eastern cottontail rabbit ranks first among game mammals in terms of the numbers taken and hours spent hunting them in North America. The snowshoe hare (*L. americanus*) historically has been an important furbearer, and several other species of hares are hunted for food and sport (Murray 2003).

Local populations of leporids can increase to such densities ("they breed like rabbits!") that they become serious crop depredators. Lethal methods such as poisoning and shooting, along with nonlethal methods such as fencing and repellents, are used in attempts to control local populations. In the western United States, ranchers and farmers historically had "rabbit drives" in which large numbers of people worked together to round up and kill thousands of black-tailed jack rabbits (*L. californicus*; Figure 16.57) in an effort to reduce their density and resultant crop damage. As noted, introduced European wild rabbits often have a negative impact on native communities. Conversely, invasive species such as the Indian mongoose (*Herpestes javanicus*) or feral dogs and cats are threats to some lagomorphs, as is habitat loss to agriculture and commercial development (Smith 2018).

FAMILIES

Ochotonidae

Of the 29 species of pikas, 27 inhabit Asia and 2 occur in western North America. Pikas commonly inhabit steppe, meadow, and forest areas, or steep, rocky (talus) slopes in alpine areas, often at high elevations. They are diurnal and live under and among boulders (Figure 16.58). Distinct differences mark species within each habitat type. Pikas in talus areas do not burrow, are relatively asocial, and have low population densities and fecundity rates. Conversely, those in steppe or forest habitats dig burrows, are more social, and have higher population densities and fecundity. Burrow systems are either permanent—used for predator avoidance, resting, and raising young in a nesting chamber—or they are temporary—used primarily for emergency escape from predators (Wei and Zhang 2018). Burrowing by pikas can alter soil nutrients as well as plant biomass and diversity (Pang and Guo 2017). Reese and colleagues (2013) found significant differences in several forelimb and hind limb indices between pikas dwelling in meadows and those in talus. Regardless, in both habitats, pikas are

Figure 16.57 **Black-tailed jackrabbit (*Lepus californicus*).** Sometimes taken by hunters, this species is more often considered a crop depredator.

extremely vocal, with differences in calls and "songs" evident among and between populations of American pikas (*O. princeps*) and collared pikas (*O. collaris*) (Trefry and Hik 2010). Calls and songs are used to maintain distinct territories and social organization. These are enhanced with scent marking from apocrine glands on the cheeks. Given the acoustic characteristics of their alarm calls to warn of predators, Hayes and Huntly (2005) found the American pika was less active during inclement weather with windy conditions that masked the calls. Lanier and Olson (2013) investigated the genetic structure of collared pika populations; Galbreath and colleagues (2010) found 5 distinct genetic lineages in American pikas.

Pikas are well known for their "haymaking" activity (Figure 16.59). An individual or breeding pair cuts and gathers vegetation throughout the summer and fall, cures it in piles in the sun, and stores it in a traditional place within the territory. This cached hay is then used for winter food. These caches can weigh up to 5 kg and can directly affect the dynamics of local plant communities and sympatric species of herbivores (Smith et al. 1990). Kohl and colleagues (2018) found gut microbial communities in

Figure 16.58 **Collared pika (*Ochotona collaris*).** Pikas look very similar to rodents. Note the talus slope habitat. Many Asian pika species live in meadow or steppe habitats.

Figure 16.59 **North American pika (*Ochotona princeps*).** Pikas are well known for their "haymaking" activities and carrying cut vegetation.

American pika populations had several "core" microbes in common, although overall the microbial communities varied significantly among pika populations. Population densities of plateau pikas (*O. curzoniae*) were positively correlated with the diversity of the gut microbial communities (Li et al. 2016). Gliwicz and coworkers (2006) found that the northern pika (*O. hyperborea*), like the American pika, gathered and stored plants selectively rather than in proportion to their availability. The potential impact of climate change on pikas, including the American pika, has been studied extensively (Beever et al. 2013), although results have been inconsistent (Galbreath et al. 2009; Millar et al. 2010; Erb et al. 2011).

Endangered ochotonids are the silver pika (*O. argentata*), which is restricted to a forested area of 107 km^2 in north central China; Kozlov's pika (*O. koslowi*), Hoffmann's pika (*O. hoffmanni*), and the ili pika (*O. iliensis*) (IUCN 2018). The Sardinian pika (*Prolagus sardus*) is recently extinct. Smith and colleagues (2018) provided thorough accounts of the paleontology and life history characteristics of the 29 pika species.

Leporidae

This family includes the rabbits and hares, which, although morphologically similar, differ in several ways. Rabbits usually build fairly well-constructed, fur-lined nests and give birth to altricial young (called "kittens"). Hares do not construct nests but instead make shallow depressions on the ground called "forms," and they have precocial young. Neonatal hares (called "leverets") are fully furred, have

their eyes open, and are able to run when only a few hours old. Rabbits have an interparietal bone in the skull, but hares do not. The karyotype of most rabbits is $2N = 42$; most hares have $2N = 48$. Based on studies using a large molecular, cytogenetic, and morphological database, Robinson and Matthee (2005) strongly supported the monophyly of the leporids. Using mitochondrial DNA markers, Wu and coworkers (2005) described North American, Eurasian, and African species groups for the Genus *Lepus*. Leporids are herbivorous, and coprophagy is common, as it is in many rodents. They reingest both soft and hard pellets, which enhances their ability to live on relatively low-quality vegetation.

Leporids are nocturnal and have strong, long hind limbs for rapid locomotion. They occur in habitats ranging from the snow and cold of the Arctic to deserts, grasslands, mountain areas, swamps, and tropical forests. One of the adaptations of species in temperate or arctic areas, such as the arctic hare (*L. timidus*) or snowshoe hare, is pelage dimorphism. Coats are white in the winter and brown in the summer. Blending in with the habitat is beneficial because leporids are potential prey to a wide variety of predators, including lynx (Genus *Lynx*), coyotes (*Canis latrans*), red fox (*Vulpes vulpes*), marten (*Martes americana*), fisher, and raptors.

Like rodents, leporids have a high reproductive potential. They can have several litters per breeding season, with several individuals per litter. Postpartum estrus occurs, so that litters are produced in fairly rapid succession. Leporids also exhibit induced ovulation, further enhancing the probability that reproductively mature females will conceive. Similar to certain species of rodents that have 3- to 4-year cycles in population density, snowshoe hare populations exhibit 8- to 11-year cycles. Density can change during this period by 2 orders of magnitude. Population increases result

from increased birth rates and survival of young; the opposite occurs during population declines. The effect of food, predators, and other factors on causation of cycles has been investigated for many decades (Krebs 1996).

In contrast to the high population densities of some leporids, several species of rabbits and hares are currently endangered. The riverine rabbit (*Bunolagus monticularis*) in the Karoo region of South Africa is critically endangered, as is the San Jose brush rabbit (*Sylvilagus mansuetus*). Endangered species include the Tehuantepec jackrabbit (*Lepus flavigularis*), restricted to the Isthmus of Tehuantepec (see Rico et al. 2008), the Hainan hare (*L. hainanus*), the volcano rabbit (*Romerolagus diazi*), the Tres Marias rabbit (*S. graysoni*), and the Omilteme rabbit (*S. insonus*) in Mexico; the robust rabbit (*S. robustus*) in the Davis Mountains of New Mexico, Texas, and Mexico; the Manzano Mountain cottontail (*S. cognatus*); the hispid hare (*Caprolagus hispidus*, which is actually a rabbit) in the foothills of the Himalayan Mountains; and the Amami rabbit (*Pentalagus furnessi*) in the Ryukyu Islands of Japan.

SUMMARY

- Rodents are the largest mammalian order with about 2,550 described species.
  - They represent about 44% of the extant species of mammals and are distributed almost worldwide.
  - Their structural and functional characteristics of locomotion and morphology are diverse, and they are highly adaptable in the many habitats they occupy.

- All rodents have a single pair of upper and lower chisel-shaped incisors, a diastema, and reduced numbers of molariform teeth.

- Convergence and parallelism of morphology and associated behavior are key themes among rodent taxa.
  - Behavior, structural similarity, and kangaroo-like bipedal locomotion are evident among some of the heteromyids, pedetids, dipodids, and certain murids.
  - The anomalurids and certain gliding sciurids show highly convergent adaptations, as do fossorial geomyids, bathyergids, ctenomyids, and some murids.

- Lagomorphs are structurally and functionally similar in many respects to rodents, and the two orders are grouped together in the clade Glires.
  - Lagomorphs have less than 4% the number of species as rodents.
  - They have more restricted habitats, morphology, and locomotion.

- Peg teeth (small pair of incisors posterior to the large, upper incisors) are the single key characteristic that defines the order.

- Some leporids are significant game animals.

- Others are introduced species that have caused significant damage in several countries.
  - However, economic importance and effect on humans of the two families of lagomorphs are minor compared with those of rodents.

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DISCUSSION QUESTIONS

1. Discuss kin selection and various factors that could contribute to eusociality and reproductive "altruism," including fossorial living or patchy distribution of resources, in species such as the naked mole-rat.

2. How might breeding be suppressed in the majority of members in a colony of naked mole-rats, such that only the queen and one male breed?

3. Convergence in rodents in terms of bipedal locomotion, fossorial adaptations, and gliding is noted in the summary. List two or three rodent taxa that show similar convergence in terms of adaptations for an aquatic niche.

4. Considering rabbits and hares, how would complexity of nest construction relate to whether neonates are altricial or precocial?

5. What is the significance of coprophagy in mammals? Besides lagomorphs, what other mammalian orders exhibit coprophagy? Why are no carnivores coprophagous?

Order: Eulipotyphla

Order Eulipotyphla

The four families discussed in this chapter have a confusing and chaotic taxonomic history. Although the four families in Order Eulipotyphla are not considered to be phylogenetically close, all were included at one time in the inclusive Order Insectivora, usually referred to as the "wastebasket" taxon for families of uncertain affinities (Simpson 1945; Butler 1972; MacPhee and Novacheck 1993; McKenna and Bell 1997; Kingdon et al. 2013; Wilson and Mittermeier 2018). As a result of modern molecular analyses, "insectivores" have been "sorted out" and comprise six orders. Three orders discussed in Chapter 11, the Order Macroscelidea (elephant shrews or sengis), Order Afrosoricida (tenrecs and golden moles), and Order Tubulidentata (the aardvark) are part of the Superorder Afrotheria. Two other orders are in the Grandorder Archonta: the Order Scandentia (treeshrews) and the Order Dermoptera (colugos) (see Chapter 14). The final order of insectivores, Eulipotyphla, is the subject of this chapter and includes four families: the Solenodontidae (solenodons), Soricidae (shrews), Talpidae (moles and desmans), and Erinaceidae (hedgehogs and gymnures). For the sake of discussion, and recalling traditional nomenclature, we will periodically refer to members of several of these orders as "insectivores."

Many insectivorous morphological characteristics are considered ancestral and probably represent characteristics common to the earliest mammals (O'Leary et al. 2013). As such, "insectivores" probably are near the ancestral stocks of many other orders of eutherians that have advanced, or more recently derived, characteristics. These 6 orders include a total of 12 families. Phylogenetic relationships among and within families often remain unresolved, although molecular analyses are providing additional insights.

MORPHOLOGY

Unlike most mammalian orders, no key character or set of characters serves to identify insectivores. This is one of the most anatomically diverse mammalian groups; each family has interesting adaptations for survival. Members of this group are generally small to medium sized, pentadactyl, with generalized plantigrade locomotion, and long, somewhat pointed snouts. Pelage of adults often is made up only of guard hairs, sometimes modified as spines, as in hedgehogs and tenrecs. The **pinnae** (external ear) and eyes usually are small or absent; the eyes of golden moles are nonfunctional and without external openings. Primitive characteristics include a small braincase and a brain with smooth cerebral hemispheres. A ring-shaped tympanic bone is present instead of auditory bullae, and the anterior vena cavae are paired. In males, the testes are usually abdominal or within the inguinal canal; if external, the scrotum is anterior to the penis. A cloaca is present in some genera. The jugal bone is reduced or absent, and the pubic symphysis is reduced.

Another ancestral insectivore characteristic is their dentition. As noted in Chapter 4, some insectivores retain tribosphenic molars, including tenrecids, chrysochlorids, solenodontids, and some soricids. Teeth are rooted, so they do not grow throughout life. The deciduous teeth are shed early and are seldom functional. The molars have four or five cusps and usually form a V-shaped (**zalambdodont**) or W-shaped (**dilambdodont**) occlusal pattern (Figure 17.1). In many species, the total number of teeth is often the same as the primitive eutherian pattern: 3/3, 1/1, 4/4, 3/3 = 44. Given the morphological diversity within the currently recognized Orders and the uncertain affinities of families, it is not surprising that Springer and colleagues (1997a) concluded that the order is not monophyletic. Using genetic analyses, they found the golden moles (see the subsequent section on Family Chrysochloridae) strongly associated with a group of taxa that includes elephant shrews, the aardvark (*Orycteropus afer*: Order Tubulidentata), and three orders discussed in Chapter 19—elephants (Order Proboscidea), hyraxes (Order Hyracoidea), and sirenians. Similar relationships were reported by Mouchaty and colleagues (2000a), and by Stanhope and coworkers (1998) who proposed the new "Afrosoricida" order to include these taxa as well as the tenrecs (see the subsequent section on Family Tenrecidae and discussion by Bronner and Jenkins 2005).

FOSSIL HISTORY

Historically, we think of the fossil "insectivores" as a diversified assemblage with approximately 150 described genera. As noted by Butler (1972:254), this is because "any early fossil eutherian not clearly related to one of the other orders is classifiable in the order Insectivora." As noted, however, because it clearly is not monophyletic, Order Insectivora is no longer recognized. The earliest fossil "insectivore," the tiny, poorly known remains of *Batodon*, dates from the mid-Cretaceous period in North America, about 100 mya. The oldest members of clearly recognizable families—soricids and talpids—date from the Eocene epoch, about 50 mya (Harris 1998). Summaries of research focusing on paleontological relationships of New World and Old World shrews can be found in Wójcik and Wolsan (1998), Hutterer (2005), and Merritt and colleagues (2005).

ECONOMICS AND CONSERVATION

Mammalian "insectivores" are of little economic importance today. Until the late 1800s, moles were trapped for their pelts, which were used for hats, apparel trim, and other purposes. Today, although they may damage lawns, fields, and gardens, moles have a relatively minor economic effect compared with rodents. Hedgehogs, moles, and shrews take harmful insects as prey, but their impact is fairly negligible compared with insectivorous bats. Because many insectivores are found in tropical areas where habitats are often rapidly lost to logging and agriculture, several species are considered threatened or endangered (see the discussion of each family).

FAMILIES

Solenodontidae

This family is represented by 1 genus and 2 extant species (Hutterer 2005b; Wilson and Mittermeier 2018). Both the Cuban solenodon (*Solenodon cubanus*; Figure 17.2) and the Hispaniolan solenodon (*S. paradoxus*), which resides in the Dominican Republic and Haiti, are considered endangered. Combined gene sequences (13.9 kilobases) from *S. paradoxus*

Figure 17.1 **Representative occlusal surfaces in "insectivores."** (**A**) Occlusal surfaces of the left upper tooth row from a European mole (*Talpa europaea*) with a dilambdodont (W-shaped) cusp pattern; (**B**) left upper tooth row from a giant otter shrew (*Potamogale velox*) with a zalambdodont (V-shaped) cusp pattern. *Adapted from Cabrera (1925).*

Figure 17.2 **Unusual insectivores—the solenodons.** The small eyes and shrew-like snout are characteristic of the endangered Hispaniolan solenodon. Prior to the arrival of Europeans, solenodons were among the largest predators within their restricted geographic area. They are quite defenseless against introduced mongooses and house cats, however. *Adapted from Flower and Lydekker (1896).*

Figure 17.3 **Use of toxin for prey capture by solenodons.** (**A**) Dorsal and (**B**) lateral views of the skull of a Cuban solenodon. Note the incomplete zygomatic arch and enlarged first upper incisor. (**C**) The large second lower incisor is deeply grooved to accommodate secretions of toxin from the submaxillary gland below it. *Adapted from DeBlase and Martin (1981).*

established that solenodons diverged from other lipotyphlan "insectivores" 76 mya in the Cretaceous period (Roca et al. 2004; Sato et al. 2016; Wible and Hughes 2016). Solenodons shelter in caves, crevices, and under logs; they construct extensive networks of tunnels reaching depths greater than 20 cm below ground (Eisenberg and Gozalez 1985). They inhabit forests of Cuba and Hispaniola to elevations of 2,000 m. They are one of the few native nonflying mammals that survived human settlement of the islands of the West Indies (MacPhee et al. 1999). Solenodons are among the largest "insectivores," with total lengths approaching 600 mm. The pelage, naked tail, claws, and pinnae are all rather long, and the eyes are small. They have a pointed, highly flexible, and sensitive shrew-like snout used in capturing prey. They inhabit rocky, brushy, or forested areas, move slowly in a zigzag path with a waddling gait, and are omnivorous. Solenodons emit high-frequency clicking sounds that probably function in echolocation. Along with certain shrews and the platypus (see Chapter 10), they are among the few mammals that use a toxin. It is produced in the submaxillary glands, located at the base of the second lower incisor, which is large and deeply grooved to accommodate the toxic secretions (Figure 17.3). Both species are considered endangered because of habitat loss and introduced predators, such as mongoose and feral cats, against which they are defenseless. Recovery of solenodon populations is also hampered by their low reproductive rate (Turvey et al. 2016).

A closely related group of from 6 to 9 species in the Genus *Nesophontes* from Cuba, Haiti, Puerto Rico, and other islands survived until the last several hundred years, with speculation that some species may have remained extant within the last 50 years. As noted by MacPhee and coworkers (1999:11), however, "There is no direct evidence at present that any species of *Nesophontes* even outlasted the close of the fifteenth century, let alone that of the nineteenth century." These recently extinct species now comprise their own family, the Nesophontidae.

Soricidae

Shrews constitute the largest and most widely distributed family of insectivores. There are about 25 genera and 448 species, although many are of uncertain taxonomic status (Hutterer 2005b; Wilson and Mittermeier 2018). This large family includes two subfamilies. The Subfamily Soricinae (the red-toothed shrews) includes three tribes found throughout much of the Nearctic, Palaearctic, and Oriental faunal regions (Figure 17.4). The Subfamily Crocidurinae (the white-toothed shrews) is restricted to Old World faunal regions (Churchfield 1990; Wójcik and Wolsan 1998; Merritt 2010). Shrews are generally small. Body mass ranges from 3 g and 35- mm head and body length for adult pygmy white-toothed shrews (*Suncus etruscus*) and pygmy shrews (*Sorex hoyi*), two of the smallest mammals in the world, to 100 g and 150-mm head and body length for the musk shrew (*Suncus murinus*). Most species of shrews weigh 10–15 g and have a head and body length of about 50 mm. Legs are short, and the feet are unspecialized, except in the elegant water shrew (*Nectogale elegans*) and the North American water shrew (*Sorex palustris*), which are semiaquatic. Species associated with wet habitats have fimbriated hind feet. Shrews have small eyes and a long, pointed rostrum. Their pelage is short, dense, and usually dark-colored. In many species, lateral glands produce a musky odor that is most noticeable during the breeding season.
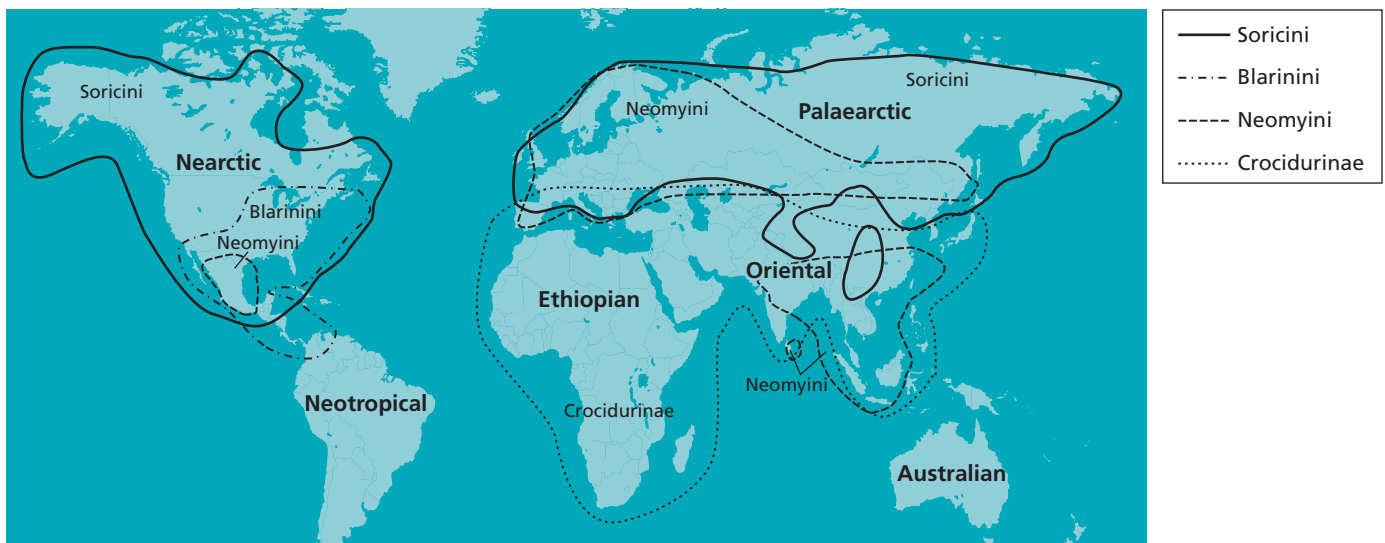
Figure 17.4 Worldwide distribution of shrews. Geographic distribution of red-toothed shrews (Subfamily Soricinae, which includes three tribes: Neomyini, Soricini, and Blarinini) and the white-toothed shrews (Subfamily Crocidurinae). *Data from Churchfield (1990).*
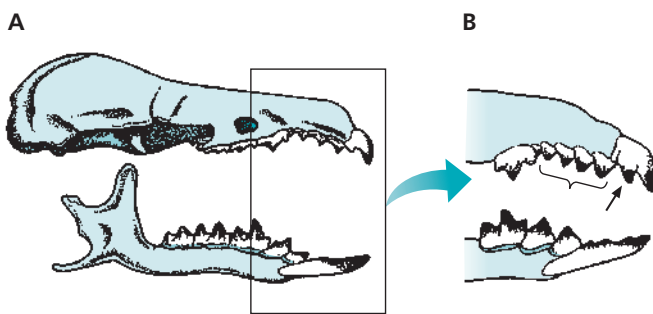
Figure 17.5 Characteristic features of shrew skulls. (**A**) A typical shrew skull. Note the lack of the auditory bullae and zygomatic arch. (**B**) The enlarged anterior portion of a red-toothed shrew showing the distinctively pigmented enamel, procumbent first lower incisor, secondary cusp on the first upper incisor (*arrow*), and unicuspids (*bracket*). The incisors function as tweezers picking up insect prey that are then passed to the sharp, multicusped posterior teeth for crushing and chewing. *Adapted from Churchfield (1990).*

Shrew skulls have no zygomatic arch and no auditory bullae. The teeth are noteworthy in several ways. The first upper incisor is large and hooked and has a posterior cusp that appears to be a distinct tooth (Figure 17.5). The first lower incisor is long and procumbent (projecting horizontally forward). The upper molars are dilambdodont. The deciduous teeth are shed prior to parturition. In members of the Subfamily Soricinae, the tips of the teeth are a deep red (see Figure 17.5). This color is caused by iron deposits (Dötsch and Koenigswald 1978; Dumont et al. 2014) and is worn down and reduced as individuals age. Shrews with pigmented teeth are thus distinguished from the white-toothed shrews (Subfamily Crocidurinae), which do not have this characteristic. The groups also differ in biogeography, behavior, and physiology (Churchfield 1990; Merritt et al.

1994; Merritt and Zegers 2014; Cornette et al. 2015). Querouil and colleagues (2001, 2005) used partial sequences of the mitochondrial 16S ribosomal RNA gene to examine relationships among genera of African Crocidurinae. Molecular phylogeny of Palearctic shrews from the Genera *Sorex*, *Crocidura*, *Neomys*, and *Suncus* were assessed using **Restriction Fragment Length Polymorphism (RFLP)** analysis of genome DNA and In Situ Polymerase Chain Reaction (IS-PCR) methods (Bannikova and Kramerov 2005). These techniques were useful in delineating two main lineages within the Palearctic Genus *Sorex* in addition to resolving other difficult phylogenetic questions arising from discordant morphological, karyological, biochemical, and mtDNA data associated with the phylogeny of shrews.

Shrews are mainly insectivorous, but many species are functional omnivores, consuming subterranean fungi. Shrews are found in many terrestrial habitats, usually with a heavy vegetative ground cover and an abundance of invertebrates. This family is a good example of the ways body size constrains aspects of life history (Merritt 1995; Taylor 1998; McNab 2006; Hoole et al. 2016). Shrews are often closely associated with water or moist habitats because they have a high respiratory water loss—a characteristic directly related to small size. The average life span of most shrews is only about a year (Figure 17.6) because they have such high mass-specific metabolic rates, again associated with small size (Taylor 1998). Shrews are too small to hibernate or migrate, although some may enter torpor. As a result, most forage throughout the year, which exposes them to extremes of weather and predators and affects life span. As noted by Merritt and Vessey (2000:235), "Daily activity patterns of shrews are controlled by metabolic requirements commensurate with their diminutive body mass and resultant high surface-to-mass ratios; they must forage often to avoid exhaustion of their energy stores. To
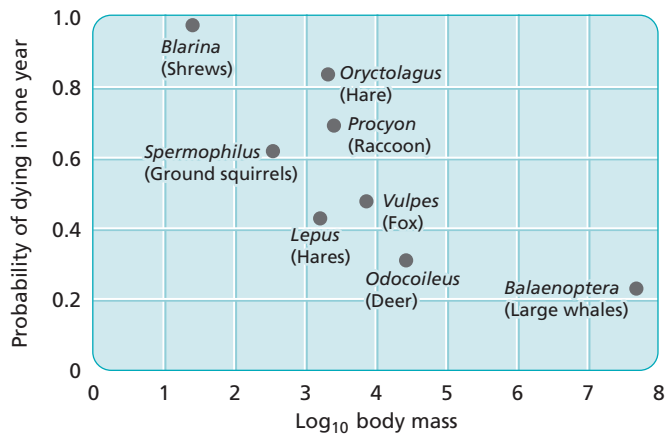
Figure 17.6 Mortality and body mass relationship.
Inverse relationship between body size in a number of different mammals and the probability of dying within the first year of life. Note that the chance of a shrew such as *Blarina* living much beyond one year is very low. *Data from Eisenberg (1981).*

Figure 17.7 Caravanning shrews. Caravanning in shrews involves a unique behavior in which each youngster grasps the base of the tail of the preceding shrew so that the mother runs along with the young trailing in a line behind her. This behavior has been reported for masked shrews (*Sorex cinereus*) and Sicilian shrews (*Crocidura sicula*).

remain homeothermic, shrews must partition a 24-h period into multiple bouts of foraging, rest, and sleep." Although several factors may affect activity in soricids, including feeding, photoperiod, precipitation, and temperature, few clear relationships are evident. Crocidurine shrews, and presumably soricine shrews as well, exhibit a behavior called "caravanning" (Figure 17.7) (Wilson and Mittermeier 2018). Churchfield (1990:33) described this behavior, which involves a mother and her young, as follows: "Each youngster grasps the base of the tail of the preceding shrew so that the mother runs along with the young trailing in a line behind her." Numerous species of soricids are threatened or endangered (IUCN 2018).

Many other aspects of these small insectivores are fascinating. Like solenodons, several species, including the short-tailed shrews (Genus *Blarina*) and European water shrews (Genus *Neomys*), have salivary glands that secrete a toxin used to immobilize prey (see Chapter 8) (Tomasi 1978; Churchfield 1990; Kita et al. 2004, 2005). Many species of soricine shrews use high-frequency sounds for interspecific communication, orientation, and prey detection (Tomasi 1979; Forsman and Malmquist 1988; Churchfield 1990; Tapisso et al. 2013; von Merten and Siemers 2012). Echolocation in shrews is not as well studied as in bats. As with sand-dwelling chrysochlorid golden moles mentioned earlier, seismic body vibrations are also reported for the piebald shrew (*Diplomesodon pulchellum*) residing in the Turan Lowland east of the Caspian Sea in Turkmenistan and Uzbekistan (Volodin et al. 2012). Vibrations of piebald shrews are generated by muscles of the body wall. Airborne waves of vibratory drumming average a frequency of 160.5 Hz. Such vibrations may be employed for exploring the density of the substrate to minimize costly digging of packed sand associated with burrowing and foraging and may be important for **agonistic** communication of piebald shrews (Volodin et al. 2012).

Venomous bites (see Chapter 7) and seismic body vibrations of shrews and solenodons noted above are certainly unique adaptations for survival; however, from the standpoint of architecture only one shrew, the hero shrew (*Scutiosorex somereni*), clearly displays the premier winning adaptations. The hero shrew, also known as the armored shrew, is a large shrew weighing from 70 to 113 g and is a native to the Congo Basin of Africa. Although its features are similar to other white-toothed shrews noted above, it is quite unique in possessing a spinal column of corrugated interlocking vertebrae adapted for supporting huge amounts of weight (see box) (Cullinane et. al. 1998; Cullinane and Bertram, 2000; Stanley et al. 2013; Kingdon et al. 2013).

Talpidae

About 18 genera of moles, desmans, and shrew-moles constitute this family; talpids are closely related to soricids (Mouchaty et al. 2000b; Hutterer 2005b). They are distributed throughout Europe, the Palaearctic region, and Asia, including Japan. In North America, they are found in southern Canada and most of the United States. Talpids are fairly diverse, ranging from moles, which are fossorial, to desmans, which are semiaquatic. Shrew-moles, the smallest talpids, are terrestrial. They are much more agile than moles, forage on the surface, and occasionally climb small shrubs. The star-nosed mole (*Condylura cristata*) of North America is unique among moles for its semiaquatic lifestyle and predilection for moist soils bordering streams and lakes. Star-nosed moles live farther north than any other North American mole; they cope with cold encountered during foraging by possessing an elevated metabolic rate and high body temperature (Campbell et al. 1999).

The morphology of talpids reflects their fossorial life. The body shape is fusiform, with short, powerful limbs and

The Hero Shrew: An Enigmatic Insectivore

Hero shrews (*Scutisorex somereni*) inhabit swampy forests of northern Zaire, Rwanda, and Uganda. Also called "armored shrews," they were first described from a single specimen from Uganda found in 1913 by Oldfield Thomas. The English name "hero shrew" has its origin with the Mangbetu people of the Democratic Republic of the Congo. The Mangbetu and other natives of the region were well acquainted with the strength of these rather large shrews—they weigh up to 90 g. Natives believed that when setting out on dangerous adventures such as hunting elephants or even engaging in warfare, they would be protected if they wore the charred body or even the heart of a hero shrew as a talisman. Medicine derived from the hero shrew would transmit invincible qualities and convey protection from spears and arrows, thereby acting as a passport to heroism. Local tribesmen demonstrated the strength of live hero shrews by standing on them. The strength of the vertebral column coupled with the strong convex curve behind the shoulder evidently protected the heart and other organs from being crushed—and shrews ran off unharmed.

This skeletal strength is derived from the unique morphology of the spinal column, which is unparalleled among mammals. There are 11 lumbar vertebrae (the typical mammalian number ranges from 5 to 6) augmented by lateral, dorsal, and ventral interlocking spines (called "apophyses"), which form a unique basket-like structure. Relative to its body mass, the spine is 4 times more robust than that of any other species of vertebrate, yet the vertebral column is quite flexible.

So what is the adaptive significance of the hero shrew's unique and remarkable spine? Authorities contend that there is no obvious behavioral or functional explanation for this unparalleled vertebral morphology. Because hero shrews reside in swampy palm forests where they establish runways around the base of trees and feed on beetle larvae and earthworms residing under dead leaf bases under tree trunks, they can use their spines and associated musculature to leverage heavy objects such as logs to gain access to aggregates of invertebrate prey below the leaf litter. For more information on these remarkable shrews, see the references.

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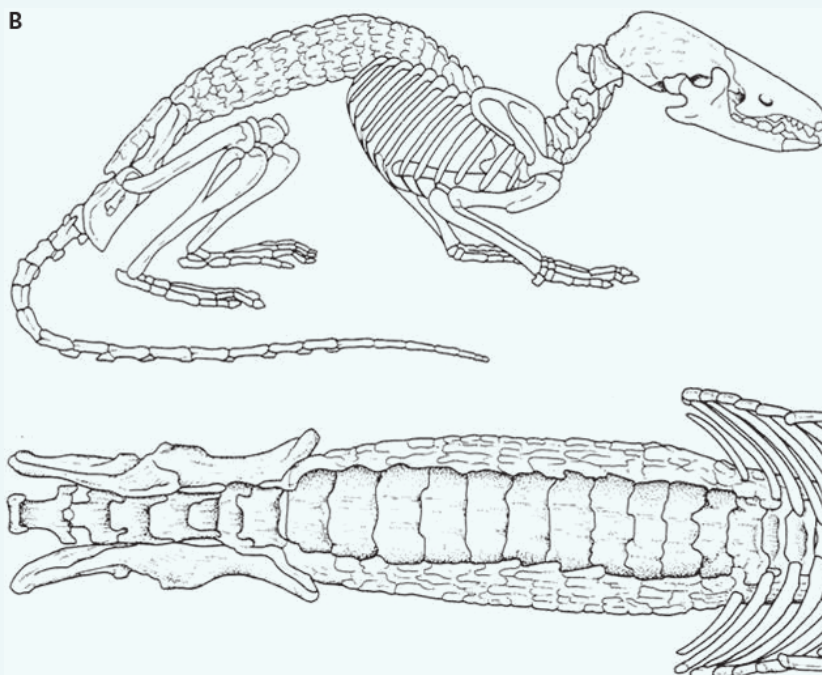
Hero shrews: a lot stronger than they look. (**A**) The hero, or armored, shrew (*Scutiosorex somereni*) inhabits forests of the Democratic Republic of the Congo. (**B**) It shows a unique vertebral column characterized by 11 lumbar vertebrae rather than the usual 5 or 6. (**C**) Vertebrae are particularly sturdy due to presence of many articular apophyses and interlocking spines forming a basket-like structure unlike any other mammal. *(B) Diagrammatic interpretation from Churchfield (1990).*

short, smooth pelage (Figure 17.8). The pinnae are reduced or absent, and the eyes are minute. The sternum is keeled for enhanced pectoral muscle attachment, which is useful in digging. The forefeet are large and paddle-like, with large claws. Because the radius articulates with the humerus, the forefeet are permanently rotated outward (see Figure 17.8) and produce the unique lateral digging motion of moles. The humerus is short and broad, again for enhanced muscle attachment, and articulates with both the clavicle and scapula to generate a great deal of force for dig-

Figure 17.9 **Mole burrow system.** Example of depth and extent of burrow construction of a mole. *Data from Arlton (1936).*

A

B

C
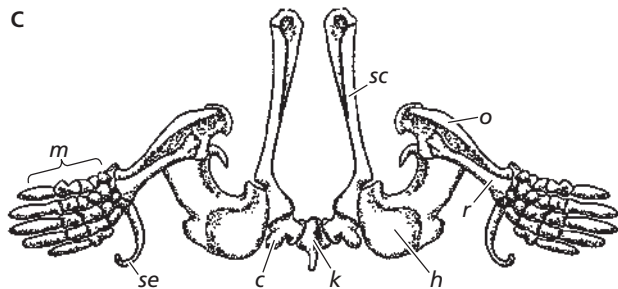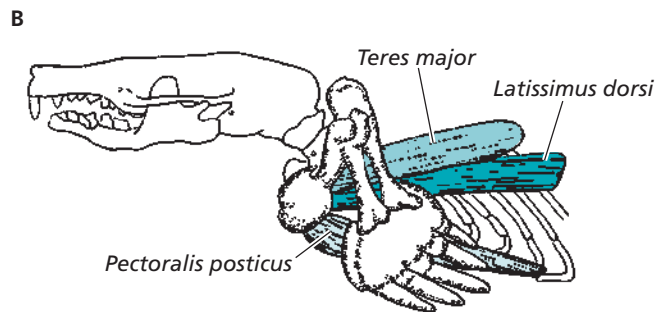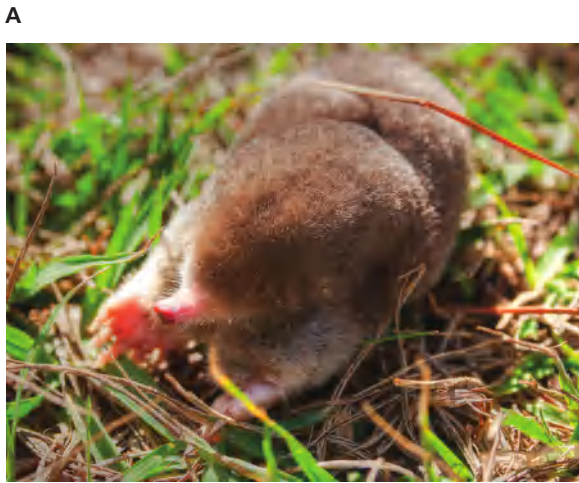
Figure 17.8 **Morphological features of moles.** (**A**) The short hair, pointed snout, fusiform body shape, and large forepaws are evident in this eastern mole (*Scalopus aquaticus*). (**B**) The massive forearm is supported and rotated by the *teres major*, *latissimus dorsi*, and *pectoralis posticus* muscles. (**C**) Forelimbs and highly modified pectoral girdle of the European mole. Note the large manus (*m*) with modified sesamoid bone (*se*), the small clavicle (*c*), keeled sternum (*k*), elongated scapula (*sc*), and elongated olecranon process (*o*) of the ulna. The humerus (*h*) is massive and rectangular and articulates with the radius (*r*). *Adapted from Gorman and Stone (1990).*

ging. The olecranon process of the ulna also is very long for enhanced attachment of the triceps muscle. As a result, the digging muscles of the eastern mole (*Scalopus aquaticus*) can generate a force 32 times its own body mass (Arlton 1936; Hartman and Yates 2003; Lin et al. 2017).

The only evidence of moles that most people see is their tunneling activity and resulting molehills of excess excavated dirt. Burrowing is generally done in moist soils. Shallow tunnels 4–5 cm in diameter and a few centimeters below the surface are made when moles search for invertebrate prey. These are not as permanent as the complex, branching network of defended tunnels that extend to 150 cm deep and include the nest chamber (Figure 17.9) (Gorman and Stone 1990; Hartman and Yates 2003). The Family Talpidae contains a diverse array of insectivores that exhibit some of the most unusual mechanosensory specializations found among mammals. Nearly all species of talpids possess small, domed mechanosensory organs called "Eimer's organs" located on their rhinarium (Catania 2000). With poorly developed eyesight and only a moderately developed sense of smell, the star-nosed mole (*C. cristata*) of eastern North America uses its impressive snout, equipped with 22 projecting nasal appendages and long whiskers, to search for prey below ground and in streams. We feature this fascinating mole and its equipment of "Eimer's organs" in Chapter 7—modes of feeding.

Restricted to the Old World, desmans have a diet consisting of aquatic invertebrates and fish. The Russian desman (*Desmana moschata*) prefers ponds and marshes with thick vegetation. Conversely, the Pyrenean desman (*Galemys pyrenaicus*) inhabits streams and rivers with clear, fast-moving water. Head and body length is about 200 mm in the Russian desman and about 140 mm in the Pyrenean desman. The tail is laterally compressed in both species and equals the head and body length. The hind feet are webbed and fimbriated (having a fringe of hairs) for additional surface area. Both adaptations help desmans to swim rapidly. Their long, flexible snouts are very sensitive and are used to locate prey under water. Desmans echolocate to maneuver and locate prey (Richard 1973), like shrews and some tenrecs. Both species are negatively affected by habitat loss,

construction of dams and roads, and water pollution. The endangered Russian desmans are harvested for their pelts. Pyrenean desmans are further reduced in number because of predation by introduced mink (*Neovison vison*). Several species of Asian moles and shrew-moles are endangered.

Erinaceidae

There are 10 genera and 26 species of extant erinaceid**s** comprising 2 subfamilies. The Subfamily Erinaceinae contains 18 species of spiny hedgehogs, and the subfamily of gymnures or moonrats (Galericinae) include 8 species of gymures, which are mostly nonspiny and have softer pelage (Hutterer 2005; Wilson and Mittermeier 2018).

Hedgehogs are found in the Palearctic, Afrotropical, and Indo-Malayan regions. They have barbless spines on the back and sides (Hutterer 2005a; Kim et al. 2017). They inhabit many different habitats, including deserts, steppes, forests, urban grasslands, parks, fields, and farmlands. As their name suggests, desert hedgehogs (Genus *Paraechinus*) inhabit arid areas in North Africa, India, and Pakistan. Long-eared desert hedgehogs (Genus *Hemiechinus*) are found from northern Africa east to the Gobi Desert of Mongolia. Hedgehogs are mainly nocturnal and terrestrial, but some are semiarboreal. Adult *Hemiechinus auritus* weigh only 40–50 g, whereas the common European hedgehog (*Erinaceus europaeus*) reaches 1100 g. All are omnivorous, feeding on small vertebrates, eggs, fruits, and carrion in addition to invertebrates. Hedgehogs are well known for their ability to employ torpor as a mechanism for energy conservation in response to reduced energy availability and/or cold (Baker et al. 2016). Daily torpor may occur at any time of the year. Body temperature does not fall below 17°C, and the hedgehog may remain in a torpid state for periods >22 hours at a time. During torpor, their body temperature falls to within a few degrees of ambient (Geiser and Ruff 1995; Webb and Ellison 1998; Boyles et al. 2017). Warm-season torpor (also called "estivation") is reported for the closely related *Hemiechinus micropus* from India. This species has survived in captivity for periods of 4 to 6 weeks without food or water (Nowak and Paradiso 1991). In Kenya, *Erinaceus albiventris* undergoes estivation during the dry season from May to October. This form of torpor may be due in part to shortages of food because temperatures are known to remain moderate for this period. (See Chapter 8 for information on dormancy in mammals.) Basing their conclusion on mtDNA analyses, Mouchaty and colleagues (2000b:64) considered "the hedgehog as the most basal eutherian taxon." However, Murphy and co-workers (2001a), who used a much more extensive data set, did not support this conclusion.

A European hedgehog has approximately 5,000 spines (Figure 17.10A). Its defensive posture is typical for a mammal with spines or scales. When threatened, it rolls into a tight ball with the spines directed outward (see Figure 17.10B). This posture is aided by paired longitudinal "drawstring" muscles, the *panniculus carnosus*, on either side

Figure 17.10 Hedgehog spines. (**A**) Lateral view of a long-eared hedgehog (*Hemiechinus auritus*). An adult hedgehog has about 5,000 spines, each 2–3 cm long. The medulla of each spine is filled with air pockets to reduce weight. (**B**) The defensive posture of an African hedgehog (*Erinaceus frontalis*) is similar to that of armadillos and scaly anteaters.

of the body. Hedgehogs have an interesting "self-anointing" behavior in which they spread large amounts of foamy saliva on the spines. This may be done as a sexual attractant during the breeding season, to reduce parasites, to clean the spines, or as additional protection from predators (Wroot 1984; Weldon 2004; D'havé et al. 2005). Several species, including the common European hedgehog, undergo true hibernation throughout the winter—the only insectivores that do. Desert hedgehogs commonly estivate (enter a dormant condition in the summer). Litter size is generally between 4 and 6, and 2 litters a year can be produced. The young are altricial (immature). At birth, their short, soft spines have not yet broken through the skin, but the spines quickly grow in length after birth (Figure 17.11) and harden within a few weeks.

Figure 17.11 Spines in a newborn hedgehog. Spines on this litter of newborn, nursing hedgehogs erupt and harden after birth.

Figure 17.13 Lesser gymnure. Gymnures are smaller than moonrats and as with moonrats they lack spines, The short-tailed gymnure (*Hylomys suillus*) weighs between 50 and 70 g and resembles a large shrew.

Figure 17.12 Moonrat (*Echinosorex gymnura*). These moonrats possess a very coarse, rough pelage consisting of a short thick underfur covered by a dense layer of long course hair. Unlike hedgehogs, moonrats lack spines. The coloration is generally black with a whitish head and shoulders; however, some individuals are white as in this photo.

The gymnures or moonrats of the subfamily Galericinae are found in Java and Borneo, the Malay Peninsula, and throughout southeastern Asia, to southwestern China (Hutterer 2005a; Jenkins and Robinson 2002; Meredith 2011; Bannikova et al. 2014; Kim et al. 2017; Wilson and Mittermeier 2018). Moonrats such as *Echinosorex gymnura* (Figure 17.12) and gymnures (Figure 17.13) lack spines and possess a very coarse, rough pelage consisting of a short thick underfur covered by a dense layer of long coarse hair. The tail is long and scaly with very short hairs. The coloration is generally black with a whitish head and shoulders; however, some individuals are white (see Figure 17.12). The head and body length of moonrats ranges from 260 to 460 mm. These large erinaceids reach up to 2 kg in mass, or about the size of a muskrat. They have a very narrow form, possibly an adaptation for securing food in narrow crevices. Moonrats are noted for their strong, pungent, ammonia-like odor, which is different than the **musk** smell of carnivores. The odor emanates from a pair of anal scent glands. Moonrats are solitary, nocturnal, and terrestrial, and they reside in hollow logs, in abandoned burrows, and under roots of trees (Gould 1978). They inhabit lowland forests, mangroves, rubber plantations, and cultivated fields. They prefer damp areas and readily enter water, where they feed on frogs, fish, mollusks, crustaceans, and insects. Moonrats breed throughout the year and typically produce 2 litters per year with an average litter size of 2; gestation period is about 35–40 days. Maximum longevity in captivity is 55 months (Nowak 1999).

Gymnures are smaller than moonrats, but like moonrats they lack spines. The short-tailed gymnure (*Hylomys suillus*) weighs between 50 and 70 g and resembles a large shrew. It has an elongate muzzle, dense, soft pelage, and conspicuous rounded leathery ears. Similar species include the shrew gymnure (*Neotetracus* [*Hylomys*] *sinensis*), which possesses a long tail, and the long-eared gymnure (*Hylomys megalotis*), which has a longer and thicker tail and larger ears (Hutterer 2005a; Francis 2008; Bannikova et al. 2014; Wilson and Mittermeier 2018). Gymnures reside in humid tropical forests typified by an abundant leaf litter, where they feed on arthropods and earthworms. Francis (2008) reported *H. megalotis* in limestone karst areas of central Laos. The Hainan gymnure (*Neohylomys hainanensis*), and dinagat gymnure (*Podogymnura aureospinula*) are endangered (IUCN 2018).

SUMMARY

Order Eulipotyphla consists of Families Solenodontidae, Soricidae, Talpidae, and Erinaceidae, which are rich in diversity of form and function.

• These "insectivores" retain many primitive eutherian characteristics, including their brain anatomy, dentition, cranial morphology, postcranial structures, and cloaca.
  ◦ As such, they are thought to be ancestral to other mammalian orders.

◦ In contrast to their primitive characteristics, many have developed highly specialized features, such as echolocation (tenrecs and shrews) and toxin in the saliva (solenodons and some shrews).

• Unlike many other orders, no key morphological character serves to identify these groups.

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DISCUSSION QUESTIONS

1. What do you think might be the functional significance of the pigmented teeth found in the soricid Subfamily Soricinae—the red-toothed shrews? Can you think of pigmented teeth in any other mammalian orders?

2. What is the adaptive significance of caravanning behavior in shrews?

3. The textbook discusses how body size influences the life-history characteristics of shrews. What other factors would you expect also are affected by small body size? What other factor would you expect also are affected by small body size in shrews?

4. How does body size influence the available range of prey of shrews? How does it influence reproductive potential and life span?

5. Why have so few species of mammals developed the use of toxins as part of their life history strategies?

6. Several possible reasons for the "self-anointing" behavior of hedgehogs were given in the text. Can you think of any others? Do any other mammals do this?

Orders: Carnivora and Pholidota

Order Carnivora

A great deal of variety exists among the 16 families and approximately 300 species in this order. Included are large terrestrial predators such as wolves, bears, and big cats, as well as well-known charismatic species such as pandas, the tiger (*Panthera tigris*), and the cheetah (*Acinonyx jubatus*). Lesser known perhaps are many small species, such as the least weasel (*Mustela nivalis*), the smallest member of the order. Carnivores exhibit broad diversity in feeding habits and degree of sociality. Most carnivores eat meat. Although it is easier to digest than vegetation, meat is much more difficult to locate, capture, kill, and consume. Thus, carnivorans (members of Order Carnivora) generally are thought of as the major group of mammalian predators because they feed primarily on animal flesh (including other mammals). Whales, insectivores, many bats, a few rodents, and some marsupial species also consume animals but are not in Order Carnivora. Carnivorans occur naturally on all continents except Australia and have adapted to diverse niches in a variety of terrestrial and aquatic habitats. In this chapter, we will use the term "carnivore" to represent the taxonomic designation for carnivorans.

There are two suborders of carnivores (Flynn and Wesley-Hunt 2005; Wozencraft 2005; Agnarsson et al. 2010), based on the structure of their auditory bullae and carotid circulation (Flynn et al. 1988; Wozencraft 1989; Figure 18.1). Suborder Feliformia (meaning "cat-like") includes 7 families: the Felidae (cats); Prionodontidae (linsangs) (Gaubert et al. 2005; Gaubert 2010); Hyaenidae (hyenas); Herpestidae (mongooses); Viverridae (civets); Eupleridae (Madagascar mongooses); and the monotypic Nandiniidae (the African palm civet, *Nandinia binotata*). There are about 56 genera of extant feliforms. The other suborder, Caniformia (meaning "doglike"), with 74 living genera, includes the families Canidae (dogs); Mustelidae (weasels); Mephitidae (skunks); Procyonidae (raccoons); Ursidae (bears); the monotypic Ailuridae (the red panda, *Ailurus fulgens*), and 3 families of aquatic carnivores—Odobenidae (walrus), Otariidae (eared seals, including fur seals and sea lions), and Phocidae (earless, or true seals). Arnason and
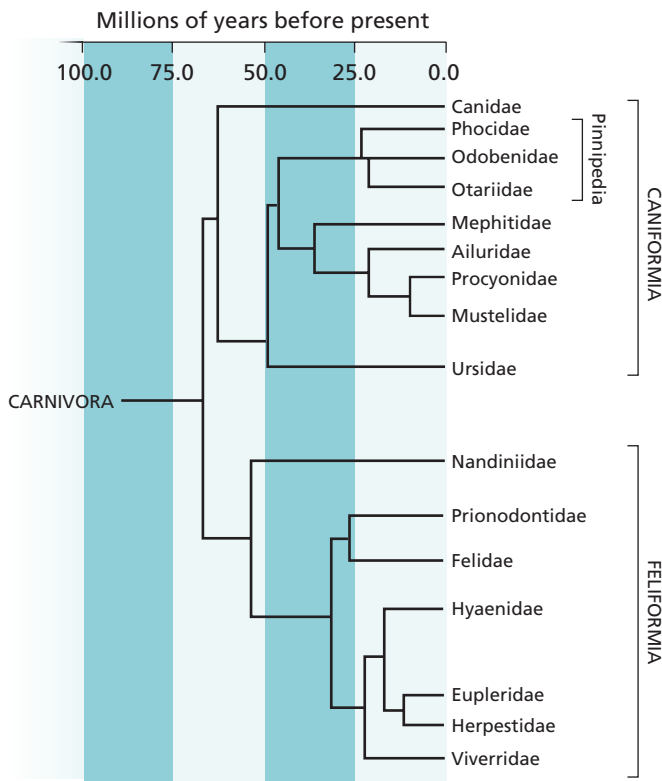
Figure 18.1 Phylogeny of extant carnivore families.
Within Suborder Caniformia, note the monophyly of the three
families of pinnipeds. Within the suborder Feliformia, the
African palm civet (Family Nandiniidae) and the linsangs (Family
Prionodontidae) are in their own families distinct from the
viverrids. The Madagascar mongooses (Family Eupleridae) are a
sister taxon to the mongooses (Family Herpestidae), and they
are most closely related to the hyaenas (Family Hyaenidae).

coworkers (2007) discussed phylogenetic relationships
among caniforms. The aquatic carnivores are referred to as
pinnipeds (meaning "feather-footed"), based on the modifi-
cation of their limbs into flippers. Unlike whales, pinnipeds
leave the water to rest, breed, and give birth. The sea otter
(*Enhydra lutris*; Mustelidae) is also essentially aquatic. Other
species of otters spend much of their time in water, as does
the polar bear (*Ursus maritimus*; Ursidae). In the past, pinni-
peds were considered either as a separate order of their own
or as a suborder within Order Carnivora, with the remaining
families grouped in Suborder Fissipedia (meaning "split-
footed") because of the individual toes on each foot. Cur-
rently, a single monophyletic order Carnivora is recognized.

Smaller species of carnivores generally have larger litters
and breed more frequently. Larger species, such as bears and
the pinnipeds, have small litters (often a single young), and
females may breed at intervals of several years. Induced ovu-
lation or delayed implantation (see Chapter 9) occur in cer-
tain species and are related to environmental or life-history
factors. Few carnivores have precocial young. Juveniles must
learn to hunt successfully under a variety of circumstances,
and an extended period of maturation and learning is often
required before these skills are acquired and individuals dis-
perse. This need to learn and adapt, as well as to develop a
high degree of coordination and dexterity, is reflected in the
high brain-to-body-mass ratio of carnivores. Rolland and
colleagues (2015) discussed the relationship between disper-
sal and latitudinal diversity in carnivores.

When hunting, individuals can be solitary, paired, or in
small groups. Smaller carnivores, such as weasels, are gen-
erally solitary and restricted to taking smaller prey. Larger
species, such as wolves, lions, hyenas, and African wild dogs
(*Lycaon pictus*), may hunt in packs. In addition to hunting
smaller prey, packs are able to prey on larger, more dan-
gerous species (Figure 18.2), which can be several times the
size of individual members of the pack (Scheel and Packer

Figure 18.2 Group hunting in lions. Hunting together allows many carnivores to take down larger prey species.

1991; Holekamp et al. 1997). Group living and associated social behavior serve to improve cooperative hunting success and, through communication of an individual's dominant or submissive status, to reduce intraspecific competitive pressure within groups. Groups can also provide communal infant care, reduce predation, and defend territories from rival packs. Caro (1994) provided a concise summary of factors affecting group living in carnivores.

Methods of hunting vary from concealment and a surprise pounce (stealth and "ambush" seen in many felids) to a stalk followed by a short, swift run (weasels) to a prolonged chase (wolves or hyenas). One of the functions of pelage in carnivores is concealment (as it is in potential prey species), and coloration is often related to hunting behavior. Generally, in cats and other groups in which concealment is critical, the pelage often has spots or stripes. Conversely, in predators such as canids, pelage is typically plain because concealment is less critical (Figure 18.3). There are exceptions to both cases, however.

As noted in the next section, species in this order exhibit several morphological and behavioral adaptations for searching out, capturing, and handling their prey so as to minimize the possibility of injury during the process. In this chapter, we explore general characteristics of carnivores as well as life-history strategies within lineages that have evolved to deal with constantly changing relations between predators and their prey.

MORPHOLOGY

The defining morphological characteristic of carnivores is the specialization of their fourth upper premolar (P^4) and first lower molar (m_1) as carnassial teeth used for shearing. Carnassials are especially well developed in the predaceous felids, hyaenids, and canids (Figure 18.4B) but much reduced in the omnivorous ursids (Figure 18.4F) and procyonids. Regardless of the relative development of carnassials, all carnivores have well-developed, elongated canine teeth.

Skulls are usually heavy, with strong facial musculature for crushing, cutting, and chewing flesh, ligaments, and bone. The relative development of facial muscle groups and associated skull shape reflect different life-history patterns and relative use of canines and cheekteeth. Van Valkenburgh (2007) noted the general convergence of craniodental feeding adaptations within the Carnivora. Carnivores often have a deep, sharply defined, C-shaped **mandibular fossa** (the portion of the cranium that articulates with the mandible). This strong hinge joint, particularly evident in mustelids (Figure 18.5A), minimizes lateral movement of the mandible as captured prey struggles and permits only a vertical (up-and-down) motion. In addition to less-developed carnassial teeth, omnivorous carnivores such as bears (Figure 18.5B) and raccoons have a relatively flatter mandibular fossa that allows more lateral motion of the jaw as the animal chews. As might be expected, the size and shape of the mandi-
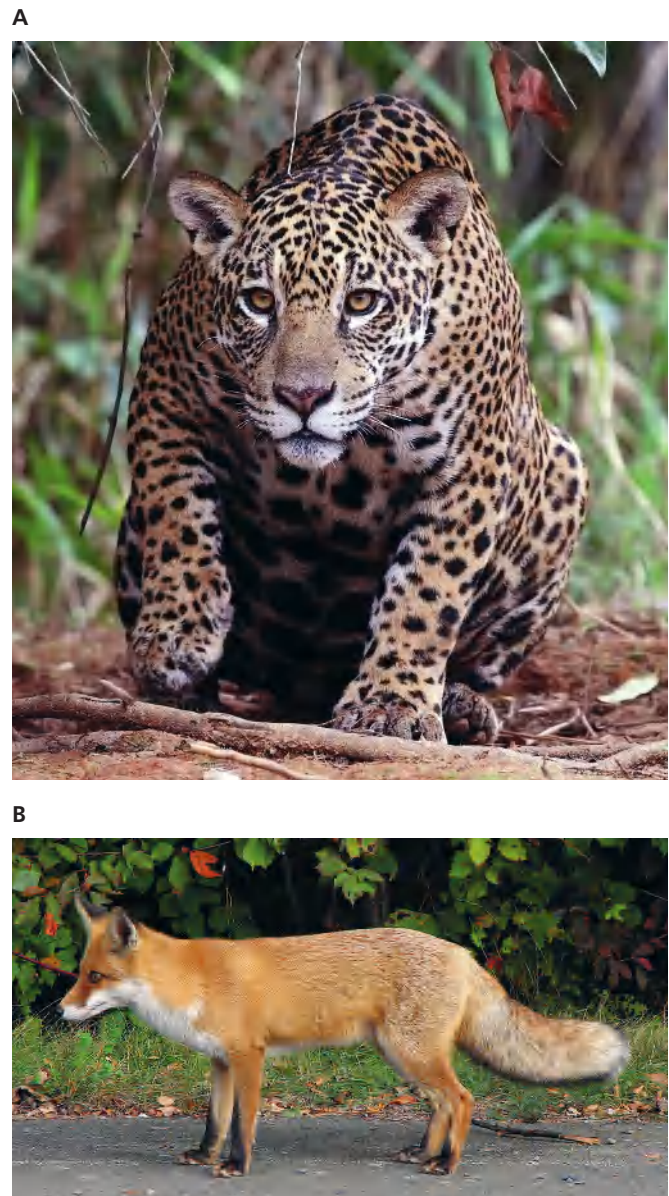
Figure 18.3 Pelage coloration of carnivores. Pelage coloration and pattern are often adapted to hunting technique. Species that hunt from concealment, including many members of the cat family, often have spots or stripes to help camouflage them, as in (**A**) the jaguar (*Panthera onca*). Species that do not hunt from concealment, such as (**B**) this red fox (*Vulpes vulpes*) usually have pelage without stripes or spots.

bles of terrestrial carnivores correspond to both phylogeny and diet (Meloro and O'Higgins 2011).

The auditory bullae in carnivores (as in other eutherians) house the tympanic membrane and inner ear. Bullae are formed either entirely from the tympanic bone (derived from the reptilian angular bone) or from the tympanic and endotympanic bones. The structure of the bullae is a criterion used to differentiate the two suborders of carnivores. In feliforms, both the tympanic and endotympanic bones form the bullae, with a septum occurring where the two meet. In caniforms, the bullae are formed almost entirely from the tympanic bone, and there is no septum. Ivanoff

Upper Carnassial tooth (p⁴)
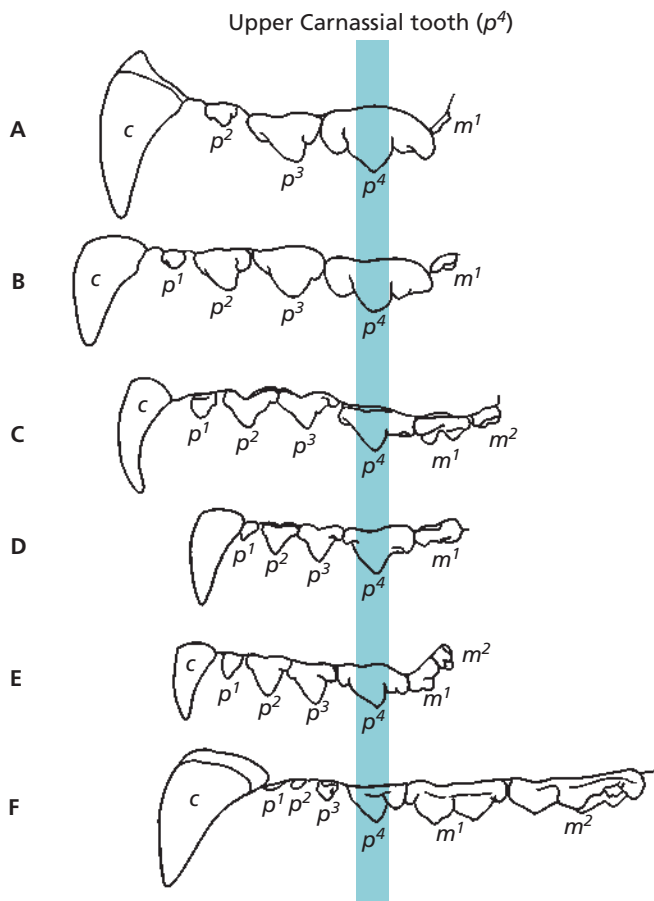
Figure 18.4 Carnassial dentition. The relative develop-
ment of the carnassial dentition in various families of carnivores
is represented by the vertical line through the maxillary
carnassial tooth (P⁴) in (**A**) a lion (Felidae); (**B**) a hyena (Hyaenidae);
(**C**) a dog (Canidae); (**D**) a marten (Mustelidae); (**E**) a mongoose
(Herpestidae); and (**F**) a bear (Ursidae). Note the large canine
tooth at the left (anterior) and the fact that the carnassial teeth
are posterior (toward the back of the jaw). Carnassial dentition
functions like a nutcracker, with the greatest force generated
closest to the articulation of jaw and skull (the fulcrum point in
a lever system), to better facilitate their crushing and shearing
function. *Adapted from DeBlase and Martin (1981).*

(2001) provided details of the auditory bullae of carnivores
and discussed formation of the septum.

All but a few carnivore species have a well-developed **os
baculum** (penis bone; Figure 18.6). Although the function
of the baculum is open to question, it may serve to prolong
copulation in species with induced ovulation. Most carni-
vores have distinctive **anal sacs** associated with secretory
anal scent glands. These occur on both sides of the anus
and produce substances that function in defense and intra-
specific communication. They are especially well devel-
oped in mephitids, mustelids, herpestids, and hyaenids.
Skunks are well known for ejecting the anal gland secre-
tion as a defensive mechanism. Weasels also have strong-
smelling scent glands, but they are not used defensively.
Anal sacs are relatively small in canids and felids and are
absent in ursids and some procyonids.
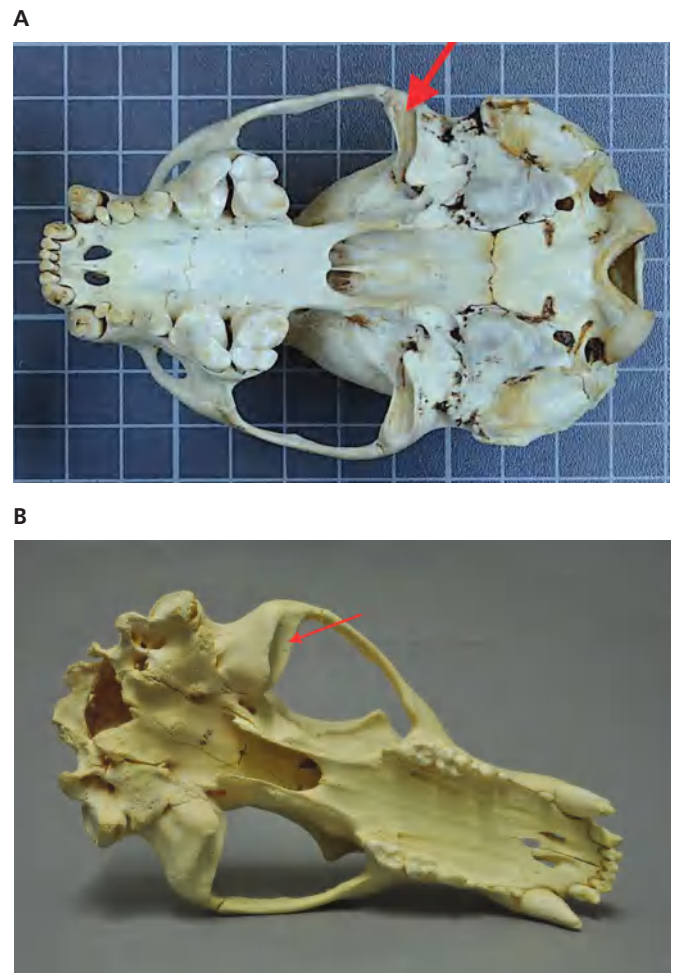
Figure 18.5 Carnivore jaw articulation. The strongly
C-shaped mandibular fossa (*arrow*) of (**A**) a river otter (*Lontra
canadensis*), a mustelid is evident, as opposed to (**B**) the flatter
mandibular fossa of an omnivorous bear.
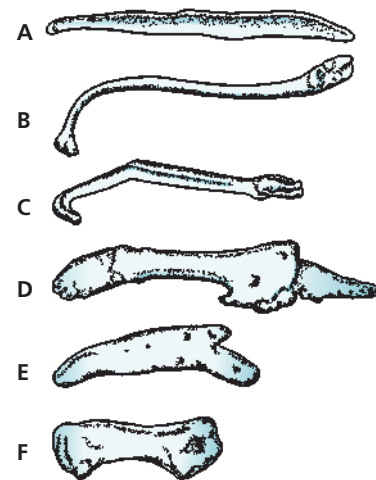
Figure 18.6 Shapes and sizes of bacula. The size and
shape of the baculum varies considerably among carnivores.
Lateral view of the baculum in a (**A**) canid (red fox, *Vulpes vulpes*
[64 mm]); (**B**) procyonid (raccoon, *Procyon lotor* [90 mm]);
(**C**) mustelid (least weasel, *Mustela nivalis* [19 mm]); (**D**) herpestid
(Egyptian mongoose, *Herpestes ichneumon* [18 mm]); (**E**) viverrid
(common genet, *Genetta genetta* [6 mm]); and (**F**) felid (lion,
Panthera leo [7 mm]). *Adapted from Ewer (1986).*

Figure 18.7 **Asian small-clawed otter (*Aonyx cinerea*).** This small otter occurs in southern India and throughout much of southeastern Asia.

Figure 18.8 **Carnivore wrist structure.** (**A**) In carnivores, the centrale, scaphoid, and lunar bones of the wrist are fused (*shaded area*), whereas in other mammals, such as a (**B**) primate, they are not. *Adapted from Macdonald (1984).*

Carnivores usually have well-developed claws on all digits. Even the unusual clawless otters (Genus *Aonyx*) have vestigial claws (Figure 18.7). In most felids and some viverrids, claws are retractile. This helps keep them sharp because they have less contact with the ground. Neither the pollex nor the hallux is opposable. The centrale, scaphoid, and lunar bones of the wrist are fused (Figure 18.8) to form a scapholunar bone, which may add support for cursorial locomotion in some terrestrial species. As in ungulates, the clavicle in carnivores is reduced or lost, which serves to increase the length of the stride and allow for faster running in cursorial species. Carnivores have an expanded braincase, but the postcranial skeleton of terrestrial species is generalized. Differences in limb structure reflect locomotor adaptations: cursorial canids and felids are digitigrade, whereas ursids and procyonids are plantigrade. Specialized morphological adaptations that allow pinnipeds to spend most of their time in water are noted in the pinniped section of this chapter.

Carnivores range in size from a body mass of about 80 g in the least weasel to 4,000 kg in bull southern elephant seals (*Mirounga leonina*)—4 orders of magnitude heavier. Sexual dimorphism is often evident, with males larger than females. This dimorphism is particularly pronounced in some pinnipeds. For example, male northern elephant seals (*M. angustirostris*) can be 6 times larger than females (Figure 18.9). Highly dimorphic taxa always exhibit polygynous mating systems; dimorphism in pinnipeds arose in the mid-Oligocene, about 27 mya (Cullen et al. 2014). Evolution in size variation from small to large species within and among carnivore families reflects the size range of potential prey species available to them.

Because meat is easy to digest, carnivores have simple stomachs with an undeveloped cecum. Nonetheless, some
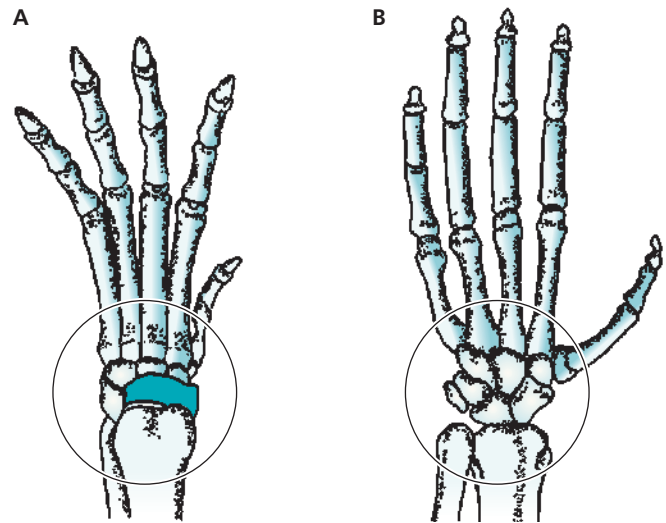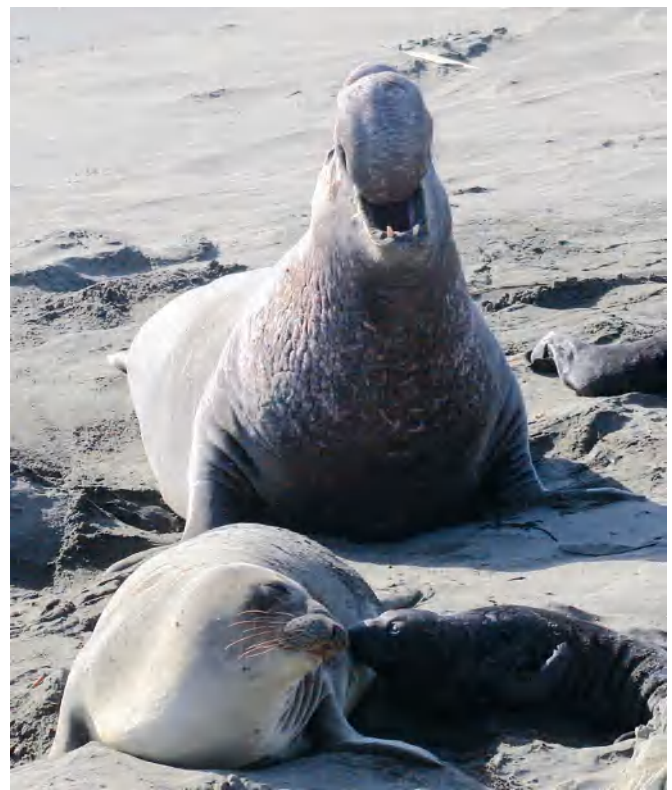
Figure 18.9 **Size dimorphism in northern elephant seals.** Male (*back*) is much larger than the female (*front*). Note the black pup to the right.

specialized feeding habits have evolved. Apart from those that eat only flesh, carnivores can be insectivorous, piscivorous, frugivorous, omnivorous, or almost completely herbivorous. Carbone and coworkers (1999) noted a direct relationship between the body mass of carnivores and the

mass of their typical prey; diet choice and body size in carnivores are closely related. The structure of the dentition, including the carnassials, is correspondingly modified (see Figure 18.4). Canids, felids, and mustelids subsist mainly on freshly killed prey. These families show correspondingly greater development in "tooth and claw," and they also have greater carnassial development and cursorial locomotion. In addition to live prey, canids, ursids, and hyaenids take a large amount of **carrion** (dead, often decaying animal matter). Because not all carnivores are strictly carnivorous (most ursids and procyonids are omnivorous), their diet varies depending on season and local availability of food. The giant panda bear (*Ailuropoda melanoleuca*) eats primarily bamboo shoots and roots and only occasionally eats animal matter (Wei et al. 1999).

FOSSIL HISTORY

The earliest archaic carnivorans were members of the extinct Order Creodonta. Like modern carnivores, they had carnassial teeth. However, a different array of premolars and molars made up the carnassial dentition in creodonts (Lewis and Morlo 2010). Currently, two extinct families of creodonts are recognized—the Hyaenodontidae and the Oxyaenidae. The earliest known mammalian genus adapted for carnivory was *Cimolestes* from the late Cretaceous period, over 65 million years ago (mya). *Cimolestes* was small, about the size of a weasel. The creodonts (Figure 18.10) extended from the late Cretaceous to the Miocene, when they became extinct, possibly through competition with modern carnivore lineages. The two stem groups of ancestral carnivores were the extinct families Viverravidae (which gave rise to caniforms) and Miacidae (which gave rise to feliforms; Figure 18.11) (Flynn and Wesley-Hunt 2005; Flynn et al. 2010). These first carnivores, with P^4/m_1 carnassial dentition, appeared in the early Paleocene (Fox et al. 2010) and are known from Asia and North America. They were in Europe by the Eocene and were extinct by the late Eocene. Unlike those of modern carnivores, the centrale, scaphoid, and lunar bones of the wrist in these early specimens were not yet fused. Modern families of carnivores began to diverge by the late Eocene, when fossils of several families are known, including canids, ursids, and mustelids. Others are recognizable only by the Oligocene, including felids, viverrids, mustelids, and hyaenids. This adaptive radiation reflected corresponding diversification of prey groups, which was in turn related to the development of more diverse vegetative biomes in the early Cretaceous period.

The earliest ancestral pinnipeds, the enaliarctids (Genus *Enaliarctos*), date from the late Oligocene and early Miocene. The earliest walruses, such as *Proneotherium repenningi* (Demere and Berta 2001) and *Pseudotaria muramotoi* (Kohno 2006), date from the early to mid-Miocene. Other early odobenids include the Genera *Neotherium*, *Pseudotaria*, and *Pelagiarctos* from the mid- to late Miocene (Berta et al. 2015).
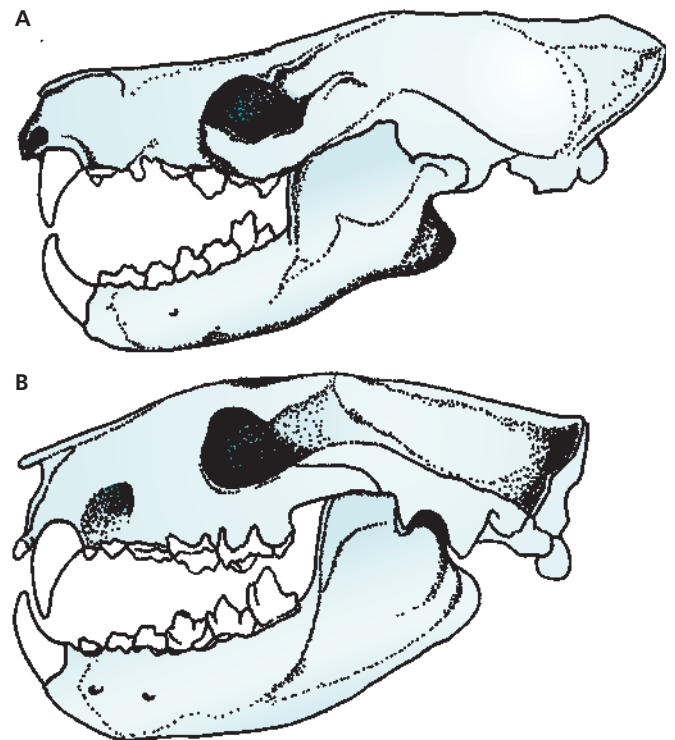
Figure 18.10 **Early creodonts.** (**A**) Skull and jaw of an early creodont, *Limnocyon* (Family Hyaenodontidae). (**B**) Unlike in the modern lineage of carnivores, the carnassial teeth in creodonts, such as *Oxyaena* shown here (Family Oxyaenidae), involved the first or second upper molars and the second or third lower molars. Skull length is about 21 cm. (**A**) *Adapted from Flynn and Wesley-Hunt (2005); (**B**) adapted from Romer (1966).*

ECONOMICS AND CONSERVATION

Many species of carnivores have close associations with humans. Domestic dogs and cats have been popular pets throughout the world for thousands of years. Likewise, numerous species of carnivores have been important as sources of furs (pelts) throughout human history. Today, raccoons (*Procyon lotor*) are trapped for their pelts, as are foxes and many species of mustelids, including mink (*Neovison vison*), river otter (*Lontra canadensis*), marten (*Martes americana*), fisher (*Pekania* [*Martes*] *pennanti*), and sable (*M. zibellina*) (see Feldhamer et al. 2003b). Many other species are useful to the agricultural industry as predators on rodents and other agricultural pests.

Conversely, carnivores are often in conflict with human economic interests. Often vilified, carnivores are viewed by many people (and historically, by wildlife management agencies) as viciously preying on innocent grass-eating herbivores as well as livestock. As a result, the density and distribution of many carnivore species have been greatly reduced. The gray wolf is a prime example. It has been extirpated throughout much of its former range in the Old World. In the contiguous 48 United States, it occurs in only about 5% of its historic range (Paquet and Carbyn

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B
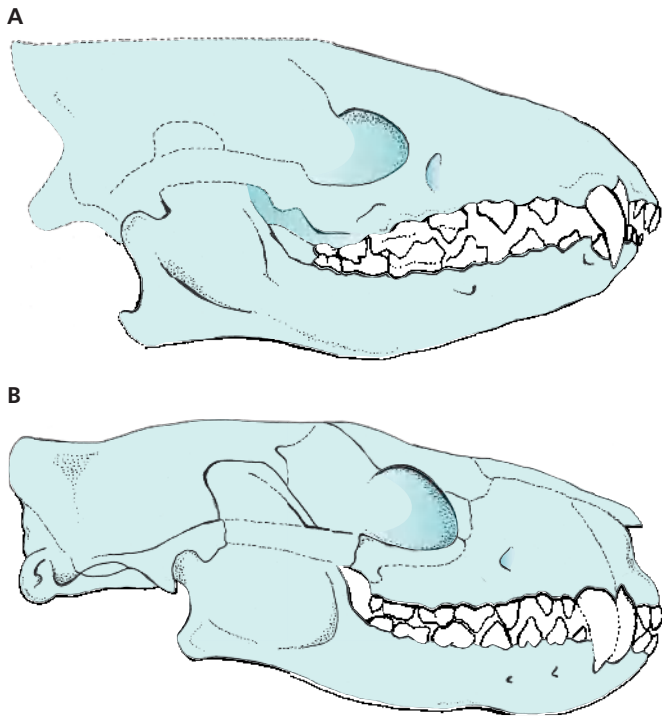
Figure 18.11 Ancestral carnivores. (**A**) Lateral view of the skull of *Protictis* (extinct Family Viverravidae); actual length about 9 cm; (**B**) lateral view of the skull of *Vulpavus profectus* (extinct Family Miacidae); actual length about 10 cm. These early taxa were ancestral to modern carnivores. *Adapted from Carroll (1988).*

Figure 18.12 Phylogeny of felid genera. Estimated divergence dates of major nodes (in mya) are given. *Modified and adapted from Johnson et al. (2006); additional currently recognized genera and species numbers from IUCN (2018).*

A

B
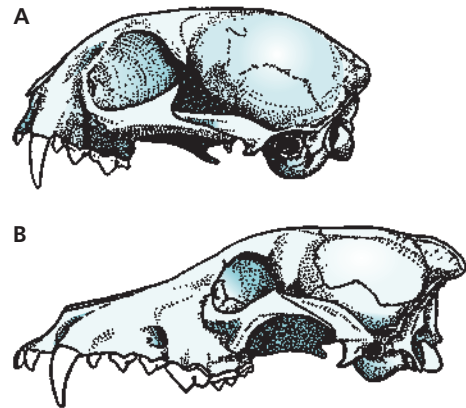
Figure 18.13 Shape of felid and canid skulls. (**A**) A felid skull typically has a short, rounded rostrum and a reduced number of molariform teeth compared with (**B**) the long rostrum typical of canids. *Adapted from Lawlor (1979).*

2003). Similarly, in the last 200 years, the grizzly bear (*Ursus arctos*) was practically extirpated in the United States (Schwartz et al. 2003). Likewise, large carnivores in Europe face serious conservation challenges (Chapron et al. 2014). Historically, large carnivores throughout the world have also been important as big-game trophies. This has resulted in serious overexploitation and range reduction of numerous species, as in the case of the tiger. In response to changing sentiments toward conservation, however, many species are beginning to recover (Mech 1995), often because of active reintroduction programs.

SUBORDERS AND FAMILIES

Feliformia

Felidae

The cat family is distributed worldwide except for Australia, New Zealand, and surrounding islands; polar areas; Madagascar; Japan; and most oceanic islands. The classification of felids has been controversial. Some authorities recognize only a few genera; however, Wozencraft (2005) considered 14 genera and 40 species within 2 subfamilies—Pantherinae (including Genera *Neofelis* and *Panthera*) and Felinae (with the remaining 12 genera). Burgin and co-workers (2018) recognized 14 genera and 42 species; the

IUCN (2018) recognized 14 genera and 38 species (Figure 18.12). All cats have a shortened rostrum (Figure 18.13), well-developed carnassials, reduced number of post-carnassial teeth, and large canines that are "highly specialized for delivering an aimed lethal bite" (Ewer 1973:5). Felids kill their prey by suffocation or by biting the prey's neck so the canines enter between the vertebrae and separate the spinal cord. Loss or reduction in size of the post-carnassial teeth is more evident in felids than in any other carnivores; total number of teeth is reduced to 28 or 30. The shortened toothrow and rostrum add to the force generated through the enlarged canines. The cheekteeth are blade-like and adapted for seizing and slicing meat from prey, rather than crushing bones, as occurs in hyaenids or canids.

Although they are morphologically similar, body masses of felids exhibit 3 orders of magnitude difference—from about 1 kg in the rusty-spotted cat (*Prionailurus rubiginosus*) of India and Sri Lanka to 300 kg in tigers. Despite size

differences, the general body morphology and musculature of felids is remarkably uniform. Males are generally 5% to 10% larger than females. Large felids are noted for their ability to roar (because flexible cartilage replaces the hyoid bone at the base of the tongue), whereas smaller species purr. As noted by Sunquist and Sunquist (2009), however, this generalization is open to question. Lions (*Panthera leo*) and leopards certainly roar, but other large felids may not, despite having a flexible hyoid. Also, elastic characteristics of the vocal cords within the larynx contribute to whether cats roar or purr. Regardless, felids exhibit a variety of vocalizations. Most cats are at least semiarboreal. They are digitigrade and have strongly curved, sharp claws to hold prey. Other than in the cheetah, claws are retractable; in the resting position the claws are held "in." The dorsal surface of the tongue is covered by posterior-directed papillae that give the tongue a "sandpaper" feeling and may help to retain food in the mouth, lap up water, groom fur, and rasp meat from bones.

Felids occur in numerous habitat types and at elevations from sea level to 6,000 m. They are strictly carnivorous and require a diet high in protein. Cats prey almost exclusively on mammals and birds, although the Asian flat-headed cat (*Prionailurus planiceps*) and fishing cat (*P. viverrinus*) consume fish, frogs, and even mollusks. Most felids are nocturnal. They are very agile and either stalk their prey or pounce from ambush. Williams and colleagues (2014) discussed the energetic advantages to felids of this strategy. Their pelage, with dark stripes, spots, or rosettes on a lighter background, is often adapted for camouflage. In adult lions, cougars (*Puma concolor*), jaguarundi (*Herpailurus jagouaroundi*), or caracal (*Caracal caracal*), however, pelage coloration is uniform. The diurnal cheetah, the fastest terrestrial mammal in the world, relies on its ability to outrun prey over short distances. Species generally are solitary or form pairs; however, lions associate in prides that include up to 18 related females, their offspring, and several unrelated males (Packer 1986). The larger species are intolerant of other species; lions are known to kill leopards, and leopards kill cheetahs.

The earliest fossil felids are from the Oligocene of Eurasia. Miocene felids are known from Europe, Asia, and North America. Following the formation of the Isthmus of Panama in the Pliocene, felids dispersed to South America (Goswami 2010). Modern felids resulted from divergence and speciation events in the late Miocene (Johnson et al. 2006).

Populations of many species of felids are decreasing either because of overhunting, habitat loss, or the fur trade. Felids considered endangered (IUCN 2018) include the Iberian lynx (*Lynx pardinus*), tiger, the Andean cat (*Leopardus jacobita*), the Borneo Bay cat (*Pardofelis badia*), and the flat-headed cat.

Prionodontidae

Formerly included within the Viverridae, the Asian linsangs include 1 genus and 2 species—the banded linsang (*Prionodon linsang*) and the spotted linsang (*P. pardicolor*) (Barycka 2007; Nyakatura and Bininda-Edmonds 2012). They occur in Southeast Asia, including the Malay Peninsula, Borneo, Java, Sumatra, and other islands, although they do not overlap geographically (Jennings and Veron 2015). These poorly known nocturnal and arboreal species inhabit coniferous forest areas from sea level to 3,000 m elevation. Both are small, with short legs, long tails, and body weights <1 kg. The fur is short and velvety, with stripes or spots, and the claws are retractile. Populations of both species are decreasing although neither is considered threatened or endangered (IUCN 2018).

Hyaenidae

Hyaenids inhabit grassy plains, brushy habitats, forests, and deserts in the Middle East, India, and Africa, where spotted hyenas (*Crocuta crocuta*) are the most abundant large carnivore. The four extant species—each in its own genus—include the aardwolf (*Proteles cristata*), which in the past has been placed in a separate family, the Protelidae, because of morphological and behavioral differences from hyenas. Currently, the aardwolf is considered the sole member of the hyaenid Subfamily Protelinae. The other subfamily, Hyaeninae, includes the three bone-crushing species: the striped hyena (*Hyaena hyaena*), the brown hyena (*Parahyaena brunnea*), and the spotted hyena.

Hyenas are fairly large carnivores; the spotted hyena reaches 80 kg in body mass. The aardwolf is the smallest member of the family, with maximum body weight of about 12 kg. Well-developed canines and large premolars make the 3 species of bone-cracking hyenas highly competent hunters, capable of killing large prey. They also are highly adapted to scavenging carcasses and feeding on carrion (especially the brown and striped hyenas), using their large carnassials (Figure 18.14A) and robust skull structure to crush bones (Tanner et al. 2008). Although the carnassials are robust, the molars are reduced in striped hyenas, are even smaller in brown hyenas, and are usually absent in spotted hyenas. Reduced molars allow for enlargement of the premolars, reduce wear on the carnassials, and increase the bite force, which is necessary to break bones (Holekamp and Kolowski 2009). Although morphological growth of spotted hyenas reaches a plateau at 20 months of age, their bite strength continues to increase until they are 5 years old (Binder and Van Valkenburgh 2000). The scavenging specialization of brown, striped, and spotted hyenas may allow them to minimize competition with sympatric canids. They regurgitate pellets of undigested material, including bone fragments, ligaments, hair, and horns. Unlike other hyaenids, the small, nocturnal aardwolf is myrmecophagous (feeds on ants and termites), which is unusual among carnivores. It takes primarily snouted harvester termites (*Trinervitermes trinervoides*), which it locates through both sound and scent and by following aardvarks that have opened the mounds (Taylor and Skinner 2000). An aardwolf can consume up to 300,000 termites a night. Reflecting

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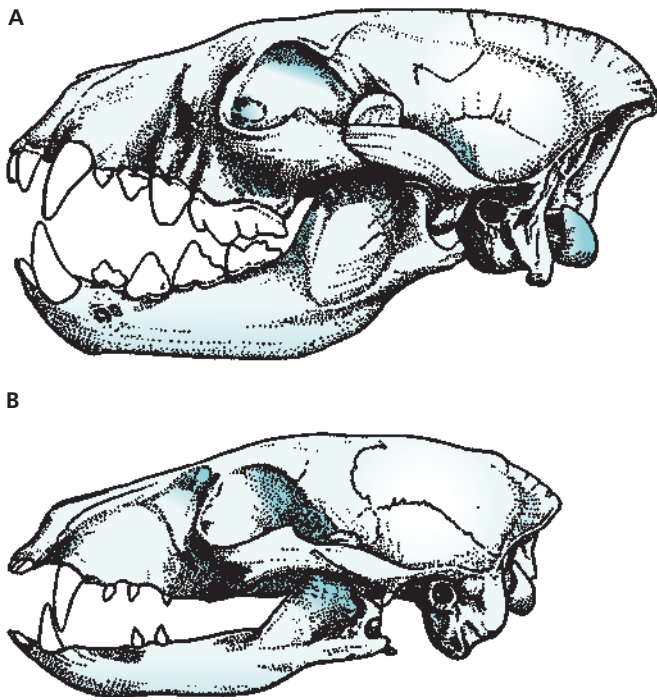
Figure 18.14 **Hyaenid dentition.** (**A**) The dentition of the striped hyena (*Hyaena hyaena*) is adapted for crushing bones, unlike (**B**) the reduced dentition of the myrmecophagous aardwolf. *Adapted from DeBlase and Martin (1981).*

these feeding habits, the dentition is weakly developed, with smaller, more widely spaced cheekteeth than in other hyaenids (Figure 18.14B), a broad tongue, and sticky saliva. The aardwolf spends the day in a den, which provides thermal stability to escape extremes of ambient temperatures and protection from black-backed jackals (*Canis mesomelas*) and other predators (Anderson and Richardson 2005).

Hyaenids are digitigrade and have nonretractile claws. The long neck and forelimbs and shorter hind limbs produce a characteristic sloping profile. Pelage is coarse, with a prominent mane in all but the spotted hyena, in which the mane is less apparent. Stripes or spots are on the dorsal pelage of all species except the brown hyena. All hyenas have **protrusible** (can be turned inside out) anal scent glands, which are dragged along the ground, depositing a paste-like substance to scent-mark territory and identify individuals (Burgener et al. 2009). Scent glands occur in both males and females. Hyaenids are unusual among carnivores in lacking a baculum.

Spotted hyenas are noteworthy for their "laughing" vocalizations, one of several types of calls used to communicate to conspecifics an individual's age, sex, and other information (Mathevon et al. 2010). Hyenas also communicate chemically by marking with their scent glands. Spotted hyenas are unique in that the external genitalia of females resemble that of males, such that it is very difficult to determine gender in the field. As noted by Frank (1997:58), the "female has no external vagina; rather, the urogenital canal traverses the hypertrophied clitoris,

which resembles a penis in size, shape and erectile ability" (Figure 18.15). Various hypotheses have been proposed to explain the evolution of this female masculinization (East and Hofer 1997; Frank 1997). It is not induced by androgen (see Holekamp and Kolowski 2009), but Hammond and co-workers (2012) concluded that the condition is tied to low levels of sex hormone–binding globulin. Population trends of striped and spotted hyenas are decreasing, but neither is considered threatened or endangered. Hyaenids diverged in the mid-Oligocene, with living hyenas representing a small remnant of the 20 extinct genera and nearly 70 described fossil species (Koepfli et al. 2006; Goswami 2010).

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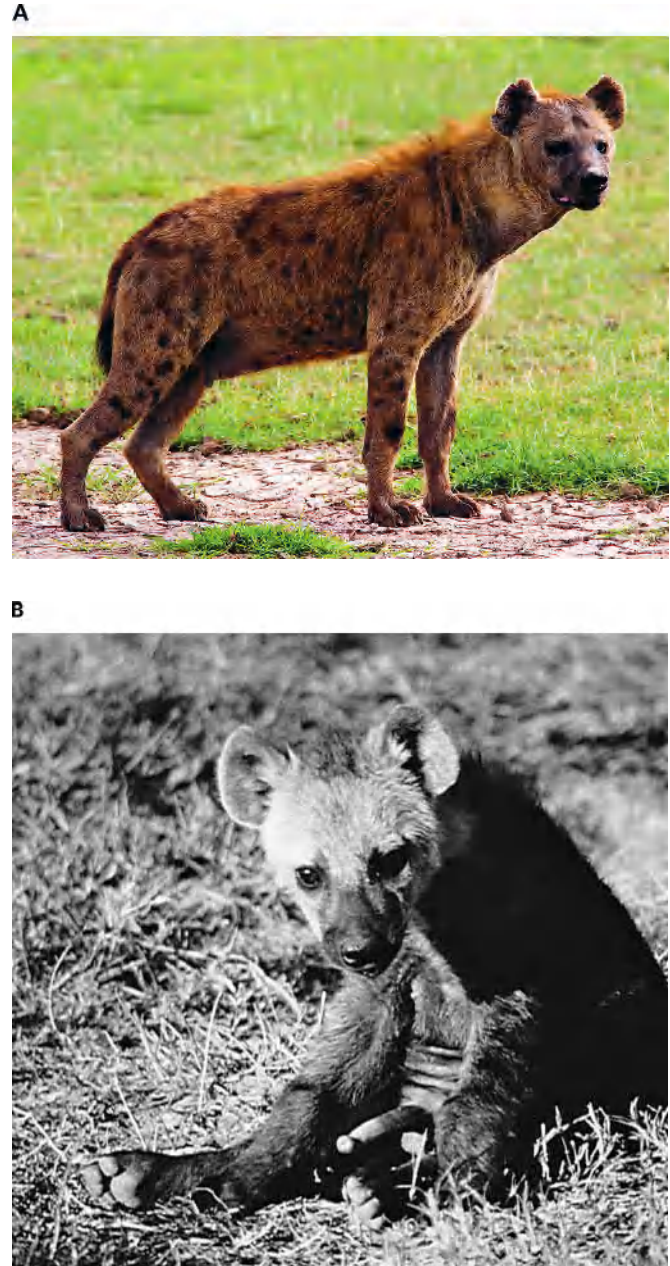
Figure 18.15 **Body morphology.** (**A**) Hyenas have a characteristic sloping profile. The high, strong shoulders provide leverage for individuals as they pull meat and hide from carcasses. (**B**) This female has an erect pseudopenis.

Herpestidae

The 13–16 genera and 35–36 species of mongooses are native to Africa, the Middle East, and Asia. Because they are fairly small and have slender bodies and long tails and snouts, herpestids were once included in Family Viverridae (civets and genets). However, they differ from viverrids based on the structure of their auditory bullae and anal sacs, which are similar to those of euplerids and hyaenids—closely related families (see Figure 18.1). Anal sacs can be everted, exposing cutaneous glands (Kingdon 1972). Several other features distinguish herpestids from viverrids (Table 18.1). Body masses of herpestids range from the dwarf mongoose (*Helogale parvula*) at 0.2 kg (Figure 18.16) to the white-tailed mongoose (*Ichneumia albicauda*) at about 5.0 kg. The coarse pelage is uniform in color, without spots, and a few species have a single stripe from the ear to the shoulder. Herpestids are grouped into 2 subfamilies—the Herpestinae and the Mungotinae. Gilchrist and colleagues (2009) discussed the phylogenetic relationships of the species in each subfamily.

Herpestids occur in a variety of grassland, savanna, and forested habitats. They are feeding generalists, taking small vertebrates, insects, vegetation, and carrion (Gilchrist et al. 2009; Bandeira et al. 2018), with associated generalized dentition. Several species are well known for their ability to feed on poisonous snakes (see box). Some species are solitary, whereas others are highly social and form groups. The banded mongoose (*Mungos mungo*), and likely most other social species, avoids inbreeding by discriminating between kin and other individuals (Sanderson et al. 2015). The best known social herpestid is the suricate, or meerkat (*Suricata suricatta*; Figure 18.17), which forms large groups of family members in which individuals cooperate

Figure 18.16 Dwarf mongoose. A common species throughout southcentral and east Africa, this is the smallest herpestid.

in activities such as rearing young and detecting predators. Meerkats have been extensively studied to test hypotheses of the evolutionary development of helping behavior by nonbreeders in a social species (O'Riain et al. 2000; Clutton-Brock et al. 2001). Manser (2001) found that meerkats give acoustically different alarm calls depending on the type of predator encountered and the level of urgency of the threat. Likewise, the dwarf mongoose (*Helogale parvula*) produces a diverse array of alarm calls depending on context and function (Collier et al. 2017; Rubow et al. 2018).

Between 1872 and 1979, the small Indian mongoose (*Herpestes javanicus*) was introduced to Asia, Africa, Europe, North and South America (Hays and Conant 2007), the West Indies, and Hawaii, as well as several national parks in the United States (Burde and Feldhamer 2003), with often devastating effects on native fauna. It preys on poultry and native fauna, especially nesting birds, and carries rabies. The population trends of several species of mongoose are unknown, but only the Sokoke dog mongoose (*Bdeogale omnivora*) and the Liberian mongoose (*Liberiictis kuhni*) are considered threatened.

Herpestids originated in the early Miocene (Patou et al. 2009; Goswami 2010). The earliest known appearance of an extant herpestid, the slender mongoose (*Galerella sanguinea*), is from the Miocene of Chad, Africa (Peigne et al. 2005).

Viverridae

The civets and genets occur only in Africa, the Middle East, and Asia (the common genet, *Genetta genetta*, occurs in Europe but was likely introduced). The 13–14 extant genera and 33–37 very diverse species that are currently recognized occupy tropical and subtropical habitats. Historically somewhat of a wastebasket taxon, viverrids once included the mongooses (now in Family Herpestidae),

Table 18.1 Morphological characteristics differentiating herpestids (mongooses) from closely related viverrids (civets and genets)

	Herpestidae (Mongooses)	Viverridae (Civets and Genets)
Tail length	Less than head and body length	Equal to or greater than head and body length
Digits	Four or five; webbing reduced or absent	Five; webbing between toes
Claws	Nonretractile	Retractile
Ears	Short and round; no bursae on lateral margins	Long and pointed; bursae on margins
Pelage	Usually uniform coloration	Usually spotted or striped
Behavior	Social, often forms groups; diurnal or nocturnal; terrestrial	Generally solitary; nocturnal; arboreal

Mammalian Resistance to Snake Venom

Most of us are familiar with pictures of cobras in their threat posture about to be attacked by a mongoose. This scenario certainly occurs in the wild, although such photos are often of staged encounters for tourists in Asia. Nonetheless, there are approximately 600 species of venomous snakes worldwide, and you may be surprised that about 50 species of mammals are known to prey on them at least occasionally. Venomous snakes have been documented as being preyed upon by a variety of didelphids, including the Virginia opossum (*Didelphis virginiana*), the southern white-breasted hedgehog (*Erinaceus concolor*) and the western European hedgehog (*E. europaeus*), two species of skunks—especially Molina's hognosed skunk (*Conepatus chinga*)—the American badger (*Taxidea taxus*), the European badger (*Meles meles*), and the honey badger (*Mellivora capensis*), several species of mongooses including the Indian gray mongoose (*Herpestes edwardsi*), the Egyptian mongoose (*H. ichneumon*) and others, and even pigs (*Sus scrofa*). Voss and Jansa (2012) listed species from 6 mammalian orders and 14 families, including 7 families of carnivores that are ophiophagous (i.e., snake eaters).

There are no consistent morphological, craniodental, or anatomical traits among the variety of mammalian species documented to take venomous snakes—and certainly not among those species that take them regularly. The only constant in this diverse array of mammalian species is that they have mechanisms for venom resistance, acquired through a relentless co-evolutionary biochemical "arms race" to defend themselves against the evolving toxins of snakes. Research in this area, comprehensively reviewed by Calvete (2017), has been ongoing for more than 100 years, with much of it focusing on biochemical factors that neutralize toxins. Relatively few ophiophagous mammalian species have been investigated with a view toward determining how they resist snake venom; however, it is likely that they do use unknown biochemical venom-resistance strategies. As noted by Voss and Jansa (2012:833), "Although multiple mechanisms of venom resistance have been identified in some ophiophagous mammals, the proteomic complexity of most snake venoms suggests that many additional mechanisms of venom resistance remain to be discovered." The approximately 50 mammalian species that are capable of preying on venomous snakes represent <1% of all species of mammals. This small percentage suggests that there are serious constraints on those species in terms of developing resistance to venom—and why so many species of snakes have evolved to use venom as part of their life history strategy.

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Figure 18.17 **Meerkats.** Often called "suricates," these highly-social herpestids inhabit dry regions of southern Africa.

linsangs (Prionodontidae), Madagascar carnivores (Eupleridae), and the African palm civet (Nandiniidae), which are now placed in their own families based on molecular data. Wozencraft (2005) recognized 4 subfamilies: the Viverrinae, which includes 3 genera and 6 species of terrestrial civets; the Paradoxurinae, which encompasses 5 genera and 7 species of palm civets; the Genettinae, with 2 genera and 17 species of genets and oyans; and the Hemigalinae, with 4 genera and 4 species of palm and otter civets (Figure 18.18). Werdelin and Wesley-Hunt (2014) showed that each subfamily occupied a distinct "morphospace." Taxonomic relationships among species in each subfamily continue to be investigated genetically and morphologically.

Dental adaptations are diverse and reflect the variety of morphological adaptations in this family. In physical appearance and life history, viverrids are small to medium size, with slender bodies, long tails, small ears, pointed snouts, and limbs that are generally short and unspecialized. The pelage usually is spotted or striped (see Table 18.1). They fill a variety of feeding niches: some viverrids are carnivorous, others are omnivorous or frugivorous, and others are scavengers. Species can be diurnal or nocturnal, can occur singly or in groups, and can be terrestrial, semiaquatic, or arboreal. They occur primarily in forested habitats, although a few species are in grasslands or savannas.

Almost all viverrids have a perineal scent gland, unique among carnivores. Glands are generally "composed of a compact mass of glandular tissue, typically lying between the anus and vulva or penis and opening into a naked or sparsely haired area, which may be infolded to form a storage pouch" (Ewer 1973:92). They produce a thick yellowish fluid called "civet" or "civet oil," which is used for scent-

Figure 18.18 Banded palm civet (*Hemigalus derbyanus*). The geographic range of the banded palm civet includes Borneo, Sumatra, Malaysia, Thailand, and Myanmar; populations are declining.

marking and functions in intraspecific communication. The structure of the perineal gland varies among species within each subfamily (Jennings and Veron 2009). Civet oil has been economically important in traditional Asian medicine as well as perfume-making for thousands of years. There are numerous farms in Ethiopia where African civets are held under very poor conditions to extract civet oil (Jennings and Veron 2009). Viverrids also are taken from the wild for food (bushmeat) throughout Africa and Asia, or raised for food in China and elsewhere.

The Malabar large spotted civet (*Viverra civettina*) is critically endangered, and the semiaquatic otter-civet (*Cynogale bennettii*; Veron et al. 2006), Owston's civet (*Chrotogale owstoni*), and the large-spotted civet (*Viverra megaspila*) are all endangered. The population status of several other species is declining or unknown (IUCN 2018).

The earliest fossil viverrids date from the Oligocene of Eurasia. They spread to Africa by the Miocene (Flynn and Wesley-Hunt 2005). Werdelin and Peigné (2010) summarized known distributions of 15 Miocene and Pliocene genera and species of African viverrids.

Eupleridae

The 7 genera and 8–9 species of Malagasy (Madagascar) mongooses (or vontsiras, a Malagasy common name) represent a monophyletic group resulting from a single radiation (Yoder et al. 2003). All carnivores in Madagascar are in this family, based on strong molecular (although not anatomical) evidence. Madagascar separated from the African mainland 155 to 170 mya. Thus, a euplerid ancestor rafted the 400 km across the Mozambique Channel to colonize the island 18 to 24 mya (Yoder et al. 2003). A remarkable adaptive radiation followed, resulting in the diverse modern euplerids seen today. Species within this family were formerly included in 2 other families—the herpestids and viverrids. The ring-tailed mongoose, or von-

tsira (*Galidia elegans*), the brown-tailed vontsira (*Salanoia concolor*), the narrow-striped mongoose, or bokiboky (*Mungotictis decemlineata*), and species in the Genus *Galidictis* were once within the Herpestidae; they now comprise the euplerid Subfamily Galidiinae. The Malagasy civet or spotted fanaloka (*Fossa fossana*), fossa (*Crytoprocta ferox*), and falanouc (*Eupleres goudotii*) were formerly placed in the Viverridae and now make up the euplerid Subfamily Eupleriinae. Goodman and Helgen (2010) recognized the western falanouc (*Eupleres major*) as a species distinct from the eastern falanouc (*E. goudotii*). Based only on differences in the cytochrome b gene of *E. major*, Veron and Goodman (2018) concluded that they do not form a monophyletic group. Veron and colleagues (2017) described the molecular systematics of the galidiinids and suggested various subspecies be recognized.

Euplerids occur only in deciduous forest habitat. Two of the smaller species, the ring-tailed mongoose and broad-striped mongoose, have similar diets but are active at different times. The medium-sized Malagasy civet and the falanoucs are nocturnal but have different feeding habits. The fossa is the largest euplerid and is active both day and night (Gerber et al. 2012); it preys primarily on lemurs (Hawkins and Racey 2008). Schneider and Kappeler (2016) discussed the social organization of the narrow-striped mongoose, where males and females live in small, same-sex groups. Several euplerids are of conservation concern because of habitat loss, human disturbance, and predation from domestic dogs (Woolaver et al. 2006). The giant-striped mongoose, or Grandidier's vontsira (*Galidictis grandidieri*), with a total population of 3,000 to 5,000 (Marquard et al. 2011), is endangered, as are the western falanouc and the bokiboky (IUCN 2018). The giant fossa (*Cryptoprocta spelea*) became extinct in the recent geological past. Goodman (2009) provided an excellent review of each species in the family. Neither the euplerids nor the nandiniids (following section) have a pre-Recent fossil record (Goswami 2010).

Nandiniidae

As noted, this monotypic family includes only the African palm civet, formerly included within the Viverridae but placed in its own family based on morphological and molecular criteria (Veron and Heard 2000; Yoder et al. 2003). Although debate over the systematic status of the African palm civet continues, most authorities place it as the sister taxon to extant feliforms (see Figure 18.1). Gaubert (2009a) noted the unique retained anatomical characteristics of palm civets, which differ from those of other carnivores. They have dense, brownish pelage with dark spots and dark bands on the tail. Palm civets occur throughout central Africa in forested habitats, where they are primarily arboreal, frugivorous, and nocturnal. They also take insects and small vertebrates opportunistically. Apparently, palm civets are easily tamed and reduce rodent pests in houses. Hassanin (2016) reported on their complete mitochondrial genome.

Caniformia

Canidae

Canids include the wolves, coyote (*Canis latrans*), foxes, dhole (*Cuon alpinus*), jackals, and the domestic dog. There are 13 genera and 37 species—if the dingo (*Canis lupus dingo*), introduced to Australia, New Guinea, and parts of Asia 3,500–4,000 years ago (Corbett 1995; Letnic et al. 2012), and eastern gray wolf (*C. lycaon*)—are considered distinct species. However, hybridization of eastern gray wolves and coyotes (von Holdt et al. 2016) and coyotes with the red wolf (*C. rufus*; Gese et al. 2015; Hinton et al. 2017a, 2017b) causes serious taxonomic uncertainty (species? subspecies? hybrids?) as well significant problems with recovery efforts of taxa such as the red wolf.

Canids are the most widely distributed family of carnivores and occur on all continents except Antarctica. The red fox (*Vulpes vulpes*) and the gray wolf enjoy the widest geographic distributions of any terrestrial mammal. Habitats of canids include hot, dry deserts, grasslands, savannas, forests, and even arctic ice. Coyotes and red foxes can now be found in suburban areas and some cities, and the Asian raccoon dog (*Nyctereutes procyonoides*) is now an invasive species in Europe (Suld et al. 2017; Mustonen and Nieminen 2018). As noted by Sillero-Zubiri (2009:352) canids are "characterized by a great flexibility of diet, opportunistic and adaptable behavior, and complex social organization with much variation within and between species." Canids generally take animal prey throughout the year; however, plant material may be taken seasonally by some species. Jackals often eat carrion, and the bat-eared fox (*Otocyon megalotis*) consumes a large amount of insects.

Many canids are solitary, whereas others—including the gray wolf, African wild dog (*Lycaon pictus*), dhole (Figure 18.19), Ethiopian wolf (*Canis simensis*), and bush dog (*Speothos venaticus*)—form packs and engage in cooperative hunting. Pack hunting allows these species to take prey that are larger than they are. Large prey can also provide sufficient resources to support large packs. Intraspecific communication by vocalizations and scent-marking is highly adapted in canids, as are visual postures including bared teeth, position of the ears and tail, and raising hair on the neck and shoulders.

Generally, canids have long limbs relative to head and body length and are adapted to pursue prey in open habitats. Canids range in body mass from 1 kg in the fennec (*Vulpes zerda*; Figure 18.20) to about 80 kg in the gray wolf. They are generally digitigrade, four-toed, and have nonretractile claws. The pollex and hallux are reduced. Pelage is generally short (the maned wolf, *Chrysocyon brachyurus*, is an exception) and uniform in color dorsally, without spots or stripes as in many felids. Coloration of widely distributed species can vary throughout different portions of their range. Canid skulls characteristically have an elongated rostrum (see Figure 18.13), with well-developed canines and carnassial teeth. Although there are a few exceptions, the typical dental formula is 3/3, 1/1, 4/4, 2/3 = 42, which is close to the primitive eutherian number of 44. An exception is the bat-eared fox (Figure 18.21), which has 46 to 50 teeth, more than any other terrestrial eutherian mammal.

Several species of canids (e.g., foxes) are hunted for sport or trapped for their fur. In the United States, the coyote has been the target of state and federal predator control programs because of livestock depredations and preying on deer fawns. The gray wolf was listed as endangered in the

Figure 18.19 **Dhole (*Cuon alpinus*).** Also called the "Asian wild dog," dholes have a wide geographic distribution from Siberia to southeastern Asia and west to India.

Figure 18.20 **Fennec fox (*Vulpes zerda*).** Found throughout dry areas of northern Africa and the Arabian peninsula, the fennec weighs only 1 kg.

Figure 18.21 **Bat-eared fox (*Otocyon megalotis*).** This species occurs in savanna areas of southern and eastern Africa and has more teeth than any other eutherian mammal.

lower 48 United States until delisting in 2012 in northern Minnesota, Wisconsin, Michigan, and the Rocky Mountain states. Hunting and trapping followed immediately, with high mortality rates amid intense controversy (Creel and Rotella 2010). Wolves remain listed in India, Nepal, Pakistan, and Bhutan. The Ethiopian wolf, dhole, Darwin's fox (*Lycalopex fulvipes*), and African wild dog are also endangered. The red wolf is critically endangered (IUCN 2018). They have been reintroduced in the eastern United States, but mortality from gunshots as well as hybridization with coyotes significantly compromise recovery efforts (Gese et al. 2015; Hinton et al. 2017b). The Falkland Island wolf (*Dusicyon australis*) was driven to extinction in the 1870s.

The earliest fossil remains of identifiable canids are from the Subfamily Hesperocyoninae, which includes 10 genera that date from the mid-Eocene to the mid-Miocene in North America. A second extinct subfamily, the Borophaginae, was also North American, with as many as 15 recognized genera dating from the early Oligocene through the Pliocene (Wang 1994; Wang et al. 1999; Tedford et al. 2009). Only members of the Subfamily Caninae left North America and spread to other parts of the world 2–7 mya (Figueirido et al. 2015; Silvestro et al. 2015).

Mustelidae

This diverse family of 22–23 genera and 64 species is the largest in the order and includes weasels, badgers, otters, martens, polecats, and the wolverine (*Gulo gulo*). Although Wozencraft (2005) recognized only 2 subfamilies, more recent studies recognize as many as 8 (see Yu et al. 2011 and references therein): the Lutrinae with 7 genera and 12 species of otters; the Mustelinae, which encompasses the American mink (*Neovison vison*) plus 2 genera and 18 species of weasels; the Helictidinae, which has 4 species of ferret-badgers in the Genus *Melogale*; the Galictidinae, which includes 4 genera and 6 species of grisons and polecats; the Melinae, which has a species of Eurasian badger (Genus *Meles*) plus the hog badger (*Arctonyx collaris*); the Martinae, which includes the wolverine, tayra (*Eira barbara*), and 8 species of martens (Genus *Martes*); and the 2 monotypic Subfamilies Taxidiinae (American badger, *Taxidea taxus*) and Mellivorinae (honey badger, *Mellivora capensis*). Larivière and Jennings (2009) provided an excellent review of the systematics and subfamily relationships of the mustelids.

Mustelids occur throughout much of the world and are absent only from Australia, Antarctica, Madagascar, the Celebes, and some other oceanic islands. Mustelids are highly specialized predators that inhabit terrestrial and arboreal habitats as well as fresh and salt water (Figure 18.22).

Mustelids have long bodies with relatively short legs and long tails. They are usually digitigrade (badgers are plantigrade) and pentadactyl and have nonretractile claws. They range in size from the 30-g least weasel, the smallest carnivore in the world, to the 45-kg sea otter (*Enhydra lutris*); the largest terrestrial mustelid is the wolverine at 18 kg. Males are generally about 25% larger than females. The carnassial teeth are well developed, and no extant mustelid has more than one molar after the carnassials. Nonetheless, diverse dental adaptations within mustelids reflect the varied life histories and diets in this family: some species are strictly carnivorous, others are omnivorous, and others are scavengers. The mandibular fossa is strongly C-shaped, which restricts the lateral movement of the mandible and allows little "give" for struggling prey (see Figure 18.5). Linnell and colleagues (2017) found that the annual survival rate for the short-tailed weasel (*Mustela erminea*) and the long-tailed weasel (*M. frenata*) was quite low because these small carnivores are preyed upon by larger carnivores, primarily predatory birds such as the barred owl (*Strix varia*).

Figure 18.22 **Giant otter (*Pteronura brasiliensis*).** Note the webbed forefeet of this endangered mustelid, which occurs in aquatic habitats throughout much of South America.

Mustelids are noteworthy for their enlarged anal scent glands. The thick, powerful-smelling secretion (musk) is used for olfactory communication and defense. Pelage is often uniform in color, although pronounced facial markings are common. Some species, such as the marbled polecat (*Vormela peregusna*), African striped weasel (*Poecilogale albinucha*), and zorilla (*Ictonyx striatus*), have a striking contrast in their black pelage with white stripes, like that of skunks. This pattern probably serves as "warning coloration" to potential predators that their anal scent glands make them hazardous to capture. Pelage dimorphism occurs in northern populations of weasels, in which fur is white in the winter when snow is on the ground. In summer, the dorsal pelage is a uniform brown. This pelage dimorphism occurs in many high-latitude mammalian species, including hares, arctic fox, and others.

Mustelids are monestrus, and many genera display both induced ovulation and delayed implantation. Although the actual gestation period is usually 1 or 2 months, because of delayed implantation, in some species the total period of pregnancy can be about 1 year. Mustelids constitute >50% of all mammalian species known to exhibit delayed implantation, which is prevalent in highly seasonal climates (Thom et al. 2004) and allows both mating and parturition to occur during optimal spring or summer seasons. A single litter per year is typical.

Mustelids are economically important—negatively, as carriers of disease or raiders of poultry farms, and positively as furbearers. Mink, sable (*Martes zibellina*), and other mustelids generate billions of dollars annually in retail fur sales. Both species are farmed in North America and Europe, as well as more recently in China. Unfortunately, species such as the sea otter, marten, and fisher were severely overharvested in North America prior to initiation of conservation and recovery programs.

The European mink (*Mustela lutreola*) is critically endangered because of habitat loss, overharvest, and competition from introduced American mink. The black-footed ferret (*M. nigripes*) is endangered. Once believed to be extinct, it has been reintroduced at 24 sites in 8 Midwestern and Western US states, 1 state in Mexico, and 1 Canadian province, although only 4 of these sites are currently considered to be self-sustaining (IUCN 2018). Other endangered mustelids include the Bornean ferret badger (*Melogale everetti*), the sea otter, the giant otter, the marine otter (*Lontra felina*), the southern river otter (*Lontra provocax*), and the hairy-nosed otter (*Lutra sumatrana*).

The fossil record of mustelids dates from the early Oligocene of Eurasia, with at least 84 recognized extinct genera—reflecting the diversity of extant mustelids. Early lineages spread to Africa and North America by the late Oligocene or early Miocene (Wolson 1993; Koepfli et al. 2008; Werdelin and Peigné 2010), and into South America after the formation of the Panamanian land bridge in the Pliocene.

Mephitidae

Skunks were formerly included in the Mustelidae because of their enlarged anal scent glands. Based on their molecular analyses, however, Dragoo and Honeycutt (1997) and Flynn and colleagues (2000) placed skunks and stink badgers in their own Family Mephitidae. As seen in Figure 18.1, raccoons (Family Procyonidae) group more closely with mustelids than do skunks. There are 4 genera and 12 species in 2 subfamilies: the Myadinae includes the Sunda stink badger (*Mydaus javanensis*) and the Palawan stink badger (*M. marchei*), which occur in Indonesia, Borneo, the Philippines, and other Southeast Asian islands. The Mephitinae encompasses the remaining 3 genera and 10 species of skunks. These occur throughout a variety of habitats in the Western Hemisphere from Canada to Argentina. Skunks are noteworthy for their striking black and white aposematic pelage patterns, which warn potential predators, as well as for paired anal scent glands that produce a noxious scented spray. As noted by Rosatte and Larivière (2003:692), "The musk is an oily, yellow sulphur-alcohol compound known as butylmercaptan and it contains sulphuric acid." Dragoo (2009) discussed the anatomy of the scent glands and skunk behavior associated with spraying. Stink badgers, striped skunks (Genus *Mephitis*), and spotted skunks (Genus *Spilogale*; Figure 18.23) have a total of 34 teeth, whereas hog-nosed skunks (Genus *Conepatus*) have 32. Mephitids are plantigrade (although spotted skunks are able to climb trees), nocturnal, and usually solitary. They are highly omnivorous, taking insects, small vertebrates, and plant material opportunistically.

Thorne and colleagues (2017) in Virginia, and Sprayberry and Edelman (2018) in Alabama examined den site selection of eastern spotted skunks (*Spilogale putorius*). Den sites were associated with heavier, more complex under-

Figure 18.23 **Western spotted skunk (*Spilogale gracilis*).** This mephitid occurs throughout the western United States and northern Mexico. It shows the contrasting black and white pelage typical of skunks.

story and midstory cover than were sites without dens. Dias (2017) found activity of the striped hog-nosed skunk (*C. semistriatus*) in northeastern Brazil was predominately nocturnal, likely in order to avoid high daytime temperatures. Likewise, the activity pattern of the Sunda stink badger in northeastern Borneo was highly nocturnal, with no seasonal or lunar effects (Vickers et al. 2017). Only raccoons and bats have more cases of rabies reported each year in North America than do skunks. Currently, none of the 21 species of mephitids is considered endangered (IUCN 2018). Dragoo (2009) provided a comprehensive review of extant mephitids.

The fossil record of this family dates from the early Miocene of Europe and the late Miocene in North America. Eleven genera are often considered to be extinct mephitids, although Geraads and Spassov (2016) suggested that the affinities of several of these are doubtful.

Procyonidae

The 6 genera and 12–14 species in the raccoon family are restricted to the New World; they typically inhabit temperate and tropical forested areas, usually near water. Their geographic distribution extends from central Canada through Argentina. Body mass ranges from about 1 kg in the ringtail (*Bassariscus astutus*) and northern olingo (*Bassaricyon gabbii*) to 12 kg or more in raccoons (Figure 18.24A); males usually weigh about 20% more than females. Helgen and coworkers (2013), in a comprehensive revision of the olingos, described a new species, the olinguito (*Bassaricyon neblina*) from the Andean cloud forests of Colombia and Ecuador. Gerstner and colleagues (2018) provided revised and expanded distributional records for the olinguito. Procyonids typically have long, bushy tails with alternating light and dark rings (except in the kinkajou [*Potos flavus*]), and black facemasks or facial marks. They are plantigrade, some have semiretractile claws, and all are adept at climbing trees. The kinkajou (Figure 18.24B) is particularly adept at climbing and moves through the forest canopy. With its prehensile tail, it can hang from limbs as it forages. Kinkajous have even more dexterous forepaws than do raccoons and can hold food with 1 paw. Procyonids have a total of 40 teeth; the kinkajou, with 38, is again an exception. Kinkajous are widely distributed from western Mexico through Central America, and south through northern South America from Bolivia to Brazil. Nascimento and coworkers (2017) examined the systematics of the kinkajou based on the mitochondrial cytochrome b gene and found 5 well-defined clades. Several prior investigators (see Agnarsson et al. 2010) have

Figure 18.24 Representative procyonids. (**A**) The crab-eating raccoon (*Procyon cancrivorus*) closely resembles the North American raccoon. It occurs from Costa Rica to Uruguay. (**B**) The kinkajou (*Potos flavus*) is a highly arboreal member of the raccoon family with a prehensile tail and somewhat questionable taxonomic affinity with other procyonids.

Figure 18.25 **White-nosed coati (*Nasua narica*).** This social procyonid ranges from the southwestern United States through Central America.

questioned the placement of the kinkajou within the raccoon family. Procyonids may be the least carnivorous of the carnivores. Dentition is generalized and adapted for an omnivorous diet, with fruit predominating in the kinkajou and olingos. The carnassials are fairly well developed only in the ringtail and cacomistle (*Bassariscus sumichrasti*). Kays and Gittleman (2001) discussed social organization in the kinkajou. Groups occur most often at denning and feeding sites, whereas most kinkajous are solitary. Conversely, the white-nosed coati (*Nasua narica*) is a highly social neotropical procyonid (Valenzuela and Ceballas 2000), with groups of up to 30 individuals (Figure 18.25). They are generally diurnal, and activity patterns did not vary seasonally in southeastern Mexico (Perez-Irineo and Santos-Moreno 2016). Breeding biology of procyonids varies geographically and seasonally among species as reviewed by Kays (2009). Nielsen and Nielsen (2007) found multiple paternity in most of the 11 raccoon litters they tested from southern Illinois. The raccoon, a popular game animal with both hunters and trappers, is one of the most commonly harvested furbearers in North America (Gehrt 2003). Populations are increasing in North America, and *P. lotor* has been introduced to numerous European countries as well as Japan. The raccoon can be a significant nest predator of bird eggs; it can also be a major focus of rabies (see Chapter 27). The pygmy raccoon (*P. pygmaeus*) is restricted to Cozumel Island off the coast of the Yucatan Peninsula, Mexico, and is critically endangered. The eastern mountain coati (*Nasuella meridensis*), endemic to the Andes Mountains of Venezuela, is endangered (IUCN 2018).

The earliest fossil procyonids are from the early Miocene of Europe, although they were gone prior to the Pliocene. They dispersed to South America in the late Miocene, well before the appearance of the Panamanian land bridge.

Ursidae

Bears historically occurred throughout North America, in the Andes Mountains of South America, in Eurasia, and in the Atlas Mountains of North Africa. They primarily occur in forested habitats, as well as in high-elevation alpine areas and tundra; polar bears (*Ursus maritimus*) occur on arctic ice floes (Figure 18.26). There are 5 genera and 8 species of extant bears, including the giant panda (*Ailuropoda melanoleuca*), which at one time was placed in a family (Ailuropodidae) along with the red panda. Historically, the systematics of ursids has been problematic. Most authorities now place bears in 3 subfamilies: the Tremarctinae, which includes only the spectacled bear (*Tremarctos ornatus*); the giant panda (Figure 18.27), which is the only member of the Subfamily Ailuropodinae, and the Ursinae, which encompasses 3 genera and 6 species (Garshelis 2009).

Body mass in bears reaches 800 kg in grizzly (brown) bears (*Ursus arctos*) and polar bears, which are the largest terrestrial carnivores. The sun bear (*Helarctos malayanus*) is the smallest ursid; males weigh only about 60 kg. Sexual dimorphism is evident in bears. Males are about 20% heavier than females in monogamous species such as the sun bear and sloth bear (*Melursus ursinus*) and up to twice as large in polygamous species. Dimorphism can vary geographically among species (McDonough and Christ 2012). All bears are plantigrade and pentadactyl and have nonretractile claws. An extended radial sesamoid carpal bone in the giant panda forms a "false thumb" that is used to strip bamboo leaves. This same convergent adaptation evolved independently in the red panda (Hu et al. 2017). The occurrence of epipharyngeal pouches, located near the pharynx and trachea, has been documented in most ursids, including the giant panda (Weissengruber et al. 2001). These pouches probably play a role in modification and amplification of vocalizations. Bears usually have a total of 42 teeth. Canines are large, but the last upper molar is reduced, and carnassials are not well developed. Molars are

Figure 18.26 **Polar bear.** Polar bears hunt seals from ice floes. This has become increasing difficult as arctic ice melts because of climate change.

Figure 18.27 Giant panda. Although the giant panda was at one time placed in its own family, currently, authorities generally agree that it should be placed in the bear Family Ursidae.

broad, flat, and relatively unspecialized, reflecting an omnivorous diet in most bears. Bears are active both day and night, and locate food primarily through their highly acute sense of smell. Zhang and colleagues (2015) found three activity peaks in giant pandas in Wolong Preserve, China—one in the morning, another in the afternoon, and at midnight. Only the polar bear is strictly carnivorous, feeding on fish and seals. Because their prey (primarily ringed seals, *Pusa hispida*) is relatively soft, polar bears can function well without highly developed carnassials. The sloth bear, like the aardwolf, is highly myrmecophagous, Asiatic black bears and sun bears consume a great deal of fruit (Steinmetz et al. 2013), whereas the diet of the giant panda is almost entirely bamboo. Nonetheless, the gut microbiota of giant pandas is similar to that of other bears, rather than to that of herbivores as might be expected (Guo et al. 2018). It is not adapted to digest cellulose, which is consistent with the large volumes of food intake and limited activity level of giant pandas. Reduced activity levels in pandas result in energy expenditure that is only about 38% of that in similar-sized mammals. Nie and colleagues (2015) found this low metabolism was related to very low levels of two thyroid hormones. As they note, pandas subsist on bamboo by a combination of physiological, behavioral, and genetic adaptations. Caro and coworkers (2017) attributed the familiar black and white coloration of panda bears to both camouflage (white pelage against winter snow; black pelage in summer wooded areas) and intraspecific communication.

In northern areas, American black bears (*Ursus americanus*), grizzlies, and Asiatic black bears (*U. thibetanus*) den in hollow trees, caves, or burrows. Polar bears use dens of ice and snow and may abandon dens due to human disturbance (Durner et al. 2006). Bears can sleep through the winter, especially pregnant females, and live off their stored body fat. This process is called "winter lethargy" rather than hiberna-

tion because body temperature, heart rate, and other physiological processes are not reduced to the same extent that they are in true hibernation (Hellgren et al. 1990; Brown 1993). Whiteman and colleagues (2015), studying polar bears in the Beaufort Sea, expected them to reduce energy expenditure because of reduced prey availability caused by climate change and melting ice. Instead of entering a type of "walking hibernation," the bears simply starved.

Bears are monestrus and exhibit delayed implantation; American and Asiatic black bears are also induced ovulators (Garshalis 2009). Young, often twins, are usually born between November and February, while the female dens. In giant pandas, females move cubs to new dens 3 to 4 times before the cubs permanently leave the den at 3 to 4 months of age (Zhu et al. 2001). Den site selection and potential population size of black bears in an area are negatively affected by numbers of roads.

Bears have been hunted for their hides, meat, and fat since prehistoric times. Most species have been eradicated throughout much of their ranges because of predation on domestic livestock; the spectacled bear of northern South America (Goldstein et al. 2006) is an example. Black bears are also illegally killed for their gallbladders, which are valuable in traditional Asian medicine. The giant panda (recently downlisted from endangered status by the IUCN), sun bear, sloth bear, spectacled bear, polar bear, and Asiatic black bear are threatened. Although the number of panda bears living in the wild has increased to an estimated 1,800, primarily in Sichuan Province, China, available habitat is reduced and more fragmented (Xu et al. 2017). About 20 extinct genera of ursids dating to the late Eocene of Europe and North America are known (Hunt 1998; Goswami 2010).

Ailuridae

This monotypic family contains only the red or lesser panda (*Ailurus fulgens*), an endangered species (IUCN 2018). The phylogenetic relationship of the red panda with other carnivores has been uncertain for 200 years. In the past, the species was placed with raccoons in the Family Procyonidae or with bears (Family Ursidae), based on morphological similarities, or included with the giant panda in Family Ailuropodidae, because both eat bamboo and have a carpal bone modified to form a "false thumb" (a fascinating convergence also found in the Miocene relative *Simocyon batalleri*; see Salesa et al. 2006). Molecular and morphological data now clearly place the red panda in its own fairly ancient family (Morlo and Peigné 2010). The species occurs in the Himalayan Mountain areas of northern India, Nepal, Bhutan, Myanmar, and south-central China, where it inhabits high-elevation forests with an understory of bamboo thickets. Red pandas (Figure 18.28), with a body weight of only 3–6 kg, feed primarily on bamboo and other vegetation (Panthi et al. 2012), with insects and small vertebrates occasionally included. Despite the low energetic and nutritional quality of bamboo, the seasonal metabolic rates of red pandas were similar to those of

Figure 18.28 **Red panda (*Ailurus fulgens*).** The phylogenetic position of the red panda has been difficult to assess for over 200 years. It currently resides in its own monotypic family.

Figure 18.29 **Pinniped body shape.** All pinnipeds have a streamlined, torpedo-shaped (fusiform) body for minimal resistance as they swim, as in this leopard seal (*Hydrurga leptonyx*).

same-sized mammals (Fei et al. 2017). Han and colleagues (2004) and Zhang and coworkers (2006) described microhabitat selection of red pandas, as well as differences from the giant panda. During the breeding season, Cao and coworkers (2016) recorded seven types of vocalizations from captive red pandas. Wei and Zhang (2009) summarized systematic and life-history information on the species. Thapa and colleagues (2018) discussed reasons for the decline in populations and potential conservation approaches.

Fossil ailurids from the Miocene and Pliocene are known from Europe and North America (Ogino et al. 2009). The earliest—the late Oligocene Genus *Amphictis*—is known only from Europe, where ailurids passed most of their evolutionary history (Morlo and Peigné 2010), despite being found today only in Asia.

Pinnipedia

The last three families of carnivores in this chapter—collectively referred to as "pinnipeds"—form a monophyletic clade (see Figure 18.1) that exhibits specialized adaptations for an aquatic existence. Pinnipeds are not as totally adapted for life in the water as are whales, manatees, and the dugong, however. Sirenians (Chapter 12) and whales (Chapter 20) spend their entire lives in the water, but pinnipeds must "haul out" onto rocky, generally inaccessible land or ice floes (where they are slow and vulnerable) to breed (in "rookeries"), give birth, or rest. When undisturbed, they may rest on manmade structures such as docks or buoys.

Being adapted to both terrestrial and aquatic conditions has caused all pinnipeds to be morphologically similar. They have a coarse pelage of guard hairs that helps protect them when they are out of the water. As in whales, body shape in pinnipeds is adapted to reduce turbulence and resistance (drag) as they swim. Thus, bodies are fusiform, with no constriction in the neck region (Figure 18.29). External genitalia are concealed in sheaths within the body

contour, as are the teats, and external ears are reduced or lost. A subcutaneous layer of fat (blubber) provides energy, insulation, and buoyancy. It also serves to maintain a streamlined body shape, which enhances hydrodynamic properties and further reduces drag.

The limbs are relatively short, stout, and modified to form paddle-like flippers. The forelimbs provide the propulsive force in otariids (eared or fur seals) and odobenids (walrus); the hind limbs serve this function in phocids (earless or "true" seals). These differences are reflected in skeletal anatomy. Otariids and the walrus have enlarged cervical and thoracic (neck and upper chest) vertebrae that support the large muscle groups associated with the forelimbs. Because the hind limbs provide propulsion in phocids, the lumbar (lower back) vertebrae are relatively large (Figure 18.30).

Most pinnipeds have generalized feeding habits, and the primary function of the teeth is to grasp and hold prey rather than to chew. Teeth in most species approach homodonty, with the premolars and molars being similar and somewhat conical (Figure 18.31). There are exceptions, however, in species that are more specialized feeders. For example, the crabeater seal (*Lobodon carcinophaga*) has distinctive cheekteeth that form a sieve to filter krill from the water. Unlike the interorbital area of terrestrial carnivores, that of pinniped skulls is long and narrow, and the braincase is longer in proportion to the facial area (see Figure 18.31).

The eyes of seals are relatively large and modified to focus underwater by means of a greater corneal curvature than occurs in the eyes of terrestrial mammals. On land, however, seals are quite nearsighted. Pinnipeds see effectively under conditions of reduced light. Like felids, deer, and some other terrestrial groups, they have a well-developed **tapetum lucidum**, a specialized membrane behind the retina. The tapetum lucidum increases light-gathering

A

B

A

B

C

D
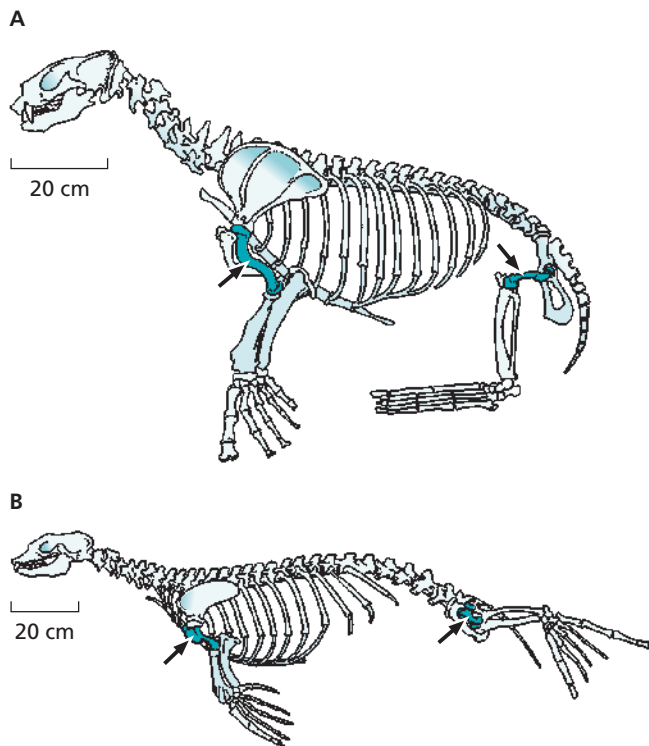
Figure 18.30 **Pinniped skeletal characteristics.** Lateral view of the skeleton of (**A**) a New Zealand fur seal (*Arctocephalus forsteri*), an otariid and (**B**) a West Indian monk seal (*Monachus tropicalis*), a phocid. Note the very short, broad humerus and femur (*arrows*) and elongated foot bones in both. In otariids and the walrus, the cervical and thoracic vertebrae and scapula are enlarged to support the primary muscle groups that power the forelimbs for propulsion. The hind limbs propel phocids through the water, and the lumbar vertebrae are enhanced for muscle attachment. *Adapted from J. E. King (1983).*

Figure 18.31 **Pinniped skulls and cheekteeth.** (**A**) Dorsal view and (**B**) ventral view of a phocid, the harbor seal (*Phoca vitulina*). Note the narrow interorbital regions, shortening of the nasal bones on the rostrum, and lack of a postorbital process in the phocid. The cheekteeth of otariids usually are single-cusped and peg-like, as in (**C**) the Steller sea lion (*Eumetopias jubatus*), whereas those of phocids are multicusped and particularly well developed, as in (**D**) the crabeater seal. *Adapted from Riedman (1990).*

efficiency by reflecting back to the retina light that has passed through but not been absorbed. All pinnipeds hear well underwater and are able to determine the direction from which sounds come. This ability is critical for locating prey, especially under reduced light conditions or in total darkness. Harbor seals (*Phoca vitulina*) and California sea lions (*Zalophus californianus*) are known to locate and follow for considerable distances the hydrodynamic trails left by fish and other potential swimming prey (Glaeser et al. 2011; Beem and Triantafyllou 2015). It is likely that many other pinnipeds can as well.

Many of the same physiological processes for diving seen in whales also occur in pinnipeds, including **bradycardia** (reduced heart rate) and shunting blood from peripheral areas to the brain and heart. Like whales, seals also have more oxygen-binding hemoglobin and myoglobin than do terrestrial mammals. The size of the spleen, and its importance in red blood cell storage, is related to diving capabilities in seals (Thornton et al. 2001). Pinnipeds do not dive as deep or remain submerged as long as whales, however (Lavigne and Kovacs 1988). Among pinnipeds, phocids dive deeper and remain submerged longer than

otariids. Aspects of dive duration and depth in pinnipeds relate to regional water conditions, seasonal variations in depth of prey species, and reproductive condition and molting (Frost et al. 2001).

Pinnipeds had been harvested for thousands of years on a subsistence basis for fur, food, and oil, with little effect on populations. Large-scale commercial hunting and resultant overharvesting of many species began in the early 1800s, and many species were "commercially extinct" by the end of the century. Today, several species are still harvested, but most populations are secure. The most serious threats to pinnipeds include incidental drowning in fishing nets, habitat degradation, and contamination of marine habitats.

Odobenidae

The only extant member of this family, once considered a subfamily of otariids, is the walrus (*Odobenus rosmarus*). Walruses have a circumpolar distribution in shallow arctic

Table 18.2   Morphological characteristics differentiating the three families of pinniped carnivores*

	Phocidae (Earless Seals)	Odobenidae (Walrus)	Otariidae (Fur Seals, Sea Lions)
External pinnae	No	No	Yes
Testes	Abdominal	Abdominal	Scrotal
Tip of tongue notched	Yes	No	Yes
Hind limbs rotate forward	No	Yes	Yes
Guard hairs with medulla	No	No	Yes
Underfur	Essentially absent	Essentially absent	Present in sea lions
Alisphenoid canal	Absent	Present	Present
Auditory bullae	Inflated	Small and flattened	Small and flattened
Transverse groove on upper incisors	No	No	Yes
Lower incisors present	Yes	No	Yes
Total number of teeth	26–36	18–24	34–38
Fused symphysis of lower jaw	No	Yes	No
Postorbital process	Absent	Absent	Present
Chromosome number	32–34	32	36

*For additional differences of the skull, middle ear, and inner ear, see Repenning (1972).

waters, where they remain near ice floes and rocky shorelines. Average body mass of adult bulls is about 1,000 kg but can reach 1,600 kg. As is typical of pinnipeds and most other carnivores, males are significantly larger than females. The skin is thick and wrinkled, and the layer of blubber, which is usually 6–7 cm thick, can reach 15 cm. Certain morphological features of walruses are shared with otariids, whereas others are similar to phocids (Table 18.2). In addition, walruses, like otariids, have naked ventral surfaces on all flippers, and the nails on the first and fifth digits of the hind flippers are rudimentary.

A significant feature in both male and female walruses is their tusks, which are enlarged upper canines (Figure 18.32). These grow throughout life and can reach as long as 100 cm in males and 60 cm in females. The crown of the tusk is composed internally of dentine and externally of cementum. Other than a small cap at the end of the tooth, which wears away during the first couple of years, there is no enamel. Tusks are used for defense, raking the sea bottom for mollusks, breaking through ice, and hanging from ice floes while remaining in the water. Among males, however, they are also weapons for establishing dominance hierarchies— dominant males are very aggressive and have larger bodies and longer tusks than subordinates.

Walruses remain in shallow water, usually diving to depths of between 10 and 100 m. Garde and colleagues (2018) studied the diving behavior of Atlantic walruses (*O. r. rosmarus*) in Arctic Greenland and Canada. Although most dive depths were 100 m or less, they recorded 4 dives >500 m. Likewise, the mean depth of foraging dives for 9 males on Svalbard, in the eastern Greenland Sea, was about 22 m, with a mean duration of only 6 minutes. The mean time spent in the water was 56 h, followed by 20 h on land (Gjertz et al. 2001). Jay and coworkers (2001) followed 4 Pacific walruses (*O. r. divergens*) in Bristol Bay, Alaska, for

Figure 18.32 Walrus tusks. These large tusks are canine teeth.

a month during the summer. Walruses were in the water almost 77% of the time, of which about 60% was spent diving. Jay and colleagues (2017) found the probability of walruses being in the water increased with higher wind speed and decreased with higher air temperature. Walruses feed primarily on clams, other bivalve mollusks, and a variety of invertebrates taken from the muddy sea bottom (Sheffield and Grebmeier 2009). Ray and colleagues (2006) suggested that the feeding activities of walruses significantly impacted sediment, nutrient flux, and biological structure of thousands of square kilometers of the sea floor. Annual walrus predation on the biomass of bivalves in northwest Greenland was estimated at 3.2% (Garde et al. 2018).

Walruses are gregarious, often huddle together, and form groups of up to 1,000 individuals. They are polyga-

mous, mating during February and March on near-shore ice floes. Following a 3-month delayed implantation period and 12-month gestation, females haul out to give birth on land, usually to a single calf, in May or June. Thus, given the lactation period, females normally mate every 2–3 years.

Walruses have been a critical biological and cultural resource for northern indigenous people for >1,000 years (Gotfredsen et al. 2018)—hunted for meat, oil, and hides; the tusks (ivory) are highly prized for artwork carvings (called "scrimshaw"). From 10,000 to 15,000 individuals are harvested annually. The most serious concern, however, is long-term impact of climate change on the loss of arctic sea ice and resultant effects on prey availability and resultant walrus populations (Beatty et al. 2016; Udevitz et al. 2017; Taylor et al. 2018).

There are about 15 known extinct genera of walruses. The earliest date from the early to mid-Miocene of the North Pacific, and include the Genera *Prototaria* and *Proneotherium* (Kohno 2006) as well as 7 other genera; they were all relatively small and did not have enlarged canines (Berta 2017). The mid- to late-Miocene walrus Genera *Pseudotaria*, *Neotherium*, and *Pelagiarctos* were from the eastern North Pacific (Boessenecker and Churchill 2013). The late-Miocene to early-Pliocene walruses *Dusignathus* and *Gomphotaria* of North America had enlarged, tusk-like upper as well as lower canines. Berta (2017) provided an excellent summary of fossil odobenids as well as other pinnipeds. Stewart (2014a) provided a comprehensive summary of all aspects of the life history of the walrus.

Otariidae

The eared seals include fur seals and sea lions in subpolar, temperate, or coastal waters of western North America, South America, Asia, southern Australia and New Zealand, and other oceanic islands. They inhabit only marine communities, unlike phocids, which also occur in freshwater and estuarine communities. Several general characteristics of the 7 genera and 15 species of otariids are noted in Table 18.2. Two otariid subfamilies have traditionally been recognized: sea lions (Subfamily Otariinae), with blunt noses and little underfur, and fur seals (Subfamily Arctocephalinae), with pointed noses and abundant underfur. However, morphological and molecular analyses (Churchill et al. 2014) show these subfamily divisions are not valid. All otariids are highly dimorphic, with males being larger than females. For example, maximum body mass of male northern fur seals (*Callorhinus ursinus*) is 5 times greater than that of females (Webber 2014); male southern sea lions (*Otaria flavescens*) are twice the size of females. The largest otariid, and one of the largest carnivores, is the Steller sea lion (*Eumetopias jubatus*): adult males are 3 m long and over 1,100 kg.

Otariids feed on fish, cephalopods, and crustaceans, usually swallowing prey whole. Chewing occurs only to tear larger prey into small enough pieces to swallow (Hocking et al. 2017). Northern fur seals in the north Pacific fed on 15 species of small squid, primarily *Watasenia scintillans*

(Mori et al. 2001). Duration of foraging trips in Afro-Australian fur seals (*Arctocephalus pusillus*) in southeast Australia increased from a mean of 3.7 days in summer to 6.8 days in winter (Arnould and Hindell 2001). Baylis and colleagues (2015) found that most female southern sea lions foraged more in deeper offshore waters than in shallower coastal waters.

Generally, otariids are much more gregarious than terrestrial carnivores (Figure 18.33), and breeding colonies of up to a million individuals can occur within limited areas. All otariids breed on land in rocky, isolated areas that are inaccessible to potential predators. Phillips and Stirling (2001) described 11 distinct calls, grouped into investigative, threat, submissive, and affiliative categories, in South American fur seals (*Arctocephalus australis*). Female otariids must leave newborn pups to forage at sea. For the subantarctic fur seal (*A. tropicalis*), Charrier and coworkers (2001:873) found that "the mother's departure date is linked to the pup's ability to recognize her voice." This ability is crucial to survival of pups in a colonial species in which females nurse only their young. Kuhn and colleagues (2006) found that by the time they are weaned, California sea lion pups (*Zalophus californianus*) can store only about 53% of the oxygen that adults can prior to diving. As a result, pups cannot forage on resources that are available to adults in deeper water; depth and duration of dives increase with age. Breeding males are polygynous and defend a territory with a group of 3–40 females. Most species exhibit delayed implantation.

The most familiar species of otariid is the California sea lion, commonly displayed in circuses and zoos. Historically, all species were harvested for meat and hides and for oil from blubber. Today, relatively few individuals are harvested for subsistence purposes. However, climate change has reduced prey availability for many otariids, with resultant changes in neonate birth weights, as well as increased genetic heterozygosity of breeding females (Forcada and Hoffman 2014).

The Galápagos fur seal (*Arctocephalus galapagoensis*), Galápagos sea lion (*Zalophus wollebaeki*; Riofrio-Lazo et al. 2017),

Figure 18.33 **Stellers sea lions.** The otariids, unlike phocids, are very gregarious.

Australian sea lion, and New Zealand sea lion (*Phocarctos hookeri*; Chilvers and Meyer 2017) are endangered. The Japanese sea lion (*Z. japonicus*) is recently extinct (IUCN 2018).

Unlike the numerous genera of early walruses, known fossil otariids are limited. The oldest is the late-Miocene *Pithanotaria starri* from California. Another fossil otariid is *Thalassoleon* from southern California and Japan. The Pliocene-Pleistocoene Genus *Hydrarctos* is known from Peru (Berta et al. 2015; Berta 2017).

Phocidae

The earless seals include 14 genera and 19 extant species. Traditionally, 2 subfamilies have been recognized, the Phocinae (northern seals) and the Monachinae (southern seals and monk seals, Genus *Monachus*). Using a large mtDNA database, Davis and coworkers (2004) found "strong support" for groupings within these subfamilies, which diverged about 15 mya (Fulton and Strobeck 2010). Phocids occur primarily in polar, subpolar, and temperate waters around the world; the Hawaiian monk seal (*Neomonachus schauinslandi*) and the Mediterranean monk seal (*N. monachus*) are the only surviving pinnipeds that inhabit tropical areas. In addition to occurring in oceans, phocids inhabit inland freshwater lakes and estuaries. The flippers of phocids are furred on all surfaces, and the nails on the hind flippers are all the same size.

Among pinnipeds, phocids are the most diverse in size. The smallest is the Baikal seal (*Pusa sibirica*), restricted to freshwater Lake Baikal, with a body mass of only 35 kg. As noted, the largest phocid is the southern elephant seal; maximum male body mass can reach 4,000 kg. Unlike otariids, phocids generally lack underfur (see Table 18.2), and the cheekteeth are multicusped (see Figure 18.31). Phocids are not gregarious and do not form large breeding colonies. Almost all phocids breed on ice. Because they are clumsy and vulnerable on land, ice floes offer several benefits to breeding individuals. It is easier for seals to move on ice than on rocks, and they have quick access to the relative safety of deep water. Cameron and colleagues (2018) found young bearded seals (*Erignathus barbatus*) associated more with the edge of the ice pack in the Bering Sea, whereas adults stayed farther north in the ice pack. Like other pinnipeds, phocids exhibit delayed implantation.

Fish and cephalopods form the diet of most species (Howard et al. 2013). The leopard seal (*Hydrurga leptonyx*; see Figure 18.29), the only pinniped that regularly feeds on warm-blooded prey, takes penguins and the young of other seals. As noted earlier, phocids dive deeper for prey and remain submerged longer than otariids and thus are the most aquatically adapted of the carnivores. Dive durations in southern elephant seals (*Mirounga leonina*) are longest in the morning and deepest at midday (Bennett et al. 2001). On land, however, phocids are less agile and mobile. They are unable to raise themselves on their front flippers and simply hunch their bodies, moving forward like inchworms.

Commercial sealing of many species, including the harvesting of young harp seals (*Pagophilus groenlandicus*), is controversial, but populations are high. The Mediterranean monk seal (*Monachus monachus*), with fewer than 700 mature individuals in the entire population (Karamanlidis et al. 2016; IUCN 2018), is endangered, as are the Hawaiian monk seal and the Caspian seal (*Pusa caspica*). The Caribbean monk seal (*N. tropicalis*), last seen in the early 1950s, is considered extinct.

Fossil phocids are highly diverse, with as many as 26 extinct genera. The oldest confirmed specimens date from the middle Miocene and occur from various Old and New World sites in both the Northern and Southern Hemispheres (Berta et al. 2015; Berta 2017). Stewart (2014b) provided a comprehensive review of the family.

Order Pholidota

Pholidotes—pangolins (also called scaly anteaters)—are included with the Carnivora in this chapter because it has long been known that the two orders are closely related sister taxa (Arnason et al. 2002; Murphy et al. 2007; du Toit et al. 2017). Pangolins are in a single family, Manidae. As was true for the aardvark, pangolins were once placed in Order Edentata based on morphological features associated with diet. Historically, a single genus (*Manis*) was recognized, but now many authorities place the 8 species of pangolins in 3 "well supported, monophyletic genera" (Gaudin et al. 2009:236; also see Gaubert 2011; Gaubert et al. 2017; Figure 18.34). Four species of pangolins are found in Africa south of the Sahara Desert: the giant ground pangolin (*Smutsia gigantea*), Temminck's ground pangolin (*S. temminckii*), the black-bellied, or long-tailed, pangolin (*Phataginus tetradactyla*), and the white-bellied, or tree, pangolin (*P. tricuspis*; Figure 18.35). Four other species of pangolins occur in Pakistan, India, Sri Lanka, Southeast Asia, southern China, and Indonesia. These are the Philippine pangolin (*M. culionensis*), an endemic to the Culion Islands of the Philippines, which differs from the closely related Malayan pangolin (*M. javanica*) in several skull characteristics and aspects of the scales, and was first described by Gaubert and Antunes (2005). The other species of Southeast Asian pangolins are the Chinese pangolin (*Manis pentadactyla*) and the Indian or thick-tailed pangolin (*M. crassicaudata*).

Pangolins inhabit forests, savannas, and sandy areas, with distribution directly related to the occurrence of ants and termites, their primary prey (Heath 1995). For Temminck's ground pangolin in South Africa, ants—primarily *Anoplolepis custodiens*—formed 96% of their diet (Swart et al. 1999). The mean duration of feeding bouts by pangolins was 40 seconds, with the abundance and size of ants the primary factors determining the number of feeding bouts on a particular prey species. More recently, Pietersen and coworkers (2016) found Temminck's ground pangolin fed very selectively on 4 species of ants (*A. steinroeveri*, *Camponotus fulvopilosus*, and *Crematogaster* spp.) and 1 ter-
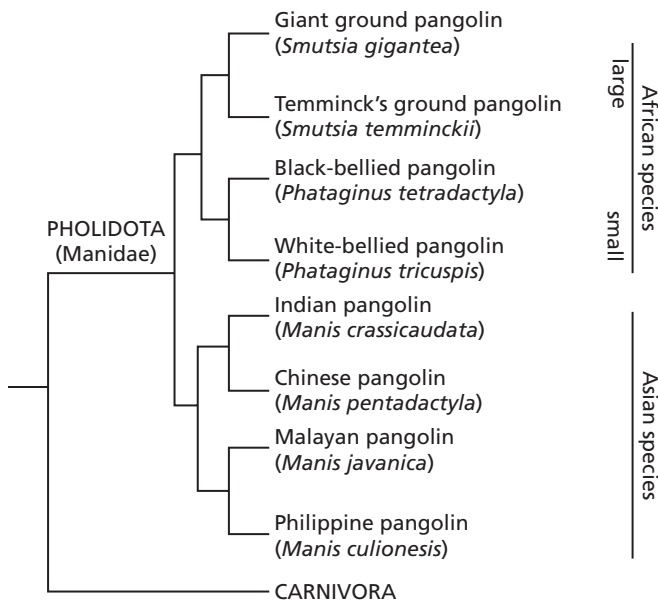
Figure 18.34 Phylogeny of extant pangolins. Alternatively, Gaubert et al. (2017) considered the Indian pangolin as sister to the Malayan and Philippine pangolins. *Modified and adapted from Gaudin et al. (2009) and DuToit et al. (2017).*

Figure 18.35 White-bellied pangolin. Note the prehensile tail wound around the tree limb.

mite species (*Trinervitermes trinervoides*), with no seasonal, gender, or age-specific differences in diet. Some pangolins are terrestrial and are strong diggers, living in large, deep burrows, whereas others are arboreal, living primarily in trees and having prehensile tails (see Figure 18.35). Even the terrestrial species are good climbers and occasionally may forage in trees. Pangolins can be active during the day but are primarily nocturnal. Occurring as solitary individuals or in pairs, they have limited vocal, visual, and auditory acuity. Olfactory communication plays a significant role in their behavior, however. Strong scent is produced from paired anal glands, and feces and urine are deposited along trails and trees. Like skunks, they may eject an unpleasant smelling secretion from the anal glands. Gestation is about 140 days. Litter size is usually 1, but occasionally

twins are produced. The young are born with soft scales that do not harden until 2 days after birth. Newborn young cling to the female's back or tail, and, if threatened, the female curls up around the neonate.

MORPHOLOGY

The ordinal name means "scaly ones" and refers to the major diagnostic characteristic of this group. With the exception of the sides of the face, inner surface of the limbs, and the venter, pangolins are covered with **imbricate** (overlapping) scales, somewhat like those of a pinecone (Figure 18.36). Scales, which are composed of keratinized

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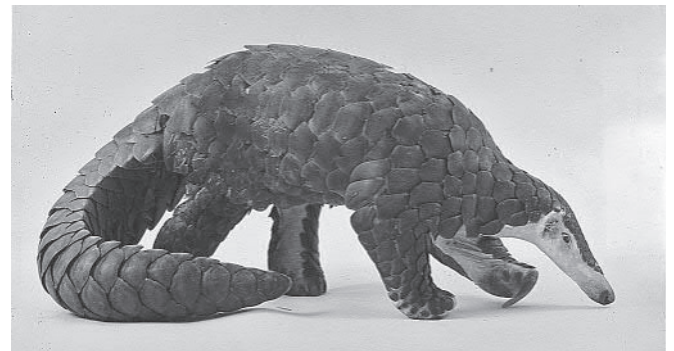
B
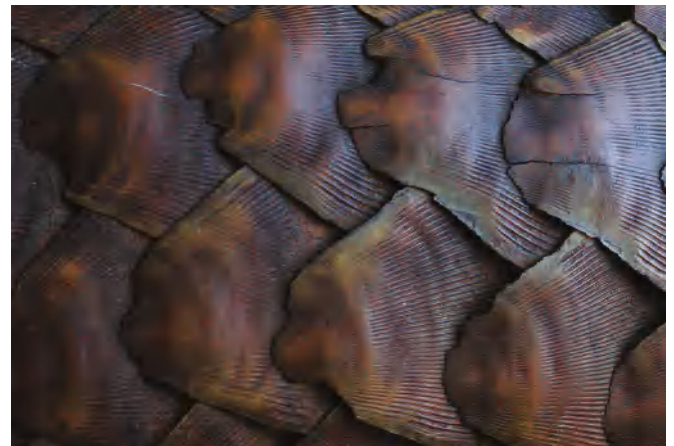
C

Figure 18.36 Morphology of a pangolin. (**A**) Dorsal view of a long-tailed pangolin (*Phataginus tetradactyla*), showing its distinctive scales; (**B**) the overlapping, pine-cone-like scales of the ground pangolin, *Smutsia temminckii*; (**C**) skull of a pangolin, showing the incomplete zygomatic arch and very simple mandible.

Figure 18.37 **Skull of Temminck's ground pangolin.** Note the incomplete zygomatic arch, very simple mandible, and lack of teeth.

epidermis and are a dark brown to yellow color, serve the same protective function as the armor of armadillos or the spines of echidnas. Wang and Sullivan (2017) reviewed the structural and mechanical properties of pangolin scales; Wang and colleagues (2016) described the nano-scale (5 μm) internal structure of scales. A pangolin has the same number of scales throughout life; they grow larger as the individual grows. Skin and scales make up 25% to 33% of the body mass of most species, although, as might be expected, scales on arboreal species such as the white-bellied pangolin are lighter and thinner than those on terrestrial species. Scales protect against predators but are nonetheless costly metabolically and provide little thermal insulation (Gaubert 2011). When alarmed, pangolins curl up in a ball, with the sharp-edged, movable scales directed outward. Pangolins can reach 1.6 m in length, with the tail comprising half the total. External ears do not occur in the 4 African species, but they are found in Asian pangolins.

All pangolins are edentate. Instead of teeth, they use a long, powerful tongue for foraging. Sticky, viscous saliva is secreted onto the tongue by a large salivary gland in the chest cavity. Tongue muscles are enclosed in a sheath and pass over the sternum and anchor on the pelvis. A pangolin's tongue is longer than its head and body length and is structurally similar to that of the giant anteater (Chan 1995; Reiss 2001). The skull is long and tapered, with a straight slender mandible and incomplete zygomatic arches (Figure 18.37). The morphology of the skull, lack of teeth, and associated lack of any strong facial muscles for chewing reflect the pangolin's highly specialized diet. Pangolins are plantigrade and pentadactyl, with large, sharp, curved claws used to break into ant and termite mounds, which they locate primarily through scent. Steyn and colleagues (2018) described the skeletal anatomy of the forelimbs of Temminck's pangolin, which are adapted for protraction and retraction (for dig-

ging) rather than for weight-bearing. As in other ant-eating species, pangolins have a stomach with a muscular, keratinized, gizzard-like pyloric region for grinding ants and termites.

FOSSIL HISTORY

Fossil material is meager, partly because pangolins lack teeth, which fossilize most easily, have low population densities, and can be misidentified by paleontologists. Interestingly, the oldest fossil material is from outside the current distribution of pangolins. The oldest known fossil pangolins are *Eomanis krebsi* and *E. waldi* from the mid-Eocene of Germany (Gaudin 2008)—even 50 mya, scales were present, as was a long, thin, toothless skull adapted for eating ants and termites (Gaubert 2011). A fossil pangolin from the late Eocene of Inner Mongolia, *Cryptomanis gobiensis*, represents the oldest and most northerly distributed Asian pangolin (Gaudin et al. 2006). It is similar anatomically to *Patriomanis americanus*, a late-Eocene pangolin from western North America (Emry 2004). Various species of the extinct Genus *Necromanis* occur in late Oligocene–early Miocene deposits of Germany and France. In contrast, the fossil record from the current range of pangolins is poor and generally dates only from the Pliocene and Pleistocene (Gaudin et al. 2009; Gaudin 2010).

ECONOMICS AND CONSERVATION

No other group of mammals is illegally trafficked more than pangolins. Native people eat African and Asian species (Carpaneto and Fusari 2000), and their scales are used for adornments. Scales are also used as good luck charms,

with entire skins being very valuable. In Asia, because powdered scales are believed to be of medicinal value, populations of the four species in this region are greatly reduced. Although it is extremely difficult to determine population levels, all species are declining. Malayan and Chinese pangolins are critically endangered (IUCN 2018), and the Indian and Philippine pangolins are endangered. Populations of Asian pangolins have declined 50%–90%, and those declines are expected to continue because of intense hunting pressure for meat and scales, forest fires, livestock grazing, and even electrocution from electric fences (Heinrich et al. 2016; Katuwal et al. 2017).

SUMMARY

- Carnivores are terrestrial or aquatic predators that usually consume other animals as a major part of their diet.

- Specialized carnivore feeding habits include insectivory (aardwolf and sloth bear), scavenging on carrion (hyenas), omnivory (black bear and raccoon), and almost complete herbivory (greater and lesser pandas).

- Two suborders of carnivores are recognized:
  - Suborder Feliformia consists of seven families: felids, herpestids, hyaenids, viverrids, euplerids, nandiniids, and the recently recognized prionodontids.
  - Suborder Caniformia includes nine families: canids, ursids, mustelids, procyonids, ailurids, mephitids, and three families of aquatic carnivores (the pinnipeds)—otariids, phocids, and odobenids.

- Morphological and behavioral characteristics of carnivores involve adaptations to locate, capture, kill, and consume prey without being injured in the process. Morphological features of carnivores include:
  - digits with well-developed claws;
  - dentition with enlarged canine teeth;
  - carnassial teeth-specialization of the fourth upper premolar (P^4) and first lower molar (m_1) for cutting and shearing (especially well developed in felids, canids, and hyaenids; less developed in more omnivorous groups, such as ursids and procyonids);
  - well-developed facial musculature;
  - articulation of jaw with the cranium typically hinged to reduce lateral motion as captured prey struggle to escape.

- Size diversity is pronounced within the order and families.
  - The largest carnivores are the elephant seals; the largest terrestrial carnivores are the polar bear and grizzly bear.

- The largest carnivores are 11,000 times heavier than the smallest carnivore, the least weasel.
- Secondary sexual dimorphism is often evident, with males being larger and heavier than females.

- Most species are solitary hunters, although wolves, spotted hyenas, lions, and some others do generally hunt in packs.

- Benefits to group hunting include:
  - ability to prey on species larger than themselves;
  - improved foraging efficiency;
  - communal infant care;
  - increased vigilance and reduced predation; and
  - defense of feeding areas from rival packs.

- The earliest carnivorous mammal, *Cimolestes*, was from the late Cretaceous period and is considered basal for modern carnivores.
  - Most families of modern carnivores had developed by the Oligocene.

- Carnivores have had a long association with humans—both positive and negative.
  - Dogs and cats are popular domestic pets throughout the world.
  - Many other carnivore species are valuable in the fur industry.
  - Most large predators have been eliminated throughout much of their range because of conflict with human economic interests.
  - Other species have been overexploited through trophy hunting or commercial harvest and are endangered as a result.

- Pholidotes occur in both Africa and Asia.

- Called pangolins, or scaly anteaters, they are covered with keratinized, overlapping scales.

- Scales serve the same protective function as the carapice in armadillos.

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DISCUSSION QUESTIONS

1. What are the adaptive benefits of delayed implantation to such carnivores as ursids and pinnipeds?

2. There is considerable genetic **introgression** among wolves and coyotes. How does this potentially impact protection of an endangered species such as the red wolf under the Endangered Species Act?

3. Sexual dimorphism is often evident among carnivores, with males being larger than females. Consider such factors as feeding and reproduction to hypothesize why size dimorphism evolved and is beneficial.

4. The red panda has been included in the past in Families Ursidae, Procyonidae, and Ailuropodidae. Speculate as to why the red panda has had (and continues to have) such a confusing taxonomic history.

5. The black-footed ferret has been reintroduced into numerous sites where it formerly existed. If you were in charge of the reintroduction, what logistical, biological, seasonal, temporal, and other factors would you need to consider? What is the difference between "hard" and "soft" releases?

6. How might the striking black-and-white warning coloration of skunks and other species have evolved? How do potential predators learn to avoid these species?

Orders: Perissodactyla and Cetartiodactyla

Perissodactyla
Morphology
Fossil History
Economics and Conservation
Families

Cetartiodactyla
Morphology
Fossil History
Economics and Conservation
Families

The perissodactyls and cetartiodactyls include the modern ungulates, which historically have encompassed hoofed, terrestrial herbivores. The Perissodactyla includes 3 families: horses, asses, and zebras (Family Equidae); tapirs (Tapiridae); and rhinoceroses (Rhinocerotidae). The Cetartiodactyla includes 10 terrestrial families: camels (Camelidae); pigs (Suidae); peccaries (Tayassuidae); mouse deer (Tragulidae); giraffes (Giraffidae); hippopotamuses (Hippopotamidae); pronghorn (Antilocapridae); musk deer (Moschidae); deer (Cervidae); and antelopes, sheep, goats, and relatives (Bovidae). Whales are also included in this order. Grouping whales within the cetartiodactyls is not intuitively obvious, but authorities now agree that whales are the sister group to the hippos. Specifically, as shown in Table 19.1, whales are now placed in Order Cetartiodactyla, in Suborder Whippomorpha, and Infraorder Cetacea (see Geisler et al. 2007; Asher and Helgen 2010). There is overwhelming evidence for this phylogenetic arrangement, including molecular genetics data (Madsen et al. 2001; Boisserie et al. 2005; Geisler and Uhen 2005; O'Leary et al. 2013), dental similarities (Theodor and Foss 2005), and paleontological and skeletal data—specifically, paraxonic feet and the double-pulley astragulus in terrestrial cetartiodactyls and early cetaceans (Gingerich et al. 2001; Thewissen et al. 2001). Because morphology and life-history characteristics of modern ungulates and whales are so different, however, we consider terrestrial ungulates in this chapter and whales in the following chapter.

The unifying characteristic of ungulates is their limb structure (Figure 19.1). Perissodactyls and terrestrial cetartiodactyls walk on the tips of their toes, which end in thick, hard, keratinized hoofs. Ungulates often have a reduced number of toes and a lengthened foot such that the **calcaneum** (heel bone) does not articulate with the fibula. The limbs are restricted to movement in a single plane and ungulates are adapted for cursorial (running) locomotion. Although dentition varies among families, cheekteeth often are hypsodont, with complex occlusal surfaces. These and other morphological and life-history characteristics of ungulates adapt many of them for living in large, open expanses of land where they can feed efficiently and outrun potential predators.

Table 19.1 Suborders and Infraorders in Order Cetartiodactyla

Suborder	Infraorder	Family
Tylopoda		Camelidae (camels)
Suina		Tayassuidae (peccaries)
		Suidae (pigs)
Ruminantia	Tragulina	Tragulidae (chevrotains)
	Pecora	Giraffidae (giraffe, okapi)
		Antilocapridae (pronghorn)
		Moschidae (musk deer)
		Cervidae (deer)
		Bovidae (hollow-horned ungulates)
Whippomorpha	Ancodonta	Hippopotamidae (hippos)
	Cetacea	10 families of toothed whales (Parvorder Odontoceti) & 4 families of baleen whales (Parvorder Mysticeti); see Chapter 20

Figure 19.1 **Hind foot structure of perissodactyls and terrestrial cetartiodactyls.** The hind feet of perissodactyls, including the (**A**) tapir, (**B**) rhinoceros, and (**C**) horse. In these "odd-toed" ungulates, the main axis of the limb passes through the enlarged third digit (i.e., they are mesaxonic). In equids, the third digit is the only one remaining (also see Figure 19.6). Representative terrestrial cetartiodactyls include the (**D**) pig, (**E**) deer, (**F**) camel, and (**G**) pronghorn. In these "even-toed" ungulates, the axis of the limb passes between the third and fourth digits (i.e., they are paraxonic). Note the vestigial second and fifth digits remain as "dew claws" in the pig and deer. For all examples, the heel bone (calcaneum) is shaded and articulates with the astragalus (*a*). (**H**) The grooved, pulley-like anterior surface of the astragalus in ungulates limits motion of the feet to a single plane. Note the fused metapodials (cannon bone, *b*) in **C**, **E**, **F**, and **G**. *Adapted from Macdonald (1984) and Kowalski (1976).*

The distributions and adaptations of large herbivores are dictated to a large extent by their forage resources.

The two orders in this chapter include a great deal of structural diversity among taxa, the result of their rich, well-documented evolutionary histories. The perissodactyls ("odd-toed" ungulates) today are a small order in terms of the number of extant species. They are a remnant of a group that flourished during the early to mid-Tertiary period. In contrast, modern terrestrial cetartiodactyls ("even-toed" ungulates—again, exclusive of the whales) encompass a diverse array of species. Today, ungulates are the most important group of mammals in terms of human commerce and economics. Many ungulate species have been translocated from their native areas and introduced throughout the world, where they are important as domesticated animals, for sport or subsistence hunting, or for ecotourism. Many other native ungulates, however, are on the verge of extinction because of poaching, overexploitation, and habitat destruction.

Perissodactyla

The three families in this order may initially appear to have little in common in terms of locomotion, life histories, and morphology. But all perissodactyls are large, terrestrial herbivores. These hindgut fermenters (that is, they do not ruminate) feed on fibrous vegetation that is often of poor quality. Like the terrestrial cetartiodactyls, they share a common morphological feature—foot structure—that defines the order.

MORPHOLOGY

As noted, the ordinal name means "odd-toed" and refers to the main weight-bearing axis of each limb passing through the enlarged third digit, a condition called **mesaxonic.** Tapirs have four digits on the forefeet and three on the hind feet, whereas rhinos have three digits on all feet. The third digit is the only one remaining in equids (see Figure 19.1). Perissodactyls have a deep groove in the proximal surface of the **astragalus** (ankle bone), which creates a pulley-like surface that limits the limbs to forward-backward movement. The skulls of all species are elongated with a lengthened rostrum. The cheekteeth are hypsodont and usually lophodont—adaptations that occur in large grazers to enhance the grinding of vegetation. Three upper
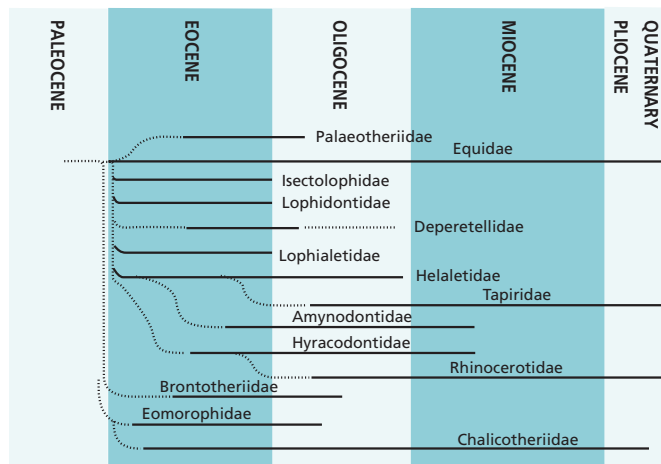
Figure 19.2 Geologic ranges of modern and extinct families of Perissodactyla. Several families of perissodactyls flourished in the early Eocene, but by the middle Miocene, only four families remained. Today, only 3 families are extant, which include only 6 genera and 16 to 18 species. *Adapted from Carroll (1988).*

Figure 19.3 Example of a recently extinct perissodactyl. Chalicotheriids remained extant in Asia and Africa until the late Pleistocene epoch. (**A**) Skeleton of the large *Chalicotherium* from the Miocene epoch of Europe; (**B**) the clawed hind foot of *Moropus*. Note the calcaneum (*c*) and astragalus (*a*). *Adapted from Carroll (1988).*

incisors are retained in the equids and tapirids. Upper incisors are reduced in number or absent in the rhinos. Perissodactyls have a simple stomach, but there is an enlarged cecum at the junction of the small and large intestines where the majority of the microorganism-aided breakdown of cellulose occurs. Food passes through the digestive system of a perissodactyl about twice as fast as through that of a ruminating cetartiodactyl. Because food is retained for less time, digestion is less efficient. For example, the digestive efficiency of a horse is only about 70% that of a cow. Perissodactyls compensate for reduced efficiency by consuming more food per unit of body mass. The enlarged cecum and colon provide storage and surface area for absorption of nutrients. Perissodactyls have a bicornuate uterus, diffuse placentation, and no baculum.

FOSSIL HISTORY

Perissodactyls originated from archaic ungulate phenacodonts (Prothero 2017) in the early Paleocene (about 65 mya). The oldest identifiable perissodactyl fossils are from the early Eocene (50 mya), possibly from India (Rose et al. 2014). By this time, several lines of radiation are evident, and about 14 families are recognized (Figure 19.2). During this period, perissodactyls far outnumbered the smaller, less diverse cetartiodactyls. By the end of the Oligocene (25 mya), however, 8 of the 14 families of perissodactyls were extinct. By the early Miocene, only the equids, tapirids, rhinocerotids, and the Family Chalicotheriidae remained. This last family included unusual ungulates with large forelimbs and short hind limbs (Figure 19.3) adapted for standing semierect to feed on tall trees (Coombs 1983). Several genera had large, retractable claws instead of hoofs.
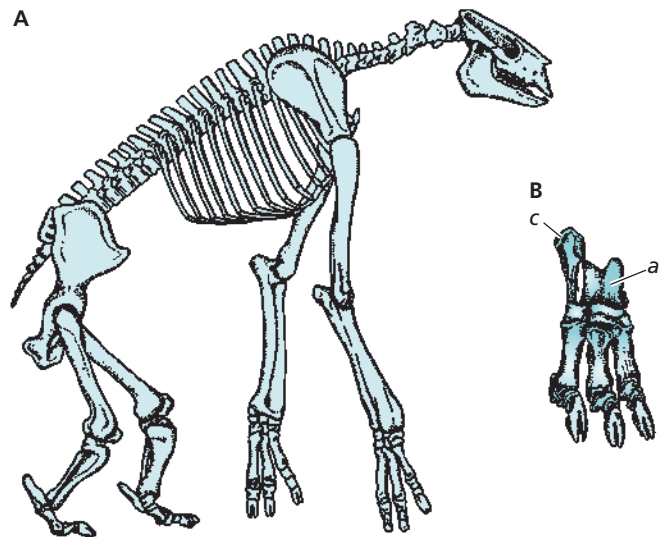
ECONOMICS AND CONSERVATION

As a domesticated species, horses are probably second only to cattle in their importance in the development of human cultural and economic systems. Domesticated in southern Ukraine and elsewhere about 5,000 years ago, horses have been introduced throughout most of the world and have been pivotal in expanding travel and exploration and changing warfare throughout history. There are about 350 recognized breeds of horses in the world today. In contrast to the cosmopolitan distribution of domestic horses through introductions, several other species of equids are either recently extirpated in the wild or endangered. Likewise, tapirs are much reduced throughout their ranges because of hunting pressure and destruction of habitat, and 3 of the 4 species are endangered. The plight of rhinoceroses is well known; all species have become prime targets of poachers for their horns and other body parts. Details of endangered species and conservation efforts are discussed in each family account.

FAMILIES

Equidae

This family has a long history of taxonomic confusion, and uncertainty remains. The current number of recognized extant species, all in the single Genus *Equus*, varies among authorities from 7 (Rubenstein 2011) to 9 (Groves and Grubb 2011; Burgin et al. 2018). Extant equids include the

Figure 19.4 **Przewalski's horse.** Also known by the Mongolian name "takhi," they are native to the steppe regions of Mongolia and China, where they are being reintroduced (see box).

Figure 19.5 **Plains zebra (*Equus quagga*).** The plains zebra—now considered conspecific with the extinct quagga—was formerly called Burchell's zebra.

African wild ass (*E. africanus*), Przewalski's horse (*E.* [*przewalskii*] *ferus*; Figure 19.4), Asiatic wild ass (*E. hemionus*), kiang (*E. kiang*), 3 species of zebras—Grevy's zebra (*E. grevyi*), plains zebra (*E. quagga*), and mountain zebra (*E. zebra*)—domestic or wild horse (*E. caballus*), and the donkey, or ass (*E. asinus*). Regardless of the exact number of species, they all have long, slender limbs, and only the third digit remains functional. Equids are well adapted for moving long distances across open habitats. Three upper and lower incisors occur in each quadrant, and the cheekteeth are large and hypsodont and have complex occlusal surfaces for grazing. Pelage color is variable in most equids, although the pattern of stripes in zebras depends on the species. Stripes are narrow and close together and extend down to the hooves in Grevy's zebra. The mountain zebra has broad stripes that do not extend to the ventral surface. The plains zebra—formerly called "Burchell's zebra" and now considered conspecific with the recently extinct quagga—has a variable pattern (Pedersen et al. 2018),

generally with broad stripes posteriorly that become narrower anteriorly (Figure 19.5). Like fingerprints in people, the stripes of individual zebras are unique. Stripes serve several purposes: they help deflect heat, reduce insect bites (Egri et al. 2012), and make it more difficult for predators to discern individuals as they move about in a herd. The neck mane on most equids is erect; it falls to the side only in the domestic horse. The body mass of wild equids ranges from about 250 kg in the donkey to 400 kg in Grevy's zebra. The body mass of domestic horses can reach 1,000 kg. Male equids are generally about 10% heavier than females.

The natural distribution of equids includes eastern Africa and from the Middle East to Mongolia. They inhabit short grasslands and desert scrublands and are never far from water. The basic social unit is a family group, generally consisting of 10 to 15 individuals and including a highly territorial male, several females, and their offspring. Young females leave the family group when they become sexually mature at about 2 years of age. Young males become sexually mature at the same age. They do not breed until they leave the family group and gain access to other females by about 5 years of age. In the plains zebra, temporary aggregations of 100,000 individuals may form, depending on season and ecological conditions.

A single offspring is usual after a gestation period of about a year. Birth and subsequent mating 7–10 days later occur during the wet season, when vegetation is most abundant. In most species, females breed in alternate years. Neonates are precocial. They begin to graze at about 1 month of age and are weaned at 8–13 months of age. Rubenstein (2011) provided a comprehensive review of equid morphology, reproduction, behavior, and ecology.

In the western United States, as of 1 March 2018, there were almost 82,000 free-ranging wild horses on public lands, up from 25,000 in 1971. They are managed by the Bureau of Land Management under provisions of the Wild and Free-Roaming Horses and Burros Act of 1971.

Return of the Takhi

The endangered Przewalski's horse is named for Russian army officer and explorer Nikolai Przewalski, who "discovered" it in 1880—although of course, it was well known by Mongolians for thousands of years. Called "takhi"—meaning "spirit" in Mongolian—these horses roamed the steppes of Mongolia and China, diverging from domesticated horses around 200,000 years ago. Takhi are stocky and compact, have light brown pelage, black tails, and short, erect manes (see Figure 19.4). A dark stripe runs from the mane to the tail; unlike in domestic horses, the mane is shed during the spring molt. By the late 1960s, takhi were extirpated in the wild because of hunting, collection of foals for European zoos, pasture competition from livestock, and periodic severe winters. By this time, several international initiatives were begun to reintroduce them in several places within their former range.

Reintroductions of large mammals are logistically difficult and involve many variables, including having a sufficient number of animals for sustainable populations, safe and efficient transportation, and release sites with necessary habitat requirements, among other factors. In the case of the takhi, these included no grazing competition from domestic horses or livestock. Although earlier European collection of takhi had contributed to their demise in the wild, because of successful breeding programs, zoos could provide a reservoir of close to 2,000 captive individuals for potential reintroduction. The first release of horses was in 1992 in two sites in Mongolia—Takhin Tal (Mongolian for "Valley of the Wild Horses") in the Great Gobi B Special Protection Area (see map) as well as Hustai National Park. These reintroductions produced mixed results, however. The Great Gobi B population increased to 138 individuals before being reduced to 50 animals because of a severe winter in 2008–2009. Additional releases and natural reproduction had increased the population to 90 by 2014. The release at Hustai National Park was the most successful and had about 300 animals by 2014. In 2004–2005, a third Mongolian reintroduction site, Khomin Tal, saw the release of 22 horses. With only 40 individuals by 2014, it remains to be seen if this site will be successful. China has also reintroduced takhi, at Kalamaili Nature Reserve, but this is currently a semi-wild herd because of the management protocol. Finally, a release at Altyn Emel National Park in Kazakhstan began in 2003, but failed due to poor habitat and the limited available area.

Reintroductions, especially of large mammals, face a number of hurdles. Some are successful but many others fail for a variety of reasons. But continued research, experience, and lessons learned from releases help strengthen future efforts and refine management priorities to conserve wild populations. It is hoped that wild, free-ranging populations of takhi will be established for future generations.

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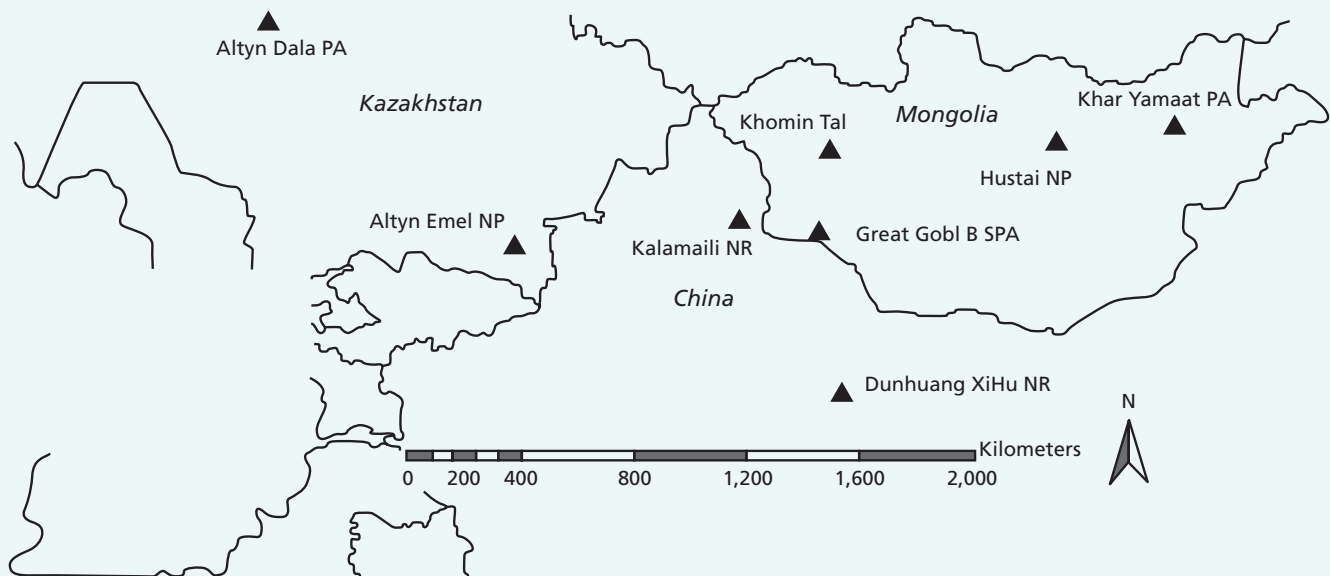
Reintroduction sites of Przewalski's horse, also called the "takhi." *Abbreviations*: NP = national park; PA = protected area; SPA = strictly protected area; SR = steppe reserve. *Figure modified from Kaczensky et al. (2016).*

Although many are adopted each year (245,000 since the start of the program) and others are rounded up and shipped to private ranches in other parts of the country, it is difficult to keep numbers at the mandated level of approximately 27,000 horses. The only alternatives to shooting horses are extensive immunocontraceptive programs (Ransom et al. 2011; 2013) to reduce foaling rates. Possible fertility control includes porcine zona pellucida (PZP), the more recently developed GonaCon, or chemical vasectomy. However, immunocontraceptives by themselves are often not effective in reducing population sizes (Hobbs and Hinds 2018).

Conversely, several other species of equids are of conservation concern. These include the African ass, which is critically endangered because of severely reduced density and limited distribution. Przewalski's horse is endangered. It was recently extinct in the wild, but now there are free-ranging, reintroduced populations in Mongolia (see box). Also, Grevy's zebra is endangered. The quagga of South Africa, uniform in color on the posterior and striped on the anterior, became extinct in the wild in 1872. The last individual died in an Amsterdam zoo on 12 August 1883.

The fossil history of equids is one of the best documented for any mammalian family. Beginning in the early Eocene, fossils show increasing body size and skull proportions, increasing size and complexity of the cheekteeth, and reduction in the number of digits (Figure 19.6). As noted by Hooker (2005:206), "Early equoids that have classically been referred to the Genus *Hyracotherium* have long been regarded as the most primitive perissodactyls." However, *Hyracotherium* may not have been a true horse (Prothero 2017). Nonetheless, many other genera of early horses are known from the Eocene, including *Protohippus*, *Eohippus*, and *Orohippus*. Keep in mind, however, that the evolution of the horse was not a ladder-like, directed, progressive process, as suggested by Figure 19.6, but a complex radiation of numerous divergent, overlapping lineages (Figure 19.7; also see Cantalapiedra et al. 2017). Numerous genera and close to 100 fossil species of horses have been described. Equids passed most of their evolutionary history in North America, with migration to the Old World during the Miocene and to Central and South America in the Pliocene and Pleistocene. Equids left no Pleistocene descendants in the New World, however, where they were extirpated about 10,000 years ago. They were reintroduced to the New World by the Spanish conquistador Hernando Cortés in 1519.

Tapiridae

The 4 species of tapirs historically have been in the single Genus *Tapirus* with a **discontinuous** geographic distribution. However, Groves and Grubb (2011) proposed 3 genera: the South American or lowland tapir (*T. terrestris*) and the mountain tapir (*T. pinchaque*), which occur in northern South America; Baird's tapir (*Tapirella bairdii*) in Mexico,

Central America, and northern South America; and the Malayan tapir (*Acrocodia indicus*) in Myanmar, Thailand, Malaya, and Sumatra. It has a chromosome complement of only $2N = 52$, whereas the New World species have a diploid number of $2N = 76$ or 80 (Houck et al. 2000). Ashley and colleagues (1996) found the lowland and mountain tapirs are close relatives, whereas the other 2 species are less closely related. Cozzuol and colleagues (2013) described a new species of tapir, *Tapirus kabomani*, based on morphology and molecular characteristics. However, other investigators (Voss et al. 2014; Ruiz-Garcia et al. 2016; Burgin et al. 2018) considered it a synonym of *T. terrestris*, as did the IUCN (2018).

Tapirs have chunky bodies with short legs and elongated heads with small eyes and ears (Figure 19.8). MacLaren and Nauwelaerts (2017) found interspecific variation in the forefeet of tapirs. The nose and upper lip form a pronounced, flexible proboscis. Like an elephant's trunk, it is used to manipulate vegetation during feeding and, during locomotion, to gather olfactory information about the environment. The cheekteeth are brachyodont and the adult dental formula for all species is 3/3, 1/1, 4/3, 3/3 = 42. Mean head and body length is 180–250 cm, and body mass reaches as much as 400 kg in the Malayan tapir. Pelage color in New World species is a uniform reddish brown to gray or black, whereas the Malayan tapir has a white body and black on the head, shoulders, and limbs (see Figure 19.8). A short, bristly neck mane is characteristic of both Baird's and lowland tapirs. The hide is very tough in all species with short, bristly hairs that protect against thorns and branches as they move through dense understory.

Tapirs inhabit heavily forested areas. The mountain tapir lives at elevations of 2,000–4,500 m; the other species range up to 1,200 m. All tapirs are nocturnal and feed on understory shoots, twigs, fruit, grass, and aquatic vegetation and occasionally on cultivated crops. Tapirs significantly affect plant ecology by dispersing seeds from a variety of plant species (Fragoso and Huffman 2000). All but the mountain tapir are associated with swamps, rivers, or other wet areas. All tapirs are good swimmers and feed or seek refuge in water. The primary predators of neotropical tapirs are jaguars (*Panthera onca*) and cougars (*Puma concolor*); for the Malayan tapir, tigers (*Panthera tigris*) are the main predators.

Tapirs are generally solitary, although they do vocalize (Gomez-Hoyos et al. 2018). Sexual maturity is reached at 3–4 years of age. Breeding occurs at any time during the year (Padilla and Dowler 1994). Usually, a single young is born after a gestation of about 395 days. Young have a reddish-brown coat and are camouflaged with white spots and lines. They stay with their mother for 6–8 months, by which time the juvenile pelage is replaced with adult pelage. All species of tapirs are declining in number and distribution from loss of habitat due to logging, agriculture, and forest clearing for cattle ranching. They are also killed as crop depredators, and neotropical species are hunted for meat and hides. The mountain tapir, Baird's tapir, and the Malayan tapir are all endangered; the South American
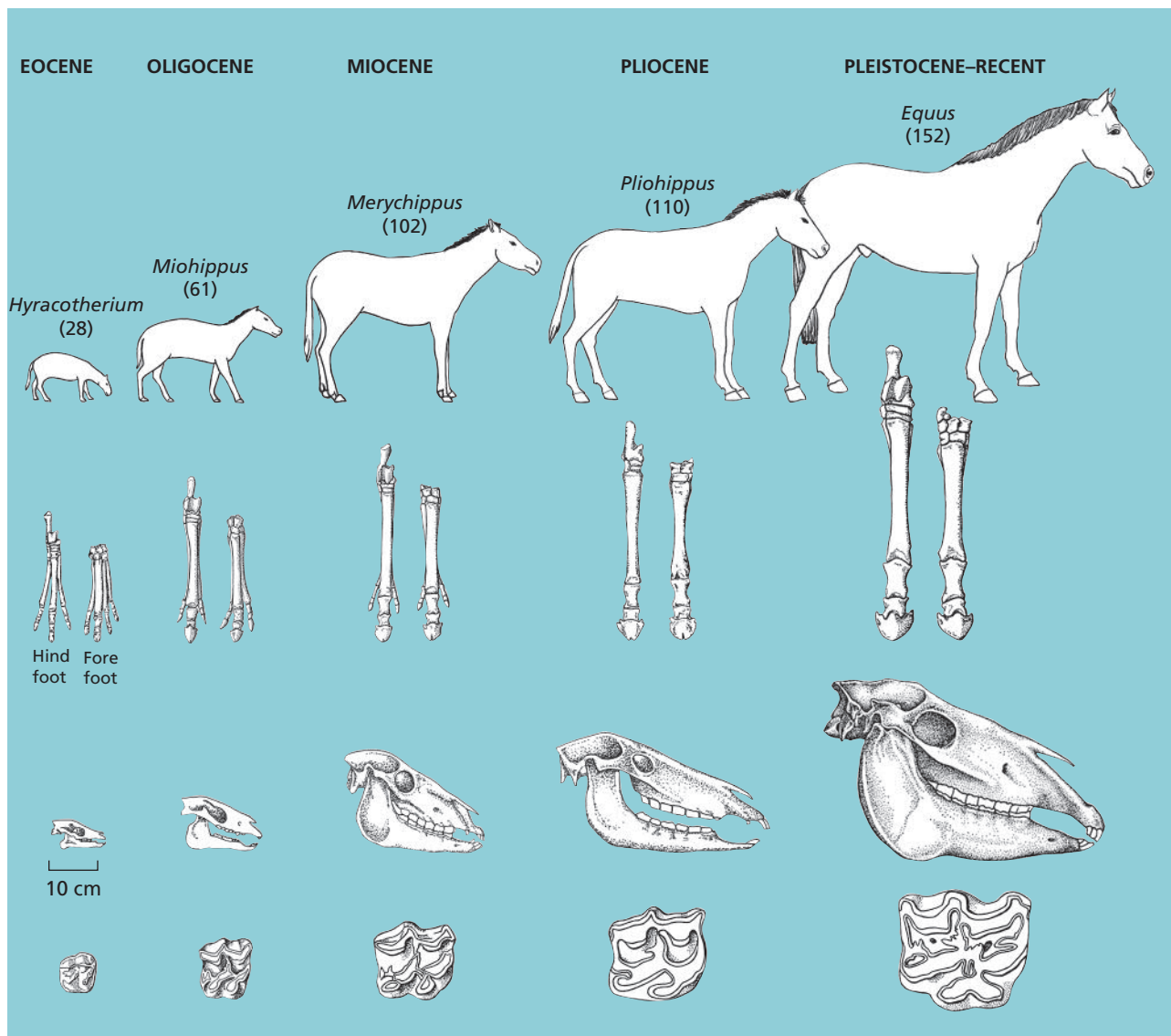
Figure 19.6 **Evolution of the horse.** The early Eocene *Hyracotherium* was a small, forest-dwelling browser. The forefeet had four toes, the skull had confluent temporal and orbital openings, and the brachyodont cheekteeth had simple enamel patterns. Note the increase in size (shoulder heights in centimeters are in parentheses), with reduction in the number of digits, changed proportions of the skull with formation of a postorbital bar, and increasing complexity of the occlusal surface of the cheekteeth in the grazing Genus *Equus* that now inhabits open areas.

tapir is threatened. Populations are slow to recover because of the low reproductive rate.

Tapirs are among the more primitive extant large mammals, given their four toes on the forefeet and brachyodont cheekteeth. Fossil tapirs are known from the early Eocene of North America (*Heptodon*), from the Oligocene (*Protapirus*), and the Miocene (*Miotapirus*). Tapirs migrated both north into Asia and south into Central and South America. Tapirs were extirpated in North America by the late Pleistocene. The combination of migration and extirpation resulted in a discontinuous geographic distribution today. The current Genus *Tapirus* dates from 20 mya in the Miocene and has changed little since then.

Rhinocerotidae

There are four genera in this family; historically, five living species have been recognized. Both white (*Ceratotherium simum*) and black rhinos (*Diceros bicornis*) occur in sub-Saharan central and east Africa. The Indian rhino (*Rhinoceros unicornis*) occurred in Pakistan and northern India, and the Javan rhino (*Rhinoceros sondaicus*) was originally in southeastern Asia from eastern India to Vietnam, Sumatra, and Java. The Sumatran rhino (*Dicerorhinus sumatrensis*), was also originally distributed throughout southeastern Asia, Sumatra, and Borneo. Rhinos are sometimes placed in two subfamilies: the Dicerotinae includes the two African species; the Rhinocerotinae the three
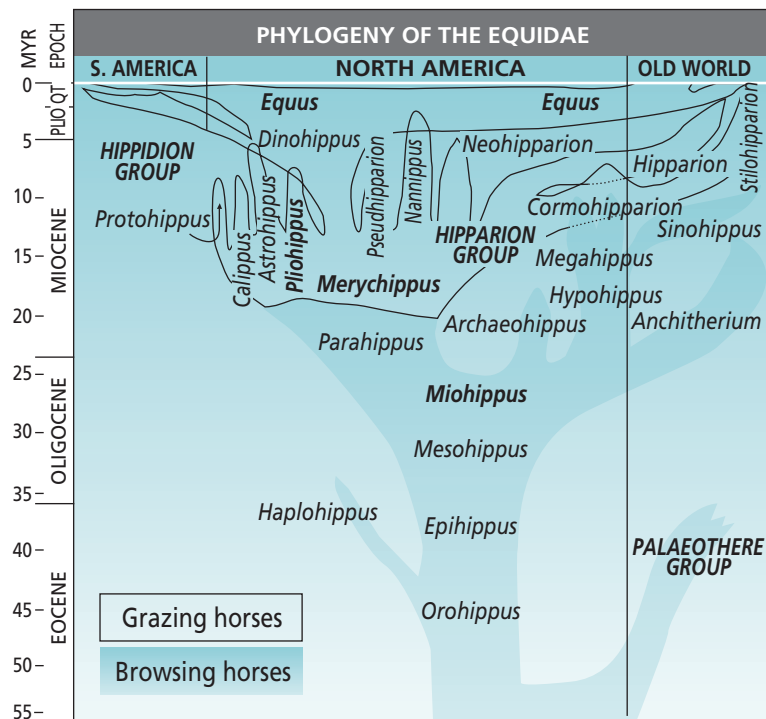
Figure 19.7 **Lineages of the horse.** Phylogeny of the horse is complex, with overlapping and divergent adaptive radiations. Genera in bold type are shown in figure 19.6.

Figure 19.8 **Malayan tapir.** The tapirids have a disjunct distribution. Only the Malayan tapir occurs in Asia; all other species are New World. Note the elongated, flexible proboscis.

Figure 19.9 **White, or square-lipped, rhinoceros (*Ceratotherium simum*).** The largest rhinoceros, white rhinos have been reintroduced to much of their former range in southern Africa.

Asian species (Dinerstein 2011). Based on morphological and genetic differences between the northern and southern subspecies of the white rhino, and their apparent geographic separation that is estimated at 1 my, Groves and colleagues (2010) believed the northern white rhino should be elevated to species level as *C. cottoni*. Other authorities have questioned this recommendation, however. Unfortunately, conservation issues related to recognizing northern white rhinos as a species are somewhat moot—as of March 2018, only two females were alive.

Rhinoceroses are well known for their large, heavyset, graviportal structure (Figure 19.9). They have small eyes

and a prehensile upper lip that extends past the lower lip in black and Asian rhinos. The upper lip is used to gather vegetation. White rhinos reach 400 cm at the shoulder, with maximum body mass of 1,700 kg. Body mass of adult male Indian rhinos (Figure 19.10)—also called "greater one-horned rhinos"—can be 2,000 kg (Dinerstein 1991; 2011). Interestingly, rhinos have one of the highest chromosome numbers among mammals—$2N = 84$ in the black rhino and 82 in the other species.

The family name ("nose horn" in Greek) refers to the rhino's horns, which are unique in having no bony core or keratinized sheath (Figures 19.11 and 19.12A) but instead are a dermal mass of agglutinated, keratinized fibers (fused hairs). Horns are conical, often curve posteriorly, and can reach 130 cm in length in the black rhino. Asian rhinos have shorter horns. The anterior horn is positioned medially over the nasal bones. If 2 horns occur, the shorter, posterior one is over the frontal bones. Neither horn is attached to the bone, however, but to the skin over a roughened section of the skull bones. The nasal bones of the skull are large and project well above and anterior to the maxillae (see Figure 19.11). Besides horn size, Asian species differ from African rhinos because their lower third

Figure 19.11 Rhino skull. Note the typical elongated nasal bones without any horn core or attachment site for the horns. *Scale*: pencil = 16 cm.

incisors are tusk-like. They can reach 9 cm in length in large bull Indian rhinos. Tusks in the Asian species are used primarily during the breeding season to establish dominance among males. Mortality of bulls from wounds sustained from these battles is not uncommon. Occasionally, females also are killed because of overly aggressive, violent courtship of males.

The geographic range of all species is confined to tropical and subtropical habitats and is greatly reduced due to human interference, poaching, and habitat destruction. Depending on the species, rhinos occupy tropical rainforests, floodplains, grasslands, and scrublands. All are dependent on a permanent water supply for frequent drinking and bathing, although the black rhinos in the desert of Damaraland, Namibia, may survive for days on the water in the vegetation they eat. Wallowing probably is necessary to help control body temperature, to reduce insect harassment, and possibly for sociality and information exchange. Rhinos forage on woody or grassy vegetation and occasionally fruits but prefer leafy material when available. They also may take agricultural crops.

Aside from mother-and-offspring pairs, rhinos are generally solitary. Small groups of immature individuals may

Figure 19.10 Indian, or greater one-horned, rhinoceros (*Rhinoceros unicornis*). Although populations are small and fragmented, overall numbers are slowly increasing.
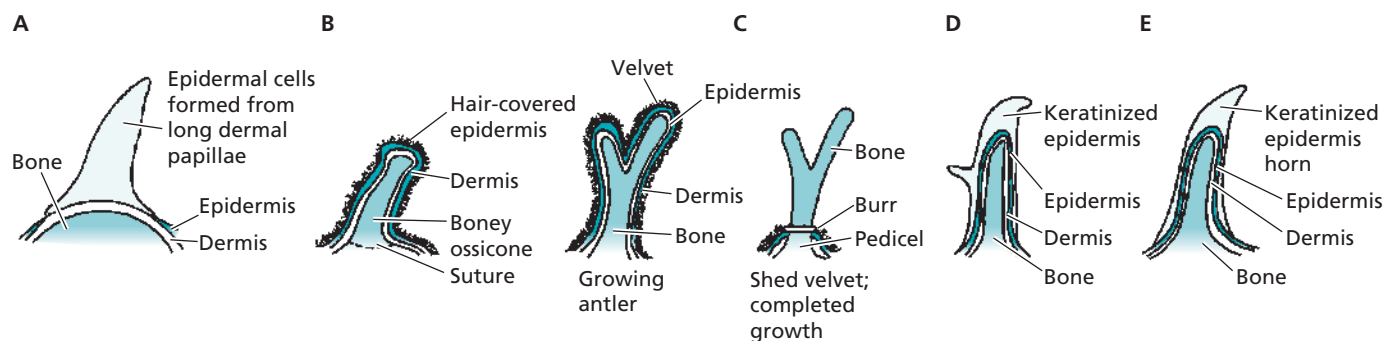
Figure 19.12 Head ornamentation in five ungulate families. (**A**) Rhinocerotidae, a perissodactyl, and four families of cetartiodactyls: (**B**) Giraffidae; (**C**) Cervidae; (**D**) Antilocapridae; (**E**) Bovidae. *Adapted from Gunderson (1976).*

form in Indian and white rhinos. Females become sexually mature at 5 years of age and bear their first calves when 6–8 years of age. Gestation is about 8 months in the Sumatran rhino and about 16 months in the other species. Births, usually a single calf, occur at intervals of 2–4 years (Dinerstein and Price 1991). Young nurse for 1–2 years, although the white rhino begins to eat solid food by 1 week of age. Males generally do not breed before 10 years of age (Ryder 1993).

Populations of all species have declined drastically during the last 150 years. As is the case with many large mammals, the quantity of forage required and low reproductive rates mitigate against recovery when populations are reduced. The black, Javan, and Sumatran rhinos are critically endangered (Moodley et al. 2017; Brandt et al. 2018; Mays et al. 2018), while the two Asian species are near extinction. Rhinos are poached for their horns, which, with other body parts, are valued in traditional Asian medicine for supposed aphrodisiac and medicinal properties. Horns have also been traditionally used for making dagger handles ("jambiya") in Yemen and other countries in the Middle East. A controversial conservation strategy in some areas has been to preemptively de-horn rhinos to reduce their appeal to poachers; several positives and negatives are associated with de-horning (Berger et al. 1993; Dinerstein 2011). White rhinos have been successfully translocated to parts of their former range in southern Africa, although as noted, northern white rhinos—possibly a separate species—are essentially extinct. For a comprehensive review of the status and conservation of rhinos, see Dinerstein (2011).

Estimates based on molecular analyses suggest that Asian and African lineages of rhinos diverged in the late Oligocene about 26 mya (Tougard et al. 2001). The extant species today represent a small fraction of the number that flourished during the Oligocene in terms of geographic range, diversity of size and feeding habits, adaptability, and abundance. Fossil evidence of the rhinocerotids dates from the late Eocene (see Figure 19.2). An early rhinocerotoid family, Hyracodontidae, was adapted for cursorial (running) locomotion. Wang and colleagues (2016) considered them the basal clade for rhinocerotoids, although Tissier and coworkers (2018) suggested the family is not monophyletic and is a "wastebasket" taxon. Members of the archaic Family Amynodontidae were better adapted to wet habitats, similar to hippopotamuses today. Both these families were extinct by the mid-Miocene. Most of the genera extant today date from the Miocene (10–25 mya). They were extinct in North America by the end of the Pliocene (2 mya), however, and never dispersed to South America. Rhinocerotids were abundant and widespread in the Old World until the late Pleistocene (about 60,000 years ago). The largest land mammal that ever lived was a rhinocerotid. The giraffe-rhinoceros (*Paraceratherium grangeri*) of Mongolia—previously referred to as *Indricotherium transouralicum* or *Baluchitherium grangeri*—was close to 6 m tall at the shoulder and almost 9 m in length. Although many estimates suggest the maximum body mass of *Para-*

ceratherium was 30,000 kg or more, an upper estimate of 15,000–20,000 kg may be more reliable (Economos 1981; Fortelius and Kappelman 1993; Prothero 2017).

Cetartiodactyla

It is important to reiterate that data from molecular genetics now place whales within Order Cetartiodactyla. In the remainder of this chapter, however, we will discuss only terrestrial cetartiodactyls—the even-toed ungulates; use of the term in this section does not include the cetaceans (Chapter 20). Compared to perissodactyls, terrestrial cetartiodactyls are much more selective feeders, which is a factor in their greater adaptive radiation. In contrast to the 3 families and approximately 18 extant species of perissodactyls, terrestrial cetartiodactyls include 10 living families and up to 550 species (Burgin et al. 2018). They are distributed almost worldwide, either naturally or through introduction. As might be expected in such a large group, there is tremendous diversity in body size and structure, and 4 suborders are now recognized (see Table 19.1). The Suborder Suina, generally considered the least derived (most primitive) group, includes 2 families: the Suidae (pigs, warthogs, and relatives) and the Tayassuidae (peccaries). The Suborder Tylopoda includes the single Family Camelidae (camels, llamas, and vicuña). Six extant families make up Suborder Ruminantia, the most derived group: the Tragulidae (chevrotains or mouse deer), the Giraffidae (giraffe and okapi), the Cervidae (deer), the Moschidae (musk deer), the Antilocapridae (pronghorn), and the Bovidae (antelope, bison, goats, sheep, and many others). All ruminants, with the exception of chevrotains and musk deer, have some type of head ornamentation in the form of horns or antlers (see Figure 19.12). The Suborder Whippomorpha includes the Hippopotamidae (hippopotamuses) as well as the toothed whales (Parvorder **Odontoceti**) and baleen whales (Parvorder **Mysticeti**). Despite the vast array of species, terrestrial cetartiodactyls share a common morphological characteristic that defines the order.

MORPHOLOGY

Like perissodactyls, the terrestrial cetartiodactyls are defined by the structure of the foot. The main weight-bearing axis passes through the third and fourth digits, a condition termed **paraxonic**. The second and fifth digits are absent or reduced and nonfunctional. There is a definite trend toward cursorial locomotion in the more derived families. The Suina exhibit semi-digitigrade locomotion, with unfused **metapodials** (metacarpals and metatarsals), in contrast to members of the Ruminantia, which are cursorial (unguligrade, more specifically—that is, walking on the tips of the toes), with metapodials fused to form a **cannon bone** (see Figure 19.1C, E–G). The astragalus bone has a

pulley-like surface above and below (see Figure 19.1H). This "double pulley" system is above the distal portions of the limbs and allows great flexion and extension. At the same time, however, the astragalus keeps distal limb motion parallel to the body. The clavicle is reduced or absent. Dentition varies in this order, with the cheekteeth ranging from bunodont and brachyodont to selenodont and hypsodont. In most families, the upper incisors and canines are reduced or absent. In some species such as pigs, peccaries, and musk deer, however, the canines form enlarged tusks. Terrestrial cetartiodactyls are diverse in their digestive anatomy, with simple, nonruminating stomachs occurring in suids and tayassuids, grading to much more complex, 4-chambered ruminating stomachs in the more derived families. Size ranges from a maximum head and body length of 0.5 m in the mouse deer to 6 m in giraffes. Maximum body mass ranges from 2 kg in the Javan mouse deer (*Tragulus javanicus*) to 4,500 kg in the hippopotamus (*Hippopotamus amphibius*). Using molecular evidence, Matthee and colleagues (2001 and references therein) concluded that this order was not monophyletic. They found that hippopotamuses were more closely related to whales than to other artiodactyls (Figure 19.13). Since then, this phylogenetic affinity has been confirmed by numerous molecular studies with better-resolved and supported evidence of the whales nested within artiodactyls (Geisler et al. 2007 and references therein; Marcot 2007). Characteristics specific to individual families are noted in the following sections.

FOSSIL HISTORY

The oldest recognized terrestrial cetartiodactyl fossil is the rabbit-sized *Diacodexis ilicis* in the early Eocene of North America (Theodor et al. 2005; 2007). The order was relatively insignificant compared with the perissodactyls but radiated a great deal throughout the Eocene and Oligocene. Of the modern families, fossil evidence for several dates to the Eocene (Figure 19.14).
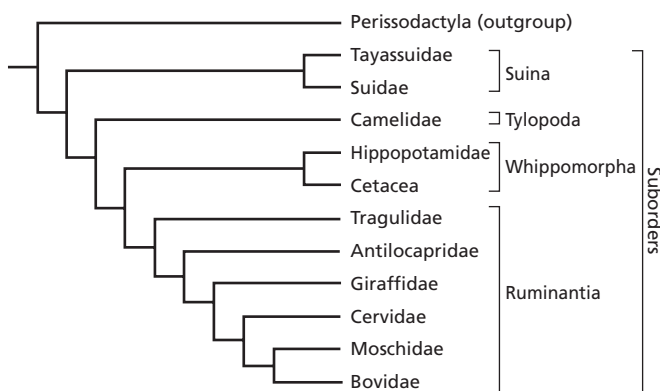
Figure 19.13 Phylogeny of Order Cetartiodactyla. Note the whales as a sister group to the hippos. Morphological as well as molecular analyses support inclusion of whales within the Cetartiodactyla. *Adapted from Marcot (2007).*
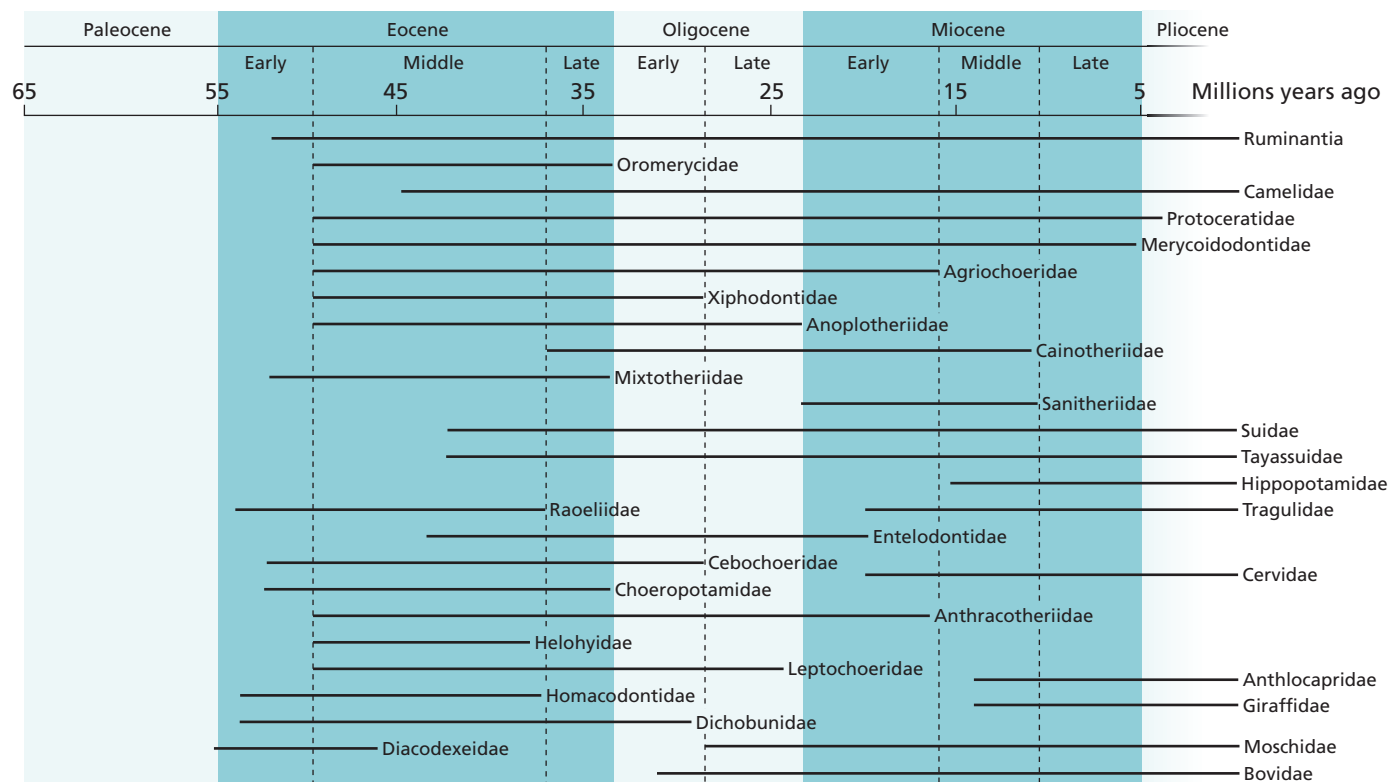
Figure 19.14 Geological ranges of fossil and living lineages of cetartiodactyls. Several lineages date from the Eocene. *Reproduced in part from Theodor et al. (2005).*

ECONOMICS AND CONSERVATION

Most families of terrestrial cetartiodactyls have had some type of economic importance to human civilizations for thousands of years. Domestic species include pigs, camels, llamas, and cattle. Some species are no longer found in the wild but survive only in domestication. Deer, the pronghorn (*Antilocapra americana*), mountain sheep and goats, numerous African antelope, and many other bovids provide meat, hides, sport hunting, and an economic base unparalleled by other mammalian groups. Many of these species are managed intensively on a sustained yield basis throughout much of their ranges.

FAMILIES

Suborder Tylopoda

Camelidae

Camels are distinct from other terrestrial cetartiodactyls and are the sole living member of Suborder Tylopoda (Greek for "pad-footed"). This family traditionally has had 3 genera and 6 species that differ greatly in size. The nomenclature of the camelids continues to be somewhat problematic. Some authorities consider the few remaining wild Bactrian camels as a separate species (*C. ferus*), with *C. bactrianus* used for domesticated individuals (Franklin 2011; Ming et al. 2017; Yi et al. 2017). The guanaco (*Lama guanicoe*) is the wild ancestor of the domesticated llama (*L. glama*; Figure 19.15). The domesticated alpaca (*Vicugna pacos*), sometimes referred as *L. pacos*, was bred from its wild ancestor, the vicuña (*V. vicugna*). Alternatively, Burgin and colleagues (2018), following Groves and Grubb (2011) placed all South American camelids in Genus *Lama*, and recognized 2 species of vicuñas.

Head and body length in the one-humped, or dromedary, camel (*Camelus dromedarius*) and the two-humped Bactrian camel (*C. bactrianus*) approaches 3.5 m, with a body mass close to 700 kg. The guanaco can reach 2.2 m in head and body length and 140 kg in body mass. The vicuña is much smaller, about 55 kg. All camelids have a small head with long snout and cleft upper lip; a long, thin neck; and long legs with the metapodials fused to form a cannon bone. Unlike the hard hooves of other ungulates, the toes of camelids have nails on the upper surface and spread out as they contact the ground, with a broad pad acting to support the mass of the animal on soft, loose sand. The dental formula in *Camelus* is 1/1, 1/1, 3/2, 3/3 = 34. New World species have 28 to 32 teeth because of additional lost premolars. Only the outer, spatulate upper incisor is retained in adults, and the cheekteeth are selenodont. Interestingly, the vicuña is the only cetartiodactyl with ever-growing incisors, like rodents. Camelids have a three-chambered, ruminating stomach and a short, simple cecum. An intriguing phenomenon in camelids involves their

Figure 19.15 **A New World camelid.** The llama, shown here, descended from the wild guanaco. Relationships among New World camelids are open to debate.

functional antibodies. Most vertebrates, and presumably all mammals, have immunoglobulin molecules made up of 4 polypeptide chains. These molecules have 2 heavy and 2 light chains. However, antibody molecules in camelids are not tetrameric but instead are dimeric—they have only the 2 heavy chains—a unique adaptation (Griffen et al. 2014; Liang et al. 2015).

The dromedary camel may once have ranged throughout the Middle East but now survives only in domestication. They were first domesticated approximately 3,500 years ago. The only remaining large, wild population was introduced into Australia (see box).

The Bactrian camel originally ranged throughout much of central Asia but now is restricted in the wild to the western Gobi Desert. Guanacos are found from sea level to 4,000 m elevation in various habitats (Sosa and Sarasola 2005) in the Andes Mountains from southern Peru to Tierra del Fuego. Vicuñas occur in the grasslands of Peru, western Bolivia, northeast Chile, and northwest Argentina at high elevations from 3,700 to 4,800 m (Arzamendia et al. 2006). All camelids are gregarious, diurnal, and herbivorous and are best suited to dry, arid environments. They can eat plants with a high salt content not tolerated by other grazers. They are well known for their ability to go long distances under difficult conditions, conserving water better than other large mammals; they may lose up to 40% of their body mass through desiccation without harm. When camels are well-fed, their humps are firm and erect. The

Camels Introduced to Australia

Dromedary camels have been used as pack animals for thousands of years, and because they do well under the harshest of environmental conditions, they have been introduced to many countries around the world. For example, they were imported into Italy near Pisa in 1622, and survived there until the 1940s. Dromedaries have also been introduced into Canada and the United States, and unsuccessful attempts were made in Russia and Europe and in South American, and Caribbean countries. But because so much of Australia is desert, camels introduced there fared better than elsewhere. They did so well in fact, that—unlikely as it may seem—Australia now has the only extant, free-ranging population of dromedary camels in the world.

The first few camels were introduced there in 1840 from the Canary Islands. From 1880 until about 1900, roughly 20,000 camels were imported. They were ideal for carrying freight and supplies into the desert interior. As motor vehicles became available in the early 1900s, however, camels were needed less, and as many as 10,000 were released into the wild. For many decades thereafter, this feral population expanded in regions inhabited by few people. As a result, damage to rangelands, cultural sites, waterholes, or other environmental impacts were "out of sight—out of mind" to the vast majority of Australians. By the early 2000s, the magnitude of the problem became more evident, as increasing environmental, economic, and social impacts caused by an estimated 1 million feral camels spread across 3.3 million km² of Australian outback. The population is estimated to increase at 8% a year—due in part to an adult survival rate of 96%. To reduce populations to manageable levels, chemical, biological, and fertility control have all been discussed. Unfortunately, little research has been conducted on camels, because, as noted, Australia has the world's only wild population. Thus, control efforts have been limited to culling (shooting) thousands of individuals. Because many Australians view culling as highly wasteful, initiatives have been made to develop commercial opportunities. One organization—the Central Australian Camel Industry Association—is made up of a variety of stakeholders whose goal is to better use the only wild population of dromedary camels for trade in meat, hides, milk, and live animals. Although many camels are exported to countries such as Saudi Arabia, culling is currently necessary to help keep Australia's population within manageable limits.

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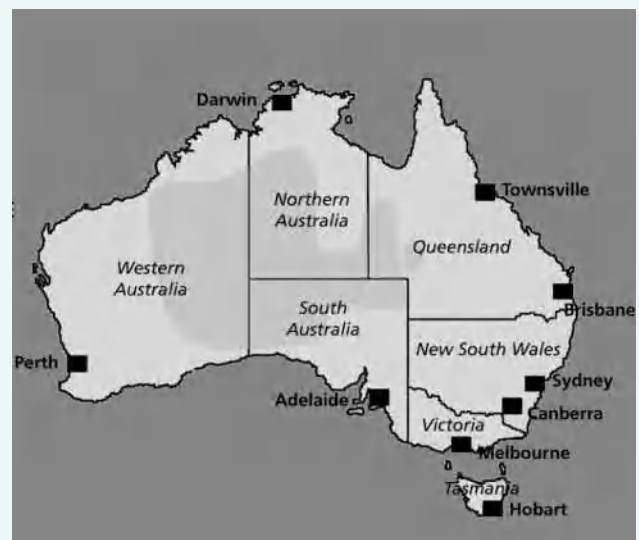
The current range of camels introduced to Australia.

hump is a fat reservoir (up to 35 kg) and shrinks, leaning to one side, when camels are nutritionally stressed. In camels, both limbs on either side of the body move in unison. This **pacing** locomotion allows for long strides with consequent lower energy expenditure. Wild camelids are social, forming groups of up to 30 individuals with different sex and age compositions depending on the season. Groups of vicuñas are highly territorial; camels are not. Camelids are induced ovulators with no defined estrous cycle. A single young (rarely twins) is born after a gestation of 300–320 days in Genus *Lama* and 365–440 days in Genus *Camelus*. All camelids have a diploid chromosome number = 74.

This family arose in North America in the early to mid-Eocene (see Figure 19.14) and was restricted to North America throughout most of the Tertiary period. Early camels, such as *Poebrotherium wilsoni* from the Oligocene, were among the most common ungulates in North America (Prothero 2017). The family expanded to both Eurasia and South America during the Pliocene. At least 35 genera and 90 species of camelids arose before the family became extirpated in North America in the late Pleistocene. Camelids have been introduced throughout the world for use as pack animals and for meat, wool, or milk. As noted by Franklin (2011:206), "Their domestication and unsurpassed ability to thrive in harsh and dry environs has [*sic*] made it possible for humans to inhabit some of the most severe corners of the world. . . . Domesticated camels facilitated unprecedented advances in economic and cultural development of human civilizations in the steppes of Eurasia, deserts of Africa, and arid Andes of South America." Both the llama and the dromedary camel have been domesticated for up to 5,000 years. In the wild, the Bactrian

camel is critically endangered (IUCN 2018) because of illegal hunting, mining development, and habitat lost to domestic animal grazing.

Suborder Suina

Suidae

There are currently 6 genera of suids; the number of recognized species varies among authorities. Meijaard and colleagues (2011) and Burgin and coworkers (2018) recognized 17 species, whereas Groves and Grubb (2011) recognized 20 species. Pigs have simple stomachs, cheek-teeth that are brachyodont and bunodont, and large, ever-growing canines—the upper pair curving up and outward to form tusks (Figure 19.16). With the exception of the desert warthog (*Phacochoerus aethiopicus*), pigs have upper incisors—unlike most other cetartiodactyls. Pigs also have short legs; heavyset bodies; thick skin with short, coarse pelage; small eyes; a relatively large head; and a prominent snout truncated at the end with a round, cartilaginous disk. Several layers of muscles are associated with the snout, which is used in rooting for food. Nostrils can be closed to keep dirt out of the nasal passages. Several species have large facial warts, most notable in the desert warthog and common warthog (*P. africanus*; see Figure 19.16A); facial warts are most prominent in males. Maximum body mass of suids ranges from 9 kg in the pygmy hog (*Porcula salvania*) to 275 kg in the Eurasian wild pig (*Sus scrofa*) and the forest hog (*Hylochoerus meinertzhageni*). The native distribution of suids is Europe, Africa (except the Sahara Desert), and Asia, including Indonesia, Borneo, and the Philippines. They have been introduced to North and South America, Australia, and New Zealand, where both feral and domestic pigs now flourish.

Suids are gregarious and often forage in groups, although solitary individuals may occur, especially of the
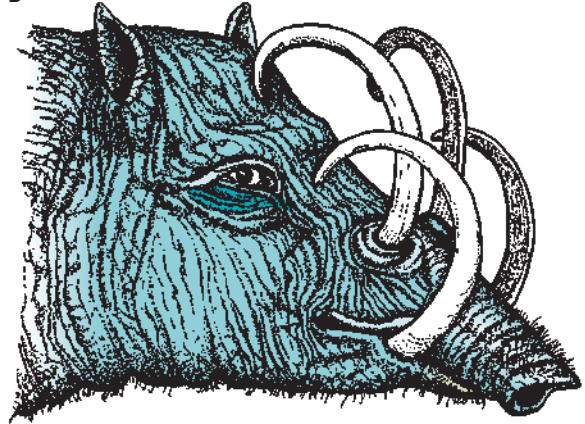
Figure 19.16 **Representative suids.** (**A**) Large facial warts, composed of dense connective tissue, are evident on this common warthog. Warts may protect the facial area from an opponent's tusks during aggressive interactions involving **ritualized** head-to-head pushing contests. (**B**) Tusks are especially pronounced in the babirusas. The upper canines protrude through the skin of the rostrum and do not occlude with the lower canines. Their function is unknown as they are too brittle and shallow-rooted to be used for fighting. (**C**) The typical wedge shape of suid skulls is evident in this Javan warty pig. Canine tusks are less pronounced than in the warthog and babirusa.

desert warthog. Habitats include tropical forests, woodlands, scrubby thickets, grasslands, savannas, and deserts. Regardless of habitats, pigs are closely associated with mud wallows, which are important for cooling and protection against biting insects and ectoparasites. Given their generalized dentition, most pigs are omnivorous. However, the Moluccan babirusa (*Babyrousa babyrussa*), the Togian babirusa (*B. togeanensis*), the Sulawesi babirusa (*B. celebensis*; see Figure 19.16B), and the forest hog are herbivores. Morphology, anatomy, and karyology of babirusas are so different from other suids that their affiliation with the family can be questioned (Meijaard et al. 2011). Suids are sexually mature by 18 months of age, although males may not have access to females until they are 4 years old. Gestation is about 100 days in the pygmy hog, 115 days in domestic pigs, and about 175 days in the desert warthog. Litter size ranges from 1 to 2 in babirusas and up to 14 in domestic pigs.

With close to a billion domestic pigs worldwide, they provide a significant source of animal protein. Many wild species are hunted for food and are of great socioeconomic importance to native people. Feral hogs are an important hunted species in California and throughout much of the southeastern United States (Sweeney et al. 2003)—they are the most widely distributed invasive ungulate in the country (Hernandez et al. 2018). Unfortunately, they carry a number of diseases, including swine brucellosis, African swine fever, and pseudorabies. These can be transmitted to domestic pigs, creating potential problems for livestock operations. Rooting activities of feral hogs, in association with their high reproductive rate, can cause severe environmental impacts including damage in many national parks throughout the United States (Burde and Feldhamer 2005). Worldwide, many species are increasingly a focus of conservation concern because of hunting pressure and habitat loss. The pygmy hog, found in a very restricted range in the foothills of the Himalayan Mountains in northeast India, is critically endangered, as is the Visayan warty pig (*Sus cebifrons*). The Javan pig (*S. verrucosus*; Figure 19.16C) is endangered, as is the Togian babirusa. The earliest suid-like fossils date from mid-Eocene deposits of China and Thailand (Harris and Li-Ping 2007). True pigs first appeared and began to diverge in the early Miocene, with about 40 recognized genera (Prothero 2017).

Tayassuidae

The 3 genera of peccaries, each with a single species, superficially resemble pigs. They have large heads and long, mobile, pig-like snouts, but with thin legs and small hooves (19.17). Peccaries are smaller than pigs; they reach only up to 30 kg body mass. The dental formula for all species is 2/3, 1/1, 3/3, 3/3 = 38. Pigs have a total of 32 to 40 teeth. The tusk-like upper canines of peccaries—which are up to 40 cm long—are sharp-edged and point downward, unlike those of pigs. Also, peccaries are found only in the New World, from the southwestern United States to central Argentina, where they occur in various habitats from desert

scrublands to tropical rainforests. Collared peccaries (*Pecari tajacu*) occur throughout this range; white-lipped peccaries (*Tayassu pecari*) are distributed from southern Mexico to northern Argentina. The Chacoan peccary (*Catagonus wagneri*) was known only from fossils until the 1970s (Wetzel et al. 1975). It is restricted to the dry, Gran Chaco region of western Paraguay, southeastern Bolivia, and northern Argentina, where all three species are sympatric. Appropriate generic names, especially for the collared peccary, have generated controversy; both *Dicotyles* and *Tayassu* have been used in the past, and lack of consensus in the taxonomy of peccaries remains (cf. Dutra et al. 2017). Using nuclear and mtDNA, Gongora and Moran (2005) found Chacoan and white-lipped peccaries formed a clade distinct from the collared peccary. A presumptive fourth extant species, *Pecari maximus*, was described from the Brazilian Amazon (van Roosmalen et al. 2007) and Bolivia (Moravec and Boehme 2009), although questions remain as to its validity (Gongora et al. 2011; Taber et al. 2011).

Peccaries are primarily diurnal herbivores; like suids, they are nonruminating. They root with their snouts as do pigs but occasionally take small vertebrates, invertebrates, eggs, fruit, and carrion. Peccaries generally form small groups of 5–15 individuals, although herds of the white-lipped peccary may number several hundred (Reyna-Hurtado et al. 2016). Subherds often form with individuals commonly moving among them (Keuroghlian et al. 2004). A rump gland is used in social communication. Breeding may occur throughout the year; in arid environments, it is affected by rainfall (Hellgren et al. 1995). The gestation period varies from 142 days in the collared peccary to 162 days in the white-lipped peccary, which exhibits promiscuous breeding (Leite et al. 2018). Litter size averages 2. Female collared peccaries attain sexual maturity by about 8 months of age, males by 11 months old. The Chacoan peccary is endangered by loss of habitat and possibly overharvesting. The collared peccary (see Figure 19.17) is hunted in Texas, New Mexico, and Arizona (Hellgren and

Figure 19.17 Collared peccaries. Morphologically similar to pigs, collared peccaries are a popular game mammal in parts of Texas, New Mexico, and Arizona.

Bissonette 2003), where populations generally are secure. It is also an important resource for meat and hides throughout Latin America. Fossil tayassuids are known from all continents except Australia and Antarctica. The oldest are from the late Eocene (see Figure 19.2) of southeastern Asia. Old World tayassuids were extinct by the end of the Miocene, but were well established in the New World, where they persist today.

Suborder Ruminantia

Tragulidae

Tragulids include 3 genera and 10 species of water chevrotains and mouse deer. The 6 species of mouse deer (Genus *Tragulus*) occur in Southeast Asia, the 3 species of spotted chevrotains (Genus *Moshiola*) are in India and Sri Lanka, whereas the water chevrotain (*Hyemoschus aquaticus*) occurs in tropical regions of west-central Africa. Sarvani and colleagues (2018) found that *Tragulus* and *Hyemoschus* were sister groups. This was surprising because the two Asian genera were expected to be most closely related. The Javan mouse deer is the world's smallest cetartiodactyl and superficially resembles a tiny, chunky deer; the largest extant tragulid is the water chevrotain at about 10 kg. Unlike deer, male chevrotains have no antlers and no facial or other body glands. The legs are thin with a cannon bone in the hind limbs; the forelimbs have a partially fused cannon bone. Molariform dentition is selenodont and brachyodont. There is a four-chambered, ruminating stomach, although the third chamber (omasum) is very poorly developed (Meijaard 2011). As in species of deer without antlers, tragulids have an enlarged, curved upper canine that extends below the upper lip. Tragulids generally are solitary and nocturnal and spend most of the day hidden in the brushy undergrowth of dense forests (Figure 19.18), usually not far from water. Their spotted pelage helps camouflage them. They feed on grass, leaves, and fallen fruit. Because they are so small, tragulids do not need large quantities of food and can be selective feeders. Gestation in *Tragulus* is 6–9 months, and a single, precocial young is born each year; the Indian chevrotain (*M. indica*) normally has twins. Tragulids are physically and sexually mature by 9 months of age. Hunting and habitat destruction have reduced populations of all species, although currently only the Balabac mouse deer (*T. nigricans*) is endangered. The earliest fossil tragulid may be *Archaeotraguludus krabiensis* from the late Eocene of Southeast Asia (Rössner 2007). During the Oligocene and Miocene the family enjoyed a worldwide distribution. The earliest African fossils are from the Miocene of Kenya (Geraads 2011; Sanchez et al. 2015).

Giraffidae

Historically, this family was considered to have only 2 living species—the unmistakable giraffe (*Giraffa camelopardalis*—
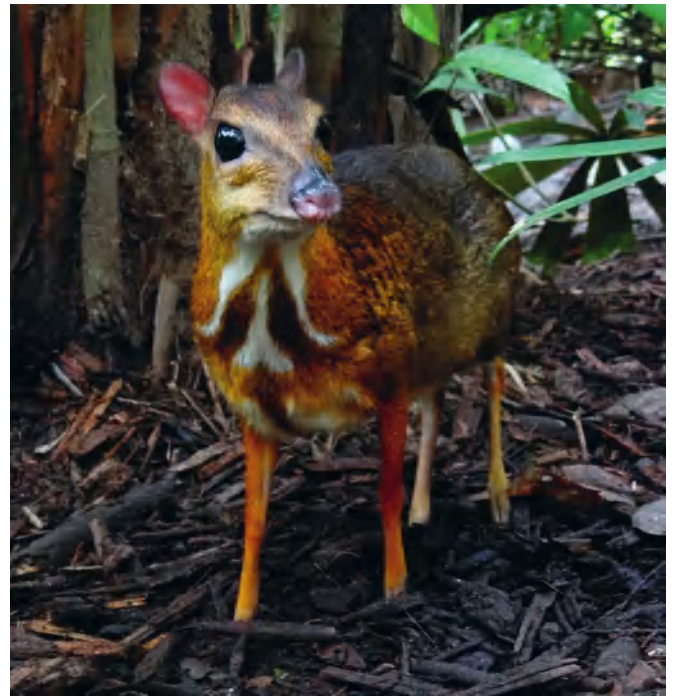
Figure 19.18 A lesser mouse deer (*Tragulus kanchil*). In male tragulids, these small cetartiodactyls have enlarged upper canines.

the species name means "spotted camel" in Greek), and the less familiar okapi (*Okapia johnstoni*). Using genetic data, geographic ranges, and pelage patterns, Brown and coworkers (2007) found 6 distinct lineages of giraffes with little gene flow between them and concluded they should be "considered evolutionarily significant units if not species." Groves and Grubb (2011)—occasionally prone toward nomenclatural exuberance—recognized 10 species of giraffes. Currently, however, 4 species are generally recognized (Fennessy et al. 2016): northern (*G. camelopardalis*); southern (*G. giraffa*); reticulated (*G. reticulata*); and Masai (*G. tippelskirchi*; Figure 19.19), although among some authorities the question remains open (cf. Berkovitch et al. 2017).

Giraffes are patchily distributed in savannas, grasslands, and open woodlands north and south throughout sub-Saharan Africa, in areas often associated with acacia trees. The okapi is restricted to dense forested areas of northeast Democratic Republic of Congo (formerly Zaire). Long legs and neck characterize both species and allow them access to forage that is out of reach of other large herbivores. Height in giraffes is attained by elongation of the leg and neck bones, although as in most mammals, giraffids have the normal number of 7 cervical vertebrae. In male giraffes, the top of the head can be 6 m off the ground, 5 m in females. Body weight of bulls can reach 1,900 kg; cows can be 1,200 kg (Skinner and Mitchell 2011). Okapis are smaller, with a crown height of about 2 m. Unlike giraffe cows, okapi cows are taller and heavier than the bulls. Even though the relative size of the heart in giraffes is the same as in other mammals (it is about 0.5% of body weight),
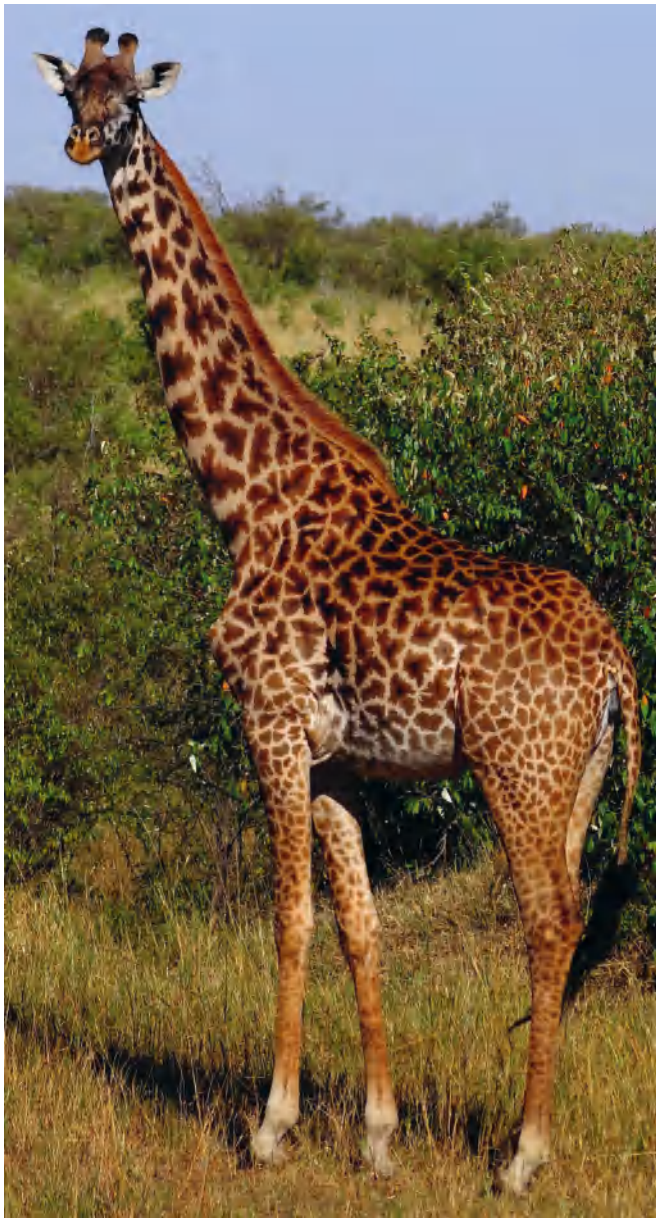
Figure 19.19 **Masai giraffe.** This female is from Masaai Mara National Park, Kenya.

Figure 19.20 **Skull of a giraffe.** (**A**) Dorsal and (**B**) lateral views of the "horns" (ossicones) of a giraffe, showing distinct sutures on the frontal/parietal area. The horns are not extensions of the frontal bone as in bovids. (**C**) Sagittal section of a giraffe skull showing the extensive sinus cavities in the roof of the cranium. Sinuses allow blood to collect when the head is lowered so blood pressure does not increase to dangerously high levels. *Adapted from Bubenik and Bubenik (1990).*

twice the normal blood pressure is generated to get blood to the head against the pull of gravity (Skinner and Mitchell 2011; Østergaard et al. 2013).

The dental formula is 0/3, 0/1, 3/3, 3/3 = 32 teeth. The canine is incisiform and bilobed. The teeth are small and brachyodont, which is unusual for a large herbivore. Giraffids are browsers, and their very long, muscular, prehensile tongues aid in forage selection. In the giraffe, the tongue can be extended almost 0.5 m and is used to pull leaves off trees. Both species ruminate and have a four-chambered stomach. The horns are short, permanent, unbranched processes (**ossicones**) over the frontal and parietal bones (Figure 19.20; see also Figure 19.12B). They are not extensions of the frontal bone but are distinct, fused

to the cranium, and covered with hairy skin. Horns are larger in bulls than in cows. Ossicones and the bilobed canine are unique to giraffids. The long, muscular neck of both species is also used in intraspecific aggressive interactions of males as they establish dominance hierarchies. Interactions involve standing side by side and "necking"— pushing each other with intertwined necks and occasionally swinging the neck and using the horns to strike an opponent's head and neck. Extensive cranial sinuses and a heavy skull help protect individuals from hammering blows. There are 2 hypotheses as to why giraffes have long necks: to feed above competing browsers, or for use in male-male combat for access to estrous females ("necks-for-sex"). It is likely both factors are important evolutionary determinants (Simmons and Altwegg 2010; although see Mitchell et al. 2009).

The 4 giraffe species have distinctive pelage patterns (Figure 19.21) with variations in color shades. In addition, the coat pattern of individual giraffes is unique. The okapi is reddish brown dorsally with distinctive striping on the legs and back of the thighs (Figure 19.22). They do not form herds but are solitary or live in small family groups. Group size in giraffes varies and can reach 30 to 50. Herd size and habitat use are reflections of seasonality, forage or water availability, sex, age, kinship, and other factors more than gregariousness (Deacon and Smit 2017; Deacon and Bercovitch 2018). Gestation is variable in both species, but averages about 450 days in the giraffe and somewhat shorter in the okapi. Females of both species give birth to a single, precocial calf approximately every 2 years. At birth, giraffe calves are 2 m tall and weigh about 100 kg. Calf mortality is very high due to predation.

Southern giraffe   *Reticulated giraffe*

Masai giraffe   *Northern giraffe*
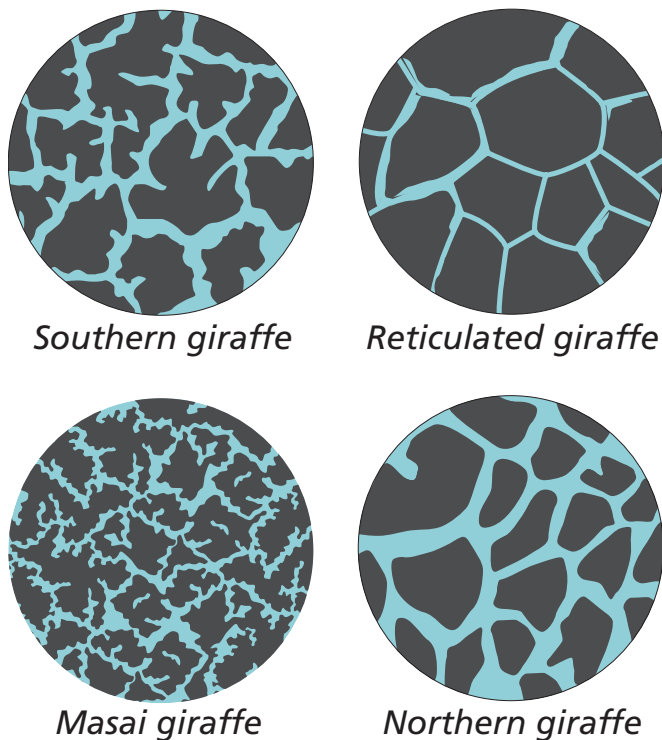
Figure 19.21 **Patterns of blotches on giraffes.** Individual giraffes have unique patterns, but the blotches also vary among the four presumptive species. *Modified from Skinner and Mitchell (2011).*

Figure 19.22 **Okapi.** This endangered member of the giraffe family has a very distinctive coloration pattern and is restricted to northeast portions of the Democratic Republic of the Congo.

Native hunters have long taken giraffes for meat and hides. Giraffes are also harvested illegally for their meter-long tail tufts, which are used to make bracelets for tourists or flyswatters. The okapi was unknown to science until 1901 and has been protected by the government since 1933 (Hart and Hart 1988); it is currently listed as endangered (IUCN 2018). Political instability of the region they inhabit is cause for concern, and okapis are still part of the bushmeat market (van Vliet et al. 2012).

Early fossil giraffes had short necks and often complex, extensive head ornamentation. The earliest known fossil giraffid is *Canthumeryx sirtense* from the early Miocene of Libya. Subsequent radiation occurred throughout the mid- to late Miocene. Solounias (2007) and Harris and colleagues (2010) provided comprehensive reviews of the paleontology of the family.

Antilocapridae

This monotypic family includes only the pronghorn (*Antilocapra americana*), which is endemic to the open grass-lands and arid regions of western North America. Pronghorns have barrel-shaped bodies and long, thin legs (Figure 19.23). Shoulder height reaches about 90 cm, and maximum body mass is 80 kg, with males being about 10% larger than females. The pronghorn is the fastest New World mammal—speed reflects their evolution as North American grassland specialists adapted to outrun speedy Tertiary predators. Speed results from their long legs, long stride, and large heart and lungs. They can attain speeds of 100 km/h for short distances. Equally impressive is their ability to sustain speeds of 70 km/hr for up to 10 km (Byers 2011). Like deer, pronghorns have several different glands for olfactory communication. Both sexes have rump glands and interdigital glands; males have a gland below each ear and on the back. Wood (2001, 2002) discussed the chemical properties and functions of glands in pronghorns.

The horns consist of a keratinized sheath over a permanent, bony core extension of the frontal bone as in the Family Bovidae. Unlike bovids, however, male pronghorns grow a new horn sheath each year under the old one, which splits and is shed following the breeding season. Horns are upright, with a posterior hook and a short, anterior branch, or prong (see Figure 19.12D). Horns on males can reach 30 cm in length. They may be absent on females; if present, they are much shorter, do not have the prong, and are shed at irregular intervals.

Pronghorns forage on grasses, forbs, and low shrubs, especially sagebrush (*Artemisia tridentata*). Males are unusual in that they defend territories from March or April until after the rut, even though breeding occurs only in the fall. Depending on her body condition, a female searches among territorial males for vigorous potential mates (Byers et al. 2006). However, rutting behavior is variable among populations (Maher 1991). The gestation period is about 250 days, and twins are the rule. Fawns are weaned when about 3 months old. During winter, large herds may form. Pronghorns migrate up to 160 km between distinct summer and winter ranges. The pronghorn is a popular game animal. In the 1920s, populations were very low. There

Figure 19.23 **Pronghorn.** The black jaw patch, found only in males, is important in male-male and male-female behavioral interactions. Horns in females are short and without a prong. Also note the white rump patch, which flares when the animal is alarmed.

Figure 19.24 **Musk deer skull.** Male musk deer have no antlers, but enlarged, tusk-like upper canines are evident. *Scale*: pencil = 16 cm.

were an estimated 13,000 pronghorns in North America in 1924, compared to an estimated 35 million in the early 1800s. Populations in the United States have recovered to about 1 million individuals because of successful management programs. Populations of the Mexican subspecies (*Antilocapra americana peninsularis* and *A. a. sonoriensis*) are endangered, however. Population densities of Sonoran pronghorns are very small, with associated loss of genetic diversity (Stephen et al. 2005; Horne et al. 2016). Also, predation rates on fawns and adults may be high (Bright and Hervert 2005). Fossil antilocaprids date from the early Miocene in North America, and were very diverse during the mid- and late Miocene (Davis 2007; Prothero 2017).

Moschidae

Formerly considered a subfamily in the deer Family Cervidae, the musk deer form a valid, monophyletic family (Su et al. 1999) with 1 genus (*Moschus*) and 7 species. Surprisingly, this family is more closely related to the Bovidae than the Cervidae, based on analyses of nuclear and mtDNA (Hassanin and Douzery 2003; Guha et al. 2007; see Figure 19.13). Musk deer are small, with head and body length between 80 and 100 cm and maximum body mass of 18 kg. The smallest species, the forest musk deer (*M. berezovskii*) and the Anhui musk deer (*M. anhuiensis*), weigh less than 10 kg. Females are about 10% heavier than males. The males do not have antlers, but as in the Chinese water deer (*Hydropotes inermis*) and tragulids (chevrotains and mouse deer), the upper canines are long and curved (Figure 19.24); upper canines of females are smaller. Musk deer occur from Sibe-

ria to the Himalaya Mountains in forested areas with dense understory vegetation. Wu and colleagues (2006) found that Siberian or taiga musk deer (*M. moschiferus*), the most widely distributed species, selected for steep, rocky, higher elevation slopes near water and away from human disturbance. Musk deer are solitary, nocturnal or crepuscular, and shy.

Males have a caudal gland that is used to wipe ("tail paste") a foul-smelling secretion on trees and rocks during the rut. Musk deer are better known (and named for) the musk gland, or "pod," that develops slightly anterior to the genital area of males. In adults, this gland contains 18–32 g of reddish brown, gelatinous, oily material. Released in the urine, it is important during the breeding season for marking a territory and attracting females. Li and colleagues (2016) as well as Fan and coworkers (2018) discussed the chemical composition of musk. It is used in fine perfumes and has been an ingredient in Asian traditional medicine for over 2,000 years. As a result, hunting and trapping pressure on musk deer has always been very high. Musk deer have been produced on game farms for over 60 years (He et al. 2014) to help ensure a reliable supply of musk and to reduce harvest pressure on wild populations. Nonetheless, 6 of the 7 species are endangered: the alpine musk deer (*M. chrysogaster*), the Himalayan musk deer (*M. leucogaster*), the Kashmir musk deer (*M. cupreus*), the forest musk deer, the Anhui musk deer, and the black musk deer (*M. fuscus*). The Siberian musk deer is threatened. Although limited today in distribution and species diversity, musk deer have an extensive fossil record from the Oligocene in Eurasia, including *Dremotherium*, the oldest fossil moschid. At least 8 fossil genera are known from the Miocene in Euasia and North America (Wang et al. 2015; Prothero 2017).

Cervidae

The arrangement of subfamilies and genera within the deer family differs among authorities (Gilbert et al. 2006; Groves and Grubb 2011). Historically, 3 subfamilies were recog-

nized: the Capreolinae (sometimes referred to as the Odocoileinae), the Cervinae, and the Hydropotinae, which included only the Chinese water deer (*Hydropotes inermis*). More recent phylogenies recognize only the Capreolinae and Cervinae, with a combined 18 genera and 52 extant species (Figure 19.25). The subfamily divisions are based on genetic data as well as the position of retained splints of the lateral metacarpals—these are proximal (called "plesiometacarpalian") in Cervinae and distal (called "telemetacarpalian") in Capreolinae (Figure 19.26). The 52 living species recognized today are many more than 25 years ago because several former subspecies are now considered full species based on genetic, morphological, or karyotypic characteristics. This trend will likely continue among species such as the red muntjac (*Muntiacus muntjak*) complex, and the red deer (*Cervus elaphus*) complex in which eastern and western Eurasian populations are likely different species.

Cervids are widely distributed and are absent only from sub-Saharan Africa and Antarctica. They are not native to Australia or New Zealand but have been introduced there as well as to many other areas. The habitats occupied by deer include deciduous forests, marshes, grasslands, tundra, arid scrublands, mountains, and rainforests. Deer range in size from the northern pudu (*Pudu mephistophiles*), with a maximum body mass of about 6 kg, to the moose (*Alces alces*) at 800 kg. Deer exhibit sexual dimorphism, with males (called "bucks," "bulls," or "stags" depending on the species) often being 25% larger in body mass and body dimensions than females (called "does," "cows," or "hinds"). Male red deer can be 90% heavier than females. Deer are also well known for their characteristic antlers, which are made of bone, are usually branched, and are supported on pedicels, which are raised extensions of the frontal bone (see Figure 19.12C). Antlers usually occur only in males. Exceptions include Chinese water deer, in which males do
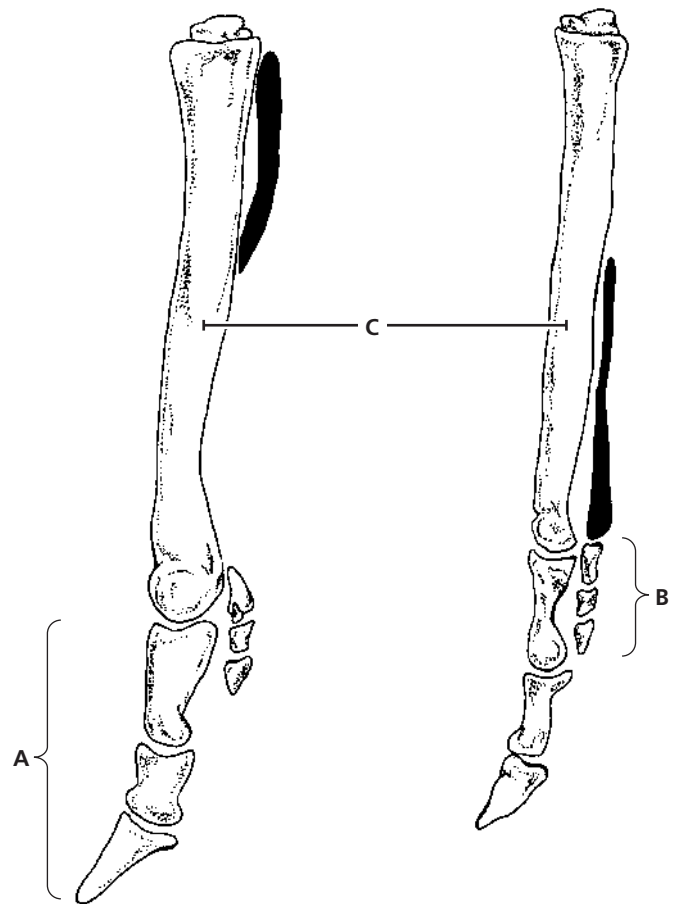
Figure 19.26 Retained splints of lateral metacarpals in deer. *Left*: Proximal (plesiometacarpalian) splints occur in Subfamily Cervinae. *Right*: Distal (telemetacarpalian) splints occur in Subfamily Capreolinae. (**A**) The three phalanges of the toe that end in the hoof; (**B**) vestigial dew claws; (**C**) fused cannon bone. *Adapted from Feldhamer and McShea (2012).*
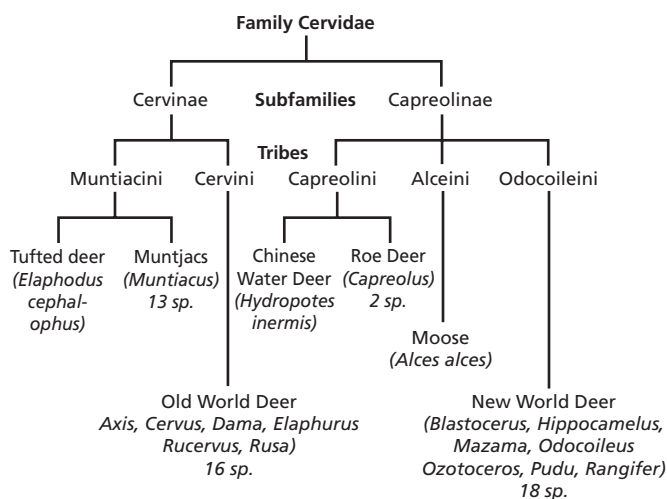
Figure 19.25 Subfamilies and tribes within the deer Family Cervidae. Placement and relationships of some genera and other taxonomic questions remain unresolved. For an alternative arrangement, see Groves and Grubb (2011). *Modified from Mattioli (2011).*

not have antlers, and caribou (*Rangifer tarandus*), in which both sexes have antlers. Antlers are deciduous—that is, they are shed each winter following the rut and regrown in the spring. Growing antlers are covered with haired, highly vascularized skin known as **velvet.** Antlers grow very fast—up to 2.5 cm/day in large species—and can temporarily draw minerals from the axial skeleton. Antler size and the number of **tines** (points) are a function of nutritional condition, genetic factors, and age. There is little correlation between individual age and the number of antler points, however. Different species of deer have a characteristic antler shape and size (Figure 19.27). Antlers are important in mating behavior, display, and success of males and, therefore, are a highly selected trait (Goss 1983; Geist 1991; Heckeberg 2017). Male deer face a trade-off in allocating energy between body weight, needed for survival in harsh winter climates, and antler growth, needed for successful reproduction (Melnycky et al. 2013).

Pelage color varies among and within species of deer. Most newborn cervids have white spots and lines on a darker
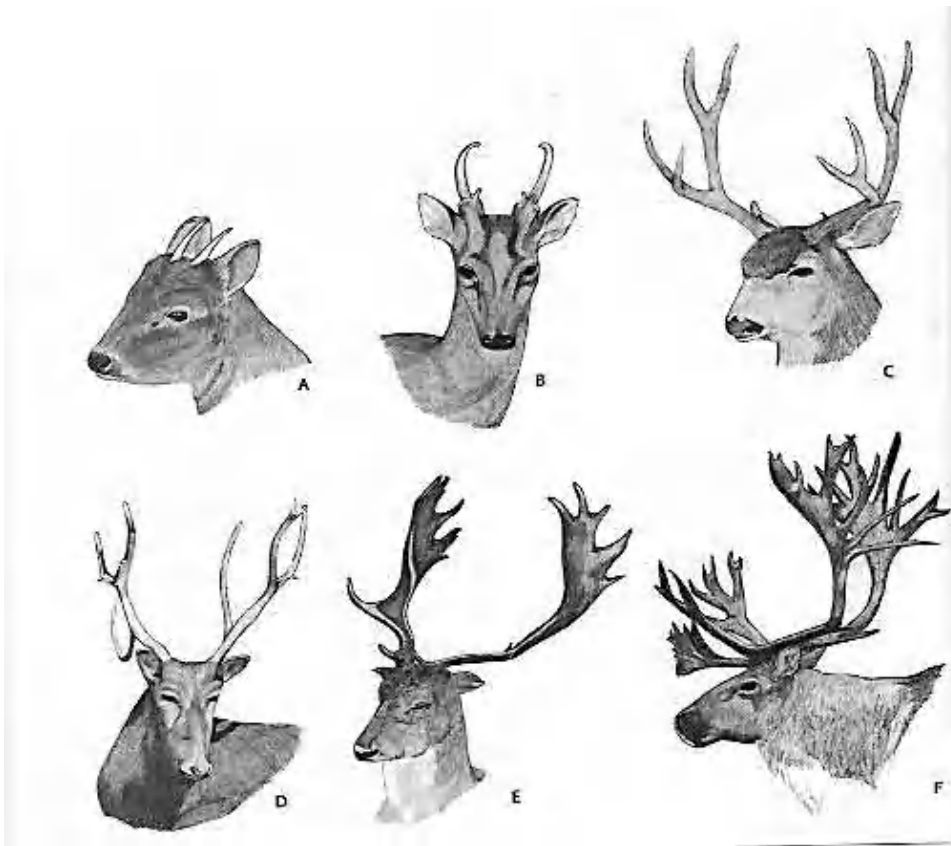
Figure 19.27 **Variations in antler structure of cervids.** (**A**) pudu; (**B**) muntjacs; (**C**) mule deer; (**D**) Père David's deer; (**E**) fallow deer; (**F**) caribou. *Drawing by Lisa Stone, from Feldhamer and McShea (2012).*

background, providing excellent camouflage; exceptions are newborn moose, caribou, marsh deer (*Blastocerus dichotomus*), sambar (*Rusa unicolor*), Philippine brown deer (*R. marianna*), Javan deer (*R. timorensis*), northern pudu, and huemuls (Genus *Hippocamelus*). Certain species maintain the spotted pattern as adults, including fallow deer (*Dama dama*), sika deer (*Cervus nippon*), chital (*Axis axis*), and the Visayan or Philippine spotted deer (*R. alfredi*). Deer have no upper incisors; they browse or graze by cutting off forage between the lower incisors and a calloused upper pad. They are herbivores, and many of the temperate species change their diet depending on the season. Deer are gregarious, with species such as caribou forming herds of 100,000 or more. Visual, auditory, and olfactory senses are acute. Several glands may be present from which herd members gain reproductive and other information about each other. Glands may be located on the face (prelacrimal), between the toes (interdigital), or on the lower hind legs (tarsal or metatarsal glands). Both sexes of sambar have a pronounced throat gland referred to as the "sore spot." Using their antlers, male deer often fight (spar with) each other to establish territories on which to attract a group of females for breeding. Maintenance by males of female breeding groups depends on the tendency of females to remain grouped, and therefore defensible, and the extent to which estrus is synchronized. Gestation is generally 6–7 months. Among cervids, only the European roe deer (*Cap-reolus capreolus*) is known to exhibit delayed implantation. From 1 to 3 young are typical in cervids depending on habitat and body condition of the female.

Deer have been hunted by humans for thousands of years for both meat and antler trophies. Likewise, deer have been depicted in arts, literature, and mythology since Paleolithic times, 35,000 years ago (Feldhamer and McShea 2012). Today, many species are domesticated to harvest both meat and antler velvet. Others have been introduced as free-ranging exotics to numerous countries outside their native range, often with unanticipated negative effects on native species (Feldhamer and Armstrong 1993). Overharvesting and habitat loss have resulted in several species becoming endangered, including the Phillipine spotted deer, the Calamian deer (*Axis calamianensis*), the hog deer (*A. porcinus*), the Mesopotamian fallow deer (*Dama mesopotamica*), the brow-antlered or Eld's deer (*Rucervus eldii*), and the southern or Chilean huemul (*Hippocamelus bisulcus*). Critically endangered cervids include the Bawean deer (*A. kuhlii*), with fewer than 250 individuals, the large-antlered muntjac (*Muntiacus vuquangensis*), and Pére David's deer (*Elaphurus davidianus*). Extinct in the wild for several hundred years, Pére David's deer has been reintroduced to parts of its original range. Schomburgk's deer (*Rucervus schomburgki*), endemic to Thailand, went extinct in the 1930s. The earliest cervid fossils (Genera *Procervulus*, *Heteroprox*, *Lagomeryx*, and *Euprox*)

are from the early Miocene of Asia and Europe (Mennecart et al. 2017); the earliest North American deer fossils (Genus *Bretzia*) date from the Pliocene. Mattioli (2011) provided an excellent review of the Cervidae.

Bovidae

This is the largest family of cetartiodactyls and includes about 54 genera and as many as 297 species—almost double the number of recognized species 20 years ago. Indicative of the number of species and diversity of the group, various authorities have recognized from 5 to 10 subfamilies. We follow Groves and Leslie (2012), who reviewed the taxonomic history of the family, and recognized 2 subfamilies and 12 tribes of bovids (Table 19.2). Designation of subfamilies and tribes is based on molecular genetics, horn structure, cranial and skeletal features, behavior, feeding strategies, and other factors. Generally, bovids have hypsodont and selenodont cheekteeth, with no upper incisors or canines; lower canines are incisiform. All species have four-chambered, ruminating stomachs. Size varies greatly, from the royal antelope (*Neotragus pygmaeus*) with a shoulder height of 25–30 cm and maximum body mass of 1.5 kg, to several species of cattle (Genus *Bos*) and elands (Genus *Taurotragus*) with body masses approaching 1,000 kg. All bovids have a pair of horns with the exception of the four-horned antelope, or chowsingha (*Tetracerus quadricornis*), which has anterior and posterior pairs of horns. Bovid horns are present on males and some females. They have a bony core, which is an extension of the frontal bone (see Figure 19.12E), and is covered with a keratinized sheath that is unbranched and rarely shed. Horns can be straight, spiraled, or curved (Figure 19.28) and grow throughout an individual's life. Like

antlers in deer, horns can function in defense against predators as well as males sparring for access to breeding females. Variation in size and shape of horns reflects the fighting behavior of the species. If a horn breaks, it does not regrow.

Wild bovids are naturally absent only from South America and Australia; domesticated bovids are distributed practically worldwide. Wild species are found primarily in Africa and Eurasia, where they occupy grasslands, savannas, scrublands, and forests. They also occur in harsher environments, including tundra, deserts, and swamplands. All are herbivores, with different tribes having different feeding strategies (Figure 19.29). Social systems are related to body size, feeding strategy, and predation pressure (Jarman 1974; Brashares et al. 2000). Generally, small species are specialized feeders in dense, closed habitats and tend to be solitary or paired. Larger species are more gregarious and occupy more open areas, where they are generalist feeders on high-fiber (more cellulose) vegetation.

Cattle, sheep, and goats have been domesticated for over 5,000 years and are an integral part of agricultural economies throughout the world. Many other species of bovids have been introduced or are hunted for meat, hides, and sport. At least 25 species throughout the world are endangered or critically endangered because of habitat loss or overharvesting. Several others have been driven to extinction in recent times, including the auroch (*Bos primigenius*), the ancestor of modern cattle, which was extirpated about 500 years ago. Given their generally large size, it is unusual to discover new species of bovids. Nonetheless, a previously unknown bovid, the critically endangered saola (*Pseudoryx nghetinhensis*), was discovered about 30 years ago in Vietnam (Dung et al. 1993). More recently, Colyn and colleagues (2010) described a new species—Walter's duiker (*Philan-*

Table 19.2   Taxonomic arrangement of subfamilies, tribes, and genera within Family Bovidae*

Subfamily	Tribe	Genera
Bovinae	Bovini	*Bos, Bubalus, Pseudoryx, Syncerus*
	Boselaphini	*Boselaphus, Tetracerus*
	Tragelaphini	*Ammelaphus, Nyala, Strepsiceros, Taurotragus, Tragelaphus*
Antilopinae	Neotragini	*Neotragus*
	Aepycerotini	*Aepyceros*
	Antilopini	*Ammodorcas, Antidorcas, Antilope, Dorcatragus, Eudorcas, Gazella, Litocranius, Madoqua, Nanger, Ourebia, Procapra, Raphicerus, Saiga*
	Reduncini	*Kobus, Pelea, Redunca*
	Hippotragini	*Addax, Hippotragus, Oryx*
	Alcelaphini	*Alcelaphus, Beatragus, Connochaetes, Damaliscus*
	Caprini	*Ammotragus, Arabitragus, Budorcas, Capra, Capricornis, Hemitragus, Naemorhedus, Nilgiritragus, Oreamnos, Ovibos, Ovis, Pantholops, Pseudois, Rupicapra*
	Cephalophini	*Cephalophus, Philantomba, Sylvicapra*
	Oreotragini	*Oreotragus*

*Groves and Grubb (2010) recognized this arrangement plus three additional genera.
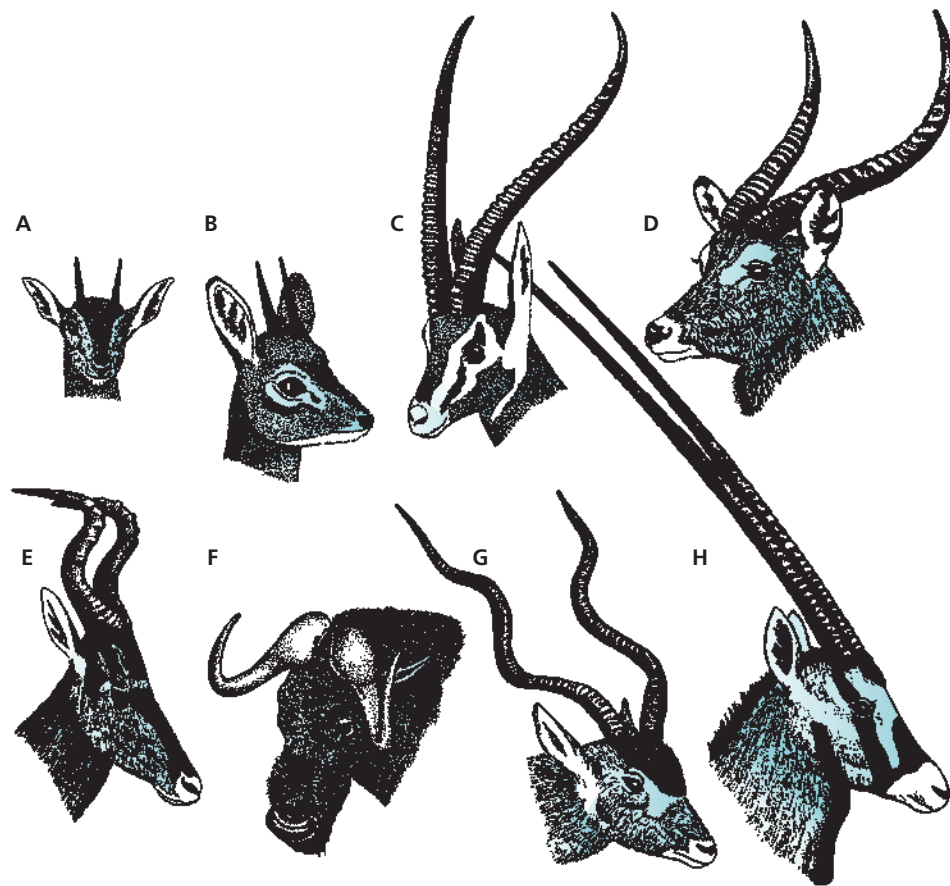
Figure 19.28 **Variety of horn shapes and sizes in bovids.** (**A**) Suni (*Neotragus moschatus*); (**B**) klipspringer (*Oreotragus oreotragus*); (**C**) Grant's gazelle (*Gazella granti*); (**D**) waterbuck (*Kobus ellipsiprymnus*); (**E**) hartebeest (*Alcelaphus buselaphus*); (**F**) gnou (*Connochaetes gnou*); (**G**) addax (*Addax nasomaculatus*); (**H**) oryx (*Oryx gazella*). Not to the same scale. *Adapted from Bubenik and Bubenik (1990).*

tomba walteri) found in Togo, Benin, and the Niger delta of West Africa. The earliest fossil bovids (*Eotragus*) date from the early to mid-Miocene in Africa and Eurasia. Bovids radiated dramatically throughout the Miocene (Prothero 2017) with about 160 known extinct genera.

Suborder Whippomorpha

Hippopotamidae

Combining "whale" and "hippo" to form the somewhat whimsical name of the suborder reflects the association of the hippopotamids as the closest relatives of cetaceans. Before molecular analyses showed their close association with whales (see Figure 19.13), hippos were grouped with the pigs and peccaries. The 2 extant species of hippos differ greatly in size. The common hippopotamus (*Hippopotamus amphibius*) has a total length up to 5.5 m and maximum body mass of 4,500 kg. The pygmy hippo (*Choeropsis* [*Hexaprotodon*] *liberiensis*) has a total length of only 2 m and maximum body mass of about 270 kg. Both hippo species are essentially without hair except for a few bristles around the snout. With-

out temperature-regulating sweat glands, both species have glandular skin that exudes a pigmented fluid that appears red and gives rise to the misconception that they "sweat blood." The fluid helps protect against sunburn and acts as an antibiotic to keep wounds from becoming infected. The cheek-teeth are bunodont, and *H. amphibius* has ever-growing, tusk-like lower canines and incisors, with the alveoli of the canines anterior to those of the incisors (Figure 19.30). Although the canines are not used in foraging, they are important in ritualized fighting to establish dominance and function as visual signals in a threatening "yawn" display.

Both species are closely associated with rivers, lakes, and estuaries and are excellent swimmers and divers. Part of their dependence on water is because of rapid evaporative water loss through the epidermis. The common hippopotamus can remain submerged for up to 30 minutes while walking along the bottom of lakes and rivers feeding on plants. Common hippos are the more aquatic of the 2 species and spend most days in the water (Figure 19.31). Individuals remain submerged throughout much of the day with only the eyes and nostrils above water.

Hippos were originally distributed throughout most of Africa south of the Sahara Desert and along the Nile
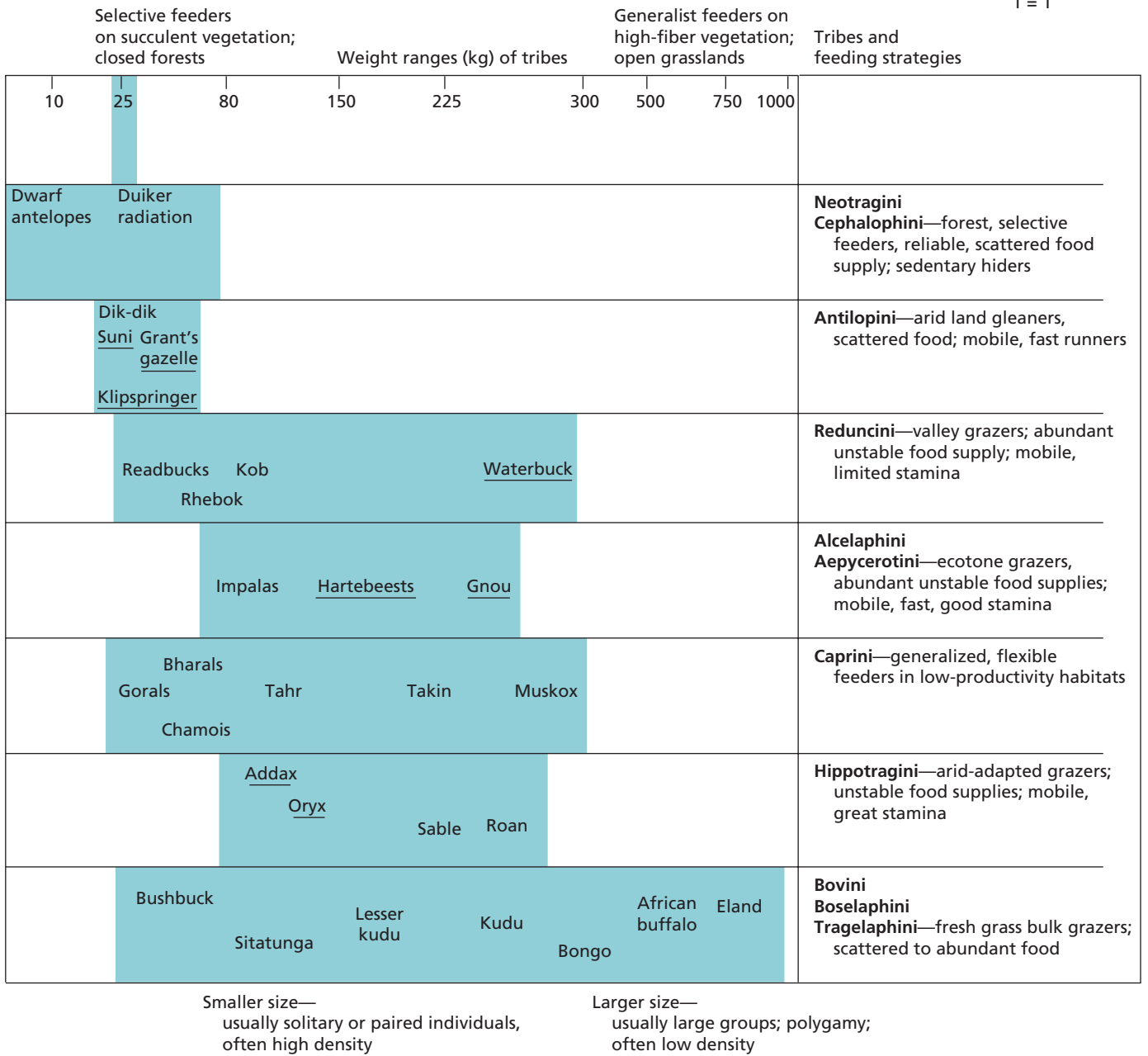
Figure 19.29 Feeding strategies of bovid tribes. Ecological niches vary, depending on the size of the species. Underlined names are species shown in figure 19.28. *Adapted from Kingdon (1979, vol. 3B); tribes from Groves and Leslie (2012).*

River. The pygmy hippo is restricted to the coastal regions of West Africa from Guinea to Nigeria. The aquatic specialization of common hippos and the geographic restriction of the more terrestrial pygmy hippopotamus may have been in response to pressure from other grazing cetartiodactyls, specifically bovids. The common hippo grazes on land for 5–6 hours each night, with grass as the primary food, although based on stable carbon isotope analyses, Cerling and colleagues (2008) reported a more variable diet than expected. Pygmy hippos consume leaves and fruit, as well as aquatic plants and roots. Hippos are not ruminants, but the stomach has septa and several

blind sacs to slow the passage of food for more efficient digestion.

Common hippos are gregarious, forming herds of up to 40 individuals, depending on availability of water. They produce a variety of sounds that serve both social and behavioral functions, as well as help individuals orient underwater in murky waters (Maust-Mohl et al. 2018). Pygmy hippos are solitary or form pairs. Although there is a great deal of variability, male common hippos generally are sexually mature when 7 years old, females by 9 years of age; pygmy hippos are sexually mature when 4 to 5 years old. A single young is born after a gestation period of 6 months

Figure 19.30 Mandible of a hippopotamus. Note the alveoli of the lower canines anterior to those of the incisors. *Photo by G. Feldhamer.*

Figure 19.31 The common hippopotamus (*Hippopotamus amphibius*). Hippos, closely related to whales, spend a great deal of time in the water, both for feeding and thermoregulation.

in pygmy hippos and 8 months in common hippos. Breeding as well as parturition usually occur in the water. Calving intervals are about 2 years but may be affected by drought. Both species have been extensively overhunted, with populations further reduced by habitat destruction. The common hippopotamus is extirpated from the Nile River Valley in Egypt. The pygmy hippo has probably never been common and has been listed as endangered since 2006. The Malagasy dwarf hippo (*H. lemerlei*) and Malagasy pygmy hippo (*H. madagascariensis*) became extinct within the last 1,000 years (Stuenes 1989) because of overhunting. The oldest known hippopotamids are from the early to mid-Miocene. For comprehensive reviews of the paleontology of hippos see Boisserie and coworkers (2011) and Weston and Boisserie (2011).

SUMMARY

- Both perissodactyls and terrestrial cetartiodactyls are defined on the basis of limb structure.
  - Perissodactyls are mesaxonic; the main weight-bearing axis of the limbs passes through the third digit.
  - Cetartiodactyls are paraxonic; the axis of the limbs passes between the third and fourth digits.
- The superior digestive efficiency of ruminants probably led to the displacement of most lineages of perissodactyls early in the Cenozoic.
  - The order today represents a remnant of a much more diverse group that lived in the early Tertiary.

- Other than the domestic horse, most species in the three surviving families of perissodactyls are severely depleted in numbers and geographic distribution.
- In contrast, terrestrial cetartiodactyls, especially the cervids and bovids, are widely distributed and are very diverse in size (from the mouse deer to hippopotamus) and life-history characteristics.
- Horns and antlers occur in five of the families discussed in this chapter for defense against predators and as part of intraspecific social behavior.

○ Rhinoceroses are the only perissodactyls with horns, although they are not made of bone and are not permanently attached to the skull.

○ Giraffes also have unusual horns that form from separate bones (ossicones) that fuse to the cranium.

○ Antilocaprids and bovids have horns formed from keratinized sheaths over bony extensions of the frontal bone; sheaths are deciduous in pronghorns but not in bovids.

○ Cervids have antlers made of bone and are branched, deciduous, and generally occur only on males.

• Horses and several species of cetartiodactyls are found worldwide, in many cases because of introductions.

○ Other species such as camels and some bovids are no longer found in the wild but only in domestication.

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DISCUSSION QUESTIONS

1. Consider Figure 19.6 depicting the evolutionary development of the horse. Why do you never see a similar figure for rodents or bats?

2. Why is it adaptive for deer to shed their antlers every year following the rut, even though it means considerable energy expenditure to regrow a new set beginning a few months later in the spring? Why not keep the same set of antlers throughout life?

3. What is the adaptive significance of antlers in female caribou? Consider the northern latitudes and the extreme climatic conditions where caribou occur. Also, keep in mind that males develop antlers before females each year and subsequently cast them in the winter before females do.

4. Camels and tapirs both passed most of their evolutionary development in North America, but radiated both north and south during the Pliocene and died out in North America during the Pleistocene. What reasons might explain why the highly mobile pronghorn antelope never left North America?

5. Considering the length of their neck, what physiological mechanisms do giraffes use to maintain blood flow to their brain or to regulate blood flow when bent down to drink?

6. What kinds of characteristics have plants evolved in response to pressure from herbivores such as perissodactyls and terrestrial cetartiodactyls?

Infraorder: Cetacea

Whales are some of the most fascinating of all mammals. Whales used to be in their own order with 2 well-defined suborders. As noted in the introduction to Chapter 19, whales now are known to be closely related to cetartiodactyls. Specifically, they are the sister group of Family Hippopotamidae (see Figure 19.13; Table 19.1). As a result, whales are no longer considered a separate order, but are in the Infraorder Cetacea (from the Greek word for "whale") within the Order Cetartiodactyla. There are 14 extant families of cetaceans in 2 parvorders: the Odontoceti (toothed whales) and Mysticeti (baleen whales) (Figure 20.1).

Whales are characterized by extremes. They include the largest animals that have ever lived—adult blue whales (*Balaenoptera musculus*) are heavier (about 136,360 kg) than the biggest dinosaurs, and reach 30 m in length. Whales also have the loudest voices, producing low-frequency vocalizations greater than 180 decibels. The sperm whale (*Physeter macrocephalus*) has the largest brain (weighing about 10 kg) of any living animal. Sperm whales endure tremendous water pressure as they dive deeper than any other mammal. Certain whale species make some of the longest migrations. Whales are all the more amazing considering that they evolved from terrestrial ancestors in the early Eocene, with all the associated anatomical, behavioral, and physiological changes necessary for a complete transition from land to water (Gatesy et al. 2013; Berta 2017). But the life histories of many species of whales remain unknown because of their relative inaccessibility and the wide-ranging movements of individuals. Only recently have advances in technology and molecular genetics allowed researchers to more thoroughly investigate the physiology, behavior, sound communication, social interactions, reproduction, phylogeny, and other aspects of whale biology. Conversely, more is known about the anatomy of whales than of many other large mammals because the whaling industry provided carcasses for hundreds of years.

In addition to the manatees and dugong (Order Sirenia; see Chapter 12), whales are the only group of mammals that are entirely marine—they never leave the water. This chapter examines many of the interrelated morphological, physiological, locomotor, and behav-
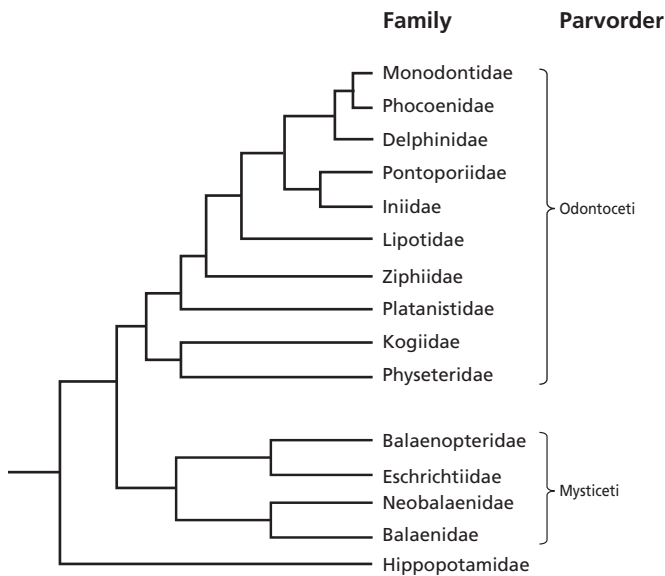
Family	Parvorder

Figure 20.1 **Phylogeny of extant whales.** There are ten families of toothed whales (Parvorder Odontoceti) and four families of baleen whales (Parvorder Mysticeti). Whales are a sister group to the Family Hippopotamidae within the Order Cetartiodactyla. *Modified and adapted from Geisler et al. (2011) and Boessenecker and Fordyce (2015).*

ioral adaptations of whales that have evolved in response to the demands of life in a marine environment.

Morphology

As noted, the extant Mysticeti (baleen whales) and the Odontoceti (toothed whales) were considered suborders but are now parvorders within the Infraorder Cetacea. The primary feature of mysticetes is their baleen plates, which take the place of teeth (see the section Mysticetes: Baleen and Filter-Feeding in this chapter). Baleen is used to strain small marine organisms from the water for food. The teeth in odontocetes generally are homodont, simple, and peg-like. Most mammals are diphyodont—they have two sets of teeth during a lifetime: deciduous and permanent. Odontocetes are monophyodont—they have a single set of teeth. Odontocetes also echolocate to orient within their environment and find prey; mysticetes do not. Several other differences exist between mysticetes and odontocetes (Table 20.1). A third group of ancient, extinct whales, generally considered "**Archaeoceti,**" had many features that were intermediate during the transition from primitive terrestrial mammals to fully marine whales (see Fossil History in this chapter).

Unlike the adaptations of fish, whose entire evolutionary history was in water, the adaptations of whales for life in the water are all secondary. That is, the morphological

characteristics of whales today are all derived from those of ancestral land mammals that made a gradual transition from land to sea about 50 mya (see Fossil History in this chapter). Gingerich (2005:235) noted that Infraorder Cetacea "is interesting from an evolutionary point of view, because it represents entry into and eventual mastery of a new aquatic adaptive zone markedly different from that of its terrestrial ancestors." Water, especially saltwater, provides a particularly buoyant environment. Thus, whales can be larger than any terrestrial mammal and still remain mobile because they never leave the buoyant environment that supports them. Nonetheless, body size varies considerably among cetaceans; more than half of all whale species are the relatively small dolphins and porpoises. Keep in mind, however, that even "small" whales are quite large relative to the average size of most terrestrial mammals. Whales range in size from Heaviside's dolphin (*Cephalorhynchus heavisidii*) and Hector's dolphin (*C. hectori*), which weigh about 40 kg and are about 1.7 m long, to the blue whale (Figure 20.2). No terrestrial mammals are the size of the large baleen whales because their skeletal support system would have to be so massive that they would be rendered immobile; there probably are metabolic and reproductive constraints against such size as well. Several interrelated features of whales are associated with life in the water, including body and skull shape, thermoregulation, and the physiology of diving, all of which we discuss next.

Table 20.1 Primary differences between the two parvorders of cetaceans: the mysticetes (baleen whales) and odontocetes (toothed whales)

Mysticeti	Odontoceti
Baleen present instead of teeth; teeth present in fetus lost before birth	Teeth present, usually homodont; exceed the primitive eutherian number in some species; monophyodont
Paired external nares ("blowholes"); located anterior to eye	A single external nare; located posterior to eye in all species except sperm whales
Facial profile convex, with no fatty "melon" present	Facial profile concave, with depression occupied by a "melon," or fatty organ
Skull symmetrical	Skull generally asymmetrical
Do not echolocate; auditory bullae (tympanoperiotic bones) attached to skull	Echolocate; tympanoperiotic bones not attached to skull
Nasal passages simple	Nasal passages with a complex system of diverticula
Mandibular condyle directed upward	Mandibular condyle directed posteriorly
Sternum consists of a single bone	Sternum consists of three or more bones

Baleen whales

Blue whale

Fin whale

Sei whale

Right whale

Humpback whale

Gray whale

Bryde's whale

Minke whale

Toothed whales

Sperm whale

Baird's beaked whale

Killer whale

Cuvier's beaked whale

False killer whale

Pilot whale

Hubb's beaked whale

Blainville's beaked whale

Risso's whale

Bottlenose dolphin

Pygmy sperm whale

Right-whale dolphin

Rough-toothed dolphin

Dwarf sperm whale

Striped dolphin

Common dolphin

Spotted dolphin

White-sided dolphin

Spinner dolphin

Dall's porpoise

Harbor porpoise

Scale
⊢—⊣ = 2 meters   Adult African elephant
(6.56 ft.)   shown for comparison

Figure 20.2 Relative sizes of baleen and toothed whales. The scale represents approximately 2 m. An adult African elephant is shown for comparison. *Data from Orr and Helm (1989).*

STREAMLINED BODY SHAPE

The general body shape of whales is the same whether they are large mysticetes or smaller odontocetes (Figure 20.3). Whales are fusiform (meaning streamlined, or torpedo-shaped), which allows them to move forward through the water with less drag. As with bats flying through air, drag on whales is a function of several factors, including the density and viscosity (resistance to flow) of water and the

size, shape, and speed of the whale moving through it. How these factors interact in fluid dynamics is suggested by the Reynolds number (Re), a dimensionless value. Of primary importance in determining Re is the product of the size and speed of an object moving through a fluid. Thus, a 0.3-mm-long zooplankton moving at 1 mm/s results in Re = 0.3. By comparison, a large whale moving at 10 m/s results in Re = 300,000,000. An excellent account of the mechanics of organisms in fluids, both water and air, is provided by Vogel (1994).

As a whale moves forward, water flows smoothly over it with minimal turbulence (referred to as **laminar flow**) because of several structural features. Little protrudes from a whale's body that would increase drag and impede the smooth, continuous flow of water. Whales have no external ears or hind limbs, for example. Hind limbs have been reduced to small, vestigial, internal innominate bones. These are not attached to the vertebral column (see Figure 20.3) but are imbedded in ventral muscles anterior to the anus. Likewise, the male has no scrotum, and testes are permanently abdominal. The penis is retractile and lies in a fold of skin (Figure 20.4A), as do the genital and mammary grooves of females (Figure 20.4B). Streamlining is further achieved by almost complete absence of body hair; subcutaneous blubber (the layer of fat under the skin) provides insulation. Several physiological features noted below maintain thermoregulation.

The forelimbs of whales are modified as flexible flippers. The humerus, radius, and ulna are shortened, whereas the digits are greatly elongated by having additional **phalanges**, or finger bones (Figure 20.4C–F). The flippers do not provide power for forward thrust, however, but act only as stabilizers. The elongated tail that ends in a dorsoventrally flattened, horizontal fluke (see Figure 20.3) generates power for locomotion. The **fluke** is supported only by connective tissue rather than by any skeletal element. Because water is denser than air and has much greater viscosity, the large surface area of the tail fluke moving up and down, which is termed **caudal undulation**, "pushes" against the water and propels a whale forward (Fish and Hui 1991; Fish 1992; Buchholtz 2001). The dorsal spinous vertebral processes provide sites for muscle attachment to raise the tail, and the **chevron bones** on the ventral portion of the anterior caudal vertebrae provide attachment for the muscles that depress the tail. Another dimensionless value, the Strouhal number (St), is used to describe the swimming efficiency of cetaceans, as well as fish. Parameters that define St include stroke frequency, oscillation amplitude of the fluke, and mean forward velocity (Rohr and Fish 2004).

The simple postcranial skeleton of cetaceans is composed primarily of the backbone, which provides attachment sites for the large tail muscles. Limbs are not needed for support because the aquatic environment provides the needed buoyancy. Cervical vertebrae are reduced in size and are often fused; most whales have little mobility of the head.

It is interesting that the stomach structure of most whales is similar to that of ruminating cetartiodactyls in
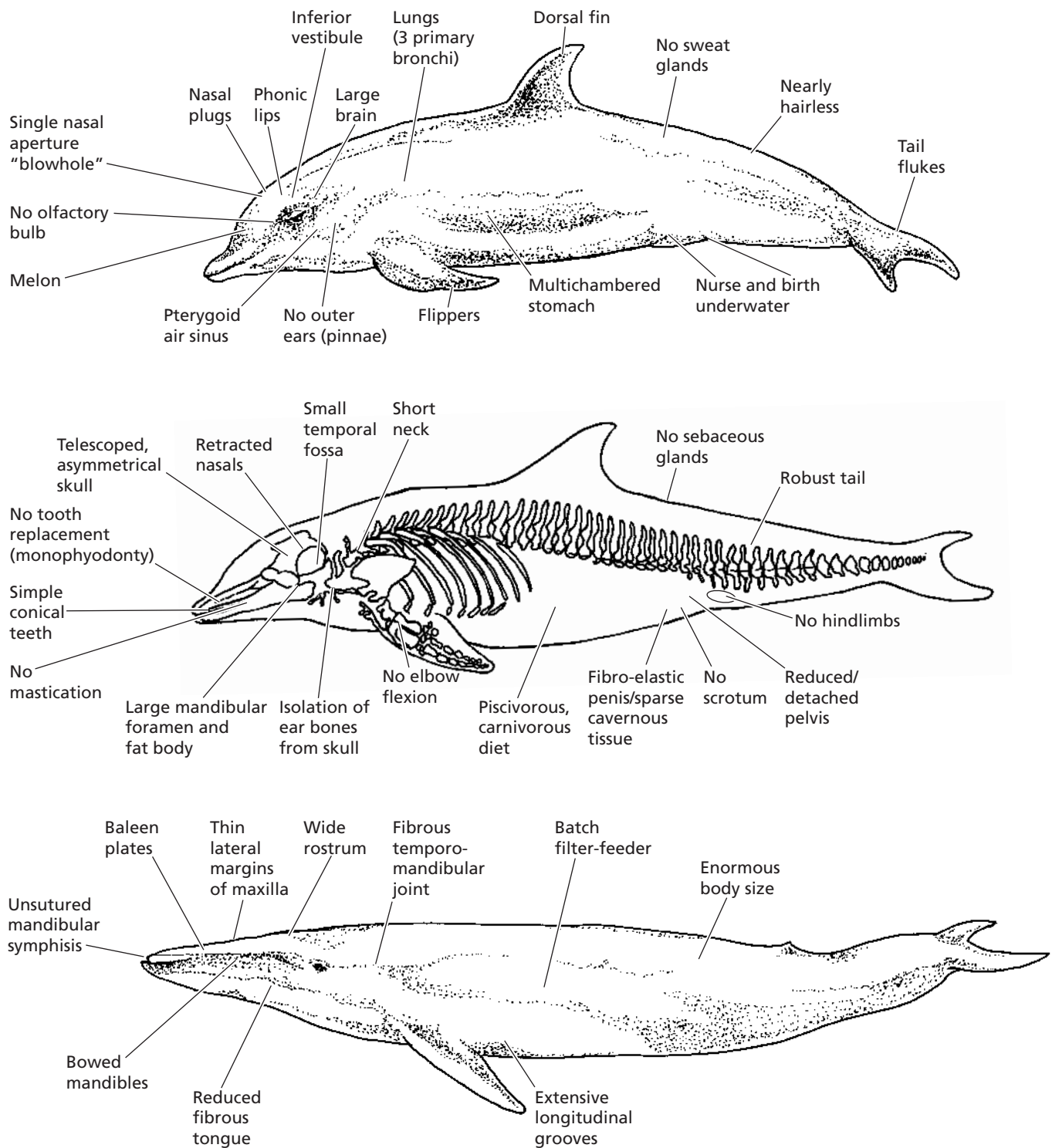
Figure 20.3 **Whale body morphology.** Note the numerous features characteristic of modern whales. Many of these, including flippers and loss of external ears, hair, and hind limbs, are adaptations for a more streamlined body to reduce drag as they swim. Dorsal fins, blowholes, telescoped skulls, an asymmetrical skull and a melon in odontocetes, and baleen in mysticetes are all unique among mammals. *Adapted from Gatesy et al. (2013).*

having three chambers (Figure 20.5), although all whales are carnivores and do not ruminate. Whales physically break down food using the highly muscular walls of the first chamber, or forestomach. No digestive enzymes are secreted in the first chamber, but they are in the second

chamber, which is the main stomach. Numerous reticular folds allow the main stomach to greatly expand. The third chamber, or pyloric stomach, is named for its numerous pyloric glands (Slijper 1979; Langer 1996). However, mysticetes and odontocetes feed in distinctly different ways on
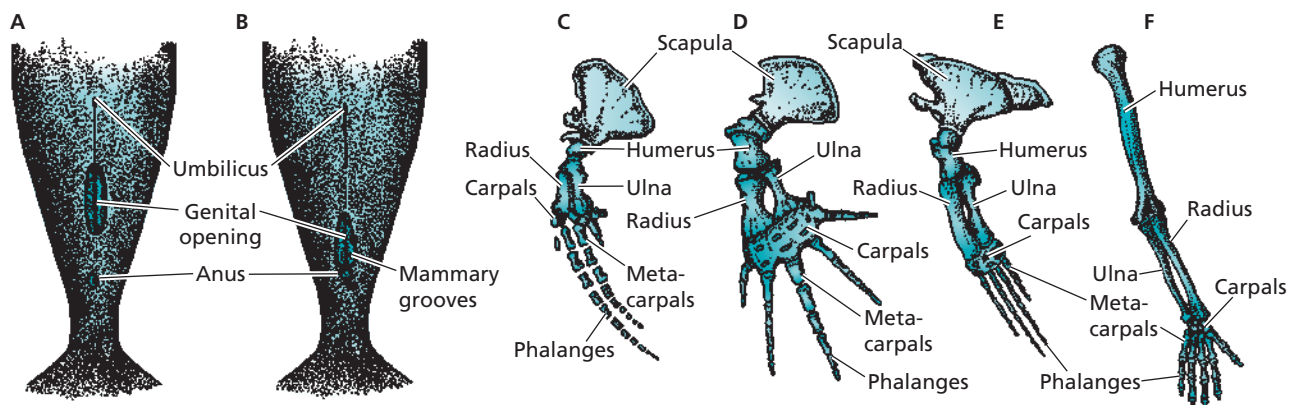
Figure 20.4 **Genital grooves and forelimbs.** Ventral view of the genital grooves in (**A**) a male whale and (**B**) a female whale. Forelimbs of whales have been modified to form paddle-like flippers, as seen in (**C**) a pilot whale (Genus *Globicephala*), (**D**) a blue whale, and (**E**) a right whale. Compared to a human arm (**F**), the humerus, radius, and ulna of whales are relatively short. The phalanges have been lengthened and increased in number. Drawings are not to the same scale. *Adapted from Evans (1987).*
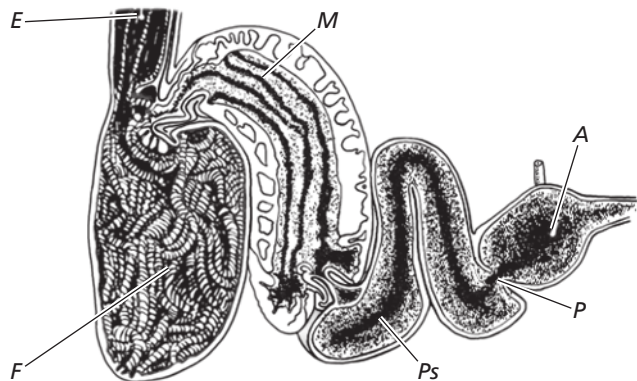
Figure 20.5 **Whale stomachs.** Several compartments are evident in the stomach of a bottlenose dolphin. *Abbreviations*: E = esophagus; F = forestomach; M = main stomach; Ps = pyloric stomach; P = pylorus; A = ampulla of duodenum. *Adapted from Slijper (1979).*

different types of prey (Figure 20.6). Nonetheless, both baleen and toothed whales lack taste receptor genes for sweet, sour, bitter, and umami—likely because they swallow prey whole without chewing (Feng et al. 2014).

SKULL STRUCTURE

Whales have highly modified, **telescoped skulls** in which posterior bones of the cranium are compressed and overlap each other. The anterior, or rostral portion, of the skull is greatly elongated through extension of the nasal, premaxillary, maxillary, and frontal bones. These bones extend posteriorly such that they overlap the parietal bones (Figure 20.7). Telescoping was in place by the Oligocene (Churchill et al. 2018) and has accommodated the posterior displacement of the external **nares** (nostrils, or "blow-

holes") to the top of the skull, so that only this portion needs to be above water for a whale to breath. In addition, odontocetes have an asymmetrical skull structure, especially around the internal nares (Figure 20.8); asymmetry is related to production of sound pulses and echolocation. Inner ear structure and function differ in mysticetes and odontocetes. Baleen whales use low-frequency, infrasonic sounds, whereas toothed whales are sensitive to high-frequency, ultrasonic sounds. Many authorities have shown that these auditory adaptations are evident in the cochlea of even the early stem archaeocetes (Geisler et al. 2014; Ekdale and Racicot 2015; Ekdale 2016; Park et al. 2016; Ritsche et al. 2018).

THERMOREGULATION

Whales face certain challenges living in an aquatic environment because of the physical properties of water. One challenge is water's very high thermal conductivity: water absorbs heat from a warm body about 27 times faster than air does. Thus, whales must maintain their body temperature in frigid polar waters or the deep, cold waters of temperate and tropical areas. Loss of body heat represents loss of energy, which must be made up by increased food intake. Thus, it benefits individuals in cold water to minimize the amount of heat they radiate to the environment. Unlike terrestrial mammals, whales have no insulating fur, nor can they burrow or construct nests to help maintain their body temperature against cold ambient conditions. Whales maintain thermal equilibrium in several ways. Because of their large size, they have a favorable surface-to-volume ratio (the "Scale Effect"). Even though they have a large surface area from which they lose heat, this area is small relative to their heat-producing body mass. Also, the subcutaneous layer of blubber acts to insulate whales. The thickness of blubber varies both seasonally and among

Figure 20.7 **Telescoping of the skull in modern whales.** Skulls of (**A**) a terrestrial mammal (the horse, *Equus caballus*); (**B**) an archaeocete whale (Genus *Basilosaurus*) with heterodont dentition; (**C**) a modern odontocete (common dolphin, *Delphinus delphis*) with homodont dentition; and (**D**) a modern mysticete (fin whale, *Balaenoptera physalus*). In modern whales, the nasal, premaxilla, maxilla, and frontal bones have extended posteriorly to overlap the parietal bones. Arrows indicate the resultant posterior movement of the nares or nostrils. Skulls are not drawn to scale. *Adapted from Slijper (1979).*

Figure 20.6 **Size ranges of food items of baleen and toothed whales.** Shown on a logarithmic scale are (**1**) calanoid copepods; (**2–3**) zooplankton; (**4**) lantern fish; (**5**) capelin; (**6**) mackerel; (**7**) small squid; (**8**) deep-water angler fish; and (**9**) large squid. *Adapted from Gaskin (1982).*
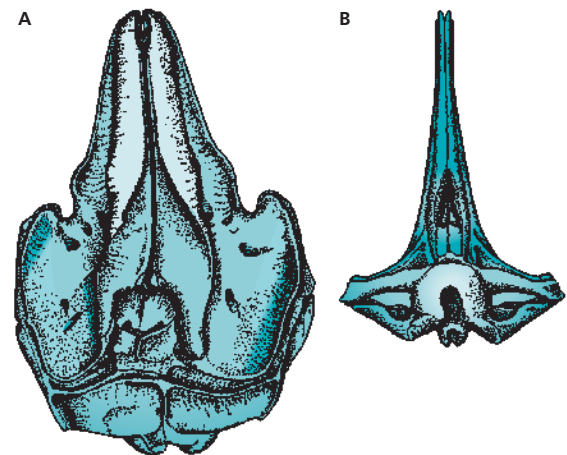
Figure 20.8 **Odontocete verses mysticete skulls.** Dorsal views of the skulls of (**A**) an odontocete, Risso's dolphin (*Grampus griseus*), and (**B**) a mysticete, the northern right whale (*Eubalaena glacialis*). Note the asymmetrical skull typical of odontocetes. Skulls are not to the same scale. *Adapted from DeBlase and Martin (1981).*

species, from 5 cm in small dolphins to as much as 50 cm in the bowhead whale (*Balaena mysticetus*). When large whales are feeding at high latitudes, blubber may represent up to 70% of their body mass (Bonner 1989).

Although blubber forms a passive means of heat retention for thermoregulation, heat can also be actively retained in whales through their well-developed countercurrent heat exchange system. This system is associated with areas of the body with little blubber or muscle, such as the flippers, flukes, and head. In these areas, a closely associated network of veins surrounds major arteries. This *rete mirabile* ("wonderful net") acts as a heat exchanger. As the warm blood in the arteries moves from the body core outward toward the cooler body surface, heat transfers to the adjacent colder blood in the returning venous system. Moreover, whales have somewhat of an advantage in thermoregulation compared with terrestrial species because large bodies of water generally maintain fairly constant temperatures.

PHYSIOLOGY OF DIVING

Whales must also face the challenges associated with diving. Because water pressure increases by 1 atmosphere (atm; 14.7 lb/in.^{2}, or approximately 1 kg/cm^2) for every 10 m increase in depth, deep-diving species face tremendous physical as well as physiological demands. At a depth of 30 m,

the pressure is 4 atm, or about 60 lb/in.^{2}; at 1,000 m, the water pressure is over 1,500 lb/in.^{2} Whales have adapted in several ways to meet these challenges. They are able to survive the extreme pressures encountered during deep dives because their bones are relatively noncompressible. Their upper airways are fairly rigid as well and are supported by bundles of cartilage, although their lungs collapse at depth.

Like all mammals, whales must breathe air or they will die. Large species, however, are able to remain submerged without breathing for prolonged periods—a little over 2 hours in sperm whales and bottlenose whales (*Hyperoodon ampullatus*). Whales can do so because they use oxygen more efficiently than terrestrial mammals. Land mammals use 4% of the oxygen they inhale with each breath, whereas whales use 12%. Oxygen is carried to the cells of the body more efficiently as well because the average **hematocrit** (number of erythrocytes [red blood cells] per volume of blood) of whales is twice that of terrestrial mammals. In addition, whales have 2 to 9 times the amount of **myoglobin** (oxygen-binding protein in muscles) found in terrestrial mammals. Extra capillaries in the alveoli of the lungs facilitate rapid gas exchange. Whales also exhibit a characteristic "diving response," which includes bradycardia (reduced heart rate) while submerged. They maintain normal arterial blood flow to the brain and heart but with vasoconstriction and reduced peripheral circulation. Nonetheless, constant blood pressure is maintained to vital organs throughout the dive—the combined result of increased blood pressure through vasoconstriction and decreased blood pressure because of bradycardia.

When people dive while breathing compressed air, the increased water pressure causes nitrogen, which makes up about 79% of air, to dissolve in tissues and body fluids. If a diver ascends too quickly from a deep dive, the decreasing water pressure causes the nitrogen to come out of solution faster than it can be taken to the lungs and exhaled. The nitrogen forms bubbles in joints or other areas of the body, resulting in the "bends," or "decompression sickness," a condition that is not only painful but can be fatal. Whales dive deep and return to the surface rapidly but are able to avoid this problem. Cetacean lungs are relatively small compared with their body size. With increased depth and pressure, their lungs begin to collapse; at a depth of about 100 m, they are completely collapsed and contain no air. Any residual air is pushed to more rigid, cartilaginous portions of the trachea and bronchioles with little or no gas exchange. Thus, an increased invasion rate of nitrogen is no longer a problem with increased depth.

Although metabolic wastes accumulate during a dive, the respiratory center of the brain has a high tolerance to carbon dioxide buildup. Whales also tolerate high levels of lactic acid, which is produced by anaerobic respiration. They repay their "oxygen debt" when they surface and breath again, rapidly ventilating their lungs. This results in the characteristic "blow." This is a vapor cloud produced by the condensation of exhaled warm air contacting cooler outside air as well as spray from a small amount of water on the blowhole. Species sometimes can be identified by the shape, height, and direction of their blow.

MYSTICETES: BALEEN AND FILTER-FEEDING

Mysticete means "mustached whale," and baleen whales are named for their most characteristic feature: their ability to filter-feed opened a new ecological niche for them. Baleen is composed of **keratin**, the same cornified protein material that makes up the horns of rhinoceroses and the fingernails of humans. Plates of baleen hang in comb-like fashion from the upper jaw only (Figure 20.9). Depending on the species, from about 155 to almost 500 compact plates occur on each side. Baleen plates in the front of the mouth are shorter; posterior baleen plates become progressively longer. The inner edge of each plate has a fringe of long, frayed filaments. These strainer-like filaments overlap each other from plate to plate and form a continuous filter. Baleen continues to grow throughout the life of an individual as the inner portion is continuously worn away. Again, depending on the species' feeding habits, baleen can be fairly short or up to 5.2 m long, as in the bowhead whale (Figure 20.10). Deméré and colleagues (2008) discussed the evolutionary transition from teeth found in early Oligocene mysticetes to later transitional forms that had both teeth and baleen, to modern bulk-feeding mysticetes with only baleen. As noted by Berta (2017:70), "The origin of bulk feeding represents a major morphological and ecological shift in mammalian evolution. This novel filter-feeding strategy is a key innovation that heralded the evolution of modern baleen whales." In addition to development of baleen, associated morphological changes included larger body size and a greatly elongated, bowed mandible because bite force was greatly reduced. The dentary bones are not fused at the mandibular symphysis so they can move separately (Berta et al. 2016). The mandibles of the larger balaenopterids are the single largest bone of any vertebrate, living or extinct (Pyenson et al. 2013). Fetal mysticetes actually have vestigial teeth that are resorbed before birth, and the maxillary and mandibular alveolar grooves close as baleen develops (see Ekdale et al. 2015 and references therein). Slijper (1979), Pivorunas (1979), and Bonner (1989) discussed details of the formation and fine structure of baleen.

Mysticetes feed on a variety of small marine organisms. **Plankton** (often referred to as "krill") have limited locomotion and form large, floating aggregations. **Necton** is another category of slightly larger and more mobile marine organisms, including fish. Baleen whales feed on both plankton and necton, collectively referred to as **zooplankton** (see Figure 20.6), as well as phytoplankton (small plantlike organisms). Mysticetes generally do so by either "skimming" or "gulping," also called "lunge feeding." Skimming (Figure 20.11) occurs in several species of mys-

A

Gum base

Upper jaw

Baleen plates

Keel of palate

Fringes forming filter mat

B

Outer fringes

Single baleen plate

Inner fringes

C

Upper jaw

Baleen plate

Bone of lower jaw

Filter mat of baleen fibers

Tongue
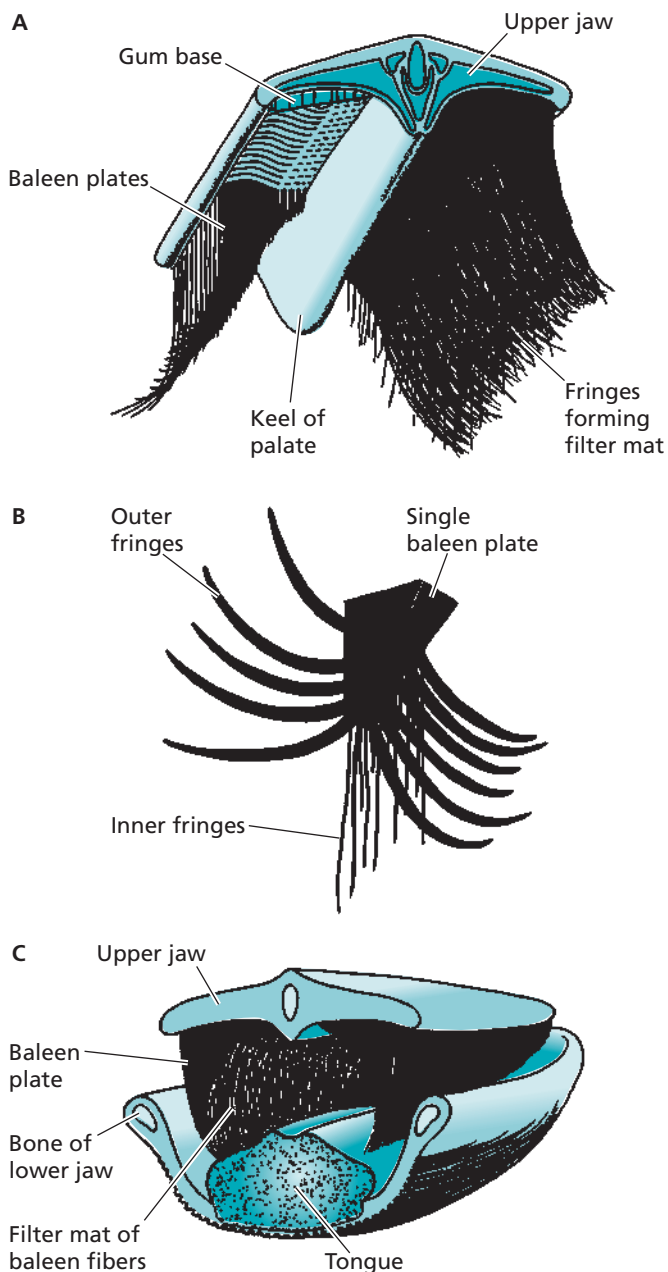
Figure 20.9 **Baleen.** (**A**) Arrangement of baleen in the upper jaw of mysticetes. Hundreds of plates may occur on each side of the mouth. (**B**) Example of a single plate. The size and number of plates vary among species. Growth is continuous as baleen is worn down from scraping by the tongue. (**C**) Transverse section through the head of a baleen whale showing the plates in place in relation to the large tongue. *Adapted from Pivorunas (1979).*

A B C D E F G H

I

J

1 m

Figure 20.10 **Size and shape of baleen plates.** Size and shape of plates are highly variable among different species. Representative plates of baleen from (**A**) minke, (**B**) sei, (**C**) Bryde's, (**D**) pygmy right, (**E**) gray, (**F**) humpback, (**G**) fin, (**H**) blue, (**I**) right, and (**J**) bowhead whales. *Adapted from Evans (1987).*

Figure 20.11 **Skim-feeding in a Bryde's whale (*Balaenoptera edeni*).** Note the baleen plates in the upper jaw.

ticetes. Individuals remain at or just below the surface. With their rostrum out of the water and mouth open, they move through large swarms of zooplankton. Water passes through the mouth and baleen, leaving a mass of zooplankton behind on the baleen. This material is scraped off by the tongue and swallowed.

The larger mysticetes (Family Balaenopteridae) are known as **rorquals**, from the Norwegian *røyrkval* meaning "grooved whale" or "tube-throated." This term refers to the longitudinal grooves or pleats on the throat and chest that allow for great expansion of the oral cavity as the throat fills with water during lunge feeding. Individuals remain submerged several hundred meters deep and open their mouth as they move forward. A huge oral cavity is created (Figure 20.12A, B) as the lower jaw is distended (aided by a loosely joined, ligamentous mandibular symphysis), the pleated throat expands, and the tongue is withdrawn into the large ventral pouch under the chest. Enormous amounts of water, filled with plankton and necton, flow into this oral cavity. Blue whales can gulp 16,000 gallons (60,560 liters, or almost 67 tons) of water at a time. This water is not swallowed but is expelled through the baleen and out the sides of the mouth as the throat and thoracic cavity contract (Figure 20.12C, D) and the tongue protrudes forward. The mass of zooplankton trapped on the baleen is scraped off with the tongue and swallowed.
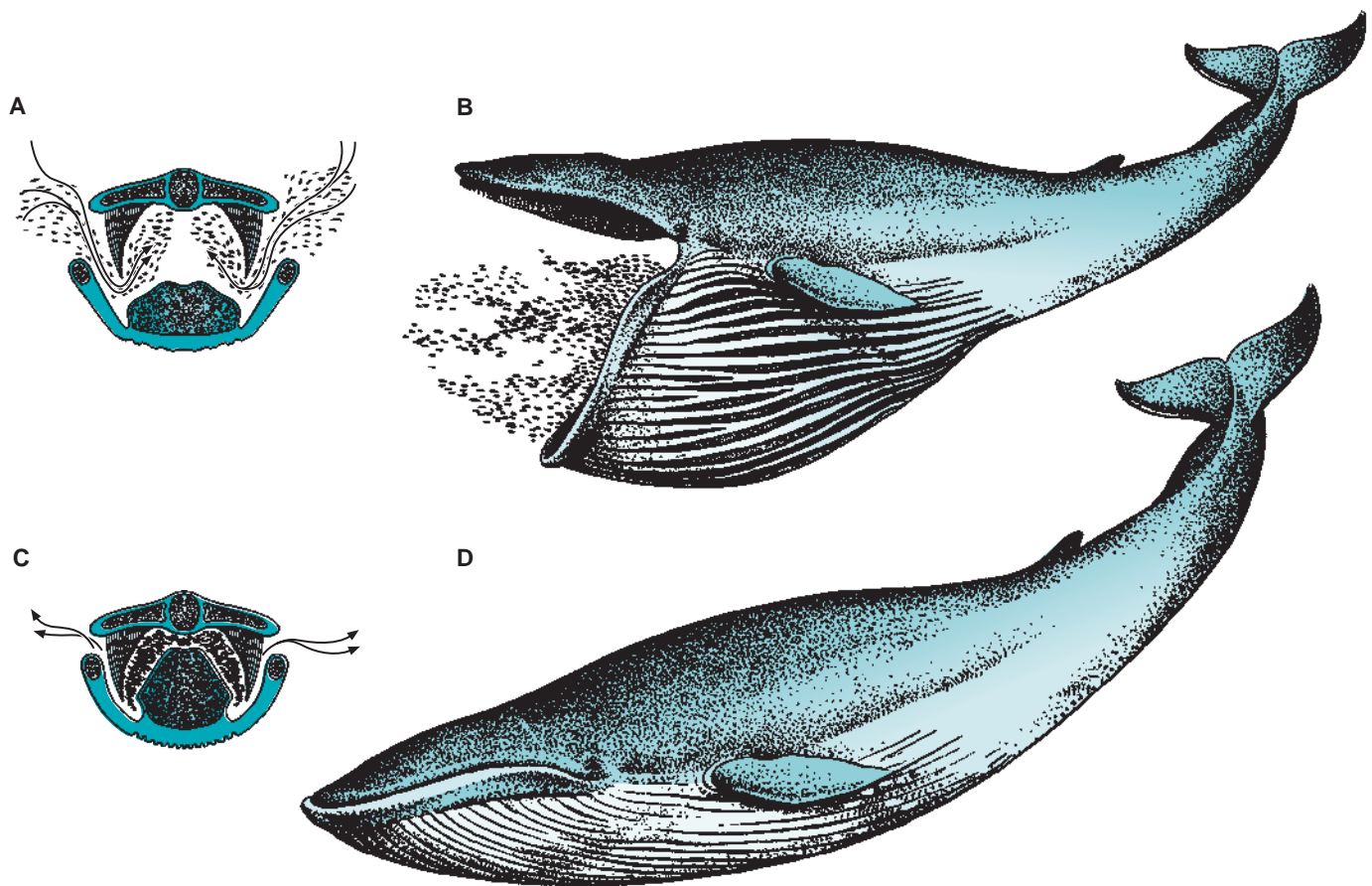
Figure 20.12 Gulping, or lunge feeding, in baleen whales. (**A**) As the mouth opens, huge amounts of water pour in along with vast quantities of plankton and necton, as the (**B**) throat grooves allow for expansion of the oral cavity. (**C**) This water is then expelled through the filter-like baleen mat as (**D**) the throat contracts, trapping the food that is scraped off by the tongue and swallowed. *Adapted from Bonner (1989).*

Several researchers have investigated the kinematics of lunge feeding and associated anatomical characteristics in mysticetes (Goldbogen et al. 2006, 2007, 2008; Potvin et al. 2009; Pyenson et al. 2012; Shadwick et al. 2013). While submerged, a whale accelerates to about 3 m/sec before opening its mouth. Engulfment of the huge volume of water is active rather than passive, there is large force exerted on the mandible, and the whale quickly slows as the drag coefficient rapidly increases.

Unlike most other predators, baleen whales do not actively pursue their prey. Krill and other zooplankton passively float on ocean currents—they cannot attempt to outrun or outmaneuver whales. Thus, baleen whales do not need great speed or agility to capture them; locating concentrations of prey is all that is necessary. Baleen whales can become large at the expense of speed because increased size affords them thermoregulatory and other benefits.

In contrast, toothed whales are more typical active predators—they must pursue and catch their prey. This necessitates a greater degree of agility and speed, with associated restrictions on body size. Not surprisingly, of the approximately 77 species of odontocetes, two-thirds are relatively small dolphins, river dolphins, and porpoises.

ODONTOCETES: DENTITION AND ECHOLOCATION

All odontocetes have teeth. The number varies among species, from a single pair of teeth in Genus *Mesoplodon* (beaked whale, Family Ziphiidae) to well over 100 pairs in some dolphins. Teeth are used to hold fish and squid, prey items that are found through echolocation. Opinion once differed about where echolocation sound pulses are produced. Several investigators argued that echolocation sounds are produced in the larynx, as is true in bats and other mammals. In contrast, Norris (1968) suggested that the larynx is not involved and that echolocation pulses originate in the complex system of the nasal plugs and air sacs that occur in the forehead region of odontocetes. This is now supported by experimental evidence from numerous studies (see Au 1993; Madsen et al. 2013 and references

therein for review). More specifically, Cranford and co-workers (1996) found numerous species of toothed whales had a constriction in each nare, just below the blowholes. Originally termed "monkey lips dorsal bursae," they are now called the "phonic lips." Air moving through the phonic lips produces echolocation clicks and whistles of different frequencies, bandwidths, and directional properties. For several species of dolphins and porpoises, it appears that the larger right phonic lips produce lower frequency clicks, and the left pair produces whistles (Madsen et al. 2010, 2013). A substantial amount of research continues to further define the anatomical and physiological parameters of echolocation in toothed whales. As the sound is generated, it is reflected by the parabolic (dish-shaped) skull and focused and modulated through air sinuses and the oil-filled "melon" in the forehead (Figure 20.13). The low-frequency echolocation sound pulses that whales emit are not as variable as those of bats, but the effective range of echolocation signals is much greater. The returning echoes are received via the relatively small, thin mandible. The mandible has an oil-filled sinus that channels the sound to the auditory bullae. The oil in the mandible and the melon is the same.

Because water conducts sound much better than air, whales receiving sound echoes could not achieve directionality or sensitivity unless they had adaptations not found in other mammals—namely, adaptations that allow them to localize and discern the direction of incoming sound waves. They are able to do so because their auditory bullae, or **tympanoperiotic** bones (containing the middle ear), are not fused to the skull. Instead, the bullae are isolated by connective tissue and a system of sinuses filled with a unique foamed, mucous emulsion (Popper 1980). As noted by Au (1993:30): "Having the bullae physically isolated from the skull and therefore isolated from each other allows [them] to localize sounds received by bone conduction." The facial morphology of the oldest known odonto-

cetes suggests that they had high-frequency hearing and echolocated (Churchill et al. 2016).

Fossil History

The distinctive morphological adaptations of whales for aquatic life are all secondarily derived—that is, they evolved from terrestrial land mammals. The earliest fossil evidence is from the early Eocene. As noted, evidence now clearly indicates whales are most closely related today to hippos (Milinkovitch et al. 1998; Geisler and Theodor 2009). Uhen (2010:189) stated that since the early 1980s, "Whale origins can be supported with a great deal of evidence from paleontology, anatomy, stratigraphy, and molecular biology," as can their transition from land to sea. Fossil (stem) whale families (Pakicetidae, Ambulocetidae, Remingtonocetidae, Protocetidae, and Basilosauridae) are collectively referred to as "archaeocetes" (Figure 20.14). They are known only from early to late Eocene deposits of the Indo-Pakistan region. These early groups showed intermediate morphological stages during transition from terrestrial to fully aquatic mammals.

The Family Pakicetidae includes several known genera (*Pakicetus*, *Ichthyolestes*, and *Nalacetus*) with terrestrial features, including well-developed fore and hind limbs for running. One of the earliest known whales is *Pakicetus inachus*. It was small (less than 2 m long), and the ear structure was primitive, with none of the adaptations for deep diving or directional hearing underwater. Pakicetids waded in shallows and likely fed on fish and other freshwater prey (Berta 2017). Within Family Ambulocetidae, the Genera *Ambulocetus*, *Gandakasia*, and *Himalayacetus* were much larger than pakicetids but were also associated with shallow, freshwater habitats for foraging. They were able to walk but also swam well using their tail and hind limbs. The 6 genera of Family Remingtonocetidae continued the transition of early whales to a more marine lifestyle, with reduced limbs in the Genus *Dalanistes* (Clementz et al. 2006) for example. Like these 3 early families, Family Protocetidae also had an Indo-Pakistan origin, but diversified rapidly with about 20 currently described genera, and radiated worldwide. Protocetids were still able to walk on land and use the forelimbs and hind limbs for swimming. They likely functioned much like modern pinnipeds (seals and walruses), spending most of their time in coastal waters foraging for fish but coming ashore to mate and give birth. They were large and took large prey; the nasal opening was posterior on the skull. The Family Basilosauridae also radiated worldwide and was contemporary with protocetids during the mid-Eocene. As protocetids went extinct during the late Eocene, basilosaurids (Figure 20.15) continued the transition to fully marine cetaceans with a corresponding increase in length (up to 20 m) and body mass, loss of external hind limbs, and development of flukes.

Figure 20.13 Echolocation in toothed whales. As in the dolphin shown here, sounds in the form of clicks and whistles are produced in the complex nasal area. Sound is reflected from the skull and beamed out through the "melon." The returning echo moves through the oil-filled channel of the lower jaw to the tympanoperiotic or ear bullae. *Adapted from Evans (1987).*
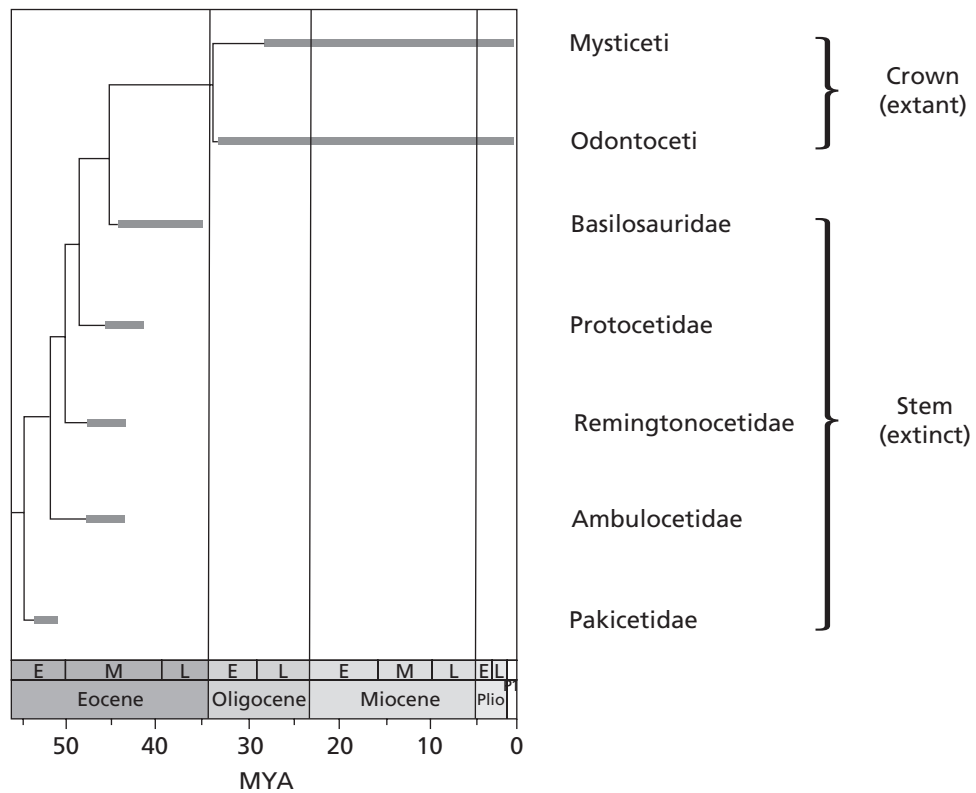
Figure 20.14 Phylogeny of extinct (stem "archaeocete") families of whales. Changes in stem whales from the early to late Eocene included reduction of limbs and movement from land to a primarily marine environment. Extant (crown) cetaceans, which never leave the water, were in place by the Oligocene. *Adapted and modified from Gatesy et al. (2013).*

Figure 20.15 Skull of a *Basilosaurus*. Note the heterodont dentition with multicusped cheekteeth in this transitional late Eocene cetacean.

Both modern parvorders—odontocetes and mysticetes—were clearly distinct by the early Oligocene (Figures 20.14 and 20.16) with marked adaptive radiation in the late Oligocene. The oldest described cetacean, and earliest mysticete, is *Mystacodon selenensis* from the Pisco Basin of Peru (Lambert et al. 2017). Another very early mysticete is *Llanocetus denticrenatus*, with a body length of 8 m, from the late Eocene of Antarctica. Although identifiable as a primitive mysticete, it had heterodont teeth and probably baleen as well, although the presence of baleen remains open to question (see Fordyce and Marx 2018). If the **palmate**, multicusped cheekteeth were present, they also may have functioned as a filter in feeding—intermediate between basilosaurids and more derived mysticetes. A wide range of other primitive, transitional mysticetes from the Oligocene is known from the fossil record (see Boessenecker and Fordyce 2015a), as are numerous genera of odontocetes. As noted, based on their skull characteristics, these Oligocene odontocetes probably echolocated. Most of the extant families of whales were recognizable by the Miocene. Thewissen (2015) and Berta (2017) provided comprehensive reviews of the early evolution of cetaceans, and new transitional fossil species continue to be described (see Marx et al. 2015; Tsai and Fordyce 2018). A good example is *Maiabalaena nesbittae* from the early Oligocene of Washington (Peredo et al. 2018). This early "baleen" whale had neither teeth nor baleen, but is believed to have been a suction feeder, as well as an intermediate stage between toothed and baleen whales.
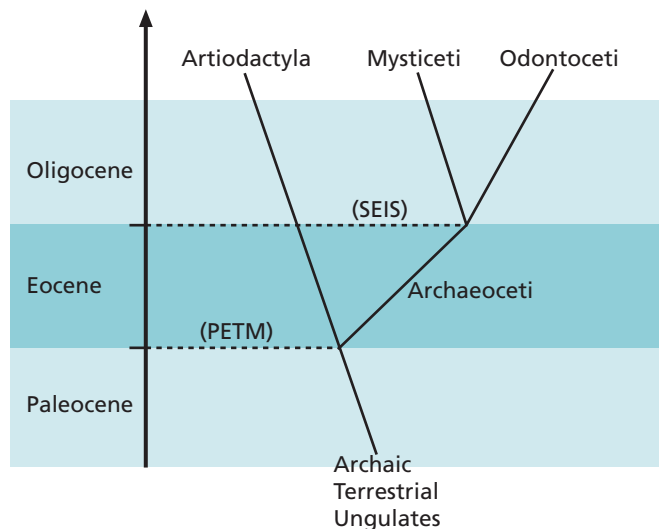
Figure 20.16 **The evolution of whales can be associated with changes in ocean temperatures.** Archaeocetes derived from terrestrial ungulates in the early Eocene, concurrent with a global warming period called the Paleocene-Eocene Thermal Maximum (PETM). Likewise, modern parvorders originated from the Archaeoceti concurrent with abrupt cooling events (small ephemeral ice sheets, or SEIS) marking the Eocene-Oligocene boundary. *Adapted and modified from Gingerich (2005).*

Economics and Conservation

Aboriginal harvest of whales dates back thousands of years, with Alaskan, Scandinavian, and other subsistence hunters using the meat and oil. These early hunting efforts were land-based and typically restricted to slower species inhabiting coastal waters. Using small boats, handheld harpoons, and nets, hunters often tried to drive whales ashore to be killed. These efforts probably had a minimal effect on populations. The extent of whaling operations soon increased, however, as did their effect on populations. Basques were taking significant numbers of right whales during the first millennium, and by the 1500s and 1600s, most European countries had entered the whale trade using large ships that operated throughout the world. Whaling in New England began during the 1600s as well. By this time, exploitation of whales had moved from a subsistence level to a commercial enterprise because of the high economic value of the meat, oil, and "whalebone" (baleen). Commercial exploitation had a pronounced negative impact on whale populations, and significant declines began.

Technological advances in the whaling industry during the 1800s increased the efficiency of whaling even more, allowing additional species to be taken. A modern, explosive harpoon gun was in use by 1864, concurrent with the replacement of sailing ships by steam-driven vessels. The early 1900s saw the development of floating factory ships. The stern slipway, on which whales are hauled directly aboard factory ships (Figure 20.17), was in use by 1925. This allowed whalers to operate more easily on the high seas. Many species were so severely depleted that they became "commercially extinct" and began to be protected from harvest.

The decimation of whale stocks and concern over future sustainable harvests caused several whaling nations to enact the Convention for the Regulation of Whaling in 1931,
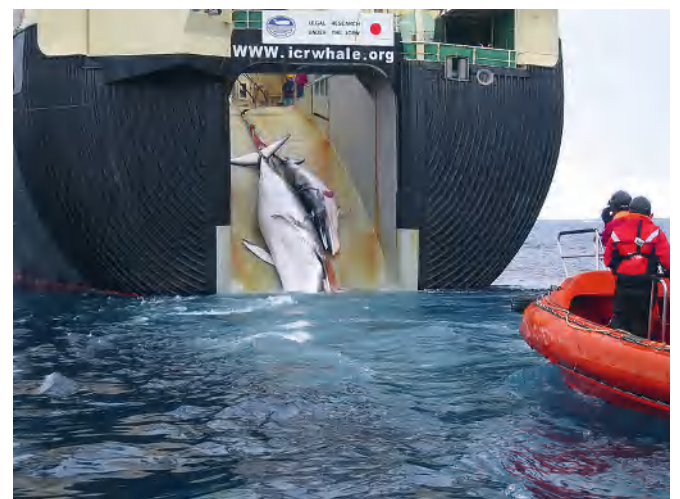
Figure 20.17 **Japanese factory ship.** Adult and subadult minke whales are on the slipway of this factory ship.

which led to the International Agreement for the Regulation of Whaling in 1937. This evolved into the International Convention for the Regulation of Whaling in 1946, which created the International Whaling Commission (IWC). The IWC had dual and conflicting purposes: whale conservation but also development of the whaling industry. It established harvest quotas on certain species and protected other species from any harvest, but it had no enforcement powers. Whale stocks, especially the larger species, continued to be overharvested due to the short-term economic interests of some countries. Today, public opinion, political pressure, various governmental agencies, and nongovernmental conservation groups work toward conservation of whales and protection of ocean habitat. In addition, the availability of alternative products to whale meat and oil has reduced the demand for whales. As of 2018, 87 countries adhered to the International Convention for the Regulation of Whaling. Nonetheless, some commercial whaling continues, generally for smaller species, by Japan, Russia, and Norway—even though they signed the convention—and occasionally other countries. Unfortunately, these commercial ventures are often conducted under the guise of "scientific research," especially by Japan (see "Legal Research" sign in Figure 20.17). Also, continued subsistence hunting of bowhead whales by Inuit peoples remains highly controversial. Nonetheless, some large species, including the eastern population of the gray whale and even the blue whale, may be increasing in number. Other species, however, including bowhead and northern right whales, have not recovered. Newton (2013) and Laist (2017) provided excellent summaries of the history of whaling; Parsons and colleagues (2013) discussed aspects of the IWC.

Parvorders and Families

MYSTICETES

Baleen whales are large, with the females generally about 5% longer and heavier than the males. The smallest mysticetes, male pygmy right whales (Family Neobalaenidae; *Caperea marginata*), are about 6 m in length. As noted, the large body size of baleen whales evolved relatively late and is associated with gulp feeding. During the late Oligocene, mysticetes and odontocetes were about the same size—only about 2.5 m long. The huge sizes of mysticetes such as blue and fin whales (*Balaenoptera physalus*) occurred from the late Miocene to the Recent (Pyenson and Sponberg 2011). During the summer, baleen whales generally feed in northern or southern polar latitudes, where they accumulate vast stores of subcutaneous fat (blubber). During the winter, they often migrate long distances to warmer, more equatorial areas. Feeding is greatly reduced during the winter because tropical waters contain less food, and whales sub-

sist off their stored blubber. Baleen whales do not echolocate, although they produce a variety of sounds. These include "moans" and "grunts" in the low-frequency range, higher-frequency "chirps" and "whistles," and very high-frequency (as much as 30 kHz, or 30,000 cycles per second) pulsating clicks. Because these vocalizations are so loud and water is such an excellent conductor of sound, they can transmit for hundreds, and possibly thousands, of kilometers. Different sounds serve a variety of communication functions, some of the most important of which are identification of sex, social status, and location.

There are 4 extant families in this parvorder; they include only 6 genera and 14 species. Thus, in terms of the number of species, baleen whales comprise only about 15% of living cetaceans. Using molecular data, Sasaki and colleagues (2005, 2006) investigated the phylogenetic relationships of baleen whales (Figure 20.18). As noted by Marx (2011), despite continuing phylogenetic studies on baleen whales, a broad consensus on relationships remains elusive, including placement of the gray whale and pygmy right whale.

Balaenopteridae

The systematics of this family of rorquals are somewhat unsettled, including the number of species in the "Bryde's whale complex." Currently, there are 8 recognized species in 2 genera. Unlike that of the balaenids, the rostrum of
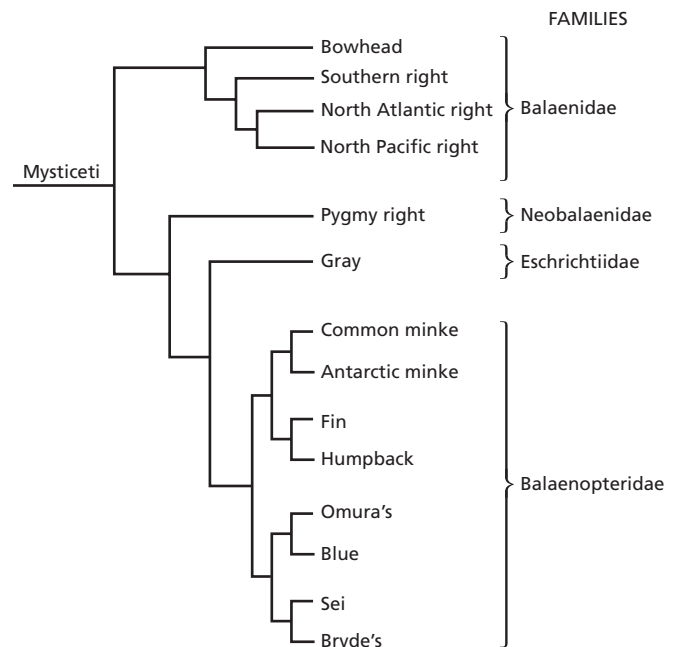
Figure 20.18 **Proposed phylogeny of the Mysticeti.** Fourteen species of baleen whales are now recognized. North Pacific and North Atlantic right whales are now recognized as distinct species, as is Omura's whale. Close association of the pygmy right whale with balaenids is supported by morphological analyses but not by molecular data. *Adapted and modified from Sasaki et al. (2005, 2006).*

balaenopterids is not highly arched, the baleen plates are short, and they meet anteriorly. The 7 species in the Genus *Balaenoptera* are long and slender, with short pectoral fins and dorsal fins that are posterior to the midpoint of the body, and numerous throat grooves. These species are the blue whale, distributed throughout all oceans; the fin whale and sei whale (*B. borealis*), also cosmopolitan in generally temperate waters; Bryde's whale (*B.* [*brydei*] *edeni*) which occurs in tropical and warmer temperate areas; the small (about 7 m total length) common minke whale (*B. acutorostrata*), which is found in all oceans; and the Antarctic minke whale (*B. bonaerensis*), which occurs throughout waters of the Southern Hemisphere. The recently described Omura's whale (*B. omurai*; see Wada et al. 2003) occurs in waters of the East Indies. While it was originally considered a third species in the "Bryde's whale complex," Sasaki and coworkers (2006) found that Omura's whale is more closely related to the blue whale (see Figure 20.18) in a lineage that diverged much earlier than that of Bryde's whale. The remaining species in the family is the humpback whale (*Megaptera novaeangliae*), which enjoys a cosmopolitan distribution but is often more sedentary and found closer to shore than the other balaenopterids. Humpbacks have a more robust body shape than other members of the family, and the flippers are very long (up to 5 m), equal to one-third of the body length (Figure 20.19). Numerous bumps cover the head, each with a single, short, sensory hair projecting from it.

Balaenopterids feed on zooplankton by gulping (also called "lunge-" or "bulk-feeding"). Kot and colleagues (2014) as well as Werth and Ito (2017) provided detailed analyses of lunge feeding behaviors. Sei whales also feed by skimming and take mainly calanoid copepods and euphausids (Prieto et al. 2012). The larger species feed almost exclusively on krill, but the smaller species may also consume small fishes (see Figure 20.6). Because lunge feeding exerts tremendous pressure on the lower jaw of balaenop-

Figure 20.19 **Humpback whale breaching.** Note the long flipper as well as the calf.

terids, the relative size of mandibles becomes larger with increasing body size (Goldbogen et al. 2007; Pyenson et al. 2013). As noted, the mandibles of blue, fin, and sei whales are the largest single bones of any vertebrate that has ever lived (Figure 20.20). Humpback whales are known to use a "bubble-netting" technique as well (Würsig 1988). In bubble netting, a whale exhales a stream of air bubbles under water as it swims in a circle. This tends to congregate the plankton inside a curtain-like column of rising bubbles. The whale, with mouth open, then moves up through the column and consumes the concentrated plankton. Sometimes, coordinated groups of up to 20 humpbacks work together bubble-netting to concentrate prey (Jefferson et al. 1993). Rorquals feed during the summer, and they live off stored body fat during winter. Seasonal feeding and breeding activities of northern and southern populations of rorquals, like balaenids, are out of phase because they are in different hemispheres. As a result, they are genetically isolated, although they are considered to be conspecific.

All balaenopterids vocalize in various ways. For example, calls of blue whales have a seasonal pattern with peaks in late summer and early fall, and daily peaks at dawn and dusk. Peak calling correlates with the vertical migration of krill (Stafford et al. 2005; Wiggins et al. 2005). Humpback whales are well known for their complex, repetitive, long-lasting songs, calls, and other social communications. Suzuki and coworkers (2006:1849) noted that a "song is a sequence of themes, where a theme consists of a phrase, or very similar phrases, repeated several times. A phrase is a sequence of several units." Songs are made up of complex series of multiple units. There are 6 basic songs with variations, and all the humpbacks in a given region sing the same song. The song changes throughout the course of a season (Cerchio et al. 2001); all individuals in a region adapt to the changes. Fournet and Szabo (2013) recognized 19 types of calls within 4 call classes in humpback whales in southeast Alaska. Songs likely have multiple functions: they help individual males compete for breeding females, promote male-male social ordering, because only mature males sing, and attract females to breeding grounds (Herman 2017; Murray et al. 2018). Singing occurs during migration at higher latitudes as well as during the breeding season (Charif et al. 2001; Clark and Clapham 2004). Fin whales off the coast of British Columbia all had a similar song (Koot et al. 2013), although geographical differences occur (Delarue et al. 2009).

Humpbacks, blue whales, and the other large rorquals were drastically overharvested throughout the early and mid-1900s. Blue, fin, and sei whales are endangered and are protected from whaling, although ship strikes remain a significant mortality factor (Berman-Kowalewski 2010). Recovery of large whales has been slow, however, and most species almost certainly will never regain their former numbers. The oldest fossil balaenopterids are from the mid Miocene. Deméré (2014) provided an excellent review of all aspects of the family.

Figure 20.20 **Skull of a blue whale.** As noted in the text, the lower jaw is the largest bone of any vertebrate that has ever existed.

Eschrichtiidae

The gray whale (*Eschrichtius robustus*) constitutes a monotypic family. Males can reach a total length of about 13 m, females about 14 m. Body weight can reach 35,000 kg. Gray whales have fairly slender bodies and small heads, broad flippers, and no dorsal fin, although the posterior third of the body has a series of low humps, or **crenulations**. Size and shape of these "knuckles" are distinct in each individual and aid in identification (Swartz 2014). There are 2 to 5 short throat grooves. They are gray, with lighter mottled areas, and individuals are covered with many barnacles and associated cyamids, or "whale lice" (Figure 20.21). Populations were eliminated from the Atlantic Ocean by the late 1700s (Bryant 1995). There currently are two populations in the North Pacific Ocean—the western occurs along the coast of Asia, the eastern along the coast of North America.

Gray whales feed during the summer in shallow waters of the North Pacific, specifically in parts of the Arctic Ocean, Bering Sea, and Okhotsk Sea. They roll on their sides and suck muddy sediment from the bottom to strain out a variety of worms, invertebrates, amphipods, and decapods (Moore et al. 2003; Swartz 2014). The 140 to 180 pairs of short baleen plates are narrow, stiff, and coarse. There is a gap in the baleen in the anterior part of the mouth, unlike in balaenopterids. Small groups of gray whales are most common, although up to 150 individuals may congregate in good feeding areas. During 6 months of feeding, a gray whale consumes over 200,000 kg of food (Swartz 2014).

Because their feeding areas freeze during the winter, in autumn gray whales migrate up to 20,000 km—one of the longest migrations of any mammalian species. They follow the Pacific coastline to calving grounds in Baja California, or the Sea of Japan. They conceive during migration and

Figure 20.21 **Gray whale breaching.** Note the short baleen and numerous barnacles and other excrescences on the body.

give birth in January or February after a 13.5-month gestation period. A single calf is born in alternate years. Calves are born in shallow lagoons where the water is calmer and warmer than in the open ocean. They are about 5 m long and weigh 800 kg. Most attacks by killer whales (*Orcinus orca*) on gray whales are on calves and yearlings (Barrett-Lennard et al. 2011).

Gray whales swim slowly in shallow waters near shore, so they have always been easy prey for whalers. The eastern Pacific population has been protected since 1946, and gray whales appear to be increasing in numbers, although nowhere near estimated pre-whaling densities (Alter et al. 2007, 2012). The eastern population was removed from the

endangered species list in 1994. The western Pacific population remains severely depleted, however. Estimated at < 100 individuals, it is critically endangered, and its survival is uncertain (Bradford et al. 2012). Fossil eschrichtiids are known from both the Atlantic and Pacific Oceans. The earliest known is *Archaeschrichtius ruggieroi* from the late Miocene of Italy (Berta 2017). Kimura and colleagues (2018) described a new species of fossil eschrichtiid, *Eschrichtius akishimaensis*, from the early Pleistocene of Japan. Swartz (2014) provided a comprehensive review of the family.

Neobalaenidae

This monotypic family includes only the pygmy right whale, which formerly was included in Family Balaenidae. Fordyce and Marx (2013) and Marx and Fordyce (2016) argued that the species is the last surviving member of the otherwise extinct Family Cetotheriidae. However, most authorities accept the more traditional alignment of Neobalaenidae with the balaenids (see Boessenecker and Fordyce 2015b; see Figure 20.1). One of the least known cetaceans, it occurs only in temperate and cold waters of the Southern Hemisphere. Records from 196 sightings and strandings of pygmy right whales over a 125-year period were associated with areas of high zooplankton productivity (Kemper et al. 2013). As suggested by the name, it is the smallest of the mysticetes—females are only about 6.5 m in total length, males about 6 m—and is about one-third the size of the North Atlantic right whale (*Eubalaena glacialis*). The flippers are small; there is a small **falcate** (curved toward the tail) dorsal fin two-thirds of the way back on the body. There are about 213–230 baleen plates per side. Like the closely related right whales, the pygmy right whale has a highly arched rostrum, with long, narrow baleen. They do not have the head callosities found on right whales, however. Large groups of >100 individuals form far offshore (Kemper 2014). Bisconti (2012) described the oldest unequivocal fossil pygmy right whale, *Miocaperea pulchra*, from late Miocene deposits of Peru. This area is now 2,000 km north of the current known range of *C. marginata*. Kemper (2014) provided a detailed review of the pygmy right whale.

Balaenidae

There are two genera and four species in this family (Churchill et al. 2012; Burgin et al. 2018). The bowhead whale (*Balaena mysticetes*), occasionally called the Greenland right whale, inhabits northern polar waters throughout the year, where its movements and habitat use are associated with seasonal changes in sea ice (Ferguson et al. 2010; Curry and Brownell 2014). Bowhead whales are often solitary. The North Atlantic right whale (or black whale) is found in subpolar, temperate, and subtropical waters of the Northern Hemisphere. Formerly included

within *E. glacialis*, the North Pacific right whale (*E. japonica*) is now considered a distinct species (Gaines et al. 2005; Curry and Brownell 2014). Warm Gulf Stream waters may represent a thermal limit in the distribution of *E. glacialis* (Keller et al. 2006). The southern right whale (*Eubalaena australis*) occurs in temperate and Antarctic waters.

Balaenids are characterized by their stocky body shape; large head (up to one-third of the total length); a narrow, highly arched rostrum and jaw line that accommodates very long, narrow baleen plates; a massive lower lip; lack of throat grooves; and no dorsal fin. Abundant **excrescences**, or **callosities**, occur on the head of *Eubalaena* (Figure 20.22), but not on bowhead whales. These are rough, horny, white or yellow patches that are covered with barnacles and "whale lice" (small amphipod crustaceans). Three species of whale lice (Genus *Cyamus*) are known to occur on right whales. The largest excrescence, termed the "bonnet," is situated just anterior to the blowholes. The pattern of excrescences is specific to each whale and can be used to identify individuals. Although not known for certain, excrescences may function in aggressive interactions with conspecifics or predators (Reeves and Kenney 2003).

Adult female North Atlantic right whales can mate with multiple males. Given the enormous size of the males' testes—about 1,000 kg—sperm competition may be an important aspect of reproduction in this species (Mate et al. 2005). Gestation is 12 to 13 months, and neonatal right whales are about 4 m long and weigh 800 kg. Postnatal growth of calves is rapid. They double in body length to about 10 m, and weigh about 13 tons, when weaned at 1 year of age (Fortune et al. 2012). Throughout the past decade, reproduction in right whales has been dramatically reduced. In some years no calves are seen during aerial surveys. Like all cetaceans, balaenids have diverse, complex communication calls. Root-Gutteridge and coworkers (2018) found North Atlantic right whales increased the number of calls

Figure 20.22 Excrescences and bonnet on the head of a North Atlantic right whale. Variation in the pattern of excrescences can be used to identify individuals.

and their duration with increasing age of individuals. Mc-Cordic and colleagues (2016) used the "upcall" of *E. glacialis* to differentiate age classes and individuals.

Large whales are believed to have long life spans, and different techniques to estimate age are now documenting this. For example, Rosa and coworkers (2013) used aspartic acid racemization (AAR) to estimate age of 42 bowhead whales. The oldest male was >100 years, the oldest female was 88. George and colleagues (2011) also estimated age in 117 bowhead whales using corpora counts, baleen, and AAR. Their oldest individual was estimated to be 133 years. As noted, mysticetes feed by either skimming or gulping (lunge feeding); balaenids are highly specialized for skimming plankton at or just below the surface. The highly arched rostrum and 250 to 350 plates of baleen facilitate skimming. Baleen is up to 5.2 m long in bowhead whales, the longest of any mysticete (see Figure 20.10). Skimming is also aided by the anterior separation of the baleen plates on each side of the jaw, which allows water to flow more easily into the open mouth (Simon et al. 2009; Figure 20.23—also see Figure 20.11). This feeding behavior also explains why throat grooves—found in the rorquals (Family Balaenopteridae), which also feed by gulping—do not occur in balaenids.

Balaenids were the "right" whales to hunt because they were slow moving and found close to land. They had a great amount of blubber (and thus oil), meat, and baleen and therefore were economically valuable. Because of their high oil content, they also have a tendency to float longer than other species after being killed. Bowhead and right whales were the first to be overexploited and dramatically reduced, and populations do not appear to be recovering, possibly because of the combined effects of predation by killer whales, hunting, net entanglement, tourism, loss of habitat, or **inbreeding depression** (Finley 2001; Fujiwara and Caswell 2001; Knowlton et al. 2012). North Pacific and

North Atlantic right whales remain endangered (IUCN 2018). Balaenids are well represented in the fossil record. The oldest is *Morenocetus parvus* from the early Miocene.

ODONTOCETES

Toothed whales are generally smaller than baleen whales. Unlike male baleen whales, male toothed whales are usually larger than females. The forehead houses a complex system of nasal sacs and a fatty melon, both of which function in echolocation. Echolocation was an integral part of the evolution of odontocetes and developed very early in archaic toothed whales. As noted, all toothed whales have an asymmetrical skull, which also functions in echolocation. Bones on the right side of the skull are larger than on the left; their single external nare is often left of the centerline. In all other respects, odontocetes exhibit bilateral symmetry. Odontocetes echolocate to find food and to orient within their environment. Ten families are currently recognized, although the Yangtze River dolphin (*Lipotes vexillifer*, the only member of Family Lipotidae) was last seen in 2002 and is likely extinct (see Lipotidae below).

Monodontidae

The 2 species in this family—the white whale or beluga (*Delphinapterus leucas*) and the narwhal (*Monodon monoceros*)—occur in polar waters along the coasts during summers and pack ice in winter. Narwhals generally inhabit deeper waters than belugas. Both have somewhat robust bodies, rounded heads, and no dorsal fin (Figure 20.24A, B). Belugas, generally found in shallow waters, are 3 to 5 m in length and weigh up to 1,600 kg. Calves are gray at birth and become progressively paler as they mature; adults are white. Calves of both species may nurse for up to 2 years. The total numbers of teeth range from 14 to 44. Narwhals are similar in size to belugas and are mottled grayish black dorsally and paler on the ventral surface. Males reach sexual maturity at about 9 years of age, females at 6 to 7 years (Garde et al. 2007), and the species appears to be very long-lived.

Dentition consists of one pair of upper teeth. The genus name of the narwhal means "one tooth" and the species name means "one horn." Tusks are the basis of the myth of unicorn horns (see box). In male narwhals, the left upper tooth develops into a long tusk (up to 3 m long and 10 kg) with a counterclockwise spiral (Figures 20.24C and 20.25). The right tooth does not usually erupt. In females, neither of these teeth usually erupts. Nweeia and colleagues (2012) examined 131 narwhal skulls and concluded that the tusk is best characterized as a canine. It has been hypothesized that the tusk is used to spear prey items, deter predators, focus echolocation signals, punch breathing holes through ice, or determine water tempera-

Figure 20.23 Feeding by skimming. In this anterior view of a right whale feeding by skimming, the separation of the baleen plates in the front of the mouth is evident, as are the large tongue and lower lips. Note the excrescences. *Adapted from Katona et al. (1993).*
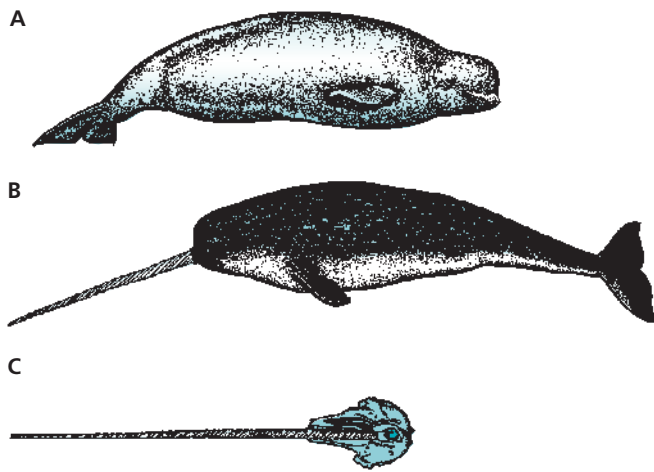
Figure 20.24 **Monodontids.** (**A**) Beluga and (**B**) narwhal whales and (**C**) the spiral tusk of the narwhal. The dorsal portion of the cranium has been removed to show the root of the large, spiral left tusk of males and the typically unerupted right tusk. *Adapted from Flower and Lydekker (1891).*

ture and salinity. Most authorities agree, however, that the tusks function as weapons for establishing dominance hierarchies among males during the breeding season (Hay and Mansfield 1989). They do not spear each other, but spar with tusks crossed at the base. Both species are gregarious, and aggregations of over 1,000 individuals may form, although groups of 10 to 15 are more common (Jefferson et al. 1993; Richard 2014). Like other social species, narwhals are highly vocal. They communicate with whistles and pulsed calls that may be specific to groups and individuals (Marcoux et al. 2012); Blackwell and coworkers (2018) described the patterns of clicks, buzzes, whistles, and trumpet-like calls of narwhals off east Greenland. Garland and colleagues (2015) classified vocalizations of belugas in the Beaufort Sea into 34 different call types. Belugas feed at or near the bottom on a variety of fishes, small squid, and mollusks. Unlike belugas, narwhals are suction feeders, opening the lower jaw to draw in water and prey. At the bottom of a dive, they turn over so the melon, used in echolocation, is pointed downward (Richard 2014). Depth and duration of diving in belugas, as well as movement behavior, varies seasonally and regionally (Barber et al. 2001; A. R. Martin et al. 2001). Belugas in the Beaufort Sea feed primarily on Arctic cod (*Boreogadus saida*) with maximum dive depths of >900 m (Hauser et al. 2015). Movement patterns of narwhals appear to be influenced by the dynamics and condition of sea ice (Laidre et al. 2004; Laidre and Heide-Jorgensen 2005), as well as the presence of killer whales (Breed et al. 2017). Colbeck and colleagues (2013) found that migrating groups of belugas around Hudson Bay were related, with primarily adult females maintaining social structure. As in other odontocetes, weaning age in belugas is highly variable, ranging from 1 to 3 years (Matthews and Ferguson 2015).

Figure 20.25 **Narwhal tusk.** Note the left (counterclockwise) spiral of this left canine tooth.

Inuits take both species for food; chewing narwhal skin is an excellent source of vitamin D. Three genera of fossil monodontids are recognized; the earliest (*Denebola*), dates from the late Miocene. Extinct species occupied temperate waters as far south as Baja California, unlike the two living species. Richard (2014) comprehensively reviewed the monodontids.

Narwhals Tusks and Unicorn Horns

Numerous mythic creatures populate the early folklore of all cultures. Sea monsters, dragons, or mermaids were how early people dealt with unknowns in the world. As early as 390 BCE, for example, ancient Greek naturalists such as Ctesias, Aristotle, and Strabo were writing on the natural history and characteristics of what they regarded as a rare, mystical, and powerful animal—the unicorn. Although details such as the color of the head vary, early writers usually described unicorns as bearded horses with cloven hooves, a lion-like tail, and a single, spiraled horn from the center of its head. When spiraled, spear-like "horns" actually began to appear in ancient European marketplaces, this was taken as further proof of the existence of unicorns. That an actual unicorn had never been captured (despite the fact many people had reported seeing them) was attributed to the fact that the animals were too fast, elusive, and acrobatic to ever be closely approached. What people considered "unicorn horns" were actually the tusks of narwhals, imported from Arctic regions by Vikings who hunted the animals as well as traded for the tusks. From these, the myth of unicorns blossomed. People from throughout most of the ancient world not only believed in their existence, but also considered unicorns to be magical and their horns to have tremendous medicinal powers, including as a cure for poison. Many illnesses were treated with powdered "unicorn horn," including plague and rabies. Regardless of the fact that patients receiving such treatments failed to recover—including Martin Luther in 1546—tusks were so prized that they were worth ten times their weight in gold.

Throughout the Middle Ages, belief in the magical and curative properties of unicorns persisted, and the "horns" remained extremely valuable. Unicorns were fashionable and figured prominently in art, tapestries, and literature. Early scholars translating the Old Testament from Hebrew into Greek believed the Hebrew word *re'em* meant "unicorn." There are nine references to them in the 1611 edition of the King James Bible, including Numbers 23:22, "God brought them out of Egypt; he hath as it were the strength of a unicorn," and Job 39:9, "Will the unicorn be willing to serve thee, or abide by thy crib?" In the Middle Ages, naturalists such as Conrad Gesner in his *Historiae Animalium*, described unicorns among the animals in the world. Despite the widespread belief in their existence, a few scholars and physicians argued against the use of unicorn "horns" as nothing more than superstition. For example, the pioneering French surgeon Ambroise Paré, one of the fathers of surgical technique and treatment of battlefield wounds, considered the use of powdered unicorn horn "useless." In 1638, the Danish zoologist and physician Ole Wurm showed that mystical "unicorn horns" were nothing other than narwhal tusks. Like other naysayers, however, Paré and Wurm were ignored. It took another 200 years for the legend of unicorns and the magical curative properties of their "horns" to eventually die out.

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Phocoenidae

Porpoises formerly were considered a subfamily within the dolphin Family Delphinidae. Unlike dolphins, which generally have a beak, the 3 genera and 7 species of porpoises have no distinct beak. Whereas porpoises were traditionally considered a sister group to delphinids, molecular analyses (Geisler et al. 2011) group them with the monodontids (see Figure 20.1). The total numbers of teeth range from 60 to 120 and are blunt with flattened crowns, in contrast to the sharply pointed, conical teeth in dolphins. Phocoenids generally are small and stocky, ranging in total length from 1.5 m in the California harbor porpoise, or vaquita (*Phocoena sinus*; Figure 20.26), to about 2.2 m in Dall's porpoise (*Phocoenoides dalli*). Most species have a short, triangular dorsal fin. Ginter and coworkers (2011) investigated the anatomy and morphology of small tubercles on the anterior edge of the dorsal fins of harbor porpoises (*Phocoena phocoena*). Although tubercles are likely to be important in hydrodynamics, their exact function is unknown. As their name suggests, the 2 species of finless porpoises (Wang et al. 2008, 2010; Jefferson and Wang 2011)—the Indo-Pacific finless porpoise (*Neophocaena phocaenoides*; Figure 20.27) and the narrow-ridged finless porpoise (*N. asiaeorientalis*)—lack the dorsal fin found in other phocoenids. Instead, there is a distinct narrow ridge. Lin and colleagues (2017) determined that the 2 species diverged about 13 mya. Porpoises are distributed in Northern Hemisphere oceans and seas, including the Black Sea, and in Asian rivers. In the Southern Hemisphere, they occur in shallow coastal waters of South America and around several island groups. The 2 species of finless porpoises and the 4 species in the Genus *Phocoena* are found close to shore in bays and estuaries. Dall's porpoise occurs in deeper offshore waters; for short distances, it can attain speeds of 55 km/h—the fastest of any cetacean (Jefferson 2014). The spectacled porpoise (*Phocaena dioptrica*) is found in both inland and offshore waters of the Southern Hemisphere.

Stomach analyses of 122 *Neophocaena* from the East China Sea found 33 prey species, primarily teleosts, with variation due to gender and age (Chen et al. 2017). Stomach contents of 339 harbor porpoises from the Baltic Sea, collected over a 32-year period, were 70% Atlantic cod (*Gadus morhua*) and herring (Andreason et al. 2017).

Figure 20.26 **California harbor porpoise, or vaquita.** This species is one of the smallest of any living whale and occurs only in the northern portion of the Gulf of California. With its very restricted range, the vaquita is considered to be critically endangered.
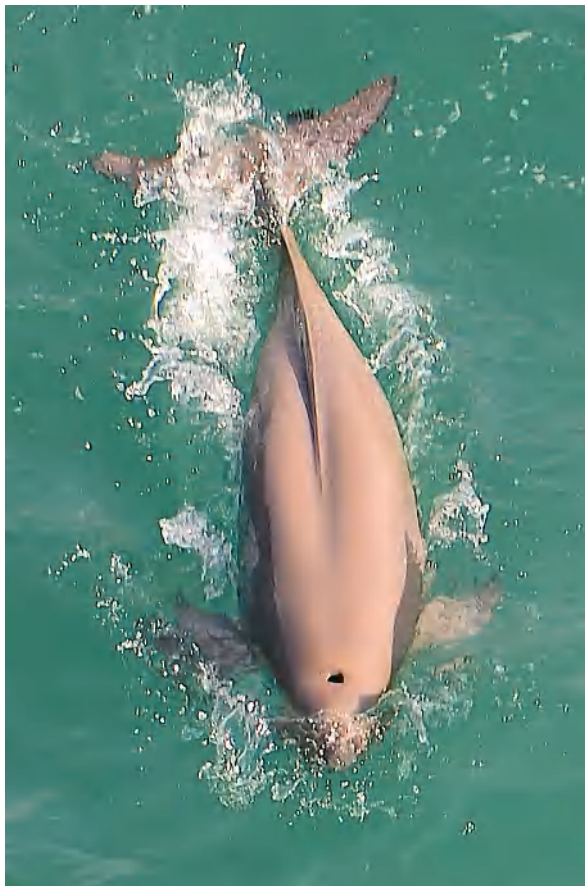
Figure 20.27 **Indo-Pacific finless porpoise.** This very small porpoise inhabits shallow coastal areas and estuaries from the Persian Gulf to East China, Indonesia, and other areas of the East Indies.

Dall's porpoises, like certain dolphins, are killed accidentally in fishing nets. They also are harvested in Japanese fisheries. Other species, including the harbor porpoise, are taken for food. The vaquita (see Figure 20.26) is geographically limited to the northern portion of the Gulf

of California, the most restricted range of any cetacean, and is critically endangered. As of 2017, the total population was about 30 individuals. The narrow-ridged finless porpoise is endangered (IUCN 2018). Demographic models by Mei and colleagues (2012) predict extinction within 100 years if current trends continue. The fossil record of phocoenids dates to the late Miocene with 13 genera currently recognized (Berta 2017). Jefferson (2014) reviewed the family.

Delphinidae

The 17 genera and approximately 38 to 40 species of dolphins are the most diverse family of cetaceans and include about 40% of extant whales. They are distributed practically worldwide in all but polar waters. Delphinids had a pronounced adaptive radiation during the Pliocene-Pleistocene (do Amaral et al. 2018), and discerning phylogenetic relationships among species has been difficult (McGowen 2011; Vilstrup et al. 2011). Molecular genetic work continues (see Jefferson and Rosenbaum 2014; Cunha et al. 2015), and new species will likely be designated. For example, the three distinct "ecotypes" of killer whales currently recognized might deserve separate species designations. Delphinids range in size from Heaviside's and Hector's dolphins (<2 m long and 40 kg) to the killer whale (9 m long and 7,000 kg). Most have a rostrum that forms a beak and a falcate dorsal fin in the middle of the back. Fins vary in size and shape among species; they reach 2 m tall in adult killer whales. Delphinids also vary in color from uniform gray or black to stripes, spots, or bands to the contrasting black-and-white patterns of the killer whale. Many morphological differences in this family are related to feeding. The total number of teeth varies among species (Figure 20.28), from 2 to 7 pairs in Risso's dolphin (*Grampus griseus*) to over 120 pairs in the spinner dolphin (*Stenella longirostris*). Feeding habits of delphinids vary in terms of the size of prey species taken, distance from shore, diving depth, and dietary niche width (Wang et al. 2012). Most dolphins, however, dive for short periods to depths <200 m. Delphinids generally take small fishes and squid. Prey of the bottlenose dolphin (*Tursiops truncatus*; Figure 20.29) is highly variable; coastal and offshore dolphins take different prey (Reeves and Read 2003). Killer whales feed on fishes, seals, marine mammals, other cetaceans, birds, and even sharks. Benoit-Bird and Au (2009) found that spinner dolphins that foraged cooperatively in groups of 16 to 28 accessed more prey than individuals that foraged alone.

Delphinids generally are gregarious and form **pods** (groups or schools) of up to 1,000 individuals, although typical group sizes are much smaller (see Evans 1987, his table 7.2). Species found closer to shore generally form smaller groups. Shark predation on bottlenose dolphins may have been a factor in the evolution of group formation, habitat use, and sociality (Heithaus 2001a, 2001b). Noren
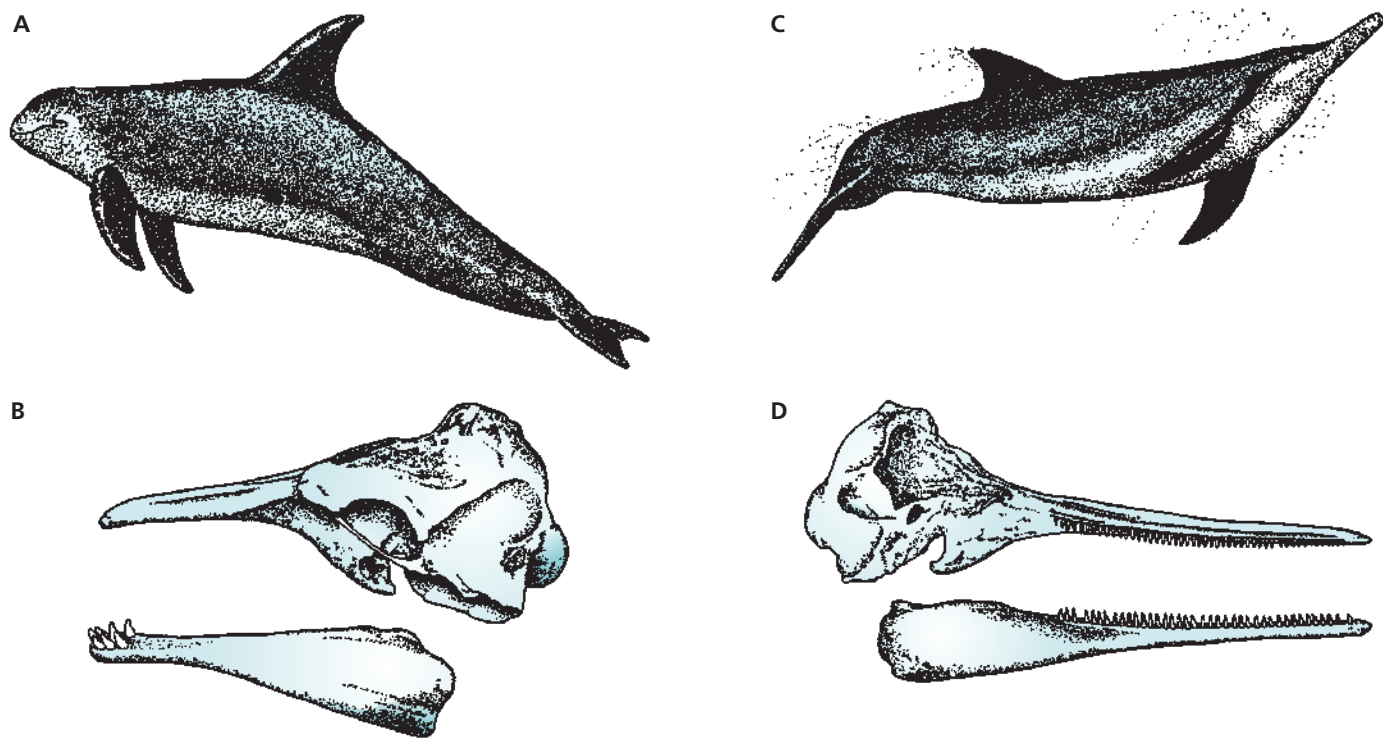
Figure 20.28 Variation in dolphin tooth number. (**A**) Risso's dolphin, or grampus (*Grampus griseus*), has (**B**) from 2 to 7 pairs of teeth, whereas (**C**) the spinner dolphin (*Stenella longirostris*) can have (**D**) a total of over 120 pairs of teeth. Note the lack of an external beak in Risso's dolphin. *Adapted from Jefferson et al. (1993).*

Figure 20.29 Bottlenose dolphin. This common dolphin is one of the best known whales, and is the cetacean most often seen in zoos and aquaria.

and colleagues (2011) determined that pregnant bottlenose dolphins were at increased risk of predation due to increased hydrodynamic drag, which lowered swimming speed. Estimated fertility rates of bottlenose dolphins in the northwest Mediterranean Sea was 29% to 41% of adult females, with a calving interval of 2.5 to 3.5 years (Rossi et al. 2017).

Spinner dolphins and pantropical spotted dolphins (*Stenella attenuata*) are the species most often captured and drowned in purse-seine nets set for tuna. Special fishing techniques have been developed in attempts to minimize losses of dolphins (Evans 1987; Berta et al. 2015). Other species of dolphins are taken for food in various parts of the world. Most species are insufficiently known to determine their conservation status, although Hector's dolphin, the Irrawaddy dolphin (*Orcaella brevirostris*), and the Indian Ocean humpback dolphin (*Sousa plumbea*) are endangered. The Atlantic humpbacked dolphin (*S. teuszii*) is critically endangered (IUCN 2018). The oldest known delphinid, *Eodelphinus kabatensis*, is from the late Miocene. Wang and colleagues (2014) thoroughly reviewed the family.

Iniidae

The taxonomic relationships of river dolphins have always been problematic; 4 families are now recognized—Iniidae, Lipotidae, Pontoporiidae, and Platanistidae (Burgin et al. 2018; IUCN 2018). They all share several morphological characteristics including a long rostrum and very small eyes. Formerly they were all included within the Family Platanistidae. The iniids now include a single genus and species recognized by the IUCN. The South American

river dolphin, or boto (*Inia geoffrensis*), occurs in the Orinoco and Amazon River basins throughout northern South America—an area of about 7 million km²—where it inhabits only fresh water. Two other taxa considered subspecies by the IUCN inhabit different river basins and are considered distinct species by other authorities (see da Silva and Martin 2014) based on molecular data: the Bolivian river dolphin or bufeo (*I. boliviensis*) occurs in the Bolivian Amazon basin, and the Araguaia River dolphin (*I. araguaiaensis*) in the Araguaia and Tocantins rivers of east-central Brazil (Hrbek et al. 2014). Iniids have the usual long rostrum and pointed front teeth, but have molariform posterior teeth for crushing fish (da Silva and Martin 2014; Berta 2017).

Also called the "pink river dolphin," the boto echolocates in an acoustically difficult environment because of shallow, turbid water and dense vegetation—not experienced by other toothed whales. Thus, amplitude, frequency and other echolocation parameters differ from those of similar-sized marine species (Ding et al. 2001; Ladegaard et al. 2015, 2017; Amorim et al. 2016). The boto is active day and night, foraging on a diverse array of fishes. It is the largest river dolphin. Adult males can reach 185 kg body weight and are significantly larger than females (maximum 150 kg), suggesting intense competition between males related to mating opportunities (Martin and daSilva 2006). Competition is further suggested by the great amount of scarring on the body and flukes of males caused by fighting with other males. Breeding in *Inia geoffrensis* takes place throughout the year, with gestation of 12–13 months. Neonates average 84 cm in length and are about 12 kg (Da Silva and Martin 2014; Martin and da Silva 2018). In some areas, the boto is illegally harvested for use as bait in the fishing industry (Mintzer et al. 2013). Fossil iniids are fairly diverse and date to the late Miocene.

Lipotidae

The Chinese river dolphin, or baiji (*Lipotes vexillifer*), is (or was) restricted to the Yangtze River system. Only a few dozen individuals were believed to be alive in the late 1990s (Zhou 2002). The last confirmed sighting was in 2002. The baiji most likely is extinct and is listed as such by the IUCN (2018). They had a long, narrow, upturned rostrum, triangular dorsal fin, and very small eyes. Maximum female body length (2.5 m) was slightly greater than that of males (2.3 m). Common group size was 3–4 individuals, and they fed on a variety of fishes. Overharvest, collision with vessels, dam construction, and industrial pollution doomed the species, although occasional unconfirmed sightings occur. As noted by Smith (2014:380), the Chinese river dolphin is the first cetacean to go extinct because of humans and "represents the loss of 20 million years of evolutionary history." Fossil remains of *Lipotes* remain unconfirmed, but closely related fossil taxa date to the late Miocene.

Pontoporiidae

The La Plata river dolphin, or franciscana (*Pontoporia blainvillei*), occurs in coastal marine waters of Argentina, Uruguay, and southern Brazil. It is one of the smallest river dolphins; mean body length of females is 1.6 m and in males 1.4 m (Botta et al. 2010). Given its small size, the extensive beak is relatively longer than in any other cetacean. Their gray-brown coloration matches the slow, turbid waters it inhabits. Dives are of very short duration, only about 20 seconds. Diet varies geographically as well as individually by season, gender, and age (Denuncio et al. 2017; Henning et al. 2018). Tellechea and colleagues (2017) found that a large percentage of the diet was made up of fishes that emitted sound, especially the striped weakfish (*Cynoscion guatucupa*). Group size can reach 30, but the franciscana is often solitary or in pairs. Cremer and coworkers (2017) recorded 10 types of whistles from franciscanas from southern Brazil. Given reversed sexual dimorphism, low testes weight, and lack of scars from intrasexual fighting, Panebianco and colleagues (2012) concluded that the species has a monogamous mating system. The fossil record is diverse, with 6 described genera, and dates to the Miocene. Fossil pontoporiids have been found from the South Pacific and North Atlantic as well as the current range. Post and colleagues (2017) described a new fossil, *Scaldiporia vandokkumi*, from the late Miocene-early Pliocene of the Netherlands.

Platanistidae

Previously, all river dolphins were included in this family, but molecular studies found that they were not a monophyletic group (Cassens et al. 2000; Hamilton et al. 2001; Nikaido et al. 2001). The family currently consists of a single genus and species—the South Asian river dolphin, or susu (*Platanista gangetica*), also called the "Ganges River dolphin." A second presumptive species, the Indus River dolphin, or bhulan (*P. minor*), is now considered a subspecies of *P. gangetica*. The susu is small, 2 to 3 m long, and is found in estuaries, turbid rivers, and inland lakes in India, Pakistan, and Bangladesh. It is similar to other river dolphins in appearance, with a long rostrum, numerous thin, pointed teeth, and small eyes (Figure 20.30). Their eyes are without lenses, so they are virtually blind. They locate prey, generally small fishes and crustaceans, through echolocation. The susu often swims on its side with a foreflipper touching the bottom. Sinha and coworkers (2010) recorded a mean dive time of 2 minutes, with surface behavior dependent on age of the animal and distance from shore. The susu is endangered and is negatively affected by dam construction, gill nets, decline in water quality, dams, siltation, and decreased prey base because of overfishing (Smith et al. 2001; Braulik et al. 2014; Chowdhury et al. 2016). Fossil records of specimens from two closely related "platanistoid" families date from the Miocene (Berta 2017; Godfrey et al. 2017).

Ziphiidae

This diverse family of 6 genera and 22 extant species of beaked whales—named for their long rostrum—occurs in all oceans. Only the delphinids are more diverse. Beaked whales are slender, with a pronounced beak and small dorsal fin. Total length ranges from about 4 m in the pygmy beaked whale (*Mesoplodon peruvianus*) to 12 m in Baird's beaked whale (*Berardius bairdii*). MacLeod and coworkers (2006) discussed distribution patterns of ziphiids. They are deep divers (up to 3,000 m) that feed on smaller species of squid (Santos et al. 2001a, 2001b; West et al. 2017) and fishes (see Figure 20.6), capturing them through suction (Heyning and Mead 1996). Baumann-Pickering and colleagues (2013) examined the echolocation pulses of 8 spe-

cies of beaked whales. Signals are species-specific, and they suggested there was a relationship between mean frequency and body size, with higher frequency in smaller whales. Blainville's beaked whales (*M. densirostris*) need only about 60 echolocation clicks to select and approach a prey item; they can classify prey at a range of >15 m (Madsen et al. 2013). Foraging dives of this species were much shallower at night than during the day, apparently to avoid predators such as sharks and killer whales (Baird et al. 2008). Shepherd's beaked whale (*Tasmacetus shepherdi*) may have up to 98 teeth, but most ziphiids have only 1 or 2 teeth in each side of the lower jaw. These teeth usually occur only in males and are used primarily for intraspecific fighting. In the Genus *Mesoplodon*—with 15 extant species, it is the most speciose of any genus of cetaceans—the single pair of teeth is quite specialized among species (Figure 20.31), and they are useful for species identification. MacLeod (2000b) suggested that these sexually dimorphic teeth aid in recognition of morphologically similar sympatric species. These male tusks may also function in sexual selection (Dalebout et al. 2008), as might several unusual bony structures found on the face, rostrum, and mandible that could be sensed by echolocation (Gol'din 2014). Like that of river dolphins, the taxonomy of ziphiids remains problematic; their natural history and conservation status are poorly known because they are uncommon, difficult to identify at sea, and spend most of their lives in deep water. Much of what is known about ziphiids comes from stranded individuals. Of 21 species of ziphiids recognized by the IUCN (2018), 19 are considered "data deficient" as far as determining their population trends. There are about 21 genera of fossil ziphiids, which first appeared in the early Miocene (Bianucci et al. 2016); there are more described fossil species than extant species, with many newly described fossils

Figure 20.30 **The South Asian river dolphin, or susu.** (**A**) Lateral view of the skull shows the numerous homodont teeth and the distinctive maxillary crests overhanging the rostrum. There are variable numbers of teeth in the upper and lower jaws. (**B**) The robust body and extremely long rostrum are evident. *Adapted from Jefferson et al. (1993).*
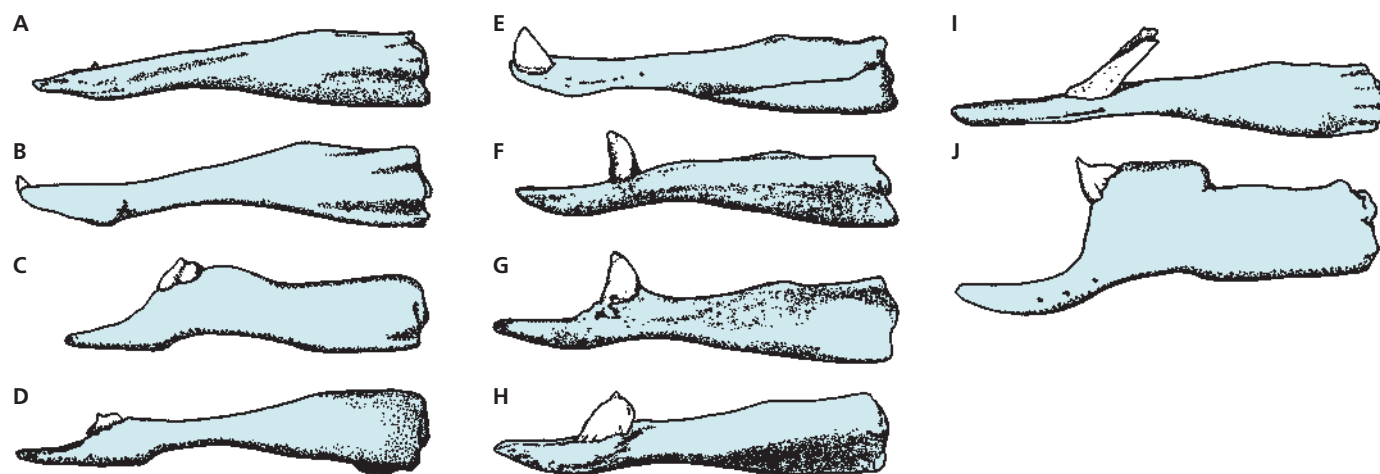
Figure 20.31 **Specialized ziphiid dentition.** Highly specialized and variable dentition occurs in the lower jaws of the ziphiid Genus *Mesoplodon*. Lateral view of the right mandible of (**A**) Gervais's beaked whale, *M. europaeus*; (**B**) True's beaked whale, *M. mirus*; (**C**) ginkgo-toothed beaked whale, *M. ginkgodens*; (**D**) Gray's beaked whale, *M. grayi*; (**E**) Hector's beaked whale, *M. hectori*; (**F**) Stejneger's beaked whale, *M. stejnegeri*; (**G**) Andrew's beaked whale, *M. bowdoini*; (**H**) Hubbs's beaked whale, *M. carlhubbsi*; (**I**) strap-toothed whale, *M. layardii*; and (**J**) Blainville's beaked whale, *M. densirostris. Adapted from Jefferson et al. (1993).*

being reported (cf. Ichishima et al. 2017; Lambert et al. 2018). MacLeod (2014) as well as Ellis and Mead (2017) provided comprehensive reviews of the natural history as well as species accounts of beaked whales.

Kogiidae

This family contains the dwarf sperm whale (*Kogia sima*) and the pygmy sperm whale (*K. breviceps*). Until recently, these species were placed in Family Physeteridae along with the sperm whale; as of 2018, the IUCN still placed them there. Pygmy and dwarf sperm whales reach a maximum length of 3.4 and 2.7 m, respectively (Figure 20.32)—significantly smaller than *Physeter macrocephalus*. They are morphologically similar, sometimes described as looking "shark-like," and difficult to differentiate at sea. Asymmetry of the skulls is exacerbated in dwarf and pygmy whales—the left passage (for breathing) is 7 times larger than the right passage (for echolocation) (McAlpine 2014). Squid predominate in the diets of both species, and there appears to be a high degree of overlap in their foraging niches (Staudinger et al. 2014). Both species are distributed worldwide and can be fairly common in tropical and temperate waters. Pygmy and dwarf sperm whales are rarely seen at sea, however, and are poorly known. They are believed to be solitary and deep diving, and they feed on small squid, fishes, and crustaceans (Caldwell and Caldwell 1989) that are taken through suction. Thornton and colleagues (2015) and Song and coworkers (2015, 2017) investigated echolocation sound formation and propagation in kogiids. Only the bottlenose dolphin is found stranded on beaches more often than pygmy sperm whales (Maldini et al. 2005). Strandings in the Atlantic may be related to exposure to the neurotoxin domoic acid, produced by certain diatoms of the Genus *Pseudonitzschia* (Fire et al. 2009). There are 5 recognized fossil genera; the oldest, *Thalassocetus*, dates from the mid-Miocene. Collareta and coworkers (2017) described a new genus and species of fossil kogiid from the late Miocene—*Koristocetus pescei*—that still preyed by raptorial feeding rather than suction feeding. McAlpine (2014) comprehensively reviewed the kogiids.
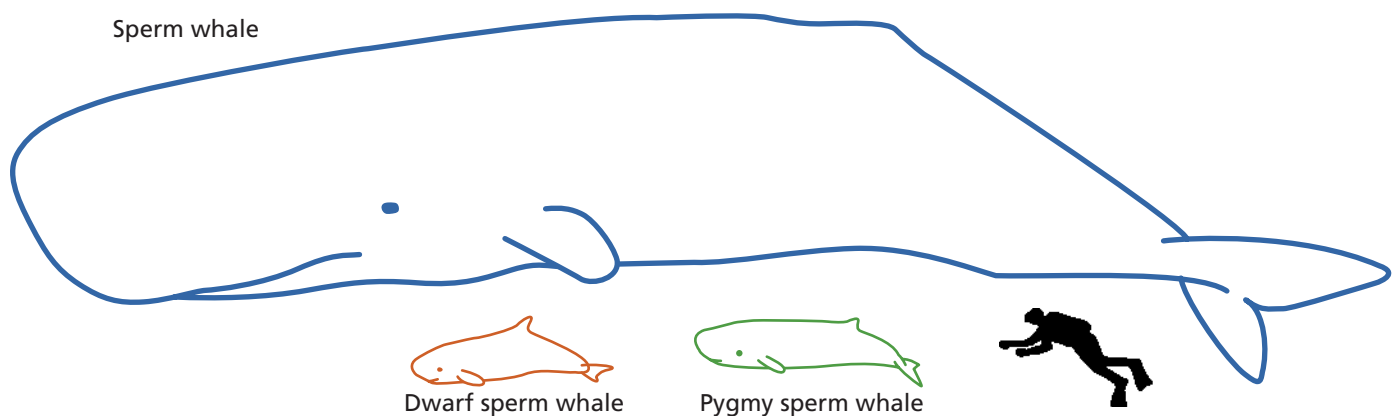
Figure 20.32 **Relative sizes of pygmy and dwarf sperm whales (Family Kogiidae).** Both kogiids are a fraction of the size of the giant sperm whale.

Figure 20.33 **Sperm whale.** Mother with calf. The huge head, small flippers, dorsal hump and crenulations are evident.
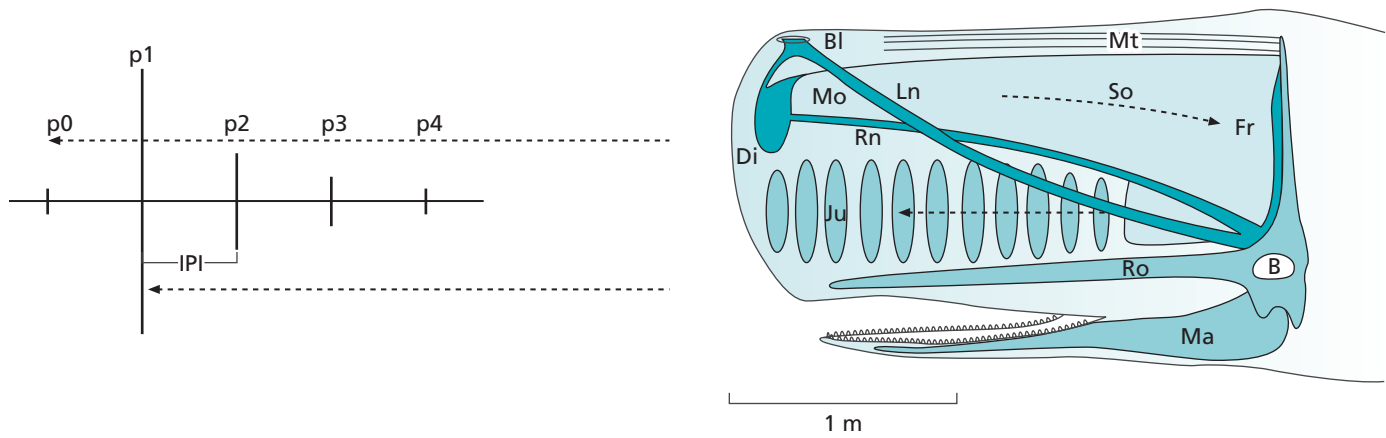
Figure 20.34 **Spermaceti organ of a sperm whale.** *Abbreviations*: B = brain; Bl = blowhole; Di = distal air sac; Fr = frontal air sac; Ju = junk; Ln = left nare; Ma = mandible; Mo = "monkey lips"; Mt = muscle/tendon layer; Rn = right nare; Ro = rostrum; So = spermaceti organ. During a sperm whale echolocation click, a small amount of the energy produced "leaks" out anteriorly (represented by p0). Most of the energy is transmitted posteriorly into the spermaceti organ and bounces off the frontal air sac to be reflected out through the junk as the primary sound pulse p1. Continued reverberations at decreasing amplitude produce pulses p2–p4 at constant intervals, producing the multipulsed clicks. *Adapted from Zimmer et al. (2005).*

Physeteridae

This monotypic family includes only the sperm whale, which occurs in all but polar oceans. Males can reach close to 20 m in total length, the largest of any odontocete, and 70,000 kg; sperm whales are the most sexually dimorphic cetaceans. The large, blunt head constitutes one third of its total length (Figure 20.33). Their flippers are small. Sperm whales have a small dorsal hump and series of posterior crenulations similar to gray whales. The thin mandible, with 18–25 pairs of teeth, is much shorter than the upper jaw, which contains sockets but no teeth.

Sperm whales have a huge, highly distinctive **spermaceti** organ (Figure 20.34), several meters long. It can account for close to 10% of the total mass of an individual (Bonner 1989). The organ is composed mainly of 2 structures, the spermaceti organ, or "case," and the "junk," both of which contain a waxy liquid, the spermaceti. In conjunction with the elaborate and convoluted nasal passages, the spermaceti organ serves as a lens to focus echolocation signals. Wahlberg and colleagues (2005:3404) suggested that "the nasal complex of the sperm whale is nature's largest sound generator." Sperm whales echolocate using "clicks" at 0.5- to 2-second intervals and "creaks," which are very rapid clicks at intervals of 20 milliseconds (Jaquet et al. 2001; Miller et al. 2004). Clicks are emitted during deep foraging dives and are suited for long-range echolocation. Creaks are analogous to the "terminal buzz" of bats and are used when a whale closes in on prey. Repetitive series of clicks, called "codas," are used for communication between individuals (Wahlberg et al. 2005; Zimmer et al. 2005) and appear to be specific to different social groups (Rendall et al. 2012). Sperm whales can reach depths of 3,200 m or more, apparently
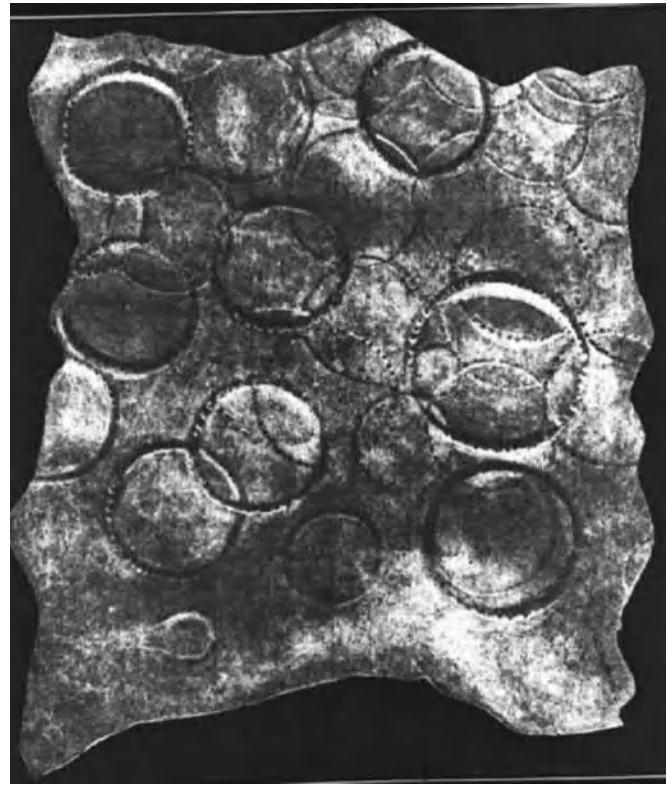
Figure 20.35 **Sperm whale skin.** This piece of skin shows the circular sucker marks from squid taken as prey. *From Murray and Hjort (1912).*

diving straight up and down, and can remain submerged for 2 hours or more (Jefferson et al. 1993). They feed mainly on giant squid (Figure 20.35), as well as smaller species of squid—from 100 g to 400 kg in weight—but also take a variety of fishes. Sperm whales exhibit com-

plex spatial-temporal social behavior and form groups of up to 20 individuals (Christal and Whitehead 2001; Gero et al. 2008) with associated complex vocalizations (Rendell and Whitehead 2005). The evolution of group formation may be partially in response to predation pressure from killer whales (Pitman et al. 2001). In addition to its well-known role in echolocation, the huge head of a sperm whale may also function as a battering ram during male-to-male intraspecific competition (Panagiotopoulou et al. 2016). Genetic analyses using mtDNA found significant differences between sperm whale populations in the Gulf of Mexico, the western North Atlantic, the North Sea, and the Mediterranean Sea. In the Atlantic, males moved among populations for breeding, whereas females exhibited greater site fidelity (Engelhaupt et al. 2009). Young are born after a gestation of 14–16 months; they weigh about 1,000 kg and swim immediately (Mesnick 2014).

Historically and recently, sperm whales have been one of the most important species in the whaling industry because of the vast amounts of spermaceti oil they contain (Reeves and Read 2003). They also are known for ambergris, a brownish, pliable, organic substance produced in the intestinal tract of some individuals. The function of ambergris remains unknown, although it may aid in digestion. Ambergris is extremely valuable as a perfume fixative ("worth its weight in gold"); pieces up to 421 kg have been found (Slijper 1979). Sperm whale hunting has been banned by the IWC since 1981, and they are considered threatened. Anthropogenic impacts occur from habitat loss, oil and gas exploration, and chemical pollution (Farmer et al. 2018). Physeterids have a very diverse fossil record dating to the early Miocene (Lambert et al. 2016; Berta 2017) and are generally recognized as the most basal odotocetes. Mesnick (2014) provided a comprehensive review of the family.

SUMMARY

- No longer considered an order, cetaceans are now an infraorder within the Order Cetartiodactyla.

- There are two parvorders—Mysticeti (baleen whales) and Odontoceti (toothed whales)—with several differences between them.
  - Baleen whales have baleen plates that hang from the upper jaw in place of teeth.
  - Baleen is used as a filter to strain small marine organisms (krill) from the water.
  - With 14 species, mysticetes account for only 15% of extant whales.
  - They are the largest whales and have sacrificed speed and agility for increased body size.
  - Toothed whales generally are smaller and more agile than baleen whales.
  - They feed on fishes, squid, and larger prey items rather than on krill.
  - Odontocetes have asymmetrical skulls, a single external nare, complex systems of nasal sacs, and large, bulbous foreheads with oil-filled melons.
  - These structural features relate to the ability of toothed whales to echolocate.

- Whales evolved from early terrestrial ungulates.
  - Cetaceans are the sister group to Family Hippopotamidae.
  - They made a gradual transition from land to sea during the Eocene epoch.
  - Intermediate stages during this transition are evident in several extinct lineages.
  - Both mysticetes and odontocetes were distinct lineages by the early Oligocene.

- Whales can be as large as they are because water provides a buoyant, supportive environment.
  - All whales have a streamlined, fusiform body.
  - There are no external ears, external hind limbs, or fur to disrupt the smooth flow of water over the body as a whale moves.
  - Forelimbs have been modified into paddle-like flippers.
  - A horizontally flattened tail fluke provides propulsion.
  - The skull is modified by "telescoping," with resultant movement of the external nares to the top of the head.
  - In place of fur, insulation is provided by a layer of subcutaneous fat—the blubber.

- Whales have several physiological adaptations for diving.
  - They have a high hematocrit and more myoglobin and use oxygen more efficiently than terrestrial mammals.
  - While submerged, they undergo bradycardia and reduced blood flow to peripheral areas of the body ("diving response").

- Whales have been hunted for thousands of years for their meat, oil, and other valuable products.
  - Most species have experienced significant population declines because of overharvesting.
  - The International Whaling Commission (IWC) was formed in 1946 to help conserve stocks of many species.
  - Through the efforts of the IWC, governments, and many conservation agencies, most nations no longer harvest whales; unfortunately, Japan continues to harvest many of the smaller species.
  - Populations of some species have begun to recover, but many others have not.

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DISCUSSION QUESTIONS

1. In contrast to whales, the seals and walrus (pinnipeds), which spend the majority of their lives in water, are heavily furred. What life-history aspects make retention of fur adaptive in pinnipeds but not in whales?

2. Sexual dimorphism is evident in whales. Why might females be larger than males in baleen whales, whereas the opposite situation occurs in toothed whales?

3. There are several ways that whales maintain their body heat in cold polar waters. Consider the other extreme: How do they dissipate heat while in tropical waters?

4. Despite conservation programs, many species of large whales have not recovered their former numbers. What negative factors that harm future recovery of whales are present in oceans today?

Order: Chiroptera

Bats are second only to rodents in the number of recognized species in the order. Currently, there are 21 recognized extant families of bats, encompassing almost 230 genera and close to 1,400 species (Burgin et al. 2018). They are a fascinating group of mammals for both the general public and professional mammalogists. In terms of feeding, reproduction, behavior, and morphology, including structural adaptations for true flight, bats show a great degree of specialization. They also exhibit an impressive range in body size, from the tiny hog-nosed bat (*Craseonycteris thonglongyai*) in Thailand, which weighs about 2 g, to fruit bats such as the large flying fox (*Pteropus vampyrus*) that weigh up to 1,200 g (Figure 21.1). Most bats, however, are relatively small, weighing from 10 to 100 g. This chapter examines the structural and functional adaptations of bats, as well as their evolutionary history and the relationships among families.

Flight and echolocation have allowed bats to be widely distributed and fill many feeding niches. Most species are insectivorous, often taking insects in flight or gleaning them from foliage. Others are carnivorous, taking small vertebrates, such as frogs, mice, and occasionally other bats. A few species (especially in Family Noctilionidae) are piscivorous—they feed on small fish. Many species of bats are nectivorous, consuming pollen and nectar from flowers (with which they have often coevolved; see Muchhala and Thomson 2009), and the fruit bats are frugivorous. Finally, the three species of vampire bats are sanguinivorous, feeding only on blood. Different feeding adaptations may occur within a given family. For example, all these feeding modes are seen among species of New World leaf-nosed bats in Family Phyllostomidae. These different feeding habits and foraging styles among bat species result in a greater variety of head shapes, dentition, and facial features than occurs in other mammalian orders.

Variation is also evident in the reproductive patterns of bats. Many species breed in the spring and exhibit the typical pattern of spontaneous ovulation (see Chapter 9). Others, however, such as some of the common bats (Family Vespertilionidae) and horseshoe bats (Family Rhinolophidae) in northern areas, exhibit **delayed fertilization**, in which mating occurs in the fall prior to migration or hibernation.

tation and rock fissures, and in various other protected places. Some species roost alone, whereas others form aggregations that can range from small (a few individuals) to very large (millions). The roosting habits of bats are adaptations that reflect the interrelationships of social structure, diet, flight behavior, predation risks, and reproduction of each species (Kunz 1982). Most species are strictly nocturnal (Speakman 1995), although diurnal activity is common in species of island-dwelling Old World fruit bats (Family Pteropodidae) and a few species in other families.

Whereas small mammals usually have several large litters per breeding season, bats are unusual in their limited reproductive potential. Although there are exceptions (usually in tropical species), bats most often produce a single litter per year, with only 1 or 2 young per litter. Thus, declining bat populations are slow to rebound. Neonates typically weigh 20% to 30% of the maternal body mass (Kurta and Kunz 1987). Hayssen and Kunz (1996) examined the relationship between litter mass and several maternal morphological characteristics in over 400 species of bats from 16 families. They found different relationships in pteropodids from those occurring in other bats, suggesting different selection pressures on reproductive traits. Bats also have much longer life spans than is typical for small mammals, sometimes exceeding 30 years. In some species, prolonged life spans may be a function of reduced metabolic rate both daily (torpor during the day) and seasonally (hibernation in winter).

Bats are important in community structure and because of the role they fill as the major consumer of night-flying insects and as pollinators of plants. Bats also are significant vectors of some serious human diseases (see Chapter 27). Despite their ability to adapt to various environments, bat populations are often negatively affected by environmental perturbations, both natural and human-induced. As a result, many species throughout the world are in danger of extinction through loss of cave and riparian (riverbank) habitats, exposure to pesticides, disease, and human exploitation.

Figure 21.1 **Large flying fox (*Pteropus vampyrus*).** This is the largest bat in the world. Throughout its broad range in Southeast Asia, it is a major plant pollinator and seed disperser. Note the large eyes and fox-like face.

Sperm is stored in the uterine tract, and ovulation and subsequent fertilization occur in spring. Birth coincides with the emergence of insect prey. Other reproductive variations occur in different species of bats, including delayed implantation and delayed development (Racey 1982; Kunz and Pierson 1994). Mating systems that occur in various families of bats were placed in the following three general categories by McCracken and Wilkinson (2000): (1) single male/multifemale groups, (2) multimale/multifemale groups, and (3) single male/single female monogamous groups. Ecological factors that affect these patterns include either male defense of females or male defense of the resources that females depend on.

Bats roost in many different places: in caves and hollow trees, under loose bark, in buildings, in understory vege-

Suborders and Superfamilies

Smith (1980) reviewed early attempts at the classification of bats. Historically, bats were divided into two suborders based on morphological and paleontological data: the Megachiroptera, which included only the Old World family of fruit bats (Pteropodidae), and the Microchiroptera, which encompassed all the other families. Given the names of these former suborders, size was one of the obvious differences between the two groups (Hutcheon and Garland 2004). There are several other morphological differences between pteropodids, which do not echolocate, and all the remaining families, which do echolocate (Table 21.1). Although the terms "megachiroptera" and "microchiroptera" continue to have descriptive value, recent phylogenies based

Table 21.1 Major differences between the Old World fruit bats (Family Pteropodidae) and the other 20 families of bats*

Family Pteropodidae	All Other Families of Bats
No echolocation, except in Genus *Rousettus*; primarily frugivores or nectivores	Echolocation for foraging and maneuvering; primarily insectivores
No tragus; continuous inner ear margin	Tragus often well developed
No nose or facial ornamentation	Nose or facial ornamentation often evident
Claw evident on second digit except in Genera *Dobsonia*, *Eonycteris*, *Notopteris*, and *Neopterx*; second finger independent	No claw on second digit; second finger closely associated with third
Cervical vertebrae not modified; head held ventrally when roosting	Cervical vertebrae modified; head is flexed dorsally from main axis of body when roosting
Tail and uropatagium usually absent	Tail and uropatagium often evident
Generally large body size; eyes usually large	Generally small body size; eyes generally small
Angular process of mandible absent, or broad and low if present	Mandible with well-developed, long, narrow, angular process
Postorbital process well developed	Postorbital process usually absent
Palate extends beyond last upper molars	

*Koopman (1984) and Simmons (1995) discuss additional differences.

on large molecular data sets, both nuclear and mitochondrial, result in the 2 Suborders Yinpterochiroptera and Yangochiroptera and 5 superfamilies (Figure 21.2) currently recognized (Amador et al. 2018). The Yinpterochiroptera include the pteropodids—Old World fruit bats that do not echolocate—and the 6 families of echolocating bats in the Superfamily Rhinolophoidea. The Suborder Yangochiroptera encompasses 14 families of echolocating bats grouped in 3 superfamilies: Emballonuroidea, Noctilionoidea, and Vespertilionoidea. Teeling and colleagues (2012) provided a concise review of past controversies surrounding morphological versus molecular-based phylogenies of bats.

Morphology

Bats are the only mammals that fly; consequently, many of their unique morphological features relate to flight. The ordinal name "Chiroptera," derived from the Greek *cheir* (hand) and *pteron* (wing), refers to the modification of the bones of the hand into a wing, the primary adaptation for flight in bats (Figure 21.3). The wing is formed from skin stretched between the arm, wrist, and finger bones. Several different muscle groups are used to keep the skin taut over the wings. Although the skin on the wings is very thin and appears delicate, it is fairly resistant to tears or punctures. The primary modification of the forelimb (wing) is its elongation, especially the forearm (radius and ulna), metacarpals, and fingers. The radius is greatly enlarged in bats—sometimes being twice as long as the humerus—and the ulna is very much reduced. Because of the demands of flight, movement is restricted to a single plane in the wrist, elbow, and knee joints of bats. The radius cannot rotate (as it does in humans), and the wrist (**carpal** bones) moves only forward and backward (flexion and extension). Thus, the wing gains strength and rigidity to withstand air pressures associated with flight. Wing membranes usually attach along the sides of the body in bats, although there are exceptions, as in Family Mormoopidae.

The pectoral area is also highly developed and modified and contributes to a bat's ability to fly. The last cervical and first two thoracic vertebrae are often fused. Along with a T-shaped **manubrium** (the anterior portion of the sternum, or breast bone), the first two ribs form a strong, rigid pectoral "ring" to anchor the wings. In conjunction with the pectoral ring, the articulating **scapula** (shoulder blade) and proximal end of the humerus are highly modified for flight. Besides their primary function in flight, wings also aid bats in thermoregulation. The thin, vascularized wing membranes dissipate excess body heat generated during flight. Additional aspects of the wings will be considered when we examine the mechanics of how bats fly.

In many species, the **uropatagium** or interfemoral membrane (between the hind limbs; see Figure 21.3) encloses the tail and also aids bats in flying. Although not necessary for flight (some species have no uropatagium), this
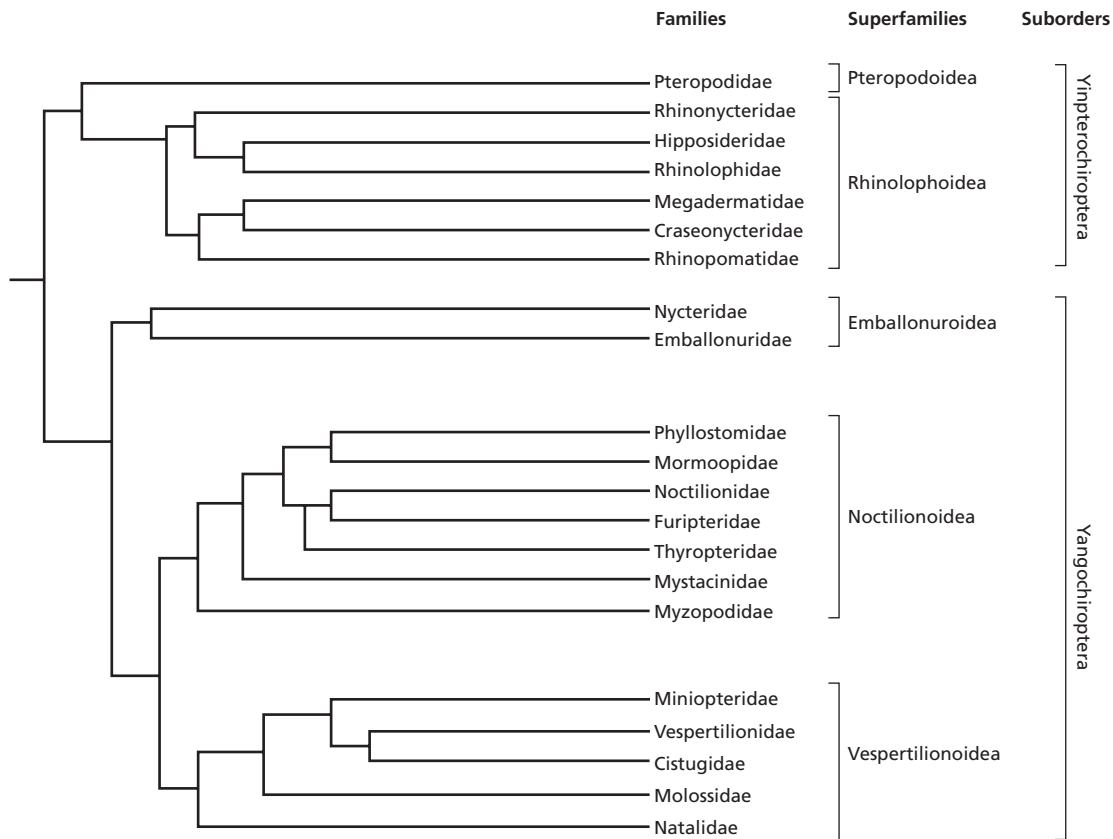
Figure 21.2 A molecular phylogeny of bats. Relationships of chiropteran families based on molecular data. Phylogenies based on morphological characters differ substantially. *Combined and modified from Simmons (2005) and Teeling et al. (2012). See Eick et al. (2005) for an alternate arrangement.*
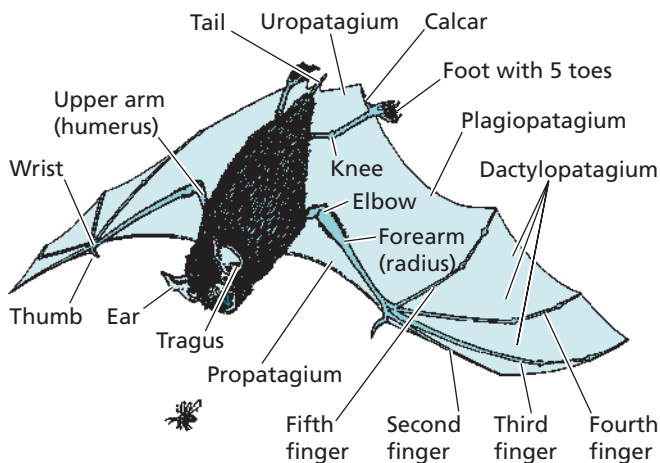
Figure 21.3 The major external features of bats. Note the humerus, elongated forearm (radius), and fingers that form the wing. The claw on the thumb (digit one) occurs in all families, although it is rudimentary in smoky bats (Furipteridae) and short-tailed bats (Myzopodidae). Not all species have an external tail and uropatagium (see Figure 21.4A). *Adapted from Macdonald (1984).*

membrane may contribute to lift and help stabilize the body during turns and other maneuvers. Aerodynamic stability is also enhanced in bats by their body mass being concentrated close to their center of gravity. The size and

shape of the uropatagium, and whether it completely encloses the tail, vary considerably among and within families (Figure 21.4A). The **calcar**, a cartilaginous process that extends from the ankle, helps support the uropatagium.

The hind limbs of bats are small relative to the wings and are unique among mammals in being rotated 180° so that the knees point backward. This aids in various flight maneuvers, as well as in the characteristic upside-down roosting posture of bats. Almost all bats roost head-down, hanging by the claws of the toes; the sucker-footed bat (*Myzopoda aurita*) is an exception and roosts with the head up. A special locking tendon (Quinn and Baumel 1993; Simmons and Quinn 1994) allows bats to cling to surfaces without expending energy.

As noted, the head and facial features of bats exhibit a great deal of diversity. Facial ornamentation, in the form of fleshy nose leafs, are conspicuous in New World leaf-nosed bats, horseshoe bats, the false vampire bats (Family Megadermatidae), and slit-faced bats (Family Nycteridae). Such ornamentation functions in the transmission of echolocation pulses because species in these families emit ultrasonic pulses through their nostrils.

"Blind-as-a-bat" is a totally misleading phrase. All bats have perfectly functional vision. Eyes are large in pteropodids but relatively small in microchiropteran bats—used here as synonymous to bats that use laryngeal echolocation.

A

B
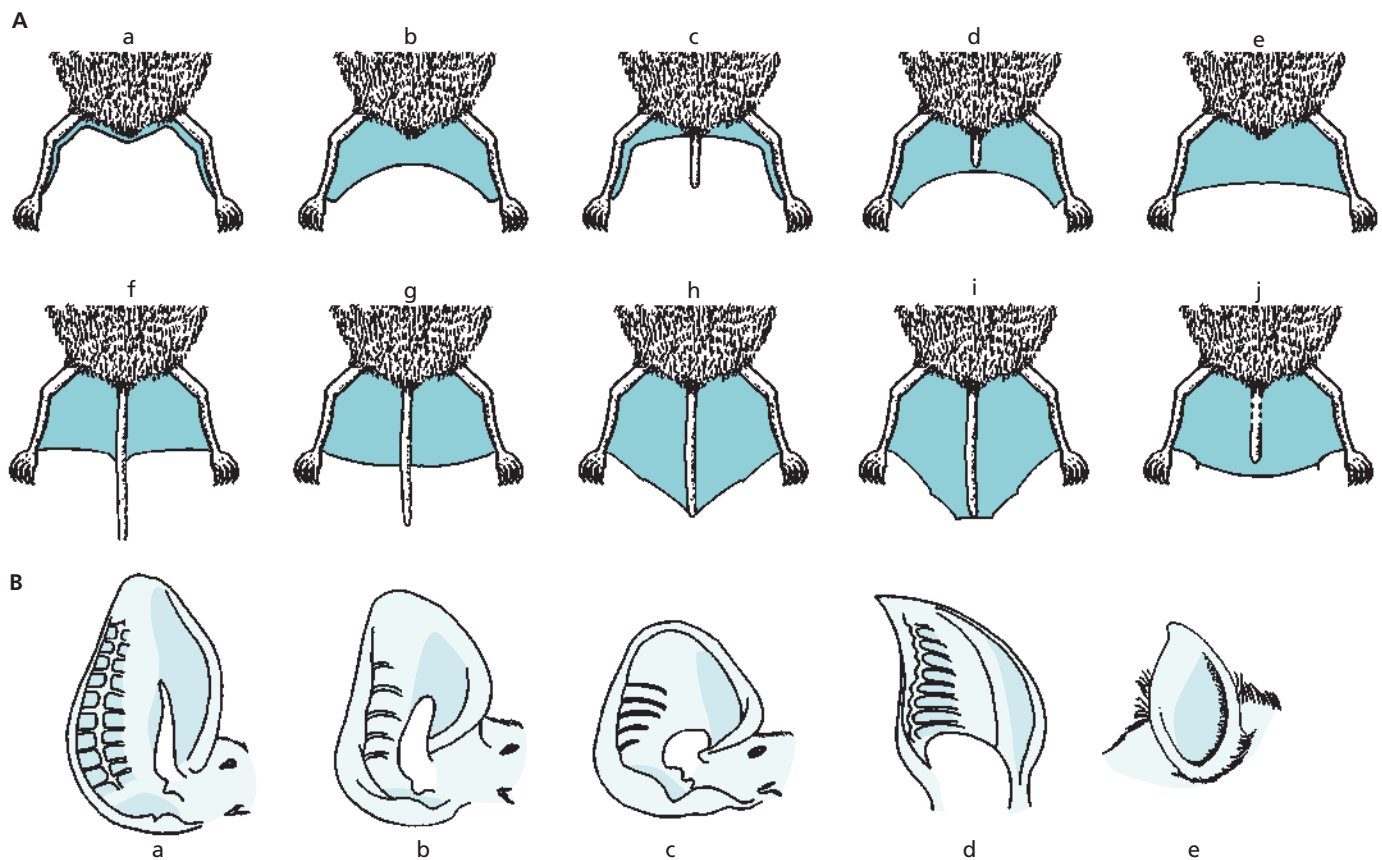
Figure 21.4 Variation in the uropatagium, tail, external ear, and tragus of representative families of bats. (A) (*a*) Fruit bats (Pteropodidae) in the Genus *Pteropus*, as well as some New World leaf-nosed bats (Phyllostomidae); (*b*) New World leaf-nosed bats; (*c*) tube-nosed fruit bats in the Genera *Nyctimene* and *Paranyctimene* (Pteropodidae); (*d*) New World leaf-nosed bats; (*e*) hog-nosed bat (Craseonycteridae), with extensive uropatagium but no external tail; (*f*) mouse-tailed bats (Rhinopomatidae) with long, thin tail free of the uropatagium; (*g*) free-tailed bats (Molossidae) with about one-half the tail free of the uropatagium; (*h*) common bats (Vespertilionidae), similar to tails in horseshoe bats (Rhinolophidae) and false vampire bats (Megadermatidae); (*i*) slit-faced bats (Nycteridae) with T-shaped tip of the tail; (*j*) sac-winged bats (Emballonuridae), fishing bats (Noctilionidae), and mustached bats (Mormoopidae) have a tail that protrudes through the uropatagium. **(B)** Representative sizes and shapes of the external ears and tragus in bats: (*a–c*) variation in size and shape of the ear and tragus in vespertilionids; (*d*) antitragus in a rhinolophid; (*e*) continuous inner ear margin without tragus or antitragus in a pteropodid. *Adapted from Hill and Smith (1984).*

Other than some pteropodids, however, most bats are nocturnal, and visual acuity is secondary. Primary perception of the environment is through acoustic orientation, both through echolocation (see section below) and audible vocalizations important in various social interactions. The importance of hearing to microchiropterans is reflected in the tremendous variety evident in the size and shape of the pinnae (external ears) among species (Obrist et al. 1993; Figure 21.4B). Most have a **tragus**, a projection from the lower margin of the pinnae (see Figure 21.4B), which is important in echolocation. Some species may also have an **antitragus**, a small, fleshy process at the base of the pinnae. An antitragus is especially evident in groups in which the tragus is absent or reduced, as in the horseshoe bats and free-tailed bats (Family Molossidae).

HOW BATS FLY

All aspects of the biology and natural history of bats are associated with their ability to fly. Compared with flight in birds, flight in bats is slow but highly maneuverable. To comprehend how a bat flies, it is necessary to understand a few basic aerodynamic terms (see Norberg 1990; Swartz et al. 2012 for detailed analyses of flight in bats). A bat (like a bird or an airplane) is able to fly because it generates enough **lift** to overcome gravity and sufficient forward propulsive thrust to overcome **drag** (Figure 21.5A). Drag is the resistance of air as a bat moves through it. Drag on a flying bat is reflected in its Reynolds number (Re). For bats, this dimensionless value is a function of the density (d) and viscosity (v) of air, flight speed (s), and wing length (L), such that $Re = dsL/v$. For most bats, Re values of 10,000 to 50,000 are typical. These are actually relatively low values; large swimming whales generate Re values of hundreds of millions.
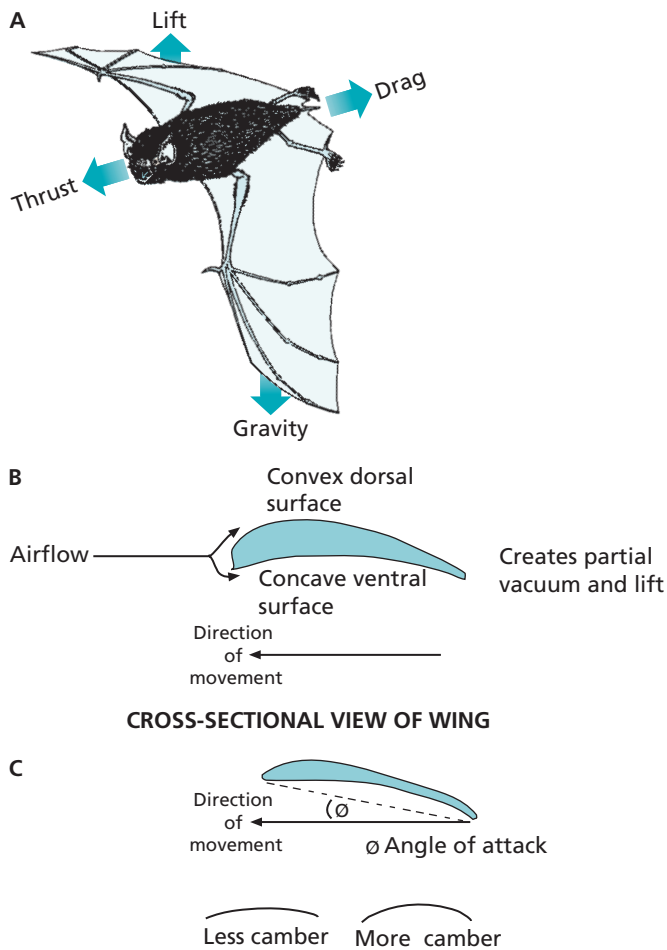
Figure 21.5 Aerodynamics of flight in bats. (**A**) In order for bats to fly, the power-producing forward thrust must overcome "backward" drag caused by air friction, while upward lift must be greater than the effects of "downward" gravity. Drag increases in proportion to the surface area of the wings and air speed, as well as increased camber and angle of attack. (**B**) Lift is created as air moves over the convex top of the wing as a bat moves forward. It has a greater distance to travel relative to the concave bottom of the wing. This produces less pressure above the wing and results in upward lift. A decrease in pressure with increased velocity of the air (or fluid) is known as "Bernoulli's Principle." (**C**) The angle of attack is the angle of the wings relative to the horizontal plane in the direction of movement; camber is the degree of curvature of the wing.

Lift and thrust are achieved in bats through the structure of the wings, in conjunction with the pectoral bones and muscles, the uropatagium, and hind limbs. The dorsal surface of the wing in bats, as in airplanes, is convex, and the ventral surface is concave, which causes air to move more rapidly over the wing than underneath it. This reduces the relative air pressure above the wing and results in lift (Figure 21.5B). In addition, to facilitate airflow, the surface of the wing is kept smooth and taut by layered elastic tissue in the wing. Generally, the greater the **camber** (the extent of the front-to-back curvature of the wing), the more lift that can be produced. Bats can adjust the camber of their wings

in response to shifting aerodynamic conditions (Cheney et al. 2014). Likewise, the greater the **angle of attack** (Figure 21.5C), the more lift that can be generated. If the camber and angle of attack are too great, however, the smooth flow of air over the surface of the wing is disrupted and becomes turbulent; lift is greatly reduced or lost completely. Poor aerodynamics and disrupted airflow are characterized by high Strouhal numbers—dimensionless values describing changing flow values—of (St) > 3.0, where St = fa/s, with f = frequency of wing beats, a = amplitude of wing beats, and s = flight speed. Bats generally have smooth flight and St values < 0.1 (Swartz et al. 2012) because they can quickly adjust both camber and angle of attack throughout the wing-beat cycle by use of several muscles in the wing, in conjunction with the movement of the wrist, thumb, fifth finger, and the hind limbs (Norberg 1990; Swartz et al. 1992, 2012).

As noted by Fenton (1985:16), "In flight the wing area proximal to the fifth digit provides lift, while the portion distal to the fifth digit acts as a variable pitch propeller providing thrust. Power comes from the contraction of nine pairs of flight muscles located on the chest and back." As a bat flies, thrust and lift are provided during the downstroke, in which the wings are fully extended and move in both a downward and forward motion. Little if any thrust or lift is developed during recovery, when the wings, partially folded to reduce drag, move upward and backward in preparation for the next downstroke. The chest muscles of bats power the downstroke and provide for lift and thrust. They are much larger than the back muscles, which function during the upstroke. In many species, the specialized scapula "locks" the movement of the humerus and stops the upstroke phase. As is the case for fixed-winged aircraft, bats require more energy for flight at low and high speeds, as opposed to intermediate speed (von Busse et al. 2013).

The shape of a bat's wing is another factor that affects aerodynamic properties. When viewed from above, wing shape varies from short and broad to long and thin in different families and species (Figure 21.6). The proportion of wing length to width is called the **aspect ratio** and results from the relative lengths of the metacarpals and phalanges of the third, fourth, and fifth fingers. A high aspect ratio—long, narrow wings—adapts a species for sustained, relatively fast flight, as is seen in many free-tailed bats. These species would be expected to forage high above the ground, predominately in open habitats, free of obstructing vegetation. A low aspect ratio—short, wide wings—is seen in bats with slower, more maneuverable flight, as in the false vampire bats, slit-faced bats, and many northern temperate species. A low aspect ratio is associated with bats that forage more often in habitats with dense, obstructing understory vegetation. Besides aspect ratio, slow, maneuverable flight can be enhanced by low **wing loading**—the ratio obtained by the body mass of the bat divided by the total surface area of the wing. The lower the wing loading, the greater the potential lift and capacity for slow flight. In general, a direct relationship exists between the wing morphology and flight patterns of bats and their foraging and
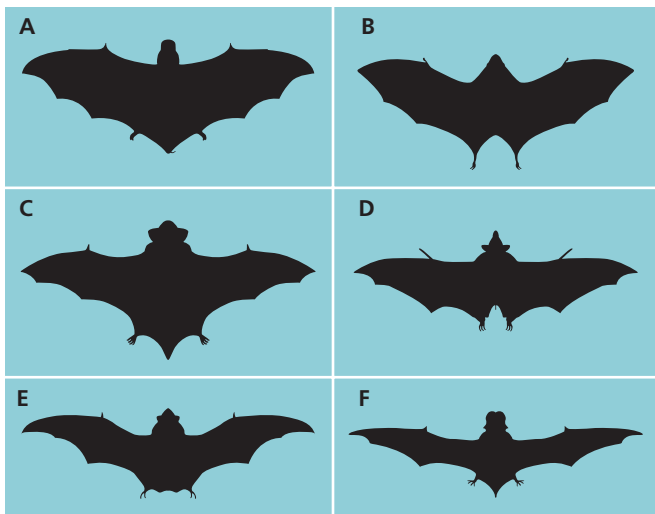
Figure 21.6 **Increasing aspect ratios of the wings in several different families of African bats.** The aspect ratio—calculated as the wingspan squared divided by the area of the wing—increases as wings become longer and thinner in different species of bats. Broader wings generally translate to slower, more maneuverable flight patterns. (**A**) Egyptian slit-faced bat (*Nycteris thebaica*) (Nycteridae); (**B**) heart-nosed bat (*Cardioderma cor*) (Megadermatidae); (**C**) Moloney's flat-headed bat (*Mimetillus moloneyi*) (Vespertilionidae); (**D**) straw-colored fruit bat (*Eidolon helvum*) (Pteropodidae); (**E**) Pel's pouched bat (*Saccolaimus peli*) (Emballonuridae); (**F**) Midas' free-tailed bat (*Mops midas*) (Molossidae). *Adapted from Kingdon (1974b).*

life-history characteristics (Altringham 1996; Stockwell 2001; Swartz et al. 2012).

ECHOLOCATION

To find prey items and maneuver within their environment, most bats **echolocate**—that is, they emit high-frequency sound pulses and discern information about objects in their path from the returning echoes. Many of the structural characteristics of bats, including their seemingly bizarre facial features, relate to echolocation. As with the relationship among wing morphology, flight patterns, and life-history features for various species, many aspects of echolocation are also species-specific and relate to foraging. Most pteropodids rely on vision and olfaction to locate food, avoid obstacles, and maneuver in their environment (although the rousette fruit bats—Genus *Rousettus*—have a limited form of echolocation using low-frequency tongue clicks). Vision involves interpreting information about objects in the immediate environment from energy received as light waves that are produced by or reflected from those objects. Microchiropterans substantially augment visual senses with hearing, in the form of a highly sophisticated system of auditory echolocation. Hearing can give the same amount of information as vision, except for color—which is not necessary for nocturnal animals.

In echolocation, a bat generates and emits high-frequency, high-intensity sounds through the mouth or nose. These sound pulses are then transmitted through, scattered by, or reflected back by objects in their path. When reflected, the returning sound (echo) is received, with altered characteristics, by the bat. The characteristics of the returning echo are altered from the original sound pulse depending on the physical features of the object, including its distance, texture, movement, shape, and size. The bat interprets these features from the echo. Although simple in concept, the actual process is extremely complex, and the sensory apparatus of bats is very sophisticated. For example, the echo from a target 1 m away returns to the bat in 6/1,000 of a second. Although 6/1,000 second is very fast, bats are able to discriminate echo delays as short as 70 millionths of a second (Suga 1990). Many species can also determine the presence of objects as thin as 0.06 mm (0.002 in.) in diameter, the width of a human hair.

High-frequency sound pulses are particularly suitable for bat echolocation because objects about 1 wavelength in size reflect sound particularly well. For example, at a frequency of 30 kHz, the **wavelength** (distance from peak to peak in a sound wave; Figure 21.7) is about 11 mm—roughly equivalent to the length of a small moth. Also, low-frequency sounds (long wavelengths) can "wrap around" small targets such as insects and eliminate any echo. The negative aspect of high-frequency sound is that it is quickly absorbed by the atmosphere and thus has limited range relative to lower-frequency sound. If they were within the range of human hearing (and some species use signals that are), the high-intensity echolocation signals of certain species would be very loud, including the signals from rhinolophids, molossids, emballonurids, rhinopomatids, and many vespertil-
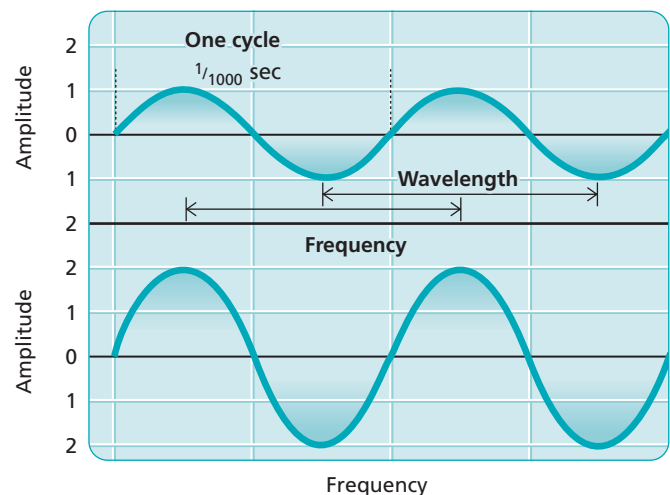
Figure 21.7 **Characteristics of a sound wave.** The upper sound wave represents a 1-kHz pure tone wave and is the same frequency as the lower one, but the amplitude is twice as great in the lower sound wave. Amplitude, or the intensity of sound, is measured in newtons per square meter. A newton equals 105 dynes (a dyne is the force necessary to move 1 gm of mass 1 cm/sec). *Adapted from Hill and Smith (1984).*

ionids. Bats avoid self-deafening from loud outgoing pulses by disarticulating the bones of the middle ear and dampening the sound. Other bats, including nycterids, phyllostomids, and megadermatids, are sometimes called "whispering bats." Their much lower-intensity signals have a less effective range than those of species using signals of higher intensity. Interestingly, insects from at least 6 orders can hear ultrasound, and many night-flying insects have devel-

oped countermeasures to evade echolocating bats (Fenton 1995; Altringham 1996; Connor and Corcoran 2012; Corcoran and Connor 2012).

Following Donald Griffin's pioneering work (Griffin 1958; Griffin et al. 1960), numerous investigators have studied the remarkable aspects of echolocation (Simmons et al. 1975; Fenton 1985; Neuweiler 1990; Popper and Fay 1995). The high-frequency sound pulses are produced by contraction of the cricothyroid muscles of the larynx (see Metzner and Müller 2016 for a detailed description of ultrasound production). When a bat is taking insects in flight, the frequency and characteristics of echolocation pulses vary depending on whether the bat is in the search, approach, or terminal phase (Figure 21.8). This variation involves changes in signal duration, loudness, and the nature and extent of frequency modulation and **harmonics** (integral multiples of fundamental frequencies that provide a broader scanning ability; Figure 21.9). All these factors change in different phases of approach to a target and under different foraging situations, as well as among different species of bats.

As noted, bats perceive a great amount of detailed information from returning echoes, including size, shape, texture, and relative motion, in addition to distance to a target (Figure 21.10). The constant-frequency (CF) component of the search phase, a pulse of constant pitch, is particularly useful for discriminating between moving objects, such as prey items, and stationary obstacles. Moving objects can be determined by their **Doppler shift**—a change in sound frequency of an echo relative to the original signal caused by the movement of one or both objects: the source (bat) or the target (insect). We observe a Doppler
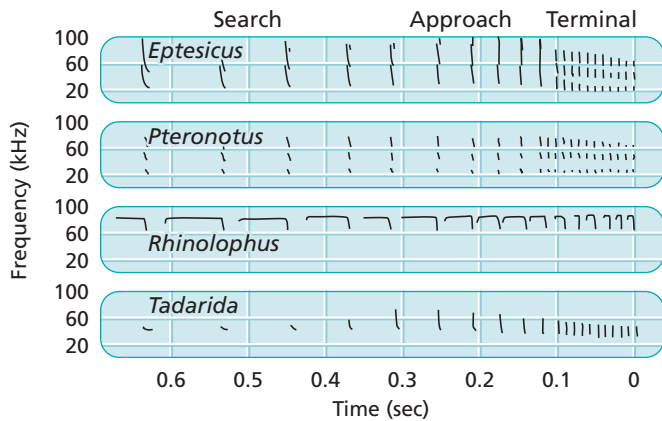
Figure 21.8 **Increased pulse repetition at terminal phase.** The increased pulse rate during the terminal phase of closing in on a prey item, referred to as the "feeding buzz," is evident in these reproductions of sonograms from four species of bats: big brown bat (*Eptesicus fuscus*) (Vespertilionidae); Wagner's mustached bat (*Pteronotus personatus*) (Mormoopidae); greater horseshoe bat (*Rhinolophus ferrumequinum*) (Rhinolophidae); and Brazilian free-tailed bat (*Tadarida brasiliensis*) (Molossidae). *Adapted from Hill and Smith (1984).*
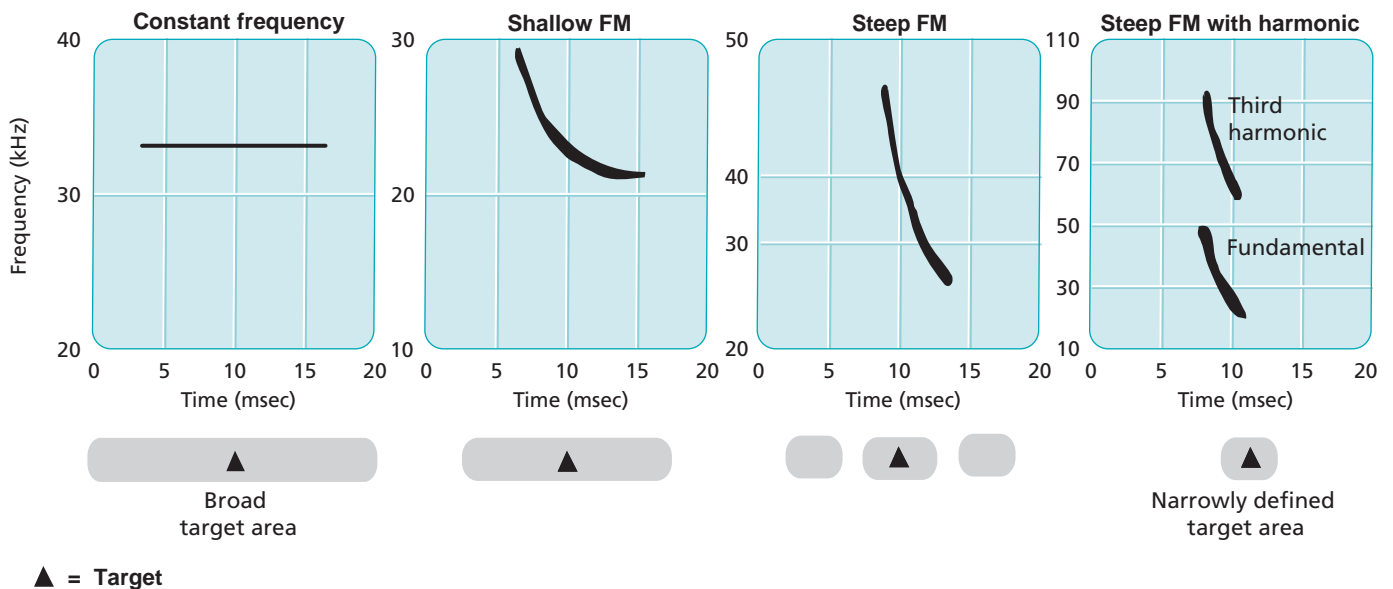
▲ = Target

Figure 21.9 **Typical pattern of frequency changes in echolocation pulses that continuously narrows the target area perceived by a bat.** Bats may use a narrow-band, long-duration, constant frequency (CF) pulse until a potential prey item (target indicated by ▲) is located. The target area (*shaded*) perceived by the bat becomes increasingly more narrowly defined as the bat shifts to broadband, shorter-duration echolocation pulses including a shallow frequency-modulated (FM) sweep, a steep FM sweep, and finally a steep FM sweep with harmonics (which are integral multiples of fundamental frequencies) that pinpoint the target and provide fine details. *Data from Fenton (1981).*
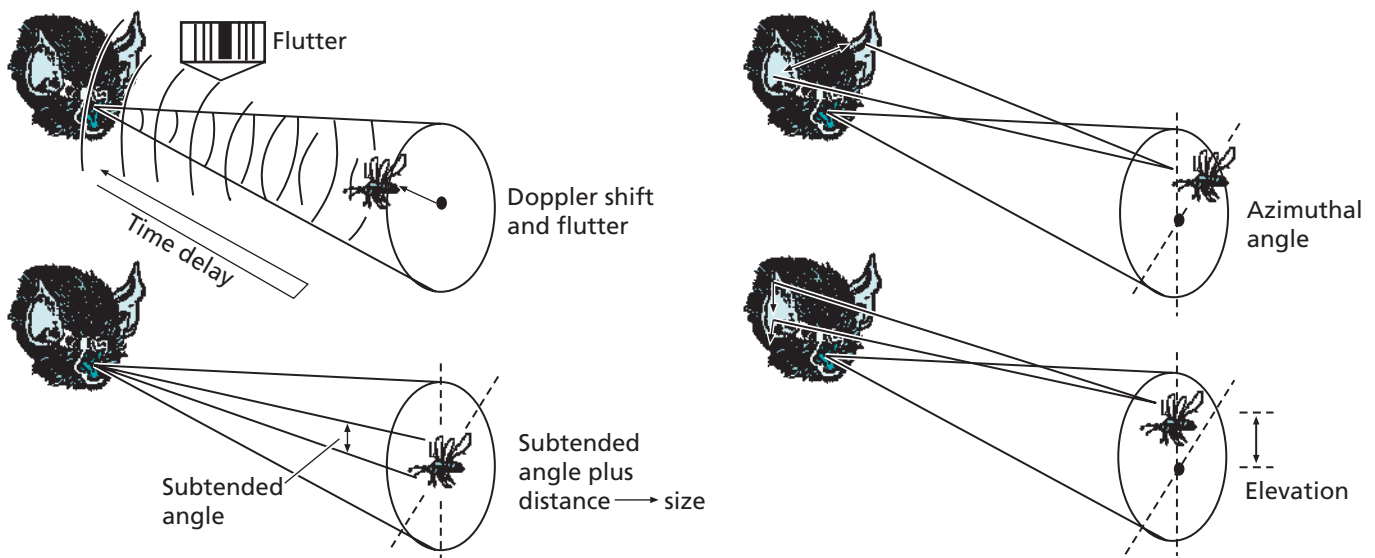
Figure 21.10 **Information gained from returning echolocation signals.** (*Top left*) Distance and relative speed of the target are indicated by the time delay and strength (in decibels; dB) of the returning pulse and by the Doppler shift. Flutters indicate the presence of rapidly beating insect wings. (*Bottom left*) The size of the target is reflected in the amplitude (subtended angle) of the returning signal in conjunction with the distance. (*Top right*) Time delay and amplitude differences between the ears convey information on azimuth (angular distance from center). (*Bottom right*) Interference patterns of the sound waves within the inner surface of the ear indicate elevation. *Adapted from Suga (1990).*

shift when a loud car races by us as we are standing still. The pitch of the engine noise sounds higher as it comes toward us because the sound waves "pile up," the wavelength becomes shorter, and the sound frequency (pitch) is higher. As the car moves away from us, the sound waves are now being "stretched out" and become longer. The sound is now at a lower frequency (also, low-frequency sound travels farther than high-frequency sound). Because a bat and its insect prey are moving relative to each other, the returning echoes may be shifted in frequency. Many species of bats compensate for this phenomenon. Hiryu and colleagues (2016) provided a detailed review of Doppler compensation in echolocating bats.

Because bats cannot transmit and receive at the same time, outgoing pulses are often of short duration so as not to obscure the returning echoes. Bats that emit short calls and listen for echoes during the intervals are characterized as having "low-duty-cycle" echolocation. The alternative is "high-duty-cycle" echolocation, which involves long, rapidly emitted, constant frequency calls (Simmons 2005b).

Broader band, frequency-modulated (FM) pulses, which go up or down, are better than CF pulses for determining the finer details of a target. Thus, the bat uses a series of FM pulses as it approaches closer to the target. Throughout the sequence, the rate of sound pulses increases (see Figure 21.8), until it is extremely rapid during the terminal phase. This is because even small movements of the prey quickly create large angular differences in its relative position the closer the bat comes. Also, many species of bats may broaden the echolocation beam to keep evasive

prey within their acoustic field during the terminal phase (Jakobsen et al. 2015). The search-approach-termination sequence is repeated very rapidly. Although these generalizations of echolocation apply to all bats, there is substantial variation and diversity among families (Table 21.2). The highly developed sensory apparatus, specialized neural anatomy, and sophisticated neural pathways of bats (Suga 1990) provide an amazing amount of detailed information about their surroundings.

Echolocation is not unique to bats; it occurs in other mammals, including some rodents, insectivores such as shrews and tenrecs, and seals. Only in the toothed whales, however, might echolocation approach the level of sophistication found in bats.

EVOLUTION OF ECHOLOCATION AND FLIGHT

Echolocation and flight are two noteworthy characteristics of bats that are interrelated in the life history of all echolocating bats. As noted in the next section (Fossil History), studies based on analyses of the articulation of the shoulder joint and enlarged scapula for flight muscles indicate that Eocene bats were capable of flight. They could also echolocate, as suggested by their enlarged cochlea and fusion of an enlarged stylohyal element to the tympanic bones (Simmons et al. 2010; Veselka et al. 2010; Thiagavel et al. 2018). Given what we see in bats today, debate about their evolution of echolocation has centered on two com-

Table 21.2 Diversity of echolocation characteristics among families of bats

Characteristics of Echolocation Call	Family of Bat
Brief, broadband tongue clicks	Pteropodidae* (Genus *Rousettus*)
Narrowband; dominant fundamental harmonic	Some Vespertilionidae, Molossidae
Narrowband; multiharmonic	Craseonycteridae, Rhinopomatidae, Emballonuridae, Mormoopidae, Thyropteridae
Short broadband; dominant fundamental harmonic	Vespertilionidae (Genus *Myotis*)
Short broadband; multiharmonic	Megadermatidae, Nycteridae, Phyllostomidae, Mystacinidae, some Vespertilionidae, Natalidae
Long, broadband	Myzopodidae
Constant frequency	Rhinolophidae, Hipposideridae, Noctilionidae

*Most pteropodids do not echolocate.

peting scenarios: (1) the early stem group of bats developed echolocation, which was later lost in pteropodids; or (2) the earliest bats did not echolocate, but this developed later as a convergent characteristic in all but the pteropodids. This question remains unresolved, but as noted, early Eocene bats could echolocate so this feature evolved early in their history (Teeling et al. 2012; 2016).

Fossil History

Fossil bats have been found on all continents except Antarctica (McKenna and Bell 1997). Nonetheless, the fossil record for bats is poor. Eiting and Gunnell (2009) estimated that there is no fossil record for 88% of the bats that ever existed. Based on occlusal surface patterns of the molars, bats are believed to have evolved from arboreal, shrew-like insectivores, although the time of divergence is unknown, and no intermediate forms have been discovered. Fossils from 9 extant families of bats have been found in early to late-Eocene deposits (Figure 21.11). Fossil remains of bats from most other families date to the Oligocene or Miocene. The earliest fossil records of bats are those of *Icaronycteris index*, from early Eocene deposits of North America (Jepson 1966), and *Onychonycteris finneyi* from the same site (Simmons et al. 2008). Many of the characteristics of *I. index* are considered primitive or unspecialized relative to modern bats. Primitive features include 38 total teeth, lack of fusion in ribs and vertebrae, lack of a keeled sternum, and several other features (Jepson 1970). Nonetheless, other specialized morphological features of modern microchiropterans did occur in *Icaronycteris* (Figure 21.12), which was fully capable of flight. Several other early Eocene bat taxa that could fly include *Archaeonycteris*, *Hassianycteris*, *Palaeochiropteryx*, and *Tachypteron*. In their essential features,

including flight and echolocation, bats have existed for over 50 million years. As summarized by Simmons (2005b:165), these Eocene bats "(1) were capable of powered flight, (2) used sophisticated echolocation like that of extant microchiropteran bats, (3) were taxonomically and ecologically diverse, and (4) were globally widespread, occurring on virtually all continents."

Megachiropterans include the fossil Genera *Archaeopteropus* from the early Oligocene of Europe and *Propotto* from the early Miocene of Africa (Butler 1978; Gunnell 2010). Despite the morphological differences noted in Table 21.1, numerous molecular and morphological studies strongly support the monophyly of bats—that is, they all derive from a common ancestral lineage.

Economics and Conservation

Bats create both positive and negative economic effects. On the negative side, bats are associated with many bacterial, rickettsial, viral, and fungal diseases (Hayman et al. 2013; Klimpel and Mehlhorn 2013). One of the fears people have is the association of bats with rabies. Rabies has been reported in numerous Old and New World species, but the percentage of infected individuals in any population generally is no more than 1% to 4%, depending on the season and whether species are solitary or colonial (Brass 1994). Carnivores such as dogs, foxes, skunks, and raccoons are much more likely to be significant vectors of rabies than bats are (see Chapter 27).

Vampire bats are directly responsible for losses of hundreds of millions of dollars to the livestock industry through disease transmission, including rabies. The distribution of vampire bats is restricted to New World tropical areas, however, as is their effect on livestock (see section
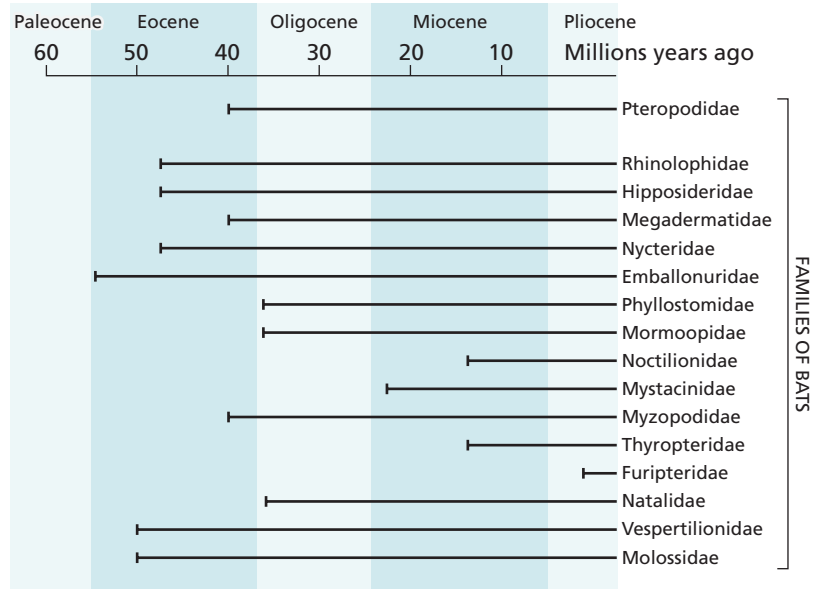
Figure 21.11 **Fossil history of living (extant) families of bats.** The fossil history of nine extant families of bats can be traced to the Eocene, with most of the remaining families documented from the Oligocene or Miocene. *Modified from Simmons (2005) and other sources.*
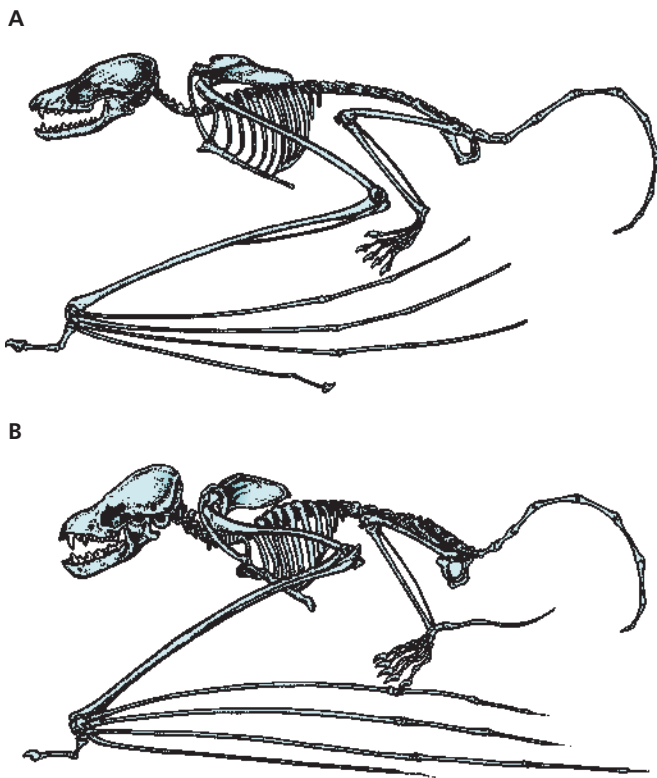
Figure 21.12 **Similarities between one of the oldest fossil bats and modern bats.** (**A**) Fossil skeleton of the bat *Icaronycteris* from the early Eocene. Note the development of the forelimb into a wing, with elongation of the phalanges, partial fusion of the radius and ulna, and dorsal position of the scapula. (**B**) Skeleton of a modern *Myotis* is similar in many respects to that of Icaronycteris. *Adapted from Jepsen (1970).*

on Family Phyllostomidae). Histoplasmosis is a fungal disease of the lungs caused by *Histoplasma capsulatum* and is associated with bat **guano** (fecal droppings) in caves, mines, and attics of houses where bats occur. This health hazard is limited, however, because relatively few people frequent such places, and infections are often mild.

On the positive side, bats are one of the most economically beneficial mammalian groups. They are the only significant predator of nocturnal insects, consuming tremendous numbers of insect pests that would otherwise damage billions of dollars' worth of agricultural crops. Bats also fill key ecological roles in many forest communities, especially as seed dispersers and plant pollinators. They pollinate hundreds of plant species of economic importance for food, timber, medicines, or fiber, including bananas, peaches, dates, and figs. Large accumulations of guano in caves have been mined in the past and used for fertilizer as well as an ingredient in gunpowder. Bats are also used in a variety of medical research programs, including studies of drugs, disease resistance, and navigational aids for the blind.

Population declines and range reductions of many species of bats throughout the world are due to cave closures and loss of foraging and roosting habitats, siltation or draining of riparian areas, insecticide accumulations, and, in the case of large Old World fruit bats, consumption by humans. A recent major mortality factor for bats in North America is white nose syndrome (WNS), an infection caused by the cold-adapted fungus *Pseudogymnoascus* (*Geomyces*) *destructans* (Lorch et al. 2011; Raudabaugh and Miller 2013). It is evident around the nose (Figure 21.13), wings, or other parts of the body. As of 2018, WNS was confirmed in 28 states (including Washing-

Figure 21.13 **White nose syndrome.** The fungus—*Pseudogymnoascus destructans*—is evident around the nose of this southeastern bat (*Myotis austroriparius*).

ton—2,100 km from the nearest known location in the Midwest) and 5 Canadian provinces. Likely originating in Europe, the fungus causes increased arousal in bats that hibernate in caves, leading to decreased survival rates and mass mortalities in 9 species (Warnecke et al. 2012; Cryan et al. 2013). This certainly ranks as one of the most severe and significant threats to bats, and millions have died, although there is evidence that some individuals from infected populations can survive (Dobony et al. 2011; Meteyer et al. 2011). Also, recent research suggests that the fungus may be susceptible to treatment with ultraviolet light (Palmer et al. 2018). Another potentially devastating impact on populations of some bat species is the proliferation of large wind turbines around the world, which can be a significant source of fatalities (Cryan and Barclay 2009; Hein and Schirmacher 2016; Zimmerling and Francis 2016). A great deal of current research is directed toward reducing bat fatalities associated with large wind turbines.

Many bat species have gone extinct in recent decades, especially endemic species of pteropodids (Kunz and Pierson 1994). In the United States, the Indiana bat (*Myotis sodalis*) and several other species are endangered. Others, such as the northern long-eared bat (*Myotis septentrionalis*), may become endangered because of population declines from WNS. Hibernacula of these species, including caves and abandoned mines, are often gated to prevent disturbance of bats. A primary goal of conservation programs is to change people's perceptions of bats through education so that they might learn to appreciate these fascinating mammals rather than fear and persecute them. The organization Bat Conservation International has taken a leading role in these educational efforts.

Suborder Yinpterochiroptera

SUPERFAMILY PTEROPODOIDEA

Pteropodidae

Historically, this large assemblage of about 45 genera and close to 200 species of Old World fruit bats was divided into 2 to 6 subfamilies based on feeding and morphological characteristics (see Simmons 2005a). Pteropodids occur throughout tropical and subtropical areas of the Old World, usually in forested or shrubby areas that provide a predictable supply of fruit. They are distributed south and east of the Sahara Desert in Africa, east through India, Southeast Asia and Australia, to the Caroline and Cook Islands in the Pacific.

Major features that distinguish the Old World fruit bats from the other families of bats ("microchiropterans") are noted in Table 21.1. Pteropodids do not echolocate, the exception being the low-intensity tongue clicking of members of Genus *Rousettus*. Holland and coworkers (2004) described the duration, amplitude, and peak frequency of tongue clicks in the Egyptian fruit bat (*R. aegyptiacus*). Pteropodids have none of the distinctive facial features related to echolocation, such as a nose leaf or enlarged tragus (Figures 21.1 and 21.14), which are found in other families of bats. They navigate primarily using vision, and anatomically their large eyes are unusual. The choroid, which surrounds the retina, has numerous **papillae**, or projections. These extend into the retina and form undulating, uneven contours. Most of the photoreceptors are rod cells, for black-and-white vision,

Figure 21.14 **Facial features of a fruit bat, Family Pteropodidae.** The large eyes, lack of facial ornamentation, and simple ears with no tragus or antitragus of this Gambian epauletted fruit bat (*Epomophorus gambianus*) can be contrasted with most echolocating microchiropterans.

although cone cells for color vision occur in some species (Pedler and Tilley 1969; Mueller et al. 2007).

Body size varies considerably among members of this family. The smaller species, such as the long-tongued fruit bat (*Macroglossus minimus*), pygmy fruit bat (*Aethalops alecto*), and spotted-winged fruit bat (*Balionycteris maculata*), weigh only about 15–20 g; the largest species in the Genus *Pteropus* weigh up to 1,200 g, a difference of 2 orders of magnitude. Wingspans may reach 2 m in some species of *Pteropus* and *Acerodon*, the largest of any bat. Sexual dimorphism is evident in greater body size in males in the Genera *Eonycteris*, *Epomops*, and *Epomophorus*. Male hammer-headed fruit bats (*Hypsignathus monstrosus*) are nearly twice the body mass of females—a greater degree of sexual dimorphism than in any other species of bat.

Dental formulae vary, with the teeth being specialized for a diet of fruit. Although some genera have 34 teeth, the more specialized nectar-feeders have a reduced number. Canines are always present, however. The molars generally have smooth surfaces, usually without cusps, but with shallow, longitudinal grooves. As noted in Table 21.1, the palate extends beyond the last molar. In frugivores, the palate has ridges (Figure 21.15) against which the tongue mashes ingested food. The juice is consumed, and pulp and seeds are discarded.

Fruit bats are primarily nocturnal, although some species may be diurnal. Large species can fly up to 100 km between roosting and foraging areas, depending on the local availability of fruit. Annually, species such as the straw-colored fruit bat (*Eidolon helvum*) can migrate 1,500 km to take advantage of seasonal food availability (Richter and Cumming 2006). Food resources are located primarily through olfaction. Pollen and nectar may make up a significant proportion of the diet in some species. Many species have bristle-like papillae on their long, extensible tongues to help collect pollen from flowers or other adaptations for frugivory or nectarivory (Mqokeli and Downs 2013). Pteropodids thus serve valuable ecological functions in pollination (Andriafidison et al. 2006) and in seed dispersal of hundreds of species of tropical plants (Seltzer et al. 2013)—a mutualistic relationship between fruit bats and bat fruit (Mahandran et al. 2018). Seeds usually are spit out or passed through the gut away from the parent tree, thus promoting dispersal. Shilton and colleagues (1999) examined retention time and viability of seeds in the gut of the short-nosed fruit bat (*Cynopterus sphinx*). They suggested that ingested seeds can potentially be dispersed >300 km from the parent plant. Additionally, many pteropodids are folivores (eat leaves), because leaves are available throughout the year in the tropics and are a predictable resource temporally and spatially (Nelson et al. 2005).
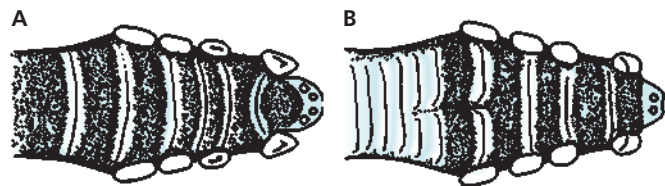
Pteropodids usually roost in trees or shrubs (Figure 21.16), although a few species use caves or buildings. Roosts often are communal, especially in the larger pteropodids. The short-nosed fruit bat roosts in "tents" it constructs in the stems or fruit clusters of various tree species—most frequently the kitul palm (*Caryota urens*) in India (Bhat and Kunz 1995; Storz et al. 2000). Concentrations of up to a million straw-colored fruit bats may occur at roosting sites (Kulzer 1969). Conversely, roosting dawn bats (Genus *Eonycteris*) are solitary. Whether species are colonial or solitary is a function of several factors, including predation pressure, food availability, roosting site availability, and breeding pattern. In American Samoa, the Pacific flying fox (*Pteropus tonganus*) forms roosting colonies in isolated areas because of hunting pressure by people (Brooke et al. 2000). Gestation periods range from 100 to 125 days; some pteropodids exhibit delayed implantation or diapause (Mutere 1965; Heideman 1989).

Pteropodids can harbor zoonotic viruses for hemorrhagic fevers (Hayman et al. 2008; Towner et al. 2009). They can also become serious crop depredators where large congregations occur. In Africa and on many South Pacific islands, loss of roosting and foraging habitats and use of bats as food for people (Wilson and Graham 1992) have severely reduced bat populations. A prime example is the Pacific flying fox population on the island of Niue, which is severely overharvested during a two-month hunting season each year (Brooke and Tschapka 2002). Likewise, hundreds of thousands of *E. helvum* are taken annually for the bushmeat trade in West Africa (Kamins et al. 2011).

Figure 21.15 Ridges on the palatal surface of fruit bats. (**A**) Six ridges occur on the palate of epauletted bats (Genus *Epomophorus*). (**B**) Additional flat, posterior serrated ridges are found in fruit bats of the Genus *Epomops*. *Adapted from Kingdon (1974b).*
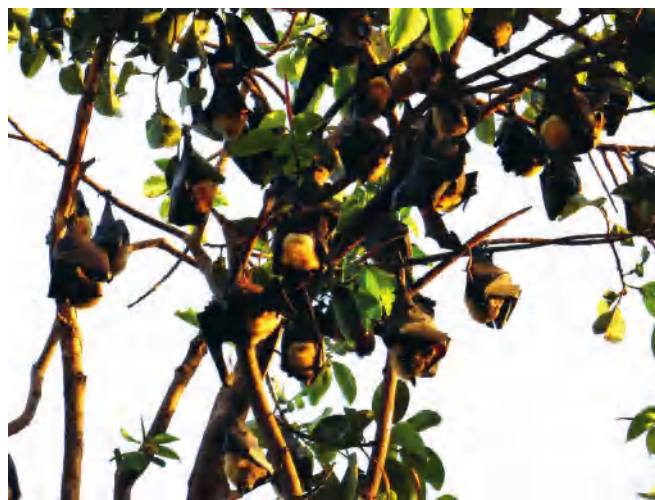
Figure 21.16 Fruit bats roosting in a tree. Communal roosts, such as these spectacled fruit bats (*Pteropus conspicillatus*) are particularly common in Old World fruit bats.

Four species have become extinct recently, including the Palau Island flying fox (*Pteropus pilosus*), the Guam flying fox (*P. tokudae*), the Percy Island flying fox (*P. brunneus*), and the Lesser Mascarene flying fox (*P. subniger*). Critically endangered pteropodids include: the Aru flying fox (*P. aruensis*), Livingstone's flying fox (*P. livingstonii*), the Vanikoro flying fox (*P. tuberculatus*), Bulmer's fruit bat (*Aproteles bulmerae*), the Philippine bare-backed fruit bat (*Dobsonia chapmani*), the Fijian monkey-faced bat (*Mirimiri acrodonta*), the greater monkey-faced bat (*Pteralopex flanneryi*), and the montane monkey-faced bat (*P. pulchra*). Several other species are endangered (IUCN 2018).

SUPERFAMILY RHINOLOPHOIDEA

Rhinolophidae

Traditionally, the horseshoe bats were divided into two subfamilies, the Rhinolophinae and the Hipposiderinae; these two taxa of Old World bats now constitute separate families based on several distinctive morphological and behavioral characteristics; additionally, the Family Rhinonycteridae was recently split from the hipposiderids (Foley et al. 2015). Rhinolophids are widely distributed throughout Europe, Africa, the Middle East, Asia, Japan, the East Indies, and northern Australia. The single genus (*Rhinolophus*) and about 100 species occur in a variety of habitats from deserts to tropical forests.

As might be expected given the large number of species, there is considerable morphological and behavioral variation in horseshoe bats. They are named for their distinctive facial ornamentation, which ranges from structurally simple to very ornate. Generally, this includes a nose leaf above the nostrils, and below and on the sides of the nostrils a flap of skin shaped like a horseshoe (Figure 21.17). Between the horseshoe and nose leaf is a median projection called the **sella**. Similar nose ornamentation occurs in Family Hipposideridae, but without the sella (Table 21.3). Nose ornamentation functions in directing the echolocation pulses (Vanderelst et al. 2012) emitted through the nostrils (not from the mouth). This "nasophonation" in rhinolophids is accomplished via their unique maxilloturbinate structure and pharyngeal modifications (Curtis and Simmons 2017; Curtis et al. 2018). All horseshoe bats take insects while in flight (referred to as "aerial hawking") in highly cluttered understory, using constant frequency echolocation calls (see Table 21.2). Primary prey are small moths and beetles. Rhinolophids generally have large ears without a tragus. Ear length correlates to call frequency—species using high frequency have smaller ears—more so than in closely related hipposiderids (Huihua et al. 2003). Kobayasi and colleagues (2012) found that echolocation-like pulses also functioned in communication between individuals within a colony of greater horseshoe bats (*R. ferrumequinum*). Li and colleagues (2014) as well as Raw and coworkers (2018) investigated the multiple acoustic mech-
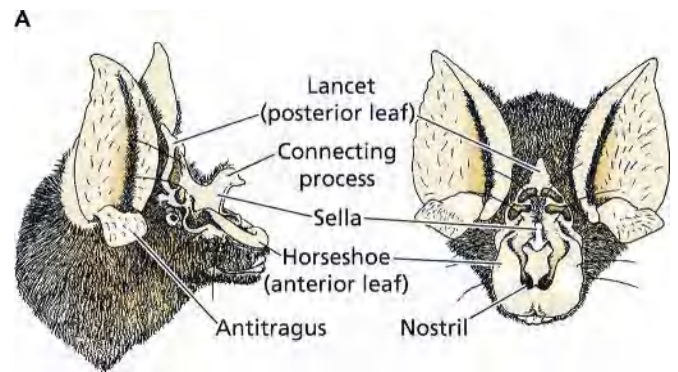
Figure 21.17 **The distinctive nose leaf of horseshoe bats.** (**A**) Note the anterior horseshoe shape, connecting sella, and posterior leaf in this broad-eared horseshoe bat (*Rhinolophus euryotis*). Horseshoe bats emit echolocation pulses through their nostrils, and this complex structure helps to beam the sound waves. (**B**) The nose leaf and horseshoe-shaped structure are evident in this greater horseshoe bat (*R. ferrumequinum*). The photo of the roosting bat has been inverted to make it easier to discern the horseshoe shape.

anisms used by rhinolophids to distinguish between echolocation calls of conspecifics and those of sympatric heterospecifics.

Rhinolophids roost singly or in small groups in caves, crevices, hollow trees, or houses. While roosting, they wrap their wings around themselves and fold up the uropatagium,

Table 21.3　Morphological and behavioral differences separating the horseshoe bats (Family Rhinolophidae) and Old World leaf-nosed bats (Family Hipposideridae)

Rhinolophidae	Hipposideridae
Three phalanges in all toes of the feet except the first	Two phalanges in all toes of the feet
A median projection (sella) extends from the nose leaf (see text)	No median projection
No sac behind nose leaf	Males often with a sac behind nose leaf, which can be everted and secretes a waxy material
Dentition: 32 teeth, with small lower premolar	Dentition: 28 to 30 teeth, no small lower premolar
Generally forage individually	Generally forage in small groups

thus appearing to be large cocoons. Species that hibernate exhibit delayed fertilization, mating in the fall, with ovulation and fertilization in the spring. Species from warmer regions ovulate and mate in the early spring. Rhinolophids commonly have a single young, with birth and lactation coinciding with the peak occurrence of insects in the spring. Hill's horseshoe bat (*R. hilli*) from Rwanda is critically endangered. Six other species are endangered (IUCN 2018).

Hipposideridae

As noted, the 7 genera and about 88 species of Old World leaf-nosed and roundleaf bats in this family are distinct from the closely related horseshoe bats (Yuan et al. 2012) from which they diverged about 42 mya (Foley et al. 2015). Like rhinolophids, the hipposiderids are widely distributed throughout Asia, the East Indies, Australia, Africa, and the Middle East, where they take a diverse array of prey, primarily beetles, moths, and flies. For example, prey of Schneider's roundleaf bat (*Hipposideros speoris*) in Sri Lanka consisted of at least 27 families of insects taken among various habitats (Pavey et al. 2001a, b). Hiryu and coworkers (2005) mounted a small telemetry microphone on the head of great leaf-nosed bats (*H. armiger*) in Taiwan to investigate Doppler-shift compensation of their echolocation pulses. The bats changed frequency depending on flight speed such that the frequency of returning echoes remained constant. In Formosa, great leaf-nosed bats used winter hibernacula that were warmer, with more stable temperatures, than non-hibernacula sites (Ho and Lee 2003). Likewise, the Formosan leaf-nosed bat (*H. terasensis*) hibernates in roosts with temperatures as high as 23°C (Liu and Karasov 2012)—which is very demanding metabolically. Lamotte's roundleaf bat (*H. lamottei*), known only from Mount Nimba near the borders of Guinea, Liberia, and Côte d'Ivoire, is critically endangered, as is the Kolar leaf-nosed bat (*H. hypophyllus*), with only 150–200 individuals known from a single cave in India. One other

species, Cox's leaf-nosed bat (*H. coxi*) is endangered (IUCN 2018).

Rhinonycteridae

This family of 4 extant genera and 6 species of trident bats was recently separated from Family Hipposideridae (Foley et al. 2015). All share characteristics similar to those of the leaf-nosed bats. Species include Percival's short-eared trident-nosed bat (*Cleotis Cloeotis*), a cave-dwelling insectivore that occurs from Zaire and Kenya south to South Africa. Trouessart's trident bat (*Paratriaenops furculus*) and Grandidier's trident bat (*P. auritus*) also occur in Africa. They were formerly included in Genus *Triaenops* but were placed in their current genus based on the work of Benda and Vallo (2009). The Persian trident bat (*T. persicus*) occurs in riparian forests and savannas in parts of the Middle East, as well as East Africa and eastern Madagascar; *T. menamena* (formerly, the rufous trident bat, *T. rufous*) inhabits tropical forests throughout western Madagascar. The orange leaf-nosed bat (*Rhinonicteris aurantia*) inhabits grasslands and forests throughout the northern portion of Australia, where it roosts in caves with sometimes up to 5,000 individuals. Two extinct genera have been described: *Brachipposideros* from the late Oligocene of France and the early Miocene in Australia, and *Brevipalatus* from the Australian Miocene.

Megadermatidae

There are 5 genera and 6 species of false vampire bats (Burgin et al. 2018). The common name reflects the historical, false belief that they feed on blood. They are found in tropical and savanna habitats throughout central Africa, India, Southeast Asia, the East Indies, and Australia. These are moderate to large bats (Figure 21.18); the Australian giant false vampire, or ghost, bat (*Macroderma gigas*) has a wingspan of 60 cm and body mass up to 170 g. Megadermatids

birds, and other bats (Marimuthu et al. 1995). The range of the ghost bat has contracted significantly, and the species now occurs in distinct, isolated populations in northern Australia (Hoyle et al. 2001), with limited gene flow between populations (Worthington Wilmer et al. 1999). Thongaree's disc-nosed bat (*Eudiscoderma thongareeae*), recently described by Soisook and colleagues (2015), appears to occur only in a 4-km² area in Thailand and is considered critically endangered (IUCN 2018).

Craseonycteridae

This monotypic family includes only the hog-nosed bat, *Craseonycteris thonglongyai*, discovered in 1973 and known from only 35 caves in Kanchanaburi Province, western Thailand, and from 8 caves in southeast Myanmar. Puechmaille and colleagues (2011) reported no gene flow and differences in echolocation between the Thai and Myanmar populations. It is the smallest species of bat and, based on body mass, among the smallest mammalian species in the world. Head and body length is about 30 mm, and body mass is about 2 g. The hog-nosed bat has large ears and tragus, and a distinctive plate on the nose. There is no external tail or calcar. Also known as the "bumblebee bat," this species has a large uropatagium and broad wings adapted for slow, hovering flight. The bats roost in small caves where they are solitary. They feed on insects taken in flight or gleaned from foliage, as well as small spiders (Hill and Smith 1981). Surlykke and colleagues (1993) described the echolocation characteristics of the species, and their relation to foraging. The species is considered threatened because of roost disturbance and loss of foraging habitat (Pereira et al. 2006; Puechmaille et al. 2009), and populations are believed to be declining (IUCN 2018).

Rhinopomatidae

The mouse-tailed bats are named for their long tails, which are nearly equal to the length of the head and body (see Figure 21.4A [f]). They are the only living microchiropterans with a tail longer than their forearm. Adults weigh from 6 to 14 g and have dark dorsal and paler ventral pelage, with naked areas on the face, rump, and abdomen. The ears are large and connected across the forehead by a flap of skin, and the slit-like nostrils are valvular. The single genus, *Rhinopoma*, contains 4 species found throughout North Africa and the Middle East, as well as India and Sumatra. These insectivorous bats occur in arid regions where they roost in caves, cliffs, houses, and even Egyptian pyramids. They are considered primitive microchiropterans based on several morphological features, including 2 phalanges on the second digit of the **manus** (hand or forefoot), unfused premaxillary bones, and an unmodified anterior thoracic region (Koopman 1984), as

Figure 21.18 Greater false vampire bat (*Megaderma lyra*). This species occurs throughout Southeast Asia.

have large ears that are united across the forehead. Wang and Muller (2009) found that skin folds uniting the ears at the midline functioned in detection and directionality of returning, faint echolocation signals in the lesser false vampire bat (*Megaderma spasma*). Megadermatids also have a divided (**bifid**) tragus and a large, erect nose leaf. All species lack upper incisors, which is unusual for bats.

Megadermatids roost in caves, trees, buildings, and bushes. Genera are variable in their feeding and roosting habits. The yellow-winged bat (*Lavia frons*) consumes insects and may be diurnal as well as nocturnal. Roosts may contain single individuals or groups of up to 100. The heart-nosed bat (*Cardioderma cor*) roosts in groups of up to 80 individuals and feeds primarily on ground-dwelling beetles and scorpions (Csada 1996). The 2 species of Asian false vampire bats (Genus *Megaderma*) and the ghost bat feed on small vertebrates, including lizards, rodents, small

well as primitive chromosomal characteristics (Qumsiyeh and Baker 1985). Levin and coworkers (2008) investigated genetic diversity and phylogeography of the greater mouse-tailed bat (*R. microphyllum*), which has an extensive geographic range. Qumsiyeh and Jones (1986) summarized life-history characteristics of the lesser mouse-tailed bat (*R. hardwickii*) and the small mouse-tailed bat (*R. muscatellum*). Hulva and colleagues (2007) found unexpected morphological diversity within these two taxa. Although mouse-tailed bats do not hibernate during the winter, they enter torpor and do not forage, living off stored body fat instead. Females are monestrus and give birth to a single young in July or August after a gestation of about 123 days. The Yemeni mouse-tailed bat (*R. hadramauticum*) is endangered. It is known from a single site in Yemen with a population of about 150 individuals (IUCN 2018). The fossil record for rhinopomatids is poor, with only late Miocene specimens from Greece reported (Hulva et al. 2007).

Figure 21.19 Northern ghost bat (*Diclidurus albus*). One of four species in the genus, the northern ghost bat occurs from Mexico to northern South America and Trinidad. It forages for insects high above forest canopy.

Suborder Yangochiroptera

SUPERFAMILY EMBALLONUROIDEA

Emballonuridae

This family comprises 14 genera and about 54 species of sac-winged or sheath-tailed bats. They enjoy a widespread distribution in tropical and subtropical habitats from Mexico to Brazil, sub-Saharan Africa, the Middle East, India, Southeast Asia, Australia, and Pacific islands eastward to Samoa. Emballonurids range in body mass from 5 to 105 g. The total number of teeth varies from 30 to 34, and dentition is adapted for an insectivorous diet; molars have a distinct dilambdodont (W-shaped) occlusal pattern.

Emballonurids roost in caves, trees, houses, crevices, or the leaves of shrubby vegetation. Some species, such as the northern ghost bat (Genus *Diclidurus albus*; Figure 21.19) are solitary, whereas the sharp-nosed bat (*Rhynchonycteris naso*) and the white-lined bats (Genus *Saccopteryx*) form groups of up to 60 individuals. The common names of the family refer

Figure 21.20 Greater sac-winged bat (*Saccopteryx bilineata*). This common emballonurid is one of four species in this New World genus.

to their distinctive morphological features. They are known as sheath-tailed bats because of the way the tail protrudes through the uropatagium (see Figure 21.4A [j]) and slides up and down with movement of the hind limbs. They are also called sac-winged bats because of glandular wing sacs on the ventral surface of the wings near the elbow. The sacs are most prominent in males, and exude a red, odiferous substance that is important in pheromone production and attraction of females. Colonies of up to 60 individuals form in daytime roosts of greater sac-winged bats (*S. bilineata*; Figure 21.20), which are very vocal, highly social, and polygynous. Colonies at day roosts consist of several harem groups—a territorial male surrounded by several females (Fulmer and Knoernschild 2012). Scent from the sacs, as well as unusually complex audible vocalizations (songs; see box), function in male courtship displays (Behr and von Helversen 2004; Voigt et al. 2005). Males produce the complex territorial songs; young males learn songs from one or more older males and may recognize individual rivals from their songs (Eckenweber and Knoernschild 2013). Songs advertise to females the quality of the male as a potential mate (Behr et al. 2006), as do visual displays and scent-marking (Voight et al. 2008). The Seychelles sheath-tailed bat (*Coleura seychellensis*) is critically endangered. It occurs on only 3 islands in the Seychelles with a population size of <100 individuals. The Antioquian sac-winged bat (*S. antioquensis*) and the Pacific sheath-tailed bat (*Emballonura semicaudata*) are endangered (IUCN 2018).

Nycteridae

There is a single genus (*Nycteris*) and 16 species of slit-faced bats. Fourteen species are distributed throughout sub-Saharan Africa and Madagascar. The Malayan slit-faced bat (*N. tragata*) occurs in Malaysia, Sumatra, and Borneo, and the Javan slit-faced bat (*N. javanica*) is on the East Indies islands of Java, Bali, and Kangean. Nycterids occur in habitats ranging from semiarid areas to savannas and tropical forests, where solitary individuals or small colonies roost in caves, trees, houses, or animal burrows. For example, Egyptian slit-faced bats (*N. thebaica*) commonly roost in aardvark (*Orycteropus afer*) burrows (Monadjem et al. 2009). Nycterids are small to medium-sized bats weighing 10 to 30 g. Head and body length is 40 to 90 mm, with tail length up to 75 mm. They have large ears and a small tragus. The common name derives from the unusual longitudinal groove throughout the facial region (Figure 21.21), which, along with the external nose leaf, functions in their low-intensity echolocation calls, emitted through the nostrils. Zhuang and colleagues (2012) found that the nose leaf in *N. thebaica* functioned as a "double-curved reflector" to enhance directionality and improve detectability of targets. The uropatagium completely encloses the tail and is partially supported by the unique, T-shaped tip of the tail (see Figure 21.4A [i]). Most species are insectivorous, but the large slit-faced bat (*N. grandis*) also feeds on frogs and other small vertebrates (Bayefsky-Anand 2005), including other

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Bat Songs

Male birds with their colorful plumage are familiar sights during the breeding season as they perch in their territories and sing equally colorful songs to attract females—each species with its own recognizable song. Bird songs relay a great deal of intraspecific information because the songs have multiple syllables and different elements that are combined and ordered in various ways depending on different social contexts. These patterns are known as "syntax." Among mammals, however, whales are one of the only groups that are known to transmit learned vocalizations with defined syntax for communication; the familiar songs of the humpback whale (*Megaptera novaeangliae*) are one example.

Given the sophisticated echolocation signals of microchiropteran bats, it might be expected that they too would be capable of complex vocal songs for social communication—and many species are. For example, the sac-winged bat (*Saccopteryx bilineata*), a polygynous species, engages in complex courtship songs. Likewise, big brown bats (*Eptesicus fuscus*) have a large repertoire of social vocalizations. Male Brazilian free-tailed bats (*Tadarida brasiliensis*) may, however, be the singing superstars among chiropterans. Research by Bohn and colleagues (2013) found that males produce ultrasonic songs that are comparable to those of birds in their complexity. With three types of phrases (chirps, trills, and buzzes) and four types of syllables, male Brazilian free-tailed bats can

rapidly adjust their songs—that is, vary the syntax—in different situations. Singing is especially evident during the breeding season as it attracts mates, but songs also function in other social and ecological contexts. Like bird songs, bat songs function as part of reproduction, territoriality, migration, and metabolic constraints of flight. A great deal of recent research, in conjunction with technological advances, has shown a widespread degree of complex social communication via songs in a variety of bat species. In addition to visual, olfactory, and tactile communication, auditory signals in the form of calls and songs are likely critical in all bat species.

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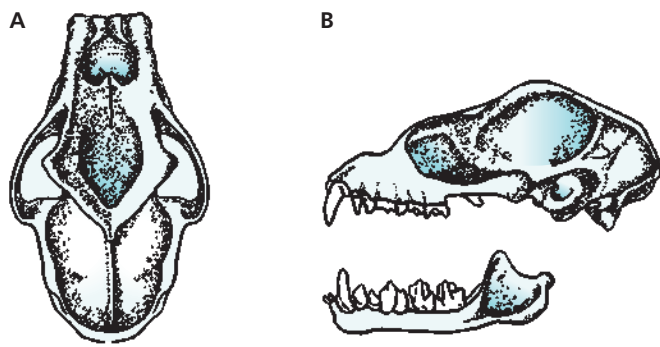
Figure 21.21 Skull of a slit-faced bat. (**A**) The dorsal aspect shows the deep concavity between the eye orbits. (**B**) Lateral view of the skull and mandible. *Adapted from Miller (1907).*

bats (Fenton et al. 1981). Griffiths (1997) described a post-laryngeal chamber that is distinctive in the two Asian species compared to nycterids from Africa. The conservation status of many species is unknown, but no nycterids are currently endangered.

SUPERFAMILY NOCTILIONOIDEA

Phyllostomidae

This large New World family of leaf-nosed bats consists of 62 genera and as many as 214 species (Burgin et al. 2018)—dozens of new species have been described since 2005 (Nogueira et al. 2012; Velazco and Gardner 2012; Botero-Castro et al. 2013 and references therein). Based on studies of dentition, nose-leaf structure, and skull features, Simmons (2005a) recognized 7 subfamilies, including the vampire bats (Subfamily Desmodontinae). Since then, several other subfamilies have been recognized or consolidated by other authorities (see Datzmann et al. 2010). Based on genetic and morphological analyses, Baker and colleagues (2016) in conjunction with Cirranello and coworkers (2016) recognized 11 subfamilies.

Phyllostomids are widely distributed from the southwestern United States through Central America, the Caribbean, and northern South America. They occur from sea level to high elevations, in habitats ranging from desert to tropical forest. Nose-leaf ornamentation is present in most genera, although it is not as pronounced as in the Old World leaf-nosed bats (Family Hipposideridae). For those genera of phyllostomids without the nose leaf, such as vampire bats and many fruit-eating species, the upper lip usually has some type of plate or other prominent outgrowth. The ears are sometimes connected at the base, and a tragus is present. A tail and uropatagium may or may not be present. Body sizes range from small species such as the little white-shouldered bat (*Ametrida centurio*), with a head and body length of 4 cm, to the largest New World species, the spectral bat (*Vampyrum spectrum*), with a head and body length of 13 cm and a wingspan of about 60 cm.

Phyllostomids also exhibit an unparalleled variety of feeding habits, probably the greatest diversity of any mammalian family (Baker et al. 2012). Many of the smaller species in the Subfamily Phyllostominae are insectivorous. Larger species in this subfamily, such as the spectral bat, the spear-nosed bat (*Phyllostomus hastatus*), and Peter's woolly false vampire bat (*Chrotopterus auritus*), are carnivorous, feeding on small vertebrates. Species within the Subfamily Glyphonycterinae also are insectivorous. Species in the Subfamilies Glossophaginae, Rhinophyllinae, Phyllonycterinae, Brachyphyllinae, Stenodermatinae, and Carolliinae feed primarily on nectar, pollen, or fruit. Datzmann and colleagues (2010) found that nectarivory arose independently in the Subfamilies Glossophaginae and Lonchophyllinae—as did the associated morphological adaptations of an elongated rostrum and tongue, reduced dentition, and hovering flight while feeding. Dietary diversification from insectivory to frugivory and nectarivory among subfamilies likely arose during the Miocene (Rojas et al. 2011).

The three species of true vampire bats in the Subfamily Desmodontinae are sanguinivorous—that is, they consume only blood. Their dentition is specialized (Figure 21.22), with large, sharp incisors for making an incision, and large canines. The cheekteeth are reduced in size, number, and complexity because blood does not require chewing. The common vampire bat (*Desmodus rotundus*) preys on mammals, especially large **ungulates** (hoofed mammals), both domestic and wild. In contrast, the white-winged vampire bat (*Diaemus youngi*) and the hairy-legged vampire bat (*Diphylla ecaudata*) prey primarily on birds.

Aspects of the biology of the common vampire bat are detailed in Brass (1994). Vampire bats make an incision about 1 cm long, 5 mm deep, and 4 mm wide (Davis et al. 2010) on the tail, snout, ears, feet, anus, or other area with sparse amounts of hair. Grooves on the sides and bottom of the tongue produce suction through capillary action while the bat laps up blood. Anticoagulant in the bat's saliva may keep the blood from coagulating for several hours. Nonetheless, blood loss is minimal, and the prey is usually unaware that it has been attacked. A vampire bat probably consumes about 25 ml/day (Wimsatt and Guerriere 1962). The open wound is subject to bacterial infections, parasites, and rabies, however. Also, vampire bats negatively impact the cattle industry by causing decreased weight gain and milk production of cows. This can make livestock ranching impractical in areas of Central and South America within the range of vampire bats (Streicker and Allgeier 2016). Voigt and Kelm (2006) used stable carbon isotope analyses to document the preference of vampire bats for cattle instead of free-ranging ungulates. They suggested that livestock, which are usually fenced in, were easier targets than free-ranging hosts. Lee and coworkers (2012) used ecological niche modeling to predict future distribution of *D. rotundus* and their impact on cattle. Zepeda Mendoza and colleagues (2018) found that common vampire bats had gut microbiota that was distinct from that of other types of bats, as well as unique aspects of their ge-

A

B

C
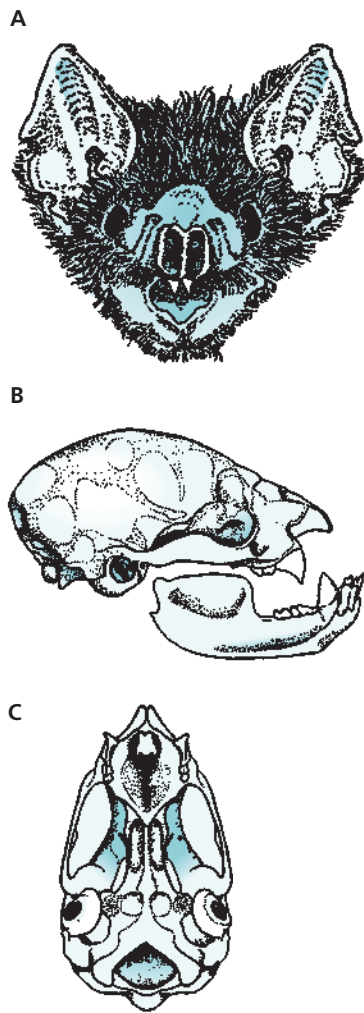
Figure 21.22 **The common vampire bat (*D. rotundus*).** (**A**) Note the flat nose and relatively large eyes. (**B**) Lateral view and (**C**) ventral view of the skull show the specialized teeth. The incisors and canines are enlarged, with great reduction in the size and number of molars. There is a total of 20 teeth; other phyllostomids have 32–34 teeth. *Adapted from Hill and Smith (1984).*

Figure 21.23 **Great fruit-eating bats (*Artibeus litura-tus*).** These individuals are on a palm frond in Panama; several species within this genus construct "tent" shelters from palm fronds.

nome involved in immune response that help protect them from viral pathogens in the blood they ingest.

Food-sharing in vampire bats (Wilkinson 1984, 1990) is a fascinating social behavior that is a rare example of re-ciprocal altruism. Vampire bats will starve to death if they do not eat for about three days. Within roosting colonies of females (males roost individually), a bat that has eaten recently regurgitates blood to a roost-mate that is close to starvation. Food-sharing occurs even between unrelated individuals but only in bats that have a close roosting as-sociation and can return the favor when necessary—a form of social bet-hedging (Carter and Wilkinson 2015, 2016; Carter et al. 2017). Blood-sharing was not observed in *D. youngi* (Schutt et al. 1999).

Phyllostomids use more types of roosts than any other family of bats—caves, trees, buildings, or the burrows of other animals, sometimes with other species of bats (Gar-bino and da Cunha Tavares 2018). Single individuals, small groups, or large clusters may occur. An example of a phyl-lostomid that forms exceptionally large colonies of 100,000 or more adults is the lesser long-nosed bat (*Leptonycteris cu-rasoae*). Although this species forages cooperatively, Flem-ing and coworkers (1998) observed no allogrooming, com-munal nursing, or food-sharing in a maternity colony. The tent-building bats (Genus *Uroderma*), the white bat (*Ecto-phylla alba*), and several species of fruit-eating bats (Genus *Artibeus*; Figure 21.23) construct a roost shelter by biting through the midrib of palm fronds, which causes the leaf to fold over and form a protective "tent." About 22 species of tropical bats are known to make tents; of these, 17 oc-cur in the New World (Rodriguez-Herrera 2018).

The Puerto Rican flower bat (*Phyllonycteris major*) and giant vampire bat (*Desmodus draculae*) are recently extinct. The Jamaican flower bat (*Phyllonycteris aphylla*), with only about 250 individuals, is critically endangered, as are the Aru flying fox (*Pteropus aruensis*), Livingstone's flying fox (*P. livingstoneii*), and the Vanikoro flying fox (*P. tubercula-tus*). Fourteen other species of phyllostomids are endan-gered (IUCN 2018).

Figure 21.24 **Wagner's mustached bat (*Pteronotus personatus*).** It occurs from Mexico to northern South America, where it forages for insects in riparian, forested areas. Note the enlarged lower lip.

Mormoopidae

The 2 genera (*Pteronotus* and *Mormoops*) and 17 species are known as mustached, ghost-faced, or naked-backed bats. Pavan and Marroig (2017) and Pavan and coworkers (2018) discussed geographic variation, diversification, and a revised taxonomy of *Pteronotus*, which now includes approximately 16 species. Mormoopids occur in semiarid to tropical forest habitats from the southwestern United States through Mexico, Central America, and the Caribbean, to northern South America. Based on mtDNA data, Davalos (2006) discussed the origin and subsequent distribution of the family, as well as species relationships. This New World family was considered a subfamily of the Phyllostomidae but gained family status based on work by Smith (1972). Mormoopids are small to medium-sized bats. All have a tail and a tragus with a secondary fold of skin, best developed in Genus *Mormoops*. This family differs from phyllostomids in that species lack a nose leaf and have very small eyes. The lips are enlarged and surrounded by numerous stiff hairs and, with a plate-like growth on the lower lip, form a funnel into the mouth (Figure 21.24). Davy's naked-backed bat (*Pteronotus davyi*) and the big naked-backed bat (*P. gymnonotus*) actually have thick pelage on their back but appear naked because their wings meet mid-dorsally, obscuring the fur. They roost in warm, humid caves and are gregarious, sometimes forming colonies of hundreds of thousands. All mormoopids are insectivorous, have long, narrow wings for rapid flight, and usually forage near water. Mora and coworkers (2013) examined echolocation in mormoopids.

Noctilionidae

Known as bulldog (Figure 21.25A), or fishing, bats, this family has a single genus (*Noctilio*) and 2 extant species distributed in tropical lowlands from northern Mexico to northern Argentina and on several Caribbean islands. Both species roost in cliffs, caves, buildings, and hollow trees lo-

A

B

Figure 21.25 **A fishing bat.** (**A**) From this close-up of the head, it is easy to see why they are also called "bulldog bats." Note the long ears and well-developed tragus, with a comb-like lateral edge, and the lack of a nose leaf. (**B**) A fishing bat taking a small fish from the water.

cated near the water. The greater bulldog bat (*N. leporinus*) has a head and body length up to 13 cm. Males can weigh 70 g and have a 50-cm wingspan. Pelage color varies from yellow to brown and apparently becomes darker in older, heavier individuals (Bordignon and de Oliveira-Franca 2004). These bats hunt at night and use their very long hind legs and large, rake-like feet with well-developed claws to scoop up small fish (Figure 21.25B), crustaceans, and aquatic insects. Prey is detected through echolocation near the surface of fresh or salt water (Schnitzler et al. 1994; Stulov 2013). These bats also take terrestrial invertebrates. Small groups usually forage together. The lesser bulldog bat (*N. albiventris*) is smaller, 8–9 cm in head and body length, with maximum body mass of about 40 g. The hind limbs are not as well developed as in *N. leporinus*, and it

Figure 21.26 **A thumbless bat (*Furipterus horrens*).** This Central and South American species is fairly common. *Adapted from Tomes (1856).*

feeds primarily on insects, again taken by echolocation; its diet also includes a small percentage of fruits and seeds (Aranguren et al. 2011). Kahn and colleagues (2014) found divergence of the 2 extant species occurred approximately 3 mya; thus, in an evolutionary timeframe, the dietary shifts between the species were very rapid. Pavan and co-workers (2013) used 1 nuclear and 2 mtDNA markers in a phylogenetic analysis of the family. They found 3 genetic lineages in *N. albiventris* that correspond to the current subspecies associated with South American river basins.

Furipteridae

The smoky bats include two genera, each with a single species. The thumbless bat (*Furipterus horrens*) is found from Costa Rica to Peru and Brazil. The smoky bat (*Amorphochilus schnablii*) occurs along coastal areas and interior valleys from western Ecuador to northwestern Chile. These bats are small: the body mass of *F. horrens* is only 3 g. They resemble funnel-eared bats in their general appearance (Figure 21.26), wing shape, inconspicuous nose leaf, ear shape, small tragus, and dense fur. Furipterids are also known as "thumbless bats" because this digit is so small and so enclosed in the wing membrane that it appears to be absent. Smoky bats are insectivorous and inhabit moist, low-elevation forested areas, where they roost in caves. Population numbers of smoky bats appear to be stable, and the species is no longer considered endangered (IUCN 2018).

Thyropteridae

There are 5 species of disk-winged bats in a single genus (*Thyroptera*). Peter's disk-winged bat (*T. discifera*) occurs from Nicaragua southward to northern South America. Spix's disk-winged bat (*T. tricolor*) is distributed from southern Mexico to Bolivia and southern Brazil. LaVal's disk-winged bat (*T. lavali*) is a rare species known from limited localities in northern South America. Gregorin and colleagues (2006) described DeVivo's disk-winged bat (*T. devivoi*) from four specimens in Brazil and Guyana. It is the sister taxon to *T. lavali*, with *T. tricolor* and then *T. discifera* as basal lineages. The most recently de-
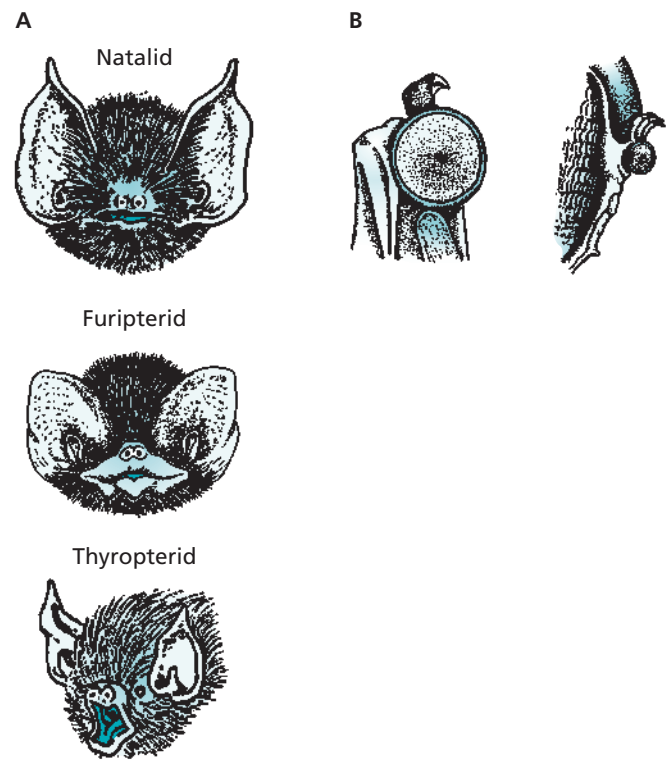
Figure 21.27 **Facial features and disk characteristics among three families of bats.** (**A**) (*Top*) Mexican funnel-eared bat (*Natalus stramineus*), (*center*) smoky bat (*Amorphochilus schnablii*), and (*bottom*) Spix's disk-winged bat (*Thyroptera tricolor*). Note the characteristic three fleshy projections on the lower lip of the smoky bat. (**B**) Adhesive disks of a disk-winged bat are larger on the wrist (*left*) than on the foot (*right*).

scribed species—Patricia's disk-winged bat (*T. wynneae*)—occurs in Brazil and Northeast Peru (Velazco et al. 2014). These bats are small: the body mass of *T. tricolor* is about 4 g. They are similar to the funnel-eared bats and smoky bats in features such as wing shape, high domed forehead, ear shape, and tragus (Figure 21.27A). The common name of these bats refers to their most striking anatomical feature: round, concave, suction disks at the base of the thumbs and on the soles of the feet. The larger thumb disks are attached by a short stalk, or **pedicle** (Figure 21.27B). Disks are used to cling to stems, leaves, and other smooth, hard surfaces. A single disk is capable of supporting an individual's body mass. These species occupy humid forests, usually near water, where they feed on insects. Adhering by their disks, they roost during the day, inside curled leaves of plants, often the fronds of banana trees (Genus *Heliconia*) or species of *Calathea* (Solano-Quesada and Sandoval 2010). Several individuals, possibly a family group, sometimes share a single leaf, which is usually used as a roosting site for only a brief time (Vonhof and Fenton 2004). Characteristics of the echolocation calls have been described for *T. discifera* (Tschapka et al. 2000) and *T. tricolor* (Fenton et al. 1999). Echolocation pulses are low intensity and include FM harmonics (see Table 21.2).
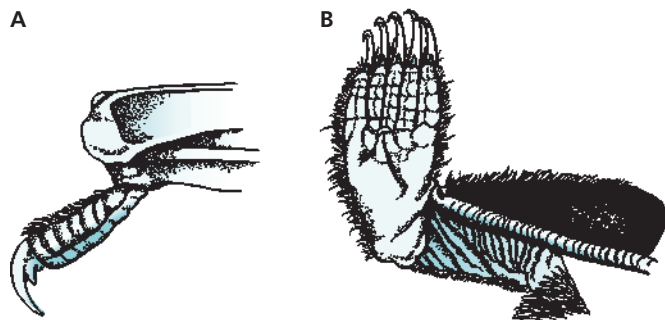
Figure 21.28 **Claws of the New Zealand short-tailed bat.** (**A**) The basal talon on the thumb is particularly evident. (**B**) Small talons also occur on the claws of the feet. Like flightless birds, these bats are highly adapted for terrestrial locomotion. *Adapted from Dobson (1876).*

Figure 21.29 **Old World sucker-footed bat (*Myzopoda aurita*).** Notice the fleshy, mushroom-shaped structure at the base of the ear. Its function is unknown. *Adapted from Thomas (1904).*

Mystacinidae

This small family of endemic New Zealand short-tailed bats includes only two species in Genus *Mystacina*. Historically, the phylogenetic position of this family has been enigmatic, with little consensus between morphological and molecular data. However, analyses by Teeling and colleagues (2012) suggest a close relationship of the short-tailed bats and noctilionoid families (see Figure 21.2). These bats occupy old-growth rainforests and have several morphological adaptations for terrestrial locomotion and capture of prey on the ground. They have very sharp claws on the hind feet and thumb, each with a small, basal talon (Figure 21.28). They also have a thick membrane along the side of the body. When an individual is not flying, the wings can be folded up, much like a sail. This makes the bats much more agile on the ground. The uropatagium can be "furled" in a similar manner. Riskin and coworkers (2006) studied the kinetics of terrestrial movement by lesser short-tailed bats (*M. tuberculata*); Parsons and colleagues (2010) found no biomechanical linkage between echolocation and limb movement when the species was walking.

New Zealand short-tailed bats roost in caves, trees, and burrows in forested areas. In a lesser short-tailed bat population at the highest latitude of the species' distribution, individuals during winter roosted alone about 50% of the time, and communally about 50% of the time. Summer roosts were in large trees, with well-insulated cavities and stable temperatures (Sedgeley 2001; 2003). Lesser short-tailed bats can remain more active than other species of bats during cold temperatures because of their ability to forage on terrestrial invertebrates. The only species of bat known to burrow, they use their upper incisors to excavate. The dentition is typical for insectivorous bats, although the diet is diverse; in addition to insects, they eat fruit, nectar, and arthropods. Two species were once widely distributed throughout New Zealand forests. The lesser short-tailed bat, the smaller of the two species with a body mass of 12–15 g, is now reduced
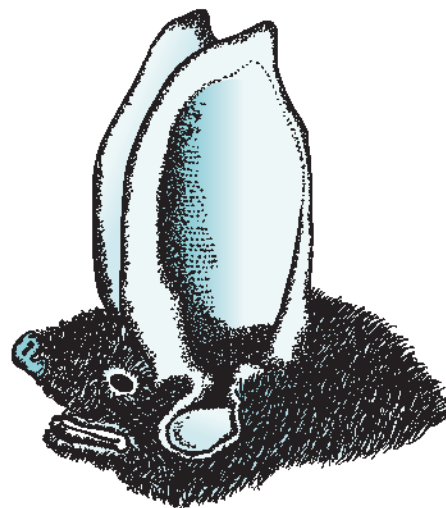
to a small number of populations and is threatened. The larger greater short-tailed bat (*M. robusta*), with a body mass of 25–35 g, was last seen in 1967 on Big South Cape Island. Although listed as critically endangered, the species is likely extinct. The fossil record of mystacinids extends to the early Miocene (Hand et al. 2015; 2018).

Myzopodidae

This family was considered to include only the insectivorous sucker-footed bat (*Myzopoda aurita*), which is **endemic** to Madagascar. A second myzopodid, Schliemann's sucker-footed bat (*M. schliemanni*), was described by Goodman and colleagues (2007) based on pelage color, cranial characteristics, and external measurements, and later confirmed using mtDNA analyses (Russell et al. 2008). Like the New World disk-winged bats (Family Thyropteridae), myzopodids have suction disks at the base of the thumbs and soles of the feet. There is no stalk associated with the thumb disk of sucker-footed bats, however. The discs in myzopodids and thyropterids also differ anatomically (Schliemann and Maas 1978). Disks probably evolved independently in each family, another example of convergent evolution. A mushroom-shaped process at the base of the ear (Figure 21.29) in myzopodids is unique. Whereas *M. aurita* is restricted to rainforest habitats on the east coast of the island, *M. schliemanni* occurs in dry forests of western Madagascar. Interestingly, *M. aurita* (and presumably *M. schliemanni*) roosts with its head up—unlike all other bats. It clings to smooth leaves, often of the traveler's palm (*Ravenala madagascariensis*), using the disks on its wrists and ankles. Riskin and Racey (2010) found that such clinging was more characteristic of wet adhesion than of suction and

that it helped explain their head-up posture. Gunnell and colleagues (2014) described 2 new species and a new genus (*Phasmatonycteris*) of fossil myzopodids from the late Eocene–early Oligocene of Egypt.

SUPERFAMILY VESPERTILIONOIDEA

Vespertilionidae

There are more species of common bats than any other family of chiropterans. They enjoy a worldwide distribution in tropical, temperate, and desert habitats and are absent only from polar, high-elevation areas and some oceanic islands. Simmons (2005a) recognized 48 genera and 407 species of vespertilionids in 6 subfamilies: the Vespertilioninae, with the most genera and species by far; as well as Subfamilies Myotinae; Kerivoulinae (see Kuo et al. 2017); Murininae; Antrizoinae; and Miniopterinae, which is now elevated to family status (see next section). Burgin and colleagues (2018) recognized 54 genera and 493 species of vespertilionids, with new species being described on a fairly regular basis. Within the Subfamily Myotinae, Genus *Myotis* (with >100 species) is the most widely distributed genus of bat, occurring worldwide. Because there are nearly 500 species in this family, there is a great deal of diversity in size, pelage coloration, and morphological features. Head and body length ranges from 3 to 10 cm, and adult body mass from 4 to 50 g. The eyes are small, and a nose leaf is absent, except for a rudimentary one in the New Guinea big-eared bat (*Pharotis imogene*) and the long-eared bats (Genus *Nyctophilus*). The ears of some species are exceptionally large, up to 4 cm in *Corynorhinus* (Figure 21.30). A well-developed tragus usually is present. The total number of teeth varies from 28 to 38, with reduced dentition usually through loss of premolars. The number of molars is always

Figure 21.30 **Large ears occur on some vespertilionid bats.** Huge ears are evident on this Virginia big-eared bat (*Corynorhinus townsendii virginianus*).

3/3, and the cusp pattern of upper molars is dilambdodont. Species generally are insectivorous, although there are a few exceptions. For example, the fish-eating bat (*Myotis vivesi*) has adaptations similar to those of noctilionids, whereas the pallid bat (*Antrozous pallidus*) feeds on scorpions, beetles, other ground-dwelling prey, and occasionally fruit.

Caves are often favored roosting sites, although vespertilionids use many different types of shelter. Depending on the species, roosting may be solitary, in small clusters of a few individuals, or in large groups of thousands. Roosts may contain more than one species, although they generally do not form mixed clusters. Because insects are unavailable during winter, species in temperate regions either migrate or hibernate. Like other hibernators, bats arouse periodically throughout the winter. Although they may fly, they do not feed (Whitaker and Rissler 1993). Hibernating species may exhibit delayed fertilization, with females segregating into maternity colonies. In tropical species, breeding (without delayed fertilization) can take place throughout the year. Nevertheless, a single neonate is typical, although again there are exceptions. Some of the smaller species have two young; litters of up to four young can occur in Genus *Lasiurus*.

In North America, the Indiana bat is endangered, as are at least 14 other species worldwide. Critically endangered species include: the Bala tube-nosed bat (*Murina balaensis*), known only from a 4 km² area in south Thailand; the gloomy tube-nosed bat (*M. tenebrosa*), not found since 1962 and likely extinct; the Armenian whiskered bat (*Myotis hajastanicus*), not found since the 1980s and also likely extinct; the Yanbaru whiskered bat (*M. yanbarensis*); the Lord Howe long-eared bat (*Nyctophilus howensis*), known only from a single skull found in 1972 and not found since; the New Caledonia long-eared bat (*N. nebulosus*); and Thomas's big-eared bat (*Pharotis imogene*), not seen since 1890 and likely extinct. The Christmas Island pipistrelle (*Pipistrellus murrayi*) was considered critically endangered but is now listed as extinct because the last individual was seen in 2009, and none has been found since then despite extensive surveys (IUCN 2018). The earliest fossil vespertilionids are from the early Eocene (Gunnell et al. 2017).

Miniopteridae

Formerly considered a subfamily of Family Vespertilionidae, the miniopterids were raised to family status based on molecular genetic data (Hoofer and van den Bussche 2003; Miller-Butterworth et al. 2007) as well as morphological differences. Known as the long-winged or bent-winged bats, they form a single genus (*Miniopterus*) and from 19 to as many as 35 species. The validity of some species and relationships among species vary widely among authorities, but a proliferation of new—formerly cryptic—species has been described, especially from Madagascar and the Comoro Archipelago (Goodman et al. 2009, 2015; Christidis et al. 2014). The family is widely distributed throughout

much of Africa, southern Europe, India, Southeast Asia, Japan, Australia, and many South Pacific islands.

These are fairly large bats. Total length is from 80 to 140 mm, with forearm lengths up to 55 mm and body weights from 6 to 20 g. They are highly gregarious and form large colonies. Miniopterids roost in caves, rock crevices, trees, and buildings, and they hibernate in colder regions of their range. The Southeast Asian long-fingered bat (*M. fuscus*), endemic to Japan, is endangered, as is the Loyalty bent-winged bat (*M. robustior*), known only from Lifou and Maré in the Loyalty Islands of New Caledonia.

Cistugidae

Like the miniopterids, this recently recognized family (Lack et al. 2010) was formerly included in Family Vespertilionidae. The cistugids include a single genus (*Cistugo*) and two rare species of wing-gland, or hairy, bats found in southern Africa—the Angolan hairy bat (*C. seabrae*) and Lesueur's hairy bat (*C. lesueuri*). These small bats formerly were grouped in the large Genus *Myotis* but differ in aspects of dentition (Kearney and Van Schalkwyk 2009) and by having wing glands that are evident in living animals, but not dried museum specimens. Hairy bats occur in arid regions, where they forage around groves of trees, taking insects in the air and by gleaning them off foliage.

Molossidae

The 19 genera and approximately 122 species (Burgin et al. 2018) of free-tailed bats are distributed worldwide from southern Europe, Africa, Asia, and Australia to the Fiji Islands. In the New World, they occur from southwestern Canada, through the United States and the Caribbean, to Central America, and most of South America. Molossids are fast-flying, aerial insectivores that occur in habitats from forests to deserts. The family name derives from the Greek *mollossus*, or mastiff—a reference to the general dog-like snout of these bats (Figure 21.31A). They are medium-sized to large bats, with head and body length from 4 to 13 cm. The large ears meet on the forehead and point forward; there is a tragus but no nose leaf. The common name results from the tail extending well beyond the outer edge of the uropatagium (see Figure 21.4A [g]; Figure 21.31B). Molecular analyses by Ammerman and colleagues (2012) suggested that molossids originated in the Paleocene. Gregorin and Cirranello (2016) produced a phylogeny of molossids based on morphological data. They found two clades, both intermixed with Old and New World genera, and several genera that were not monophyletic. Amador and coworkers (2018) felt the family should be thoroughly revised.

Molossid fur is short and fine. In the two species of *Cheiromeles*, the hair is so short and sparse that they are called "naked bats." Schutt and Simmons (2001) described unique characteristics of the thumb and calcar for the greater na-

Figure 21.31 Free-tailed bats (*Tadarida*). (A) A free-tailed bat from South Africa, likely *T. aegyptiaca*; (**B**) close up of the tail and uropatagium of a Mexican free-tailed bat (*T. brasiliensis*). Note the long hairs of the feet. This common molossid may form aggregations of millions of individuals. They also engage in sophisticated singing, especially during the mating season.

ked bat (*Cheiromeles torquatus*) and the lesser naked bat (*C. parvidens*). They suggested that these structures could be related to a greater amount of quadrupedal locomotion in these species compared to other molossids. Other free-tailed bats often have sensitive, erectile tufts, or crests, of hair between the ears, associated with glands. In the Genera *Tadarida* and *Molossus*, males have throat glands. Molossids generally are swift aerial insectivores with high-aspect-ratio wings (see Figure 21.6F).

The dentition is typical of insectivorous bats; total number of teeth ranges from 26 to 32, depending on the

species. Lee and McCracken (2005) analyzed fecal pellets from 3 colonies of Brazilian free-tailed bats (*Tadarida brasiliensis*) in Texas and documented extremely diverse remains from 12 orders and 35 families of insects. Unlike most other bats, *T. brasiliensis* can forage at very high altitudes—900 m or more above the ground (McCracken et al. 2008). Molossids do not hibernate, although species in north temperate regions, such as the mastiff bat (*Eumops perotis*) and Brazilian free-tailed bat, may migrate and go into torpor during the winter. They roost in caves, buildings, trees, rock crevices, and on foliage. They can be solitary, roost in small groups, or form extremely large aggregations. Brazilian free-tailed bats are especially gregarious; large numbers congregate in the southwestern United States. For example, an estimated 20 million *T. brasiliensis* have been reported from a single cave in central Texas. Carlsbad Cavern, in New Mexico, is famous for its large colony of free-tailed bats. These are the largest aggregations of any species of mammal. Because accurate estimates of colony sizes are very difficult to make, however, some historical estimates may be exaggerated (Hristov et al. 2010). Five molossid species are currently endangered (IUCN 2018): the São Tomé free-tailed bat (*Chaerephon tomensis*), the equatorial dog-faced bat (*Molossops aequatorianus*), the Mauritian free-tailed bat (*Mormopterus acetabulosus*), the blunt-eared bat (*Tomopeas ravus*), and the Fijian free-tailed bat (*Tadarida bregullae*).

Natalidae

The 3 genera (*Natalus*, *Chilonatalus*, and *Nyctiellus*) and 11 or 12 species of funnel-eared bats occur from northern Mexico to northern South America, and on many Caribbean islands. Tejedor (2011) in a taxonomic revision of the family recognized 12 species. Natalids are small bats. Head and body length is 35 to 55 mm, and adults weigh from 4 to 10 g. The long, soft dorsal pelage is yellow to reddish brown. The tragus is short, and the large ears are funnel-like, giving the family its common name. The forehead region is domed, and there is no nose leaf. Adult males have an unusual mass of glandular sensory cells, the "natalid organ," below the skin of the forehead. The wings are long and slim (a high aspect ratio), and natalids have an erratic, butterfly-like flight as they consume insects. These bats roost alone or in small clusters far back in caves and tunnels in lowland areas with high humidity. Morphological analyses suggested that natalids were most closely related to two other small New World families, the Furipteridae (the thumbless bats) and the Thyropteridae (the disk-winged or sucker-footed bats). However, molecular analyses (Dávalos 2005) placed funnel-eared bats in close association with the Vespertilionidae and Molossidae (see Figure 21.2). The Jamaican greater funnel-eared bat (*Natalus jamaicensis*) is critically endangered because of very limited distribution, habitat loss, and low population size.

SUMMARY

- Bats are second only to rodents in the number of species in the order, and represent unparalleled diversity among mammals.
  - No order is more diverse in feeding niches used: they are insectivorous; frugivorous, nectarivorous, carnivorous, piscivorous, or sanguinivorous.
  - Bats are also diverse in their reproductive patterns: they exhibit spontaneous ovulation, delayed fertilization, delayed implantation, or delayed development.
  - Roosting ecology likewise varies among species: bats can roost in large colonies of millions, in smaller aggregations, in clusters of a few individuals, or be solitary.
  - Roosting habits depend on interrelated characteristics of social organization, foraging ecology, predator avoidance, and reproduction.

- All bats have highly modified forearms and hands that form wings, and they are the only mammals that fly.
  - There is diversity in the shape of wings, quantified in measures of aspect ratio and wing-loading capacity.
  - These measures reflect the habitat, foraging characteristics, degree of maneuverability, and general life history characteristics of bat species.

- Bats are also diverse morphologically.
  - Most bats are small—many are <10 g body mass.
  - The largest bats are in Family Pteropodidae (Old World fruit bats); they can reach 1,200 g and have wingspans close to 2 m.
  - Unlike other bats, pteropodids have simple facial characteristics—no nose leaf or other ornamentation, relatively large eyes, and ears without a tragus—and they do not echolocate.

- All other families of bats (microchiropterans) echolocate.
  - They sense their immediate environment and "locate" food or objects from the echoes returned from high-frequency sound pulses.
  - Species differ in the characteristics of sound-pulse duration, timing, frequency modulation, intensity, and length of signals.

- Several species of bats worldwide are critically endangered or have recently gone extinct because of loss of roosting and foraging habitat, cave closure, insecticide accumulation, and other adverse influences. Despite the many positive economic benefits provided by bats, this fascinating group of mammals continues to suffer because of human misconceptions and unfounded fears.

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DISCUSSION QUESTIONS
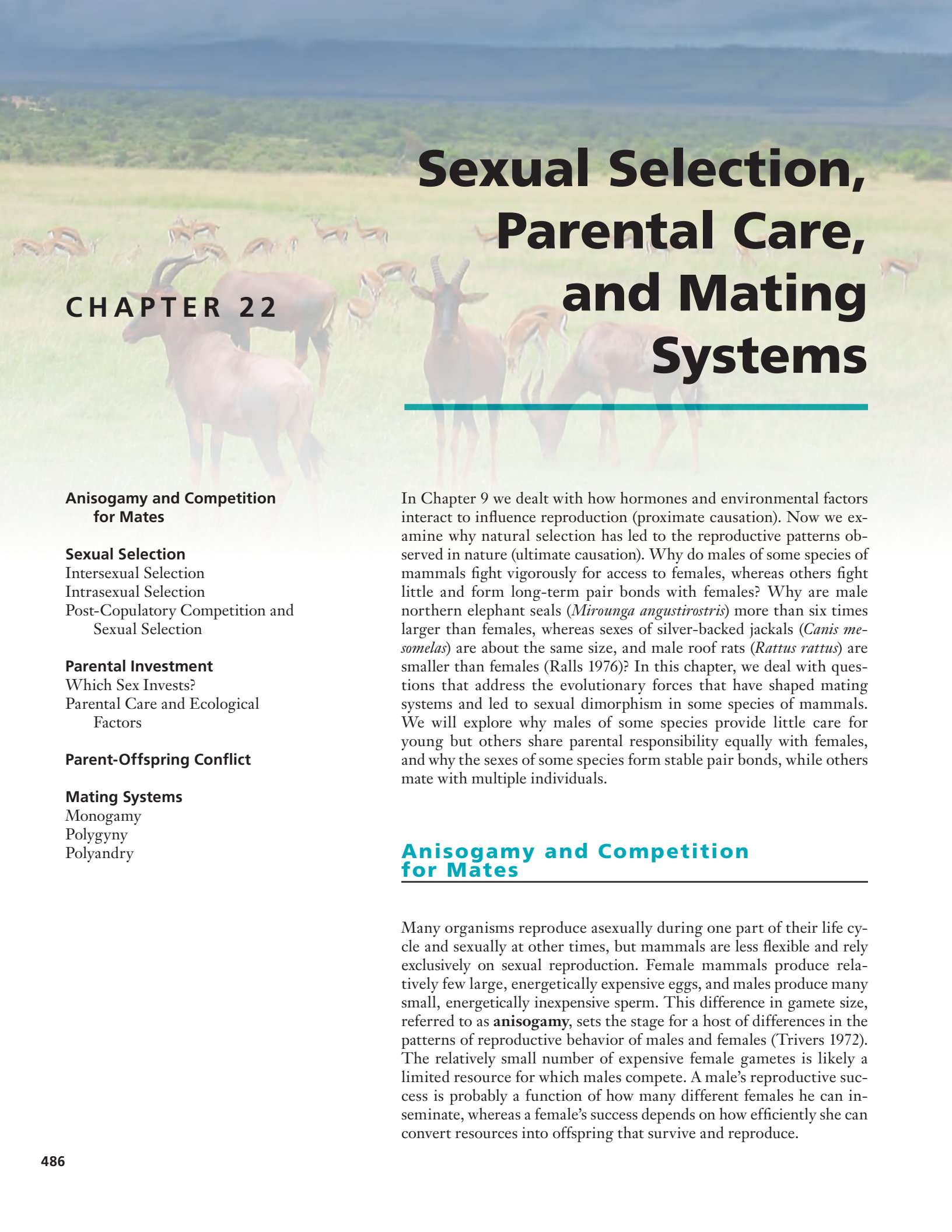
1. Given the active dispersal abilities of bats because of their ability to fly, why have the large fruit bats (Pteropodidae) never dispersed to tropical areas of the New World. Likewise, why have myzopodids remained endemic to Madagascar, and mystacinids never dispersed beyond New Zealand?

2. What kinds of technological difficulties do you suspect may have limited early investigators in their studies of bat echolocation? What kinds of technological advances have allowed researchers to study bat echolocation in the field and the laboratory, as well as movement patterns and foraging ecology of bats?

3. Vampire bats have highly specialized diets consisting only of blood. How might this specialization have arisen during the evolution of these bats? Why do you think vampire bats are restricted in their distribution to tropical areas? Given convergent evolution in other features of bats, why has sanguinivory never arisen in any Old World bats?

4. Generally, there is an inverse relationship in mammals between body size and litter size—small species have larger litters than large species. Nonetheless, most bats are small, and they have small litters (usually one young). Why?

5. Likewise, there is a direct relationship between mammal body size and life span—larger species generally live longer than smaller species. How do bats fit this pattern?

Behavior and Ecology

In Part 4, we tie together the structural, functional, and ordinal characteristics of mammals and consider what mammals do as they interact with their environment and each other. We explore these ideas in the context of the discipline of **behavioral ecology**, which is the study of evolutionary causes and fitness consequences of behavioral decisions. In Chapter 22, we examine reproductive behavior—acquiring mates and caring for young—and the evolutionary and ecological drivers that shape the diversity of mating systems exhibited by mammals. Almost all mammals are social (i.e., live in groups) at some time in their lives, and in Chapter 23, we focus on social behaviors among individuals and how selection has shaped evolution of sociality in mammals. Chapter 24 explores how mammals obtain resources required to support survival and reproduction (e.g., food, water, shelter, mates), and how the distribution of those resources influences patterns of space use and movement. Chapters 25 and 26 address mammals in the context of population and community ecology. These two chapters form a continuum that begins with single-species populations, expands in scope to include interactions among different species, and finally includes the structure and function of mixed-species communities.

Sexual Selection, Parental Care, and Mating Systems

In Chapter 9 we dealt with how hormones and environmental factors interact to influence reproduction (proximate causation). Now we examine why natural selection has led to the reproductive patterns observed in nature (ultimate causation). Why do males of some species of mammals fight vigorously for access to females, whereas others fight little and form long-term pair bonds with females? Why are male northern elephant seals (*Mirounga angustirostris*) more than six times larger than females, whereas sexes of silver-backed jackals (*Canis mesomelas*) are about the same size, and male roof rats (*Rattus rattus*) are smaller than females (Ralls 1976)? In this chapter, we deal with questions that address the evolutionary forces that have shaped mating systems and led to sexual dimorphism in some species of mammals. We will explore why males of some species provide little care for young but others share parental responsibility equally with females, and why the sexes of some species form stable pair bonds, while others mate with multiple individuals.

Anisogamy and Competition for Mates

Many organisms reproduce asexually during one part of their life cycle and sexually at other times, but mammals are less flexible and rely exclusively on sexual reproduction. Female mammals produce relatively few large, energetically expensive eggs, and males produce many small, energetically inexpensive sperm. This difference in gamete size, referred to as **anisogamy**, sets the stage for a host of differences in the patterns of reproductive behavior of males and females (Trivers 1972). The relatively small number of expensive female gametes is likely a limited resource for which males compete. A male's reproductive success is probably a function of how many different females he can inseminate, whereas a female's success depends on how efficiently she can convert resources into offspring that survive and reproduce.

Several features of mammalian reproduction further promote differences in reproductive behavior between the sexes: fertilization occurs in the oviducts, so it is certain that the female is the biological parent of offspring born to her, but paternity is not as certain. Also, only female mammals gestate and lactate, which limits the investment males can make in offspring. One result of these differences is that the sexes are likely to follow different strategies to maximize their reproductive success. Bateman (1948) demonstrated in laboratory populations of fruit flies (*Drosophila melanogaster*) that nearly all the females mated, but some males mated several times while others failed to mate at all. Consequently, the variance in mating success was higher for males than for females, and males that copulated the most sired the most offspring. Females, on the other hand, needed to mate only once to produce the maximum number of offspring. The slope of the regression line between mating success and reproductive success is referred to as the **Bateman gradient**, and the sex with the steepest slope (usually males in mammals) is likely to experience the strongest selection pressure on traits that enhance mating success (Andersson 1994). More recently, studies have demonstrated that females of some species can benefit from mating with multiple males, and others have questioned the results of Bateman's original experiments (Gowaty et al. 2012). Nonetheless, the concept of Bateman gradients "represents one of the cornerstones of modern evolutionary theory" (Clutton-Brock 2017:2).

When reproductive success is determined over an animal's entire life (lifetime reproductive success), the differences between the sexes can become more evident, especially in species where male-male competition for access to grouped females is intense. For example, male African lions (*Panthera leo*) have a much higher variance in lifetime reproductive success than females (Packer et al. 1988; Figure 22.1), which experience nearly equal lifetime reproductive success within a pride (Packer et al. 2001). The term
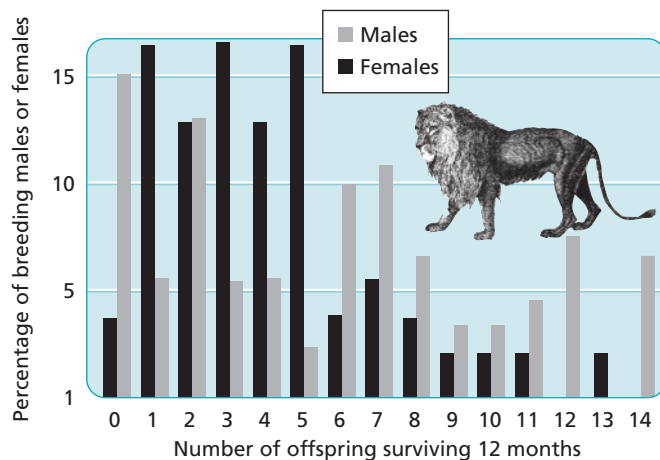
reproductive skew is used to describe the degree to which breeding in group-living species is monopolized by a subset of individuals in one sex relative to the other. For African lions, reproductive skew would be higher in males than females. However, a recent review of reproduction across polygynous mammals suggested that reproductive skew among males, when evaluated over their lifetimes, might be less than expected because of the short tenure of breeding males in groups (Lukas and Clutton-Brock 2014).

Availability of potential mates can also influence competition for mating opportunities and selection for traits associated with securing mates. The sex ratios of populations of most species tend to be about 50:50 at birth or hatching, but they can deviate significantly among adults. The **operational sex ratio** (**OSR**) considers only the reproductively active members of the population—specifically, it represents the ratio of males to females that are ready to mate at a particular time (Figure 22.2). Deviations in this ratio can have a large influence on the mating system, as members of the more abundant sex compete for access to members of the scarcer one (Emlen and Oring 1977). Both the Bateman gradient and the OSR reflect competition for mating opportunities and the potential for selection to act

Figure 22.2 Mammals with contrasting operational sex ratios. (**A**) Roosevelt elk (*C. c. roosevelti*) breed annually and synchronously, and consequently, most adults of both sexes are ready to mate at the same time. (**B**) In contrast, white rhinoceros (*Ceratotherium simum*) females can give birth at any time of year at 2.5- to 3-year intervals. Hence, the operational sex ratio is skewed towards males since most adult males but only a few females will be ready to mate at any given time.

Figure 22.1 Lifetime reproductive success for African lions. Female reproductive success varies little; most females produce 1–5 surviving offspring. Male reproductive success varies widely; males sire 0–14 offspring. *Data from Packer et al. (1988).*

on traits that influence an individual's mating success (Kokko et al. 2012).

Sexual Selection

Differences between the sexes can be dramatic, and other than the reproductive organs, they cannot be readily explained as products of natural selection. In *The Descent of Man, and Selection in Relation to Sex* (1871), Charles Darwin introduced the concept of **sexual selection**, a process that produces morphological and behavioral traits that affect an individual's ability to acquire mates. He believed that sexual selection was a different process than natural selection because it could produce traits that might reduce an individual's survival and thus oppose natural selection. It is likely that many mammalian traits are acted upon by both types of selection, but an important point to remember is that the *net effect* on an individual's fitness must be positive for a sexually selected trait to persist.

Sexual selection can be divided into two types: one in which members of one sex choose certain mates of the other sex (**intersexual selection**), and a second in which individuals of one sex compete among themselves for access to the other sex (**intrasexual selection**). A result of either mechanism is that the sexes evolve to look (and behave) differently—that is, they are **sexually dimorphic**.

INTERSEXUAL SELECTION

Often, individuals of one sex (usually the males in mammals) "advertise" that they are worthy of an investment; then members of the other sex (usually females) choose among them. Fisher (1958) developed a model for how exaggerated traits could evolve. Suppose a male trait (e.g., antlers or bright colors, Figure 22.3) is preferred by females, for whatever reason. If the trait is heritable, then females that mate with males exhibiting the trait are likely to produce male offspring with that trait and female offspring that prefer that trait when choosing a mate of their own. Further development of the trait proceeds in males, as does the preference for it in the females, resulting in what has been called **runaway selection**.

Sexually selected traits can become so exaggerated that survival of the males is reduced. In these cases, natural selection favoring less ornamented males would be expected, and the trait exhibited by males would reflect the opposing forces of natural and sexual selection. An often-cited example of runaway sexual selection in mammals is that of the extinct Irish elk (*Megaloceros giganteus*). The enormous antlers of Irish elk—much larger than those of the extant North American elk or wapiti (*Cervus canadensis*)—apparently functioned for social display (Figure 22.4), but little evidence supports the notion that heavy antlers directly caused their extinction (Barnosky 1985).

Alternatives to Fisher's runaway selection hypothesis are several "good genes," or **indicator models**, which assume that the trait favored by females in some way indicates male fitness. One is the **handicap hypothesis** proposed by Zahavi (1975). Agreeing that sexual selection can produce traits that are detrimental to survival, he added that such traits are both costly to produce and linked to superior qualities in the males. Important to this hypothesis is the notion of **truth in advertising**: the male's handicap must be honest and linked to overall fitness. Only in this way do females benefit by choosing to mate with a male with this handicap. Antlers of deer could be viewed as a handicap because any male that can bear the energetic and nutritional cost of such structures and still survive must be fit indeed. One problem with this model is that when a male with a handicap is picked by a female, not only are his favorable traits passed on to his offspring but so are the genes for the handicap, which should be selected against. In addition to selecting for good genes, genetic compatibility or dissimilarity also might influence mate choice by females. When fitness is higher in heterozygous offspring, females might be expected to choose mates with genotypes that are dissimilar to their own, and indeed, this pattern is evident in studies examining the major histocompatibility complex (MHC) loci (Clutton-Brock and McAuliffe 2009).

Although Darwin and Fisher thought of sexual selection as a process distinct from natural selection, some biologists argue that the two are inseparable. Kodric-Brown and Brown (1984) claimed that most sexually selected traits are aids, rather than handicaps, to survival. Thus, a male deer with a big set of antlers may be dominant over other males and may have better access to a food supply. They further argue that the sexually selected trait must be a reliable indicator of the male's condition. Thus, the trait must not be entirely genetically fixed but rather must also be influenced by environmental conditions.

Evidence for an indicator role for a sexually selected trait comes from a different hypothesis put forth by Hamilton and Zuk (1984). Working with birds, they argued that sexually selected traits have evolved to reveal an animal's state of health—specifically, resistance to parasites or disease. They predicted that if brightness of plumage is linked to overall condition, such that brighter males are relatively disease-free, then they would be preferred as mates. Some experimental evidence, mostly from birds, supports the Hamilton-Zuk hypothesis, but the idea is still controversial, and alternative explanations have been proposed. In a study of a provisioned colony of mandrills (*Mandrillus sphinx*), the most brightly colored primate, there was no correlation between the redness of the face or rump of either sex and parasite loads or measures of immune system function (Setchell et al. 2009). Thus, there was no evidence that bright colors were indicators of overall health in this species under the study conditions. So far, however, there are very

Figure 22.3 Secondary sexual characteristics of male mammals. Traits that function in male-male competition, for example enlarged canines on Siberian musk deer (*upper left*) or large tusks and bodies in African elephants (*upper right*), are influenced by intrasexual selection, whereas traits that attract potential female mates like bright colors in the Mandrill (*lower right*) are likely shaped by intersexual selection. Many male characteristics (e.g., large antlers on moose, *lower left*) could be favored by both types of selection if they are used to compete with other males for access to mates, but also serve as a signal of male quality that attracts females.

few tests of the Hamilton-Zuk hypothesis, but application of modern genomic techniques to host-parasite systems provides promise for a robust test of the hypothesis in mammals (Balenger and Zuk 2014).

In addition to the size or color of sexually selected traits, the symmetry of paired traits also might indicate fitness. **Fluctuating asymmetry** (FA) refers to random deviations from bilateral symmetry in paired traits (Andersson 1994). This means, for example, that when a paired trait, such as horns or canines, is measured for length, thickness, or

some other attribute, the right and left sides may differ. These deviations are thought to reflect the inability of the organism to maintain developmental homeostasis (i.e., symmetry) in the presence of environmental variation and stress (Beasley et al. 2013). Greater asymmetry is associated with environmental factors, including low food quality and quantity, habitat disturbance, pollution, and disease, and with genetic factors, such as inbreeding, hybridization, and mutation. For example, the stress of vegetation removal caused an increase in asymmetry of mandible development

Figure 22.4 Male of the extinct Irish elk. The enormous antlers of Irish elk were much larger than those of modern-day elk and might have been a consequence of runaway sexual selection.

in least shrews (*Sorex cinereus*; Badyaev et al. 2000). Northern elephant seals suffered a severe loss of genetic diversity after overhunting by humans at the end of the 19th century. After this genetic "bottleneck," there was an increase in asymmetry of several bilateral skull characteristics (Hoelzel et al. 2002). Some studies have supported the contention that symmetrical individuals are likely to be dominant, have higher fitness, and be preferred as mates. For example, female mountain goats (*Oreamnos americanus*) with more symmetrical horns exhibited better body condition, greater body mass, and higher dominance than those with asymmetrical horns (Côté and Festa-Bianchet 2001), male fallow deer (*Dama dama*) with symmetrical antlers were dominant over those with asymmetrical antlers (Maylon and Healy 1994), and male oribi (*Ourebia ourebi*) with symmetrical horns had larger harems than did asymmetrical males (Arcese 1994). However, other studies of mammals have not documented links between FA and fitness correlates (e.g., Kruuk et al. 2003; Ginot et al. 2018), and much remains to be learned about the causes and consequences of FA.

INTRASEXUAL SELECTION

Intrasexual selection involves competition among individuals of one sex (usually males in mammals), with the winner gaining access to mating opportunities with the opposite sex. Competition often occurs before mating, and traits like those associated with male-male combat are selected. Many male ungulates in deer (Family Cervidae) and African antelopes (Family Bovidae) are typically solitary or live in all-male groups for most of the year; as the breeding season approaches, they engage in highly ritualized displays and combat, often using their antlers or horns. The winners of these contests gain dominance and do most of

the mating. Other male traits favored by intrasexual selection include large body size in species that engage in combat involving sparring (pushing; e.g., bison, elephants) and enlarged canines in males that inflict biting or slashing wounds during combat (e.g., equids, musk deer, primates; see Figure 22.3).

Both types of sexual selection can operate at the same time on the same traits, and often it can be difficult to determine which type of selection is operating to produce an observed effect. Secondary sexual traits such as large body size or head ornamentation might also be indicators of male status or quality, and careful experiments are needed to disentangle the selective forces at work (Charlton 2013). One such study experimentally manipulated antler size in white-tailed deer while segregating males to isolate female choice from the effects of male-male competition (Morina et al. 2018). Moreover, females might subtlety exert control over the choice of a mate even in systems with strong male-male competition. For example, Alaska moose (*Alces alces gigas*) exhibit a harem breeding system in which one male attempts to defend a group of females from rivals. Females vocalize loudly when a smaller male attempts to copulate, which draws the attention of other males, often inciting competition and ensuring that the female mates with the most dominant male (Bowyer et al. 2011). Indeed, given the obvious nature of male-male competition for mates in many species of mammals, the role of female mate choice in determining mating success has often been overlooked (Clutton-Brock and McAuliffe 2009).

POST-COPULATORY COMPETITION AND SEXUAL SELECTION

Competition among males to sire offspring does not necessarily cease with the act of copulation. Females of some species may mate with several males during a single estrous period, creating the possibility of **sperm competition**—that is, a situation in which sperm from different males compete to fertilize eggs within the female's reproductive tract (Parker 1970). Similarly, females might evolve strategies to choose which sperm inseminate their eggs; this strategy is referred to as **cryptic female choice** (Thornhill 1983). As before mating, opportunities for sexual selection arise to influence both processes (i.e., male-male competition and female mate choice) following copulation, and both sexes exhibit adaptations to exert their control.

Male strategies include mate-guarding behavior after copulation and the coagulation of ejaculate forming a copulatory plug in the female reproductive tract; both of these strategies reduce the chance of sperm displacement by subsequent males. Copulatory plugs have been documented in numerous mammals including rodents, bats, primates (Edward et al. 2015), and at least one carnivore, the masked palm civet (*Paguma larvata*; Jai et al. 2002), and recent studies have confirmed their role in sperm competition (Sutter et al. 2015; Mangels et al. 2016). Other male
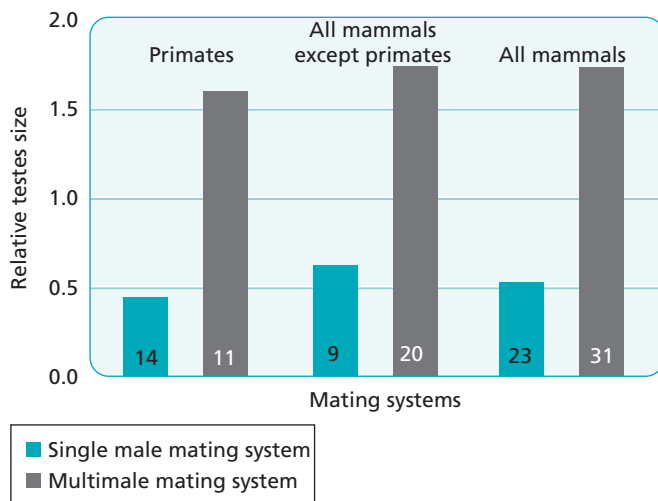
Figure 22.5 Mean relative testes size of mammals in relation to mating system. Sample sizes are at the bottom of each column. Species in which more than one male mates with a female have relatively large testes. *Data from Kenagy and Trombulak (1986).*

adaptations include increasing the number of sperm released, adjusting sperm allocation to the situation, or altering the timing of copulation relative to ovulation (Ginsberg and Huck 1989; Stockley 2004). For example, in nonhuman primates, the amount and quality of sperm that the male produces are related to the type of mating system. In gorillas (*Gorilla* spp.) and Bornean orangutans (*Pongo pygmaeus*), the winners of male-male competition have relatively unchallenged access to females. In common chimpanzees (*Pan troglodytes*), however, several males may attempt to mate with a female in estrus. Møller (1988) argued that, in this case, competition takes place in the female's fallopian tubes and that the male with the most and best sperm fertilizes the egg. In fact, chimps have larger testes than other apes and produce a high-quality ejaculate—greater numbers of more motile sperm. Among mammals in general, a similar relationship exists: species in which only one male has access to one or more females have smaller testes than do species in which more than one male has access to females (Kenagy and Trombulak 1986; Figure 22.5). Similarly, across mammals, relative testes size (controlled for body mass) is positively correlated with the rate of multiple paternity among species that produce >1 young per litter (Soulsbury 2010).

Female adaptations for post-copulatory mate choice that influence which sperm fertilize the eggs have received attention only recently (Firman et al. 2017). Numerous female-mediated processes that could bias fertilization toward the sperm of particular males have been documented and proposed. These include variation in timing and duration of mating, differential ejection, incapacitation, or retention of sperm, as well as a suite of physiological mechanisms, such as contractions of the female reproductive tract, that favor transportation of some sperm over

others to the vicinity of the ova. Indeed, selection for sperm of particular genetic makeup (e.g., MHC compatibility) has led to the "molecular sperm passport hypothesis," which suggests that molecular interactions between the sperm and the female reproductive tract form the basis for post-copulatory female mate choice (Holt and Fazeli 2015). Females of many mammalian species can store sperm in their reproductive tracts for 1–2 weeks, and some bats store sperm for several months (see Chapters 9 and 21), resulting in additional opportunities for female mate choice (Birkhead and Møller 1993; Holt and Fazeli 2016).

Sexual conflict regarding reproduction also continues post-conception. Over 50 years ago, Hilda Margaret Bruce documented that female lab mice terminated pregnancies and became sexually receptive when exposed to unfamiliar males (or their odors), a phenomenon that became known as the "**Bruce effect**" (Bruce 1959). The effect has been demonstrated in other captive situations with rodents and horses, but only indirect and anecdotal evidence supported the effect in natural populations, leading to suspicion that it was an artifact of captivity (Wolff 2003). Recent evidence, however, supports the effect in a wild Old World primate, the gelada (*Theropithecus gelada*). Research in Ethiopia documented that 80% of females terminated pregnancies following replacement of the dominant male in the group (Roberts et al. 2012). Females that terminated pregnancies had shorter interbirth intervals, suggesting that the response might be a strategy by which females reduced the costs of **infanticide** by the new dominant male.

Such infanticide represents a form of competition between the sexes with respect to reproduction that continues following birth. Infanticide by males has been documented in >50 species of primates, as well as rodents, dolphins, equids, and carnivores including bears and lions (Palombit 2015). A sexual selection hypothesis was initially forwarded to explain infanticide by northern plains gray langurs (*Semnopithecus entellus*). After a strange male took control of a group and drove out the resident male, he killed the young sired by the previous male (Hrdy 1977a). Because females that lost their young soon became sexually receptive, and the new resident male could inseminate them, infanticide was viewed as a sexually selected strategy to enhance access to mating opportunities. Other selective advantages of infanticide (e.g., improved condition and subsequent fertility of females or reduction in competition for resources) potentially accrue to males and vary across mammalian taxa and social systems (Palombit 2015). Numerous female strategies have been proposed to counter infanticide, and indeed, infanticide has been suggested as one factor leading to evolution of sociality in mammals. However, an analysis of >250 mammalian species suggested that infanticide is a consequence rather than cause of sociality (Lukas and Huchard 2014). Instead of forming groups to protect against infanticide, females are more likely to counter the risk of infanticide by promiscuous mating, which results in paternity uncertainty.

Parental Investment

Although most animals provide no care for their offspring, one or both parents provide at least some care in all species of mammals. The extent of parental care varies widely among different mammalian species. Parental care can take many forms, but all female mammals provide prenatal care in the form of gestation and lactation. Parental care in primates can last for several years, up to 25% of the offspring's life span, whereas care in some rodents and hares lasts only a few weeks. We define **parental investment** as any behavior that increases the offspring's chances of survival at the cost of the parent's ability to rear future offspring (Trivers 1972). Because an egg requires a greater investment of energy than a sperm, and only female mammals gestate and lactate, male and female parental strategies are expected to differ, and this difference is another source of conflict between the sexes.

WHICH SEX INVESTS?

Factors other than anisogamy can affect the contribution of each sex to parental care. Trivers (1972) reasoned that confidence of parentage might explain which sex cares for the young. In species in which internal fertilization occurs and in which sperm competition could take place, the male has no way of "knowing" whether his sperm fertilized the egg. He might therefore be inclined to desert the females with which he has copulated and seek additional mating opportunities. The female, on the other hand, is certain of her genetic relationship to the offspring, so she invests more in current offspring.

Because gestation and lactation are restricted to females, males can do relatively little to provide direct care for the young. In mammals with relatively advanced (precocial) young at birth, the opportunities for male investment are even lower. In contrast, species with young that are relatively undeveloped (altricial) at birth often require biparental care, and males potentially can share the investment with the females more evenly (Zeveloff and Boyce 1980).

Competition among males of some mammalian species is intense. For example, mating by northern elephant seals takes place on land in dense colonies; males establish dominance hierarchies, and only the high-ranking males breed (Le Boeuf 1974; Le Boeuf and Reiter 1988; Haley et al. 1994). Typically, less than one-third of the males copulate at all, and the top 5 males do at least 50% of the copulating (Figures 22.6 and 22.7). The males make no investment in offspring beyond the sperm, and they probably have no way of knowing which young are their own because pups are born a year after copulation.

Why then do males in about one out of ten mammalian species provide paternal care? From an evolutionary perspective, males are expected to provide care when the fitness benefits of their investment in current offspring out-

Figure 22.6 **Extreme sexual dimorphism in elephant seals.** Two males fight to establish dominance. Males differ strikingly from females; are about three times larger; possess an enlarged snout, or proboscis; and have cornified skin around the neck. In this highly polygynous species, males invest nothing in their offspring other than DNA from sperm.
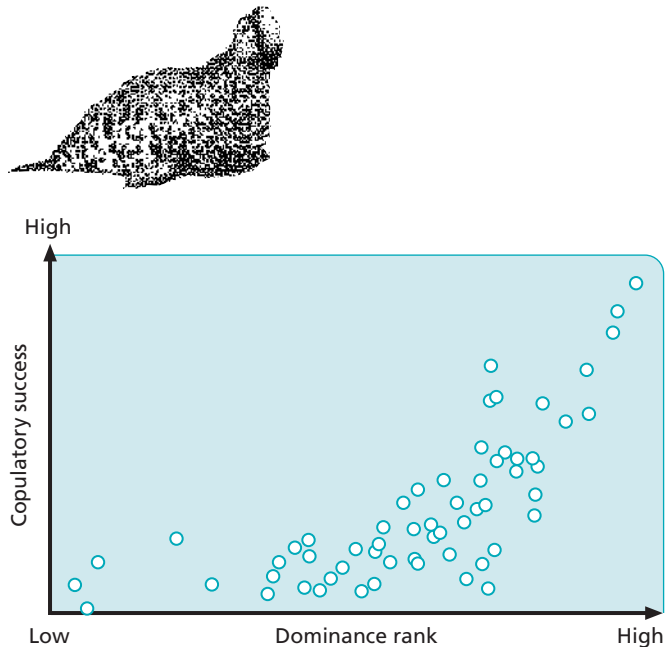
Figure 22.7 **Dominance and sex in elephant seals.** Copulatory success as a function of dominance in elephant seals for 72 males is shown here. *Data from Haley et al. (1994).*

weigh the lost opportunity costs that accrue from not seeking additional mates. Therefore, species with altricial young and systems in which alternative mating opportunities are limited should favor the evolution of paternal care. But research also suggests that care-giving fathers might reap additional benefits. An analysis of male parental care in >500 mammalian species documented that species with paternal care had shorter lactation periods, faster growth of young, and more frequent breeding, suggesting that male care enhanced both female fecundity and male reproductive success (West and Capellini 2016). In another

recent analysis, Stockley and Hobson (2016) suggested that male care in the form of food provisioning led to the evolution of larger litters among mammalian species.

Although paternal care in mammals in general is relatively uncommon, it occurs in a diversity of forms and extents in some primates, carnivores, and rodents. Paternal care is pronounced in titi monkeys (*Callicebus*) and owl monkeys (*Aotus*), which live in family units consisting of the adult pair and 2–4 young. Each year, females give birth to a single infant, but males carry the infants more than females (as much as 90% of the time), and infant titi monkeys develop stronger bonds with their fathers than mothers (Fernandez-Duque et al. 2009). As a group, canids are characterized by cooperative forms of breeding (Macdonald et al. 2004), and in the monogamous silver-backed jackals, the sexes share more or less equally in care for young (Moehlman 1983). Both parents defend the territory and hunt cooperatively, and males appear to play a crucial role because, in cases in which the father disappears, the female and her offspring die (Moehlman 1986).

Young mammals also can receive **alloparental care** (care provided by an individual other than a genetic or social parent) from siblings, other family members, and even unrelated individuals. Although the best studies involve rodents, primates, and social carnivores, alloparental care has evolved in diverse mammalian lineages (Rosenbaum and Gettler 2018).

PARENTAL CARE AND ECOLOGICAL FACTORS

Finding mates and caring for young take extra energy, which can make parents more vulnerable to predators. The term **reproductive effort** denotes both the energy expended and the risk taken for breeding that reduces reproductive success in the future. Individuals are faced with the decision, conscious or otherwise, of whether to breed now or wait until later. If they choose to breed now, they need to decide if some effort should be spared for another attempt later.

Several environmental factors influence the investment parents make in their young after birth. For example, species adapted to stable environments tend to have a larger body size, develop more slowly, enjoy a longer life span, and bear young at repeated intervals (**iteroparity**) rather than all at once (**semelparity**). Semelparity is very rare in mammals (see Chapter 25). These stable conditions favor production of small numbers of young that receive extensive care and thus have a low mortality rate. Such species are sometimes said to be *K*-**selected** because populations are usually at, or near, *K*, the **carrying capacity** of the environment (Pianka 1970; Boyce 1984). Intraspecific competition is likely to be intense, and the emphasis is on producing few, high-quality offspring rather than large numbers (e.g., gorillas, bears, whales).

In contrast, species adapted to fluctuating environments often have high reproductive rates, rapid development, and small body size, and they provide relatively little parental care. Their populations tend to be controlled by physical factors, and their mortality rates are high. Such species are said to be *r*-**selected**, where *r* refers to the reproductive rate of the population (Pianka 1970; Boyce 1984). For example, meadow voles are *r*-selected: They mature at an early age and have larger, more frequent litters than other, similarly sized rodent species.

In environments in which survival of offspring is low and unpredictable, selection should favor parents that "hedge their bets" and put in a small reproductive effort each season. The predictions of **bet-hedging** thus seem to contradict those of *r*- and *K*-selection. In unstable, unpredictable environments, *r*-selection should operate, yielding high reproductive rates. Bet-hedging theory, however, predicts low reproductive rates and the spreading of reproductive effort across many breeding seasons. These and other problems have led many researchers to reject the whole concept of *r*- and *K*-selection (Stearns 1992), but some mammalogists still find it a useful way to broadly classify patterns of mammalian life history. For a further discussion of life-history traits, see Chapter 25.

Prolonged dependency and extensive parental care also are favored when a species, such as many larger felids and canids, depends on food that is scarce or difficult to obtain. Much effort is spent searching for prey, and in some species, cooperation is needed for the kill. During the prolonged developmental period, the young benefit from considerable learning through play and observation of parents. Experimental evidence has documented adult wild meerkats (*Suricata suricatta*) teaching prey-handling skills to pups by providing them with opportunities to interact with live prey. Adults initially incapacitate prey (e.g., biting and removing the stingers from scorpions) and adjust their efforts as the pups become more skilled (Thornton and McAuliffe 2006). The Old World monkeys (Family Cercopithecidae) and the great apes (Family Hominidae) have the longest periods of dependency. These species typically have an infancy of 1.5–3.3 years and a juvenile phase of 6–7 years, which together make up nearly a third of the total life span. The prolonged dependency in these large-brained species may be related to their complex social life, in which they must recognize and remember interactions with many individuals across long spans of time.

Parent-Offspring Conflict

Anyone who has raised children or grown up with a sibling has observed frequent disagreement between parent and child. It is not unusual to see a mother rhesus monkey (*Macaca mulatta*) swat her ten-month-old infant or raise her hand over her head, thereby pulling her nipple from its mouth. Frequently, the infant responds by throwing a temper tantrum. Much of the conflict can be viewed as a disagreement over the amount of time, attention, or energy

the mother should give to the offspring (i.e., the infant wants more than the parent wants to give).

Trivers (1974) put forth the hypothesis that conflict arises because natural selection operates differently on the two generations. To maximize her lifetime reproductive success, the mother should invest a certain amount of time and energy in current offspring and then wean the young and invest in new young. The mother's optimum investment is a tradeoff between investment in current young and effort toward future reproduction. The current offspring, however, profits from continued care until the cost to its mother is twice the benefit (since the offspring shares half its mother's genes). At this point the offspring's own fitness also starts to decline because the offspring benefits to some extent from having its mother produce future, related offspring. Trivers's (1974) approach, based on the coefficient of relationship and kin selection (discussed in Chapter 23), makes intuitive sense, but has been challenging to test rigorously under natural conditions. Recent work with free-ranging domestic dogs suggested that conflicts between mothers and pups with respect to food-sharing increased as the pups aged and the mother reduced cooperation, presumably to invest in future reproductive efforts (Paul et al. 2015).

Among species of birds, where there is typically more than one young in the nest, begging displays often appear to be extravagant and costly, as would be predicted if offspring were trying to manipulate their parents into providing more food than the parents would choose. Begging behavior as a form of parent-offspring conflict, however, has been less studied in mammals. In gray seals (*Halichoerus grypus*), the single pup emits begging calls more often when hungry than when satiated, and the mother responds to these begging calls by presenting her nipples (Smiseth and Lorentsen 2001). Begging therefore seems to be an honest signal of need. Given the lack of predation on the isolated islands on which these seals breed, begging is not likely to be very costly. Thus, in this species, there is little indication that begging has become extravagant and costly, as predicted if parent-offspring conflict were at work.

Mating Systems

As noted, anisogamy prevails in all mammals, with females investing more in each egg than males invest in

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Siblicide in Mammals

Conflict is not always limited to parents and offspring; siblings can aggressively compete with one another over the distribution of parental care. Pigs (*Sus scrofa*) are born with razor-sharp teeth that they use in fights with siblings to gain access to favored teats for nursing (Fraser 1990; Fraser and Thompson 1991). Among spotted hyenas (*Crocuta crocuta*), litters are usually twins, and pups are also born with fully erupted canines and incisors.

Spotted hyenas are unusual in that young are precocial, and both sexes have high levels of circulating androgens at birth. Fighting begins within 48 hours after birth, and if littermates are of the same sex, one is often killed (Frank et al. 1991). Siblicide in this species appears to be facultative, in that it occurs most frequently when food is in short supply (Smale et al. 1999; Wahaj et al. 2007; Hofer and East 2008). Mothers typically intervene and sometimes punish their cubs when they fight. Where sibling aggression is extreme, mothers may take steps to reduce its impact, providing private nursing bouts for the subordinate cub and even temporarily housing same-sex twins in separate dens (White 2008).

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Dentition of spotted hyena on day of birth. Canines are 6–7 mm long; incisors are 2–4 mm long. Teeth are used in combat with siblings.

each sperm. This difference sets the stage for male-male competition for access to females and for attempts by males to mate with more than one female, a condition referred to as **polygyny**. Polygyny results in greater variation in reproductive success for males than for females; for each male that fertilizes the eggs from a second female, another male is likely to fertilize none, as was shown for lions at the beginning of this chapter (see Figure 22.1). Sexual selection tends to act more strongly on males than on females in polygynous species; however, not all mammals are polygynous.

In trying to evaluate the adaptive significance of differences in mating systems, researchers must look at ecological factors as well as historical ones. For example, group size may be related to predation pressure and food distribution. In the open plains, where large predators are present and food is widely distributed and often clumped, omnivorous primates and grazing mammals such as ungulates live in large groups in which mating with several members of the opposite sex is likely for both males and females. In densely forested areas, where communication over long distances is difficult, small family units and monogamy are more common; the same is true where food is uniformly distributed. Thus, the spatial distribution of resources (food, nest sites, or mates) influences the type of mating system (Figure 22.8).

Classifications of mating systems have traditionally been based on the extent to which males and females associate (bond) during the breeding season. **Monogamy** refers to an association between one male and one female at a time and includes an exclusive mating relationship between pair members. **Polygamy** incorporates all multiple-

mating, nonmonogamous mating systems. The following multiple mating systems are subsets of polygamy. As noted, polygyny is association between one male and two or more females at a time. **Polyandry** is association between one female and two or more males at a time. **Promiscuity** refers to the absence of any prolonged association between males and females and multiple mating by at least one sex.

MONOGAMY

In monogamous systems, neither sex is able to monopolize more than one member of the opposite sex. Monogamy is relatively rare in mammals. In an early analysis, 5% of mammal species were judged to be monogamous (Kleiman 1977). A more recent phylogenetic analysis of more than 2,500 species concluded that the number was closer to 9% (Lukas and Clutton-Brock 2013), with some 61 independent evolutionary transitions from the ancestral solitary condition. Facultative (i.e., optional) monogamy may occur when densities are low and the home range of a male overlaps with that of only a single female. Obligate monogamy typically occurs when investment from the male is necessary for offspring survival. When the habitat contains scattered, renewable resources or scarce nest sites, monogamy is the most likely strategy. If there is no opportunity to monopolize mates, an individual benefits from remaining with its initial mate and helping to raise the offspring. The formation of long-term pair bonds also seems advantageous because less time is needed to find a mate during each reproductive cycle, and experienced parents might be better at raising offspring. Risk of predation and infanticide are other possible factors promoting monogamy. Predation risk also results in some species living in small social units and behaving secretively to reduce the chances of being eaten.

Despite being relatively rare, monogamy is reported in most mammalian orders, with the bulk of examples coming from Primates (29% of extant species) and Carnivora (16%; Lukas and Clutton-Brock 2013). Among primates, the forest-dwelling marmosets and tamarins are all monogamous, and male care in the form of carrying infants is extensive. There is disagreement about the evolutionary causes of monogamy in primates, with some arguing that males bond with a single female to reduce infanticide by other males (Opie et al. 2013) and others that females tend to be so widely dispersed that males cannot monopolize more than one at a time (Lukas and Clutton-Brock 2013). The larger carnivores, especially canids such as jackals, foxes, and wolves, are nearly all monogamous; males feed, defend, and socialize with offspring (Macdonald et al. 2004). Among Rodentia, monogamy has been documented in marmots (*Marmota*) and beavers (*Castor*), as well as some voles (*Microtus*) and mice (*Peromyscus*) (Waterman 2008).

Clumped distribution
of resources

Uniform distribution
of resources

High potential
for polygamy

Little potential
for polygamy
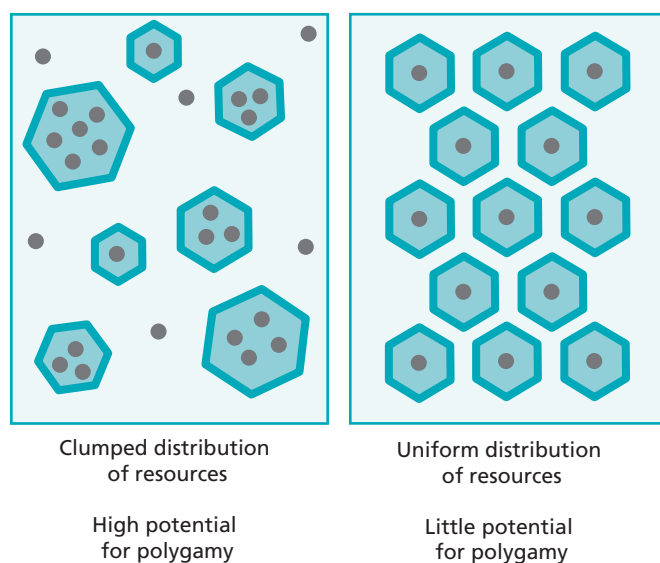
Figure 22.8 The influence of the spatial distribution of resources on the ability of individuals to monopolize those resources. Dots are resources, and hexagons are defended areas. Uniform distribution of resources on the right offers little opportunity for monopolization; monogamy is the likely mating system here. *Adapted from Drickamer et al. (2002).*

POLYGYNY

In polygynous systems, individual males monopolize more than one female. Several forms of polygyny have been described in mammals. In **resource defense polygyny**, males defend areas containing feeding or nesting sites critical for reproduction, and a female's choice of a mate is influenced by the quality of the male and the resources within his territory. Territories that vary sufficiently in quality may cross the **polygyny threshold**—the point at which a female may do better to join an already mated male possessing a good territory rather than an unmated male with a poor territory (Orians 1969).

Female defense polygyny may occur when females are gregarious for reasons unrelated to reproduction, as when females herd for protection against predators or gather around resources such as food, water, or nesting sites. Some males monopolize females and exclude other males from their breeding groups. In many species of sea lions and seals (Families Otariidae, Phocidae), the females haul out on land to give birth, and they mate soon after. The females are gregarious because there are limited numbers of suitable sites, and the males monopolize the females for breeding. Intense competition among males results in marked sexual dimorphism and a large variance in male reproductive success, as already described for northern elephant seals (see Figure 22.7; Haley et al. 1994). Many mammalian species are probably facultatively polygynous. In habitats where males cannot monopolize feeding or nesting resources, monogamy is likely, whereas habitats with clumped resources and/or concentrations of females tend to favor polygyny. Thus, variation in mating systems within species might be dependent on ecological and demographic conditions.

If males are not involved in parental care and have little opportunity to control resources or mates, **male dominance polygyny** may develop. When female movements or concentration areas are predictable, the males may concentrate in such areas and pool their advertising and courtship signals. Females then select a mate from the group of males. These areas are called "leks"; males congregate and defend small territories within them to attract and court females. Leks do not contain resources (food or nesting sites); rather, they are purely display sites for mate choice and copulation. Females select a mate, copulate, and then leave the area and rear their young on their own. Often, older or more dominant males occupy the preferred territories or have the most attractive displays and thus do most of the copulating.

Male hammer-headed fruit bats (*Hypsignathus monstrosus*), from central and western Africa, display at traditional sites along riverbanks (Bradbury 1977). Each territory is about 10 m apart, and the males emit a loud clanking noise to attract females. Once chosen, a male copulates with the female and resumes calling immediately. Some males, for whatever reason, have much higher success than others at attracting females, and in one year, 6% of the males achieved 79% of the copulations. As might be expected, this spe-

Figure 22.9 **Topi, an African ungulate, on a lek.** Larger and older topis (*Damaliscus lunatus*) defend small territories without resources near the center of the lek, where females come to select their mates.

cies shows extreme sexual dimorphism, with males nearly twice the size of females. Each male has a huge muzzle that ends in flaring lip flaps and a large larynx associated with the clanking sound it makes.

Leks also form during the breeding season in several species of ungulates, such as Uganda kob (*Kobus kob*), topi (*Damaliscus korrigum*), and fallow deer (*Dama dama*). In topi (Figure 22.9), males defending clustered territories near the center of the lek attained the most matings; those males were larger and older, but also suffered more wounds than males at the periphery (Bro-Jørgensen and Durant 2003). The reproductive success of lekking male fallow deer also varies widely, with a few males having spectacular success while most males do no breeding at all (Appolonio et al. 1992).

In the absence of territory or dominance, **scramble polygyny** can operate, as males try to obtain copulations. Where females are widely dispersed, as with the territorial North American red squirrel (*Tamiasciurus hudsonicus*), males must leave their territories to search for mates. Home ranges of males were nearly ten times larger during the breeding season, and this search effort was positively related to both mating success and reproductive success of males (Lane et al. 2009).

POLYANDRY

In polyandrous systems, females monopolize more than one male. We have already pointed out that in most mammal species, females provide the bulk of parental care, with males seeking new mates and investing little in offspring. Under certain circumstances, polyandry might be expected if food availability at the time of breeding is highly vari-

able or if breeding success is very low due to high predation on the young. True polyandry should result in role reversal, with large females competing for smaller mates, female ornamentation via intersexual selection, male parental care, and female dispersal in search of mating opportunities. Such a pattern does not occur in mammals, although there are dozens of species of birds that exhibit these traits, and except for egg-laying, the male does all the parenting alone.

In many species of mammals, however, females mate with more than one male, and multiple paternity within litters is common (Dobson et al. 2018). Such systems are usually referred to as **promiscuous** rather than polyandrous because males also mate with multiple females, males provide little or no care of offspring, and no lasting bond exists between the partners.

Several species of larger canids show many of the features of true polyandry. Although mainly monogamous, the African wild dog (*Lycaon pictus*) sometimes exhibits polyandry; females are occasionally mated by several males, males provide extensive care of pups, and females are the dispersing sex (Macdonald et al. 2004).

SUMMARY

- In mammals, as in almost all other vertebrates, sexual reproduction is the only option.

- The gametes of the two sexes differ anatomically, with females producing few large eggs and males producing many small sperm. This condition (anisogamy) contributes to males and females following differing reproductive strategies.

- In most mammalian species, males attempt to mate with more than one female, and variation in reproductive success is more pronounced among males than females.

- Intersexual selection involves mate choice between the sexes, with females usually making the choice in mammals.
  ○ Intersexual selection can lead to the evolution of elaborate secondary sexual characteristics, particularly in males.

- Intrasexual selection involves competition within one sex (usually males) for access to mating opportunities with the opposite sex.
  ○ Competition can take place before copulation, after copulation (in the form of sperm competition and cryptic female mate choice), after conception via pregnancy termination, or even after birth as infanticide.

- Parental investment in offspring is generally greater by females than males, as males seek additional mates and leave the female to care for young; however, in some species, males provide extensive care.

- Species living in harsh, unpredictable environments or suffering high juvenile mortality rates tend to have high reproductive rates and provide little care compared with those adapted to stable environments.

- Offspring often seem to want more attention or food than the mother is willing to give and resist attempts by the mother to wean them.
  ○ Such parent-offspring conflict reflects the fact that parents share only half their genome with an offspring.

- Most mammals have polygynous mating systems in which males are able to monopolize more than one female.
  ○ In such systems, males are often larger and more ornamented than females, and they provide little if any care of offspring.

- In some orders, especially Carnivora, food is difficult to obtain, and both parents share in caring for offspring; these conditions lead to monogamy.

- Polyandry, in which females monopolize more than one male, is rare in mammals.
  ○ It has, however, been reported in some of the larger canids, where females enlist the help of several males to raise offspring.

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DISCUSSION QUESTIONS

1. Sexual selection is often proposed to explain many of the morphological differences between male and female mammals. Can you think of selection pressures other than competing for mates that might produce such differences? How might you design a study to tease apart the different selective forces?

2. As you have seen in this chapter, polygyny is common in mammals. In birds, however, social monogamy is the rule (even though many participate in extra pair copulations). What ecological and behavioral factors might explain the difference in mating systems between these two groups?

3. Why is polyandry so uncommon in mammals? What sorts of ecological and phylogenetic circumstances might favor polyandry?

4. Numerous factors contribute to conflicts between the sexes with respect to caring for young. Under what circumstances should the sexes share parental duties more evenly?

5. Clutton-Brock (2007) pointed out that sometimes sexual selection acts in an opposite way than we usually think about for mammals—that is, sometimes intrasexual selection results in female-female competition, and male choice among female mates results in strong intersexual selection. Can you think of some in mammals in which this might occur? (Hint: there are some mammalian examples in Clutton-Brock's publication).

Social Behavior and Communication

In this chapter, we first define social systems and explore the range of sociality and social behaviors exhibited within mammalian taxa. Next, we discuss the costs and benefits of cooperative behavior in general and consider how selection has influenced the evolution of sociality in mammals. For overviews of sociality in different groups of mammals, refer to the chapters in Part 3. Finally, because communication among individuals is an integral component of sociality, we finish with an exploration of communication by mammals.

Sociality has evolved independently in many groups of animals, ranging from invertebrates to primates. The complexity of social behavior might be expected to increase as organisms move from simple to more sophisticated, yet by some criteria, just the opposite is true: some invertebrates, such as the Portuguese man-of-war (Genus *Physalia*), ants, and slime molds, form colonies of individuals that cooperate much more extensively than mammals do (Wilson 1975; Pennisi 2009).

The Sociality Spectrum

Social systems encompass the ways that individuals of the same species interact, including mating systems, parent-offspring interactions, competition, and cooperation among related or unrelated individuals. In its simplest definition, social means group living, but this includes a wide range of variation from mammals that live in family units consisting of parents and offspring (e.g., North American beavers, *Castor canadensis*) to assemblages numbering in the millions (e.g., nursery colonies of Mexican free-tail bats, *Tadarida brasiliensis*).

Sociality occurs to varying degrees in all mammals, and we can think of a spectrum of sociality across taxa (Figure 23.1). At one end are species that are typically solitary as adults. This includes many carnivores (e.g., bears, cats, skunks) and omnivores (e.g., opossums, armadillos), as well as herbivores (e.g., pocket gophers, rhinos, sloths). However, even mammals that are considered solitary often form tem-

Figure 23.1 **Sociality spectrum.** Sociality varies across taxa and sometimes throughout the life of a mammal. Patterns of sociality range from (**A**) solitary (e.g., wolverines, *Gulo gulo*) to (**B**) group-living, as in prairie dogs (*Cynomys*), to (**C**) highly social (eusocial) as exhibited by the subterranean naked mole-rat (*Heterocephalus glaber*).

porary associations with other individuals, for example between mothers and offspring or mates during breeding. Therefore, the division between solitary and group-living species is somewhat misleading, and individuals of most species will occur in association with conspecifics at least occasionally (Krause and Ruxton 2002).

At the opposite end of the spectrum are species that always live in groups and that would be unlikely to survive away from the group. This extreme sociality, seen most often in insects of the Order Hymenoptera, is referred to as **eusocial**. Three traits characterize eusocial organization: (l) cooperation in the care of young; (2) reproductive castes, with nonreproductive members caring for reproductive nest-mates; and (3) overlap among generations such that offspring assist parents in raising siblings (Wilson 1975). Among mammals, only two species of African mole-rats (Family Bathyergidae), the naked mole-rat (*Heterocephalus glaber*) and the Damaraland mole-rat (*Cryptomys damarensis*), exhibit true eusociality (Bennett et al. 2000). Between the extremes of solitary and eusocial is a wide range of social aggregations; indeed, the other members of the Bathyergidae include both solitary species

and social species that exhibit a diversity of cooperative breeding strategies (Burland et al. 2002). A **society** is a group of individuals of the same species that is organized in a cooperative manner, typically extending beyond sexual and parental behavior.

Why Mammals Live in Groups

Living in social groups is often assumed to be superior to living a more solitary life, yet costs and benefits are associated with each. In a classic paper on evolution of social behavior, Alexander (1974:328) wrote that "there is no automatic or universal benefit from group living. Indeed, the opposite is true: there are automatic and universal detriments." Those universal costs are competition for resources and increased transmission of parasites. The literature on potential costs of group living is small relative to that exploring the benefits—a situation that Krause and Ruxton (2002) attribute to a deficiency of research more than a lack

of real costs. Most of the benefits of sociality can be related to two ecological factors: predation risk and foraging success, especially as influenced by the distribution of food resources (Alexander 1974; Krause and Ruxton 2002). Sociality is favored when the benefits of being with others outweigh the costs of living in a group. However, Silk (2007) cautions that we have much work to do to link sociality in mammals to fitness consequences for individuals.

BENEFITS

Protection Against Predators

Predation risk can be influenced by group size in at least two different ways. First, detection of and communication about danger are more rapid when individuals are in groups. According to the "many eyes" hypothesis, individuals in large groups need to spend less time watching for predators and consequently can spend more time on other activities such as feeding (Pulliam 1973; Olson et al. 2015). Indeed, decreased vigilance by individuals in groups has been documented in many group-living mammals (Caro 2005). Second, if a predator is going to kill one animal, then being in a larger group reduces each individual's chances of being the one killed; this is known as dilution of risk (Bertram 1978). Both of these benefits can accrue to prey living in groups, and it can be difficult to separate them. One study that examined both the effects of predator detection and dilution of risk on plains zebra (*Equus quagga*) documented that vigilance decreased with group size in zebra-only herds (dilution), but that the effects were more complex in mixed-species herds (Schmitt et al. 2014). Similarly, vigilance by bighorn sheep (*Ovis canadensis*) females differed with reproductive status such that maternal females benefited from increased detection of predators while nonreproductive females gained more from numerical dilution of risk (Rieucau and Martin 2008). Careful observations and analyses are often required to disentangle the multiple ways that social groups reduce predation risk for prey animals (Fairbanks and Dobson 2007).

In addition to the size of the group, the location of an animal within a group can also influence the probability of being killed by a predator. In a classic publication, Hamilton (1971) suggested that individuals could reduce their "domain of danger" by associating with others. He called this the "selfish herd" effect and demonstrated mathematically that an animal's position in a group could reduce exposure to predators, such that individuals surrounded by others would be safer, and that the safest place to be was in the center of the group. Finally, being in a group also can reduce an individual's chances of being killed by a predator by making it more difficult for the predator to focus on one animal; the result is predator confusion (Bertram 1978; Krause and Ruxton 2002).

Not all prey animals are passive in response to predators, and some mammals can and do mount effective counteras-

Figure 23.2 **Group defense against predation.** When threatened by predators, musk oxen (*Ovibos moschatus*) adults form a circle facing outward with the calves in the center. This group defense of young is one benefit of sociality in this species, which lives in open, treeless areas where hiding from predators is not an effective option.

saults. In these cases, sociality facilitates group defense, which can increase each individual's probability of survival and which thus represents yet another way that predation risk can influence group formation (Caro 2005). This antipredator strategy is also used in defense of vulnerable young mammals. Adult musk oxen (*Ovibos moschatus*), which live on the open treeless tundra, form a defensive perimeter around calves in response to attacks by wolves (*Canis lupus*) and other predators (Berger 2018; Figure 23.2).

Finding and Obtaining Food

Living in groups can make finding and obtaining food easier in several ways. Sharing information about food resources (whether intentionally or not) is believed to favor the evolution of sociality. For diurnally foraging animals, this might involve watching conspecifics in the group (Beauchamp 2007), but for nocturnal foragers like bats, information about food resources might be obtained by listening to auditory cues produced by foraging individuals. Dechmann and colleagues (2009) studied the lesser bulldog bat (*Noctilio albiventris*), which lives in social groups and forages on flying insects over water. Occurrence of such swarming insects can be unpredictable in both space and time, but by eavesdropping on the sounds made by foraging group members, the bats appeared to forage more efficiently. In addition, long-lived mammals remember the locations of high-quality feeding areas (Merkle et al. 2014), and this information is likely transmitted to subsequent generations. Ungulate migrations are often driven by seasonal changes in forage, and, as Jesmer and coworkers (2018) demonstrated, cultural transmission of information about seasonal food resources and migratory routes influenced the evolution of migratory behavior in moose (*Alces*

alces) and bighorn sheep. Such mechanisms are likely important across many terrestrial and marine mammals that exhibit migratory behaviors (Avgar et al. 2013).

In addition to facilitating information-sharing about food resources, sociality can also expand foraging options if group-living animals can access food that might be avoided by solitary individuals. For example, bison (*Bison bison*) are more likely to graze in open meadows when in larger groups because of the antipredator benefits of grouping (Fortin et al. 2009). Similarly, carnivores are sometimes able to hunt larger, more agile, or more dangerous prey when doing so in a group. Wolves (MacNulty et al. 2014) and African lions (*Panthera leo*; Schaller 1972) are able to take large species of prey—such as bison in the case of wolves and African buffalo (*Syncerus caffer*) in the case of lions—that would be nearly impossible to kill alone. Furthermore, groups might increase predation success not only as a function of numbers, but also because of a division of labor among individuals. For example, in group hunts, individual female African lions typically form one side of a "winging" hunting approach (Stander 1992), and similar hunting-role specialization has been documented in bottlenose dolphins (*Tursiops truncatus*) in which one individual drives fish toward a group of closely-spaced "barrier" individuals (Gazda et al. 2005; Jaakkola et al. 2018).

Finally, by foraging or hunting in groups, animals can reduce the probability that others will steal their food. Such theft (known as **kleptoparasitism**) can be carried out by conspecifics or by other species. Indeed, kleptoparasitism may sometimes influence sociality in sympatric carnivores such as cheetahs (*Acinonyx jubatus*), African lions, spotted hyenas (*Crocuta crocuta*), and wild dogs (*Lycaon pictus*). A review across African carnivores suggested that on average, carnivores potentially share food resources with over 20 other species (Caro and Stoner 2003).

Opportunities for Social Learning and Culture

Social learning is the process of acquiring knowledge by observation of or interaction with another individual, usually of the same species (Hoppitt and Laland 2013). Scientists disagree about a precise definition of **culture**, but most believe that it involves a suite of specific behaviors shared among individuals in a social group and that those behaviors have been acquired via social learning. The advantages of social learning are frequently suggested as important for mammals in general, and primates and cetaceans in particular. Dependence on learning provides for greater behavioral plasticity, but it requires a long period of physiological and psychological dependence. Large-brained and highly social species, such as dolphins and primates, spend as much as 25% of their lives dependent on parents or other relatives, and many examples of culture have been proposed for these species,

An experimental demonstration of how social learning could affect foraging decisions comes from a study of wild vervet monkeys (*Chlorocebus pygerythrus*) in Africa (van de Waal et al. 2013). Experimenters fed corn that was made distasteful and colored with a dye to members of four different groups. Within several months group members rarely sampled the distasteful corn but readily ate plain corn dyed with a different color. After four more months, in the absence of offering corn, during which time infants were born into the groups and new males joined from outside, all group members, both old and new, were offered palatable corn, which was now dyed with the formerly distasteful color, and all avoided it. This tendency of naïve animals to conform to group habits could, in the long run, be highly adaptive.

A second example involving a cultural change in feeding behavior involves humpback whales (*Megaptera novaeangliae*) feeding on small fish in the Gulf of Maine (Allen et al. 2013). In 1980, one whale was observed using a new technique associated with the typical pattern of bubble-feeding, in which it smacked the water several times with its tail fluke, causing the school of prey fish to concentrate even more (Figure 23.3). This "lobtail" technique spread throughout the population in a manner that was consistent with social learning, as documented by network-based diffusion analysis, and was not random; that is, individuals adopting the practice of lobtailing were associated with individuals that were skilled in it (Allen et al. 2013).

Other Potential Benefits

Other potential fitness benefits for mammals that form social groups include reduction in energy expenditure associated with thermoregulation via huddling (Gilbert et al. 2010). Such energy savings are likely to be most important for nonhibernating small mammals (see Chapter 8); however, even larger-bodied mammals might reap thermal benefits from sociality. For example, research on

Figure 23.3 **Fluke of a humpback whale used in lobtail feeding.** Some humpback whales (*Megaptera novaeangliae*) smack the water with the ventral side of their flukes, which concentrates prey fish. Network analysis demonstrated that this behavioral pattern is transmitted culturally.

free-ranging vervet monkeys demonstrated that during cold winter months, individuals with more social partners experienced smaller daily fluctuations in body temperature and higher minimum temperatures (i.e., became less hypothermic) than did animals with fewer social partners (McFarland et al. 2015). This benefit can lead to the formation of aggregations, as with large clusters of bats. Social groups also provide opportunities for gaining access to other important resources (e.g., nests, burrows, potential mates).

COSTS

Intraspecific Competition for Resources

Competition for food and other resources (e.g., resting sites, mates, shelters) can increase with group size, resulting in a potential reduction in fitness or increased effort to attain resources. For example, a meta-analysis across primate species found that distance traveled each day increased as a function of group size and that larger groups spent more time feeding, presumably because of faster depletion of food resources and competition within the group (Majolo et al. 2008). The relationship was not affected by diet or other ecological factors. That study also revealed a negative effect on female fecundity, as have other primate studies, which reported reduced reproductive rates and slower growth of infants in larger groups (Borries et al. 2008). For group living to evolve in these species, the benefits (e.g., reduced predation on young) are expected to be greater than the negative effects on reproduction.

Spread of Parasites and Diseases

Food is not the only thing shared among individuals in a social group. A large number of empirical and theoretical studies support the relationship between parasite infections and host density or group size. Two recent meta-analyses confirmed a positive relationship between sociality and the intensity and prevalence of contagious parasites across diverse taxa, including mammals (Rifkin et al. 2012; Patterson and Ruckstuhl 2013). However, not all parasites are affected by sociality in the same way, and a review across mammals identified several characteristics of both the hosts and parasites that can affect patterns of parasitism (Altizer et al. 2003). For example, male Richardson's ground squirrels (*Urocitellus richardsonii*) had higher loads of **endoparasites**, whereas females had greater infestations of ectoparasites; these differences may have been influenced by differences in sociality between the sexes (Waterman et al. 2013). However, Spickett and colleagues (2017) found that environmental conditions were a much better predictor of parasite load than was sociality in two species of African rodents (*Rhabdomys*)—one social and the other solitary.

Other Potential Costs

Numerous other potential costs of group living have been proposed. Although not well studied in mammals, larger groups can be more obvious to predators, which could counter the benefits of group size with respect to predation risk. Aggressive encounters among conspecifics are likely to be elevated in larger groups, thereby resulting in higher levels of stress, energetic expenditures, and the potential for injury. Parental care misdirected to nonoffspring and killing of young by nonparents are other potential negative consequences of living in groups. Brazilian free-tailed bats (*Tadarida brasiliensis*) roost in caves in dense colonies containing millions of bats (see Chapter 21). Mothers returning from a night's foraging for insects have to find their own infant among the thousands present. Most of the time, they find their own young by vocalization, but 17% of the time mothers nursed offspring other than their own (McCracken 1984). Female white-footed mice (*Peromyscus leucopus*) with young are aggressive toward strange adults; in the absence of the mother, intruders usually kill the pups (Wolff 1985). One consideration in evaluating disadvantages of sociality is that costs can be manifest as opportunity costs or constraints on behavior rather than direct fitness costs (Krause and Ruxton 2002). Such negative effects are likely to remain undetected and are challenging to quantify without careful research design.

How Social Behavior Evolves

A behavior is considered a social behavior when it has fitness consequences (either positive or negative) for two or more individuals. Social behaviors can be classified into four types (Table 23.1) based on how they affect the fitness of the animal performing the behavior (the actor) and the recipient (Hamilton 1964). Two of the four types of social behavior benefit the recipient and are *potentially* cooperative behaviors (as discussed below). The other two types—selfish and spiteful—are detrimental to the recipient, and therefore, cannot be considered cooperative. Behaviors that increase fitness for both the actor and recipient are considered **mutualistic**. Behaviors that cost the actor but benefit the recipient are classified as **altruistic**. There are many examples of apparently altruistic behaviors in nature, such as alarm-calling to warn conspecifics about danger, providing care for unrelated young, or sharing food. These acts may appear to be altruistic but could actually confer direct fitness benefits to the actors. For example, caring for unrelated young allows inexperienced individuals to gain parenting skills that enhance their ability to raise their own offspring—a direct fitness benefit to the actor. Helping sisters, brothers, or cousins—who share a percentage of the actor's genome— also enhances an actor's fitness. Thus, acts of apparent al-

Table 23.1   Classification of social behaviors based on their effects on the fitness of both the actor and the recipient (Hamilton 1964). A behavior is classified as cooperative if it has a positive effect on the recipient's fitness (bold) *and* has been under selection because of that benefit (West et al. 2007).

Effect on Actor	Effect on Recipient	
	+	**–**
+	**Mutualistic**	Selfish
–	**Altruistic**	Spiteful

truism often can be explained in terms of inclusive fitness and kin selection (also discussed below).

A behavior is classified as **cooperative** when there is a benefit to the recipient (either mutualist or altruistic) *and* when the behavior has been under selection because of the positive effect on the recipient's fitness (West et al. 2007). This last distinction excludes behaviors that benefit the recipient incidentally, as a by-product. West and colleagues (2007) provided an example that illustrates this last point clearly: dung produced by an elephant strongly benefits reproduction by dung beetles, but defecation in elephants certainly did not evolve because it benefited beetles. Examples of cooperative behaviors include group hunting by carnivores, group defense against predators, and communal care of offspring (Figures 23.2 and 23.4).

INDIVIDUAL VERSUS GROUP SELECTION

A basic element of sociality is cooperation. Individuals work together, often sacrificing personal gain, to achieve a common goal that benefits the social group. How such altruistic behaviors could evolve has long puzzled biologists, given our understanding of natural selection favoring traits that enhance the fitness of individuals (and the genes that promote those traits). In fact, when reflecting on social insects, Darwin (1859) wrote that this conundrum was potentially fatal to his theory of evolution. He reasoned, however, that cooperation might evolve if it benefited members of a family that helped each other. Subsequent biologists assumed that groups with cooperating individuals would be more successful than those without cooperators—a type of **group selection**. However, such systems are vulnerable to cheaters that might reap the fitness benefits of cooperation, without paying any fitness costs. The logical extension of such free-loading behavior is that genes for cheating would spread in the population and swamp out genes for altruistic behaviors. Such ideas are at odds with natural selection acting on individuals and genes.

In recent years, there has been a resurgence of interest in group selection in the form of a modified model called "multi-level selection" (Traulsen and Nowak 2006). The idea is that not only does individual selection act within groups in which individuals compete with one another, but also selection might operate among groups, such that cooperating groups would be favored if the average fitness of individuals in a cooperating group was greater than that of individuals in a noncooperating group. Such ideas are nuanced and hotly debated (Lehmann et al. 2007; Gardner 2015), and here we focus on potential explanations for the evolution of cooperation among mammals that are consistent with the well-developed ideas of individual and gene selection.

COOPERATION AMONG KIN

In the 1960s, William Hamilton (1963, 1964) developed Darwin's ideas about families cooperating and presented a theory that did not invoke group selection, but instead incorporated both the gene and the individual as units of selection. He reasoned that the offspring of relatives also contributed to an individual's fitness tally because relatives share genes in common by descent. Therefore, helping relatives to survive and reproduce ultimately helps to spread shared genes, and cooperation should arise when the combined propagation of shared genes is greater than that resulting from individual reproduction.

It now becomes necessary to consider an individual's fitness as including both a direct component, measured by the reproductive success of its own offspring (direct fitness), and an indirect component (indirect fitness), measured by the reproductive success of its relatives other than its own offspring. These two components together make up an individual's **inclusive fitness**. Hamilton concluded that inclusive fitness could explain the evolution of eusociality in insects, thereby resolving Darwin's conundrum.

In its simplest form, Hamilton's **kin selection** theory suggests that if a gene that causes altruistic behavior appears in the population, the gene's success depends ultimately not on whether it benefits the individual carrying the gene but on the gene's benefit to itself. If the individual that benefited by the act is a relative of the altruist and therefore more likely than a nonrelative to be carrying that same gene, the frequency of that gene in the gene pool increases. The more distant the relative, the less likely it is to carry that gene, so if the gene is to spread, the ratio between the benefit to the recipient and the cost to the altruist must be greater. This relationship, called "Hamilton's rule," can be expressed algebraically as follows:

Figure 23.4 **Cooperative behaviors.** Many group-living mammals perform cooperative behaviors such as group hunting, communal rearing of offspring, and collective defense against predators or conspecific competitors. Such cooperative behaviors are common among (**A**) social canids such as wolves (*Canis lupus*), (**B**) have been well studied in members in of the Family Herpestidae (e.g., meerkats), and (**C**) characterize long-lived species like cetaceans (e.g., orcas).

$$b/c > 1/r,$$

where *b* is the benefit to the recipient, *c* is the cost to the altruist, and *r* is the coefficient of relationship—that is, the proportion of genes shared by the two participants by way of descent from a common ancestor. In full siblings, who share half their genes, $r = 1/2$, and therefore *b/c* must exceed 2 for altruistic genes to spread. In other words, if an individual more than doubles the fitness of a sibling through an altruistic act that causes that individual to leave no offspring, genes promoting that behavior could spread through the population. The more distant the relative, the lower *r* is, and the higher the benefit-to-cost ratio (*b/c*) must be. Thus, for first cousins, $r = 1/8$, so *b/c* must exceed 8. Of course, the control of an altruistic behavior pattern most likely involves more than one gene, but it is assumed that the same principles apply.

Examples of kin selection have been widely documented in mammals. Sharing prey among related individuals (e.g., killer whales, *Orcinus orca*; Wright et al. 2016) or providing warning calls to relatives when predators are nearby (Caro 2005) are examples of behaviors that benefit kin at a potential cost to the actor. A uniquely mammalian exam-ple of kin selection is the nursing of nonoffspring (allonursing) by related mothers (Figure 23.5). Indeed, relatedness among females has been positively correlated with allonursing in diverse species, including in African lions (Pusey and Packer 1994), sperm whales (*Physeter macrocephalus*; Konrad et al. 2018), and reindeer (*Rangifer tarandus*; Engelhardt et al. 2016). Among gray mouse lemurs (*Microcebus murinus*) in Madagascar, adult females typically form small daytime sleeping clusters. These groups consist of close female relatives that regularly groom and nurse offspring other than their own and adopt related dependent young after their mother's death (Eberle and Kappeler 2006). Finally, among the highly social meerkats (*Suricata suricatta*) of the Kalahari Desert, about half of the litters born are allonursed, and being a close relative of the biological mother is one of the factors important in predicting the likelihood of allonursing (MacLeod et al. 2013).

COOPERATION AMONG NON-KIN

The idea that kinship favors evolution of cooperative behavior among mammals has much support, but it cannot explain

Figure 23.5 **Communal nursing in lions.** Females nurse young born to other pride members, a trait that may have evolved via kin selection because pride females often are closely related.

cooperation among unrelated individuals. In the 1970s, Robert Trivers (1971) formulated the concept of **reciprocal altruism**—"You scratch my back, and I'll scratch yours." The idea is that individuals may cooperate and behave altruistically if there is a chance that they will be the recipients of such acts at a later time. Such a situation is similar to a behavior that is mutually beneficial, except that a time delay is involved in reciprocity whereas the benefits to both the actor and recipient are simultaneous in mutually beneficial behaviors. According to Trivers (1971), natural selection acting at the level of the individual could produce altruistic behaviors if, in the long run, those behaviors benefit the organism performing them. He first showed that if altruistic acts are dispensed randomly to individuals throughout a large population, genes promoting such behavior disappear because there is little likelihood that the recipient will pay back the altruist. If, however, altruistic acts are dispensed nonrandomly among nonrelatives, genes promoting them could increase in the population if some sort of reciprocation occurs. The factors that affect that likelihood are (l) length of life span—long-lived organisms have a greater chance of meeting again to reciprocate; (2) dispersal rate—low dispersal rate increases the chance that repeated interactions will occur; and (3) mutual dependence—clumping of individuals, as occurs when avoiding predation, increases the chances for reciprocation. In any social system, nonreciprocators (cheaters) can be expected; as cheating increases, altruistic acts become less frequent.

A classic example of reciprocity in mammals was first described in common vampire bats (*Desmodus rotundus*; see Figure 21.22) in Costa Rica by Wilkinson (1984). At night, these bats feed on blood, primarily from cattle and horses, and then return to a hollow tree to roost during the day. Given their high metabolic rate, individuals that do not obtain a blood meal within three days will starve, but most bats that do feed take in more than they need and will sometimes regurgitate blood into the mouths of roost

mates that did not feed that evening. Wilkinson demonstrated that both relatedness and association contributed significantly to the pattern of exchange, such that close relatives and associates were fed more often than would be expected by chance. In a captive colony, Carter and Wilkinson (2013b) manipulated both prior association and relatedness and demonstrated that the best predictor of food-sharing was association—in other words, having previously received food from the recipient. Relatedness was a relatively minor factor, as was harassment by individuals who had not shared previously, but relatedness became more important in decisions about blood-sharing when the bats perceived danger (Carter et al. 2017).

An interesting line of research has developed to explain extremely high levels of cooperation among humans in large groups where opportunities for reciprocity are limited. The idea is that because individuals develop reputations, those who have a reputation of being helpful are more likely to receive help, even from people with whom they have not interacted in the past (Nowak 2006). Research exploring this concept in nonhuman mammals is quite limited, but it is conceivable that such relationships might contribute to the evolution of cooperation in long-lived and highly social species such as primates. Indeed, some experimental evidence suggests that chimpanzees (*Pan troglodytes*) can infer reputations by observing interactions among other individuals (Subiaul et al. 2008).

As discussed previously, in some situations, both the actor and recipient benefit from a behavior simultaneously, with no apparent cost to either. Such mutually beneficial behaviors are similar to reciprocal altruism in the long run, except that there is no delay in returning the favor. The phrase "mutually beneficial" helps to distinguish this type of within-species cooperation from interspecific mutualism (e.g., removal of ectoparasites from ungulates by oxpeckers), which is explored in ecology (West et al. 2007). Common mammalian behaviors that result in immediate fitness benefits for all participants include huddling during cold weather to reduce the energetic costs of maintaining body temperature (see Chapter 8; Gilbert 2010) and cooperative defense exhibited by many carnivores (Smith et al. 2017) and primates (e.g., by black howler monkeys, *Alouatta pigra*; Van Belle et al. 2014). Immediate mutual benefits provide a simpler explanation for cooperation than reciprocity, and Clutton-Brock (2009) suggested that many cases of cooperative behavior among non-kin are likely selected via mutually beneficial consequences.

Although both reciprocal and mutually beneficial behaviors result in willing cooperation, another line of research has examined how cooperation might be enforced by punitive behaviors, sometimes referred to as punishment or policing (Cant 2010; Singh and Boomsma 2015). For example, among cooperatively breeding mammals, dominant females sometimes suppress reproduction by subordinate females or evict them from the group if they attempt to reproduce, presumably to reduce competition with their own offspring and the potential for infanticide

by the subordinate mothers. Such interactions have been documented in meerkats (Young et al. 2006; Bell et al. 2014) and primates (Baniel et al. 2018). Other forms of manipulation also can be used to coerce or induce cooperation among kin or non-kin, and indeed, many types of cooperation likely result from a combination of such forces (Clutton-Brock 2009).

Communication

Almost all social interactions involve some form of communication or transmission of information from one animal to another. Mammals communicate information to conspecifics and to other species through visual, auditory, tactile, olfactory, and other signals. A **signal** is a behavior or morphological structure that a sender uses to transmit information to a receiver with the condition that it has evolved for that purpose. Additionally, a signal results in a change in the receiver's behavior in a way that has, on average, positive fitness consequences for both the sender and receiver (Smith and Harper 2003).

Signals are typically honest communications, even when the sender and receiver have a conflict of interest, although why they are reliable has been an active area of theoretical and empirical research. Several mechanisms are believed to keep signals generally honest: some explanations involve costs associated with producing the signals and others entail retaliation or loss of credibility associated with dishonesty (Davies et al. 2012; Laidre and Johnstone 2013). In addition, over the long run selection would favor receivers that ignored unreliable or manipulative signals, and such systems would become evolutionarily unstable. An important caveat is that signals need not *always* be honest, but they must be reliable often enough that the system does not break down.

Animal communication research is inherently interdisciplinary and involves many fields including ethology, evolutionary biology, biological engineering, psychology, and more recently, neuroscience. As might be expected, much debate about terminology and interpretation of concepts has emerged in the scientific literature. Ruxton and Schaefer (2011) provided a review and suggested resolutions for disagreements about definitions. Additionally, Kaplan (2014) traced the development of animal communication research and the disparate approaches that characterize the fields of sociobiology and cognitive science. We direct interested readers to those reviews; this is an exciting and expanding area of research that will undoubtedly advance our understanding of mammalian social behavior.

PROPERTIES OF SIGNALS

Animal signals can be divided into two general types. **Discrete** signals are categorical behaviors that are stereotyped or unvarying, either on or off; they do not vary in intensity. In contrast, **graded** signals are variable across a continuous range of qualitative or quantitative measures, and they communicate information by their intensity. For example, among some species of primates, females signal fertility through receptive behaviors and/or sexual swellings of the anogenital region. Both the behaviors and the swellings increase to a maximum around the time of ovulation in female crested macaques (*Macaca nigra*; Figure 23.6), thereby indicating that they serve as honest graded signals about female reproductive status (Higham et al. 2012).

The type of information transmitted in signals also can be divided into two general categories. Signals can be **internally referential** (also called "intrinsic")—providing information about some attribute of the sender (e.g., state of urgency, age, social status). Or they can be externally or **functionally referential**—providing information about the environment beyond or events apart from the sender. A review of functionally referential vocalizations in mammals identified three common subjects of these vocaliza-
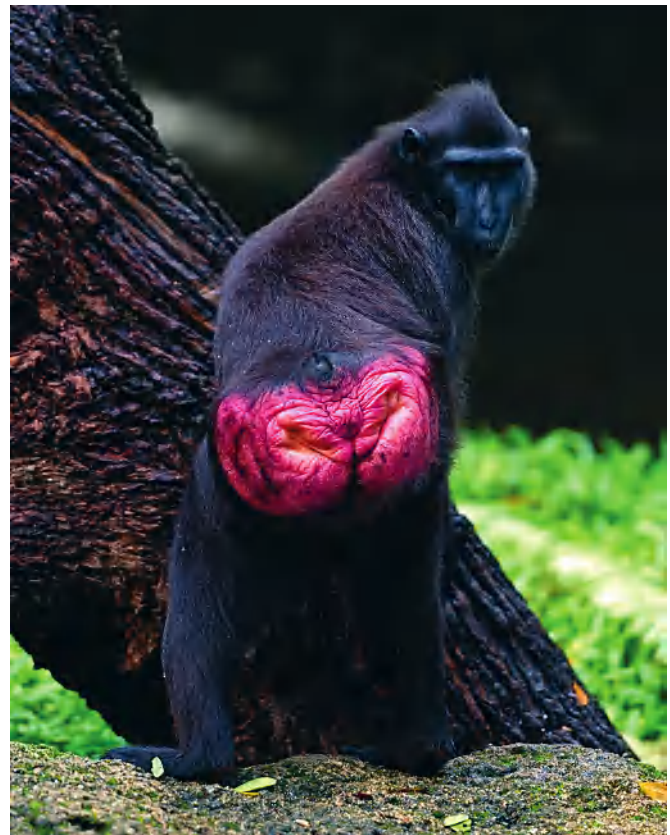
Figure 23.6 Sexual swellings of crested macaques.
Sexual swellings of the anogenital region in some species of primates such as the crested macaque (*Macaca nigra*) increase around the time of ovulation, serving as an honest signal of reproductive status.

tions: alarm calls, food calls, and social vocalizations (Townsend and Manser 2013). Although most commonly documented and studied in primates, alarm calls that identify the type of predator threat and potentially even individual attributes of the predators are also produced by other social mammals, including Gunnison's prairie dogs (*Cynomys gunnisoni*; Slobodchikoff et al. 2009). In some alarm calls, both internally and externally referential information that can affect the response of receivers is encoded. For example, yellow-bellied marmots (*Marmota flaviventris*) responding to alarm vocalizations assess reliability of individual alarm-callers and adjust the time they spend evaluating potential risk accordingly (Blumstein et al. 2004). North American beavers have a range of vocalizations, but perhaps their most significant behavioral signal is tail-slapping. Males and females, of all ages, tail-slap as a warning to family members of potential danger, as well as to drive off a predator. Tail-slapping by adults elicits the most response; kits (young) elicit the least response (Baker and Hill 2003; see Chapter 16).

Communication can be influenced not only by the information transmitted, but also by the social and ecological contexts in which a signal is given and received, as well as the relationship between the interacting individuals. For example, responses of wild chacma baboons (*Papio cynocephalus ursinus*) to grunt vocalizations depended on the type of grunt as well as the social and ecological context, including the difference in dominance rank between the sender and receiver (Rendall et al. 1999).

An intriguing property of signals is the potential to convey additional information through use of **syntax**, which is a set of rules that govern combinations of elements (sounds or words), which impart a particular meaning. In human speech, syntax is very important. Contrast the different meanings when the order of words is changed in the following phrases: "The bear eats Steve" versus "Steve eats the bear." Laboratory-reared chimpanzees are reported to use syntax as they communicate with one another and with their human companions (Savage-Rumbaugh 1986; Savage-Rumbaugh and Brakke 1990). In wild mammals, the evidence is less robust. Studies of white-handed gibbons (*Hylobates lar*; Clarke et al. 2006) and Campbell's monkeys (*Cercopithecus campbelli*; Ouattara et al. 2009) demonstrated that these animals combined sound elements following rules to form sequences associated with external events. However, these examples fall short of demonstrating actual use of syntax. Stronger support for compositional syntax was recently documented in birds (Suzuki et al. 2018). Humpback whales (*Megaptera novaeangliae*) are known to transmit learned vocalizations with defined syntax, as are Brazilian free-tailed bats (Bohn et al. 2013; Toth and Parsons 2018; see Chapter 21 breakout box). This remains an active area of research in highly social mammalian species.

MODES OF COMMUNICATION

As noted, mammals communicate and perceive signals using multiple senses (e.g., olfactory, visual, auditory, and others). Communication that simultaneously uses multiple **sensory channels** is termed **multimodal** or multisensory. The environment and the type of information being sent influence what sensory channels are likely to be used. Table 23.2 summarizes some of the properties of signals traveling via different channels. Multimodal signals can contain information that is redundant across senses (backup signals) or information that is novel or nonredundant (multiple messages) across the different senses (Partan and Marler 2005; Hebets et al. 2016).

Olfactory

Olfaction is a highly developed sense that plays a central role in social communication in mammals, and most species have two separate chemosensory systems with independent

Table 23.2   General properties of the major sensory channels of communication used by mammals

Signal Property	Sensory Channels			
	Olfactory	Auditory	Visual	Tactile
Range	Long	Long	Medium	Short
Transmission rate	Slow	Fast	Fast	Fast
Travel around objects	Yes	Yes	No	No
Night use	Yes	Yes	Little	Yes
Fade-out time	Slow	Fast	Fast	Fast
Locate sender	Difficult	Varies	Easy	Easy
Cost to send signal	Low	High	Medium	Low

Data from John Alcock (1989).

neural pathways. Receptors for the primary system are located within the nasal cavity, which is enlarged and complex in most mammals. The dorsal portion of the nasal cavity is lined with olfactory epithelium that contains chemoreceptors that can detect over 1,000 volatile molecules (Lledo et al. 2005). These airborne odorant molecules become dissolved in the mucus covering the epithelium, creating nerve impulses that are transmitted to the olfactory bulb. The secondary chemosensory system, the **vomeronasal** (or Jacobson's) **organ**, is located between the nasal passages and the mouth, near the vomer and nasal bones in the nasal septum. It opens into the roof of the mouth in most mammals. This system detects primarily nonvolatile chemical compounds often contained in liquids (water, urine, or other secretions). These odorants include **pheromones**, which are chemical signals that are released by an animal and elicit responses in other individuals, usually of the same species. In the past, the two chemosensory systems were believed to function independently, with the vomeronasal organ restricted to reception of pheromones and the main olfactory system detecting chemical signals from the environment (e.g., from food or predators); however, this is not always the case and sometimes input from the two systems is integrated.

Pheromones are especially important in social communication among mammals, and most involve mate identification and attraction, spacing mechanisms, or alarm. The sources of these products include urine, feces, the sexual accessory glands, and a number of specialized skin glands. For example, Belding's ground squirrels (*Urocitellus beldingi*) produce distinct odors from at least five specialized glands located in the mouth area, the back, the ears, the foot pads, and the anus. Each of these products contains information that uniquely identifies a particular individual, creating a singular bouquet that can be used in social situations (Mateo 2006). White-tailed deer (*Odocoileus virginianus*) and other members of Family Cervidae produce pheromones from multiple glands, including the tarsal and metatarsal glands on the hind legs, as well as glands between the toes and in front of the eyes, which are used in scent-marking behaviors (Figure 23.7).

Olfactory investigation by ungulates and some other mammals, especially felids, is characterized by the **flehmen response** (Figure 23.8), a retraction of the upper lip exhibited soon after contact with an odor source of interest. The animal usually adopts a head-up posture for several seconds, inhaling with the nostrils at least partially occluded, which brings air and chemicals into the mouth and the openings of the vomeronasal organ. This behavior pattern is especially common in males during the breeding season when investigating females and sites where females have urinated, but also occurs in adults and juveniles of both sexes in other social contexts.

Many of the pheromones produced by mammals function as a means of identifying individuals, sex, reproductive status, or marking territories. Because these substances often are associated with the urinary and digestive systems,
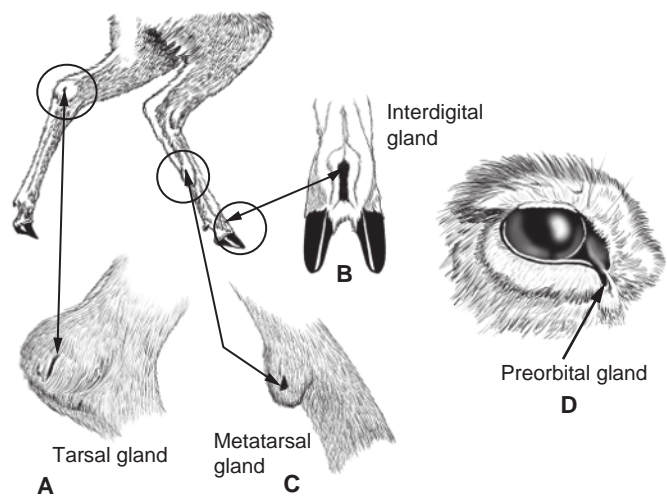
Figure 23.7 **Scent glands of white-tailed deer.** (**A**) Tarsal glands are located on the inner surfaces of the hind legs. (**B**) Interdigital glands are located between the hooves of each foot. (**C**) Metatarsal glands are found on the outer surface of the hind legs. (**D**) Preorbital glands are located at the front of each eye. *Adapted from Halls (1984).*

eliminative behavior is often highly specialized. In white rhinos (*Ceratotherium simum*), territorial adult males perform ritualized urination and defecation behaviors used to scent-mark their territories. Recent experimental work isolated the volatile organic compounds released from rhino dung and demonstrated that they convey information about sex, age, and territorial status (Marneweck et al. 2017). Likewise, male pronghorns (*Antilocapra americana*) exhibit a paw-urinate-defecate sequence to convey the same information. Spotted hyena clans mark the boundaries of their territories by establishing latrine areas. In addition, hyenas also engage in "pasting." Both sexes possess anal glands that open near the rectum. When pasting, the hyena straddles long stalks of grass, and as the stems pass underneath, the animal everts its anal gland and deposits a strong-smelling yellowish substance on the grass stems (Kruuk 1972; Drea et al. 2002; Figure 23.9). Odor-producing bacteria in the glands themselves are a principle source of olfactory signals. Bacterial communities are more similar among hyenas from the same social group than among those from different groups, and this most likely leads to clan-specific odors (Theis et al. 2012).

Auditory

Auditory signals are another prominent mode of mammalian social communication. Mammals are unique among vertebrates in possessing pinnae (external ears), which function to focus and direct sound waves to the ear canal and the eardrum (tympanum; Figure 23.10). The pinnae contribute to the acute sense of hearing of most mammals, although they have been lost secondarily in some species including fossorial mammals, cetaceans, and phocid seals.

Figure 23.8 Flehmen response behavior. Mammals often exhibit a characteristic flehmen behavior when sampling scents encountered in the environment. The upper lip is retracted and the animal inhales with the nostrils at least partially occluded, which helps to draw the odorant molecules into the openings of the vomeronasal organ located in the roof of the mouth in most mammals. Flehmen behavior is common in ungulates (e.g., Malayan tapir, *upper left*; Burchell's zebra, *right*) and felids (e.g., Sumatran tiger, *lower left*).

The three bones of the middle ear (auditory ossicles) transmit vibrations from the tympanum to the inner ear, where they are converted into nerve impulses transmitted to the brain via the auditory nerve.

Mammals can create and detect a surprisingly wide range of sounds, but the ability of almost all mammals to hear high-frequency sounds (>10 kHz) sets them apart from other vertebrates. High frequencies facilitate localization of the source of a sound. Interestingly, some fossorial species, such as mole-rats (Bathyergidae) and pocket gophers (Geomyidae), lack the ability to detect high-frequency sounds, presumably because of an absence of selection for localizing sounds in subterranean environments (Heffner and Heffner 2008).

Ultrasonic vocalizations (frequencies >20 kHz, which are above those audible to humans) are produced by a variety of mammals. Some of the vocalizations of canids are well above the range of human hearing, as are the echolocation sounds of most bats (see Chapter 21). Vocalizations by bats, however, also include social calls that function in

Figure 23.9 Pasting as a form of territorial marking.
Spotted hyena (*Crocuta crocuta*) pasting by depositing anal gland secretions on a grass stalk that is bent over between the legs. The second hyena in this photo is examining the scent mark.
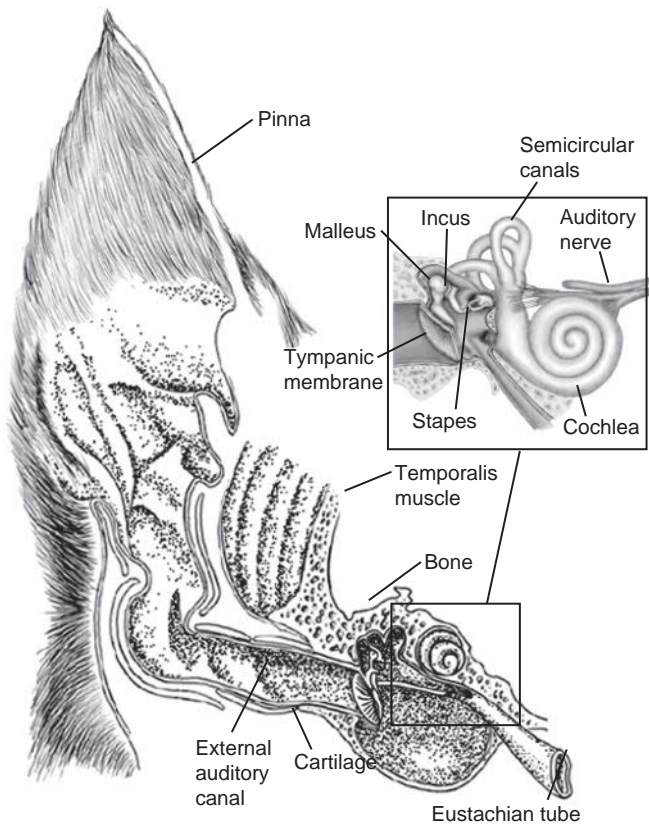
Figure 23.10 Mammalian ear. Features of the ear include an external pinna for collecting sound, the ossicles of the middle ear for transmitting the sound pressure, and the organ of Corti in the inner ear for transducing the pressure signal to neural impulses. The semicircular canals, important for balance, are located in the inner ear. *Adapted from Stebbins (1983).*

communication. For example, male Brazilian free-tail bats produce ultrasonic songs during the mating season to attract females (Bohn et al. 2013). Young mice also produce ultrasonic vocalizations when separated from their mothers, and recent work suggests that male mice "sing" to attract

females (see box). Such vocalizations contain information about kinship and individual identity, which females can use in selecting a mate (Hoffmann et al. 2012a, 2012b). For some mammals, vocalizations in the ultrasonic range might provide private channels of communication that are not detectable by predators. For example, Richardson's ground squirrels give alarm calls in both the audible and ultrasonic ranges and appear to adjust their use depending on proximity of conspecifics and threats (Wilson and Hare 2004, 2006). Other investigations suggest that flying squirrels (*Glaucomys* spp.; Murrant et al. 2013) and at least one nocturnal primate, the Philippine tarsier (*Tarsius syrichta*; Ramsier et al. 2012), also vocalize in an ultrasonic range that might elude eavesdropping by predators. As in bats, use of ultrasonics in some of these species may also function to avoid noise clutter of lower frequencies.

In addition to ultrasonic sounds, some species of terrestrial mammals produce very low frequency (infrasonic) sounds. Both Asian elephants (*Elephas maximus*) and African savanna elephants (*Loxodonta africana*) use very low frequency "rumbles," in the range of 14–35 Hz, to communicate over distances of several kilometers (Payne et al. 1986, Poole et al. 1988; see Chapter 12). These calls are used for long-distance coordination of group movements, location of mates, and even the identity of family members (McComb et al. 2003). Baleen whales also use low-frequency sounds for long-distance communications, and recent simulations based on skull morphology suggest that the infrasonic vibrations are conducted and amplified by a receiving whale's skull before being transmitted to the ear bones (Cranford and Krysl 2015).

A wide diversity of mammals (e.g., mole-rats, kangaroos, rabbits, deer, elephants) also uses low-frequency seismic vibrations to communicate, often generated via percussion on the ground (Randall 2001). Desert rodents such as kangaroo rats have greatly inflated auditory bullae (see Figure 16.15C), which make them sensitive to low-frequency sounds and vibrations such as those produced by snakes and other predators. Banner-tailed kangaroo rats (*Dipodomys spectabilis*) defend their territories by foot-drumming (Randall 1984), producing sounds in the 200–2,000-Hz range. Both Asian and African elephants also appear to send and detect low-frequency seismic signals (O'Connell-Rodwell 2007).

Visual

Vision functions in communication for most, but not all mammals, and is generally more important for diurnal than nocturnal species. Like those of other vertebrates, mammalian eyes contain both **rods** for black-and-white vision, which are sensitive to low levels of illumination, and **cones** for color vision in relatively bright light. Diurnal mammals have a greater proportion of cones, and nocturnal ones have relatively more rods. Many nocturnal species also have a tapetum lucidum behind the retina, which enhances night vision by reflecting light back through the

Why Do Mice Sing?

Adult males of several species of mice produce ultrasonic vocalizations in the presence of females—a fact that suggests that they are involved in mate choice. When presented with playbacks, females were more attracted to ultrasonic sounds of novel males and showed a preference for unfamiliar, unrelated versus familiar siblings (Musolf et al. 2010). Spectrographic analyses of these songs points to many similarities with bird songs, in that they are made up of discrete syllables that differ from one male to another in ways that denote individual and kinship signatures (Hoffmann et al. 2012a, 2012b).

Someone with good hearing in the high-frequency ranges might be able to hear the piercing trills of neotropical singing mice (Genus *Scotinomys*) in the cloud forests of Central America (Burkhard et al. 2018). These diurnal, insectivorous rodents use such calls to attract mates, as evidenced by playback experiments using wild-caught mice (Pasch et al. 2011). Females approached speakers playing faster trill rates, and trill rates were found to be under control of testosterone, given that castrated males produced slower, less preferred trills.

Singing also plays a role in mediating interspecific competition in these mice. The Chiriqui singing mouse (*S. xerampelinus*) occupies the high forest mountains of Panama and Costa Rica. At lower elevations, it is replaced by Alston's singing mouse (*S. teguina*). Behavioral trials and removal experiments indicate that *S. xerampelinus* is behaviorally dominant and excludes *S. teguina* from higher, cooler altitudes (Pasch et al. 2013). Song playback experiments indicate that the subordinate species is silenced and repelled by heterospecific song, whereas the dominant species responds to heterospecific song with approach and song rates comparable to responses to conspecifics. Thus, singing appears to contribute to setting the habitat distribution boundaries of these two closely related species (Pasch et al. 2013, 2017).

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This singing mouse (*Scotinomys teguina*) is vocalizing, using very high frequencies, in the Costa Rican rainforest.

retina and thereby increasing the light available to the photoreceptors. Some fossorial mammals have greatly reduced visual acuity. It was long believed that subterranean mole-rats were blind; however, experimental evidence supports their having a limited ability to respond to light (Kott et al. 2010). Marsupial moles (*Notoryctes*) have vestigial eyes 1 mm in diameter, with no lens, and a greatly reduced optic nerve; the 21 species of golden moles (Chrysochloridae) have fused eyelids covered with skin.

Visual communication is accomplished via **displays**, which are usually defined as a subset of signals that involve structures or ritualized behaviors with visual components (e.g., movement, color, posturing). Such displays communicate information from the sender to the receiver and are used in a diversity of contexts, including courtship, aggression, territoriality, and reconciliation. In agonistic encounters, displays often precede direct aggression and can reduce energy expenditure and the potential for injury to both the sender and receiver by avoiding escalation of the conflict. Visual displays are often incorporated into multisensory signals and accompanied by auditory or olfactory components.

Given that diurnal mammals generally have more visual acuity than nocturnal ones, it is not surprising that many displays have been described for diurnal social species. Primates rely on a rich suite of social displays including facial expressions, gestures, and postures, and they are also the most colorful mammals. In many species, color as well as size of genitals and secondary sexual characteristics can indicate social status as well as reproductive state (see Figure 23.6). Many primates display their teeth in a ritualized yawn that can convey information ranging from aggression to empathy, depending on the intensity of the facial gesture (Leone et al. 2014). Although behavior of diurnal species is better studied, it has been shown that nocturnal mammals also communicate via displays. For example, during aggressive

Figure 23.11 **Female olive baboon grooming a juvenile.** In addition to removing ectoparasites and other foreign matter from the skin and hair, grooming acts as "social cement," solidifying social bonds among group members. Although most grooming occurs between close relatives, it increases between unrelated males and females during the mating season.

Figure 23.12 **Cortical representation of body parts in the somatosensory cortex of the brain of the star-nosed mole.** (*Top*) The actual proportions of the various body parts. (*Bottom*) The relative size of each body part as it is represented in the somatosensory cortex. In addition to the huge area represented by the star, note also the large representation of the forelimbs. The latter could be linked to the use of forelimbs in the excavation of tunnels. *Redrawn from Catania and Kaas (1996).*

encounters male Seba's short-tailed fruit bats (*Carollia perspicillata*) exhibit a suite of ritualized visual displays that involve posture, approach, folding/unfolding the wings, and eventually, boxing by contacting the opponent with the wrist (Fernandez et al. 2014).

Tactile

Tactile sense, or touch, can be an important sensory channel for acquiring information for mammals, although it is perhaps less important for signaling. Touch in mammals is activated by pressure-responsive nerve cells near the surface of the skin. Additionally, most mammals have whiskers (vibrissae) that serve as active tactile sensing organs. Among mammals, touch is also an important component of affiliative behaviors in social groups. In many species, grooming is an important social activity that functions not only to remove ectoparasites but also as "social cement" in the reaffirmation of social bonds (Figure 23.11).

One of the most unusual structures among mammals is the snout of the star-nosed mole (*Condylura cristata*). It consists of 22 fleshy, mobile appendages. Scanning electron microscope images reveal that these rays are densely populated with mechanosensory structures called "Eimer's organs," which are very sensitive to touch (Catania 1999). When microelectrode recordings were made in moles' brains following stimulation of the rays, the receptive field for the star was a huge area in the somatosensory cortex (Figure 23.12; Catania and Kass 1996). One clear function

of these structures, which is especially important for underground living, is to locate and identify food items (Catania and Henry 2006).

Electric Field

Although several studies suggest that some species of aquatic mammals can detect the weak electric fields produced by prey animals, the function of these fields in social communication is undocumented. Two monotremes, the aquatic platypus (*Ornithorhynchus anatinus*) and terrestrial echidnas (Tachyglossidae), use sensors on their bills or beaks to detect the electric field produced by invertebrate prey (see Chapter 10), although the system is much reduced in echidnas (Czech-Damal et al. 2013). Aside from monotremes, the only other mammal known to detect electromagnetic fields is a species of dolphin. The hairless vibrissal crypts on the rostrum of the Guiana dolphin (*Sotalia guianensis*), structures originally associated with mammalian whiskers, detect weak electric fields comparable in strength to those produced by the fish upon which they prey (Czech-Damal et al. 2012).

SUMMARY

- Sociality occurs to varying degrees across all mammals.
  - A society can be defined as a group of individuals of the same species, organized in a cooperative manner that extends beyond sexual behavior.
  - Cooperation often involves seemingly altruistic behavior in which individuals help others at a cost to themselves.

- Potential benefits of group living include protection from predators via several mechanisms, finding and obtaining food, opportunities for social learning, and energy savings via social thermoregulation.

- Potential costs of group living include increased competition for resources, spread of parasites and diseases, attraction of predators, elevated intraspecific aggression, and potential interference in reproduction.

- Kin selection can explain altruistic behaviors and evolution of cooperation among related individuals.

- Individuals can maximize their inclusive fitness (direct fitness + indirect fitness) by helping relatives that share genes by common descent.

- Other explanations are needed to understand evolution of cooperation among unrelated individuals.
  - Reciprocity and mutually beneficial behaviors can lead to evolution of cooperation among non-kin.
  - Sometimes individuals coerce or induce cooperation from other members of a group using manipulative behaviors.

- Almost all social interactions involve some form of communication or transmission of information.

- Signals have evolved for the purpose of communicating information, and they have, on average, positive fitness consequences for both the sender and receiver.

- Primary channels of communication among mammals include the olfactory, auditory, and visual senses.

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DISCUSSION QUESTIONS

1. How might you make the case that colonial invertebrates such as the Portuguese man-of-war or slime molds have more "perfect" societies than does a group of chimpanzees?

2. Many ground squirrel species give alarm calls when predators are near. Craft a hypothesis that invokes only *individual selection* to explain evolution of this behavior. Next, craft an explanation that involves *kin selection*. What information is needed to test both of your hypotheses and how might you go about gathering that information?

3. Although signals are generally honest forms of communication, there are many examples of animals providing dishonest or manipulative information when the sender and receiver have a conflict of interest. Can you imagine some scenarios in which such **deceit** might arise?

4. Odor, sound, and vision are the three primary sensory modalities used for communication among mammals. What are some costs and benefits of using each mode to communicate information? Can you think of examples when communication of the same information across senses might be redundant and examples when the information communicated is complementary?

Movement Patterns and Spatial Relationships

Mammals require temporally and spatially diverse elements of habitat that include food, water, and cover. Patterns of movement and space use link many aspects of mammalian ecology and are important for effective conservation and management of their populations. Those movements inform how mammals use home ranges, disperse into new areas, or migrate back and forth among seasonal ranges. Movement patterns of mammals are classified in terms of fidelity to an area along a continuum from nomadic species to those exhibiting territoriality (Figure 24.1; Koprowski and Fairbanks 2013).

Knowledge of the life-history characteristics of mammals is required to understand their movement patterns as well as selection and use of resources. Additionally, structure of landscapes can affect selection of habitats, patterns of movement, and sizes of home ranges or territories. Therefore, understanding how habitat patches and the spatial configuration of those patches affect the distributions of mammals requires information about how mammals perceive and respond to variation in their environment (Kie et al. 2003; Hefty and Stewart 2018).

Mammals exhibit short-distance movements within a home range as well as long-distance movements. Those long-distance movements include both **dispersal**, which is generally one-way movement away from known areas to new areas where home ranges are then established; and **migration**, which is defined as movement back and forth between ranges. Dispersal is generally permanent, whereas migration includes return movements, often seasonally, between locations or seasonal ranges.

Home Range

In 1943, Burt defined **home range** as the area traversed by an individual animal during its normal activities of food-gathering, mating, and caring for young. Although individuals may make occasional exploratory movements outside of the home range, those movements should not be considered as part of it. The idea of home range did not
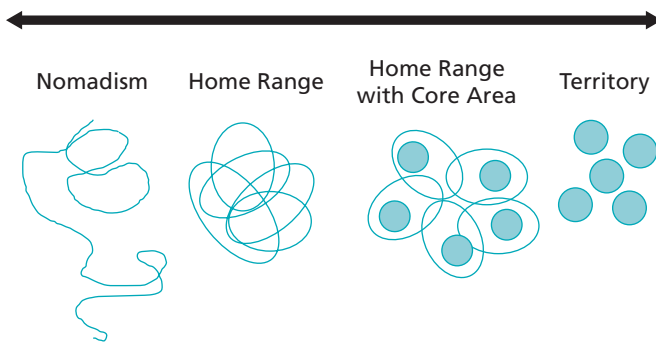
Figure 24.1 Described patterns of space use by mammals. Those representative patterns are a continuum, which is based on use of space and level of defense. *Redrawn from Koprowski and Fairbanks (2013).*

originate with Burt, however. Darwin (1861) observed that animals restrict their movements to home regions that are much smaller than one might expect from observations of mobility (Burt 1943; Börger et al. 2008). Moreover, Seton (1909) observed that wild animals do not roam at random and that each individual has a home region. Mammals exhibit site fidelity to a given area or home range and in general spend much of their reproductive life in an area that is often much smaller than their capabilities for movement (Hooten et al. 2017). Home ranges therefore provide a link between movements of animals and the distribution of resources that are necessary for survival and reproduction in a given area (Börger et al. 2008). Home ranges are not defended, and they may overlap home ranges of other individuals of the same species (Koprowski and Fairbanks 2013). Not all portions of a home range are used on a daily basis, and use of space within the home range arises from activities including searching for or acquiring food, water, and shelter, as well as finding mates or mating opportunities.

Sizes of home ranges vary depending on multiple factors related to life-history characteristics, such as sex, body size, diet, and age class, and to environmental factors such as season, habitat structure, or availability of resources. In mammalian herbivores, the size of the home range generally increases linearly with increasing body size. In carnivorous mammals, however, home-range size increases at closer to an exponential rate with increasing body size, meaning that the size of the home range increases at a greater rate than does body size. In polygynous mammals, home ranges of males generally tend to be larger than and often overlap home ranges of females. Male southern, naked-tailed armadillos (*Cabassous unicinctus*) had an average home range size of about 2 km², whereas female home ranges averaged about 0.5 km² (Desbiez et al. 2018). Armadillo home ranges also overlapped at the external boundaries, although the core areas of highest use did not overlap (Desbiez et al. 2018). Conversely, a meta-analysis of multiple studies of wild pigs (*Sus scrofa*) in the southern United States reported no differences in sizes of home ranges between males and females (Garza et al. 2017).

Sizes of home ranges may vary seasonally or with changes in availability of resources. Female home ranges, especially, appear to be determined by distribution of food resources (Johansson et al. 2018), and, in general, home-range sizes tend to decrease with increasing availability of resources. Home ranges and core areas of use by mule deer (*Odocoileus hemionus*) in a desert environment were smaller in places where water was more abundant (McKee et al. 2015). Home-range sizes of Iberian ibex (*Capra pyrenaica*) were smaller and more stable during seasons when resource availability was highest (Viana et al. 2018). Southern flying squirrels (*Glaucomys volans*) traveled longer distances and expanded their home ranges during summer when day length was longer and temperatures were warmer (Nelson and Sagot 2018). Mountain lions (*Puma concolor*) in the Sierra Nevada Mountains in California had smaller home ranges during winter when mule deer were concentrated on winter range (Pierce et al. 1999; Dellinger et al. 2018). Conversely home ranges of mountain lions during summer when mule deer moved off winter range were larger (Dellinger et al. 2018). Johansson and colleagues (2018) also observed smaller home ranges of male snow leopards (*Panthera uncia*) during winter when distribution of prey was clumped. Female snow leopards showed little seasonal variation in home-range size, but males reduced sizes of their home ranges during the mating season. Home-range sizes of male brown bears (*Ursus arctos*) increased in homogenous landscapes; this change suggested that the spatial distribution of food was more important than seasonal variation in food resources (Mangipane et al. 2017).

Territory

An area occupied more or less exclusively by an individual, pair, or group and defended by overt aggression or advertisement is a **territory**. Territorial animals exclude, or attempt to exclude, conspecifics from specific areas through auditory, visual, or olfactory signals and sometimes through aggressive interactions (Brown and Orians 1970; Giuggioli et al. 2011). To demonstrate territoriality, an individual, mated pair, or group must have exclusive use of some space and exhibit some form of defense of that area. Additionally, territories are smaller than home ranges, and although home ranges may overlap, territories do not. Territoriality often results in a uniform distribution of individuals in a given area. Mammals use multiple behavioral mechanisms to defend territories, including scent-marking, aggression, patrolling, and active defense. Although singing is common in birds to establish and maintain territories, it is uncommon in mammals with the exception of some primates and bats. The African heart-nosed bat (*Cardioderma cor*) uses low-frequency songs to establish foraging territories and to re-establish those territories each night (Smarsh and Smotherman 2017). When researchers played recorded

songs, the bats responded with aggression, and their songs became faster and lower in frequency (Smarsh and Smotherman 2017).

The key to when an animal should establish a territory seems to be related to **economic defendability** (Brown 1964; Fryxell et al. 2014; Koprowski and Fairbanks 2013), meaning that benefits of territorial defense need to outweigh the costs of defending an area. Defense of territories, however, incurs costs through energetic loss during defense, lost time and opportunities for foraging, and risk of territory loss (Figure 24.2; Koprowski and Fairbanks 2013). A benefit of territory defense is in exclusive access to resources in that defended area; therefore, a territory should consist of needed resources for survival and reproduction. Eurasian beavers (*Castor fiber*) that established medium-sized territories occupied them longer compared with beavers that had small or large territories (Mayer et al. 2017). Those findings suggest that large territories were too costly to defend, while small territories likely did not have sufficient resources to support the individuals defending the area. Moreover, high-energy food sources are more likely to be defended than low-energy sources. Food caches created and used by many central-place foraging species, such as ground squirrels or woodrats (*Neotoma* spp.), are often actively defended territories (Eisenberg 1981).

Although food is the resource that is defended, other resources can be critical and thus the focus of competition (Maher and Lott 2000). Males of some mammal species defend territories to acquire mates. Male arctic ground squirrels (*Urocitellus parryii*) defend territories against other reproductively active males (Lacey and Wieczorek 2001). Although females typically mate with several males, the male on whose territory she resides usually mates with her first, and paternity analysis has demonstrated that the first male to mate with an estrous female usually sires her off-

spring (Lacey et al. 1997). Territorial behavior may also be a strategy associated with life-history stage. Male cheetahs (*Acinonyx jubatus*) in Namibia exhibited two different behavioral strategies: resident males or small groups of resident males defended small territories, which covered a portion of ranges of solitary females (Melzheimer et al. 2018); nonterritorial males, termed "floaters," roamed over much larger areas and had somewhat overlapping home ranges. Males that switched strategies usually began as floaters; then, as they reached maturity with increased body mass they switched to territorial behavior.
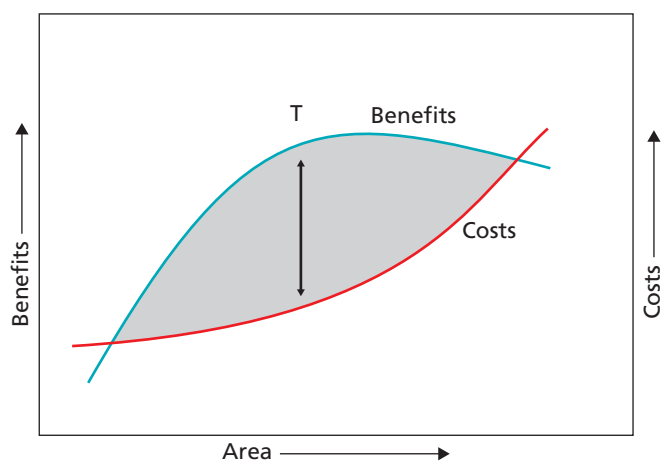
A mating system involving a peculiar type of territory is the **lek**. In a lek, the only resource that the organism defends is the space where mating takes place. Feeding occurs away from the lek. Males of species that defend leks are likely to have evolved elaborate ornaments, such as horns or antlers (Figure 24.3). Males arrive early in the breeding season and through highly ritualized agonistic behavior stake out their plots. Certain territories or displaying males appear to be more attractive to females than neighboring ones, indicated by some males breeding more often than others. Female choice is an important aspect of lek-breeding species, because females move through the area and choose the males with which they mate. While on the lek, the males do little or no feeding; they spend all their time and energy patrolling the boundaries, displaying to other males, and attempting to attract females into their area (Clutton-Brock and McAuliffe 2009). Although lek mating systems are relatively rare among mammals, they occur in some ungulate species, such as topi (*Damaliscus lunatus*; Bro-Jørgensen 2003) and blackbuck (*Antilope cervicapra*; Isvaran 2005), and in other mammals, including African hammer-headed bats (*Hypsignathus monstrosus*; Bradbury 1977). The factors that influence the lek in which females choose to mate are not clear, but females typically prefer dominant males that are centrally located in the breeding areas (Clutton-Brock and McAuliffe 2009).

Figure 24.2 Costs and benefits of territoriality. Territoriality is possible only when the benefits of defending an area outweigh the costs (*gray shading*). The optimal territory size for a given area and set of resources is where the benefits exceed the costs by the greatest amount (*T*). *Redrawn from Koprowski and Fairbanks (2013).*

Figure 24.3 Uganda Kob (*Kobus kob thomasi*) on lek. Those antelopes use mating territories, called "leks," as display grounds for females during the mating season. Lek territories tend to be restricted to mating activities and generally are not resource based (Deutsch 1994).

Habitat and Selection of Resources

Habitat is defined as the place where an animal lives, but of course the concept of habitat is much more complex. Descriptions of habitat need to be species-specific because each species has a unique set of morphological and psychological requirements, and often additional behavioral adaptations that are suited to a specific suite of resources or conditions in a given area (Mannan and Steidl 2013). Habitat is thus further understood to be the area that contains the necessary resources, including food, water, and cover, to promote residency for a species and allow it to survive and reproduce (Morrison et al. 2006; Mannan and Steidl 2013). Environmental conditions that allow species to persist are also included in habitat requirements and generally refer to ranges of temperature and precipitation in an area. Therefore habitat provides for the needs of mammals, which include shelter from inclement weather, access to food and water, places to avoid predators, and access to breeding areas and mates. If a species of mammal occupies an area and reproduces successfully there, then its needs are met and it can compete with other species successfully. Understanding how animals select the habitats in which they reside is central to conservation of mammalian populations. There are good reasons for mammals to be selective of habitats and resources that they need to successfully survive and reproduce in an area, which ties directly to their reproductive fitness.

Habitat or **resource selection** is the process by which an animal chooses a resource; the use of that resource is usually compared with what resources are available. Use of the resource must be greater than availability of that resource in a given area to infer selection (e.g., use > availability). Conversely, avoidance of some aspect of habitat means that use of the resource is less than the availability of that resource (e.g. use < availability). **Preference**, on the other hand, is the likelihood that a resource will be selected if offered on an equal basis with others (Johnson 1980; Manly et al. 2002).

An important aspect of habitat selection and use is that if a resource is readily abundant, it may not show selection if use of that resources is in proportion to its availability (e.g., use = availability), but that does not necessarily mean that the resource does not have value to the individuals using it. In fact, the resource may be very important even if it does not show selection per se (Johnson 1980; Bowyer and Bleich 1984; Manley et al. 2002). Researchers need to be careful when using selection to understand the importance of specific resources, and it is prudent to use several methods to infer the importance of components of habitat or available resources for conservation and management of mammalian populations (Bowyer and Bleich 1984; Manly et al. 2002).

SPATIAL SCALE

Evaluating habitat selection is strongly affected by spatial scale and distribution of resources. Spatial scale ranges from the geographic range of the species, to area occupied by a population, to an individual home range, or an important site within a home range, such as a bed or nest site, or a food cache (Johnson 1980). Interpretation of habitat selection needs to be relative to the appropriate spatial scale to understand how species or individuals use and move through their habitat (Kie et al. 2002; Bowyer and Kie 2006). Indeed, Bowyer and Kie (2006) demonstrated that some mammals made decisions concerning their spatial distributions well beyond the size of their home range. Kie and colleagues (2002) used several habitat metrics including patch shape, habitat graininess, and others to identify the most explanatory scale for predicting the home-range size of mule deer. The largest scale, some 2000 m, was the best predictor of home-range size of mule deer. Moreover, about 95% of the home ranges of 80 mule deer sampled were smaller than the spatial scale that best explained their size (Bowyer and Kie 2006). Some types of resources may be selected by individuals at different spatial scales than others (Bowyer and Kie 2006). At the scale of the population, during winter muskoxen (*Ovibos moschatus*) selected travel routes, feeding sites, feeding craters, and plant species (Schaefer and Messier 1995). At smaller scales, muskoxen selected for greater abundance of graminoids and less snow cover.

SELECTION OF RESOURCES AND LIFE-HISTORY CHARACTERISTICS

Selection of habitats is a process that has been honed by natural selection to ensure that individuals live in areas that contain the resources necessary to maximize their survival and reproduction (Jaenike and Holt 1991; Mannan and Steidl 2013). Therefore selection of habitats or resources is strongly linked to evolutionary fitness. Individuals that selected habitats with the types and amount of resources necessary for their survival and reproduction tend to be more successful than individuals that were less effective in selecting the appropriate resources. Over multiple generations, those individuals that were better at selecting the appropriate resources leave more progeny; and patterns of habitat use and selection that we observe are the outcome of those processes over long time scales. Additionally, patterns of resource use by individuals are a consequence of the effects of selection of resources on reproduction and survival, which ultimately determine the fitness of an individual (Boyce and McDonald 1999).

Understanding how resources are selected, and which resources are selected more often than others by individual mammals, provides information about their requirements for survival and reproduction in a given area (Johnson 1980; Manley et al. 2002; Bowyer and Kie 2006). How animals select resources is affected by multiple factors including age,

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Role of Genes and Environment on Habitat Selection

Stanley C. Wecker (1963) conducted one of the classic studies on habitat selection in mammals on deer mice (*Peromyscus maniculatus*). This species, a common North American rodent, is divided into many geographically variable subspecies; two are the larger, long-eared, long-tailed forest form (*P. m. gracilus*) and the smaller, short-eared, short-tailed grassland (prairie) form (*P. m. bairdii*). The grassland subspecies does well in forest-like laboratory conditions where its food preference and temperature tolerance are similar to those of the forest subspecies. Thus, researchers assumed that the avoidance of forests in the prairie deer mouse is a behavioral response (Harris 1952).

Wecker's objective was to assess the genetic basis of this behavior and to test the importance of "habitat imprinting" (Thorpe 1945). He constructed an enclosure halfway in a forest and halfway in a grassland, released the grassland subspecies in the middle, and recorded their locations. The animals he tested were of three basic types: (l) wild-caught in grassland; (2) offspring of wild-caught parents, reared in a laboratory; and (3) reared in a laboratory for 20 generations. Both wild-caught mice and their offspring selected the grassland half of the enclosure, whatever their previous experience. Laboratory stock and their offspring showed no preference, whether or not they had been raised in forest conditions. By contrast, laboratory stock reared in a grassland enclosure until after weaning showed strong selection for the grassland when tested later.

Wecker reached the following conclusions:

1. The choice of grassland environment by grassland deer mice is predetermined genetically.
2. Early grassland experience can reinforce this innate preference but is not a prerequisite for subsequent habitat selection.
3. Early experience in forest or laboratory is not sufficient to reverse the affinity of this subspecies for the grassland habitat.
4. Confinement of these deer mice in the laboratory for 12 to 20 generations results in a reduction of the hereditary control over the habitat selection response.
5. Laboratory stock retains the capacity to "imprint" on early grassland experience but not on forest.

Wecker also suggested that learned responses, such as habitat imprinting, are the original basis for the restriction of this subspecies to grassland environments; genetic control of this preference is secondary.

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sex, and season, as well as activity patterns and behaviors of the animals being studied. At a broader scale, temperature and precipitation are the main factors that limit the distribution of life on Earth, but food, water, and cover from inclement weather, as well as the presence of competitors, predators, and conspecifics also affect decisions of animals to select an area (Mannan and Steidl 2013). For example, moose (*Alces alces*) are well adapted to cold, but not higher temperatures; therefore, their distributions are limited to northern areas. Physical factors, such as light, soil structure, fire regimes, and chemical factors, such as pH and nutrient availability, are important as well. Each organism has a range of tolerances for a variety of physical and chemical factors in their environment, and much of their behavior is directed toward staying within these limits. Adaptations of mammals to some of these environmental conditions were discussed in Chapter 8.

Risk of predation and competition can restrict habitat use, especially in small mammals. Dune hairy-footed gerbils (*Gerbillurus tytonis*) live in vegetated islands in a sea of sand in the Namib Desert of southwestern Africa (Hughes et al. 1994). Individuals preferred sites around bushes or grass clumps over open areas and were more active on new-moon nights than on full-moon nights. They also gave up feeding at seed trays sooner in open areas and on full-moon nights (Figure 24.4). These differences were likely caused by greater risk of predation in open areas and when the moon was full. When four-striped grass mice (*Rhabdomys*

pumilio), a close competitor of the gerbil, were removed, gerbils increased foraging activity, especially in the grass clumps. Conversely, Villepique and colleagues (2015) reported that rather than abandon preferred habitat, Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*) continued to select the same areas where mountain lions actively hunted in their winter range. Those authors concluded that bighorn sheep did not trade off benefits of forage for reduced predation risk. Rather, those sheep selected for areas of high solar radiation, correlated with high vegetation productivity, while still demonstrating antipredator behavior by also selecting for steep, rugged terrain.

The value of habitats may not necessarily be based upon the amount of time they are used by individuals. For example, habitats for sleeping may be less crucial for survival than water sites, where individuals may spend only a few minutes drinking (Boyce and McDonald 2003). Mule deer in the Mojave Desert selected strongly for sources of water within their home ranges, especially during seasons when water was limited and their water requirements were highest (Figure 24.5; McKee et al. 2015). Beatty and colleagues (2016) looked at selection of resources by Pacific walrus (*Odobenus rosmarus*) relative to loss of sea ice and potential alteration of arctic food webs. Sea ice is important as resting substrates for foraging walruses. Based on Bayesian models of resource selection, walrus strongly selected areas with high biomass of benthic prey (bivalve mollusks that live in soft sediments in the ocean floor) distance to land
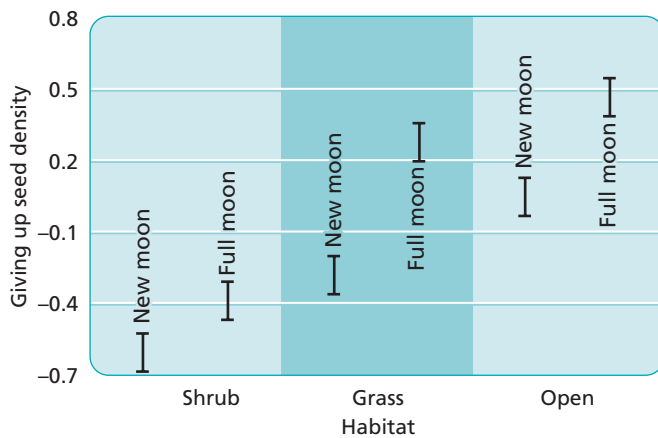
Figure 24.4 The effect of predation risk on habitat use in hairy-footed gerbils. Values along the y-axis are giving up densities (GUDs) for seeds (log10 scale) in food trays containing seeds mixed with sand that were placed in different habitats. High values mean that gerbils left the trays when many seeds were still present. Bars denote 95% confidence intervals. Gerbils gave up at higher seed densities in open areas and on full-moon nights. *Data from Hughes et al. (1994).*

Figure 24.5 Seasonal habitat selection by mule deer in the Mojave Desert. Selection coefficients with 95% confidence intervals from analysis using resource selection functions. Note that values greater than 0 indicate selection, values less than 0 indicate avoidance, and those values where the confidence intervals cross the dotted line do not differ from 0. These results indicate strong selection for sources of water and higher elevation sites, especially during summer. *Redrawn from McKee et al. (2015).*

and distance to sea ice. Distance to sea ice was the most important habitat component in their models, meaning that it explained the most variation with respect to selection of resources while foraging; amount of prey biomass was the next most important component. Those results indicate that with climate change, loss of sea ice will have major effects on foraging ecology of walrus as well as strong effects on the spatial structure of arctic food webs in the future.

Dispersal

Dispersal is the primary mechanism leading to gene flow within and between populations (Matthysen 2012). Dispersal is generally described as a permanent movement in a single direction to establish a home range in a new area. Dispersal of an individual from the place where it was born to the place where it sets up a home range and reproduces is termed **natal dispersal**. Individuals may disperse or remain near their maternal home ranges for their entire lives (Johnson and Gaines 1990). Dispersal also occurs at other stages of the life of an animal, including between successive sites of reproduction; this type of dispersal is termed **post-breeding**, or **breeding dispersal** (Greenwood 1980; Dingle 1996; Koprowski and Fairbanks 2013). Distances dispersed may vary dramatically among individuals, such that some may move to the nearest available home range, and others may move considerable distances before establishing a home range.

Mechanisms for dispersal may also vary considerably among individuals or species. An individual might be forced out of the natal area by its parents or other residents,

or it might respond involuntarily to increases in testosterone levels associated with sexual maturation and then disperse (Fryxell et al. 2014). Stenseth and Lidicker (1992) recognized two forms of dispersal among mammals. **Presaturation dispersal**, which is often seen in small mammals, occurs when juveniles leave the maternal home range even when population density is low. The mechanism for presaturation dispersal seems to be that parents forcibly evict juveniles from their home ranges or juveniles leave because they are driven by some innate behavior. **Saturation dispersal** has more commonly been observed in large mammals and is density-dependent in that dispersal occurs when the population reaches a threshold density resulting from food limitation. Saturation dispersal has been observed in wood bison in the boreal forest (Larter et al. 2000; Fryxell et al. 2014).

Dispersal consists of three stages: emigration, or moving out of natal or current home range; transfer or movement between locations; and immigration, or entering the new home range (Mabry and Stamps 2008b; Koprowski and Fairbanks 2013). Moving away from known ground is risky because individuals are unfamiliar with the location of food, shelter, and areas to escape from predators, and they are no longer in the presence of familiar neighbors and relatives. Recall from Chapter 23 that cooperative behavior can evolve by both kin selection and reciprocal altruism. Both of those behavior patterns require that individuals remain in the vicinity of relatives or associates. In general, dispersers tend to have lower survival rates than

those that remain in the natal area, but there are exceptions to that rule. For example, survival of San Joaquin kit foxes (*Vulpes macrotis mutica*) was higher for dispersing males than for philopatric (tending to remain in a particular area or near a particular site) males that remained in the natal area (Koopman et al. 2000). Given these costs, however, there must be considerable benefits for dispersal behavior to be so widespread.

Benefits of dispersing tend to fall into three broad categories: avoidance of inbreeding, reduced competition for mates, and reduced competition for resources (Fryxell et al. 2014). The primary cause of dispersal from the natal site has been argued to be the avoidance of inbreeding (Fryxell et al. 2014). The costs of inbreeding, referred to as **inbreeding depression**, have been documented in many laboratory and zoo populations (Ralls et al. 1979), but only recently studied in natural populations. Inbreeding depression manifests itself through reduced reproductive success and survival of offspring from closely related parents compared with offspring of unrelated parents. Inbreeding depression is caused by increased homozygosity of the inbred offspring and the resulting expression of deleterious recessive alleles. Nevertheless, there are instances in small populations where inbreeding has had no deleterious effects (Keane et al. 1996). Therefore, the effects of inbreeding depend on past population size and mating patterns. Populations with a long history of outbreeding tend to show the most severe effects once inbreeding takes place. This result is likely because recessive mutations accumulate in the population during outbreeding without ill effect, but are more likely to be present in both parents and thus passed on to offspring when inbreeding takes place. For example, males from a small inbred population of lions showed lower testosterone levels and more abnormal sperm than did males from a large outbred population (Wildt et al. 1987). Presumably, these inbred prides are more prone to extinction than outbred prides. Nevertheless, populations that have survived episodes of inbreeding in the past, such as the cheetah, may tolerate current inbreeding with few ill effects, in part because the deleterious recessive alleles already have been selected out of the population (Shields 1982).

If one or the other sex disperses, the chance of mating between related individuals lessens. Among black-tailed prairie dogs (*Cynomys ludovicianus*), young males leave the family group before breeding, whereas females remain. Also, adult males usually leave groups before their female offspring mature (Hoogland 1982). Among primates such as vervet monkeys (*Chlorocebus aethiops*), males usually leave the natal group at, or shortly after, sexual maturation (Cheney and Seyfarth 1983). They usually transfer to a neighboring group with age peers or brothers (Figure 24.6). Several years later, they may again transfer alone to a third group. Cheney and Seyfarth (1983) argued that this pattern of nonrandom movements followed by random movements minimizes the chances of mating with close kin. Packer (1977) reported that a male baboon that failed to disperse
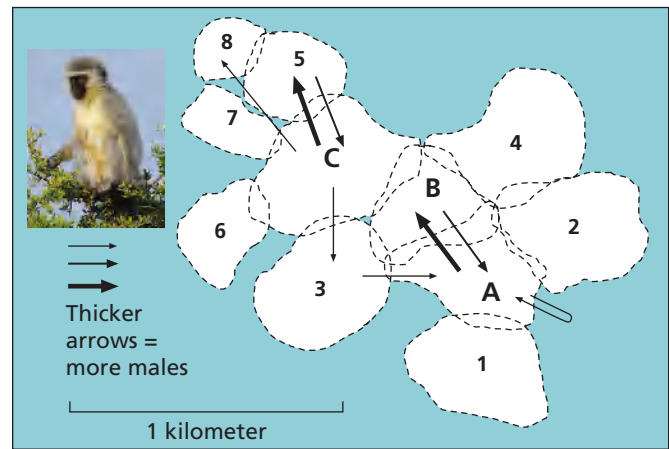
Figure 24.6 **Group transfer by natal and young adult male vervet monkeys from three social groups over a 5-year span.** Arrows indicate direction of movement. Letters indicate ranges of regularly censused groups. Only groups with ranges adjacent to the main study groups are shown. Males usually transferred to neighboring groups with brothers or age peers. *Data from Cheney and Seyfarth (1983).*

at sexual maturity and then mated with relatives produced offspring with lower survival rates than the offspring of outbred males. Thus, a real cost in reduced fitness seems to be associated with inbreeding.

In many species of animals, members of one sex disperse from the place of birth before breeding, whereas members of the other sex are **philopatric**, breeding near the place where they were born. Among mammals, males usually disperse, but the opposite is true in birds (Greenwood 1980). Nevertheless, a small proportion of female mammals will disperse as well, but they tend to move shorter distances (Koprowski and Fairbanks 2013). Mating system has an important effect on patterns of dispersal among mammals (Greenwood 1980, 1983). Generally, in polygynous or promiscuous species, males disperse because male reproductive success is limited by the number of mates, so competition for mates is important, and they are more likely to find new mates by dispersing. For example, male African lions (*Panthera leo*) typically leave the natal pride at sexual maturity and attempt to breed with females from other prides. In polygynous mammals, females invest more in offspring than do males, so their reproductive success is limited by competition for resources. Females compete for resources and tend to be philopatric, because finding food is easier when you are familiar with the area (Fryxell et al. 2014). Dispersal may therefore reduce competition for either resources or potential mates. Exceptions to male-biased dispersal in mammals include African wild dogs (*Lycaon pictus*) and plains zebra (*Equus* [*burchelli*] *quagga*): in both species, females are usually the dispersers. Additionally in species that tend towards monogamy, including Mongolian gerbils (*Meriones unguiculatus*), wolves (*Canis lupus*), and black capuchin monkeys (*Sapajus nigritus*), both

Dispersal Distances in Red Foxes

The red fox (Vulpes vulpes) is a very adaptable mid-sized predator that has colonized the majority of the northern hemisphere. Thus, red foxes have one of the largest geographic ranges of any terrestrial mammal. Nevertheless, because of their relatively small body size, tracking pathways during dispersal has been difficult. Previous knowledge has been gained by capture-recapture studies and use of very high frequency (VHF) telemetry, which relies on straight-line distance rather than actual pathways to document movements. Additionally, these data may miss animals that dispersed long distances because they move away from study area boundaries, so researchers are unable to determine how far they went or whether they dispersed and settled far away or died along the route. Therefore, foxes may be moving much greater distances than have been recorded.

Advances in global positioning system (GPS) telemetry have allowed transmitters to be much smaller, last longer, and have an improved signal. Walton and colleagues (2018) were able to use GPS telemetry to document dispersal pathways by red fox in Norway and Sweden. They were able to record detailed dispersal pathways and document long distances moved.

During the study 30 out of 101 foxes dispersed, and 6 of those foxes, 1 female and 5 males, traveled straight-line distances greater than 60 km. Cumulative distances ranged from 132 to 1,036 km. The longest distance moved was by a sub-adult female. The 2 foxes that moved the longest distances returned to settle in areas that they had previously explored.

The dispersal distances recorded by these researchers were much greater than expected based on body size of the foxes. Also, dispersal events happened relatively quickly—most occurred within two weeks, which illustrates potential for rapid colonization of new habitats. An important finding of this research is that total distances traveled during dispersal events were much longer than the distance between original and settlement locations.

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sexes disperse equally (Arthur et al. 1993; Boyd and Pletscher 1999; Wang et al. 2017; Tokuda et al. 2018).

In cooperatively breeding mammals, dispersal often differs between the sexes. Torrents-Ticó and colleagues (2018) looked at dispersal by both sexes of cooperatively breeding Damaraland mole-rats (*Fukomys damarensis*). Their results indicated that dispersal probability of both sexes was strongly affected by rainfall, with increasing rainfall also increasing probability of dispersal. After dispersing, males were more likely than females to join established groups and replace the resident breeder. Males were more often faced with competitors from outside their groups, whereas females faced higher competition within their groups.

Dispersal from the natal site may be a function of the reduction of competition with conspecifics for food, shelter, or mates (Dobson 1982; Moore and Ali 1984). As we pointed out in Chapter 23, gestation and lactation by females mean that males tend to provide little or no direct care for offspring. Most species of mammals are polygynous—that is, males mate with more than one female. Males may be forced to disperse as they compete for access to females. Although the inbreeding-avoidance hypothesis predicts that one sex should disperse, it does not predict which sex should disperse; the competition hypothesis predicts that males should be the dispersing sex in polygynous species. According to Greenwood (1980), in such systems the reproductive success of males is limited by the number of females with which they can mate, and males are likely to range farther than females as they search for mates. Females, on the other hand, are limited by resources (food and nesting sites) that can best be obtained and defended by staying at home. Among group-living mammals, females typically form the stable nucleus, and the males attempt to maximize their access to them, frequently moving from one group to another.

Hamilton and May (1977) proposed a somewhat different competition model in which animals disperse to avoid local resource competition with close relatives and thus avoid lowering their indirect fitness. In a new habitat, they are likely to be competing with nonrelatives and therefore would suffer no such fitness cost. These models are not contradictory, but more research is needed on both the proximate and ultimate causes of dispersal.

Migration

Migration is one of the most widely observed phenomena in the animal kingdom and occurs across the globe in a wide range of taxa ranging from fish to birds to mammals (Figure 24.7; Berger 2004; Dingle and Drake 2007; Dingle 2014). Migration is defined as a round-trip journey between discrete home ranges not used at other times of the year (Sinclair 1983; Fryxell and Sinclair 1988; Berger 2004). Migrating mammals use all three means of vertebrate locomotion—flying (bats), swimming (marine mammals), and walking or running (ungulates)—to make long-distance movements back and forth between seasonal ranges. Causes of migration are to increase access to high-quality food that is seasonally available, avoid seasonally harsh environments, and reduce the risk of predation (Fryxell and Sinclair 1988; Alerstam et al. 2003). Fluctuations of resources in seasonal environments are probably the most likely cause of migration in most species (Dingle 2014).

Migratory behavior is adaptive if those individuals that migrate achieve greater reproductive fitness than those that remain resident (Avgar et al. 2014; Bleich 2018). Shaw and Couzin (2013) showed that migration tends to occur when distribution of resources is more affected by seasonality than by patchiness of habitats. Migration, therefore, allows animals to exploit seasonal peaks of resource abundance and to avoid sharp declines in resource availability by moving to areas with more stable resources, even if they are of lower quality, during the harshest seasons of the year. Migration has been observed to be long distance, including those iconic movements made by caribou (*Rangifer tarandus*) and wildebeest (*Connochaetes taurinus*), but migration
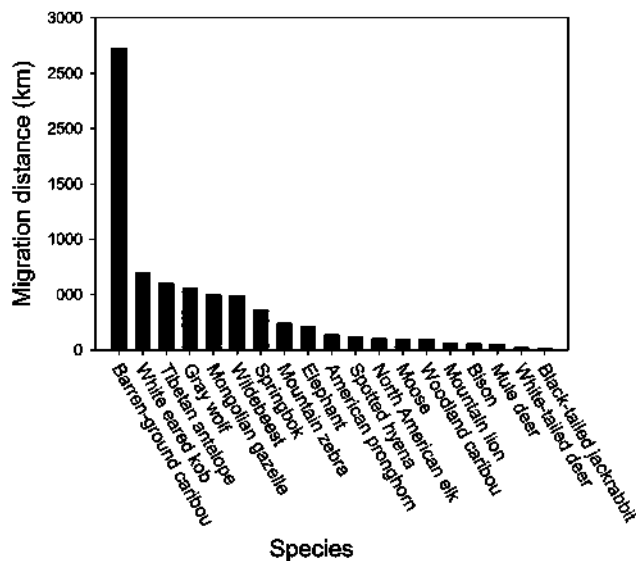
distances may be short as well. For example, in areas where mammals move up in elevation to exploit high-quality resources at high elevation during summer and move down in elevation to avoid harsh weather during winter.

There are costs to migratory movements, and the benefits of migrating must outweigh the costs of those distance movements to be favored by natural selection. Energetic costs of migration vary by form of movement: swimming appears to be the least costly, flying is intermediate, and running incurs the highest cost per unit of body size (Nielsen 1972; Alerstam et al. 2003). In addition to the cost of locomotion, terrestrial migrants encounter topographical constraints such as mountains, anthropogenic barriers such as roads that hinder movements on migratory pathways, and periodic weather events, all of which can increase risk during migratory movements. Bleich (2018) noted several mass mortality events of mule deer in the Sierra Nevada Mountain range in California, where mule deer slipped on ice that in certain instances persisted year around and caused excessively dangerous conditions. In the autumn of 2017, a mass mortality event occurred when 76 mule deer slipped on ice and plunged to their deaths at Bishops Pass, California. The same type of mortality event had also been observed in the same area in 1952 and again in 1995 (Jones 1954; Bleich and Pierce 2001).

Migration is a surprisingly complex phenomenon and requires information about timing and duration of movements in temporal and **circannual** periods for the animal, physiological adaptations for its metabolism, behavioral adaptations to respond to weather and other dangers during the movements, and control of orientation and navigation between and within seasonal ranges (Berthold 2001; Alerstam et al. 2003). Because the ability of animals to complete migration is dependent on energy reserves to fuel migratory movements, some of those reserves may need to be replenished during **stopovers** on the migratory pathway (Alerstam et al. 2003; Sawyer and Kauffman 2011). The process of migration tends to alternate between periods of transportation and refueling (Åkesson and Hedenström 2007). Migrants also use what are known as stopovers, or habitat patches along the migration route where animals rest and forage to renew energy reserves (Alerstam et al. 2003; Dingle and Drake 2007; Sawyer and Kauffman 2011). Ungulates, birds, and marine mammals have been observed to use stopovers during migration (Alerstam et al. 2003; Lyons et al. 2015). Ungulates have also been observed to use stopovers during both spring and autumn migration and on both long- and short-distance migratory movements. Sawyer and Kauffman (2011) observed that mule deer spent about 95% of their time in stopovers during long-distance spring migrations.

In order to migrate and return, animals need to have information on positioning through both orientation and navigation. Orientation requires animals to keep a compass course, and animals may also use information from the Earth's magnetic field, the sun, including light polarization, and stars (Åkesson and Hedenström 2007). Because

Figure 24.7 **Migration distances by terrestrial mammals around the world.** Note that barren-ground-caribou migration distances are substantially longer than those of any other terrestrial migrants. *Redrawn from Berger (2004).*

orientation is based on the sun and polarized light, mammals must have an internal mechanism to compensate for shifting time and for movement of the sun across the sky. Such a mechanism has been demonstrated in a wide range of animals, although it is not well understood in most vertebrates (Horváth and Varijú 2004; Åkesson and Hedenström 2007). Navigation requires use of additional information from landmarks to move from a starting point to a specific goal (Åkesson and Hedenström 2007; Mueller and Fagan 2008). Migrants find their way to a goal even when experimentally displaced from their original pathways, which demonstrates the ability to navigate over long distances. Although mammals have strongly demonstrated the ability to use both orientation and navigation in their migratory movements, we generally do not know specifically what mechanisms are used in the process (Bauer et al. 2011).

Migration strategies of terrestrial animals can be classified as **obligate** if they migrate every year or **facultative** if they migrate some years but not others (Cresswell et al. 2011). Although these behaviors have typically been observed in ungulates and birds, they may occur in other species of mammals as well. Obligate migrators tend to respond to cues such as photoperiods, which trigger migratory behaviors. Facultative migrators may respond to more flexible cues, such as weather events, to initiate migration, and in years with mild weather they may remain resident and not migrate at all.

Partial migration is described at the population level when some individuals in a population migrate, but others do not (Lundberg 1988; Chapman et al. 2011; Avgar et al. 2014). In populations where partial migration is observed, migratory behavior ranges from residents that never migrate to obligate migrants that go every year (Cagnacci et al. 2011; Henderson et al. 2018). Partial migration was observed in populations of European roe deer (*Capreolus capreolus*), and whether individuals migrated depended on both winter severity and landscape topography (Cangacci et al. 2011).

BATS

As the only mammals with true flight, bats (see Chapter 21) might be expected to show migratory behavior comparable to that of birds. Compared with bird migration, which has been extensively studied, the biology of migration in bats is less well known (Stepanian and Wainwright 2018). Migration in bats is extremely difficult to study because bats are mostly nocturnal flyers and their body size is relatively small, both of which make them difficult to mark and follow on migratory journeys (Chapman et al. 2014).

Migration is thought to be a relative rare strategy in bats, with only around 3% of bat species estimated to use migration (Fleming and Eby 2003). Most species of bats use hibernation rather than migration as the primary strategy to overcome periods of low availability of resources in seasonal environments. Hibernation is generally an energetically less costly way of dealing with cold temperatures or lack of food during seasons of low resource availability. Nevertheless, migration does occur in several species of bats, some of which make impressive migrations in terms of distance and numbers of animals migrating. In Kasanka National Park in Zambia, about 5–10 million straw-colored fruit bats (*Eidolon helvum*) seasonally migrate into and out of the park (Richter and Cumming 2005; Chapman et al. 2014). In Family Vespertilionidae, migration has been observed in 23 out of 316 classified species (Bisson et al. 2009).

Information about bat migration often comes from the seasonal appearances and disappearances at roosting sites coupled with recoveries of banded individuals (Fenton and Thomas 1985). Moreover, advances in technology are making it easier to track and tag species of bats for their entire migration (Hedenström and Lindström 2014). Richter and Cumming (2008) attached satellite transmitters to tropical fruit bats in Africa and documented them migrating up to 2,500 km seasonally. In a study involving the banding of more than 73,000 little brown bats (*Myotis lucifugus*), individuals migrated more than 200 km from hibernation caves in southwestern Vermont into Massachusetts and neighboring states for the summer (Davis and Hitchcock 1965).

Fleming and Eby (2003) observed long-distance migration in species of bats that occupy temperate regions and use trees for roost sites, but migratory behavior was also combined with hibernation at wintering areas. Swifter flying species, such as the hoary bat (*Lasiurus cinereus*) and Mexican free-tailed bat (*Tadarida brasiliensis*), move great distances. Hoary bats migrate from summer ranges in the Pacific Northwest, as far north as Alaska, south into central California and Mexico for the winter (Griffin 1970). In winter, they are not found above 37°N latitude, a limit probably set by the distribution of flying insects (Griffin 1970). Free-tailed bats seem to have both migratory and nonmigratory populations. Those in southern Oregon and northern California are year-round residents, but those in the southwestern United States migrate south into Mexico for the winter (Dingle 1980). A population of free-tailed bats in the Four Corners area (where Colorado, Utah, New Mexico, and Arizona meet) have a well-established flyway through the Mexican states of Sonora and Sinaloa west of the Sierra Madre Oriental Mountains. Nevertheless, long-distance migration is not restricted to bat species in temperate regions. Seasonal shifts in rain patterns trigger migration in some species of African bats (Fenton and Thomas 1985). For instance, West African fruit bats of Family Pteropodidae migrate distances of 1,500 km each year, moving into the to the Niger River basin with the seasonal rains (Thomas 1983).

CETACEANS

Cetaceans (Chapter 20) have some of the longest documented migration distances of any mammals. Most species of baleen whales spend summer months feeding on plankton in the highly productive Antarctic and Arctic

waters. As winter approaches in each area, whales migrate to warmer subtropical and tropical waters. Food supply does not drive this winter migration, however tropical waters are less productive than colder waters near the poles. In fact, whales do not feed during migration or at their wintering grounds in the tropics. Instead, they rely on fat deposits. Winter migration in baleen whales toward equatorial areas therefore appears to be driven by reproduction and survival of young. Conversely, summer migration toward the poles seems to be for the purposes of acquiring high-quality food (Shaw and Couzin 2013). One potential benefit of moving to warmer water is the energy savings from reduced heat loss, especially for young. Young whales are born in the tropical breeding grounds, and lactating females with their newborn young move toward feeding areas in the Arctic or Antarctic as spring approaches. Breeding cycles of species that breed near shore, such as the humpback whale (*Megaptera novaeangliae*) and the gray whale (*Eschrichtius robustus*), are fairly well known (Figure 24.8). Humpback calves are born in September, and lactating females begin the trek back north with their calves in the spring, usually after males and newly pregnant females have already left (Dingle 1980; Dingle 2014).

Gray whales have some of the longest documented migration lengths of any species (Figure 24.9). Western North Pacific gray whales were once considered to be extinct, currently number about 130 individuals (Mate et al. 2018). Western Gray whales have exhibited some of the longest documented migration distances; one individual was recorded to have migrated over 22,000 km round trip (Mate et al. 2018).

PINNIPEDS

Many species of seals and sea lions (Chapter 18) migrate thousands of kilometers from island breeding and molting areas to oceanic feeding areas. Island breeding sites are

Figure 24.9 **Migration routes of western gray whales.** Pathways of marked whales indicate migratory movements from Russia along the west coast of North America to Baja California. *Redrawn from Mate et al. (2018).*

Figure 24.10 **Elephant seals on the California coast in autumn.** Seals haul out on the beach to rest following migratory movements.

Figure 24.8 **Breaching gray whale in Guerrero Negro Bay, Mexico.** Gray whales have some of the longest recorded migration distances.

chosen because they are relatively free of predators. Northern elephant seals (*Mirounga angustirostris*; Figure 24.10) breed on island rookeries off California, migrate to foraging areas in the North Pacific and Gulf of Alaska, and later return to the islands to molt. Using geographic location-time-depth recorders, Stewart and DeLong (1995) found that seals travel linear distances of up to 21,000 km during the 250 to 300 days they are at sea. Each individual makes 2 round-trip migrations per year, returning to the same foraging areas during post-breeding and post-molt movements (see Figure 24.10). Males migrate farther north than females, where they feed off the Alaskan coast.

Data-recording tags can do double duty by providing information about ocean temperature and salinity (Pala 2006). Nine elephant seals tagged in 1998–1999 covered an average of 4,634 km over 67 days, with an average dive duration of 20 min and average depth of 428 m (Boehlert et al. 2001). Those tags provided a wealth of information about ocean conditions at different depths. These and other data have been added to the World Ocean Database.

UNGULATES

Ungulates migrate long distances worldwide. In North America, long-distance migration of terrestrial ungulates is observed in caribou, moose, mule deer, and pronghorn (*Antilocapra americana*). In Africa, long-distance migrations are made by wildebeest and plains zebra among others. In central Asia, Saiga antelope (*Saiga tatarica*), Mongolian gazelle (*Procapra gutturosa*), and Tibetan antelope (*Pantholops hodgsonii*) also exhibit large-scale migratory movements. Those species by no means complete the list of migratory ungulates (Berger 2004). One of the most spectacular migrations in northern species is that of the barren-ground caribou (Figure 24.11). Herds migrate north to calving grounds above the timberline in spring and return south in winter, covering distances of more than 500 km (Figure 24.12; Nicholson et al. 2016).

The mass migrations of wildebeests in East Africa are also spectacular. The Serengeti population spends the wet

Figure 24.11 **Migratory caribou from the Western Arctic Herd, Alaska.** Caribou were observed crossing the Kobuk River in Kobuk Valley National Park during autumn migration.
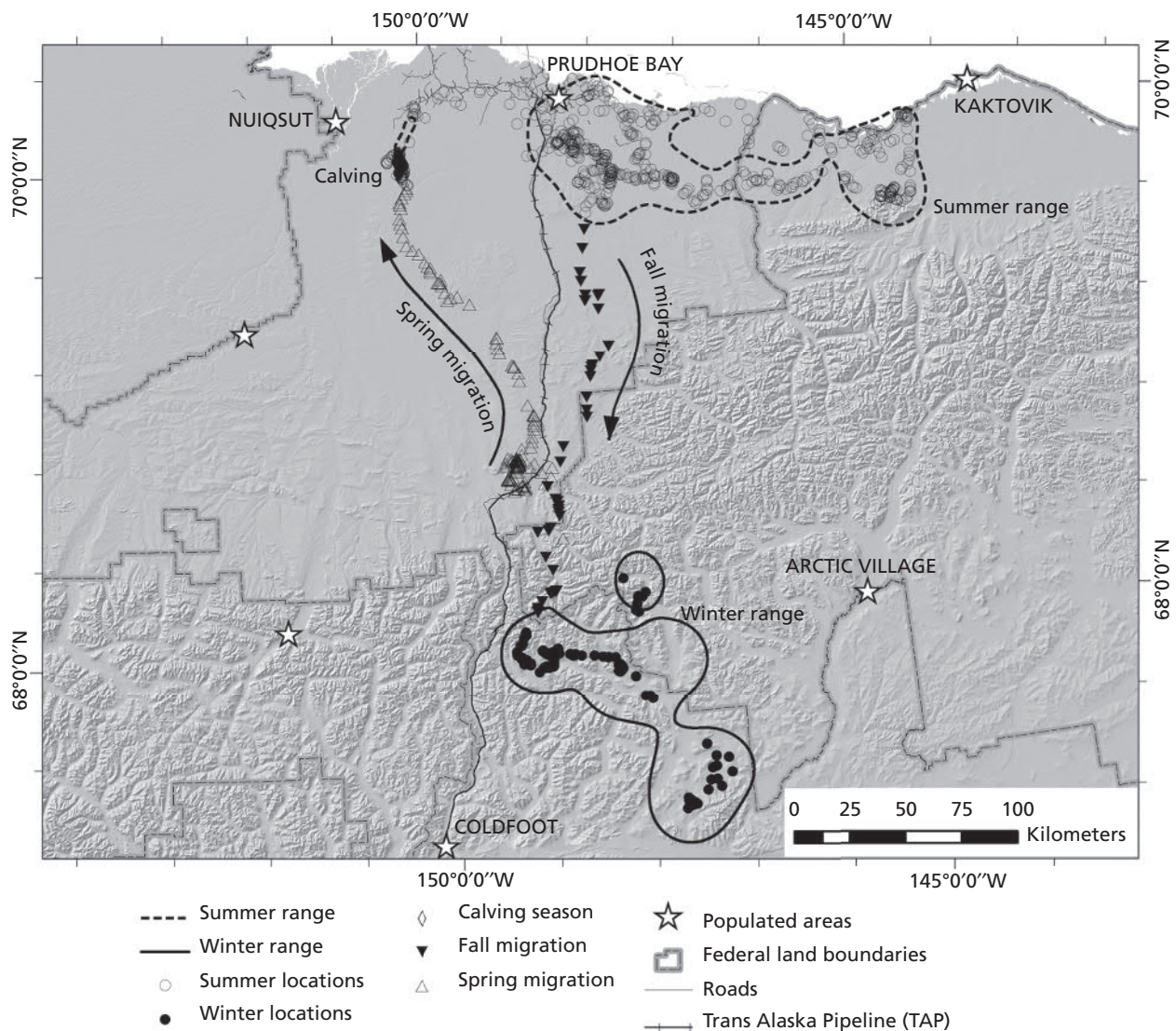
Figure 24.12 **Seasonal movements of one caribou in northern Alaska during 2004.** Herds of caribou migrate north to birthing grounds in spring and return south for winter. *Figure from Nicholson et al. (2016).*

season, usually December through April, in the southeastern Serengeti plains of Tanzania, where short grasses are lush and calving takes place. Large migratory herds form at the beginning of the dry season, in May and June, as millions of animals move, sometimes in single file, northwest toward Lake Victoria. In July and August, near the end of the dry season, herds move northeastward into the Masai-Mara of Kenya and return south to the breeding grounds between November and December. These patterns can vary considerably, however, depending on the timing of rainfall (Dingle 1980).

In the past decade, substantial research has been conducted on long-distance migration of other terrestrial ungulates in North America, including moose, mule deer, pronghorn, and North American elk (*Cervus canadensis*). Those species move into high-elevation summer ranges that are relatively free of snow and then move to milder winter ranges at lower elevations (McCullough 1985; Sawyer et al. 2016; Monteith et al. 2018). Mule deer and pronghorn both have long-distance migrations in Wyoming and Nevada with corridors that stretch over 100 km (Sawyer

and Kauffman 2011; Simpson et al. 2015; Sawyer et al. 2016). Those ungulates show partial migration in their populations as well as resident, facultative, and obligate strategies. Additionally, within populations migration distances may vary. In a population of migratory mule deer in Wyoming, both the timing of migration and the time spent on seasonal ranges varied with the distance of migration. Mule deer that moved longer distances spent more time in migratory movements and less time on seasonal ranges than did short-distance migrants (Sawyer et al. 2016).

During spring migration use of stopovers allows ungulates to move along with changing phenology of vegetation, a process that has been described as "surfing the green wave" (Sawyer and Kauffman 2011; Bischof et al. 2012; Aikens et al. 2017). Moving with changing phenology allows individuals to access forage during early growth when energy, protein, and digestibility of forage are highest (Hebblewhite et al. 2008; Monteith et al. 2018). Such strategies allow for replacement of fat and protein losses over winter as individuals are moving back to summer ranges (Monteith et al. 2013, 2018).

SUMMARY

- Studying movement patterns of mammals provides information on how mammals use the landscape and form home ranges, disperse into new areas, or migrate back and forth among seasonal ranges.

- Selection of resources by mammals occurs at multiple spatial scales from the range of the population, to home ranges, to areas of concentrated use within home ranges.

- Individuals select resources and habitats to maximize their chances of survival and successful reproduction, thereby enhancing their reproductive fitness.

- Individuals may disperse or remain in the natal area to breed, and in mammals males typically disperse while females remain philopatric.

- In polygynous mammals, dispersal reduces competition between males for mates. For females, which compete for resources for rearing young, remaining in an area that is familiar enhances the ability to find resources for successful reproduction and predator avoidance.

- Causes of dispersal include inbreeding avoidance and reduced competition for mates or resources.

- Migration in mammals has been well documented in bats, cetaceans, pinnipeds, and ungulates.

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DISCUSSION QUESTIONS

1. In contrast to mammals, most species of female birds disperse farther from the natal site to breed than do males. Why might this be so? Consult the references in Greenwood (1980, 1983).

2. Review the life history of a mammalian species of your choice. Try to explain the dispersal patterns of each sex in light of our discussion of both proximate and ultimate causation.

3. Long-distance migration occurs in many species of mammals, especially ungulates, marine mammals, and bats. What other mammals might migrate long distances? How do energy costs affect whether animals migrate or not? Do all species of migratory mammals use stopovers? Why or why not?

Populations and Life History

Populations are groups of individuals of the same species that are present at the same place and time (Gotelli 2008). Because a population has the potential to reproduce, it is meaningful to refer to birth and death rates, sex ratios, abundance, and **age structure** (Cole 1957; Gotelli 2008; Mills and Johnson 2013). Thus, populations have both temporal and spatial components. Not all individuals in a population are identical, however; individuals differ in terms of genotype, sex, age, and size, among other things, as well as in how they react to stressors or changes in their environments. Those differences in life-history tactics among individuals affect natality, mortality, and other vital rates that drive population dynamics. A central problem for mammalian ecologists for decades has been to understand and predict the population dynamics of mammals. In this chapter, we consider processes that affect populations of mammals—that is, how populations grow and what biotic and abiotic factors affect them in nature. We also examine life-history tactics of individuals and explore trade-offs made by mammals as they allocate resources to reproduction and survival.

Population Processes

Populations of mammals increase via births, or **natality**; they decrease via deaths, or **mortality**; or they change in numbers via movements through dispersal. Movement into a population is **immigration**, whereas movement out of a population is **emigration**. A simple mathematical expression describes population growth:

$$N_{t+1} = N_t + B - D + I - E, \qquad (25.1)$$

where, N_{t+1} = population size during the next time period, N_t = current population size, B = births, D = deaths, I = immigration, and E = emigration. Births are generally quantified in mammals using mean litter size and number of litters per year for an adult female. Nonetheless, not

all juveniles survive; thus only a portion is recruited into the population. We regard an individual as recruited if it has entered the breeding portion of the population. Deaths are described at the population level through mortality rates. Both immigration and emigration are mediated through dispersal (Mills 2013).

Age structure and sex ratios are other vital rates that influence mammal populations. Age structure is the proportion of individuals in each age class, which is a generalization based on grouping animals according to similarities in survival and fecundity—usually young, juveniles, subadults, or adults. Sex ratios, particularly the proportion of females in a population, are directly linked to reproductive potential and population growth. Sex ratios may vary among age classes, especially in populations that exhibit polygyny or are managed by harvest.

Mammals exhibit different types of survivorship, which can be represented graphically by curves showing the pattern of mortality across different age groups. There are three general types of **survivorship curves** illustrated in Figure 25.1. Type I illustrates relatively high survival after the first year until a certain age at which most members of the population suffer mortality. Most large mammals show type I survivorship curves (Figure 25.2). White-footed mice (*Peromyscus leucopus*), and probably many other small mammals, show a type II curve, in which mortality rates are more or less constant across ages (Schug et al. 1991). Type III survivorship curves, in which mortality rates are highest at early stages of development, are characteristic of invertebrates and some fish but rarely seen in mammals, because of the larger investment female mammals make in their offspring through gestation and lactation (Clutton-Brock et al. 1983).
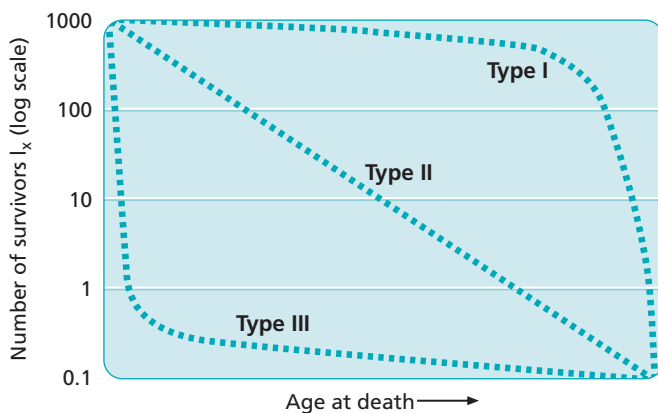
Figure 25.2 Survivorship curves of African ungulates.
After the first few years, most African ungulates resemble type I curves, with the exception of the warthog, which resembles a type II curve. *Data from Pianka (1994).*

LIMITATION AND REGULATION OF POPULATIONS

Limiting factors are defined as those that cause mortality or affect births. Although many factors, such as food, water, and shelter, must be present for any mammalian population to survive, typically only a single factor limits the population growth at any one time. Tests for limiting factors can be conducted by manipulating the amount of one factor while holding others constant and recording changes in the population. For example, if food is the limiting factor, an increase in the population will result if the food supply is augmented.

Regulation is the process by which a population tends to return to its equilibrium size. Density-dependent factors affect population growth differently depending on the number (or density) of animals in a population; at low population densities, they contribute to increased population growth (i.e., lower mortality and higher reproduction), and the opposite is true at high population densities. This type of density-dependent feedback is said to regulate a population because it tends to drive the population back toward an equilibrium. Not all limiting factors regulate populations, however, when they act in a density-dependent manner, they become regulating. A predator pit, for example, can result in a prey population being maintained at low

Figure 25.1 Hypothetical survivorship curves. Type I represents low mortality rates early in life, with most individuals dying at an old age. Type II represents constant mortality rates at all ages. Type III represents high mortality rates early in life. Most mammal species show type I or type II curves. *Adapted from Krebs (2008).*

density by density-dependent predation (Person et al. 2001; Bowyer et al. 2005, 2014). Intraspecific competition received much attention as a regulatory factor in the past because it is the only one that is "perfectly" density-dependent. In other words, the intensity of competition among members of the same population is likely to vary directly with the size of the population; as the population increases, so does competition for limited resources. Unsuccessful competitors may leave the area, die, or have lower reproductive success.

Other biotic regulatory factors, such as predation, disease, and interspecific competition, include other species of organisms that, in turn, are affected by other agents; thus, these biotic regulators are not perfectly density-dependent. For example, predation involves a complex relationship between predator and prey. Although wolves (*Canis lupus*) eat caribou (*Rangifer tarandus*), they are not necessarily the regulators of the caribou population. Because the wolf population is affected by factors other than the numbers of caribou, such as diseases or the abundance of alternative prey species, wolves will not track the caribou population exactly. An outbreak of disease might reduce the size of the wolf pack and allow the caribou to "escape" control and begin to approach ecological **carrying capacity**. Intraspecific competition among the caribou, however, varies directly with the population density and the limiting or regulating resources.

Population Growth and Equilibrium

RATE OF INCREASE

The per capita rate of growth, or the finite rate of growth, is referred to as "lambda" (λ), which describes the change in population size, or abundance, by a discrete time step. That time step is usually estimated in years, but other time steps may be more appropriate depending on the species in question. Lambda can be determined by the abundance in this year N_t compared with the following year N_{t+1} using the equation:

$$\lambda = N_{t+1} / N_t \qquad (25.2)$$

If $\lambda > 1$, the population is increasing, if $\lambda = 1$, the population is replacing itself (i.e., is stationary), and if $\lambda < 1$, the population is declining. Lambda easily converts to percentage change per year by subtracting λ from 1 and multiplying by 100. Therefore if $\lambda = 1.10$, then the population increased by 10% over the course of the year (Mills and Johnson 2013). To determine population growth in continuous time, we use the intrinsic, or instantaneous, rate of growth indicated by r; where $r =$ births–deaths. Those two measures of population growth are interrelated, and taking the natural log of

λ is equal to r. If $r > 0$, the population is increasing, if $r = 0$, the population is replacing itself, and if $r < 0$, the population is declining. Populations are inherently variable over space and time, and to understand population dynamics of mammals (or any species for that matter) that variation must be addressed (Mills 2013; Mills and Johnson 2013).

Factors in nature that keep populations from increasing indefinitely are traditionally divided into two types: those that are density-independent, and those that are density-dependent. Density-independent factors include storms, fires, floods, or other conditions that kill individuals without regard to how many are present or their nutritional condition. Density-dependent factors include food supply, shelter, predators, competitors, parasites, and disease. Effects of such factors on the population are stronger when density is high and weaker when density is low. Exponential population growth is a form of density-independent growth, because population growth does not slow with increasing numbers of animals, as it does in logistic (density-dependent) growth. Both density dependence and density independence are measurable parameters of a species' population dynamics as well as being related to life-history characteristics of that species (for review, see Bowyer et al. 2014).

EXPONENTIAL, OR DENSITY-INDEPENDENT, GROWTH

Populations of all organisms have a great capacity for increase, perhaps best illustrated by the human population of the world that was increasing at 2% per year in the 1960s and doubling every 35 years. The English economist Thomas Malthus was perhaps the first to realize that populations had the potential to increase exponentially while the means to support them did not (Malthus 1798). Arithmetical growth takes place by adding a constant amount during each time interval, but **exponential** growth occurs in proportion to the number already present. Populations increase exponentially because as each individual matures, it begins to breed along with the rest of the population (Figure 25.3). Similarly, in a savings account in which the interest is compounded, the interest begins earning interest along with the principle. The more often the interest is compounded, the faster the savings grow. In *On the Origin of Species*, Darwin (1859:64) wrote, "There is no exception to the rule that every organic being naturally increases at so high a rate, that, if not destroyed, the earth would soon be covered by the progeny of a single pair." Darwin pointed out that even one of the slowest breeding animals, the elephant, would increase from a single pair to nearly 19 million in just 750 years if unchecked.

The rate of growth of a population undergoing exponential growth at a particular instant in time is a differential equation:

$$\frac{dN}{dt} = rN, \qquad (25.3)$$
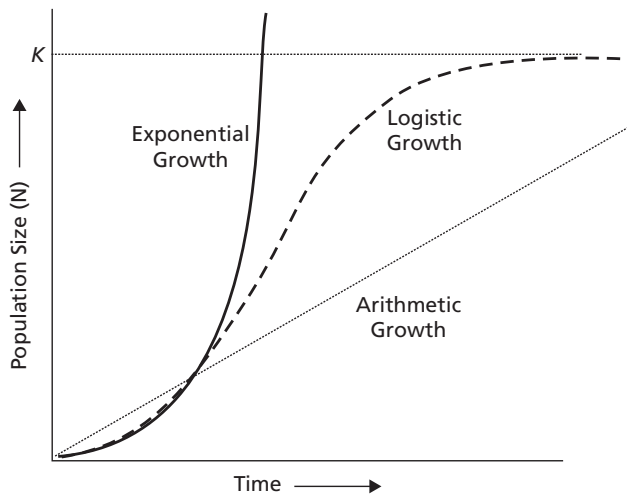
Figure 25.3 Arithmetic, exponential, and logistic growth curves. The exponential curve increases more slowly at first but then accelerates past the arithmetic curve, which increases at a steady, incremental pace throughout. The logistic curve shows sigmoidal increase, where it is similar to exponential increase until it reaches an inflection point where it becomes S-shaped and reaches an asymptote at ecological carrying capacity (*K*). *Adapted from Cunningham and Saigo (1997) and McCullough (1979).*

Figure 25.4 Population growth of a herd of reindeer. Reindeer were introduced to St. Matthew's Island in the Bering Sea in 1944. In the absence of predators and with little hunting, the population increased exponentially until 1965. Subsequently, the population crashed to only 42 individuals in 1966, largely because of overgrazing of habitat. *Redrawn from Klein 1968.*

where N = the number of individuals in the population, t = the time interval, and r = the intrinsic rate of natural increase. If a closed population is assumed, then immigration and emigration are zero. Thus, population growth is described as the change in population size (dN) that occurs during an interval of time (dt). Exponential population growth (see Figure 25.3) is also referred to as density-independent growth, because population growth does not slow with increasing numbers of animals, and the mortality rate is generally independent of population size.

If the number of individuals is plotted against time, the result is a curve that becomes increasingly steep during exponential growth (see Figure 25.3). For example, in 1944, 5 male and 24 female reindeer (caribou) were introduced to St. Matthew Island, a 332-km^2 island in the Bering Sea off Alaska. In the absence of predators and with very little hunting, numbers increased rapidly, reaching a peak of about 6,000 in 1965 (Figure 25.4; Klein 1968). The population then crashed to only 42 animals in 1966, largely because the habitat was overgrazed. In another example, a population of 23 caribou introduced to Adak Island in 1958 and was counted intermittently over 54 years (Ricca et al. 2014). Even with harvest occurring in that population, it increased from the original 23 animals to about 2,900 animals by 2012. Smaller species of mammals, with shorter generation times, can have even higher growth rates. Under laboratory conditions, vole populations can double in as little as 79 days (Leslie and Ranson 1940).

Another example of exponential population growth was observed in pale field-rats (*Rattus tunneyi*), a species native to mainland Australia (Short et al. 2017). From late 1995 to 2000, about 190 individual rats per month were caught in Herrison Prong, an area that previously had not been considered good habitat for this species. That population peaked in 2000 and collapsed by July 2001. The years 1995 to 2000 were characterized by very high rainfall that led to higher than normal grass cover. When the precipitation returned to the level typical of low rainfall years in 2001, loss of grass cover along with high herbivory by rabbits and high predation seemed to have led to the population collapse (Short et al. 2017).
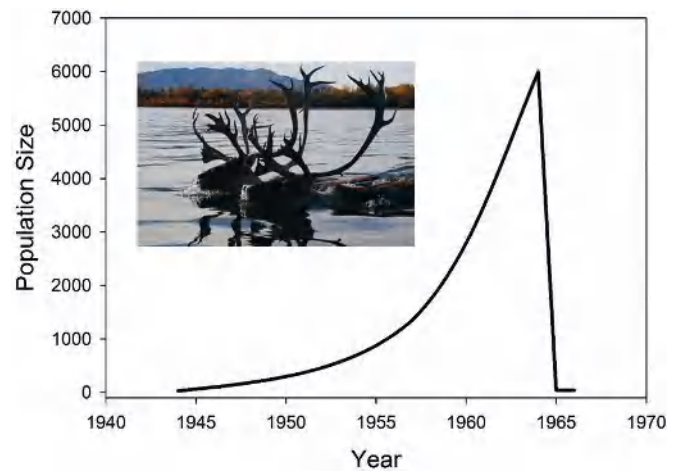
LOGISTIC, OR DENSITY-DEPENDENT, GROWTH

Populations of mammals do not increase indefinitely. As density rises, the presence of additional conspecifics causes increased intraspecific competition for resources, which reduces the birth rate, increases the death rate, or triggers emigration, and then population growth slows or stops. One model for such growth, the **logistic equation**, yields a sigmoid, or S-shaped, curve (see Figure 25.3). Numbers increase slowly at first, then increase rapidly, as shown by Equation 25.3. Then, however, the growth rate begins to slow as numbers approach an upper limit, or asymptote. The upper limit is often called the "ecological carrying capacity," or the equilibrium density, which is the number of animals in the population in equilibrium with their habitat and food supply (Kie et al. 2003).

Equation 25.3 can be modified to give the equation for logistic growth where K = the carrying capacity:

$$\frac{dN}{dt} = rN\frac{(K-N)}{K}. \qquad (25.4)$$

The term in parentheses is a density-dependent term that ranges from 0 to 1. When N is very small relative to K, then the term $(K-N)/K$ is close to 1. When the term in parentheses is 1, Equation 25.4 becomes the same as Equation 25.2, and the population increases exponentially. As N approaches K, $K-N$ approaches 0, and the density dependent term approaches 0. At that point, the whole right-hand part of the equation goes to 0, and so the growth rate, shown on the left side, is also 0, and population growth stops. If N should exceed K, the growth rate would be negative, and the population would decline. The logistic model is for density-dependent population growth, because of the slowing of growth of the population as intraspecific competition for resources increases and the population approaches carrying capacity. In this simple model, the population growth rate declines linearly with increasing population size, but the relationship is typically curvilinear (Sibly et al. 2005).

Logistic growth may be considered in several ways, and biologists often discuss forms of logistic growth (Figure 25.5). In addition to the characteristic S-shaped curve shown in Figure 25.5A, plotting the recruitment rate against the carrying capacity yields Figure 25.5B. Plotting the number of young recruited relative to the breeding population yields Figure 25.5C. Each of these figures is shown as symmetrical above and below the inflection point, although most species depart at least somewhat from a linear relationship (McCullough 1979). The inflection point (Figure 25.5) indicates that point where population growth rate is highest, exponential growths shifts to logistic growth, and population growth begins to slow as a function of increasing intraspecific competition for resources. Recruitment rate and recruitment number indicate more than just the birth rate of the population because those parameters also reflect when an individual has survived and grown to the point that it enters the breeding portion of the population. Recruitment rate is highest near the y-intercept of the recruitment-rate line (see Figure 25.5B), because the recruitment rate of the population, in the absence of efficient predators and limited resources, is near to the maximum rate of increase for that species in that particular environment. The recruitment rate declines with increasing population density until it reaches carrying capacity, which is a theoretical equilibrium point where births = deaths so the recruitment rate becomes 0. Unlike recruitment rate, the number of individuals recruited into the population (see Figure 25.5C) is greatest at about one-half K (if the parabola is symmetrical) because the greatest number of recruits into a population is a combination of both population size and recruitment rate. At very low densities, the rate of recruitment is high, but the population size is small, so the number recruited is relatively low. Conversely, at very high population density, the population size is high, but few animals are recruited into the population because the mortality rate is much higher and reproductive rate is lower when per capita resource availability is low. The inflection point on the curve showing number of recruits is the point in population growth where the density is low enough and the recruitment rate is high enough that intraspecific competition for resources is not strongly affecting reproduction, and the population is at its highest productivity.

Some species, however, have extremely strong density dependence in their life histories. For those species, the recruitment rate curve is fairly constant, resembling a plateau, until the population approaches carrying capacity and r declines precipitously when density-dependence causes the recruitment rate to decline sharply. This growth is characteristic of some species such as bighorn sheep and elephants (Figure 25.6; McCullough 1992, 1999).

Density dependence occurs in a population when the density or abundance of the population affects individuals, which then affects the population growth rate, which is a function of population density relative to carrying capacity
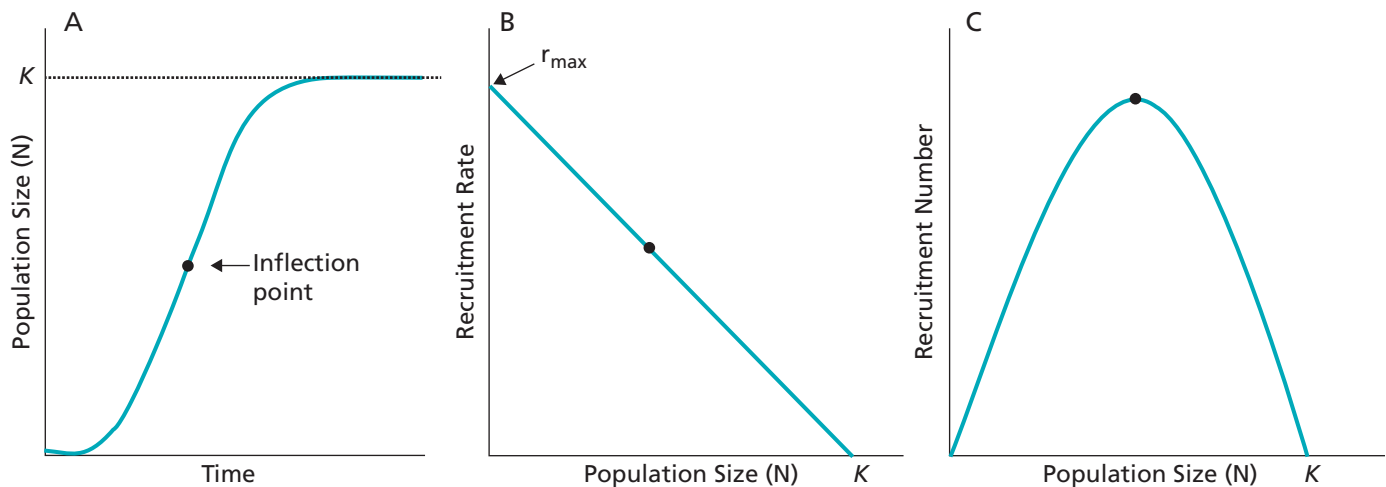
Figure 25.5 **Forms of logistic population growth.** (**A**) Population size (*Y*) against time (*X*); (**B**) recruitment rate (*Y*) against population size (*X*); (**C**) number of young recruited into the adult population (*Y*) against population size (*X*). *Note*: the inflection point on each curve is represented by • and shows the highest productivity in a population; *K* refers to ecological carrying capacity, the equilibrium point where births = deaths. *Redrawn from McCullough (1979).*

(Bowyer et al. 2014). Density dependence is usually thought of relative to negative feedbacks that cause decreased vital rates (such as reproduction) as a result of increased intraspecific competition for resources, usually food. Positive density dependence occurs when the vital rates and population growth are positively related, which has also been described as "inverse density dependence." Positive density dependence may be caused by mechanisms such as cooperative defense, where more participants lead to higher individual survival and reproduction, which in turn increases population growth.
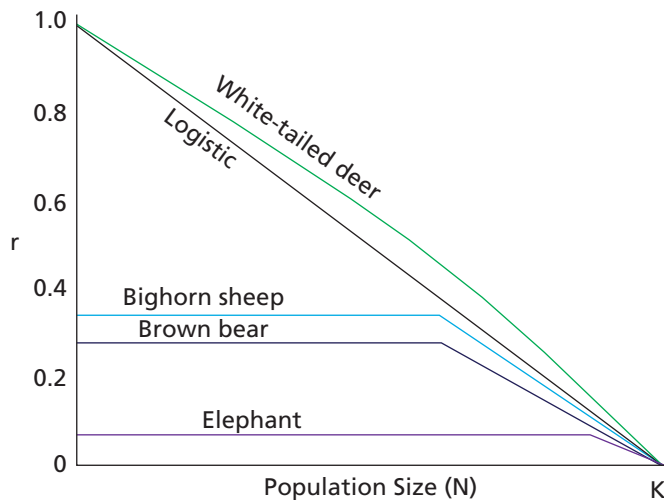
Figure 25.6 **Relationship of intrinsic rate of growth r (y-axis) against population size (x-axis).** This is shown for species with increasingly strong (*top to bottom*) density dependence in their life histories. *Redrawn from McCullough (1992).*

The best examples of the role of density dependence in population dynamics from natural populations are large mammals that often are managed as game species. Vital rates of large mammals respond to resource limitation in a sequence that is highly predictable and is a consequence of a slow pace-of-life strategy, beginning with lower survival and recruitment of young, and continuing with increased age at first reproduction, reduced fetal rates or litter sizes, and decreased pregnancy rates in adults. Decreased survival of adults is generally the last vital rate that is affected by resource limitation (Gaillard et al. 2000; Eberhardt 2002; Bowyer et al. 2014; Monteith et al. 2014). Table 25.1 describes what is expected when populations are at low density versus high density relative to ecological carrying capacity (Kie et al. 2003; Stewart et al. 2005; Monteith et al. 2014). In an experimental test of population density of North American elk (*Cervus canadensis*) nutritional condition, body mass, and pregnancy rates of adult females, as well as recruitment of young, were documented to be lower in the high-density population than the low-density population (Stewart et al. 2005).

Nutritional condition of mule deer in the Sierra Nevada, California, was strongly related to population growth, such that nutritional condition of adult females in March was a strong predictor of λ the upcoming year (Figure 25.7; Monteith et al. 2014). Equation 25.4 assumes a linear decline in population growth rate with density, producing the logistic growth curve shown in Figure 25.5B, but in reality the density-dependence function may be convex or concave. In a synthesis of long-term population data from 79 species of mammals, Sibly and colleagues (2005) noted that the relationship is usually a concave curve, meaning that population growth rate slows rapidly as populations begin to increase,

Table 25.1 Life-history characteristics of ungulates that reflect the relative differences in populations at low density (below the inflection point of recruitment number curve) or at high density, close to ecological carrying capacity (*K*)

Life-History Characteristic	Population size at low density relative to *K*	Population size at or near *K*
Nutritional condition of adult females	Better	Poorer
Pregnancy rate of adult females	Higher	Lower
Age at first reproduction in females	Younger	Older
Yearlings pregnant, or reproduction in the first year	Usually	Seldom
Pause in annual production by adult females	Less likely	More likely
Body weight of neonates	Heavier	Lighter
Litter size[a]	Higher	Lower
Survivorship of young[b]	Higher	Lower

Modified from Kie et al. (2003).

[a]No variation in some species in litter size
[b]In the absence of efficient predators
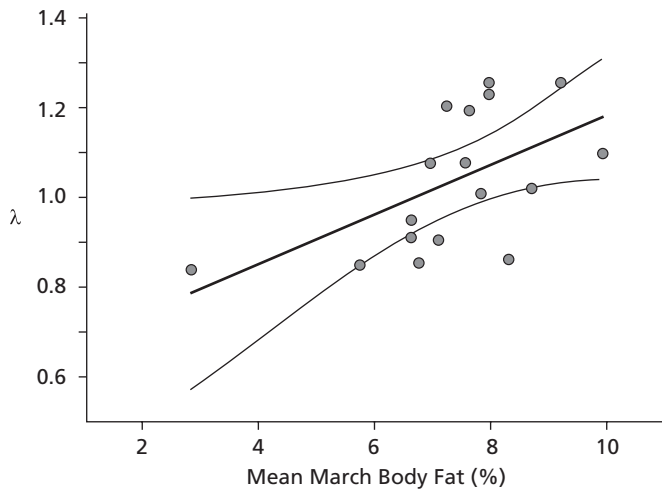
Figure 25.7 Nutritional condition of females and population growth. Estimated effect (±95% CI) of mean ingesta-free body fat measured in spring from adult female mule deer on population growth (λ). Data are from a population of mule deer in the Sierra Nevada, California. *Redrawn from Monteith et al. (2014).*

then remains low as the population slowly approaches the carrying capacity (*K*).

Life History

LIFE-HISTORY TRAITS

Life-history traits, including size at birth, litter size, age at maturity, and degree of parental care, are those that directly influence fecundity and survival. Natural selection recognizes only one currency: successful offspring. Although all organisms have presumably been selected to maximize their own lifetime reproductive success, mammals vary widely in the relative amounts of energy they expend on activities that enhance fecundity versus those that enhance survival. The principle of energy allocation states that individuals should maximize fitness by optimally allocating resources among growth, maintenance, and reproduction (Williams 1966). Such allocation of energy among life-history traits results in tradeoffs, and the traits that are most competitive for limited resources are survival and reproduction (Clutton-Brock et al. 1983; Travecchia et al. 2005; Morano et al. 2013). Much of life-history theory examines tradeoffs, particularly tradeoffs between reproduction and survival. Long-lived species have evolved strategies for energy allocation to maximize reproductive success in their lifetime by placing greater emphasis on adult survival and less on any single reproductive event (Gaillard and Yoccoz 2003; Hadley et al. 2007; Morano et al. 2013). Individuals may adopt a risk-sensitive alloca-

tion of resources to reproduction, in which investment in reproduction varies among years to increase survival and allows for energy to be allocated to future attempts at reproduction when conditions are more favorable (Bardsen et al. 2011; Morano et al. 2013). As a result of this behavior, survival is relatively stable, allowing reproduction to be more variable in stochastic environments (Gaillard and Yoccoz 2003; Hamel et al. 2010). Morano and colleagues (2013) observed that North American elk adopted a risk-sensitive allocation to reproduction. Adult survival was maintained through variation in reproductive effort, resulting in stable adult survival and more variable rates of reproduction. The probability of adult females becoming pregnant increased with increasing nutritional condition (e.g., body fat) (Figure 25.8). The costs associated with reproduction in elk, similar to other long-lived mammals, resulted in tradeoffs between current and future reproduction, with survival remaining relatively constant (Morano et al. 2013). Large mammals tend to favor life-history strategies consistent with a density-dependent or slow pace-of-life strategy described by Ricklefs and Wikelski (2002), in which adult survival is maximized, resulting in greater variability in reproductive output.

Aspects of reproduction, such as when to breed and how many young to produce, are subject to natural selection and influenced by variation in climatic conditions. For example, red squirrels (*Tamiasciurus hudsonicus*) in Yukon, Canada, have begun breeding earlier each year in response to increasing spring temperatures, advancing 18 days in 10 years. Some of this shift is a variable response to increased food availability, but the rest is a heritable response to selection (Réale et al. 2003). Heffelfinger and co-workers (2017) reported that in the Mojave Desert of California, survival of juvenile mule deer was strongly af-
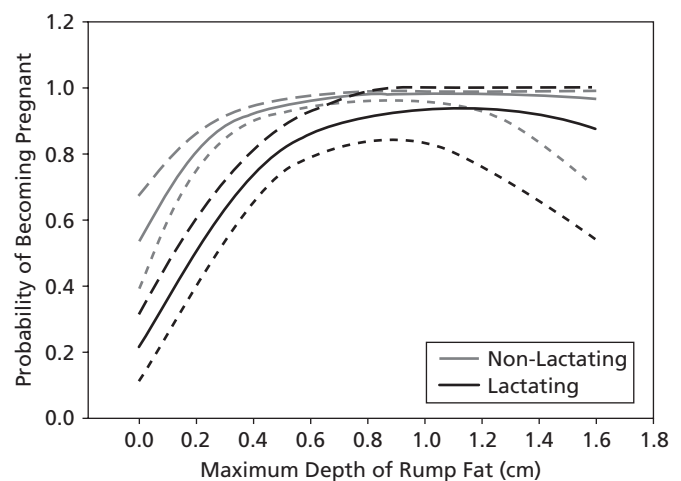
Figure 25.8 Nutritional condition and pregnancy rates in elk. The effects of nutritional condition of North American elk on the probability of becoming pregnant, and effects of recruiting a young the previous year (indicated by females lactating at capture) versus not recruiting an offspring the previous year. *Redrawn from Morano et al. (2013).*

Figure 25.9 Neonatal mule deer from Mojave Desert. Juvenile survival tends to be more variable than adult survival, and in arid environments, survival is strongly tied to precipitation and nutritional condition of the mother.

fected by spring precipitation prior to parturition. Thus, timing of precipitation corresponded with increased forage quality and quantity, which led to increased nutritional condition of maternal females. Therefore, young that were born in years with the highest precipitation had the largest body size and the highest survival (Figure 25.9).

SEMELPARITY VERSUS ITEROPARITY

Some organisms, such as annual plants, insects, and some fish, reproduce only once during their entire lifetimes. These "big bang" breeders are called **semelparous** (from the Latin *semel*, meaning "once," and *pario*, meaning "to beget"). They exert a huge effort during their reproductive episode and then die. Semelparity seems to be favored when extensive preparation for breeding is necessary or favorable environmental conditions are ephemeral or uncertain. Although very few mammals exhibit this type of reproductive strategy, some marsupial mice (*Antechinus* spp.) from Australia are semelparous in that the males reach sexual maturity, mate during a brief period, then physically decline and die shortly thereafter (Cockburn et al. 1985). Most other mammal species are **iteroparous** (from the Latin *itero*, meaning "to repeat")—that is, able to breed more than once during their lifetimes.

PACE OF LIFE

One approach to understanding the diversity of life-history patterns is to place them on a continuum, with species that mature early and have high reproductive rates and short generation times (fast) at one end, and those that mature late and have low reproductive rates and long generation

times (slow) at the other end (McCullough 1979; Promislow and Harvey 1990; Riklefs and Wikelski 2002). Oli (2004) used the ratio of the fertility rate to the age at first reproduction to quantify the tempo of life for 138 populations of mammals. At one end are species with high fertility rates and a short time to first reproduction (a high ratio), and at the other end are those with low fertility and longer time to first reproduction (a low ratio). Although "slow-paced" mammals were often relatively large in body size, the relationship is not always simply a matter of large animals such as elephants having slow life histories and small animals such as mice having fast life histories. Overall, "fast" mammal species reach sexual maturity earlier, have higher population growth rates, die younger, and have lower survival rates than "slow" mammal species.

Many large mammals, especially ungulates (see Chapter 19), are slow-paced or density dependent in their life histories and exhibit characteristics that include large body size, long life span, low adult mortality, delayed reproduction, high maternal investment in young, and variable survival rates of young (Bowyer et al. 2014). These species will trade off reproduction to protect survival (Martin and Festa-Bianchet 2010; Bowyer et al. 2014; Monteith et al. 2014) and will trade off current reproduction in favor of future reproduction (Morano et al. 2013). Adult survival thus tends to be high and relatively stable, while survival of young is more variable (Gaillard et al. 2000). As a result, survival and recruitment of young may the best indicator of population performance (Gaillard et al. 1998). Moreover, population dynamics of large mammals are strongly affected by intraspecific competition, which varies in intensity depending on the population density relative to ecological carrying capacity (*K*). Those slow-paced populations show density-dependent rates of increase (see Equation 25.4).

Characteristics of mammals that are fast paced or density independent in their life histories include small body size, many litters per year, large litter sizes, early age at first reproduction, short life span, and low maternal investment in individual offspring. Species with fast-paced life histories tend to trade survival for successful reproduction because their short lifespans tend to preclude tradeoffs between current and future reproduction (Ghalambor and Martin 2001; Bowyer et al. 2014). Population growth of those species is more likely to be affected by density-independent factors, with populations rarely reaching carrying capacity except under unusual environmental conditions or controlled conditions in experimental settings (Bowyer et al. 2014).

Cycles

Population cycles are relatively common in the Northern Hemisphere (Andreassen et al. 2013). Cyclic populations follow a predictable pattern of four steps: increase, peak,

decline, low (Krebs et al. 1973). Mammals are unusual in having a number of species that cycle, ranging from 3–4 years in smaller species such as certain voles (*Microtus* spp.) and lemmings (*Lemmus* spp.), to 9–11 years in larger species such as snowshoe hares (*Lepus americanus*) and lynx (*Lynx canadensis*) (Figure 25.10). The existence of cycles, and the reasons they occur, has fascinated and puzzled mammalogists and ecologists ever since Charles Elton (1924) introduced the subject (Krebs et al. 1973). True population cycles have constant periods, vary in amplitude, and are rare in nature (Figure 25.11). Moreover, population cycles are not known to occur in the Southern Hemisphere or in the tropics (Sinclair and Gosline 1997). An example of a cyclic species is the Siberian brown lemming (*Lemmus sibiricus*) at Barrow, Alaska, which has cycles of about 4 years (Figure 25.12). During one of the increases, breeding starts in autumn, and by spring, large numbers of lemmings are present, many of which become prey for snowy owls (*Nyctea scandiaca*), arctic foxes (*Vulpes* [*Alopex*] *lagopus*), weasels (*Mustela*), and other predators. During the summer, the population crashes to a low level, where it remains for 1–3 years.

Many agents, including extrinsic factors, such as changes in food quantity or quality, parasites, disease, predators, and intrinsic factors, such as physiological stress from crowding and changes in gene frequency, have been proposed to explain these cycles (Pianka 1994). Predation has received substantial support as a driver of population cycles, but more recently extrinsic factors related to trophic interactions also have been proposed to either generate or at least contribute to cycles in rodents and lagomorphs (Berryman 2002; Andreassen et al. 2013). Researchers have tended to focus on one or two factors. For instance, Hanski and colleagues (1991) have argued that small, specialist predators such as weasels, which are major predators at high latitudes in Scandinavia, increase the amplitude of the cycles. These authors contend that larger, generalist predators, which are more important at lower latitudes, tend to stabilize rodent populations. Others have argued that single-factor explanations are unlikely and that multifactorial explanations are needed to explain multiannual fluctuations. In these models, extrinsic and intrinsic factors act synergistically and sequentially to produce cycles (Lidicker 1988; Andreassen et al. 2013; Radchuk et al. 2016). A problem with these models is that they are complex and difficult to test.

While working with voles that have three- to four-year population cycles, Chitty (1960) noticed that populations continued to decline even under seemingly favorable environmental conditions. Voles from declining populations were highly aggressive, intolerant, and bred poorly; voles from increasing populations were mutually tolerant and rapid breeders. He postulated that a change took place in the quality of animals in a declining population. Through

Figure 25.10 **The lynx-hare cycle in North America.** This is one of the most spectacular examples of a population cycle. Populations of lynx follow population increases and declines of snowshoe hares with a time lag.
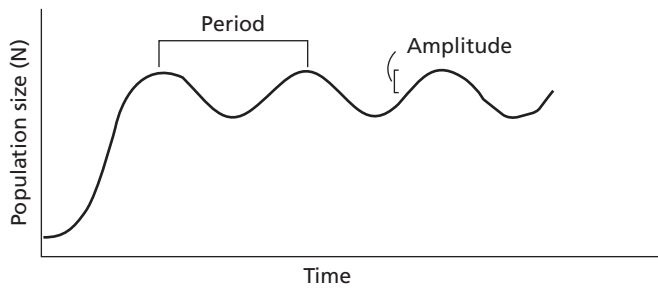
Figure 25.11　Diagram of a population cycle. The period is the amount of time it takes a population to go through a complete cycle. Amplitude is the difference between the maximum population size and the population size at the midpoint of the curve. In general, periods tend to be fairly consistent for a particular population, but amplitudes are more variable.
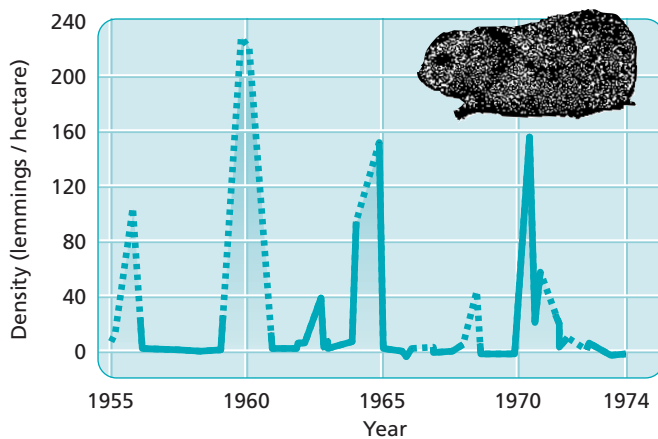
Figure 25.12　Lemming population cycles. Estimated lemming densities in the coastal tundra at Barrow, Alaska, for a 20-year period. *Data from Batzli et al. (1980).*

Figure 25.13　Chitty's model of population regulation in mammals. In response to increased population size and social contact, aggressive individuals with low reproductive rates are selected, leading to a decline in population. Modifications of the model emphasize the role of dispersal of certain phenotypes in causing the decline. This model predicts genetic changes in populations as different genotypes are favored at high versus low densities. *Data from Chitty (1967) and Krebs (1964).*

natural selection, the proportion of aggressive individuals increased, and even though they could compete in crowded conditions, their reproductive rates were low, and the population declined (Figure 25.13). Although it seems unlikely that a change in gene frequency could take place over a span of only a few years, dispersal of animals of one genotype can produce a rapid change in the gene frequency in the rest of the population. Myers and Krebs (1971) reported that the frequency of one allele in the blood serum of voles was significantly different in dispersers than in residents. The behavioral changes reported in vole populations have not been linked to specific genes, however. Evidence from the laboratory shows that the age of puberty can be shifted in house mice (*Mus musculus*) after only a few generations of artificial selection (Drickamer 1981). The low birth rates observed in peak populations in the wild could be caused, in part, by selection for late-maturing individuals.

Tamarin (1980) emphasized the role of dispersal itself as a regulating mechanism. If dispersal is blocked by a fence or is blocked naturally, as on islands, regulation fails and high populations and depleted resources result—the **fence**

effect (Krebs et al. 1973). Fences can be social as well as physical (Hestbeck 1982, 1988). When neighboring densities are low, animals are able to disperse into them. If the neighboring densities are high, dispersal may be blocked because the surrounding habitat is occupied by hostile competitors. Blocked dispersal could thus lead to high population densities, followed by population crashes as resources are used up.

In the high arctic tundra of northeast Greenland, the Nearctic collared lemming (*Dicrostonyx groenlandicus*) is the main source of food for no less than 4 vertebrate predators, making it one of the world's simplest predator-prey communities (Gilg et al. 2006). Lemmings follow a 4-year cycle, with peak densities more than 100 times those of trough densities. The most specialized predator, the short-tailed weasel (*Mustela erminea*), shows a delayed numerical response such that maximum weasel predation rates precede the lowest lemming densities and maintain low prey densities for at least two successive years. In addition, minimum predation rates by weasels occur during the winter preceding lemming peaks, which suggests that weasels are the main drivers of the cycle.

The role of climate in synchronizing population dynamics of multiple species has been documented in the high-arctic island of Svalbard, Norway (Hansen et al. 2013). Ground icing, the result of warm winter rains on top of frozen ground, makes tundra plants less available to
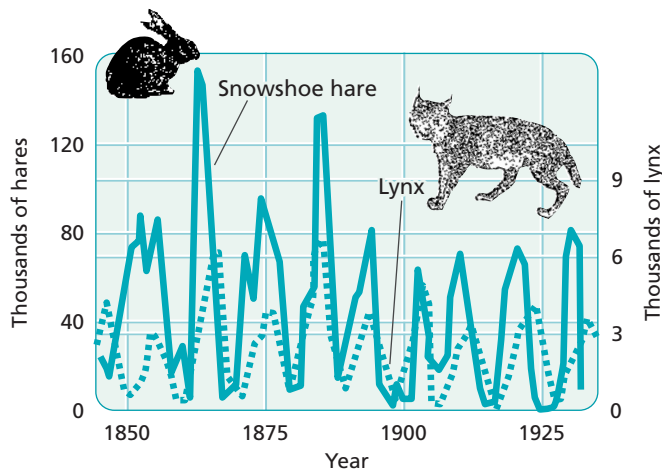
Figure 25.14 Population cycles of the lynx and the snowshoe hare. Comparison of population cycles of both species in the Hudson Bay region of Canada, as indicated by fur returns to the Hudson Bay Company. *Data after MacLulilch (1937) in Ricklefs (1990).*

reindeer, East European voles (*Microtus levis*), and rock ptarmigan (*Lagopus muta*), which depend on them for food. All three populations thus fluctuate in synchrony and produce similar fluctuations (lagged by one year) in a major predator of voles and ptarmigan, the arctic fox (Hansen et al. 2013).

The most spectacular example of a population cycle is the snowshoe hare-lynx cycle in the boreal forests and tundra of North America (Figure 25.14). Among the factors used to estimate abundance of hares and their mammalian predators are the numbers of furs brought in by trappers to the Hudson Bay Company (MacLulich 1957; Tyson et al. 2010). Each cycle is about ten years in length, and the lynx and hare populations are highly synchronized, with the peaks in lynx numbers following those of the hare by one to two years. One hypothesis for the cause of these cycles examines time delays in the interaction of three **trophic** (feeding) levels: the winter food supply of hares, the number of hares, and the number of predators (primarily lynx and great horned owls, *Bubo virginianus*; King and Schaffer 2001). A second hypothesis includes only two trophic levels: hares and their predators.

Mathematical models and laboratory experiments demonstrate that cycles can occur in the absence of any regular environmental fluctuations. The logistic equation (Equation 25.4) produces population cycles for certain values of r, the intrinsic rate of natural increase, when the response of population growth to density is time-delayed— either damped or increasing oscillations result. This result has been confirmed in laboratory populations of invertebrates, but field tests are lacking. Mathematical models of predator-prey interactions also predict stable cycles under certain conditions, which may explain the lynx-hare cycles. Keith (1983) concluded, however, that food shortage during the winter initiates the decline in hare density, with predators playing a secondary role. Lynx density seems to depend on hare density, so the lynx is food-limited, but whether hares are limited only by predators or by both food and predators is unclear (Keith 1987).

In an experiment designed to test the role of food and predators on hare density, supplemental food and mammalian predator abundance were manipulated on 1-km² plots in the Kluane region of the Yukon, Canada (Krebs et al. 1995, 2018). Mammalian predators were excluded from some plots by means of electric fences. Food supplementation tripled the population density of hares during the peak and decline phases of the population cycle, however, when predator exclusion was combined with food addition, hare density increased 11-fold. The proximate cause of death for most hares was predation, but interestingly, food limitation did not cause the documented decline in reproduction that followed the population high. Subsequent research has supported the hypothesis that the collapse in reproduction results from chronic stress related to elevated predation risk and that reduced survival and reproduction persist in subsequent generations because offspring of stressed mothers also experience lower survival and reproduction (Sheriff et al. 2010, 2011). This latter effect is believed to prolong the low phase of the hare cycle and delay the subsequent increase in the hare population.

The topic of population cycles continues to be an active area of research by mammalian ecologists from many countries. The value of long-term data and experiments for developing a more complete understanding of the causes and consequences of population cycles is even more critical now in the face of changing climates and habitats.

SUMMARY

- Populations increase via natality and immigration and decrease via mortality and emigration.

- All species of mammals are capable of exponential increase in numbers, resulting in an increasingly steep growth curve; however, such increase rarely occurs in nature because of the operation of regulating factors (food, predators, disease, and others).

- Life-history traits affect reproduction and survival.

- Most mammals are iteroparous, breeding repeatedly during their lives.

- Some populations of mammals show exponential growth (for limited time periods), and others show logistic growth, with densities gradually approaching the limit that can be supported by the environment.

- Density dependence and density independence are both factors in population growth and important aspect of life histories.

- Mammal species can be placed on a fast–slow continuum, with those that mature early and have high reproductive rates and short generation times (fast) at one end, and those that mature late and have low reproductive rates and long generation times (slow) at the other end.

- Studies attempting to correlate weather, food, and predators with population cycles indicate that all of those factors are important, but chronic stress of avoiding predation also affects survival and reproduction of species that exhibit population cycles.

- At high latitudes, densities of a few species cycle, typically every ten years for larger mammals such as snowshoe hare and lynx and every three to four years for smaller mammals such as voles and lemmings.

- Food, climate, local weather, and predators have been implicated in cycles, and there is some evidence that cycles are synchronized by large-scale climate fluctuations.

SUGGESTED READINGS

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DISCUSSION QUESTIONS

1. Inspection of survivorship curves for African ungulates (Figure 25.2, top right panel) indicates that warthogs are a special case. Suggest possible reasons for this outlier.

2. Understanding factors affecting the size and growth rate of populations is a central problem in ecology and mammalogy. Why has social behavior been implicated in so many of the theories of population regulation?

3. The following is an example of exponential growth. Before working it out, intuitively choose between two alternatives. (1) During a given month (31 days), you receive a penny on day 1, and that doubles on each successive day (i.e., exponential growth)—so you have 2 cents on day 2, 4 cents on day 3, 8 cents on day 4, 16 cents on day 5, and so on until day 31; or (2), you can have a total of $100,000! If you want to end the month with the most money, which do you choose? If you chose the exponentially increasing pennies, what is your total at the end of the month? Mathematically, what would be the easiest way to arrive at this total?

Community Ecology

In this chapter, we focus on the interactions among species and the effect those interactions have on both the living and nonliving features of their environment; together these form the subject of **community ecology**. Therefore, a fundamental aspect of community ecology is interactions among trophic levels. Interactions among species affect the relative abundance of populations (see Chapter 25), contribute to natural selection among phenotypes, and thus influence the evolution of coexisting species. Vellend (2010) suggested that community ecology could be broken down into four distinct processes: selection, drift, dispersal, and speciation. Those processes ultimately explain why there are so many different species of mammals. Populations of different species interacting in an area at the same time make up a **biological community**. A more inclusive term is **ecosystem**, which includes the biotic (living) components (i.e., the community) plus the abiotic (nonliving) components. Communities and ecosystems are not simply random assemblages of species but have similar patterns of assemblages geographically. Understanding so-called assembly rules is a central problem in ecology, and the study of mammalian communities has played a significant role in this research. **Community structure** encompasses patterns of species composition and abundance, temporal changes in communities, and relationships among locally coexisting species. At the simplest level, community ecology can be studied by looking at interactions between two species, which we do first in this chapter. Then we explore more complex and larger-scale patterns of mammalian diversity. Our goal is to explain how populations (single species) are integrated into larger biological levels of organization.

Mammalogists have played important roles in understanding of the interactions among populations. One of the first North American community ecologists was C. Hart Merriam, a mammalogist who developed the concept of "life zones." Working in the San Francisco Mountains of northern Arizona, Merriam (1894) concluded that temperature defined floral and faunal zones, forming elevational bands up the sides of mountains and latitudinal bands from the equator to the north and south poles. Early researchers viewed communities as interrelated units responding collectively to abiotic factors (reviewed by

Mares and Cameron [1994]). The degree to which communities can be considered discrete units rather than random assemblages of populations has been hotly debated by ecologists, as we discuss later in this chapter.

Ecological Niche

Each mammalian species occupies one or more habitats, has certain physical and chemical environmental tolerances, and performs a specific role in the community. Joseph Grinnell, who worked with birds and mammals in the early 1900s, was one of the first ecologists to use the term **niche**, by which he meant the habitat a species occupies as a function of its physiological and behavioral attributes (Grinnell and Swarth 1913). The term was defined somewhat differently by Elton (1927) to include an organism's functional role in the community in terms of its trophic (feeding) level (Mares and Cameron 1994). Today, most ecologists include both the distributional and functional components in considering a niche to be the total of adaptations of a species to a particular environment (Pianka 1994). Ecologists can never know all the parameters necessary to define a niche completely, so they emphasize those factors that potentially limit distribution and abundance and those for which organisms compete.

Most studies of mammals provide information potentially useful in determining niche attributes of individual species. Laboratory studies can determine physiological tolerances of a species to such conditions as heat, cold, and moisture (see Chapter 8). Measuring a species niche in the

field is more difficult, however, because biotic and abiotic factors often interact to produce unpredictable results. Competitors, predators, and symbionts affect the distribution, population dynamics, and niche of most species.

Species Interactions and Community Structure

As noted, species do not exist in isolation, but live and interact in a community of other organisms. Those interactions include competition, commensalism, ammensalism, mutualism, predation, parasitism, and facilitation (Table 26.1). Interactions may occur between individuals in the same or different trophic levels. Predation and parasitism generally occur among trophic levels; however cannibalism is a form of predation occurring within the same trophic level. Commensalism, mutualism, ammensalism, and competition also may occur within or among trophic levels.

COMPETITION

Competition results in a negative effect on all competitors not only because some will lose access to the resource, but also because all spend energy to use or defend the resource. Competition may be **exploitive**, where one species uses up the resource before the other. **Interference competition** occurs when one species attempts to prevent the other species from accessing the resource. Gotteli (2008) described these two types of competition by way of an example in

Table 26.1   Forms of interactions among 2 or more species with definitions. Those interactions can be positive (+), negative (–), or have no effect (0).

Interactions among species	Effect on each species	Description
Competition	– / –	Two or more species use or defend a resource that is in short supply, resulting in the reduced availability of the resource to the other.
Predation	+ / –	One species kills and eats the other; thus, one species benefits to the detriment of the other.
Parasitism	+ / –	Symbiosis in which one species derives nourishment from the second, and the second species is harmed in the interaction.
Commensalism	+ / 0	Symbiosis in which one species benefits from the interaction, and the other species is unaffected.
Mutualism	+ / +	Symbiosis in which both species benefit from the interaction.
Ammensalism	– / 0	Interaction in which one species is negatively affected with no effect on the other.
Facilitation	+ / + or 0 / +	One species has a positive effect on other species without direct contact.

Based on Gotelli (2008) and Mittleback (2012).

which two people are sharing a milkshake using two straws: exploitive competition would occur if one person uses his or her straw to consume the whole milkshake before the other. Interference would occur if one person reached over and pinched the other's straw shut. **Territoriality**, described in Chapter 24, is an example of interference competition, where a resource or resource area is defended from other competitors.

In the previous chapter we discussed population growth and addressed competition within species, termed "intraspecific competition." When individuals of the same species compete for limited resources such as food or shelter, density-dependent changes in population growth occur (see Equation 25.2). Other species can also compete for those resources, thereby affecting rates of population growth of all species. Equation 25.2 can be modified to include the effect of species 2 competing with species 1 by adding a term called the "competition coefficient" ($a_{1,2}$):

$$\frac{dN}{dt} = r_1 N_1 \left(\frac{K_1 - N_1 - \alpha_{1,2} N_2}{K_1} \right) \qquad (26.1)$$

where the subscripts 1 and 2 refer to values for species 1 and species 2. Notice that the density-dependent term in parentheses now contains a term including the number of individuals of species 2. When $a = 1$, the interspecific competitor, species 2, has the same effect on population growth of species 1 as another member of species 1, and interspecific competition is intense. As a declines, approaching 0, the last term of the equation approaches 0, and the effect of species 2 on species 1 can be ignored. A similar equation can be written to describe the effect of species 1 on species 2, where the coefficient of competition is $a_{2,1}$. This equation is too simple to actually model competition in nature, but it serves as a starting place to develop hypotheses and design experiments to further understand this important ecological process.

Interspecific competition also affects the habitat and food preferences of different species. In the absence of competition, a species occupies its **fundamental niche**, the full range of environmental conditions and resources in which the species can maintain a viable population in a given region. In the presence of competing species, however, the species may be restricted to a narrower **realized niche**, where some habitats or resources are not available because they are occupied by competitors (Hutchinson 1957). If the competitors are strong enough, a realized niche can become so small that local extinction (extirpation) results. This line of reasoning has led to the **competitive exclusion principle**, first described by Gause (1934), which states that two species cannot coexist for long on a single limiting resource, or, put more simply, that complete competitors cannot coexist (Hardin 1960). If two competing species coexist in a stable environment, they do so as a result of differentiation of their realized niches (Ricklefs and Miller 1999). Therefore, if no differentiation takes

place, then one species will exclude the other. For competitive exclusion to occur, there must be extensive niche overlap, such that competing species require the same resources (May 1974; Carmel et al. 2017), and one species much outperform the other in defending or using those resources (Kramer and Drake 2014; Carmel et al. 2017). Because of the link between degree of niche overlap and intensity of competition, this principle has helped to shape the field of community ecology. Although this principle makes intuitive sense and has been widely accepted by ecologists, it is difficult to confirm experimentally.

One way to visualize interspecific competition is to look at only one niche component at a time, picking the one that is likely to be most limiting for the competitors. Consider several species of desert rodents feeding on differently sized seeds from various plants. It is relatively easy to determine what types of seeds are stored for later consumption because seeds can be collected from the cheek pouches of trapped animals. The feeding niches of the rodents can be inspected by plotting seed size on one axis and the utilization (consumption) rate on the other. In the hypothetical example shown in Figure 26.1, each of the three species shown has a roughly normal, or bell-shaped, utilization curve. Niche width (w), measured by the standard deviation around the mean, and the distance between utilization peaks (d) indicate the amount of interspecific competition. When d is large and w is small, little overlap occurs, and the coefficient of interspecific competition is small (Figure 26.1A). When d is small and w is large, overlap is great, and the coefficient is large. In this case, d might increase or w might
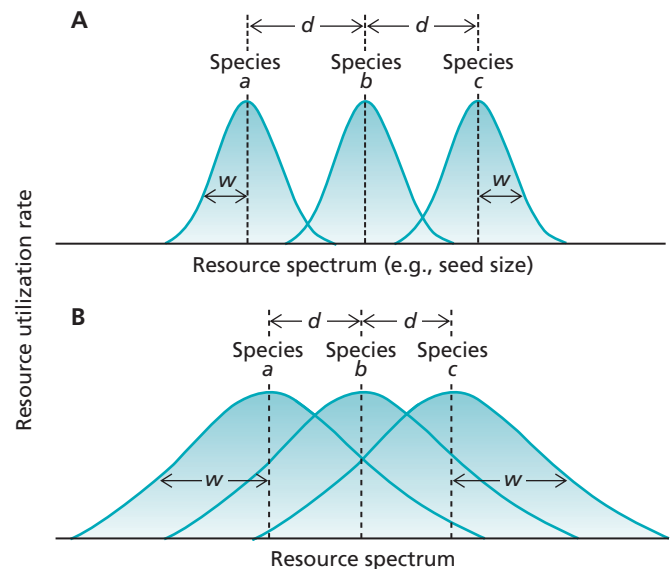
Figure 26.1 Resource utilization curves for three species coexisting along a one-dimensional resource spectrum. The term d is the distance between adjacent curve peaks; w is the standard deviation of the curves. (**A**) Narrow niches with little overlap ($d > w$), that is, relatively little interspecific competition; (**B**) broad niches with great overlap ($d < w$), that is, relatively intense interspecific competition. *Data from Begon et al. (1996).*

decrease, leading to reduced competition. Another outcome is that one species would be eliminated from the area. If possible, more than one niche dimension needs to be examined because coexisting species can overlap extensively in one niche dimension but only slightly in another (Schoener 1974).

How different do two species need to be to coexist in the same general habitat? If species overlap on one niche axis, they may coexist by separating on another axis. Although there are potentially a large number of niche axes, generally researchers tend to look at three primary niche axes: habitat, food, and time (Pianka 1974; Schoener 1974; Hearn et al. 2016). Competitors may overlap on two of the three axes but separate on the other, and thus they can coexist. Resource partitioning results from an evolutionary history of competition, where currently we observe overlap on one or two axes, but separation on the other. Hearn and colleagues (2016) looked at resource partitioning among an assemblage of five species of felids, ranging in sizes, in Borneo and observed separation on each of those three niche axes. However, differences in carrying capacity among the competing species, environmental fluctuations, and the importance of other niche parameters can all affect the outcome.

One way to indirectly evaluate a niche is to assess morphological traits related to important functions, such as feeding. The number of species packed into a niche space can be estimated by comparing morphological distances between nearest neighbors. Fenton (1972) used several dimensions to define morphological space among different species of bats. One was the ratio of ear length to forearm length; the higher the ratio, the larger the ears and the more important echolocation is presumed to be in the foraging behavior. A second was the ratio of third and fifth digits of the wing bones, yielding an index of wing shape (basically, length-to-width ratio). A high ratio indicates a long, thin wing shape, whereas a low ratio indicates a short, broad wing shape (called "aspect ratio"). The former favors high-speed flight, whereas the latter favors low-speed flight and greater maneuverability. Plotting both ratios together provides an insight into the niche space occupied by different species (Figure 26.2). In temperate zone communities in Ontario, bat species are small insectivores, and the points are clustered fairly closely. In the tropics, bats fill many other roles, such as fruit-, nectar-, fish-, and even blood-eaters, and the scatter of the points reflects the wide range of wing and ear shapes. Other studies of bats (Findley and Black 1983; Schum 1984) have confirmed that external morphology, habitat use, and diet are correlated and that variation in morphology increases with the number of species present.

Several factors provide indirect evidence of the importance of competition in natural communities of mammals. One is the distribution of species, in both the presence and the absence of presumed competitors. For instance, two species of felids, the Canada lynx (*Lynx canadensis*) and the bobcat (*L. rufus*) have broad geographic ranges, but occur
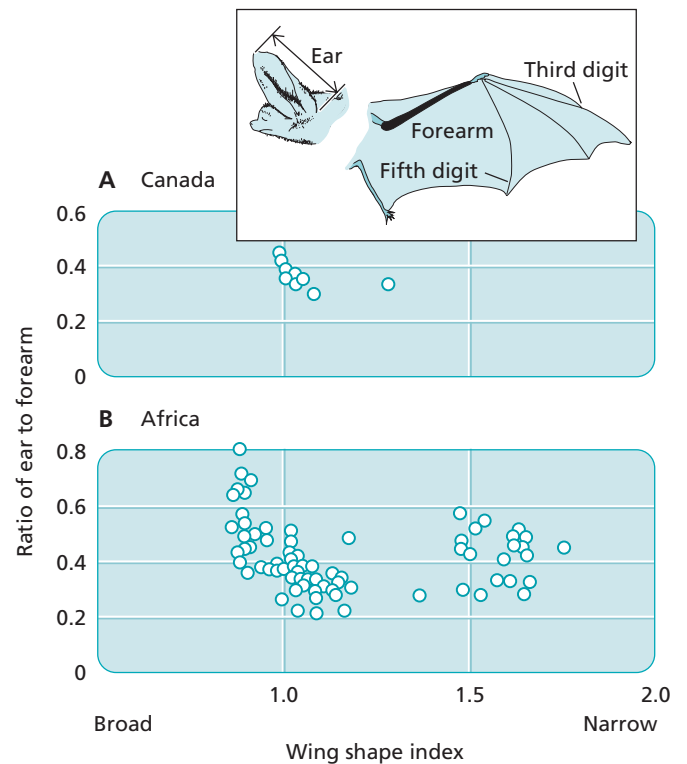
Figure 26.2 **Niche space of insectivorous bats of (A) southeastern Ontario, Canada, and (B) Cameroon, Africa.** The horizontal axis is the ratio of the lengths of the 3rd and 5th digits of the hand, and the vertical axis is the ratio of ear length to forearm length. *Data from Fenton (1972).*

in sympatry in some parts of the northern and western United States. In **sympatric** areas (where ranges of species overlap), lynx niches were different from those of bobcats, and lynx were more reliant on snow cover (Peers et al. 2013). In areas of sympatry with lynx, bobcats increased their niche breadth. The assumption is that in the presence of competition, each species reduces niche overlap, but in that instance only lynx reduced niche breadth (Peers et al. 2013). Conversely, lynx niches showed **competitive release**, and were larger in the absence of bobcats.

Introductions by humans provide indirect evidence of competition, especially when mainland species are introduced on islands (see Chapter 28). The result is often extinction of the native island species, presumably due to competitive exclusion. Thus, introduction of the placental canids, the dingo (*Canis lupus dingo*) and red fox (*Vulpes vulpes*), into Australia was a factor in the extirpation of marsupial fauna such as the Tasmanian wolf, or thylacine (*Thylacinus cynocephalus*), and the Tasmanian devil (*Sarcophilus harrisii*). In the case of the thylacine, however, shooting them because of livestock depredation was also a significant factor in their ultimate extinction (See Chapter 10). Based on fossil evidence, the disappearance of both the Tasmanian wolf and the Tasmanian devil from southern Australia coincided with the arrival of the dingo to that region. Both marsupial species survived on Tasma-

Figure 26.3 **White-tailed deer (left) and sika (right).** Sika were introduced to Maryland in 1916, and populations increased as white-tailed deer declined.

nia because the island was cut off from the mainland before the dingo got to the southwestern mainland of Australia.

In the United States, introduced species of deer have had a negative effect on native species. Sika (*Cervus nippon*), native to Japan and the East Asian mainland, were introduced into Maryland's eastern shore in 1916 (Figure 26.3). During the 1970s and 1980s, the proportion of white-tailed deer (*Odocoileus virginianus*) harvested declined sharply, from 75% to 35%, and that of sika deer showed a corresponding increase, from 25% to 65% (Feldhamer and Armstrong 1993). Such negative correlations, however, do not demonstrate a cause-and-effect relationship. Sika introduced into Great Britain have also impacted communities through genetic introgression with native red deer (*C. elaphus*).

Character Displacement

Other observational evidence for competition comes from comparisons of morphology and behavior of individuals in the presence or absence of close competitors. When the ranges of two similar species overlap (i.e., their distributions are sympatric), the species tend to differ more from each other than when their ranges do not overlap (i.e., their distributions are **allopatric**). This shifting of traits in areas where both species are present has been referred to as "**character displacement**." In northern Europe, where the Eurasian pygmy shrew (*Sorex minutus*) and the common shrew (*S. araneus*) overlap extensively, the pygmy shrew has a significantly smaller lower jaw than it does on islands off the coasts of England and Sweden, where the populations of the two species of shrew are allopatric (Malmquist 1985; Figure 26.4). In this study, jaw measurements of the larger, common shrew did not shift. Skull size is related to prey
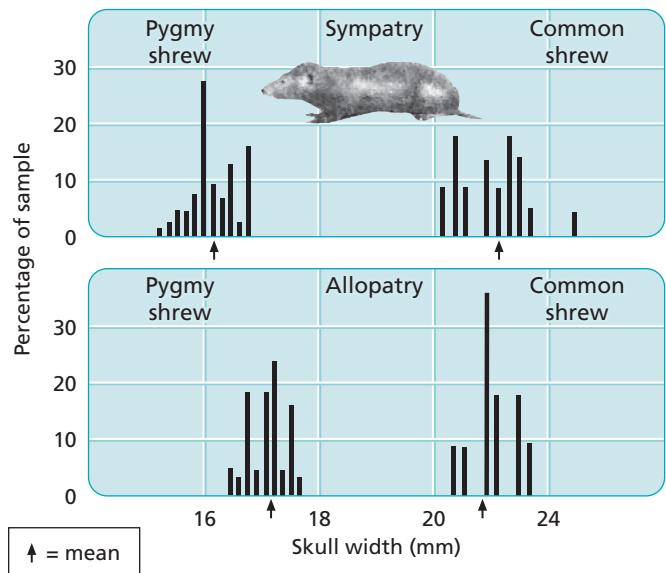
Figure 26.4 **Character displacement in shrews.** The pygmy shrew and the common shrew are allopatric on islands off the coast of Sweden but sympatric on the mainland. Note that the measure of skull width is smaller for the pygmy shrew in sympatry. *Data from Malmquist (1985).*

size—that is, individuals with larger skulls can eat larger prey than those with smaller skulls. The inference is that in zones of overlap, one or both of the species diverge in prey-size selection, leading to reduced competition and coexistence of both species.

Two species of bats, the long-eared myotis (*Myotis evotis*) and the southwestern myotis (*M. auriculus*), coexist at several sites in New Mexico where their ranges overlap. When Gannon and Rácz (2006) measured mandibles of the two species from museum specimens, they found that they differed more in sympatry than in allopatry. This finding is

consistent with the idea that the bats shifted diets in regions where they both were present. Based on the differences in mandible shape, the researchers surmised that in sympatry *M. evotis* specializes on hard-bodied beetles, while *M. auriculus* specializes on soft-bodied moths. Conversely, Arregiotia and colleagues (2018) observed no morphological size differences in two species of sympatric yellow-shouldered bats (genus *Sturnira*) in Mexico. Moreover, interspecific differences in forearm length in those bats were constant whether they were in sympatry or allopatry.

Although usually restricted to closely related species, character displacement can occur among more distantly related taxa on a community-wide basis. Three sympatric small cat species in Israel are strongly sexually dimorphic, and the sexes can be treated separately for comparison (Dayan et al. 1990). The average canine diameters for the six "morphospecies" were remarkably evenly spaced, consistent with the idea that niche partitioning of prey size occurs among species and between sexes. These cats are exclusively carnivorous, and canine teeth are used to kill prey. The canines are well adapted to wedge between the vertebrae of the prey's neck, severing the spinal cord or hind brain. Larger prey would clearly require thicker canine teeth, making canine diameter a good predictor of the size of prey captured. Dayan and colleagues (1990) argued that the evenly spaced sizes indicate character divergence to reduce competition for prey. Although competition for food is the presumed explanation, it is also possible that sexual selection has played a role in canine size. Males of these species may use canines for display or fighting with other males, as do many polygynous species of primates. Thus, canine size may be affected by male-male competition for access to females as well as by size of prey.

Two color morphs of North American black bears (*Ursus americanus*) occur in British Columbia. The white morph, also known as the Kermode, or Spirit bear, coexists with more common black morphs. Based on genotyping hair, the highest frequency of white morph—43% of the population—occurs on Gribbell Island (Ritland et al. 2001; Reimchen and Klinka 2018). A mechanism that can maintain the polymorphism in the population would occur if niche differentiation occurred between the two morphs and affected fitness. Field observations indicated that the white morph was more effective at capture of salmon during daylight, but the black morph was more effective at night (Klinka and Reimchen 2009; Reimchen and Klinka 2018). The white morph is usually closer to marine habitats whereas black morphs are more common in forested habitats. Those observations were also supported by studies using stable isotope analysis of hair. For a review of ecological character displacement, see Dayan and Simberloff (2005).

One of the ways two or more species can coexist is to evolve different body sizes, thus essentially dividing an occupied area into different feeding niches and avoiding competition. A ratio in length of 1:1.3 was suggested for the minimum difference between two closely related competitors to permit coexistence (Hutchinson 1959), prompting a number of investigators to compare body size at the community level. Numerous species of seed-eating rodents occupy the deserts of the southwestern United States. When Brown (1975) compared the rodent communities in the Sonoran Desert with those of the Mojave and Great Basin Deserts, he noticed that the distributions of body sizes of different species were remarkably similar (Figure 26.5). Brown also observed that species of similar size tended to "replace" one another in different habitats. Thus, the 7-g silky pocket mouse (*Perognathus flavus*) in the Sonoran Desert was replaced by the 7-g little pocket mouse (*P. longimembris*) in the Great Basin Desert, and the 11-g western harvest mouse (*Reithrodontomys megalotis*) was replaced by the 12-g pale kangaroo mouse (*Microdipodops pallidus*). In addition, when the same species was present in both deserts, it was displaced in body size, filling a gap. For example, the deer mouse, *Peromyscus maniculatus*, was 24 g in the Sonoran Desert but only 18 g in the Great Basin Desert.

Removal Experiments

Observational studies can provide only indirect, correlational evidence of the importance of competition in structuring ecological communities. One way to provide direct evidence of interspecific competition is to remove one of the competitors and monitor the response of the other species. In one such study, three sympatric species of small mammals—the white-footed mouse (*Peromyscus leucopus*), the golden mouse (*Ochrotomys nuttalli*), and the northern short-tailed shrew (*Blarina brevicauda*)—were captured, marked, and released in a pine plantation in Tennessee (Seagle 1985). A number of vegetation characteristics were recorded at each capture site to determine the microhabitat preferences for each species. When white-footed mice were removed from one grid, golden mice demonstrated competitive release by shifting their microhabitat preference from open forest to areas with more fallen logs, denser canopy development, and denser understory.

Four species of chipmunks (*Tamias* spp.) are found along an altitudinal-vegetational gradient on the eastern slope of the Sierra Nevada, California. The chipmunk species are contiguously allopatric—that is, their ranges are adjacent but not overlapping—and each is restricted to its own vegetational community along the gradient (Figure 26.6). Chappell (1978) conducted a series of observations and experiments to reveal the physiological and behavioral factors that might produce this distribution. For example, captures of the least chipmunk (*T. minimus*) increased in wooded areas at higher elevations, where the yellow-pine chipmunk (*T. amoenus*) was removed. Behavioral observations confirmed that *T. amoenus* was dominant to *T. minimus*, suggesting that competitive exclusion was responsible for the failure of *T. minimus* to colonize the wooded zones. Where *T. minimus* had been removed, however, *T. amoenus* failed to invade. The failure of the socially dominant *T. amoenus* to move down slope into the sagebrush zone in the absence
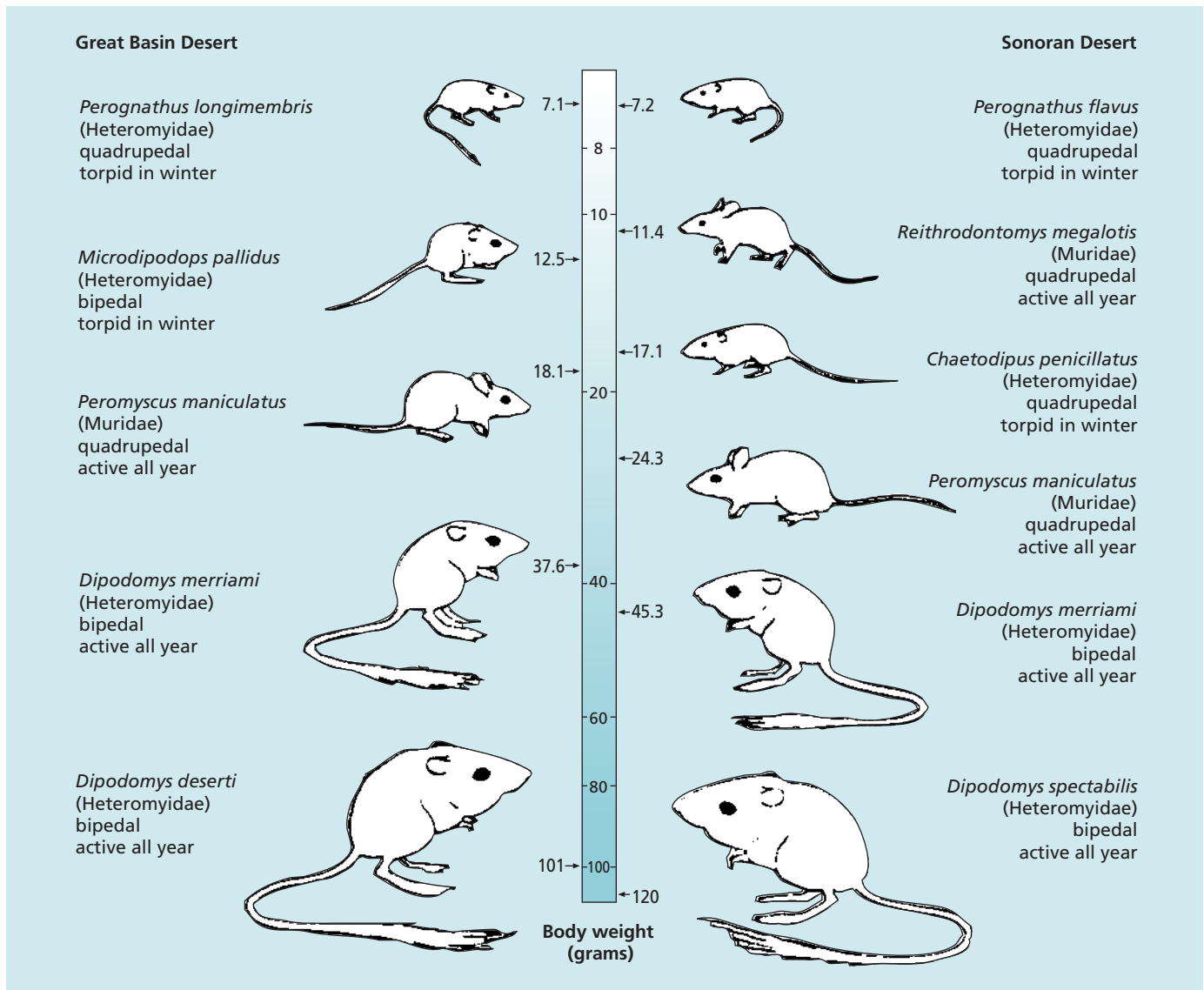
Figure 26.5 **Convergence in structure between a community of six rodent species from the Sonoran Desert and a community of five rodent species from the Great Basin Desert.** Numbers are average weights (grams). Note the similarities in body size, form, taxonomic affinity, and other characteristics between species occupying similar positions in each community. Also notice the displacement in body size in *Peromyscus maniculatus* and *Dipodomys merriami* (both are larger in the Sonoran Desert) to compensate for the different numbers and sizes of coexisting species. *Data from Brown (1975).*

of *T. minimus* is probably due to physiological constraints: *T. amoenus* is not adapted to tolerate the hot, dry conditions at lower elevations. In this example, both behavioral and physiological factors affect the distribution of species.

Not all removal studies provide clear-cut results. Along the Mediterranean coast of Israel is a narrow strip of sand dunes, of recent origin, perhaps only a few hundred years old. Two species of seed-eating gerbilline rodents occupy the area, and they show considerable overlap in diet and microhabitat preference (Abramsky and Sellah 1982). The larger species, Tristram's jird (*Meriones tristrami*), colonized the dunes from the north. It can live on sand as well as other soil types. The smaller species, Anderson's gerbil (*Gerbillus andersoni*), colonized from the south, and it is

found only on sand. When alone, *M. tristrami* occupies sand. Where the two species are sympatric, however, *G. andersoni* occupies sand and *M. tristrami* occupies soil types other than sand. The exclusion of *M. tristrami* from the habitat it prefers when alone (sand) has been interpreted as resulting from interspecific competition. When *G. andersoni* was removed from an area containing both species, it was expected that *M. tristrami* would expand its habitat and occupy the sand areas, showing competitive release. No such effect was observed, however, which suggested that competition was not responsible for the different substrates occupied. One interpretation of these results is that these species did, in fact, compete in the past and that habitat selection is under genetic control. Thus, genetic changes in
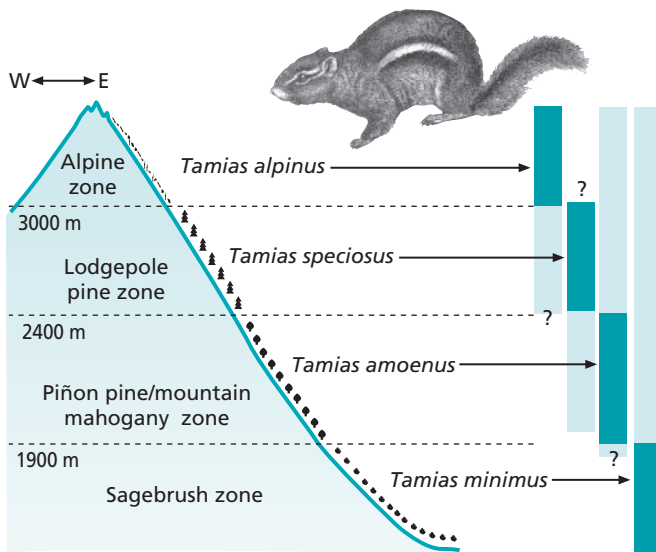
Figure 26.6 **Distribution of four species of chipmunk on the eastern slope of the Sierra Nevada, California.** Dark portions of bars denote realized niches; entire bars show fundamental niches. *Data from Chappell (1978).*

the population of *M. tristrami* in areas of overlap with *G. andersoni* might have led to its failure to occupy sand in the absence of the other species. This phenomenon has been referred to as "the ghost of competition past."

PREDATION

In Chapter 25 we discussed predation from the perspective of prey population dynamics and whether predators regulate prey populations. Predation usually involves interactions between trophic levels, where one species benefits to the detriment of another. Predation is defined as occurring when individuals consume all or part of other live individuals (Fryxell et al. 2014). There are four types of predation:

1. Herbivory, which occurs when animals consume green plants or their seeds or fruit. Generally, plants are not killed, but seed predators often kill the seeds.
2. Parasitism occurs when one species, the parasite, feeds on another, the host, which it usually does not kill. Parasites are usually much smaller than the host, but there are exceptions.
3. Carnivory, where the predator kills and eats the prey in the manner that we typically associate with predation.
4. Cannibalism, where the predator and prey are the same species and therefore they are part of the same trophic level.

Predators can respond to changes in density of prey by two primary mechanisms: change in behavior, termed the **functional response**, or change in numbers through reproduction, immigration, or emigration termed the

numerical response. Functional responses were first described by Holling (1959), and consist of three primary types. For a type-I functional response a predator must search randomly for prey, have an unlimited appetite, and spend a constant amount of time searching (Figure 26.7). For large ranges of prey densities these assumptions are unrealistic because no predator has an unlimited appetite, and because handling time (time it takes to kill, eat, and digest prey) increases, and constant search time also is unrealistic. At relatively low densities reindeer feeding on lichens approximates a Type-I functional response, but that pattern does not occur at high densities of reindeer (White et al. 1981; Fryxell et al. 2014). Type-II response curves
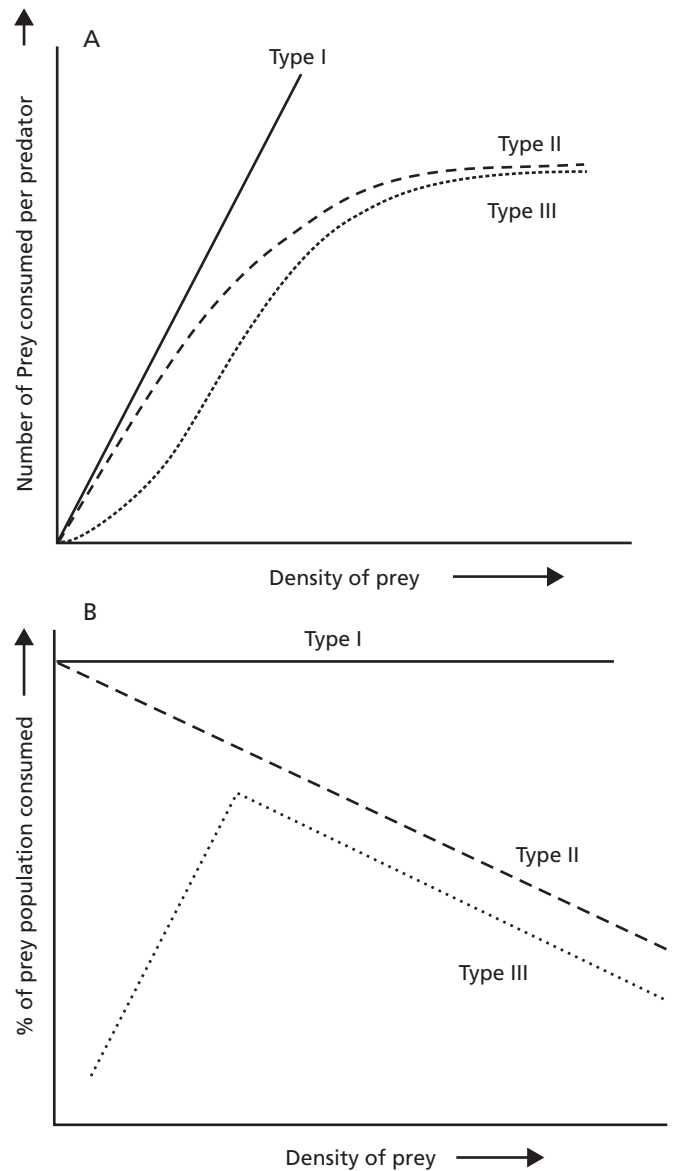
Figure 26.7 **Functional response curves, behavioral responses to predators to increasing density of prey.** (**A**) Types of functional responses curves are shown as the number of prey eaten per predator per unit time. (**B**) Curves are plotted as the percentage of the prey population eaten by predators. *Redrawn from Fryxell et al. (2014).*

show a slower increase of prey taken by predators, which reaches an asymptote where satiation occurs. At that point predators cannot continue to take more prey through changes in behavior alone (Figure 26.7A). When a Type-II curve is represented as the percentage of the prey population taken by predators (rather than numbers of individual prey; Figure 26.7A), a decreasing trend of prey is taken with increasing density of prey (Figure 26.7B). This result indicates that although numbers of prey removed are increasing, the percentage of the population removed by predators is actually declining. Finally, the Type-III response curve is S-shaped, and shows slow increase in predators using prey at low densities, faster at intermediate density, and then reaching an asymptote similar to the Type-II curve. The S-shaped curve illustrates predators switching among types of prey. When there are two prey types—one common and one rare—predators use the common prey type. The predator eventually switches prey type as the "rare species" becomes more common (Figure 26.7A). Again, functional responses involve changes in behavior of predators relative to changing prey density.

Another way predators can respond to increasing prey density is numerically through reproduction, immigration, or emigration. Thus, as prey density increases, more predators survive and produce more offspring through increased fecundity. As the predator population increases, predators consume more prey. Predator density often increases to an asymptote, which may be determined by interference competition, such as territoriality. There is some evidence, however, that based on prey availability, territory size of predators shrinks to support a higher density of predators (Pierce et al. 2000). Territoriality can also result in high rates of dispersal. For example, wolves at high density have high rates of dispersal—about 20% for adults and 50% for juveniles (Ballard et al. 1987; Fuller 1989; Fryxell et al. 2014).

Risk of Predation

Food partitioning is one way in which communities are structured, but risk of predation (i.e., nonconsumptive or indirect effects of predators on prey) can also be important. Rodents in the Great Basin Desert in Nevada partition the microhabitat so that kangaroo rats and kangaroo mice forage in the open, whereas pocket mice and deer mice forage near bushes. The former have hyperinflated auditory bullae, associated with high auditory acuity, and elongated hind legs, associated with bipedal locomotion. These adaptations aid in the detection of, and escape from, predators such as long-eared owls (*Asio otus*), coyotes (*Canis latrans*), kit foxes (*Vulpes macrotis*), and gopher snakes (*Pituophis melanoleucus*). Dice (1945) showed that owls find prey more easily under moonlight than starlight. In a field experiment, illumination that simulated moonlight was added to some grids by means of lanterns, and shadows were created at some sites by means of parachute canopies (Kotler 1989). In general, illumination led to reduced foraging in open microhabitats. Food in

the form of bird seed was added to some bush sites and to other open sites. The bipedal species responded positively to additional food in both bush and open sites, whereas the quadripedal species responded only to food in the bush sites. Kotler (1989) concluded that both risk of predation and resource availability interacted to affect foraging behavior and habitat choice. Thus, both predators and distribution of resources need to be considered when trying to predict the species composition of a community.

Among African carnivores, lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*) not only exhibit kleptoparasitism by stealing kills from cheetahs (*Acinonyx jubatus*), but they also prey on them. Playback studies show that cheetahs actively moved away from calls of lions and hyenas (Durant 2001). They also stopped hunting and moved away from high concentrations of prey (gazelles) to avoid lions and hyenas, and exhibited different behavioral strategies when handling and consuming prey (Hilborn et al. 2018). Male cheetahs and females without young, minimized time at kills and reduced kleptoparasitism by being less vigilant and eating quickly to shorten handling time. Conversely, females with dependent young prioritized vigilance rather than speed to prevent young from being killed by those larger predators. Increased vigilance allowed females and young increased time spent handling prey, which allowed inexperienced young time to consume prey (Hilborn et al. 2018)

KEYSTONE SPECIES AND TROPHIC CASCADES

Some species appear to play critical roles in the community, such that "not all species are created equal." Although mammals typically account for only a small fraction of the biomass and energy flow in most ecosystems, they sometimes regulate the structure and dynamics of the entire community. **Keystone species** are those whose functional role in a community is disproportionately greater than predicted by their abundance alone (Fryxell et al. 2014). Removal of a keystone species from its community generally has a large effect on community composition, diversity, and function. Keystone species are often, but not always, apex or top predators.

Removal of keystone species has caused what has been termed a "trophic cascade" (Paine 1980). Predators, especially apex predators, are important components of ecosystem and community functioning, because as the top rung of the trophic ladder, they tend to regulate the food web below (Terborgh et al. 2010). Apex vertebrate predators tend to be large-bodied and move at a landscape scale; thus they often tie together the dynamics of communities that appear to be distinct (Terborgh et al. 2010). Eliminating those predators destabilizes ecosystems, which sets off a chain reaction that eventually cascades down the trophic levels to the lowest one. The community that results after loss of an apex predator inevitably has lower biodiversity and sometimes fewer trophic levels than the original community (Terborgh et al.

2010). Therefore, apex predators are important for maintaining high levels of biodiversity in ecosystems that they inhabit. Reintroductions, such as wolves to Yellowstone National Park, can help to reestablish a beneficial cascade.

Sea otters (*Enhydra lutris*) prey extensively on sea urchins along the coast of the western United States. Fur traders decimated otter populations from 1741 to 1911, except for a few remnant populations in Alaska and central California. Subsequently, after protection, sea otter populations were reestablished over much of their original range, sea urchins became sparse, and algae communities (mainly kelp) thrived. In areas where sea otters remained absent, sea urchins became abundant and eliminated much of the kelp and associated marine species—exhibiting a trophic cascade when otters are lost from the ecosystem (Estes et al. 1978).

When sea urchins were experimentally removed from plots on Torch Bay, Alaska, where no otters were present, a complex association of several species of kelp developed. Similar effects were seen when otters were transplanted into areas with high densities of sea urchins. The sea urchins were quickly depleted by the otters, and the kelp community developed several years later (Duggins 1980; Figure 26.8). Sea otters, therefore, exert a profound effect on community structure and fit the definition of keystone species.

Sea otter numbers declined once again over much of Alaska's west coast in the 1990s, at rates as high as 25% per year, and numbers continue to be low. The evidence points to increased predation by killer whales (*Orcinus orca*) as the cause (Estes et al. 1998). As predicted by the decline in sea otters, sea urchin biomass increased 8× while kelp density declined 12× in the same decade. There are 2 possible explanations for increased predation on otters by killer whales. One is that killer whales feed mainly on seals in this region, but seal populations have plummeted, possibly as a result of declining fish stocks. In response, killer whales appear to have shifted to sea otters as prey. The other and more likely explanation for the decline of seals, sea lions, and sea otters is increased predation by transient pods of killer whales. Killer whale predation on those marine mammals may be caused by the decline of larger whales, upon which killer whales also feed (Springer et al. 2003, 2008; Williams et al. 2004; Estes et al. 2009).

Sea otters are also playing a key role in the recovery of beneficial eelgrass beds in a nutrient-laden estuary in central California. Sea otters there are at the top of a four-level trophic community. Their recovery has led to a reduction in crab populations, which, in turn, has led to increased growth of eelgrass at the expense of harmful algae (Hughes et al. 2013).

Although keystone species often are apex predators, herbivores also can act as keystone species in ecosystems they inhabit. The African savanna elephant (*Loxodonta africana*) and the forest elephant (*L. cyclotis*) occupy forest edge, woodland, and brushland habitats. Elephants feed on browse (twigs, shoots, and leaves) supplemented by grass. While foraging on bark, elephants destroy the shrub understory and girdle trees, causing loss of woodland and the creation of grassland (Figure 26.9). Once the forest canopy is opened up, fire accelerates the process. In large parts of sub-Saharan Africa, the vegetation has shifted from woodland to grassland as a result of elephants. Additionally, mesobrowsers, including impala (*Aepyceros melampus*), greater kudu (*Tragelaphus strepsiceros*), nyala (*T. angasii*), and black rhino (*Diceros bicornis*), which occupy the same area as elephants, also have an effect on reduction of woody browse in that they target earlier life stages of woody species than do elephants (O'Kane et al. 2011). Ultimately, this change is disadvantageous to the elephants and mesobrowsers, because they need woody species for browse, but it works to the advantage of grazing ungulates (Laws 1970; de Boer et al. 2015).

More than one species can play a keystone role in the same community. Species occupying a particular trophic level can be subdivided into **guilds**, or groups of species that exploit a common resource base in a similar fashion. In the Chihuahuan Desert, several species of kangaroo rats (*Dipodomys*) form a seed-eating guild (Brown and Heske

Figure 26.8 Sea Otters and trophic cascades. When otters are lost from an ecosystem, urchins increase and cause loss of kelp communities; the result is an urchin barren (**A**). Conversely, when otters are present, otters consume sea urchins, which allows kelp communities to flourish. See the kelp at the surface near the otter and in background (**B**).

Figure 26.9 Elephants as a keystone species. By destroying shrubs and trees, elephants promote grassland, which in turn favors grazing ungulates.

1990). When these rodents were excluded from this desert shrubland, a chain of events occurring over 12 years changed it to desert grassland. In the absence of kangaroo rats, annual plants with large seeds increased in number, raising the vegetative cover to the point where ground-feeding birds could no longer forage on grass seeds. This led to the increase in grasses. Both selective foraging by kangaroo rats on large seeds and soil disturbance from foraging, caching, and burrowing tend to maintain the shrub desert. Of the 15 species of rodents that live in the Chihuahuan Desert, Brown and Heske (1990) considered the kangaroo rats to form a **keystone guild** of large-seed eaters.

Predator Removals and Introductions

A straightforward way to test the role of predation in regulating communities is to remove the predators. Researchers predict that herbivore densities, normally kept in check by predators, would rapidly increase and plant biomass would decrease, causing a trophic cascade. Such experiments are ongoing in South America as areas are flooded by dams designed to provide hydroelectric power. In one such project in Venezuela, 4,300 km^2 were flooded, forming many islands (Terborgh et al. 2001). Large predators, which need large home ranges, quickly disappeared from these islands, and population densities of herbivores increased considerably. Howler monkeys (*Alouatta*), several rodent species, iguanas (*Iguana*), and leaf-cutter ants (*Atta*), reached densities of 10× to 100× those on the mainland. This outcome demonstrates the importance of top-down control of ecosystems in which predators keep herbivore populations sufficiently in check such that food is not limiting. In a few decades, these hyperabundant herbivores are predicted to reduce the once species-rich forests to a small group of herbivore-resistant plants.

Another example of a trophic cascade comes from the introduction of predators on islands. In the late 19th and early 20th centuries, arctic foxes (*Vulpes* [*Alopex*] *lagopus*) were introduced to more than 400 islands in the Aleutian archipelago to bolster the collapsing fur trade (Croll et al. 2005). Several islands remain fox free, however, and now serve as controls in this unwitting experiment. Breeding seabird densities are now almost 100× higher on the fox-free islands than on fox-infested islands. The reduction of seabirds by fox predation has led to a reduction in bird guano input to the ocean. The resulting loss of nutrient input from the ocean has, in turn, led to a transformation from tall grasses to a dwarf shrub/forb community on the fox-infested islands (Croll et al. 2005).

The recent reintroduction of wolves into Yellowstone National Park has led to a decrease in the elk population. That decrease has led to an increase in fruit-producing shrubs, upon which elk had browsed. This increase in shrubs has led to increased consumption of berries by threatened grizzly bears (*Ursus arctos*). These results suggest a trophic cascade involving increased predation by wolves on elk, a reduced elk population, decreased herbivory, and increased production of plant-based foods that may aid grizzly bears (Ripple et al. 2014). Additionally, the bears benefit by feeding on elk carcasses after displacing the wolves that killed them.

Increasing evidence is thus accumulating that adding or removing top predators (often mammals) leads to large-scale changes in entire ecosystems. Furthermore, there is evidence that these apex predators are more sensitive to climate change, as indicated by higher temperatures, than are the lower trophic levels (Voigt et al. 2003). Therefore, models predicting the effects of climate change on ecosystems need to incorporate these cascading interactions as we increasingly risk losing the top trophic levels (Zarnetske et al. 2012).

MUTUALISM

Interactions involving mammals and members of other taxa can be mutualistic, in which both species benefit either directly or indirectly. "Mutualism" is defined as cooperation between species (West et al. 2007). Examples of direct mutualism, in which both species are in contact, include seed dispersal by rodents, pollination of many species of plants by bats, removal of ectoparasites by birds from larger species, often mammals (see Chapter 23), and digestion of cellulose by the endosymbionts within the rumens of their ungulate hosts (see Chapters 7 and 19). An example of a mutualistic relationship between birds and mammals is between the African honey guide (*Indicator indicator*) and the African honey badger (*Mellivora capensis*). The bird vocalizes and "leads" the badger to a bee's nest. The badger opens up the nest and feeds on honey, while the honey guide consumes wax (Vaughan 1986). Oxpeckers (*Buphaga* spp.) eat the ticks they remove from large African ungulates to the benefit of both the bird and mammal (West et al. 2007). Unfortunately, as domestic cattle replace na-

Sea Otters and Global Warming

Some mammal species can have a disproportionate impact on community dynamics, sometimes acting indirectly via trophic cascades. As noted, along the north Pacific coast, where sea otters are present, they feed heavily on sea urchins, and the kelp forests flourish. Where sea otters are absent, sea urchins become abundant and feed on living kelp, thereby eliminating the kelp forests (Table 26.2).

What could this relationship have to do with global warming? We know that CO_2 is a long-lived and potent greenhouse gas, acting to warm the atmosphere and the earth below. Kelp has a high rate of CO_2 uptake via photosynthesis, and much of this carbon ends up sequestered (locked up) in the deep ocean. Wilmers and colleagues (2012) estimated the amount of carbon sequestered in sediments in the presence and absence of the kelp forests. Sequestration of carbon was >10× in areas with sea otters than without them due to the difference in abundance of kelp. The researchers were even able to put a monetary value on the ecosystem services provided by sea otters, estimating its value on the European Carbon Exchange in the hundreds of millions of dollars. Of course, the carbon locked up in this system is a tiny fraction of the total released as CO_2 by burning of fossil fuels, but restoration of predator effects in other ecosystems worldwide could add up to a substantial sum.

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Schmitz, O. J., C. C. Wilmers, S. J. Leroux, et al. 2018. Animals and the zoogeochemistry of the carbon cycle. Science 362:eaar3213.

Table 26.2 Sea otters as a keystone species: Changes in sea urchin and kelp densities in response to the reintroduction of sea otters

	Mean Density (no./m² ± SD)*		
	Torch Bay (no otters) n = 80	Deer Harbor (otters present <2 y) n = 24	Surge Bay (otters present <10 y) n = 80
Urchins			
Strongylocentrotus franciscanus	6 ± 7 (79%)	0.03 ± 0.03 (4%)	0
S. purpuratus	4 ± 13 (31%)	0.08 ± 0.06 (8%)	0
S. droebachiensis	6 ± 14 (65%)	0.2 ± 0.1 (12%)	0
Kelps			
Annuals	3 ± 7 (33%)	10 ± 5 (100%)	2 ± 5 (28%)
Laminaria groenlandica	0.8 ± 5 (6%)	0.3 ± 0.6 (21%)	46 ± 26 (99%)
Samples with no kelp	(64%)	(0%)	(0%)

Data from Duggins (1980).

*Numbers in parentheses are the percentage of those quadrats in which the species or group were observed. n = number of 1.0 m² quadrats.
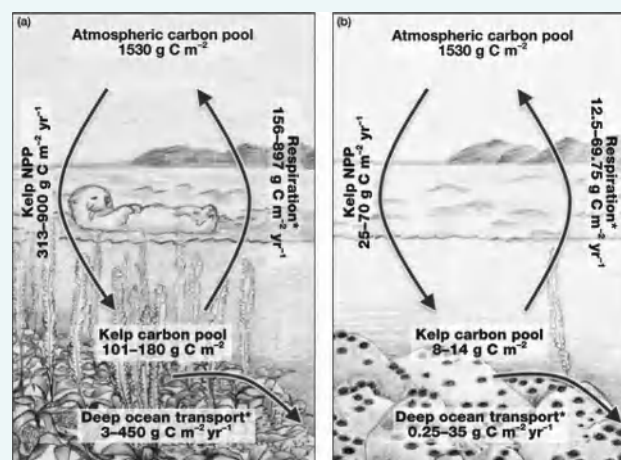
Impact of sea otters on the carbon cycle. (**A**) In areas where sea otters are present there are well-developed kelp beds and significant sequestration of carbon via loss in the deep ocean. (**B**) In the absence of sea otters, sea urchins flourish and consume the kelp, resulting in little sequestered carbon. *Data from Wilmers et al. (2012).*

tive species of ungulates, oxpeckers have declined in number, in part because cattle are treated with pesticides that eliminate the oxpecker's food supply.

Indirect mutualism involves positive effects without direct contact between the species. Commensal relationships, in which one species benefits and the other is more or less unaffected, include that between cattle egrets (*Bubulcus ibis*) and cattle (Genus *Bos*; Heatwole 1965). The egrets feed on insects stirred up by the cattle, which benefits the egrets and does not affect cattle. Another example of commensalism is the substrate provided for barnacles attached to a whale's skin.

Community Function

ENERGY FLOW AND COMMUNITY METABOLISM

One way to view the interconnectedness of communities is to trace the flow of **energy** through different trophic levels. Although often presented as linear food chains for the sake of simplicity, most communities are really interconnected in a web-like fashion. Energy enters the community as electromagnetic light energy from the sun. Converted by photosynthetic plants into chemical energy (in the form of sugars), it is then available to animals. Under natural conditions, green plants convert less than 1% of the light energy available to them. In an old-field community in Michigan studied by Golley (1960), meadow voles (*Microtus pennsylvanicus*) consumed about 2% of the plant material available to them, and least weasels (*Mustela nivalis*) ate about 31% of the available voles (Figure 26.10). In this linear food chain, so little energy was converted into weasels that a larger carnivore dependent on weasels for food could not be supported. Of course, many other organisms and energy pathways existed within this community, and most of the plants were eaten by herbivorous insects. A more complex food web (Figure 26.11) depicts trophic interaction in the alpine tundra in the central Rocky Mountains. Actually measuring the flow of energy in such a system would be extremely difficult. While food webs were traditionally thought of as being relatively static, relying on the persistence of species making up the community, more recently, they have come to be considered to be dynamic and flexible, accommodating changes in species composition (de Ruiter et al. 2005).

Grodzinski and French (1983) measured the production efficiency of small mammal populations in nine ecosystem types in Europe and North America. "Productivity" refers to the addition of new tissue in the form of growth of individuals plus new individuals from reproduction. Production was divided by respiration to give production efficiency. Efficiency was lowest for shrews (0.7%) and highest
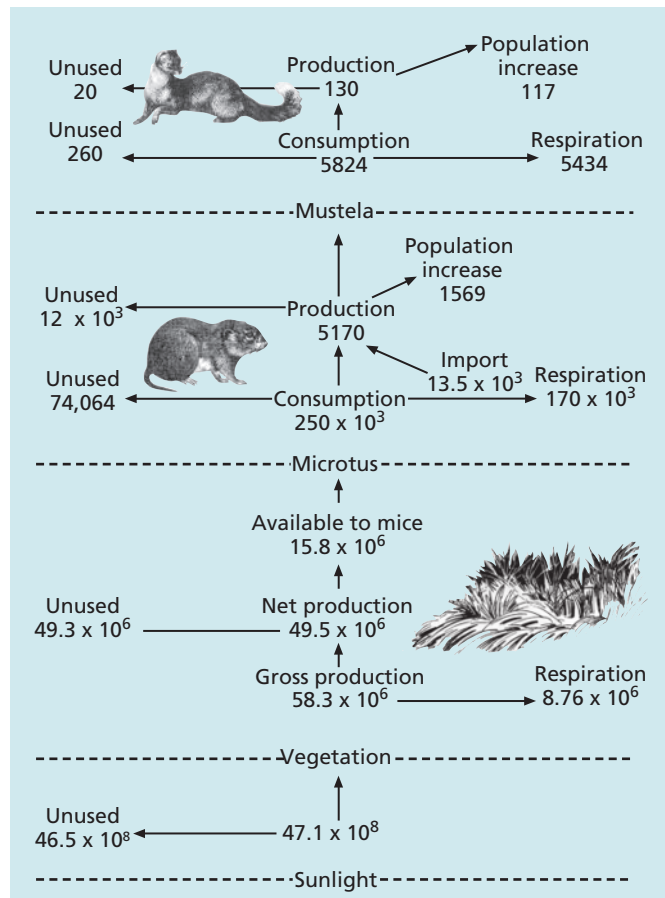
Figure 26.10 **Energy flow diagram of a portion of a food web in an old-field community in southern Michigan.** Numbers are in calories per hectare per year. *Data from Golley (1960).*

for rodents (3.4%). Efficiencies were low for shrews and rodents compared with poikilotherms because of the high respiratory cost of homeothermy in small mammals.

Although mammals typically do not account for a large proportion of energy flow in communities, their biomass can be quite high, resulting in a large "standing crop." Furthermore, the total effect of mammals on vegetation can be much greater than the amount assimilated. Common voles (*Microtus arvalis*) in agricultural fields in Poland destroyed as much as 13× more vegetation than they actually used to fulfill their energy requirements (Grodzinski et al. 1977). Mammals affect the vegetation in many ways, including cutting, trampling, burrowing, and nesting in it. Finally, because of their large size, long life, and high activity, some species of mammals play dominant roles in the community by influencing vegetation and other animals, as we have described with elephants, sea otters, and other keystone species.

COMMUNITY DEVELOPMENT

Ecological succession is the replacement of species in a habitat through a regular progression of stages leading ulti-
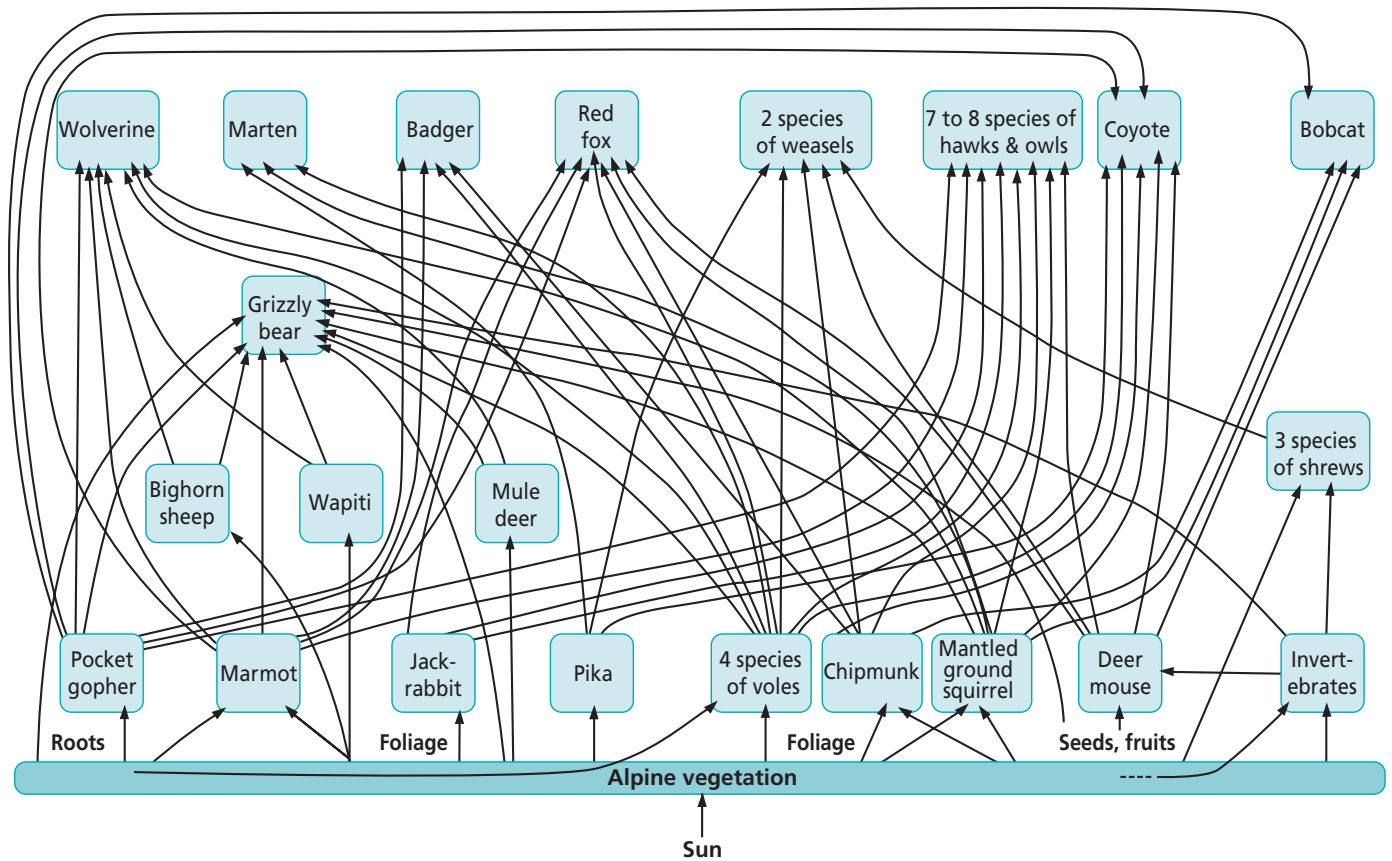
Figure 26.11 **Food web in the alpine tundra community of the Beartooth Plateau.** Insectivorous and herbivorous birds are not included. *Data from Hoffman (1974).*

mately to a stable state in the **climax community**. Species occupying early successional communities tend to have a fast pace of life, with high dispersal rates, rapid growth rates, and high reproductive rates (see Chapter 25). Those in later stages are more likely to be slow paced in their life histories, with lower dispersal rates, delayed maturation, and lower reproductive rates.

Old-field succession, in which fields are monitored for varying numbers of years following abandonment from agriculture, is often studied. The diversity of species typically increases during succession, although it may decline somewhat at the climax. In one study in Minnesota, a census of small mammals was taken for 18 fields that ranged in age from 2 to 57 years since abandonment from agriculture (Huntly and Inouye 1987). The youngest fields were dominated by short-lived, introduced Eurasian plant species. In middle-aged and older fields, native species of prairie grasses dominated. Woody shrubs were found only in fields older than 50 years and were never common. Of the 6 species of small mammals trapped, white-footed mice (*Peromyscus leucopus*) were caught in fields of all ages, whereas meadow voles and masked shrews (*Sorex cinereus*) tended to be caught in older fields. Generally, the number of small mammal species increased with the age of the field; this increase was associated with a striking increase in plant nitrogen, a measure of

primary productivity (Figure 26.12). Thus, mammal communities change as the vegetation changes.

Researchers assume that mammals respond to changes in vegetation, but mammals may affect the vegetation and thus the course of succession. Voles can extensively influence vegetation, especially during high-population years (Batzli and Pitelka 1970; Grodzinski et al. 1977). In the Serengeti, grazing by large herds of ungulates has a profound effect on the vegetation by increasing energy and nutrient flow rates. McNaughton (1985) argued that mammals and plants have both coevolved traits, resulting in interdependence rather than a relationship in which animals gain and plants lose.

Community Patterns

ISLAND BIOGEOGRAPHY

Much of what we currently understand about the ecological and evolutionary processes shaping patterns of biodiversity comes from knowledge gained from researchers
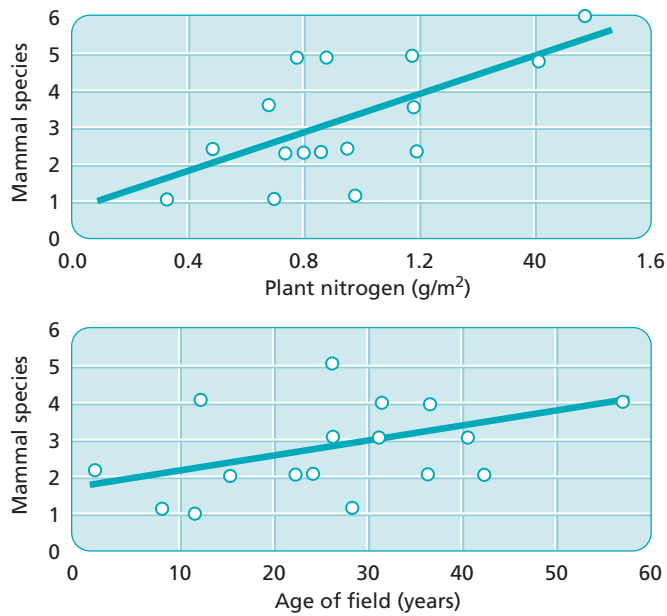
Figure 26.12 Effect of secondary succession on small mammal communities. Total number of species of small mammals in fields as a function of field age (years since abandonment from agriculture) and nitrogen content of vegetation (g/m²). *Data from Huntly and Inouye (1987).*

working on islands (Santos et al. 2016). MacArthur and Wilson (1967) developed a model that predicts a dynamic equilibrium of the number of species on islands. Although the species identity changes through time, the total number remains constant as new species colonize and resident species become extirpated. Immigration rates by new species are affected by island size: smaller islands are smaller targets and therefore have lower colonization rates. Extinction rates are higher on small islands, in part because population sizes are smaller. Also important is the distance of the island from the colonizing pool of species on the mainland; islands farther away also have lower immigration rates (Figure 26.13). Thus, small islands equilibrate at fewer species than large islands, and distant islands equilibrate at fewer species than near islands. Some researchers have worked in discrete habitats in the context of islands, including mountain tops (described as sky islands) and fragments of forests and lakes (Santos et al. 2016). In addition, the theory of island biogeography has been used as the conceptual basis for research on fragmented habitats.

It makes sense that the number of species should increase as the area being sampled increases. Larger areas typically have more habitats, which reduces the chances that an individual species will become extirpated. The re-

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Experiments with Large Mammalian Herbivores in East Africa

Many populations of the large, iconic mammals on African savannas are declining, and some areas are experiencing extirpations. In the 1990s and early 2000s, in an effort to better understand the population dynamics of large mammals, three long-term experiments at the Mpala Research Centre in Kenya were initiated to examine the factors that drive variation in the way large mammalian herbivores influence both plant communities and ecosystem processes.

The three experiments included the Kenya Long-Term Exclosure Experiment (KLEE) established in 1995, the Glade Legacies and Defaunation Experiment (GLADE) established in 1999, and the Ungulate Herbivory Under Rainfall Uncertainty experiment (UHURU) established in 2008. KLEE was designed to examine the effects of three guilds of wild and domestic large herbivorous mammals on community and ecosystem processes in an area with high-quality black cotton soils. That experiment included manipulation of densities of domestic cattle and controlled burns. GLADE was designed to examine the effects of all large herbivores combined with paired exclosures on nutrient-poor soils and nutrient-rich patches created by glades (treeless areas derived from abandoned livestock corrals). The emphasis of GLADE is to examine the interaction between soil nutrients and large herbivores on red soils. Finally, the UHURU experiment was designed to test the effects of three size-specific guilds of wild large herbivores on both under- and overstory plants, and small mammals on the red soil ecosystem.

Loss of large mammalian herbivores from savannah ecosystems in Africa may lead to alternative stable states that are much different than those that have existed for millennia. Livestock may compensate for the impact of losses of wild herbivores in herbaceous communities, but not communities dominated by woody plants. The interactions between cattle and wild herbivores are more complex than assumed; cattle and large wild herbivores were not always detrimental to one another. Responses of the plant community varied by ecosystem. On the productive ecosystem on black cotton soil, plants responded quickly to removal of herbivores. On red soils, which are somewhat less productive, vegetated plots responded within 5 years. However, bare patches took much longer to be revegetated after removal of herbivores—about 18 years. Large herbivores exert a diverse range of effects on the plant community and on smaller consumers that exist in those communities. Goheen and colleagues (2018) also observed competition and compensation across guilds of herbivores, including rodents. Finally, they observed evidence of trophic cascades and indirect effects on community, including small mammals, reptiles, and birds.

These long term experiments have highlighted he importance of large herbivores in savannah ecosystems. The research of Goheen and colleagues (2018) provides an important link between the fields of community ecology, landscape ecology, and conservation.

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A

B
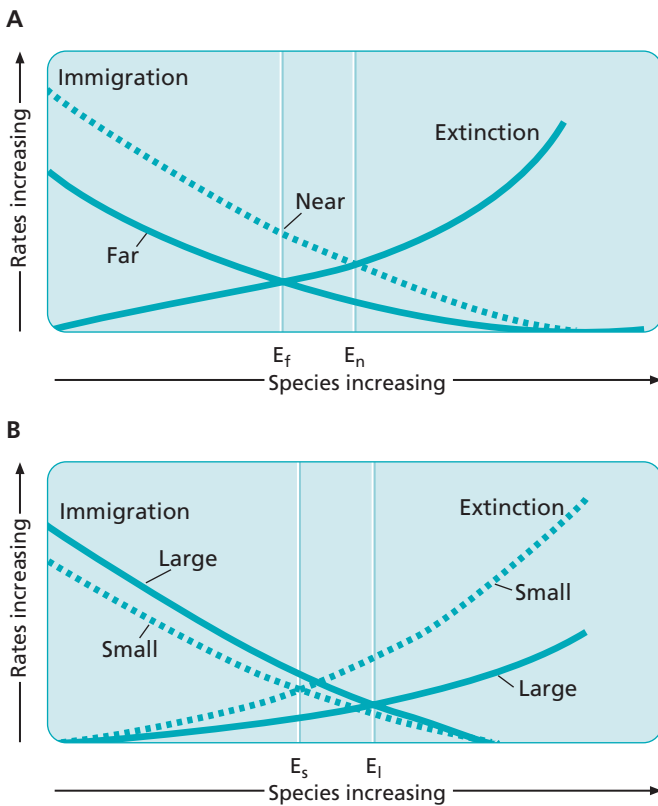
Figure 26.13 Equilibrium numbers of species on islands as a function of immigration and extinction rates. In (**A**), an island far from a colonizing source or mainland should equilibrate with fewer species, E_f, than on an otherwise identical near island, E_n. In (**B**), a large island equilibrates with more species, E_l, than a on small one, E_s, at the same distance from the mainland. Equilibrium numbers are shown where immigration and extinction curves intersect. *Data from Robert MacArthur and Wilson (1967).*

lationship, called the **species-area relationship**, can be described by the equation

$$S = cA^z, \qquad (26.2)$$

where S = number of species, c = a constant measuring the number of species per unit area, A = area being sampled, and z = a constant measuring the slope of the line relating S and A. The exponent z is typically in the range of 0.2–0.3 for mammals (Mártin and Goldenfeld 2006).

The application of island biogeography theory to mammalian communities has met with mixed results. Compared with birds and insects, mammals are relatively poor dispersers across water. For instance, Lawlor (1986) compared isolated, oceanic islands with so-called land-bridge islands, those that were connected to the mainland at the end of the Ice Age. The species-area curve for oceanic islands is nearly flat (z is low relative to land-bridge and mainland areas). Oceanic islands have fewer species than predicted from equilibrium theory, probably because colonization rates are so low for mammals.

Island size and distance from the mainland were evaluated in the Thousand Islands region of the St. Lawrence River in New York (Lomolino 1986). For species such as the red fox and raccoon (*Procyon lotor*) to be present, islands had to be above a critical size. For other species, such as deer mice, both island size and distance from the mainland were important factors in determining presence or absence of a species.

The Great Basin of North America consists of a vast "sea" of sagebrush desert interspersed at irregular intervals by isolated mountain ranges (islands). The upper slopes of these mountains have cool, mesic (moist) conditions and are well vegetated. The mammal species on these mountaintops (above approximately 2,500 m) are derived from the boreal faunas of both the Sierra Nevada Mountains to the west and the Rocky Mountains to the east. As can be seen from Figure 26.14, more species were found as the area of the mountaintop "island" increased, showing a linear relationship on log scale and approaching the number found in the saturated "mainland" areas (Brown 1971). Nevertheless, "islands" close to the "mainland" did not tend to have more species than those farther away, and the rate of colonization by new

A

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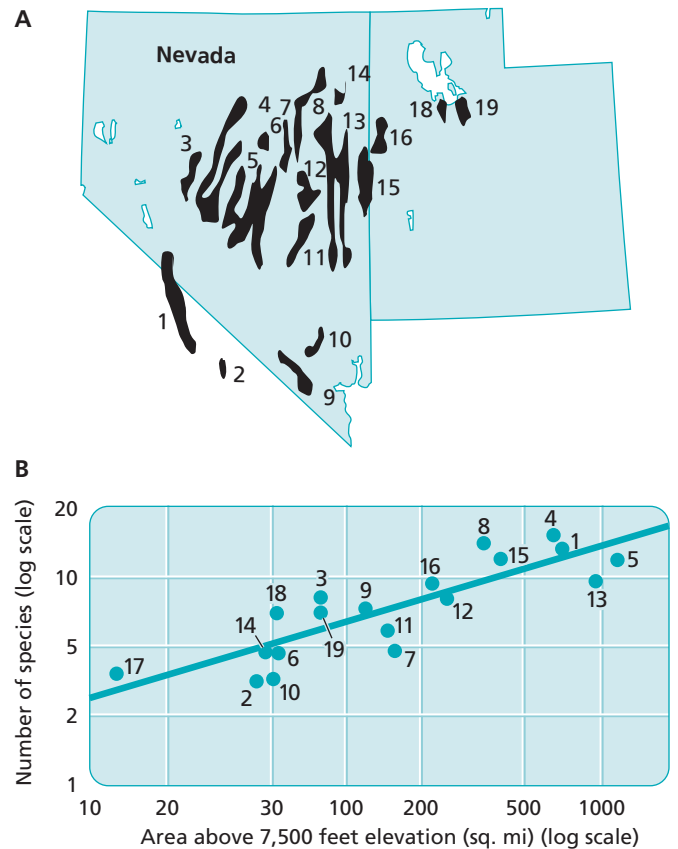
Figure 26.14 Island biogeography applied to mountaintops. (**A**) Map of the lower Great Basin region of the western United States showing the isolated mountain ranges between the Rocky Mountains on the east and the Sierra Nevada on the west; (**B**) species-area relationship for the boreal mammal species. Numbers refer to sample areas on the map. *Data from Brown (1978).*

species was much lower than on true oceanic islands. These habitats were all connected at the end of the Pleistocene epoch, when rainfall was higher, and they probably shared the same species of mammals. After postglacial climate change took place and rainfall declined, mountaintops became isolated, and they gradually lost species of mammals. Because of the extreme isolation and relatively poor dispersal powers of mammals, immigration rates of new species were probably very low, as Lawlor (1986) also found.

The species-area relationship shown in Equation 26.2 depends mainly on the statistical properties of distances between conspecific individuals; it best describes communities where the individuals within each species cluster together and where there are many rare species but only a few common species; these conditions are common to most ecological communities. The relationship does not directly involve processes such as competition or immigration or the effects of landscape variability (Mártin and Goldenfeld 2006).

SPECIES DIVERSITY

Because of the ever-increasing encroachment of humans into natural communities throughout the world, there is much interest today in **biodiversity**. Biodiversity has two main components: **species richness**, which is simply the number of species in an area, and **evenness**, the relative abundance of individuals within each species. Thus, a community that is made up of 10 species of mammals is more diverse than one with only 5. At the same time, in a comparison of 2 communities with 5 species each and a total of 100 individuals, the community with abundances of 20, 20, 20, 20, and 20 would be considered more diverse than one with 92, 2, 2, 2, and 2. Therefore, combining species richness and evenness is required to address species diversity in communities. Two diversity indices often used by mammalian ecologists are the Shannon-Wiener index and Simpson's index. Both use richness and evenness to compare communities and evaluate species diversity (Krebs 1999). In many communities, a few species are abundant, and a large number is relatively rare. Large-scale patterns of species richness are often apparent; for example, the diversity of mammals in the United States increases from east to west and from north to south.

Invasive species are a major threat to biodiversity, often having detrimental effects on populations of native species, ecological communities, and ecosystem processes (Bellard et al. 2016; Lurgi et al. 2018). Invasive species can affect populations of native species directly by predation, competition, or hybridization, as well as by spreading novel diseases (Doherty et al. 2016; Lurgi et al. 2018). Additionally, there are indirect effects on native species from disruptions of the functioning of ecosystems and habitats. Food webs have been used for decades to help understand community dynamics (May 1973; Pimm 1984). Lurgi and colleagues (2018) used food webs to model the effects of removal of European rabbits (*Oryctolagus cuniculus*) on other key species in a model arid ecosystem in Australia. They used a simplified food web to examine ecological interactions (Figure 26.15). Their simulation indicated that removal rates of up to 40% of rabbits immediately benefited native herbivores, but removal rates over 40% would delay the positive effects of rabbit management. At removal rates over 40% two factors reduced the effectiveness for native small mammals: increased competition for resources with kangaroos (*Macropus*); and increased predation by mesopredators (foxes and cats) on the native small mammals. The presence of dingos, apex predators in the ecosystem, has also reduced populations of cats (*Felis catus*) and red foxes, which are mesopredators (Letnic et al. 2012). Increased predation on alternative prey by cats following removal of rabbits has also been shown empirically (Murphy et al. 2004).

LANDSCAPE ECOLOGY

A relatively new branch of ecology, called **landscape ecology**, is concerned with understanding population and community relationships within a large geographic region. Mammalogists have understood the influence of landscapes on animal distribution and abundance since the pioneering work of Merriam (1894), but only recently have methods been developed to quantify the effects of spatial scale on community structure. An important application of this approach is in the design of nature reserves, discussed more fully in Chapter 28. Problems such as movements of individuals through habitat patches differing in size and shape, responses to habitat fragmentation, design of connecting corridors, and patterns of dispersal across habitat patches are modeled. This discipline explores the behavior of individuals, populations, and communities as they respond to different features of the environment at different spatial scales (Forman and Godron 1986; Merriam and Lanoue 1990). New techniques include computer simulations based on fractal geometry, analyses using geographic information systems (GIS) satellite imagery, and remote sensing.

Landscape ecology has great potential for helping researchers predict the effects of habitat fragmentation, one of the major causes of species extinctions. Classical island biogeography theory focuses on species richness as well as patterns of colonization and extinction as a function of habitat patch size and isolation, and it assumes that the surrounding matrix (e.g., water) is homogeneous. For these and other reasons, it has met with mixed results when applied to terrestrial systems, as noted earlier in this chapter. Landscape ecology, on the other hand, incorporates information about how landscape patterns of many types influence reproduction and dispersal of local populations. Such studies can be done on natural landscapes or on experimental plots where the arrangement of habitat elements can be manipulated (Diffendorfer et al. 1995).

At the population level, it is important to understand how mammals living in isolated habitat fragments move through less suitable areas to get to more suitable ones (Merriam 1995). Studying how animals move about their
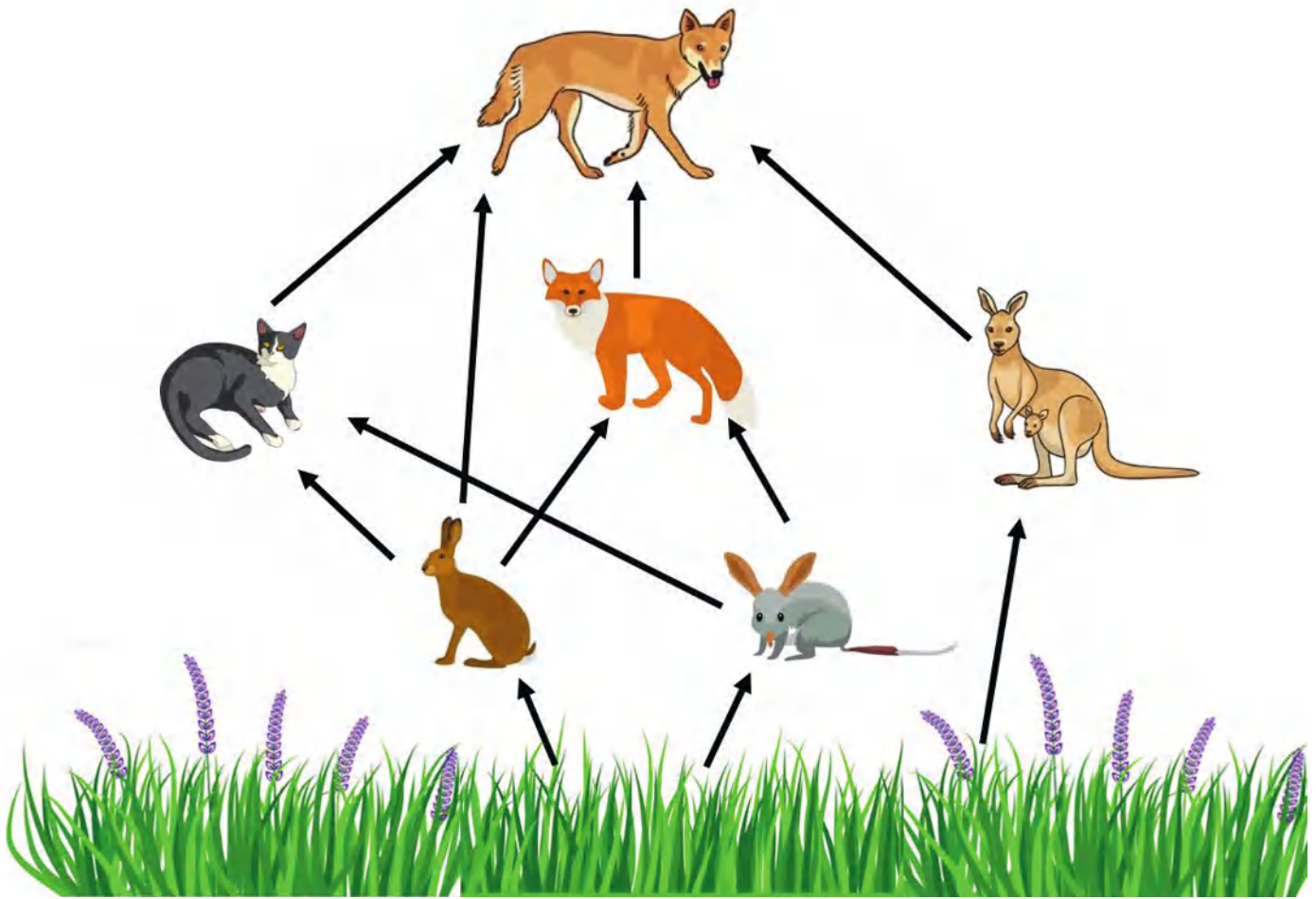
Figure 26.15 Simplified food web in an arid portion of Australia that includes both native and invasive species. Arrows between animal pictures indicate ecological interactions. Those interactions are among either trophic levels, consumer-resource relationships, or amensalistic, between dingos and mesopredators. Apex predator is dingo (*Canis lupus dingo*), mesopredators are domestic cat (*Felis catus*) and red fox (*Vulpes vulpes*), herbivores are kangaroo, European rabbit (*Oryctolagus cuniculus*), and bilby (*Macrotis lagotis*). Invasive species are domestic cat, European rabbit, and European red fox. *Redrawn from Lurgi et al. (2018).*

home ranges and territories (Chapters 24) is not sufficient; ecologists must also study the spatial structure of the landscape mosaic and how dispersing animals move through it. Local interbreeding populations can be connected to other populations via dispersal, forming **metapopulations** (Hanski 1996). Metapopulations or "population of populations" are usually defined as a group of populations that occur in patches of suitable habitat, surrounded by areas of unsuitable habitat. Those local populations are connected by dispersal of individuals, and if a local populations goes extinct, it may be reestablished by colonists from the other population. When patches of habitats are unequal in quality, metapopulations may also incorporate **source-sink dynamics** (Pulliam 1988). High-quality habitats (source) support populations where birth rates exceed death rates and individual disperse to lower quality habitats (sink), where death rates exceed birth rates. Those populations in high-quality habitats have a low probability of extirpation, unlike sink habitats, which are maintained by immigration of individuals from source populations.

Bighorn sheep (*Ovis canadensis*) are a good example of a species that in many ecosystems show metapopulation structure (Bleich et al. 1990). Historically bighorn sheep occurred in distributions that were naturally fragmented because they prefer habitat that consists of open patches of steep cliffs that occur as "sky islands" on mountains. Those mountains are usually separated by dense forests, deserts, or areas of inhospitable habitat. Epps and colleagues (2018) studied a metapopulation of desert bighorn sheep in the Mojave Desert in California. After a pathogen spread across an interstate highway that had been assumed to be a barrier to gene flow, they looked for changes in metapopulation structure that may have influenced connectivity among subpopulations. Using various genetic techniques, they detected changes in distributions and movements that established new links between some subpopulations and decreased links among others.

Researchers know that immigration and emigration are important population forces (see Chapter 25), but they often have little idea of what the boundaries of a

population actually are. For example, in a long-term study of white-footed mice in a small, isolated 2-ha woodlot in Ohio, it had been assumed that the population was essentially defined by the boundaries of the woodlot. Live-trapping mammals in the surrounding agricultural fields, however, revealed that mice were making extensive use of cropland at certain times of the year (Cummings and Vessey 1994). In eastern Ontario, near the northern edge of its range, this forest-dwelling species has adapted to living in cornfields year-round, where densities were similar to those in wooded areas (Wegner and Merriam 1990). Densities were quite low compared with those in other studies, and the spatial scale over which the mice moved was unusually large.

Landscape ecology can also be viewed at the community level and above, where patches of the same community types are studied in a spatially explicit way (Lidicker 1995). Properties of landscapes that can be studied at this level include spatial configuration (the dispersion of patches), edge-to-area ratios (sizes and shapes of patches), and connectedness (links among patches of the same community type).

MACROECOLOGY

At a still larger scale is the study of **macroecology**, which explores patterns of body mass, population density, and geographic range at the scale of whole continents (Brown and Maurer 1989; Brown 1995). It involves the nonexperimental (i.e., nonmanipulative) investigation of relationships among populations, including patterns of abundance, body size, metabolic rates, geographic distribution, and diversity. Such large-scale studies require massive amounts of data on distributions, densities, and body sizes of representative species in each community before meaningful statistical patterns can be seen. Most of these data have already been collected for mammals, at least in temperate regions. The goal of macroecology is to identify and explain emergent statistical patterns in terms of general processes that can then be applied to unstudied areas. One statistical pattern already discussed is the species-area curve (see Equation 26.2), which shows how the number of species increases with the area sampled. The species-area relationship can be studied at all spatial scales, from the smallest microhabitats to entire continents, and it has provided much insight into how communities are assembled.

Other patterns involve attributes of individual organisms. When the number of species of terrestrial mammals in North America is plotted against average body mass, one finds that there are many more small species than large ones, and a strong peak in mass occurs between 50 and 100 g (Brown and Maurer 1989; Figure 26.16A). When smaller spatial scales are used, however, as when comparing deciduous forest, desert, or still smaller patches of relatively uniform habitat, the distributions become flatter,
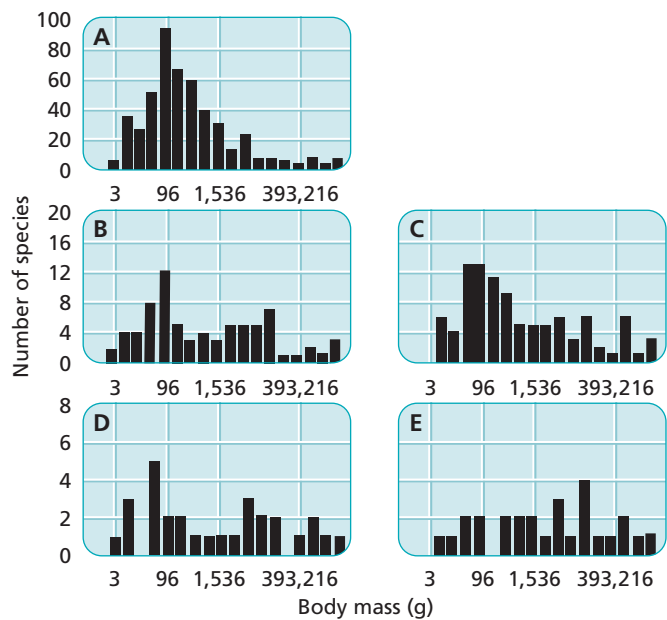
Figure 26.16 Frequency distributions of body masses (log scale) among species of North American land mammals. Distribution for the entire continent, for land mammals within (**A**) biomes, (**B**) northern deciduous forest, and (**C**) desert; and for land mammals within small patches of relatively uniform habitat within each of these biomes—(**D**) Powdermill Reserve and (**E**) Rio Grande Bosque. *Data from Brown and Maurer (1989).*

giving approximately equal numbers of species in each size category (see Figure 26.16B–E). Why are there so many small species, and why does the pattern shift as the scale changes? One possible explanation for this shift is interspecific competition, which reduces the number of similarly sized species in the same habitat. Large species could be relatively rare at the continental scale due to energy constraints; smaller populations are more likely to go extinct. Finally, Brown and Maurer (1989) hypothesize that a greater number of small species exist at the continental scale because they have smaller geographic ranges and replace one another more frequently across the landscape than do large species. These small species tend to be specialized because they need high-quality food to maintain their relatively high metabolic rates.

In the last few decades the availability of phylogenies has enabled community ecologists to explore the role of genetic relatedness and evolutionary history in determining the species present at a particular place and time (Webb et al. 2002; Tucker et al. 2017). Attempts have also been made to incorporate phylogenetic community ecology into macroecology. For example, analyses of the large-scale assemblages of African carnivores revealed that they are phylogenetically nonrandom, showing a pattern of clade growth characterized by early biome-filling radiations followed by competitive sorting within the biomes of the African continent (Cardillo 2011).

SUMMARY

- Biological communities consist of interacting populations of organisms in a prescribed area.
  - Important to the study of any species is the concept of ecological niche, which involves an organism's habitat and functional role in the community.

- A central goal of community ecology is to understand the factors, such as climate, ecology, and phylogeny, which determine the species that make up a community.

- Interspecific competition affects both the distribution and abundance of species.
  - The competitive exclusion principle states that complete competitors cannot coexist indefinitely.
  - The best evidence of competition comes from removal experiments, in which species are experimentally removed and the response of the presumed competitor is monitored.

- Predators also can be important forces in structuring communities.
  - Keystone species are those that play a primary function role in the distribution and abundance of many other members of the community.
  - Trophic cascades exist when the addition or removal of a keystone species causes cascading effects at lower trophic levels.

- Risk of predation can also act to structure communities; prey species may modify their foraging behavior and habitat choice to reduce predation risk.

- Mutualistic relationships, in which both species benefit, are common but have not been well studied in mammals.

- Several studies have documented the flow of energy through the mammalian component of ecosystems.
  - Some species of mammals play important roles by controlling other components of the ecosystem.

- Mammals show changes in both species composition and abundance in response to ecological succession.

- Studies of islands, varying in size and isolation from mainland habitats, have shown that communities consist of species in dynamic equilibria that result as new species colonize and resident species go extinct.

- Landscape ecology is the study of the distribution of individuals, populations, and communities across multiple spatial scales.

- Macroecology explores patterns of body mass, population density, and geographic range at a continental scale.

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DISCUSSION QUESTIONS

1. Character displacement is usually considered to be a result of competition among closely related species in sympatry. For what other reasons might species show character displacement?

2. Niche dimensions often shift as a result of competition and resource partitioning among sympatric species. Design an experiment to determine if niches shift without competition. Is there a way to determine if competition is occurring without a removal experiment? If the niches do not change, what conclusions can you draw?

3. How do functional and numerical responses differ from each other with respect to the prey population? What about the predator population? How would you determine what kind of functional response is occurring when observing interactions between predators and prey? How would those relationships change with multiple species of predators?

4. The theory of island biogeography has been applied to the design of conservation areas for terrestrial species on continents. How might island biogeography a be applied to habitat conservation for terrestrial species of different body sizes—for example, meadow voles, rabbits, red fox, deer, wolves. What about for species such as bighorn sheep, which show strong metapopulation structure?

5. Which of the following paragraphs best describes mammalian communities? Muster as much support as possible for your position. You may wish to consult an ecology textbook, such as Krebs (2008), Ricklefs and Miller (1999), or Begon et al. (2006).

   a. The distribution of individual species in space and time suggests that each species responds to its own unique set of requirements independently of the effects on other species. Community boundaries are best understood as being arbitrarily defined units, more for the convenience of the investigator, than as highly integrated levels of organization.
   b. Communities include closely integrated species with complementary functional roles. Predictable patterns of species distribution and guild composition reflect the close **coevolution** of species in response to interspecific competition.

PART 5

Special Topics

Parasites and Zoonotic Diseases

In this chapter, we consider several **zoonoses** (from the Greek words *zoo*, meaning animals, and *noses* meaning diseases), which for our purposes are defined as diseases transmitted from nonhuman mammals to people. Mammals are sometimes a primary reservoir, or source, of the infective organism of human zoonoses. Of 335 emergent disease events from 1940 to 2004 identified by Jones and colleagues (2008), 60% were zoonotic. Of these, almost 72% originated in wildlife and were caused by viruses, bacteria, protozoans, nematodes, or prions. Reservoirs can enable a disease to persist in an area at moderate to low levels, which is termed an **enzootic** phase. When various factors amplify the occurrence and distribution of an enzootic disease, it becomes **epizootic.** Arthropod parasites often serve as **vectors** (carriers) of viruses, bacteria, or other **microparasites** to humans and other mammalian species. These microparasites are the **etiological**, or causal, agents of the disease. We will concentrate on a few common or historically important zoonoses as well as on some relatively recent diseases with which mammalogists should be familiar. Understanding mammalian zoonoses is important because of the roles they play in the evolution and life histories of species (Childs 1995). Many animal species can be reservoirs for pathogens, and monitoring, preventing, and controlling zoonotic diseases remain a serious challenge to public health, especially in developing countries (World Health Organization 2004; CDC 2018). Additionally, there are now several zoonotic pathogens—those causing plague, tularemia, anthrax, Ebola, and others—that are considered to be bioterrorism weapons (Barras and Greub 2014; D'Amelio et al. 2015).

Mammalian Parasites and Diseases

Numerous species of parasites and diseases are associated with mammals. We will note examples of mammalian parasites and diseases that affect humans. Space does not permit a discussion of most zoonoses; for more detailed information on zoonoses and other mammal-related

diseases, see Palmer and coworkers (2011), Conover and Vail (2015), Bauerfeind and colleagues (2016), and the Centers for Disease Control and Prevention, National Center for Emerging and Zoonotic Infectious Diseases, Division of Vector-borne Diseases (CDC 2018).

PROTISTANS

A number of protistan species are pathogenic. For example, African sleeping sickness, or trypanosomosis (Figure 27.1), which occurs throughout central Africa, is caused by two subspecies of the flagellated parasite *Trypanosoma brucei*: *T. b. rhodesiense* (East African sleeping sickness) and *T. b. gambiense* (West African sleeping sickness). Antelope, domestic livestock, and many other mammalian species serve as reservoirs for trypanosomosis. The vectors are several species of tsetse fly (Genus *Glossina*). In people infected with *T. b. gambiense*, sleeping sickness progresses from headache and fever to muscular and neurological involvement and eventually to coma and death. People infected with *T. b. rhodesiense* usually die before these symptoms develop. About 70,000 new cases of sleeping sickness occur annually, although many others are probably unreported. Untreated, the disease is fatal in 100% of cases within several months (Gibson 2011). Past epidemics have killed hundreds of thousands of people (Maguire and Hoff 1992).

A closely related trypanosome protozoan, *T. cruzi*, causes American trypanosomosis, or Chagas disease (after the Brazilian physician who described it in 1909). Reservoirs include over 150 mammalian species, particularly domestic cats and dogs, as well as bats, armadillos, marsupials, and rodents. Over 35 species of blood-sucking "assassin bugs" or "kissing bugs" (Hemiptera, Reduviidae) are the vectors. This disease is a leading cause of cardiovascular death in Mexico, Central, and South America, where 8 to 10 million people are infected, with 21,000 deaths annually (Reisenman et al. 2010; Rassi et al. 2012; Bern 2015). In the United States, *T. cruzi* occurs predominately in the South, where the Centers for Disease Control (CDC) consider it one of 5 "neglected parasitic infections."

Leishmaniasis is a complex of zoonotic diseases (Bauerfeind et al. 2016; see their table 4.5) common to tropical and subtropical regions in South America, southern Europe, and Asia. They are caused by about 20 species in Genus *Leishmania*. The reservoirs of these diseases, which are transmitted through the bite of sandflies (Family Psychodidae), are primarily canids and rodents, but include several other mammalian groups as well. In humans, *Leishmania donovani* causes Dum Dum fever, also called "kala-azar." After an incubation period of several weeks, respiratory or intestinal infection and hemorrhage occur. If untreated, kala-azar is invariably fatal. An estimated 1 million new cases of leishmaniasis occur annually, with a total of about 12 million people infected worldwide (Gramiccia 2011).

Finally, several species of Genus *Plasmodium*—the causative agent of malaria—infect numerous species of mammals, including rodents, nonhuman primates, and humans. Five species of *Plasmodium* cause several varieties of malaria in people; most deaths are caused by *P. falciparum*. Malaria has been known for thousands of years; in 2016 there were an estimated 216 million cases worldwide, with 445,000 fatalities, mostly in Africa (CDC 2018).

PLATYHELMINTHS, NEMATODES, AND ARTHROPODS

Hundreds of mammalian species are infected with platyhelminths and nematodes and are often the primary hosts or reservoirs from which hundreds of millions of people become infected. Two classes within the Phylum Platyhelminthes are entirely parasitic and common in humans and other mammals. The Class Trematoda includes both visceral and blood flukes. The Class Cestoidea includes the tapeworms. The dwarf tapeworm (*Vampirolepis* [*Hymenolepis*] *nana*), commonly carried by mice, infects up to 50 million people worldwide. Annually, an estimated 200 million people contract schistosomiasis, which is "second only to malaria as the most devastating parasitic disease" of humans (CDC 2018). Three species of the blood fluke *Schistosoma* (Figure 27.2) infect humans; most live in sub-Saharan Africa. Dogs, rodents, and domestic livestock are the main reservoirs.

Nematodes are generally called "roundworms," and there may be 500,000 species worldwide. Thousands are parasitic and are carried by numerous mammalian hosts. Nematode infection occurs most often in tropical and subtropical developing countries with poor sanitation facilities. Nematode hookworms infect over 400 million people a year. Intestinal roundworms may infect as many as 25% of people worldwide. As noted by Roberts and colleagues (2012:377), "Some of the most dreaded, disfiguring, and debilitating diseases of humans are caused by nematodes."

Arthropods are the largest phylum of animals, with over a million described species. Arthropods include ticks, fleas, mites, flies, mosquitoes, and lice. They are **metameric** (segmented) and have a chitinous exoskeleton. They can serve as either intermediate or **definitive hosts** for viruses, protists, platyhelminths, and nematodes. Although most species are of no medical importance, some arthropods are
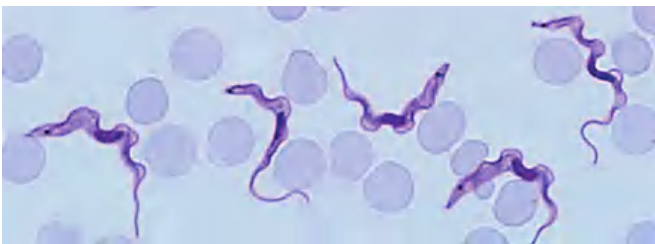
Figure 27.1 **Protistans.** *Trypanosoma* is the protozoan genus responsible for African sleeping sickness and Chagas disease.

Figure 27.2 Mature blood fluke parasite *Schistosoma masoni.* One of three species of *Schistosoma* that infect humans, the thin female lives in the gynecophoral canal of the larger male.

mammalian parasites that are among the most significant vectors in the transmission of vector-borne zoonoses.

Vector-Borne Zoonoses

PLAGUE

In the past 1,500 years, plague has killed more people and has had a greater effect on human history than any other zoonotic disease (Twigg 1978; Lewis 1993; Bauerfeind et al. 2016). The etiological (infectious) agent is the Gram-negative bacterium *Yersinia pestis*, and fleas are the primary vectors. There are more than 1,500 species of fleas, most of which are probably capable of plague transmission (Krasnov et al. 2006), although female oriental rat fleas (*Xenopsylla cheopis*) are the best-documented plague vectors (Figure 27.3). They transmit bacteria as they feed on an infected animal, often black rats (*Rattus rattus*) or brown (Norway) rats (*R. norvegicus*). Over 200 mammalian species, primarily rodents, are naturally infected with plague (Poland et al. 1994). In the United States, many rodents carry plague (Gage et al. 1995), especially ground squirrels and the deer mouse (*Peromyscus maniculatus*). Recently, Dean and colleagues (2018) found that the second plague pandemic in Europe may not have been spread by rats, as commonly believed, but by human fleas (*Pulex irritans*) and body lice (*Pediculus humanus*).

In about 12% of infected fleas, bacteria multiply rapidly and within 9–25 days fill their gut. When these "blocked" fleas try to feed on humans or other mammalian species,

Figure 27.3 Oriental rat flea (*Xenopsylla cheopis*). The gut filled with blood can be clearly seen.

blood enters their gut and picks up bacteria. Because their gut is blocked, blood is regurgitated back into the wound, and plague bacteria enter the host. More specifically: an adult female flea consumes blood from an infected vector → bacteria rapidly multiply in flea's gut → gut is clogged with bacteria and flea is "blocked" → flea bites person and regurgitates bacteria into wound → person is infected. People also can pick up the bacterium through handling animal tissues or inhaling droplets from infected, coughing people (Prentice 2011).

There are 3 clinical types of plague: bubonic, septicemic, and pneumonic. Bubonic plague is the most common and least infectious; bacteria concentrate in the lymph nodes of the armpits and groin, where, after a 2–8 day incubation period, they cause extreme swelling (Figure 27.4). These swollen areas are called **buboes**—thus, the name "bubonic plague." Because of internal bleeding and necrosis of tissue under the skin, these areas turn black. Historically, bubonic plague has been referred to as the "Black Death." Mortality can occur as quickly as 2 to 4 days after symptoms occur. Untreated, the human mortality rate for bubonic plague initially was about 75%. Today, 40%–60% of untreated cases are fatal.

In septicemic plague, bacteria infect the entire bloodstream, rather than concentrating in lymph nodes and producing buboes. Pneumonic plague results when the bacteria in human hosts move to the lungs. The lungs fill with a frothy, bloody fluid—a hemorrhagic bronchiopneumonia. Droplet-borne bacteria are highly infectious and may be spread directly from person to person without the need of intermediate fleas. The human mortality rate for untreated septicemic or pneumonic plague is 100%, and following onset of symptoms, life expectancy is only 1–8 days.

Since the 6th century C.E., three large-scale outbreaks of plague over wide geographic areas (**pandemics**) have been recorded, although strains of *Y. pestis* emerged in human populations in Europe at least 5,000 years ago (Rasmussen et al. 2015). The first large-scale outbreak—called the "Justinian Plague" after the emperor Justinian I—

Figure 27.4 Plague symptoms. A bubo (lymphadenitis) such as shown here typically occurs in people infected with bubonic plague.

began in Arabia and spread to Egypt in C.E. 542 and to the Roman Empire and Europe between 558 and 664 (Acha and Szyfres 2001). An estimated 100 million people died. The second pandemic, the Black Death of Europe, probably began in China in 1334, spread to Europe along major trade routes (Yue et al. 2017), where it killed about 60% of the population, and reached England in 1348. Over 50 million people died as periodic **epidemics** (outbreaks affecting many people in an area) continued throughout Europe until the mid-1600s. Following this pandemic, it took 200 years for Europe to regain the population level it had in 1348 (Twigg 1978). The last plague pandemic (the Modern Plague) broke out in China and India in the 1860s and continued until the 1930s, killing 12 million people throughout Southeast Asia, South Africa, and South America.

Plague is not just of historical interest, however. Several areas throughout the world continue to harbor the disease, with 1,000 to 3,000 cases reported each year—95% from sub-Saharan Africa, especially Madagascar (Figure 27.5A). Plague is also endemic in rodent populations in localized focal areas in the Middle East, China, and Southeast Asia, as well as western North America (Maher et al. 2010; Walsh and Haseeb 2015; Figure 27.5B). Although human deaths still occur from plague each year, it is treatable with a variety of antibiotics if properly diagnosed. However, given the ability of microorganisms to mutate rapidly and become immune to antibiotics, as well as the ability of people to travel anywhere in the world in a matter of hours, the potential exists for new outbreaks of plague. Also, plague is now categorized as a "bioweapon" for potential use by terrorists (Froude et al. 2011).

LYME DISEASE

Named for the town in Connecticut where it was first recognized in the United States in 1977, Lyme borreliosis has steadily increased in occurrence, with about 39,000 cases

reported in the United States in 2015. There are hundreds of thousands of cases annually in Europe and Asia. Lyme disease is the most common vector-borne illness in the Northern Hemisphere (Mead 2015; Kilpatrick et al. 2017). The etiological agent is the spirochete (corkscrew-shaped), Gram-negative bacterium Genus *Borrelia*, currently with about 37 named species. *Borrelia burgdorferi* causes Lyme disease in North America, whereas *B. garinii*, *B. afzelii*, and *B. valaisiana* are the causative agents in Europe and Asia. Another group of about 12 species of *Borrelia*, carried by mice and other small mammals, causes the closely related tick-borne relapsing fever worldwide. Pratt and colleagues (2016) described *B. mayonii*, a new species causing Lyme disease in the Upper Midwest, United States. The vectors are ticks of the *Ixodes ricinus* complex, found throughout North America, Europe (where the disease was originally described), and Asia (Lane et al. 1991). The disease correlates closely with distribution of the deer tick (*I. scapularis*) in the northeastern and midwestern United States and the western black-legged tick (*I. pacificus*) in the western United States. In Europe, the main vector is *I. ricinus*, whereas it is *I. persulcatus* throughout Asia. Numerous mammalian species, primarily rodents, are reservoirs for Lyme disease throughout the world. The main reservoirs in central and eastern North America are white-footed mice (*Peromyscus leucopus*) and white-tailed deer. In the western United States, the primary reservoir is the dusky-footed woodrat (*Neotoma fuscipes*). In Europe, the main rodent reservoirs are the bank vole (*Myodes glareolus*) and wood mice (Genus *Apodemus*). Ostfeld and colleagues (2006) attempted to predict the extent of occurrence of Lyme disease based on key determinants such as climate, density of rodents and deer, and abundance of acorns—a primary food resource. Reliability of such predictive models may be best at local rather than landscape scales (Schauber et al. 2005).

Ticks likely transmit the spirochete to humans through saliva, but only after 24 to 36 hours of attachment (Piesman et al. 1991; White 1993). Ticks pass through three developmental stages: larva, nymph, and adult (Figure 27.6). They are most likely to transmit Lyme disease during the nymph stage. They actively feed during this developmental stage but are unlikely to be noticed because of their small size (about 1 mm). Although larval ticks also feed and are even smaller (0.5 mm), they rarely carry the infection. Adult ticks can also transmit Lyme disease, but because of their relatively large size they are much more likely to be noticed and removed in less than the time necessary to transmit infection.

Symptoms of Lyme disease may include fatigue, fever, muscle and joint pain, and often a characteristic bull's-eye-shaped skin rash (Figure 27.7). This rash (*erythema migrans*), seen 3–30 days after infection, lasts 2–3 weeks. When diagnosed early, antibiotics successfully treat Lyme disease. Unfortunately, positive diagnosis often is difficult because the diversity of symptoms varies from patient to patient. For example, a rash does not form in 20%–30% of cases (Barbour and Fish 1993). Conversely, a rash can result from an allergic reaction to the tick saliva rather than infection from
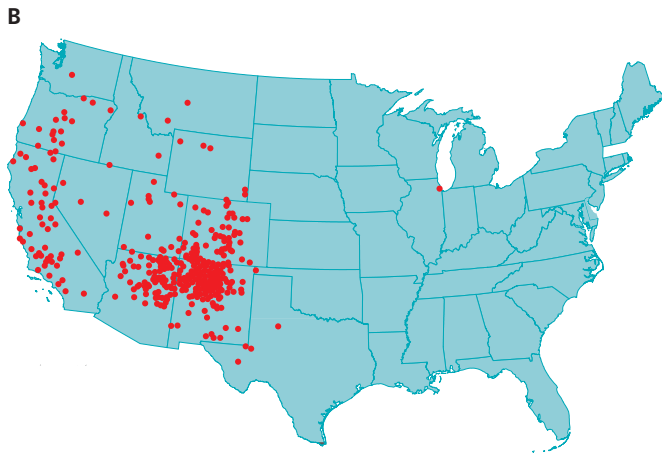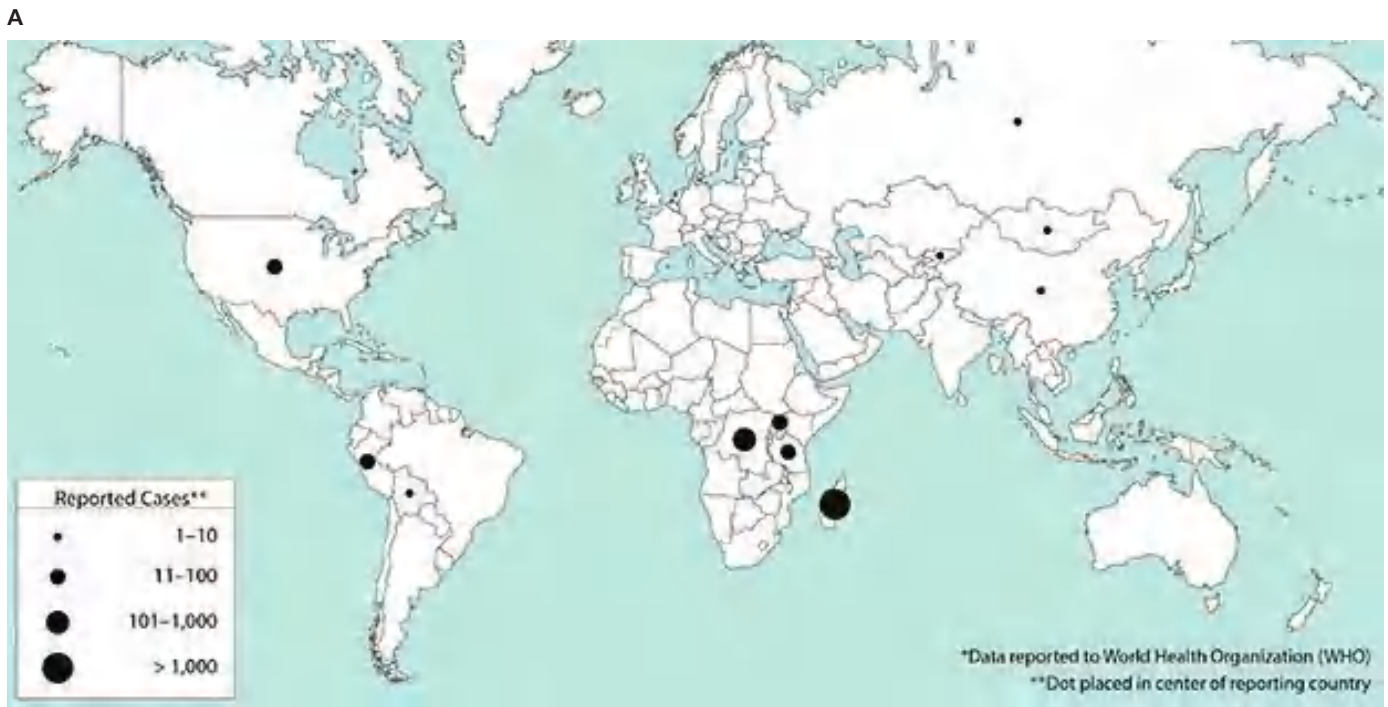
Figure 27.5 Distribution of plague. (**A**) Countries reporting plague, 2010–2015; (**B**) cases of plague reported in the United States, 1970–2016. *Data from Centers for Disease Control and Prevention (2018).*
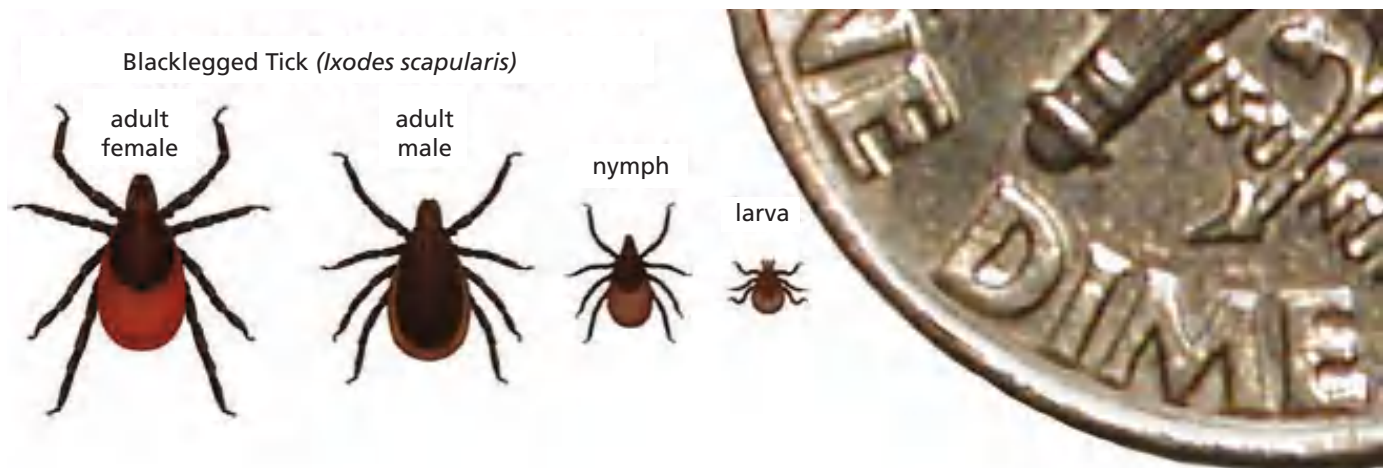
Figure 27.6 Developmental stages of ticks. Ticks have three developmental stages: larva, nymph, and adult. They are most likely to transmit Lyme disease during the nymph stage. *From Centers for Disease Control and Prevention (2018).*

Figure 27.7 Lyme disease rash. This "bulls-eye" rash does not occur in all infections. *From Centers for Disease Control and Prevention (2018).*

Lyme disease. Clinically variable, Lyme disease can produce either acute or chronic disease. If untreated, it is rarely fatal but infection can be disabling, leading to severe arthritis; nervous system involvement, including numbness, pain, or meningitis; and occasionally, cardiac arrhythmia (O'Connell 2011).

ROCKY MOUNTAIN SPOTTED FEVER

Rocky Mountain spotted fever (RMSF), first reported in 1896 in Idaho as "black measles," is another well-known tick-borne zoonosis caused by a rickettsial bacterium, *Rickettsia rickettsii*. The name of this disease is actually a misnomer, as it occurs from western Canada through the United States, Mexico, and Central America to Brazil. Other rickettsial diseases in the United States and worldwide include rickettsiosis, ehrlichiosis, granulocytic anaplasmosis, and human monocystic ehrlichiosis (Biggs et al. 2016), but RMSF is the most important in the Western Hemisphere. Parola and coworkers (2013) reviewed numerous other diseases caused by various species of *Rickettsia* in Europe, Asia, Africa, and Australia. Transmission of *R. rickettsii* is transovarially; that is, female ticks pass the infection to their offspring. Nonetheless, the bacterium probably would not be maintained without the small mammals that serve as "amplifying" hosts (Gage et al. 1995) because *R. rickettsii* negatively affects the survival and reproduction of the ticks that carry it (McDade and Newhouse 1986; Socolovschi et al. 2009).

Numerous species of rodents and lagomorphs serve as hosts for the ticks that carry RMSF, as do the opossum (*Didelphis virginiana*), carnivores, and deer. In the eastern United States, the American dog tick (*Dermacentor variabilis*) is the primary vector. In the western United States, the usual vector is the Rocky Mountain wood tick (*D. andersoni*). The brown dog tick (*Rhipicephalus sanguineus*) is a common vector in the southwestern United States and Mexico. Several species of ticks in the Genus *Amblyomma* carry RMSF from Mexico to Argentina (Biggs et al. 2016). Ticks must remain attached 10–20 hours to transmit infection. Clinical symptoms occur 3–12 days after inoculation and may include fever, headache, skin rash, and anorexia, with eventual vascular damage, kidney failure, and central nervous system involvement (Clements 1992). About 4,500 cases of spotted-fever group rickettsiosis a year are reported in the United States. Antibiotics are successful in treating RMSF; untreated case fatalities are about 20%–25% (Drexler et al. 2016).

TULAREMIA

Tularemia occurs worldwide in the Northern Hemisphere from above the Arctic Circle to 20°N latitude. This zoonosis is also known as "rabbit fever" or "deer-fly fever" in North America and "lemming fever" in Europe and Russia. It is most commonly associated with lagomorphs, usually rabbits (Genus *Sylvilagus*) or hares (Genus *Lepus*), and is maintained primarily through the tick-lagomorph cycle. However, the causative agent, the bacterium *Francisella tularensis*, a Gram-negative coccobacillus, has been documented in over 100 mammalian species (Gage et al. 1995; Sjöstedt 2005), including voles (Genera *Microtus* and *Myodes*), beavers (*Castor canadensis*), and muskrats (*Ondatra zibethicus*). Humans can contract the disease in several ways: through direct contact with infected animals; from biting flies (Family Tabanidae) or ticks—primarily the lone star tick (*Amblyomma americanum*), American dog tick, and Rocky Mountain wood tick; or from water contaminated by urine from infected animals. The incubation period to onset of symptoms is 3–5 days. Several types of tularemia have been described; all begin with fever, chills, muscle and joint pain, and malaise and lead to respiratory involvement. The seriousness of the disease varies among individuals depending on the route of infection, bacterial load, and which of the 4 subspecies of *F. tularensis* is acquired (Hopla and Hopla 1994). Tularemia is successfully treated with antibiotics. If treated, mortality rate is <2%. Prior to antibiotics, mortality rate was 15%–50% (Pearson 2011). Tularemia infection was much more prevalent in the early 20th century. In the United States, an average of only 144 cases a year was reported from 1997–2016 (CDC 2018). There are approximately 800 cases annually in Europe.

Nonvector Zoonoses

The remaining zoonotic diseases we discuss do not involve arthropod vectors but are caused by direct transmission of viruses or prions. The first, rabies, has an ancient history, whereas the hemorrhagic fevers and prion diseases have been recognized as a concern only relatively recently.

RABIES

People have feared the ravages of rabies, a fatal encephalomyelitis disease, for over 4,000 years (see box). The causative agents of rabies and related diseases (hemorrhagic fevers; see next section) are distinct molecular strains of RNA-viruses in Family Rhabdoviridae, Genus *Lyssavirus* (the Greek *lyssa* means "madness"). Lyssaviruses occur almost worldwide in numerous mammalian hosts. Current classification recognizes 16 genetically distinct phylogroups or species (Banyard and Fooks 2017—see their table 1; Velasco-Villa et al. 2017). Of these, 14 are closely associated with bats, which carry a higher proportion of zoonotic viruses than any other mammalian order (Mortlock et al. 2015; Anthony et al. 2017; Olival et al. 2017). Unfortunately, this fact often overshadows the numerous positive ecosystem services provided by bats and associated conservation efforts (Lopez-Baucells et al. 2018; see Chapter 21).

Rabies virus is transmitted to humans most commonly through bite wounds or cuts and less commonly through mucous membranes or from inhalation. After inoculation, the virus infects the nervous system. In humans, symptoms generally appear 1–3 months after exposure, with fever, headache, and unusual tactile sensations as well as apprehension, agitation, disorientation, hypersalivation, and paralysis. Once symptoms appear, death generally occurs in 100% of cases within 7 days (Krebs et al. 1995; van de Burgwal et al. 2016). The few people known to survive rabies have suffered severe neurological impairment. Other mammalian carriers also succumb to the infection.

In addition to bats, carnivores are a prime reservoir for the maintenance and transmission of rabies worldwide, especially in developing countries. In North America, primary hosts are raccoons (*Procyon lotor*), striped skunks (*Mephitis mephitis*), red foxes (*Vulpes vulpes*), and various species of bats (Figure 27.8). In Europe, the red fox is the main vector, with the raccoon dog (*Nyctereutes procyonoides*) important in Eastern Europe (Holmala and Kauhala 2006). Rabid vampire bats in Central and South America, principally *Desmodus rotundus* (see Chapter 21), primarily affect the cattle industry, but they can also infect humans. Rabies infection in humans is relatively rare in developed countries because vaccines are almost 100% effective. In the United States, only 1 or 2 people a year die from rabies. Control-

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Historical Aspects of Rabies

People in the ancient world were well aware of rabies for millennia. Eshnunna was a city-state in ancient Mesopotamia (now in modern-day Iraq), and the 56th law of the Eshnunna Code from over 4,000 years ago concerned the owner of a *kalbum segûm*—a rabid dog. It stated, "If a dog is vicious and the authorities have brought the fact to the knowledge of its owner, [if nevertheless] he does not keep it in, it bites a man and causes [his] death, then the owner of the dog shall pay two-thirds of a mina of silver." If the dog bit and killed a slave, the fine was proportionately less. These laws were incorporated into the better-known Code of Hammurabi, created around 1760 BCE by the sixth king of Babylonia.

The earliest known surviving medical description of rabies is that of the Greek philosopher Democritus about 500 BCE. The Greek Hippocrates, born about 460 BCE and considered the "father of medicine" (physicians today take the Hippocratic Oath) also described several of the symptoms of rabies. Aristotle, writing about rabies in his *Natural History of Animals* noted, "Dogs suffer from the madness. This causes them to become very irritable and all animals they bite become diseased." Numerous other famous ancient writers also discussed rabies, including Horace and Ovid. The Romans considered the infectious agent of rabies a poison—for which the Latin word was "virus." Several early Romans wrote about rabies, including the physi-

cian Celsus, sometimes called the Roman Hippocrates. Of rabies he wrote, "The Greeks call it hydrophobia, a most wretched disease, in which the sick person is tormented at the same time with thirst and fear of water, and in which there is little hope."

Given both the fascination with and fear of rabies, possible treatments for infected people and domesticated animals were a topic of numerous writers for the next 2,000 years. The earliest report of rabies in the Americas was in 1703 in Mexico, and it was common in the American colonies by the mid-1750s. Today, developed countries experience very few cases, because preventative rabies vaccines have been available for 100 years. But in less-developed regions of the world, such as parts of Africa and Asia, rabies still claims up to 59,000 people a year. Rabies is almost always 100% fatal. But it is also 100% preventable through preexposure vaccine, postexposure treatment, controlling mammalian species that can act as vectors, and public education. The organization End Rabies Now (www.endrabiesnow.org) works to provide these services at affordable costs in developing countries.

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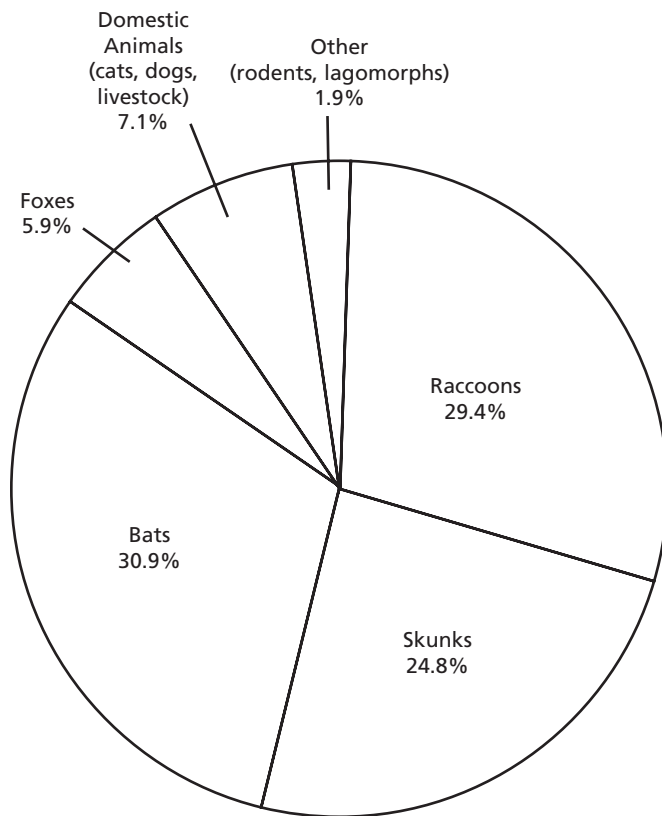
Figure 27.8 Rabies in the United States. The frequency of 5,508 cases in 2015. *Data from Centers for Disease Control and Prevention; Birhane et al. (2015).*

ling rabies, however, costs over $300 million in the United States each year, including operating diagnostic laboratories in all 50 states. It remains a significant health problem in less-developed countries (Krebs et al. 1995). Over 59,000 people a year die of rabies worldwide, primarily in Asia and Africa. Despite the close association of bats and lyssaviruses, 99% of deaths are from domestic dog bites. Vaccination could solve much of this problem (Warrell 2012; Mansfield et al. 2016). Much research is directed toward developing vaccines to reduce the incidence of rabies in wildlife populations (Banyard and Fooks 2011).

HEMORRHAGIC FEVERS

Hemorrhagic fevers encompass numerous different zoonotic viral diseases among the 9 orders and 86 currently recognized families of viruses (ICTV 2017). These negatively stranded RNA viruses are often spread directly from bats, rodents, and other mammalian hosts to humans. Lassa fever is one of a variety of human diseases caused by species in the Genus *Lassavirus*, a rhabdovirus. Lassa fever occurs in western Africa and is highly lethal. It is carried by a variety of bat species as well as the Natal multimammate rat (*Mastomys natalensis*), and there are 100,000–300,000 new cases a year and about 5,000 deaths. Argentine, Bolivian, Brazilian, and Ven-

ezuelan hemorrhagic fevers also occur (Childs et al. 1995). Untreated, these diseases are fatal in 10%–30% of cases.

Hantaviruses are caused by various species of bunyaviruses within the Genus *Orthohantavirus*. In Europe and Asia, hantaviruses cause a variety of zoonotic diseases (Jonsson et al. 2010), collectively referred to as "hemorrhagic fever with renal syndrome," in up to 200,000 people a year. First recognized in the United States in 1993, hantavirus pulmonary syndrome (HPS) occurs primarily in the Southwest and secondarily in the Midwest and Southeast. To date, it has been identified in 34 states as well as Canada, Panama, Argentina, Bolivia, Brazil, Chile, Paraguay, and Uruguay. Symptoms of HPS, like all viral hemorrhagic fevers, include fever, muscle aches, headache, and cough. Rodents are the reservoir of the virus—primarily the deer mouse, the hispid cotton rat (*Sigmodon hispidus*), white-footed mouse, and rice rat (*Oryzomys palustris*) in North America. Worldwide, more than 39 different strains of hantavirus are currently recognized. That each one is generally associated with a single rodent species suggests a long history of coevolution (Yates et al. 2002; Jonsson et al. 2010). The contagion is spread, often in dry, dusty areas, through infected rodent saliva or excreta inhaled as aerosols, or directly through broken skin (including bites) or contact with mucous membranes. Fatality rates can be 40%. Few cases of HPS have been identified compared with other zoonoses—728 in the United States as of January 2017. However, given the high mortality rates and the large number of researchers who work with wild rodents, mammalogists should be aware of the potential hazards and observe measures to minimize exposure.

Among the filoviruses, there are 5 known species in the Genus *Ebolavirus* that cause Ebola hemorrhagic fevers, 4 of which infect humans (ICTV 2017). Highly pathogenic, Ebola virus was first noted from outbreaks in 1976 in the Republic of Congo and Sudan, where they resulted in over 600 deaths. Periodic outbreaks in Africa continue to occur, and by 2015 there were 28,600 cases and 11,300 deaths (Carroll et al. 2015). The typical fever, headaches, and muscle aches begin 4–16 days after infection and progress to kidney and liver involvement. Eventually, patients can begin bleeding both internally and externally. The natural reservoirs and hosts of the Ebola virus are a variety of bat species (Plowright et al. 2015; ICTV 2017). Yang and colleagues (2019) recently reported on a new filovirus—called Menglà virus—carried by fruit bats (*Rousettus*) in China. It is closely related to the Ebola and Marburg viruses.

There potentially is a large number of emerging zoonotic viral diseases; two coronaviral diseases are Severe Acute Respiratory Syndrome (SARS) and Middle East Respiratory Syndrome (MERS). Numerous different strains of SARS are carried primarily by the Chinese horseshoe bat (*Rhinolophus sinicus*) as well as the Himalayan palm civet (*Paguma larvata*; ICTV 2017). Overall mortality is 15%, although it increases to 50% in older people. The primary

Table 27.1 Prion diseases

Disease	Natural Host
Scrapie	Sheep and goats
Transmissible mink encephalopathy (TME)	Mink
Chronic wasting disease (CWD)	Mule deer; elk
Bovine spongiform encephalopathy (BSE)*	Cattle
Kuru	Humans
Creutzfeldt-Jakob disease (CJD)	Humans
Gerstmann-Sträussler-Scheinker syndrome (GSS)	Humans
Fatal familial insomnia	Humans

Adapted from Bauerfeind et al. (2016).

*"Mad cow" disease.

Figure 27.9 Deer with visible signs of chronic wasting disease. Note the emaciated condition and lethargic posture.

carrier of MERS is the dromedary camel (*Camelus drome-darius*; Chu et al. 2018; Dudas et al. 2018); mortality rate is 60%, again increasing in older patients.

SPONGIFORM ENCEPHALOPATHIES

A very different form of infection from those discussed previously is a group of transmissible, progressive, neuro-degenerative diseases that afflict mammals (Table 27.1). The infectious agents in each are **prions**—small, modified forms of self-propagating protein. Prion diseases, or spongiform encephalopathies, are characterized by large vacuoles (open areas) that occur in the cortex and cerebellum of the brain. These produce loss of motor control, dementia, paralysis, and eventually death. One of these prion diseases is bovine spongiform encephalopathy (BSE), or "mad cow" disease. It occurs primarily in the United Kingdom; only 5 cases of BSE were reported in the United States and 22 cases in Canada from 1993 to July 2017. Since 1996, a variant form of Creutzfeldt-Jakob disease transmitted from BSE has been reported, but in only 227 people worldwide. Of more urgent concern in North America is chronic wasting disease (CWD). The only known hosts for CWD are deer (Figure 27.9)—mule deer (*Odocoileus hemio-*

nus), white-tailed deer, elk (*Cervus elaphus*), reindeer (*Rangifer tarandus*), and exotic sika deer (*Cervus nippon*). The disease was first recognized in 1978. Symptoms of infection include extreme weight loss, excessive salivation and urination, listlessness, tremors, and unusual behavior (Williams et al. 2002). Infected animals probably die within a few months. Endemic to the tricorner region of Colorado, Wyoming, and Nebraska, CWD has been documented in 24 states, 2 Canadian provinces, as well as Norway, Sweden, Finland, and Korea as of 2019.

In other infectious agents, genetic information is transmitted through nucleic acids. Besides being proteins, prions are unique disease agents because they appear to be *both* infectious and hereditary, with the disease mechanism believed to be a spontaneous change in protein structure. To date, there is no evidence of transmission to humans. However, evidence suggests that people can be infected by ingestion of prion-infected animal products (Belay et al. 2004). As might be expected, this is a very active area of current research (DeArmond and Prusiner 1995; Saunders et al. 2012; Potapov et al. 2013; Haley et al. 2018).

SUMMARY

- Many parasites are vectors of disease-causing organisms.

- Organisms that cause disease are called "etiological agents."
  - Mammalian species serve as reservoirs for many diseases that can infect humans.

- Several zoonoses are discussed, representative of viral, bacterial, protistan, platyhelminth, and arthropod parasites.

- Many of these zoonotic diseases, including rabies and hemorrhagic fevers, have a high human mortality rate.
- Throughout history, for example, plague has killed hundreds of millions of people.

- Other important zoonotic diseases have been discovered relatively recently: Lyme disease, the Ebola and hantaviruses, and protein-based prion diseases.

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DISCUSSION QUESTIONS

1. As shown in Figure 27.8 a large percentage of animals testing positive for rabies are bats. Why might this be a highly biased percentage—that is, one that is not representative of the number of bats in a given population infected with rabies?

2. Investigate current control methods for one of the zoonoses discussed in the text. Specifically, what efforts may be effective for breaking the transmission cycle, enhancing host resistance, destroying the infectious agent, or destroying the vector? You can also check the website of the Centers for Disease Control and Prevention.

3. What role does the mobility of mammalian hosts play in coevolutionary development of host-parasite assemblages? Why might host-specific relationships be more likely to develop in pocket gophers than in white-tailed deer?

4. We noted that relatively few studies have investigated the effects of parasitism on the dynamics of host populations. Discuss some of the practical difficulties in designing such a study.

5. Over 100 years ago, Robert Koch, a German medical bacteriologist, developed a set of procedural steps for identifying the causative agent of a disease. These procedures, Koch's Postulates, are still used today. Try to determine necessary steps for identifying the causative agent of a disease, then look up Koch's procedures.

Conservation

The gray wolf (*Canis lupus*; Figure 28.1A) once roamed over most of North America. Its range was reduced over the past 200 years so that it almost disappeared from the contiguous 48 states (Figure 28.1B). Extirpation of the wolf over much of its range occurred primarily through hunting and trapping, because they were considered dangerous to people and predators on livestock. In the mid-1800s, there were tens of millions of bison (*Bison bison*) throughout North America. By 1900, fewer than 500 were left in the wild, and soon the only remaining bison were in reserves. Again, people were the major factor in the dramatic decrease in numbers.

Madagascar—an island about 587,000 km² in size—is home to more species of strepsirrhine primates than any other location on Earth. During the past 50–80 years, tremendous declines in numbers have occurred for most species. Several endemic primates found only on Madagascar are on the verge of extinction (see Chapter 15), with about 80% currently listed as endangered. Disease, poaching, and habitat destruction are the causes of these severe declines in population densities. Close to 50% of the forests that are necessary for these primates have been cut down; land is used for agriculture and the wood for fires and construction. Another striking loss was that of the baiji (*Lipotes vexillifer*), or Chinese river dolphin, which has been declared extinct (Smith 2014; see Chapter 20). The growing human population along the Yangtze, and associated development and pollution, almost certainly doomed this dolphin.

About 200 mammalian species throughout the world are critically endangered; at least another 450 are endangered (Ceballos et al. 2015; IUCN 2018). The percentage of threatened species varies across mammalian orders, with groups that include large-bodied mammals having generally higher values (Figure 28.2; Bowyer et al. 2019). Additionally, data necessary to evaluate threat status are unavailable for >800 mammal species that are categorized as "data deficient" by the IUCN. Mammalian orders that include the largest numbers of species in this category are Primates (Chapter 15), Cetartiodactyla (Chapter 19), Eulipotyphla (Chapter 17), Chiroptera (Chapter 21), and Rodentia (Chapter 16).

In this chapter, we consider how we integrate knowledge about individual species, populations, community structure, and landscape

A

B
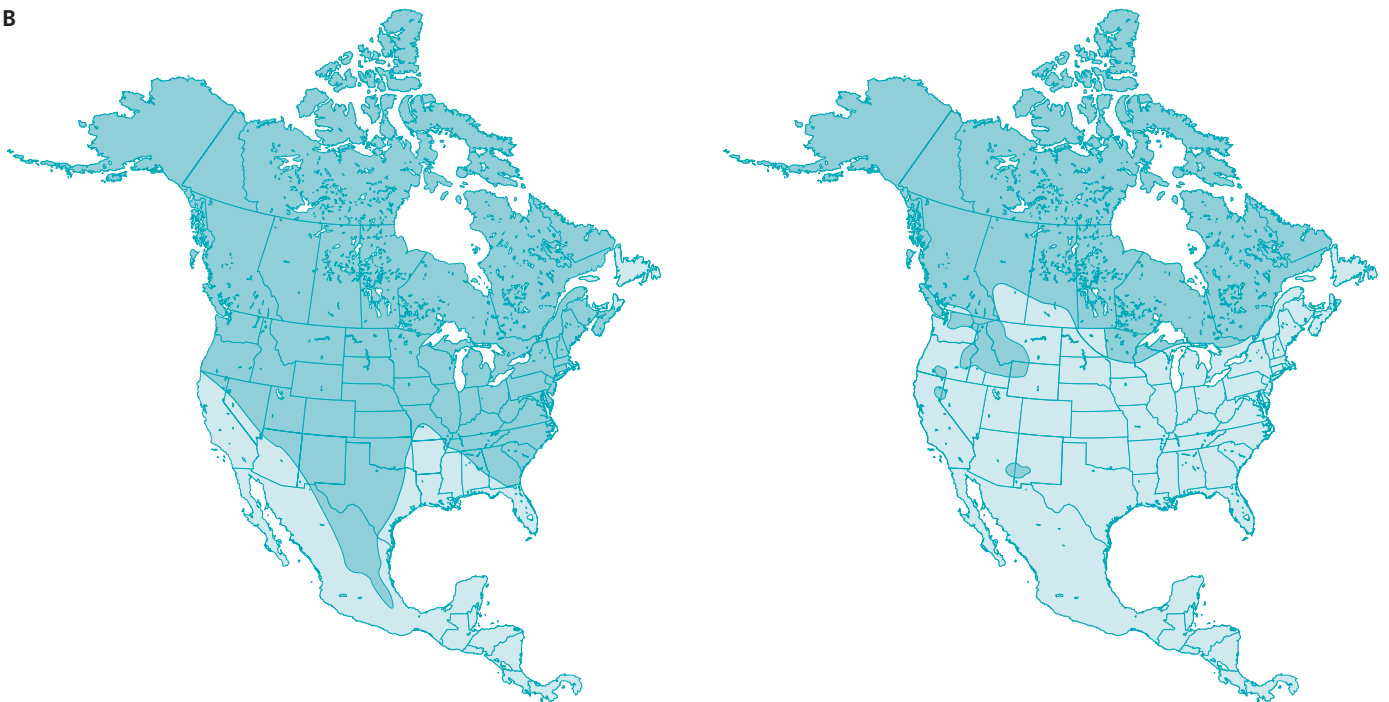
Figure 28.1 Wolves. (A) The wolf is a predator and scavenger, living alone or in packs that hunt as a unit. (**B**) Its range once encompassed much of North America (*left*) but is now restricted to the northern portion of the continent (*right*).

ecology to inform conservation strategies. What factors are responsible for the continuing decline in some mammal populations? Why are some species on the verge of extinction while others are increasing in numbers and distribution? Finally and most importantly, what are potential solutions to these problems?

Nature of the Problem

Some indigenous peoples still live in close association with their environment as their ancestors did for thousands of years. For most cultures, however, this was not the case. The land and associated resources were considered expendable commodities to enhance living standards. These commodities were overused or degraded with little consideration for sustainable development or future generations. There was little balance between the need for resource management and the needs of ever-increasing human populations.

In North America and other parts of the world, a conservation ethic was eventually born and gained momentum. Establishment of Yellowstone National Park (1872) in the American West and the Adirondack Forest Preserve in upstate New York (1885) were among the first actions taken to preserve wilderness areas on a large scale. In 1908,
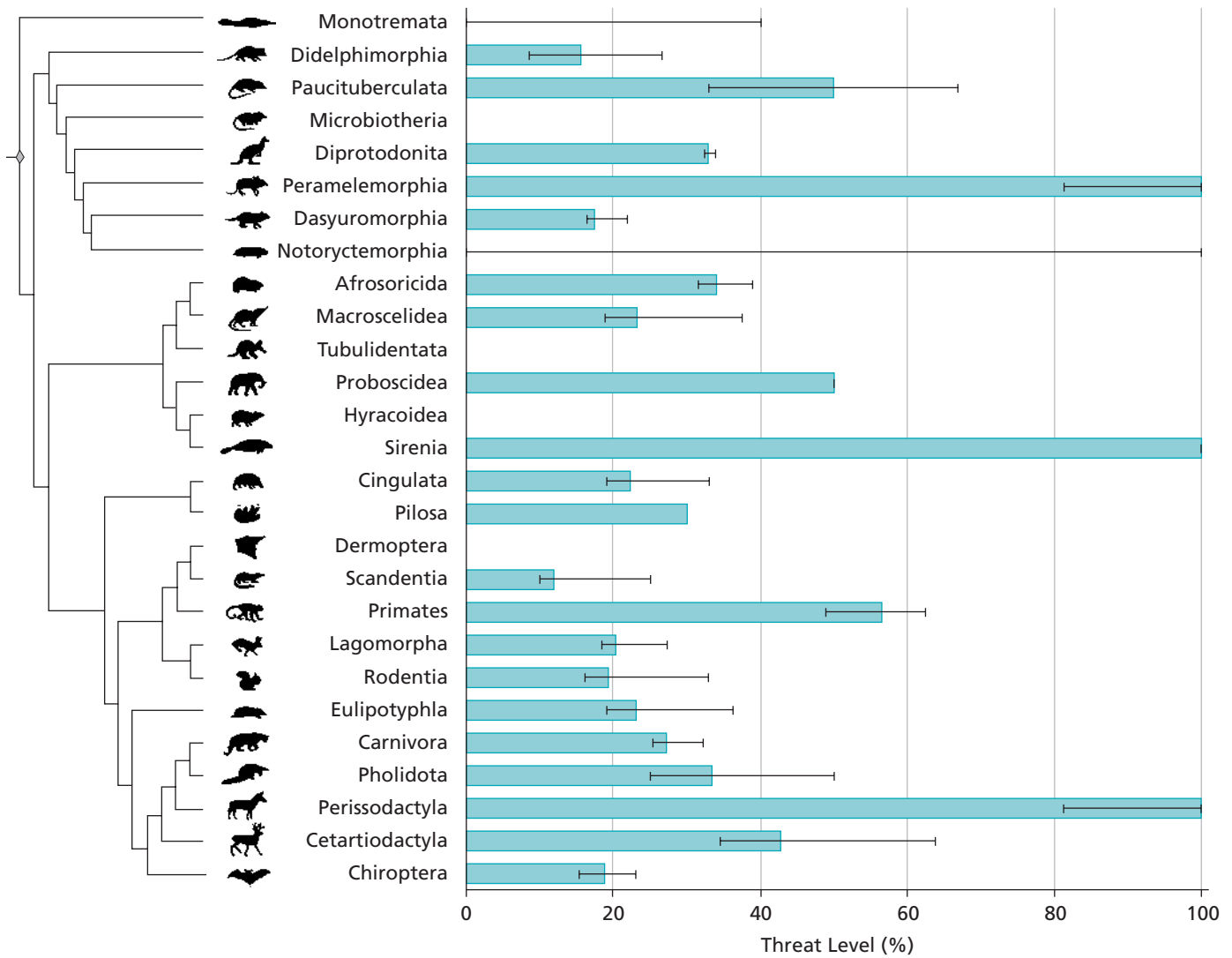
Figure 28.2 **Threat levels for 27 orders of mammals.** Percentage of species in the order that are threatened = [(VU + EN + CR + EW) / (Total – DD)] × 100. *Abbreviations*: VU = vulnerable, EN = endangered, CR = critically endangered, EW = extinct in the wild, and DD = data deficient. The error bars represent the upper and lower bounds for threat levels considering the DD species as threatened (*upper bound*) or not (*lower bound*). *Figure from Bowyer et al. (2019).*

President Theodore Roosevelt established the National Conservation Commission, headed by Gifford Pinchot. The natural resources inventory, completed by this commission, resulted in the withdrawal of more than 200 million ac (80 million ha) from further settlement. This greatly increased the numbers of national parks and forests.

The Works Progress Administration (WPA) and Civilian Conservation Corps (CCC) under President Franklin Roosevelt resulted in employment for millions during the Great Depression and a prodigious number of natural resource conservation projects throughout the United States. Other key agencies founded at this time were the Soil Conservation Service, the Natural Resources Board, and the Tennessee Valley Authority. The Wildlife Restoration Act of 1937 provided for exploration and remediation of conservation and resource problems. In the 1960s, legislative actions in the United States included the Clean Air Act

(1964), the National Wilderness Act (1964), the Endangered Species Act (1973), and the Marine Mammal Protection Act (1972), as well as bills establishing numerous additional national parks, monuments, wilderness areas, and scenic rivers. The general awakening to environmental concerns such as climate change, pollution and diminishing supplies of nonrenewable natural resources led to the first Earth Day in 1970. Many factors contribute to declining mammalian diversity, including some that are specific to various taxa and others that interact. But the need to maintain **biodiversity** on a global scale has become a concern for people in many countries.

As we entered the new millennium, threats facing terrestrial and marine mammals on a worldwide scale were apparent. Hoffmann and colleagues (2010) used an exhaustive worldwide database to document an increase in the expected rate of extinctions for mammal species. Prime causes of

biodiversity loss in terrestrial mammals were agriculture, logging, overexploitation, and invasive species. Threats are even greater for marine mammals and include pollution, accidental mortality, and harvest (Schipper et al. 2008). Although the factors that threaten mammals are diverse and differ geographically (Davidson et al. 2017), most are influenced by human activities. In response, conservation goals and strategies have been proposed on local and global scales (Schipper et al. 2008; Hoffman et al. 2011; Rondinini et al. 2011a, 2011b, 2011c). Conservation strategies entail setting priorities. Should efforts and funds be expended on individual species or broader-scale habitat conservation? Do we emphasize biodiversity hotspots or other geographical regions proactively? How do we quantify the socioeconomic cost effectiveness of efforts? How do we best coordinate conservation initiatives? How do we accommodate shifting political leadership in both undeveloped and developed countries? And of course, the specter of global climate change hangs over all conservation planning (Carwardine et al. 2008; Rondinini et al. 2011a, b; Brum et al. 2017).

HUMAN POPULATION

About 10,000 years ago, the world population was approximately 5 million people. By 1 C.E. it had grown to between 200 and 300 million. It took almost 2,000 years—until the Industrial Revolution of the 19th century—until world population reached 1 billion people. Exponential growth followed, with the second billion reached in 1930, the third billion in 1960, the fourth only 15 years later, and the fifth in 1987. As of December 2018, world population was >7.67 billion people and was increasing at 1.09% annually—about 83,000,000 people a year. Projections estimate 11 billion people by 2088 (www.worldometers.info /world-population/).

The major consequence of the ever-increasing human population is a need for additional land, water, and other resources for food production, including crops and pasture for livestock, fuel, and housing. As a result, critical habitats for numerous mammalian taxa are transformed for human use or fragmented and polluted by increased industrial, commercial, and agricultural activities. The consequences for mammals (and other wildlife) can be devastating. At least 96 species of mammals have gone extinct in the last 500 years (Burgin et al. 2018), most due to human impacts.

HABITAT DESTRUCTION AND DEGRADATION

The loss of tropical rainforest habitats is well documented and publicized. Over 45% of the original tropical rainforest of the world has been destroyed, much since 1940. Currently, 7.3 million ha (18 million ac) are lost annually to logging, burning, roads, dam building, mining, and associated activities. Most tropical soils in these forest ecosystems are

relatively poor quality because most nutrients are in the vegetation. Thus, a cleared area is productive for crops for only a few years. The land is then abandoned, and people move on to repeat the process in another nearby locale. Water runoff leaches any remaining nutrients from the soil. The secondary growth that replaces the destroyed area is a poor substitute for the original native forest. Considerable forested areas in the temperate zones have been eliminated as well. Community structure, diversity, and abundance of small mammals, primarily rodents and bats, are adversely affected by forest destruction (Fenton et al. 1998; Medellin et al. 2000). Many larger mammalian species are also severely affected by deforestation. As noted in Chapter 15 (Primates), a variety of primates occur on Madagascar, where more than 80% of the original forest has been removed, and the nearby Comoros Islands. Of the 5 endemic families of primates on Madagascar (Cheirogaleidae, Lepilemuridae, Indriidae, Lemuridae, and Daubentoniidae), 21 species are considered critically endangered, and another 48 are endangered (IUCN 2018). Similarly, many New World primates are endangered because of the loss of forest habitat, as are Old World great apes—chimpanzees (Genus *Pan*), gorillas, and orangutans (Genus *Pongo*)—due primarily to the destruction of their forest habitats. Other well-known mammalian species are negatively impacted by deforestation. Populations of giant pandas (*Ailuropoda melanoleuca*), for example, are diminished throughout much of their range in China, due in part to destruction of their bamboo forest food resource (Figure 28.3).

Many other habitats, including grasslands, prairies, savannas, and a variety of wetlands have all been usurped by humans, with negative consequences for mammal species. Most of the historical range of the American bison on the Great Plains is now used for agriculture. Several species of prairie dogs (Genus *Cynomys*) have likewise been dramatically reduced. Their habitat has been taken for agriculture and development, and they have been poisoned or shot as pests (Hoogland 2003). The drastic reduction of the black-footed ferret (*Mustela nigripes*) is directly related to declines of prairie dogs, their primary prey. In China, extensive cultivation of wetlands for rice and other grain crops led to the loss of Père David's deer (*Elaphurus davidianus*) in the wild (Figure 28.4). Likewise, Schomburgk's deer (*Rucervus schomburgki*), endemic to Thailand, was driven to extinction by the early 1900s. Several other species of deer and other larger mammals are endangered as well—usually due in large part to habitat loss.

Besides cutting down, burning, draining, or plowing under, habitat loss or depletion for mammals and other wildlife can also be caused by anthropogenic degradation, including (1) acid rain, introduction of toxic wastes, synthetic chemicals, oil spills; (2) fragmentation; and (3) invasive exotics.

The effects of acid rain are largely due to fossil fuel consumption. Emissions of sulphur dioxide and nitrogen oxides from factories and vehicles combine with water in the atmosphere to form sulphuric acid and nitric acid in pre-

Figure 28.3 Habitat destruction. Giant pandas (*Ailuropoda melanoleuca*) are declining precipitously throughout much of their range in China because of the loss of the bamboo forest habitat that is their home and source of food.

Figure 28.4 Value of captive herds. Père David's deer once roamed much of northeastern China but ceased to exist in the wild centuries ago, when its swamp habitat was taken over for cultivation. However, unlike some other animals that have been driven to extinction in such scenarios, these deer were maintained in captive herds. Although never domesticated, sizable herds of Père David's deer live in many parks and reserves today, and reintroductions have been started in China.

cipitation. Acid rain is most noticeable in the eastern United States and neighboring areas of Canada, as well as in parts of Eastern Europe and many areas of China. Degradation of forests and soils, as well as lakes, streams, and other waterways associated with acid rain undoubtedly has adverse effects on mammals—although impacts are difficult to quantify, as are effects of industrial wastes and by-products, pesticides, and polychlorinated biphenyls (PCBs).

An array of organic compounds used in agriculture or pest control persist in the environment and can negatively impact ecological integrity on a landscape scale for many decades. Carnivores, which are high on the food web, are most likely affected by biomagnification of dangerous chemicals, which become more concentrated as they move from producers to top-tier consumers. A prime example is the polar bear (*Ursus maritimus*). Spread through atmospheric and ocean circulation, organic chemicals become concentrated in arctic waters and eventually high concentrations accumulate in the tissues of polar bears (Amstrup 2003). Similarly, sea otters (*Enhydra lutris*) are susceptible to high body burdens of organochlorines as well as contamination from oil spills (Bowyer et al. 1995; Bodkin 2003; National Commission 2011). Biomagnification of chemical hazards also affects numerous species of bats worldwide, as

do many other anthropogenic hazards (Voigt and Kingston 2016). Other chemical pollutants introduced into the environment can act as **endocrine disrupters.** These chemicals mimic the effects of hormones or otherwise interfere with normal functioning of the endocrine system within an organism. Negative effects include infertility, abnormal development, and cancers (Colburn et al. 1996; WHO 2013).

Habitat fragmentation is another type of habitat modification in which a contiguous area of similar habitat is divided into smaller parcels. Fragmentation can benefit some mammalian species, especially habitat generalists and those adapted to early seral vegetation communities. For example, fragmented landscapes in much of the central Atlantic states and the Midwest have benefited white-tailed deer (*Odocoileus virginianus*) by creating interspersion of good cover with food resources. Many species, however, are negatively affected by habitat fragmentation, because of overall loss of habitat, because smaller habitat patches are less likely to support viable populations, and because of a host of habitat changes that accompany habitat fragmentation (Haddad et al. 2015). In addition, habitat fragmentation can interact synergistically with other factors such as livestock grazing, invasive species, and human exploitation to negatively affect mammals (Hobbs 2001; Peres 2001).

Roads and highways also fragment habitats, increasing edge effects and often negatively affecting local species. Experimental translocations of small mammals (white-footed mice [*Peromyscus leucopus*] and eastern chipmunks [*Tamias striatus*]) demonstrated that they were reluctant to cross road surfaces, regardless of traffic volumes (McGregor et al. 2008), and analyses of genetic patterns in wood mouse (*Apodemus sylvaticus*) populations support this contention (Ascensão et al. 2016). A review of genetic con-

sequences of roads on wildlife demonstrated pervasive effects on patterns of genetic diversity and differentiation, especially for large mammals (Holderegger and Di Giulio 2010). Furthermore, roads may facilitate access by humans, thereby opening areas to exploitation of resources and increasing the spread of exotic species. Indeed, attempts to understand the diverse ecological effects of roads and opportunities for mitigation have led to the new subdiscipline of "road ecology" (van der Ree et al. 2015). Recently, much effort has focused on creating road-crossing structures that promote movement of wildlife to reconnect populations and habitats fragmented by roadways.

Livestock grazing also can degrade grassland habitats by changing vegetation communities, helping to spread invasive plants, and altering historic fire regimes. These changes can reduce forage availability for native herbivores and alter habitat structure that provides security and thermal cover for small mammals. Riparian (riverbank) habitats, which can provide critical resources for mammals and other vertebrates, are also vulnerable to erosion from trampling.

A specialized example of habitat degradation is human activities in caves. Caves are a limited resource, and bats that use them for roosting or hibernation tend to be concentrated in them; consequently, if the caves are closed, damaged, or suffer persistent disturbances, bats are negatively affected. Bat species whose habitat has been degraded in this manner and have suffered declines in North America include the gray bat (*Myotis grisescens*), the endangered Indiana bat (*M. sodalis*), and Townsend's big-eared bat (*Corynorhinus townsendii*). Cave closures are also a factor in the decline of woodrats (*Neotoma*) in the eastern United States.

DISEASE

Numerous diseases have the potential to seriously impact wild mammal population densities. Some occur throughout broad geographic regions, whereas others are more restricted, but from a conservation standpoint all warrant management efforts to mitigate impacts. A relatively recent disease in North America—although probably not in Europe—is white nose syndrome in bats. As we noted in Chapter 21, it is caused by the cold-adapted fungus *Pseudogymnoascus destructans*, which occurs most often on the nose (see Figure 21.13) and wings. Unfortunately, this disease has spread very rapidly since it was first discovered in 2006 (see box), and in some states, bat species considered common a few years ago are now threatened or endangered. On a more positive note, researchers have found that ultraviolet light may be able to kill the fungus (Palmer et al. 2018). Also, a few individual bats may have immunity and survive from infected colonies. Nonetheless, given the low reproductive rate of bats, it will take many decades (if not centuries) for affected species to fully recover; some species may never regain their former numbers.

Equally devastating is the cancerous devil facial tumor disease (DFTD), which occurs in the Tasmanian devil (*Sarcophilus harrisii*), the largest extant carnivorous marsupial (see Chapter 10). The species is restricted to Tasmania, and inbreeding has greatly reduced genetic diversity, including the major histocompatibility complex (MHC). These are proteins on cell surfaces that are part of the immune system. Infectious disease agents are usually considered to be bacteria, viruses, parasites, fungi, or prions. Cancer is generally not considered to be contagious. Unfortunately, DFTD is (Pearse and Swift 2006; Metzger and Goff 2016). Two strains have been detected, the first in 1996, the second in 2014 (Pye et al. 2016). Because Tasmanian devils are highly aggressive and bite each other in the face during fights, DFTD spreads rapidly among populations (Hamede et al. 2012). Infected individuals usually die within a few months. Although the same chemotherapy used on humans may be a useful treatment in the future (Stammnitz et al. 2018), the population of devils has declined by 60% and continues to plummet.

As discussed in Chapter 27, prions are a type of infectious agent. **Prions** are spontaneously modified proteins that appear to be *both* infectious and hereditary. They cause several diseases that occur in mammals, primarily ungulates (see Table 27.1) as well as people. Prion diseases form large, open areas in the brain (called a "spongiform encephalopathy"). In deer, this is called chronic wasting disease (CWD). Infected individuals suffer weight loss, excessive salivation, tremors, lost motor control, paralysis, and death. In North America, CWD infects mule deer (*Odocoileus hemionus*), white-tailed deer, elk, reindeer (*Rangifer tarandus*), moose (*Alces alces*), and introduced sika deer (*Cervus nippon*). As of August 2019, CWD has been documented in at least 24 states from New York to Montana and south to Texas, and it occurs as well in Canada (Alberta and Saskatchewan), Norway, Finland, and South Korea (Centers for Disease Control and Prevention, www.cdc.gov/prions/cwd/occurrence.html). Research on how CWD is transmitted and its potential to infect people is an important area of research as well as of critical concern to deer hunters and operators of deer farms.

The African outbreaks of the Ebola virus, the resulting loss of human life, and the potential for spread to other continents have been well documented. However, humans are not the only primates that die from Ebola infections. In addition to population loss caused by poaching and **habitat destruction**, critically endangered gorillas (*Gorilla gorilla*) and endangered chimpanzees (*Pan troglodytes*) have suffered catastrophic declines because of Ebola infection (specifically, the Zaire strain, or ZEBOV). The mortality rate for infected gorillas may be 99%, and it is the leading cause of death. Susceptibility and severe population loss have been well documented for many decades (Walsh et al. 2003; Leroy et al. 2004; Bermejo et al. 2006), and large percentages of local populations continue to be lost. Only recently has vaccination of gorillas and chimpanzees against ZEBOV to protect against continued dramatic population declines appeared feasible (Warfield et al. 2014; Tsuda et al. 2015).

Finally, diseases such as rabies or hemorrhagic fevers in wild mammals can be transmitted from domestic animals.

Conservation Challenges for Bats

In addition to many of the threat factors outlined in this chapter, such as habitat degradation and human exploitation, bats are challenged by two threats that have emerged since 2000: increased wind-energy infrastructure globally and in North America, the spread of white nosed syndrome. These two factors are now the leading causes of mortalities in bats (O'Shea et al. 2016). In the United States and Canada, the number of bats killed by wind turbines during 2000–2011 was estimated to range between 0.84 and 1.7 million, but that estimate is almost certainly conservative (Arnett and Baerwald 2013), and given the rapid increase in wind energy production, that number likely increases by >500,000 annually. Tree-roosting bats that undertake long-distance seasonal migrations (e.g., hoary bats [*Lasiurus cinereus*], eastern red bats [*Lasiurus borealis*], and silver-haired bats [*Lasionycteris noctivagans*]) appear to experience the greatest mortality at wind farms. Data on bat populations are lacking from many regions of the world; nonetheless, global increases in wind-energy facilities suggest that their effects on bats are likely to continue to increase in magnitude.

White nose syndrome (WNS) is a deadly disease caused by a nonnative fungus (*Pseudogymnoascus destructans*) that was first documented on bats in New York in 2006. Since then, WNS has continued to spread west across the United States and Canada. The disease gets its common name from a white, fuzzy growth that forms on the muzzle, ears, and wings of infected bats during hibernation. This growth causes skin lesions that disrupt torpor cycles during hibernation, resulting in increased warming and depletion of stored body fat, and higher rates of evaporative water loss during winter (McGuire et al. 2018). WNS was unknown until it was detected in North American bats; subsequent research has documented the fungus on bats in Europe and Asia, although mass mortalities are not associated with infections in those regions, and evidence suggests that the fungus was introduced from Europe. WNS has infected 9 species of bats (Warnecke et al. 2012; Cryan et al. 2013) that hibernate in caves or abandoned mines throughout 24 states and 2 Canadian provinces. Three species (northern long-eared bat [*Myotis septentrionalis*], little brown bat [*Myotis lucifugus*], and tricolored bat [*Perimyotis subflavus*]) have experienced some of the largest declines.

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White-nose syndrome. The white growth associated with WNS is apparent on the muzzle of this tricolored bat.

From an economic standpoint, most research is focused in the opposite direction—on disease transmission from sympatric wildlife populations to domestics, primarily livestock (cf. Caron et al. 2013). But transmission can also be in the opposite direction. As noted by Wiethoelter and colleagues (2015:9662) "Infectious diseases at the wildlife-livestock interface threaten the health and well-being of wildlife, livestock, and human populations, and contribute to significant economic losses to each sector." Various local and global factors operate in the transmission of diseases between wild and domestic animals, including ecosystem changes, movement of people, increased demand for livestock products, and increased human population growth and resultant incursion on wildlife habitats (Martin et al. 2011; Perry et al 2013).

INVASIVE SPECIES

Exotics are species introduced by people either directly or indirectly into regions where they do not occur naturally. Also called "alien" species, they are considered **invasive species** when they spread and cause ecological changes to a native environment. Quantifying the percentage of introduced species that become invasive is difficult, but the "tens rule" is often cited (Williamson and Fitter 1996).

That is, about 10% of introduced species establish a viable population, and of these, about 10% become pests (i.e., invasive). As noted by Lever (1985:1) in his superb book on introduced mammals entitled *Naturalized Mammals of the World*, "Man is an inveterate and incorrigible meddler, never content to leave anything as he finds it but always seeking to alter and—as he sees it—to improve. . . . One of the ways in which man has sought to modify the natural environment is by the introduction of animals (principally mammals and birds) and plants throughout the world."

Increased biodiversity is usually considered a good thing for communities and ecosystems, so it may seem counterintuitive that introduction of an exotic species (increased biodiversity) is a problem. But native species of plants and animals in a region did not co-evolve with nonnative exotics. Usually, introduced species do not spread far and eventually die out, but occasionally severe unintended consequences result, to the detriment of native flora and fauna. Although an exotic may provide positive commercial or ecological benefits, this is usually not the case. Invasive mammalian species can modify habitats (deer in New Zealand; North American beavers [*Castor canadensis*] in Tierra del Fuego; camels in Australia), compete with native species (sika deer and white-tailed deer in North America; Eastern gray squirrel [*Sciurus carolinensis*] in Great Britain and Italy), potentially bring in parasites and disease (rinderpest from introduced cattle in southern Africa), or hybridize with native species (sika deer and red deer in Europe; see also Hybridization section below).

Humans have been introducing exotics for many thousands of years, deliberately or inadvertently, usually with little ecological impact. Large mammalian species, such as cervids and bovids, obviously were introduced on purpose. Fallow deer (*Dama dama*), for example, have been introduced to numerous countries in Europe, North and South America, Australia, and New Zealand. The latter two countries have been popular destinations because neither has native deer species. In New Zealand, people have introduced eight species of cervids beginning in the 1850s. The exotics competed with native fauna, over-browsed vegetation, and caused severe erosion. Many smaller mammalian species, such as brown rats (*Rattus norvegicus*), black rats (*R. rattus*), and house mice (*Mus musculus*), which were common stowaways aboard early sailing ships, found new homes throughout the world. Rats became the major vector for bubonic plague, which has killed more people worldwide than any other zoonotic disease. Again considering New Zealand, the long-term difficulty caused by introduction of the European wild rabbit (*Oryctolagus cuniculus*) has been well documented (Norbury and Jones 2015; King 2017) and serves as a cautionary tale. Examples of similar mammalian introductions—and associated extinction of native fauna—often on islands like New Zealand are too numerous to mention (see Simberloff 2013). Now, because of rapid travel worldwide, transoceanic introductions—not only of mammals, but plants, other vertebrates, invertebrates, or disease agents—are common.

Detection, assessment, control, and eradication of invasive species, including disease agents that can be used in bioterrorism, are a major concern of wildlife management agencies and other governmental organizations. Grice (2009) and Parkes and Panetta (2009) discussed stages of invasive establishment, detection, and management options for control or eradication.

SPECIES EXPLOITATION

Throughout human history, people have hunted wildlife. Long before today's deer hunters, Paleolithic peoples hunted deer for meat and to use their hides for clothing and their antlers and bones for tools (Feldhamer and McShea 2012). Subsistence hunters in many parts of the world continue to depend on big and small animals for survival. Whereas subsistence and regulated sport hunting are legitimate practices in many countries and may cause no adverse effects on mammal populations, hunting for commercial purposes has devastated populations. For example, historic market-driven harvest of beavers in North America resulted in widespread extirpations. In contrast to the current systems of regulated hunting in Europe and North America, illegal hunting or trapping (i.e., poaching) occurs in numerous countries, especially in tropical areas, and threatens diverse mammal communities (Bowyer et al. 2019). Cardillo and colleagues (2005) found significant differences among mammalian populations due to overharvest. Larger species with long-lived individuals and longer generation times were more vulnerable to extinction than were small mammals with short life spans and shorter generation times.

As noted in Chapter 20, populations of most large species of whales are endangered because of centuries of overharvest. Both baleen and toothed whales have been hunted for a variety of purposes, including meat for human and animal consumption, bone meal, spermaceti (a waxy solid used in ointments and cosmetics), and ambergris (used as a fixative in perfumes). Harvest of whales was sustainable until the advent of harpoon guns, steam-powered ships, sonar, and floating "factory" ships (see Figure 20.17). International treaties protect whales from hunting, although several nations persist in taking some whales each year and are attempting to remove the bans for some species. There are now major threats to whales from encounters with ships, entanglement in fishing nets and lines, and degradation of the ocean from pollutants and noise. Other species, especially porpoises and dolphins, also become ensnared in nets used for catching fish and other seafood and drown because they cannot reach the surface to breathe.

Sea otters are another example of an overexploited marine mammal. Beginning in the late 1700s, they were trapped in large numbers for their pelts. By the early 20th century, their numbers had greatly diminished. Recovery of sea otter populations in the northern Pacific Ocean was made possible via protection and reintroduction. The restoration of sea otters provided a natural experiment

Figure 28.5 Goeldi's marmoset (*Callimico goeldii*). This small South American primate (now included in Family Cebidae) is considered threatened, in part because of the pet trade.

that resulted in >40 years of outstanding ecological research into marine food webs, species interactions, and consequences of loss and return of mammalian apex predators (Estes 2016; see Chapter 26).

Illegal trafficking of terrestrial mammalian species has reached epidemic proportions but receives little attention compared to drug or arms trafficking. Mammals are taken illegally for bush meat, jewelry, and medicine (Felbab-Brown 2017; Nuwer 2018). Some mammal populations have significantly declined because they are captured for the pet trade, including species such as Goeldi's marmoset (*Callimico goeldii*; Figure 28.5) and Diana monkeys (*Cercopithecus diana*). Historically, numerous primate species were exported for use in medical testing and experiments because of their close evolutionary relationship to humans. Among the best-known cases of trafficking of mammal products is the poaching of elephants for ivory. In Africa and Asia, ivory is believed to have special powers; when carved and decorated, it is valued as an art object in many human societies. The limited supply of ivory, primarily from elephants and walruses (*Odobenus rosmarus*), puts a premium on this commodity. The result is extensive poaching of wild elephants, most often in Africa.

Similarly, many mammals are killed for use in traditional Chinese medicine (TCM), which has been practiced for >2,500 years and treats roughly one quarter of the world's population. TCM is growing in acceptance among Western cultures and was recently acknowledged by the World Health Organization (Cyranoski 2018). Products from many mammals are used in TCM treatments including musk obtained from musk deer (*Moschus*) and bile harvested from the gallbladders of bears (*Ursus*). The horns of rhinoceroses are valued for their use in treating a diversity of ailments, although they are also prized as sheaths and handles for knives in some Middle Eastern cultures (see Chapter 19). Such practices led to extensive poaching of the critically endangered black rhinoceros (*Diceros bicornis*) as well as the white rhinoceros (*Ceratotherium simum*). One conservation practice to save rhinoceroses involved cutting off their horns, thus removing the incentive for poachers to kill them (Figure 28.6). The efficacy of dehorning has been debated, however, and possible behavioral side effects may result from the practice (Berger et al. 1994; Berger and Cunningham 1998). Dehorning also raises questions about generating legal harvest and trade in animal products like rhino horns that might (or might not) reduce the illegal black market. Such
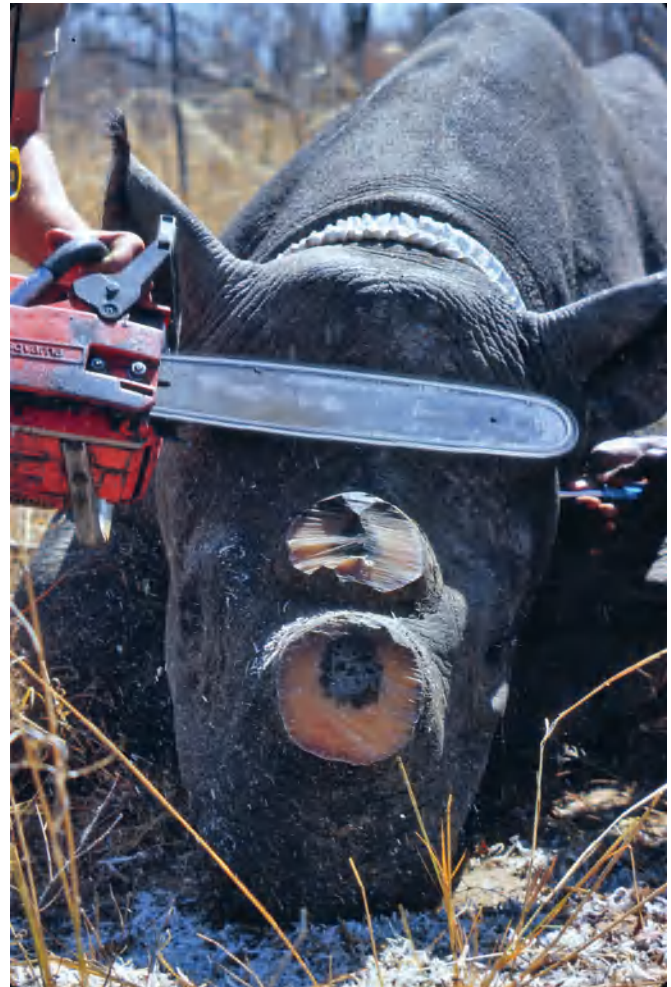
Figure 28.6 Dehorning a black rhino. Chainsaws were used to remove horns on immobilized African rhinos to reduce the incentive for poachers to kill them. Rhino horns are composed of keratin and regrow from an area of vascularized tissue near the base (visible as the dark region at the center of the horn base).

topics are hotly debated and demonstrate the interconnected nature of economics, international law, and conservation.

New tools to combat poaching are based on forensic methods, especially DNA technologies. DNA sequencing can be used to identify where body parts have been taken. It is possible to know whether elephant ivory is of African or Asian origin, and even to identify tusks in different shipments from the same individual elephant (Wasser et al. 2018). The population from which a tiger (*Panthera tigris*) was poached can now be traced with the aid of database information built on DNA analyses; for example, the Nepal Tiger Genome Project (Karmacharya et al. 2018) facilitates use of molecular forensic evidence to combat illegal trade in wildlife parts. These techniques provide some redress for poaching, but thus far have not succeeded in reducing the threat posed by this type of hunting.

ISLANDS

Isolated from nearby landmasses, islands have, through geological time, developed unique faunas and floras. The size, age, and distance of an island from either a continent or other islands can influence the number of species present through different rates of colonization and extinction (MacArthur and Wilson 1967). As noted, island ecosystems are particularly susceptible to invasive species (Simberloff 2013). Of the documented cases of mammalian extinctions since the end of the 15th century, a large percentage has been island endemics (Ehrlich and Ehrlich 1981; Reid and Miller 1989; Cooke et al. 2017; Upham 2017). Principles of island biogeography often apply to fragmented habitats as well, with isolated remnant areas functioning as terrestrial "islands."

The introduction of an exotic predator or competitor can severely harm mammalian island endemics. Such was the case for mongooses (*Herpestes javanicus*) introduced on Caribbean and Hawaiian islands for rodent control. Brown rats and black rats introduced to Madagascar, possibly as long as 2,000 years ago, decimated much of the native small rodent fauna (Goodman 1995; Brouat et al. 2014). The solenodons on Hispaniola (*Solenodon paradoxus*) and Cuba (*S. cubanus*) have both been driven nearly extinct by a combination of predation, competition from rats (Borroto-Paez and Mancina 2017), and loss of habitat. In New Zealand, bat species, most notably the long-tailed wattled bat (*Chalinolobus tuberculatus*) and the short-tailed bat (*Mystacina tuberculata*), have been almost eliminated by introduced dogs, cats, weasels (*Mustela*), and rats. Other introduced mammalian species on islands include feral pigs (*Sus scrofa*), gray squirrels, house mice, European wild rabbits, red foxes (*Vulpes vulpes*), nutria (*Myocastor coypus*), and others. Because native, island-based endemics do not have other source populations from which recolonization can occur, their demise is hastened without effective conservation measures. Eradication of invasives involves nonlethal and lethal methods. Fencing can be used to exclude pigs or goats for example. Lethal methods include trapping, shooting, and poisoning (Bull and Courchamp

2009; Parkes and Nugent 2009). New research and refined methods in vertebrate pest control are constantly being developed, including advances in fertility control.

HYBRIDIZATION

Invasive species can also impact rare native species through hybridization (Avise and Hamrick 1996; Rhymer and Simberloff 1996). Introgression can occur through intentional introduction of an exotic or through habitat modification that allows otherwise separated species to mix. An example is the interbreeding of feral house cats (*Felis catus*) with wild cats (*F. sylvestris*) in areas of Great Britain (Hubbard et al. 1992; Witzenberger and Hochkirch 2014). Attempts to reintroduce the red wolf (*Canis rufus*) in eastern North America have been compromised because of significant genetic introgression from coyotes (*C. latrans*; Wayne and Jenks 1991; vonHoldt et al. 2016; Waples et al. 2018).

Hybridization also occurs from conservation attempts that involve enhancing the stock of a rare species or subspecies by crossbreeding with a closely related taxon. **Outbreeding depression** can occur when the new stock is less adapted to local conditions. Mammalian examples of outcrossing for conservation purposes include the Florida panther (*Puma concolor coryi*), wisent, or European bison (*Bison bonasus*), and wood bison (*Bison bison athabascae*; Fergus 1991; Hostetler et al. 2013; Ochoa et al. 2017). Introgression permanently alters the original species' gene pool.

CLIMATE CHANGE

In the past 40 years, anthropogenic climate change has become the dominant conservation issue impacting all biodiversity on the planet. Scientific papers abound (a Web of Science search on "climate change" in December 2018 yielded 416,153 papers), as do hundreds of books. Very few mammals, either terrestrial or marine, are not affected to some extent by climate change and increasing temperatures, which began with the Industrial Revolution in the 19th century. Temperatures continued to increase through much of the 20th century—and the world continues to get warmer each decade. Rising temperatures affect mammalian species in a variety of ways. Large-scale effects include changes in community structure, which influence diet options, and habitat alterations, which affect spatial relations or nesting sites. Other changes occur on smaller scales and can include temperature regulation and physiological tolerances, as well as seasonal reproduction. The first mammalian extinction attributed to climate change was confirmed in 2016 (Fulton 2017). The Bramble Cay melomys (*Melomys rubicola*), a relatively large rodent species in the Family Muridae (Figure 28.7), inhabited a single, tiny island off the northwestern coast of Australia. It was repeatedly inundated as a result of sea-level rise, flooding, and coastal erosion, all attributed to climate change. This ex-

Figure 28.7 **Bramble Cay melomys (*Melomys rubicola*).** This species was declared extinct in 2016; this is the first extinction of a mammal attributed to climate change. The rodent was endemic to one island (Bramble Cay) and suffered habitat loss and degradation resulting from rising sea levels and repeated inundation of its habitat by sea water.

ample illustrates yet another class of climate change effects that could endanger island and coastal-dwelling mammals.

One of the most studied environments with regard to effects of climate change is the Arctic, home to many species of marine mammals as well as terrestrial species. Many whale and seal species inhabit Arctic waters that are already adversely affected (Moore and Huntington 2008), as are marine ecosystems worldwide (Laidre et al. 2008; Hoegh-Guldberg and Bruno 2010). Given anthropogenic climate change, the Arctic may be seasonally ice-free by 2040 or earlier (Polyak et al. 2010). Seals remain at sea, using ice flows for rest, birth, and other activities. Walrus tend to feed at the edges of sea ice, diving from perches to feed on clams and other organisms. As ice melts, there are fewer locations suitable for the seals and walruses. Perhaps the most publicized effect will be the loss of polar bears (Derocher et al. 2004; Vongraven et al. 2018). Because polar bears have elevated metabolic needs, they require a high-energy diet (Pagano et al. 2018), and melting sea ice means loss of access to their primary, high-fat food source: ringed seals (*Phoca hispida*). Polar bears obtain approximately two-thirds of their annual food intake during the six weeks that ringed seals are on ice raising pups. Growth, survival, and reproduction are all tied to access to this lipid-rich diet, and declining sea ice was the primary reason for listing polar bears in the Endangered Species Act in 2008.

A terrestrial example of the effects of a warmer climate on mammals is the American pika (*Ochotona princeps*). This cold-adapted lagomorph inhabits higher elevations in the mountainous regions of the western United States (see Chapter 16). Beginning as early as the 1930s, localized populations of pikas began to disappear. More recent surveys indicate accelerated losses of colonies (Beever et al. 2003, 2010, 2013; Waterhouse et al. 2018). Pikas are expected to move to higher elevations as climate warms to maintain the same general ecological conditions for which they are adapted. When they reach the highest elevations and can go no farther, the populations are expected to become extirpated. However, some evidence suggests that subsurface

matrices in talus slopes inhabited by pikas could provide microclimate refuges that facilitate daily and seasonal behavioral thermoregulation (Millar et al. 2016).

As climate changes, some mammalian species may benefit, particularly those that have a greater degree of flexibility in terms of physiological tolerances or the ability to change diet. However, the vast majority of mammals—like most other vertebrate and invertebrate species—are likely to suffer significant losses in species diversity, with reduced abundance and distribution of surviving taxa. Anthropogenic climate change and its impact on loss of biodiversity will be a tragic legacy for humankind.

Approaches to Solutions

Three critical factors that contribute to the demise of mammalian species are habitat loss, climate change, and the growing human population, which drives the first two factors. Mammalian species conservation is most critical precisely where growth rates of the human population are at their highest levels—in Africa, parts of Latin America, and Southeast Asia (Davidson et al. 2017). More people translates to more wildlife habitats lost to agriculture, more fossil fuels burned and accelerated climate change, more soil erosion and water pollution, and more species lost to extinction. It will be extremely difficult for any conservation programs we develop to succeed without reduction in growth of the human population and significant changes in human behavior and attitudes about resource use and conservation.

To conserve remaining wildlife, several measures are important, including continued establishment and maintenance of reserves, where native mammals and their communities and ecosystems have an opportunity to survive. Governments and nongovernmental agencies have aided in the establishment of new reserves as well as the addition of lands to existing reserves. In the United States and some other countries, sport hunters have helped provide funding for habitat acquisition and wildlife research to protect species. In conjunction with the establishment of reserves, there are many national and international laws and treaties concerning hunting, trading, exporting, and other practices that directly affect mammals and other threatened or endangered fauna. In many countries, however, law enforcement and education are lacking. Corruption also allows poaching and related activities to flourish. Many nations face increasing pressure from development, mining, or oil interests to permit exploration in ecologically fragile regions or areas that are designated reserves. Future enforcement and conservation of land and endangered species is obviously critical.

Establishment of protected areas and enforcement of laws, however, will not be sufficient to achieve long-term conservation goals for mammals. Part of effective conservation must involve stakeholders, especially because humans dominate so much of the Earth's surface. Conservation

strategies thus need to be extended to encompass working landscapes outside of protected areas and private lands, as well as consideration of the effects of conservation on local people and their livelihoods (Kareiva and Marvier 2012). Aldo Leopold recognized the critical connections between people and conservation 70 years ago when he wrote, "There are two things that interest me: the relation of people to each other, and the relation of people to land" (Meine 2010).

International treaties and agreements potentially benefit endangered mammals. The signatories and parties to the Commission on International Trade in Endangered Species (CITES) have agreed to regulate the import and export of many animal species. Trade in products such as ivory and rare furs is regulated or banned altogether. In a similar manner, starting in 1946, the International Whaling Commission (IWC) began overseeing the hunting of whales, which contributed to the virtual cessation of whale hunting. Note, however, that many nations ceased whaling simply because the whale populations had already become so greatly diminished as to make them "economically extinct." Nonetheless, several nations continue to harvest whales.

The IUCN's Species Survival Commission is a worldwide network of over 8,000 researchers, agency personnel, zoologists, botanists, and many others with expertise in plant and animal groups. For mammals, there are 30 specialist groups who advise the IUCN on listing categories for all species. In 1981, the American Association of Zoos and Aquariums created the Species Survival Program for endangered species housed in zoos and aquariums. This program covers the most critically endangered species and may involve breeding animals in captivity for eventual reintroduction or translocation to previously occupied regions. The basic components of a Species Survival Plan include designating a species in one of three categories (green, yellow, or red), based on estimated population size, and its probability of surviving 10 years, based in part on assessment of genetic diversity; appointing a coordinator for the plan; organizing a management group; facilitating cooperative agreements with other international associations; compiling a species studbook; formulating breeding and transfer plans; and compiling an animal care manual for the species. Combinations of cooperative multinational governmental efforts, numerous nongovernmental groups, and conservation organizations may help at-risk mammalian species recover former numbers and distribution. For others, however, it is most likely too late (see Ceballos et al. 2015).

Reintroduction is sometimes undertaken to reestablish populations of an extirpated species and to restore its influence on the ecosystem. Reintroduction of gray wolves into the Greater Yellowstone ecosystem in the western United States is an example of a successful reintroduction program. The reintroduction not only established a secure wolf population, but also resulted in a complex trophic cascade that affected other mammalian species including elk, grizzly bears (*Ursus arctos*), and cougars (*Puma concolor*), as well as greatly enhancing recovery of riparian vegetation (Beschta and Ripple 2016; Smith et al. 2017; Boyce 2018). Other

Figure 28.8 Black-footed ferret. Once thought to be extinct, this endangered member of the weasel family has been successfully bred in captivity and reintroduced to many parts of its former range.

mammals that have been translocated to reestablish populations include black-footed ferrets (*Mustela nigripes*; Jachowski et al. 2011; Grassel et al. 2016; Figure 28.8), elk, and woodrats (Feldhamer and Poole 2008; Peles and Wright 2008). These and many other mammals are likely to be "conservation-reliant species," meaning that they will require continued management to sustain their populations so that they do not decline and become vulnerable to extinction (Scott et al. 2010). The ultimate goal of such management is to bring the species to the point where the threats are neutralized and the species no longer requires intervention. The following case studies explain extensive efforts to do just that.

Case Studies

ARABIAN ORYX

Arabian oryx (*Oryx leucoryx*; Figure 28.9) once roamed over most of the Arabian peninsula, as far north as today's countries of Kuwait and Iraq. Overhunting and modern weapons quickly reduced numbers by the early 1900s to a few, very small, scattered populations. The last wild Arabian oryx was probably killed in 1972 (Henderson 1974). Fortunately, captive populations already existed in several locales. The first captive breeding program, with the ultimate goal of reintroduction in the wild, was established in the United States and then at several zoos in Europe (Ochoa et al. 2016). A problem faced in the initial stages of this effort was that few animals were available for breeding. Additional stocks of Arabian oryx were discovered, however, in private collections at several locations in the Arabian peninsula. Because maintaining genetic diversity is critical to the survival of reintroduced animals, a studbook—a record of all of the captive oryx, their locations, breeding status, and genealogy—was established.

Student Conservationists Who Are Making a Difference

Many professional biologists and students are members of the American Society of Mammalogists (ASM), an international organization dedicated to advancing the science and conservation of mammals. Each year, the ASM recognizes outstanding contributions of individuals to mammalian conservation with two awards. The **Aldo Leopold Award** honors a professional biologist, and the **William T. Hornaday Award** recognizes a current undergraduate or graduate student who has made significant contributions to the conservation of mammals and their habitats. Hornaday was a pioneer in conservation in the United States, who was responsible for many early wildlife protection laws and instrumental in saving the northern fur seal and the American bison from extinction.

The future of mammals relies on all of us, and especially the next generation of scientists, conservationists, and engaged citizens. What will you do to help support wildlife and wild lands? The future of mammals is in your hands.

Kristoffer Everatt from Nelson Mandela University, South Africa, was the 2018 recipient of the Hornaday Award. Kris was completing his PhD in Zoology studying the effects of poaching on the ecology of lions.

Roberto Salom-Pérez was the 2017 recipient of the Hornaday Award. Roberto is a Costa Rican biologist working on a PhD in a joint doctoral program between University of Idaho and CATIE University in Costa Rica. Roberto's work helped build a foundation for the Jaguar Corridor Initiative.

Héctor E. Ramírez-Chaves received the 2016 Hornaday Award. Héctor is a Colombian biologist who was pursuing a PhD at the University of Queensland in Australia. Héctor's work examined patterns of species richness and endemism in neotropical mammals.

José F. González-Maya was the 2015 Hornaday Award recipient. José was a PhD student at Instituto de Ecología, Universidad Nacional Autónoma de México. José is widely recognized for his contributions to mammal conservation in northern Latin America and for his work with the IUCN.

Erin Baerwald, who was pursuing a PhD at the University of Calgary, Canada, was the 2014 recipient of the Hornaday Award. Erin's research explored the causes and extent of bat fatalities related to wind-energy turbines, and she worked with industry to design operational mitigation to reduce bat fatalities.

Figure 28.9 Arabian oryx. These modest-sized ungulates, up to 1.4 m long and weighing about 55 kg, formerly inhabited much of the Arabian peninsula. Conservation efforts have succeeded in reestablishing Arabian oryx populations at several locations.

Figure 28.10 California Channel Islands fox (*Urocyon littoralis*). This island endemic has recovered from extremely low population numbers with the aid of a complex recovery strategy and has attained nearly the same numbers as recorded historically.

By the 1970s, the breeding program was successful. The first site selected for reintroduction of Arabian oryx to the wild was in Oman (Stanley-Price 1989). The area had rocky outcrops, summer high temperatures of 47°C and winter lows of 7°C, and periods of relatively lush vegetation. In 1980, release into this site occurred in stages. After confinement in small enclosures for several months, oryx were then maintained in a larger, 1-km² enclosure for 2 years. Finally, in 1982, a herd of 10 animals was released into the wild. Herds set for release consisted of specific numbers of males and females, adults and young, based on knowledge of the species and its reproductive patterns. The interest in preserving this species resulted in the establishment of captive breeding populations in Bahrain, Qatar, the United Arab Emirates, Oman, Jordan, and Saudi Arabia. Regular meetings of the Coordinating Committee for Conservation of the Arabian Oryx provided international communication, cooperation, and a united effort for more reintroductions throughout the original range of the species. After the initial reintroduction, oryx were released in Saudi Arabia (in 1990 and 1995), Israel (1997), the United Arab Emirates (2007), and Jordan (2014).

Education and local interest play vital roles in the success of such projects. The local people in Oman, the Harasis, act as wardens in protecting the oryx, as gamekeepers in managing the stock, and as aides in scientific observations of the animals. Listed as endangered from 1986 through 2008, the Arabian oryx is now categorized as vulnerable (threatened) instead of endangered (IUCN 2018), with approximately 1,220 reintroduced individuals in the wild.

CHANNEL ISLANDS FOX

The endemic Channel Islands gray fox (*Urocyon littoralis*; Figure 28.10) inhabits six of the California Channel Islands off the southern coast. There are six recognized subspecies, one on each island: *U. l. littoralis* (San Miguel Island); *U. l. santarosae* (Santa Rosa Island); *U. l. santacruzae* (Santa Cruz Island); *U. l. catalinae* (Santa Catalina Island); *U. l. dickeyi* (San Nicolas Island); and *U. l. clementae* (San Clemente Island). Four of the subspecies had severe population declines in the 1990s, in part because of low population densities associated with island endemics, as well as being further exacerbated by heavy predation by golden eagles (*Aquila chrysaetos*). These eagles initially preyed on the young of introduced feral hogs (Roemer et al. 2001) and eventually replaced native bald eagles (*Haliaeetus leucophalus*). Also, canine distemper virus (CDV) negatively impacted foxes on Santa Catalina Island. By 2004, the island fox was listed as endangered by the U.S. Fish and Wildlife Service and critically endangered by the IUCN.

Recovery efforts involved captive breeding on San Miguel in 1999 and Santa Rosa a year later with the goal of reintroducing the foxes. Reintroduction was successful, with high survival and reproduction rates in the wild. Likewise, a vaccine developed to combat CDV was successful. In addition, golden eagles were removed and relocated in northeast California. Recovery efforts also involved removal of >4,000 feral hogs, as well as reintroduction of bald eagles—which do not prey on the foxes—to discourage the return of golden eagles. Currently (IUCN 2018), the Channel Islands gray fox is listed as "near threatened" with a population of >4,000 mature individuals. Finally, with the removal of feral hogs, natural vegetation is recovering as well.

SUMMARY

- The decline of mammal species can be caused by interrelated factors:
  - Human population growth continues exponentially and places extraordinary pressure on resources.
  - Habitat destruction, for development and to provide land for agriculture for increasing human population, is a global problem.
  - Habitat degradation includes chemical alterations due to pollutants, introductions of nonnative and invasive species, and the fragmentation of habitats.
  - Overharvest of some mammalian taxa can be a significant factor threatening species with extinction; however, regulated legal harvest can benefit some populations.

- Introduced species—also called "alien," or "exotic," species—are a major threat to plant and animal communities when they spread and become invasive.

- Islands are a special case in mammal conservation.
  - Island ecosystems are vulnerable to disturbances such as introduction of exotic species.

- Hybridization can occur through introductions and can alter the gene pool of rare species.

- Anthropogenic climate change is now recognized as a primary cause of loss of fauna and flora, including mammals.
  - As temperatures rise and habitats change, some mammals may be able to adapt; many others will face—and some already face—severe threats resulting in either extinction or serious loss of abundance and distribution.

- Approaches that can help mammalian conservation include:
  - setting aside reserves, parks, and refuges to protect threatened species and their habitats;
  - involving people as stakeholders in conservation efforts and extending conservation outside of protected areas;
  - enforcing national and international laws governing harvest and trade in wildlife;
  - reintroducing extirpated species and restoring habitat with the aim of establishing sustainable populations that no longer require intervention.

SUGGESTED READINGS

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DISCUSSION QUESTIONS

1. If you were placed in charge of a reintroduction project for eastern woodrats, what considerations—logistical, population genetics, economics, community ecology, and public relations—would you need to address to maximize the chance of successful reintroduction? What criteria would you use to define a "successful" introduction?

2. One of the biggest sources of conflict facing those who work on species conservation is economic development. Can you think of examples of ways in which corporations and conservationists have been able to cooperate, providing for the interests of both groups?

3. Climate change has its major impact through warmer temperatures. What sorts of changes will occur as temperatures rise where you live? What might be the consequences for small mammals? How might these be different for large mammals?

A

ablation The destruction of tissue by electrical or chemical techniques.

abomasum The fourth and last chamber of the stomach of a ruminant, often called the "true stomach."

accidental host A host in which a parasite does not normally occur.

active dispersal Ecological dispersal events in which individuals move by terrestrial locomotion or flight.

adaptive Making an individual more fit to survive and reproduce in comparison with other individuals of the same species.

adaptive hypothermia A group of energy-conserving responses of mammals and birds characterized by the temporary abandonment of homeothermy.

adaptive radiations Diversification of many species from a common ancestor through evolutionary time.

adrenocortical hormones Hormones produced by the cortex of the adrenal gland.

age structure The proportion of individuals in a population in different age classes.

agenesis A tooth missing from the dental complement that is normally found in a species.

aggression Behavior that appears to be intended to inflict noxious stimulation or destruction on another organism.

agonistic behavior Behavior patterns used during conflict with a conspecific, including overt aggression, threats, and retreats.

agouti Hair pigments that exhibit mixtures or banding from pheomelanin and eumelanin.

albinism The condition in which all hairs are white because of an absence of pigment, caused by a genetic mutation.

alignment In molecular evolution, the definition of homologous sites within homologous DNA or protein sequences; homologous sites are typically placed in the same column (hence "aligned") of a data matrix, the rows of which are the individual sequences.

Allee effect The unfavorable consequences of undercrowding, as when individuals fail to breed because group numbers are below some critical density.

allelopathic The direct inhibition of one species by another using noxious or toxic chemicals.

Allen's rule The biogeographic "rule" that states that extremities of endothermic animals are shorter in colder climates than those of animals of the same species found in warmer climates.

alliance A long-term association between two or more individuals in which they cooperate against a third party, as in dominance interactions.

allograft A piece of tissue or an organ transferred from one individual to another individual of the same species; a successful foreign transplant.

allometric Referring to a condition in which the relative sizes of body parts change during the growth of an organism.

alloparental care Care provided for young by individuals other than the genetic parents.

allopatric Occurring in different places, usually referring to geographical separation of populations. Compare to **sympatric**.

altricial Neonates that are born in a relatively undeveloped condition (eyes closed and with minimal fur present) and require prolonged parental care; as opposed to precocial.

altruistic Behaviors that reduce the fitness of the actor while increasing the fitness of the recipient.

alveolus The socket in a jaw bone for the root(s) of a tooth.

ambergris A form of excrement of sperm whales.

ambulatory locomotion Walking; usually associated with a plantigrade foot posture.

amphibious mammals Those that spend time in both terrestrial and aquatic habitats.

amphilestids A family of triconodont mammals that was extant for about 50 million years from the Mid-Jurassic to the Early Cretaceous.

ampullary glands Small, paired accessory reproductive glands in some male mammals that contribute their products to the semen.

anal sacs A paired glandular area in carnivores that produces secretory substances.

anestrus The nonbreeding, quiescent condition of the reproductive cycle of a mammal.

angle of attack The angle of the wings of a bat relative to the ground (i.e., the horizontal plane in the direction of movement).

angora Continuously growing, long, flowing hair that may or may not be shed.

anisogamy The condition in which the female gamete (ovum) is larger than the male gamete (sperm).

annual molt A rapid process during which most hairs are replaced each year in species living at temperate and northern latitudes.

anomaluromorphs Two families of rodents in the Suborder Anomaluromorpha, the springhares and scaly-tailed flying squirrels.

Anomodontia A suborder of the Therapsida. These mammal-like amniotes were primarily herbivorous and were extinct by the Late Triassic.

anosmic Without the sense of smell.

antagonistic actions Having opposite effects, as hormones on target tissues.

anterior pituitary gland The anterior lobe of the pituitary gland.

antitragus A small fleshy process on the ventral margin of the pinnae of bats, often those that lack a tragus.

antlers Paired processes that are found only on the skull of cervids (deer); made entirely of bone, they are branched and shed yearly.

apocrine gland A type of sweat gland found on the palms of the hands and bottom of the feet of mammals; highly coiled structures located near hair follicles (sudoriferous glands).

apomorphic Characters that are derived or are of more recent origin.

appendicular skeleton The portion of the postcranial skeleton that consists of the pectoral and pelvic girdles, arms (forelimbs), and legs (hind limbs).

aquatic mammals Those that live most of the time in water but come onto land periodically for certain activities such as breeding and parturition.

arboreal Living or moving about in trees.

Archaeoceti An extinct order of whales that had features intermediate between terrestrial mammals and fully marine species.

arousal The third, or final stage, of the cycle of dormancy, characterized by shorter periods of dormancy and increases in body temperature; usually occurs in late winter.

articular bone A bone in the mandible of lower vertebrates and primitive mammals; becomes the malleus bone in the middle ear of modern mammals.

ascending ramus The upward curving branch of the jaw, which articulates with the base of the skull; the vertical portion of the dentary bone.

aspect ratio The ratio of the length of a wing to its width; short, wide wings have a low aspect ratio.

association cortex Regions of the cortex that are not specifically identifiable as sensory or motor cortex, where information is processed and integrated across the various sensory modalities.

astragalus One of the ankle bones; in ungulates, its pulley-like surface limits motion to one plane.

atlas The first cervical vertebra; it articulates with the occipital condyles of the skull anteriorly and with the axis posteriorly.

auditory bulla The auditory (hearing) vessicle with the tympanic floor derived from only the petrosal plate and ectotympanic bone.

autocorrelation As used in radiotelemetry, locations or fixes that are too close together in time—that is, dependent on the previous location.

awns The most common guard hairs on mammals, having an expanded distal end with firm tips and a weak base. They exhibit definitive growth and usually lie in one direction, giving pelage a distinctive nap.

axial skeleton The skull, vertebral column, ribs, sternum, hyoid aparatus, and laryngeal skeleton of a vertebrate.

axis The second cervical vertebra; it articulates anteriorly with the atlas.

B

background extinction The permanent loss of a species from the biosphere due to normal ecological processes associated with gradual environmental change.

baculum A penis bone found in certain mammalian orders; also called "os penis."

baleen The fringed plates of keratinized material that hang from the upper jaw of mysticete whales. Baleen grows throughout the life of an individual and is used to filter small marine organisms from the water for food.

basal metabolic rate The rate of energy conversion in a resting animal with no food in its intestine, at an ambient temperature that causes no thermal stress.

Bateman gradient The relationship between reproductive success and the number of mates obtained by each sex, which is usually a steeper slope for male than female mammals.

behavioral ecology The study of evolutionary causes and fitness consequences of behavioral decisions by animals.

Bergmann's rule The biogeographic "rule" that across groups of endotherms, smaller-bodied species and populations will occur in warmer climates and larger ones will occur in cooler climates.

bet-hedging Spreading of risk, or reducing the chance of catastrophic failure to survive and reproduce. Bet-hedging leads to more frequent but less intense bouts of reproduction.

bicornuate Type of uterus in eutherian mammals that has a single cervix and the two uterine horns fused for a part of their length (found in insectivores, most bats, primitive primates, pangolins, some carnivores, elephants, manatees, dugongs, and most ungulates).

bifid Divided into two equal parts.

bifurcated Paired; with two corresponding halves.

binomial nomenclature A system of naming species in which each species is designated with a two-word name consisting of a genus name followed by a specific epithet (e.g., *Homo sapiens*).

biodiversity The living plants, animals, and other organisms that characterize a particular region or country or the entire Earth.

biogeography The study of the patterns of distribution of organisms, including both living and extinct species.

bioinformatics The scientific discipline devoted to methods for storing, manipulating, and analyzing biological data.

biological classification The grouping of organisms into ordered categories according to their attributes, reflecting their similarities and consistent with their evolutionary descent.

biological communication An action on the part of one organism (the sender) that alters the probability of occurrence of behavior patterns in another organism (the receiver) in a fashion adaptive to either one or both of the participants.

biological community An association of interacting populations, usually defined by the nature of their interaction in the place in which they live.

biological control Using a species of organism to reduce the population density of another species in an area through parasitism or predation.

biological species concept (BSC) A definition of species in which actual or presumed reproductive isolation is the sole criterion for recognizing a species.

biome A broad ecosystem characterized by particular plant life, soil type, and climatic conditions.

bipartite A type of uterus in eutherian mammals that is almost completely divided along the median line, with a single cervical opening into the vagina (found in whales and most carnivores).

blastomeres Early cleavage cells.

blubber A thick subcutaneous layer of fat below the dermis that prevents heat loss from the body core and provides energy, insulation, and bouyancy to whales, seals, and walruses.

body hair The outer layer of hair or fur; also called "guard hair."

bootstrapping A process involving construction of replicate sets of data using the parameters of the original data to provide for subsequent analyses.

Bowman's capsule A part of the kidney; the invaginated distal portion of the uriniferous tubule, which contains the glomerulus; also called "renal capsule."

brachiation Using the forelimbs to swing from branch to branch.

brachyodont Cheekteeth with low crowns found in certain omnivorous mammals such as primates, bears, pigs, and some rodents; as opposed to hypsodont.

bradycardia A reduced heart rate associated with diving or torpor.

breasts Milk-producing glands unique to mammals; see **mammae**.

breed Individuals of the same species that have a uniform, heritable appearance.

breeding dispersal Dispersal that occurs at or between successive sites of reproduction; also known as "post-breeding dispersal."

bristles Firm, generally long hairs that exhibit angora growth, such as in the manes of horses or lions. Bristles function in communication, augmenting or accentuating facial expressions or body postures.

brown adipose tissue A special type of fat packed with mitochondria; the site of nonshivering thermogenesis in eutherian (placental) mammals.

Bruce effect In mice, the effect of a strange male, or his odor, that causes a female to abort and become receptive.

buboes Swollen lymph nodes.

bulbourethral glands In male mammals, the small paired glands that secrete mucus into the urethra at the time of sperm discharge; also called "Cowper's glands."

bunodont Low-crowned teeth that have rounded, blunt cusps used primarily for crushing.

C

caching The handling of food for the purpose of conserving it for future use; synonymous with "food-hoarding."

calcaneum The heel bone; largest and most posterior of the ankle bones.

calcar A process that extends medially from the ankle of bats and helps support the uropatagium.

calcarine fissure A shallow groove or sulcus separating convolutions of the brain; located on the internal walls of the cerebral hemispheres.

callosities Hardened, thick areas on the skin; for example, rough patches or outgrowths found on certain species of whales (same as excrescences) or ischial callosities in cercopithecid primates.

calyx A small collecting area for the renal pyramids found within the mammalian kidney.

camber Considered in cross section, the amount of curvature in a wing.

caniform Dog-like.

canine Unicuspid tooth posterior to the incisors and anterior to the premolars. If present, there is never more than one canine tooth in each quadrant.

caniniform Canine-shaped.

cannon bone Metapodials that are fused to form a single long bone in many unguligrade species.

capacitation The physiochemical changes in the spermatozoa that enable them to penetrate the protective covering of cells surrounding the oocyte.

cardiac muscle Heart muscle.

carnassial Blade-like, shearing cheekteeth found in most carnivores; the last upper premolar and the first lower molar in extant mammals; most highly developed in felids and canids.

carnivorous (carnivory) Consuming a diet of primarily animal material (characterizing meat-eating members of the Order Carnivora, marsupial dasyurids, and others).

carpal A group of bones of the forefoot, which are distal to the radius and ulna and form the wrist.

carrion Animal matter after it is dead and often decaying.

carrying capacity (*K*) The number of individuals in a population that the resources can support; the equilibrium density reached in a logistic growth curve.

castorimorphs Members of three rodent families in the Suborder Castorimorpha, beavers, kangaroo rats and mice, and pocket gophers.

caudal (vertebrae) The most posterior vertebrae; the number varies with tail length.

caudal undulation Vertical motion of the tail of a marine mammal to produce forward momentum.

cavernous sinus A network of small vessels immersed in cool venous blood located in the floor of the cranial cavity and important in heat exchange in certain carnivores and artiodactyls.

cellulolytic Cellulose-splitting enzymes.

cementum A layer of bony material that covers the roots of teeth and helps keep them in place. In many species, cementum annuli (rings) correlate with the age of the individual.

center of origin The location where a particular taxon arose.

centers of diversity Geographic regions that have a large number of species per unit area.

cerebral cortex The upper main part of the brain, consisting of two hemispheres.

cervical (vertebrae) The most anterior vertebrae, numbering seven in most mammals.

cervix The tip of the uterus that sometimes projects into the vagina.

character displacement Divergence in the characteristics of two otherwise similar species where their ranges overlap; thought to be caused by the effects of competition between the species in the area of overlap.

characters In systematic biology, all heritable features of organisms.

cheekteeth Dentition that is posterior to the canines—that is, premolars and molars.

chevron bones Found on the ventral part of the caudal vertebrae of marine mammals; sites for attachment of the muscles that depress the tail.

chorioallantoic placenta A type of placenta found in eutherians and peramelemorphians (bandicoots and bilbies) and composed of two extra-embryonic membranes: an outer chorion and an inner vascularized allantois. Highly vascularized villi enhance nutrient exchange and mechanical connection to the uterine lining.

chorionic villi Finger-like projections of the embryonic chorion that form in a chorioallantoic placenta and penetrate the endometrium; they contain capillaries of the embryo's umbilical bloodstream, which provide a high surface area for maternal-fetal exchange of nutrients and gases.

choriovitelline placenta A placenta formed by the embryonic yolk sac and chorion; found in all marsupials except bandicoots; lacks villi and has a weak mechanical connection to the uterine lining.

circadian rhythms Activity patterns with a period of about 24 hours.

circannual rhythms Seasonal activity patterns with a period of about one year.

clade A monophyletic group.

cladistic biogeography An approach to historical biogeography that seeks to reconstruct the relationships of areas based on the distribution and phylogenies of species occuring in those areas.

cladistics A process by which unweighted, nonmetric characters (traits) are used to organize organisms into taxa on the basis of joint descent from a common ancestor.

cladogram A simple representation of the branching pattern or phyletic lineage, which does not attempt to represent rates of evolutionary divergence.

clavicle The bone connecting the scapula and sternum.

claviculate Having a clavicle, the bone connecting the scapula and sternum.

claws Structures that occur at the ends of the digits, grow continuously, and consist of two parts: a lower, or ventral, subunguis, which is continuous with the pad at the end of the digit, and an upper, or dorsal, unguis.

cleidoic A type of egg laid by amniotes, including a shell that is permeable to heat and gases.

climax community The end point of a successional sequence; a community that has reached a steady state.

climbing An often arboreal locomotion involving the use of the forelimbs and hind limbs to grasp branches and other objects to move about the habitat.

cline A pattern of monotonic change in some character among individuals of a species along a geographic transect through the species' range.

clitoris The small erectile body at the anterior angle of the female vulva; homologous to the penis in the male mammal.

cloaca A chamber into which the digestive, reproductive, and urinary systems empty and from which the products of these systems leave the body.

closed-rooted Teeth that do not grow throughout the life of an individual, as opposed to open-rooted teeth.

coagulating glands Anterior prostate glands of some mammals; upon ejaculation, the secretion of these glands, when mixed with the secretions of the seminal vesicles, sometimes forms a viscous substance that constitutes a "copulatory plug" left in the vagina.

coalescent theory A stochastic model relating genetic variation in a population to the demographic history of the population.

cochlea The spirally coiled tubular cavity of the inner ear containing necessary organs for hearing.

coevolution In parasite-host relationships, reciprocal evolutionary changes that result in close association of certain species of parasites with certain host species.

cohort life table The age-specific survival and reproduction of a group of individuals of the same age, recruited into the population at the same time and followed from birth to death. Compare to **static life table**.

cold-blooded Pertaining to any animal whose body temperature remains close to that of ambient temperature; includes all animals except birds and mammals; poikilothermy, ectothermy.

colostrum A special type of protein-rich mammalian milk secreted during the first few days before and after birth of young; contains antibodies that confer the mother's immunity to various diseases to the young.

commensal(ism) Different organisms living in close association with each other; one is benefited and the other is neither benefited nor harmed; in close association with humans.

community ecology The study of the interactions among species and the effect those interactions have on both the living and nonliving features of their environment.

community structure Patterns of species composition and abundance, temporal changes in communities, and relationships among locally coexisting species.

comparative phylogeography A research program that uses genealogical concordance among multiple codistributed species to infer common historical processes that have shaped the geographic history of regional biotas.

competition The attempt of two or more organisms (or species) to use the same limited resource.

competitive exclusion principle The hypothesis that two or more species cannot coexist on a single resource that is limiting to both.

competitive release The expansion of range of one species that sometimes occurs when a competing species is removed.

composite signal In communication, a signal that is made up of more than one signal.

concealed ovulation The absence of any behavioral or morphological changes associated with estrus.

conduction The movement of heat from regions of high temperature to regions of low temperature.

Condylarthra A diverse lineage of Paleocene herbivores, a generalized ancestral order, from which arose several orders including proboscideans, sirenians, cetaceans, perissodactyls, and artiodactyls.

condyle A rounded process at the end of a bone, providing for an articulation with a socket of another bone. Occipital condyles provide articulation between the skull and the vertebral column.

cones Retinal receptors for color vision.

conservation The care, protection, and management of natural resources. The term also refers to the preservation of resources from waste and to the restoration of natural resources.

conspecific Individuals or populations of the same species.

context In communication, stimuli other than the signal that are impinging on the receiver and might alter the meaning of a signal.

continental drift The movement over geological time of the large land masses of the Earth's surface as a result of plate tectonics.

convection Movement of heat through a fluid (either liquid or gas) by mass transport in currents.

convergence (convergent) (1) The presence of a similar character for two taxa whose common ancestor lacked that character. (2) The evolution of similar morphologies by distantly related lineages that inhabit regions with similar ecological, geological, and climatic conditions.

convergent evolution The evolutionary origination of similar derived characters in species whose most recent common ancestor did not possess such characters. Derived similarities due to convergence are homoplastic, not homologous.

cooperative A behavior that benefits the recipient and that has been under se-

lection because of the positive effect on the recipient's fitness.

coprophagy Feeding upon feces (as in shrews, lagomorphs, rodents); also called "refection."

copulation plug A plug of coagulated semen formed in the vagina after copulation; found only in certain species of mammals.

core area The area of heaviest use within the home range.

corpora albicans The degenerated corpus luteum formed after the birth of the fetus or after the egg fails to implant in the uterus; also called "white bodies."

corpora cavernosa A mass of spongy tissue surrounding the male urethra within the penis.

corpus callosum The bundle of nerve fibers that integrates the left and right hemispheres of the brain in eutherian mammals.

corpus luteum An endocrine structure that forms from the remnants of the ovarian follicle after ovulation. The corpus luteum ("yellow body") secretes progestins that support the uterine lining for blastocyst implantation.

corridor route A faunal interchange where there is minimal resistance to the passage of animals between two geographic locations.

cortex (1) The structure that surrounds the medulla and makes up most of the hair shaft. (2) The area of the kidney that contains the renal corpuscles, convoluted tubules, and blood vessels.

cortisol An adrenal cortical hormone.

cosmopolitan Essentially worldwide geographic distribution.

cotyledonary placenta A type of chorioallantoic placenta in which the villi are grouped in well-shaped rosettes separated by stretches of smooth chorion.

countercurrent heat exchange An arrangement of blood vessels that allows peripheral cooling particularly of appendages and at the same time maintains an adequate blood supply without excessive heat loss.

countershading Having ventral body pelage that is more lightly colored than pelage on the dorsal surface.

cranium The upper portion of the skull including the bones that surround the brain.

crenulations A series of low humps or ridges on the back of gray whales.

crepuscular Activity concentrated near sunrise and sunset.

crown The portion of a tooth that projects above the gum, composed of enamel and dentine.

crown group A monophyletic group consisting of the all the extant descendants of a particular ancestral species, as well as the extinct lineages derived from that ancestor; for example, crown group Marsupialia includes all the descendants of the common ancestor of didelphimorphians, paucituberculates, and australidelphians.

crypsis Pattern of camouflage in which the color of the pelage matches that of the substrate; most commonly found in small, terrestrial mammals.

cryptic coloration A pelage pattern that matches the general background color of the animal's habitat.

cryptic female choice The ability of females to influence which sperm fertilize their eggs during and after copulation with multiple males; this is accomplished via diverse behavioral, physical, and chemical mechanisms.

culture A suite of specific behaviors shared among individuals in a social group that have been acquired via social learning.

cup-shaped discoid placenta The type of chorioallantoic placenta that is a variation on the discoidal arrangement of the placenta.

curation The task of assembling and maintaining a systematic collection, including a database of information associated with each specimen.

cursorial A type of locomotion in which at least a portion of the time is spent running.

cusp A projection or point on the chewing surface of a tooth. Molariform teeth have several cusps, including a protocone, metacone, and so on.

cuticle The thin, transparent, outer layer of the hair; forms a scale-like pattern on the surface.

cycle of dormancy The three phases of dormancy: entrance, period of dormancy, and arousal.

cycle sequencing A modification of the Sanger chain-termination DNA-sequencing protocol that uses the polymerase chain reaction to amplify template molecules and incorporate dideoxy nucleotides; can be performed with smaller amounts of template than are required for standard Sanger sequencing.

Cynodontia The diverse group of theriodont therapsid reptiles from which mammals evolved.

D

data matrix In phylogenetics, a summary of the variation in characters from which a phylogeny is estimated; typically, species are the rows, characters are the columns, and character states are the cell values.

deceit In communication, the sending of misleading information.

decidua The uterine mucosa in contact with the trophoblast.

deciduous placenta The type of placenta in which a portion of the uterine wall is torn away at parturition.

definitive hairs Hairs that attain a particular length and are shed and replaced periodically.

definitive host A host in which a parasite reaches sexual maturity.

Dehnel's phenomenon The observation that reduction in the body size of the common shrew (*Sorex araneus*) in autumn is accompanied by shrinkage in the size of the skull.

delayed development A condition found in some neotropical bats and characterized by a reduced growth rate of the embryo following implantation; differs from delayed fertilization in that the blastocyst implants shortly after fertilization, but development is very slow.

delayed fertilization An adaptation of certain species of hibernating bats where mating occurs in late summer or autumn. Following copulation, sperm floats free in the uterine tract during the winter; ovulation then occurs in the spring, followed by fertilization and implantation.

delayed implantation The postponement of embedding of the blastocyst in the uterine epithelium for several days or months.

deme A local population within which individuals theoretically mate more or less at random.

dendrogram A tree-like diagram of the relationships in a phylogeny.

density dependence Effects on a population that tend to change with changing population density.

dentary bone The single bone of the lower jaw or mandible in mammals.

dentine Hard, dense, calcareous (containing calcium carbonate), acellular material under the enamel in a tooth; mesodermal in origin.

dermis The part of the skin that consists of connective tissue and is vascularized; located beneath the epidermis.

destructive sampling Permanent removal of some or all tissue associated with a standard museum specimen (e.g., study skin, skeleton, spirit specimen) for biochemical analysis.

developmental biology The scientific study of ontogeny (embryonic development) encompassing both anatomical and genetic aspects.

diaphragm A muscular partition that separates the thoracic (chest) and abdominal cavities.

diastema A gap between adjacent teeth—for example, between incisors and cheekteeth in rodents, lagomorphs, artiodactyls, and perissodactyls.

didactylous Often used to refer to marsupial orders in which the digits are unfused, and each has its own skin sheath; as opposed to syndactylous.

didelphous Pertaining to the female reproductive tract of marsupials in which the uteri, oviducts, and vaginas are paired.

diestrus The final stage of the estrous cycle; cornified cells are rare and some mucus may be present in a vaginal smear; progesterone levels increase, reach a peak, and then decline.

diffuse placenta The type of chorioallantoic placenta in which the villi are expansive and distributed over the entire chorion.

digastric digestive system Consists of a complex, multichambered stomach with cellulose-digesting microorganisms that enable mammals to derive nutrients from highly fibrous foods; enables rumination, or foregut fermentation.

digitigrade A foot posture associated with cursorial locomotion; the metacarpals and metatarsals are elevated off the substrate, such that only phalanges make contact with the ground.

dilambdodont Tooth cusps and associated ridges arranged in a W-shaped pattern.

dimorphic Having more than one form, size, or appearance; usually referring to the difference between males and females of a species.

dioecious Pertaining to an organism in which male and female reproductive organs occur in different individuals.

diphyletic A group whose members are descended from two distinct lineages.

diphyodont Two sets of teeth during a lifetime. In the typical mammalian pattern, deciduous teeth ("milk," or "baby," teeth) are followed by permanent counterparts.

diprotodont Dentition in marsupials, specifically the Paucituberculata and Diprotodontia, in which the lower jaw is shortened and the single pair of lower incisors is elongated to meet the upper incisors; as opposed to polyprotodont.

discoidal placenta The type of chorioallantoic placenta in which the villi are limited to one or two disc-shaped areas.

discontinuous distribution A condition that occurs when a widespread species becomes restricted to or split into isolated geographic locations.

discrete In communication, signals that are all or none.

disease The deviation from a normal, healthy state; illness with specific causes and symptoms.

disjunct distribution A gap between the ranges of sister species or larger monophyletic groups.

disjunction The geographic isolation of sister groups.

dispersal (1) Movements that occur within the lifetime of the individual, as, for example, when it leaves its natal site. (2) Long-term movement patterns involving species in a historical zoogeographic sense.

displays Behavior patterns that convey messages from one individual to another.

disruptive coloration Patterns of stripes or colors on fur, which stand out from the basic background fur pattern.

diurnal Active primarily during daylight hours and quiescent at night.

DNA-DNA hybridization Measures similarity between strands. The DNA is heated, and the strands separate but remain intact. When the strands are allowed to cool, they collide with one another by chance, and complementary base pairs again link together. When DNA from a single species has been used, cooling results in homoduplexes. When DNA samples from two species are heated and cooled together, heteroduplexes are formed. Strands are separated and tested for thermal stability by slowly raising the temperature and assessing the mixture for DNA strand disassociation.

DNA fingerprinting A process in which DNA is cleaved by restriction enzymes, resulting in repetitive units of 16–64 base pairs in length. The fragments are run on gels and visualized by the Southern blot method. The band patterns produced in this manner are unique to each individual.

DNA sequencing The exact listing of the order of the four nucleotide bases (A [adenine], G [guanine], T [thymine], C [cytosine]) within a section of DNA.

Docodonta An order of Late Jurassic mammals known only from the remains of complex tooth and jaw fragments.

domesticated Individuals or species that are bred in captivity to benefit a human community that controls breeding, territory, and food supply.

Doppler shift The apparent change in sound or light frequency caused by movement of the source or the receiver.

dormancy A period of inactivity in which an animal allows its body temperature to approximate ambient temperature.

drag As an object moves through a medium, drag is the resistive force from friction with resulting loss of momentum. Friction results from resistance to movement of water or air and the size, shape, and speed of the object moving through it.

Dryolestidae A diverse family of early omnivorous mammals in Order Eupantotheria, which were extinct by the Mid-Cretaceous.

ductus deferens The tube that carries sperm from the epididymus to the cloaca or urethra in male mammals; also called "vas deferens."

duplex A type of uterus in which the right and left parts are completely unfused and each has a distinct cervix; found in lagomorphs, rodents, aardvarks, and hyraxes.

E

eccrine glands Sweat glands with separate ducts that lead to the body surface, through which water is forced outward. Found throughout the body, they are

important as a means of evaporative cooling in mammals.

echolocate Emit high frequency sound pulses and gain information about the surrounding environment from the returning echoes.

ecological biogeography The subdiscipline of biogeography that seeks to explain current species in terms of interaction between organisms and the ecosystems in which they occur.

ecological dispersal Movements that occur within the lifetime of the individual, as, for example, when it leaves its natal site.

ecological succession The replacement of populations in a community through a more or less regular series to a stable end point (see **climax community**).

ecology The scientific study of interactions between organisms and their environment.

economic defendability A state in which the defense of a resource yields benefits that outweigh the costs of defending it.

ecosystem The interacting biotic (living) components (i.e., the community) plus the abiotic (nonliving) components in a defined area.

ectoparasites Parasites that occur on or embedded in the body surface of their host.

ectothermy The maintenance of body temperature primarily by sources outside (*ecto*) the body; cold-blooded, poikilothermy.

edentate Without teeth. True anteaters, pangolins, and the monotremes are all edentate.

Eimer's organs The sensitive tactile organs located on the snouts of moles and desmans.

embryonic diapause A period of arrested development of an embryo at the stage of the blastocyst (70- to 100-cell stage); found in some kangaroos and wallabies.

emigration The movement of individuals out of a population.

enamel The outer portion on the crown of a tooth. Dense, acellular, and ectodermal in origin, it is the hardest, heaviest, most friction-resistant tissue in vertebrates.

endangered species Species that are likely to go extinct in all or a major portion of their range as a result of human activities and natural causes.

endemic Having a restricted geographic range.

endemism The biogeographic phenomenon in which a species or larger clade occurs only in a restricted area.

endocrine disrupters Chemical compounds that mimic the effects of hormones, facilitating or inhibiting processes normally regulated by the endocrine system; particularly important during prenatal and early postnatal development.

endocrine glands Specialized groups of cells that produce chemical substances that are released into the bloodstream.

endometrium The inner lining of the uterus in which blastocysts implant during gestation.

endoparasites Parasites that occur inside the body of their host.

endotheliochorial placenta The arrangement of the chorioallantoic placenta in which the chorion of the fetus is in direct contact with the maternal capillaries.

endothelioendothelial placenta The arrangement of the chorioallantoic placenta in which the maternal and fetal capillaries are next to each other with no connective tissue between them.

endothermy The maintenance of a relatively constant body temperature by means of heat produced from inside (*endo*) the body; emphasis is on the mechanism of body temperature regulation; homeothermy, warm-blooded.

energy The ability to do work.

entoconid One of the accessory cusps found in the lingual portion of the talonid of lower molars.

entrance In hibernation, the first stage of the cycle of dormancy; characterized by decrease in heart rate, reduction in oxygen consumption, and decrease in body temperature.

enucleate Without a nucleus. Red blood cells (erythrocytes) in adult mammals are enucleate.

enzootic A disease affecting animals only in certain areas, climates, or seasons.

epidemic A severe disease outbreak affecting many people, often over a widespread area.

epidermis The outer layer of the skin, which consists of three layers: the outer stratum corneum, the middle stratum granulosum, and the inner stratum basale.

epididymis A coiled duct that receives sperm from the seminiferous tubules of the testis and transmits them to the ductus deferens.

epipubic bones Paired bones extending anteriorly from the pelvic girdle. Seen in early reptiles, they occur in monotremes and almost all marsupials.

epitheliochorial placenta The arrangement of the chorioallantoic placenta typified by having six tissue layers, with the villi resting in pockets in the endometrium; the least modified placental condition.

epizootic Rapid, widespread disease; epidemic.

erythrocytes Red blood cells.

estivate (estivation) A period of several days or longer in summer during which a mammal allows its body temperature to approximate ambient temperature.

estradiol An important estrogen.

estrogen Any of the C_{18} class of steroid hormones, so named because of their estrus-generating properties in female mammals; produced by developing ovarian follicles, under the control of follicle-stimulating hormone. Biologically important estrogens include estradiol, estrone, and estriol.

estrous cycle A sequence of reproductive events, including hormonal, physiological, and behavioral, that typically occur at regular intervals in a female mammal; generally divided into four stages: proestrus, estrus, metestrus, and diestrus.

estrus The period during which female mammals will permit copulation (adj., "estrous"); specifically, when ovulation occurs; detected via vaginal cytology or behavior; also called "heat."

ethology The scientific study of animal behavior, especially from an evolutionary perspective.

etiologic The specific causal agent in a disease.

eumelanin Pigment mixtures that provide shades of black and brown.

Eupantotheria An order of early mammals with tribosphenic teeth from which more advanced, therian lineages evolved by the Mid to Late Cretaceous.

eusocial (eusociality) Describing a social system involving reproductive division of labor (that is, castes) and cooperative rearing of young by members of previous generations.

euthemorphic An often square molar with four major cusps (protocone, hypocone,

paracone, and metacone). Various modifications occur in different mammalian groups.

eutherian (Eutheria) Placental mammals.

evaporation The conversion of liquid into vapor.

evaporative cooling Cooling due to absorption of heat when water changes state from a liquid to a vapor. Heat is absorbed from the surface at which the change of state occurs and is carried away with the water vapor produced.

evenness The relative abundance of individuals within each species in a community.

event-based methods Analytical approaches in historical biogeography, which use phylogeny and process models to reconstruct evolutionary events such as speciation, extinction, dispersal, or vicariance within the history of a single monophyletic group.

excrescences Hardened, thick areas on the skin; rough patches or outgrowths found on certain species of whales (same as callosities).

exemplars In systematic biology, species selected for inclusion in a phylogenetic study to represent larger, presumably monophyletic groups.

exotic Nonnative; a species introduced to an area in which it does not occur naturally.

exploitation A type of competition in which organisms passively use up resources; also called "scramble competition." Contrast with **interference competition**.

exponential (growth) In reference to rates of increase (or decrease) in population size in which the number present (N) is raised to a power. Accelerating population growth as rate of change depends on the number of organisms present.

extinction The loss of a species, which is often a natural process and the ultimate fate for all species.

F

facultative An organism that is not dependent on establishing a parasitic relationship but can do so if the opportunity arises.

facultative delayed implantation A form of delayed implantation in which the delay occurs because the female is nursing a large litter or faces extreme environmental conditions.

facultative migration strategy Involves individuals that migrate some years, but do not necessarily migrate every year. Generally, when environmental conditions are mild, these individuals remain resident rather than migrate.

falcate Curved or hooked.

faunal interchange Active long-term species dispersal movements.

fecundity The number of offspring produced during a unit of time.

feliform Cat-like.

female defense polygyny A mating system in which males directly control access to females by competing with other males.

female reproductive system Reproductive organs of females consisting of a pair of ovaries, a pair of oviducts, one or two enlarged uteri, a vagina, and a cervix.

fence effect The tendency of populations to reach high densities when surrounded by a fence or natural barrier.

fenestrated Describing an area of a skull with light, feathery, lattice-like bone structure.

feral Wild or free-ranging individuals or populations that were once domesticated.

fertilization The penetration of an egg by a sperm, with the subsequent combination of paternal and maternal DNA.

field metabolic rate The rate of energy use in an animal engaging in normal activities under natural conditions.

filiform Thin and thread-like in shape.

filter route A faunal interchange where only certain species move between land masses because of some type of barrier.

fimbriation (fimbriated) Having stiff fringe of hairs between the toes to aid species, such as shrews, in locomotion.

flagging behavior Alarm signaling, as with the use of the tail or rump patch.

flehmen A retraction of the upper lip exhibited soon after contacting an odor source of interest, which brings air and chemicals into the mouth and the openings of the vomeronasal organ.

flight (powered) Volant locomotion in the aerial environment through the use of beating wings.

fluctuating asymmetry (FA) Random deviations from bilateral symmetry in paired traits, such as horns.

fluke The horizontal, dorsoventrally flattened distal end of a whale's tail.

focal animal sampling The recording of all occurrences of specified behavior pat-

terns or interactions of a selected individual or individuals during a period of prescribed length.

folivorous (folivory) Consuming a diet of leaves and stems (characterizing koalas, gliders, ringtail possums, sloths, pandas, dermopterans, various megachiropterans, primates, and rodents).

follicle A small cavity or pit. In the reproductive system of mammals a group of follicles enclose a single egg immediately under the surface of the ovary.

follicle-stimulating hormone (FSH) A hormone produced by the anterior pituitary gland that stimulates development of ovarian follicles and secretion of estrogens; stimulates spermatogenesis, Leydig cell development, and testosterone production in males.

food-hoarding The handling of food for the purpose of conserving it for future use; synonymous with "caching" or "storing."

foramen magnum An opening at the base of the skull that provides the pathway for the spinal cord to enter the brain.

foramina Openings in bone—for example, in the facial region for the eyes and at the base of the skull for the spinal cord.

foregut fermentation The digestive process characterized by mammals that possess a complex, multichambered stomach with cellulose-digesting microorganisms that enable them to derive nutrients from highly fibrous foods. Also called "rumination"; requires digastric digestive system.

fossorial Digging under the ground surface to find food or create shelter.

frugivorous (frugivory) Consuming a diet of fruit (characterizing pteropodid and phyllostomid bats, phalangerids, and primates such as indrids, lorisids, cercopithecids, colobines, and pongids).

functionally referential Signals that communicate information about ongoing external events or objects apart from the sender.

functional response The change in the rate of consumption of prey by a predatory species as a result of a change in the density of its prey. Compare to **numerical response**.

fundamental niche The full range of conditions and resources in which the species can maintain a viable population. Compare to **realized niche**.

fur The most common underhair; consists of closely spaced, fine, short hairs.

fusiform A cigar- or torpedo-shaped body form tapered at both ends.

G

gait A pattern of regular oscillations of the legs in the course of forward movement.

gamete A mature, haploid, functional sex cell (egg or sperm) capable of uniting with the alternate sex cell to form a zygote.

general adaptation syndrome (GAS) The situation in which nonspecific stressors, such as heat, cold, or defeat in a fight, produce a specific physiological response.

gene tree A branching diagram depicting the mutation history of alleles at a locus.

genome All the hereditary information encoded in the DNA or RNA or a cell or organism, including both genes and nongenic sequences.

geographic information systems (GIS) Computer software programs used to store and manipulate geographic information.

gestation The length of time from fertilization until birth of the fetus.

ghost lineage The existence of a clade prior to the earliest occurrence of its fossil representatives, inferred from the oldest fossils of its sister group.

glans penis The head or distal end of the penis.

gliding The aerial locomotion involving the use of a membrane (patagium) to provide lift, but without any active power.

glissant The gliding locomotion found in colugos, "flying" squirrels, and other species where patagia provide extended surface areas.

global positioning system (GPS) A system that uses satellite-based radio signals and a receiver to obtain the latitude and longitude at any location on the Earth's surface.

Gloger's rule The biogeographic "rule" that states, "Races in warm and humid areas are more heavily pigmented than those in cool and dry areas."

glomerulus The minute, coiled mass of capillaries within a Bowman's capsule of the mammalian kidney.

graded In communication, signals that are analog or continuously varying.

granivorous (granivory) Consuming a diet of primarily fruits, nuts, and seeds.

graviportal A mode of locomotion in large species in which the limbs are straight, pillar-like, and adapted to support great mass. Species such as elephants and hippopotamuses have their legs directly under the body, sacrificing agility for support.

group selection Selection that operates at the level of genetic lineages (groups).

guano Bat fecal droppings that often accumulate in large amounts where colonies roost.

guard hair The outer layer of hair or fur (overhair) comprised of three types: awns, bristles, and spines.

guilds Groups of species that exploit a common resource base in a similar fashion.

gummivorous (gumivory) Consuming a diet of exudates from plants such as resins, sap, or gum (characterizing marmosets, mouse lemurs, petaurid gliders, and Leadbeater's possum).

H

habitat An area that contains the necessary resources, including food, water, and cover, and promotes residency through survival and reproduction by a species.

habitat destruction A condition in which the expanding human population exerts strong negative effects on a variety of habitats in an effort to meet agricultural and industrial needs. Habitats are altered such that some or all of the original fauna and flora can no longer exist in the community.

habitat fragmentation A condition in which the continuous area of similar habitat is reduced and divided into smaller sections because of roads, fields, and towns.

hair Cylindrical outgrowths from the epidermis composed of cornified epithelial cells; a unique feature of mammals.

hair horns The "horns" of rhinoceroses. These consist of agglutinated, kertinized fibers similar to hairs that develop above the nasal bones. They are not homologous to the true horns of bovids.

hallux The first (most medial) digit of the pes (hind foot); the big toe in humans.

handicap hypothesis In sexual selection, the hypothesis that apparently deleteri-

ous sexual ornaments possessed by males are attractive to females because they indicate that the males bearing them have such vigor that they can survive even with the handicap.

haplotypes Alleles at a locus defined by their DNA sequences or restriction site maps.

harmonics Integral multiples of a fundamental sound frequency.

heat The period during which female mammals will permit copulation (adj., "estrous"); specifically, when ovulation occurs; detected via vaginal cytology or behavior; also called "estrus."

heat load The sum of the environmental and metabolic heat gain.

heimal threshold The depth of snow required to insulate the subnivean (below the snow) environment against fluctuating environmental temperatures.

hematocrit The number of red blood cells per unit volume of blood.

hemochorial placenta The arrangement of the chorioallantoic placenta that lacks maternal epithelium; villi are in direct contact with the maternal blood supply.

hemoendothelial placenta The arrangement of the chorioallantoic placenta in which the fetal capillaries are literally bathed in the maternal blood supply. This arrangement shows the greatest destruction of placental tissues and least separation of fetal and maternal bloodstreams.

herbivorous (herbivory) Animals that consume plant material.

heterodont Teeth that vary in form and function and generally include incisors, canines, premolars, and molars.

heterothermic (heterothermy) Refers to animals that at times exhibit high and well-regulated body temperatures (homeothermic) and at other times exhibit body temperatures that are close to that of the environment (ectothermic).

hibernation A form of adaptive hypothermia characterized by profound dormancy in which the animal remains at a body temperature ranging from 2° to 5°C for periods of weeks during the winter season.

hindgut fermentation A process in which food is completely digested in the stomach and passes to the large intestine and cecum, where microorganisms ferment

the ingested cellulose; also called a "monogastric system."

historical biogeography The subdiscipline of biogeography that deals with past changes in species ranges, as well as the causes and evolutionary consequences of those changes.

homeothermy The regulation of a constant body temperature by physiological means regardless of external temperature; endothermy, warm-blooded.

home range The area in which an animal spends most of its time engaged in normal activities.

homing The process of returning to a home range, nest site, or den.

homodont Teeth that do not vary in form and function; often peg-like in structure, as in toothed whales and some xenarthrans.

homologous In evolutionary biology, an adjective that applies to the same character in two or more organisms or species and was inherited from a common ancestor that also had the character.

homology In Darwinian terms, similarity of specific traits among species due to common ancestry.

homoplasy In systematic biology, a term that describes the occurence of similar, derived characters in two species due to convergent evolution; a mistaken hypothesis of homology.

hooves Large masses of keratin (the unguis) completely surrounding the subunguis; found in the ungulates (perissodactyls and artiodactyls); a specialized variation of claws.

hormones Chemical substances that are released into the bloodstream or into body fluids from endocrine glands and that affect target tissues.

horns Processes in bovids, formed from an inner core of bone, that extend from the frontal bone of the cranium, are covered by a sheath of keratinized material, and are derived from the epidermis.

hydric Wetland habitats; as opposed to xeric (very dry) areas.

hyoid apparatus A series of bones located in the upper throat region that are modified remnants of the gill arches in ancestral fish. The hyoid supports the base of the tongue and larynx.

hypocone A cusp that is posterior to the protocone and lingual (toward the tongue) in upper molars. It is labial (toward the cheek) in lower molars (where it is called a "hypoconid"). The addition of this cusp often forms quadritubercular molars.

hypoconid One of the accessory cusps found in the labial portion of the talonid of lower molars.

hypoconulid One of the accessory cusps found in the posterior portion of the talonid of lower molars.

hypodermis The innermost layer of the integument, consisting of fatty tissue; the base of each hair follicle is located in this layer, along with vascular tissues, parts of sweat glands, and portions of the dermal sensory receptors.

hypothalamic-pituitary portal system The vascular connection between the hypothalamus and pituitary gland.

hypothalamus The part of the midbrain, located below the thalamus, that contains collections of neuron cell bodies (nuclei). Sensory input to the hypothalamus comes from other brain regions and from cells within the hypothalamus that monitor conditions in blood that passes through the region. The hypothalamus is the key brain region for body homeostasis; it is the mammalian "thermostat."

hypothermia A conditon in which the temperature of the body is subnormal.

hypsodont Cheekteeth with high crowns, often with complex folding ridges; as opposed to brachyodont.

hystricognathous A mandible in certain rodents; in ventral view, the angular process is lateral to the alveolus of the incisor (as opposed to sciurognathus).

hystricomorph Rodents in which the infraorbital foramen is greatly enlarged.

I

ideal free distribution The distribution of individuals among resource patches of different quality, which equalizes the net rate of gain of each individual; assumes that organisms are free to move and have complete knowledge about patch quality.

imbricate Overlapping, as in fish scales, for example.

immigration The movement of individuals into a population.

implantation The attachment of the embryo to the uterine wall of the female mammal.

inbreeding depression The reduced reproductive success and survival of offspring from closely related parents compared to offspring of unrelated parents. It is caused by increased homozygosity of the inbred offspring and the resulting expression of deleterious recessive alleles.

incisors Usually unicuspid teeth anterior to the canines that are used for cutting or gnawing.

inclusive fitness The sum of an individual's direct and indirect fitness. Direct fitness is measured by reproductive success of one's own offspring (descendant relatives), and indirect fitness is measured by the reproductive success of one's nondescendant relatives.

incrassated Thickened or swollen.

incus The second of the three bones of the middle ear in mammals (ossicles); derived from the quadrate bone.

indicator models Models of sexual selection that assume that the trait favored by females in some way indicates male fitness.

induced ovulation Ovulation that occurs within a few hours following copulation; the act of copulation serves as a trigger for ovulation.

infanticide The killing of young.

infrasound Sound frequencies of less than 20 Hz.

insectivorous (insectivory) Consuming a diet of insects, other small arthropods, or worms.

insensible water loss The mechanism by which water is lost by diffusion through the skin and from the surfaces of the respiratory tract; also called "transpirational water loss."

in situ hybridization Experimental procedure in which nucleic acid probes are chemically bound to chromosome spreads such that specific DNA sequences can be localized on the chromosomes.

integument The outer boundary layer between an animal and its environment; the skin.

interference competition A form of competition in which organisms defend or otherwise control limited resources; also called "contest competition." Contrast with **exploitation competition**.

interleukin Any of several compounds that are produced by lymphocytes or monocytes and function especially in regulation of the immune system.

internally referential In communication, signals that contain information about the sender.

intersexual selection The selection of characteristics of one sex (usually males) based on mate choices made by members of the other sex (usually females).

intrasexual selection Selection favoring characteristics of the sexes based on competition among individuals of the same sex (usually males) for access to members of the other sex (usually females).

introgression The mixing of gene pools.

invasive species A nonnative species introduced into a new area by humans, which damages the native ecosystem.

island rule Posits that large mammals on islands tend to be smaller than their mainland relatives, whereas small mammals on islands tend to be larger than their mainland relatives.

iteroparity (iteroparous) The production of offspring by an organism in successive bouts. Compare to **semelparity (semelparous)**.

K

karyotype The characteristic number and shapes of the chromosomes of a species.

keratin A tough, fibrous scleroprotein found in epidermal tissues (in hard structures such as hair and hooves, for example).

keratinized Made of keratin.

key adaptation A novel trait that evolved in the ancestor of a monophyletic group and facilitated the evolutionary diversification of that group.

keystone guild A group of species exploiting a common resource and controlling the distribution and abundance of many other members of the community.

keystone species Species that control the distribution and abundance of many other members of the community, often by limiting a particular species of prey or by manipulating the vegetation community.

kidneys Paired, bean-shaped structures in mammals located within the dorsal part of the abdominal cavity; the principal organ that regulates the volume and composition of the internal fluid environment.

kin selection The selection of genes due to an individual's assisting the survival and reproduction of nondescendant relatives that possess the same genes by common descent.

kinship The possession of a common ancestor in the not-too-distant past.

kleptoparasitism A type of feeding accomplished by stealing food from another individual; literally, parasitism by theft.

krill Small marine organisms fed on by baleen whales.

K-selection Selection favoring slow rates of reproduction and growth, characteristics that are adapted to stable, predictable habitats. Compare to **r-selection**.

L

labia majora Two large lateral folds of skin that border and cover the vulva area.

labia minora Two lateral folds of skin that cover the vaginal opening and are largely covered by the labia majora.

lactation The production of milk by mammary glands.

lactogenic hormone A hormone—namely, prolactin (PRL)—that is produced by the anterior lobe of the pituitary gland, induces lactation, and maintains the corpora lutea in a functioning state in mammals (originally called "luteotropic hormone" [LTH]).

lactose A 12-carbon sugar present in the milk of mammals.

lambdoidal crest A bony ridge at the rear of the cranium.

laminae Ridges on teeth that may have distinct cusps.

laminar flow The smooth movement of air or water over a surface with a minimum of turbulence.

landscape ecology The study of the distribution of individuals, populations, and communities across different levels of spatial scale.

laparoscopy The use of fiber optic techniques to perform a laparotomy.

laparotomy An internal examination of the female reproductive tract to determine the condition of the ovaries and uterus.

law of the minimum The idea that only a single factor limits the growth of a population at any one time.

lek An area used, usually consistently, for communal courtship displays.

lesion Wound; an area of tissue destroyed via electrical or chemical means.

Leydig cells The interstitial cells between the seminiferous tubules in the testes, which produce androgens in response to luteinizing hormone secreted by the anterior pituitary gland.

life-history traits Traits including size at birth, litter size, age at maturity, degree of parental care and others that directly influence fecundity and survival.

life table A summary by age of the survivorship and fecundity of individuals in a population.

lift The upward force created as air moves over the top of a wing.

locomotion A form of movement. Running, jumping, gliding, swimming, or flying are all types of locomotion that occur in various mammals.

logistic equation The mathematical expression for a sigmoid (S-shaped) growth curve in which the rate of increase decreases in linear fashion as population size increases.

loop of Henle A long, thin-walled kidney tubule present only in mammals and some birds. The concentrating ability of the mammalian kidney is closely related to the length of the loops of Henle and collecting ducts.

lophodont An occlusal pattern in which the cusps of cheekteeth form a series of continuous, transverse ridges, or lophs, as in elephants.

lophs Elongated ridges formed by the fusion of tooth cusps.

lower critical temperature The temperature at which an animal must increase its metabolic rate to balance heat loss.

lumbar (vertebrae) The lower back vertebrae that number from four to seven in mammals; sometimes partially or entirely fused.

luteinizing hormone (LH) A hormone produced by the anterior pituitary gland that stimulates corpora lutea development and production of progesterone in females.

lysozyme A crystalline enzyme-like protein that is present in tears, saliva, milk, and many other animal fluids and is able to destroy bacteria by disintegration.

M

macroecology The patterns of body mass, population density, and geographic range at a continental scale.

macroparasites Parasites that are larger and have longer generation times than microparasites; they usually do not reproduce entirely within or on the host.

male dominance polygyny A mating system in which males compete and acquire dominance ranks that influence their access to females, with higher-ranking males obtaining more mates.

male reproductive system Reproductive organs of males consisting of paired testes, paired accessory glands, a duct system, and a copulatory organ.

malleus The first of the three bones of the middle ear in mammals (ossicles). The "hammer" connects the tympanic membrane (eardrum) and the incus; derived from the reptilian articular bone.

mammae Milk-producing glands unique to mammals (sing., "mamma"); see **breasts**.

mammalogy The study of animals that constitute Class Mammalia, a taxonomic group of vertebrates in the Kingdom Animalia.

mammals All species belonging to the taxon Mammalia.

mammary glands (mammae) Milk-producing, hormone-mediated glands, unique to mammals; similar to apocrine glands in development and structure.

mandible The lower jaw, consisting of paired dentary bones that meet anteriorly at the mandibular symphysis and articulate posteriorly with the squamosal bones of the cranium to form the jaw joint.

mandibular fossa A part of the cranium with which the mandible (lower jaw) articulates.

manubrium The long, lever-type arm of the malleus that attaches to the tympanic membrane (eardrum); also the anterior (uppermost) portion of the sternum.

manus The forefoot; together, the carpals, metacarpals, and phalanges.

marine mammals Mammals that spend their entire lives in the ocean and never come onto land.

mark-recapture study An experimental procedure for studying the characteristics of wild populations; individuals are captured, marked, released, and (perhaps) captured again at a later time. Recapture rates can be used in conjunction with other data and assumptions to estimate population parameters.

marsupium An external pouch formed by folds of skin in the abdominal wall. Found in many marsupials and in echidnas, the marsupium encloses mammary glands and serves as an incubation chamber.

masseter One of three main masticatory muscles of mammals that functions to close the mouth by raising the mandible. Pronounced in herbivorous mammals, the masseter aids with the horizontal movement of the jaw.

mass extinction The sudden, catastrophic, and simultaneous extinction of many species on a global scale.

mass-specific metabolic rate The rate of energy necessary per gram of body mass; refers to energy demands within the tissues of an animal.

maxilla One of a pair of large bones that form part of the upper jaw, carrying teeth; it also forms portions of the rostrum, hard palate, and zygomatic arch.

meaning In communication, how the recipient of a message interprets that message.

medulla (1) The central portion or shaft of the hair. (2) The internal area of the kidney divided into triangular wedges called "renal pyramids."

melanin A group of brown pigments produced in certain dermal chromatophores (melanophores). These pigments absorb ultraviolet radiation. They are injected into growing hair cells to give pelages their distinctive colors.

melanism A condition in which an animal is generally all black, due to a genetic mutation.

meroblastic The type of egg cleavage in reptiles, birds, and monotremes in which only part of the cytoplasm is cleaved due to a large amount of yolk.

mesaxonic Having a weight-bearing axis of a limb pass through the third digit, as in perissodactyls.

mesial drift Molariform dentition that is replaced horizontally rather than vertically. As anterior teeth wear out, they move forward and are replaced from the rear of the jaw by posterior teeth; occurs in macropodids, elephants, and manatees.

message In communication, information about the state of the sender.

metabolic rate Energy expenditure measured in kilojoules per day.

metabolic water Water produced by aerobic catabolism of food; also known as "oxidation water."

metacone A cusp that is posterior to the protocone. It is labial (toward the cheek) in upper molars and lingual (toward the tongue) in lower molars (where it is called a "metaconid").

metameric Segmented; repeated body units.

metapodials A general term for both the metacarpal and the metatarsal bones.

metapopulation A set of local populations, or demes, linked together via dispersal.

metatherian (Metatheria) Marsupial mammals.

metestrus The third stage of the estrous cycle in which leucocytes appear among the cornified epithelial cells in a vaginal smear, corpora lutea are fully formed, and progesterone levels are high.

microfauna Symbiotic ciliated protozoans and bacteria in the forestomach or cecum of herbivores, which break down cellulose and other plant materials.

microparasites Parasites that are microscopic and have rapid regeneration times generally within the host.

microsatellite markers Tandem repeats of short DNA sequences, usually multiples of two to four bases.

migration A persistent movement across different habitats in response to seasonal changes in resource availability and quality. In mammals, these typically are round-trip movements, and the individual returns to the same breeding and wintering areas each year.

milk A fluid containing water, fat, and protein that is produced by the mammary glands of mammals and provides postnatal nourishment to young offspring.

mitochondrial DNA (mtDNA) All or part of the circular DNA molecules found within mitochondria. In mammals, mtDNA is just over 16,000 bases long and contains 2 ribosomal RNA genes, 13 protein-coding genes, 22 transfer RNA genes, and one large non-coding ("control") region.

molar A nondeciduous cheektooth that has multiple cusps and is posterior to the premolars.

molecular biology Study of the structure and function of biochemical compounds in the context of cellular processes.

molecular clock A model of sequence evolution for a particular gene or pro-

tein in which the rate of substitution is the same in all lineages of organisms of a particular group.

molecular cytogenetics Application of molecular methods, particularly in-situ hybridization of nucleic acids, to the study of chromosomes.

molting The seasonal replacement of definitive hair and sometimes angora hair.

monestrous Having a single estrous period or heat each year.

monogamy (monogamous) A mating system in which a single male and female pair for some period of time and share in the rearing of offspring.

monogastric system A digestive system in which food is completely digested in the stomach and passes to the large intestine and cecum, where microorganisms ferment the ingested cellulose; required for hindgut fermentation.

monophyletic group (clade) A group consisting of an ancestral species, all of its descendants, and nothing else.

monotypic Having only one member in the next lower taxon. For example, the aardvark is a monotypic order. It has only one family, one genus in that family, and one species in the genus.

monozygotic polyembryony Reproductive process in some armadillos in which a single zygote splits into separate zygotes and forms several identical embryos all of the same sex.

morphology The scientific study of anatomy.

morphometrics The measurement of the characteristics of organisms, including such features as the skeleton, pelage, antlers, or horns.

mortality Death, usually expressed as a rate.

mosaic evolution A pattern wherein the different components of an existing structure evolved at different rates through evolutionary time.

multimodal In communication, signals that involve the use of two or more sensory modalities

multiparous Describing a female that has had several litters or young; often with evidence of placental scars of different ages.

Multituberculata An order of herbivorous mammals with large lower incisors and molariform teeth with numerous large cusps. It existed for 120 million years from the Late Jurassic to the Late Eocene.

musk Secretions from scent glands found in mustelids and a variety of other mammalian species.

musth The reproductive period in male elephants.

mutualism (mutualistic) A mutually beneficial association between different kinds of organisms.

mycophagous (mycophagy) Consuming a diet of fungi (characterizes many sciurids, murids, and the marsupial Family Potoroidae).

mycorrhiza The mutualistic association of the mycelium of a fungus with the roots of a seed plant.

myoglobin A protein in the muscles that binds oxygen.

myometrium The thick muscular wall surrounding the highly vascular endometrium in mammals.

myomorph Rodents in which the infraorbital foramen is small to moderate in size.

myrmecophagous (myrmecophagy) Feeding primarily on colonial insects such as ants and termites. Many mammalian families are primarily or secondarily myrmecophagous.

Mysticeti A modern parvorder of baleen whales; species that have two external nares and a symmetrical skull and do not echolocate.

N

nails A specialized variation of claws that evolved in primates to facilitate better gripping ability and precision in object manipulation by the hands and feet. Only the dorsal surface of the end of each digit is covered by the nail.

nares External nostrils, or "blowholes," in whales.

natal dispersal More or less permanent movements from the natal site to a site where reproduction takes place.

natality Birth, usually expressed as a rate.

nectarivorous (nectarivory) (also nectivorous, nectivory) Consuming a diet of nectar; found in about six genera of bats and marsupial honey possums.

necton Larger marine organisms with movements independent of waves and currents.

neonates Newborn animals.

neotony The retention of juvenile characteristics in an adult.

nephrons Functional units of the mammalian kidney; consisting of the Bowman's capsule and a long, unbranched tubule running through the cortex and medulla and ending in the pelvis.

next-generation sequencing High-throughput methods of DNA sequencing that rely on parallel processing of many sequence reactions, usually of short template fragments, followed by computerized assembly of overlapping fragment reads into a full-length sequence.

niche The role of an organism in an ecological community, involving its way of living and its relationships with other biotic and abiotic features of the environment.

nictating membrane A thin membrane that functions as a "third eyelid" in certain species.

nocturnal Exhibiting peak activity during hours of darkness and resting when there is daylight.

nondeciduous placenta A type of placenta that separates easily into embryonic and maternal tissue at parturition, resulting in little or no damage to the uterine wall.

nonshivering thermogenesis Means of heat production in mammals that does not involve muscle contraction.

norepinephrine A catecholamine found in sympathetic postganglionic neurons of mammals, which stimulates production of heat by brown adipose tissue; also called "noradrenaline."

nulliparous A female that has never given birth; shows no evidence of placental scars or pregnancy.

numerical response A change in the population size of a predatory species as a result of a change in the density of its prey. Compare to **functional response**.

numerical taxonomy A system in which individuals are organized into taxa based on unweighted estimates of overall similarity.

nunatak Refugia found within ice sheets during periods of glaciation; pockets of variable size that were not covered by the advancing glaciers.

nutritional condition A measure of how well a particular individual at a particular time has assimilated the nutrients necessary for normal metabolism.

nutritional requirements The types and minimum amounts of nutrients needed by an individual, or characteristic of a species, to meet the metabolic costs of normal activity.

O

obligate delayed implantation A form of delayed implantation in which the delay occurs as a normal, consistent part of the reproductive cycle, as in armadillos.

obligate migration strategy Used by individuals that migrate every year regardless of environmental conditions.

obligate parasites Organisms that must spend at least part of their life cycle as a parasite.

observability (1) Extent to which habitat permits regular, direct observation. (2) The fact that when species are watched, individuals may be seen for different portions of the time period depending on age, sex, or dominance status.

occlusal The surfaces of upper and lower teeth that contact each other during chewing. Occlusal surfaces of teeth have one or more cusps.

Odontoceti A modern parvorder of toothed whales; species with a single external nare, asymmetrical skull, and echolocation.

omasum The muscular third chamber of the stomach of a ruminant.

omnivorous (omnivory) Consuming both animal and vegetable food (characterizing most rodents, bears, raccoons, opossums, pigs, and humans).

open-rooted Teeth that grow throughout the life of an individual, as opposed to closed-rooted teeth.

operational sex ratio (OSR) The number of reproductively active males and females in a population, expressed as a proportion.

organizational effects Morphological, physiological, and behavioral differences in adults resulting from prenatal exposure to hormones that alter the developmental trajectories of various cells and tissues.

os baculum A bone in the penises of certain mammals; also called "baculum" and "os penis."

os clitoris A small bone present in the clitoris in some mammal species. Homolo-gous to the baculum (or os penis) in males.

osmoregulation The maintenance of proper internal salt and water concentrations; this function is performed principally by the kidneys in mammals.

os penis A bone in the penises of certain mammals; also called "os baculum" and "baculum."

os sacrum Fused sacral vertebrae in mammals.

ossicles (auditory) In mammals, the three bones (the malleus, incus, and stapes) of the middle ear that transmit sound waves from the tympanic membrane (eardrum) to the inner ear.

ossicones Short, permanent, unbranched processes of bone that form the horns in giraffes.

outbreeding depression A condition that occurs when new genotypes produced by crossing stocks are inferior to the original native stock; the new stock is at a disadvantage with respect to adaptation to local conditions, possibly because of the breaking up of coadapted gene complexes.

outgroup Any group (taxon) used for comparisons in a phylogenetic analysis; the outgroup cannot contain any members that are part of the study group.

ova Eggs shed from an ovary (sing., ovum).

ovaries The female gonads; the site of egg production and maturation (sing., ovary).

oviducts The ducts that carry the eggs from the ovary to the uterus; also called "Fallopian tubes."

oviparous Able to reproduce by laying eggs, as in monotremes; unlike therian mammals, which are viviparous.

ovulation The releasing of an egg by the ovary into the oviduct.

oxytocin A hormone produced by the posterior pituitary gland, which causes rhythmical contractions of the uterus during parturition and enhances milk "letdown."

P

pachyostotic Describing bones that are very dense.

pacing A gait in which both legs on the same side are raised together.

Paenungulata A group within the generalized ancestral Order Condylarthra from which evolved elephants, dugongs, manatees, and hyraxes.

palmate Flattened or web-like.

palynology Studies of pollen preserved in bogs and other moist places. Because plants that are characteristic of a region at a given time reflect the existing climate, knowledge of flora requirements can be used to describe past climate conditions.

panbiogeography A method of defining ancestral biotas by plotting disjunct distributions of many groups on a map and connecting them by lines to form "tracks."

pandemic A large-scale disease outbreak over a wide geographic area.

Pangaea A large landmass formed by all the continents about 200 million years ago, prior to their drifting apart.

panting A method of cooling characterized by very rapid, shallow breathing that increases evaporation of water from the upper respiratory tract, as occurs in canids and small ungulates.

papillae Small, protruding projections.

paracone A cusp that is anterior to the protocone. It is labial (toward the cheek) in upper molars and lingual (toward the tongue) in lower molars (where it is called a "paraconid").

paraxonic Having a weight-bearing axis of a limb pass through the third and fourth digits, as in artiodactyls.

parental investment Any investment in offspring that increases its chances of survival and reproduction at the expense of the parents' ability to invest in other offspring.

parental manipulation The selective providing of care to some offspring at the expense of other offspring so as to maximize the parents' reproductive success.

parous Describing female mammals that are pregnant or show evidence of previous pregnancies (e.g., possess placental scars).

parsimony In phylogenetics, the criterion that the best estimate of relationships among a set of species is that which minimizes the number of state changes in a set of characters for those species.

parsimony analysis of endemicity (PAE) A numerical method for identifying areas of endemism and the relationships among them based on the presence or absence of species at specific localities across a larger region.

partial migration Population-level effect in which some individuals in a population migrate and others remain resident.

parturition The process of giving birth in mammals.

passive dispersal Movements in which the dispersing organisms have no active role.

passive integrated transponder (PIT) A technology used for radiotracking. PIT tags include an integrated circuit programmed with a unique identification code that is transmitted when the tag is in proximity to a transceiver.

patagium An integumentary membrane stretching from the body wall to the limbs or tips of digits; it serves as the airfoil in gliding mammals and as the wing in bats.

path integration A process by which an organism uses internal spatial localization to return from an outward-bound trip; also called "ideothetic reckoning" or "dead reckoning."

pectinate A comb-like structure with several prongs or projections in a row.

pectoral girdle Bones of the shoulder region providing for articulation of the forelimbs; the scapula and clavicle or only the scapula form the shoulder joint in most mammals.

pedicel (pedicle) (1) A short supporting stalk or stem. (2) In deer, the extension of the frontal bone on which the antlers occur.

pelage All the hairs on an individual mammal.

pelagic The open ocean; away from coastal areas.

pelvic girdle The bones of the hip region, providing for articulation of the hind limbs and consisting of the paired ilia, ischia, and pubic bones.

pelvis A large cavity within the mammalian kidney; the renal pelvis empties into the ureter.

Pelycosauria One of two orders within the reptilian Subclass Synapsida. Pelycosaurs had more primitive characteristics than the other order, the Therapsida.

penis The male copulatory organ through which sperm are deposited in the female reproductive tract and urine leaves the body.

pentadactyl Having five digits. The hands and feet of humans are pentadactyl, as are those of insectivores.

Peramuridae A family of Jurassic mammals that probably gave rise to the lineage of advanced therians, that is, mammals of metatherian-eutherian grade.

perineal swelling The swelling and sometimes reddening of tissues in the anogenital region of some primates in estrus produced by the actions of estrogen.

period of dormancy The second stage of the cycle of dormancy characterized by leveling off of body temperature; usually occurs in early winter; see **dormancy**.

phalanges Bones of the fingers and toes; the distal-most bones in the manus and pes.

phenotype matching A mechanism by which kin may recognize one another. Individuals use kin whose phenotypes are learned by association as a reference.

pheomelanin (xanthophylls) Pigment mixtures that produce various shades of red and yellow.

pheromones Airborne chemical signals that elicit responses in other individuals, usually of the same species.

philopatric Living and breeding near the place of birth.

phylogenetic biogeography An approach to understanding the historical biogeography of a group of species by combining a reconstructed phylogeny with the "peripheral isolation" model of speciation.

phylogenetic classification The principle that only monophyletic groups should be recognized with formal taxonomic names.

phylogenetics (phylogeny) The evolutionary history of various groups of living organisms.

phylogenetic species concept (PSC) A definition of species in which a species is the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent.

phylogeny The sequence of speciation events in the history of a group of species since their most recent common ancestor.

phylogeography The study of biogeographic history, including living forms, fossils, and geology, and using molecular tools.

phylogram A tree diagram attempting to represent the degree of genetic divergence among the taxa represented by the lengths of the branches and the angles between them.

piloerection Fluffing of the fur.

piloting The use of familiar landmarks to locate food or shelter.

pinnae External ears that surround the auditory meatus and channel sound-waves to the tympanic membranes (eardrums); not found in many marine and fossorial mammals.

Pinnipedia (pinnipeds) Literally, "feather-footed"; aquatic carnivores that include the seals and walrus.

piscivorous (piscivory) Consuming a diet composed primarily of fish (characterizes bulldog bats [*Noctilio*]).

pituitary gland The master gland of the endocrine system; located below the hypothalamus.

placenta A highly vascularized endocrine organ developed during gestation from the embryonic chorion and the maternal uterine wall (endometrium); connects to the umbilical cord through which nutrient and waste exchange occurs between mother and fetus.

placental scar A pigmented area on the uterine wall formed from prior attachment of a fetus.

plankton Floating plant and animal life in lakes and oceans; movements are primarily dependent on waves and currents.

plantigrade Walking on the soles of the hands and feet.

plate tectonics The theory that the earth's crust, including the surfaces of continents and the ocean floors, is made up of a series of geological plates.

plesiomorphic Character states that arose earlier, are ancestral to, and more primitive than derived states; for example, laying eggs is the plesiomorphic state of mammalian reproduction, ancestral to live births.

pods Groups, schools, or herds of animals; specifically applied to whales.

poikilothermy Pertaining to animals whose body temperature is variable and fluctuates with that of the environment; includes all animals except birds and mammals; cold-blooded, ectothermy.

pollex The first (most medial) digit of the manus (forefoot); the thumb in humans.

polyandry A mating system in which females acquire more than one male as a mate.

polyestrous Pertaining to species that exhibit several periods of estrus, or heat, per year.

polygamy (polygamous) A mating system in which both males and females mate with several members of the opposite sex.

polygyny A mating system in which males attempt to mate with multiple females, but females mate with a single male. This is the most common mating system in mammals.

polygyny threshold The point at which a female will benefit more by joining an already mated male possessing a good territory rather than an unmated male on a poor territory.

polymerase chain reaction (PCR) A procedure for preparing large amounts of DNA from small amounts of sample.

polymorphism Character variation among individuals within a species.

polyprotodont Dentition in several orders of marsupials in which the lower jaw is equal in length to the upper jaw and the lower incisors are small and unspecialized; as opposed to diprotodont.

populations Groups of organisms of the same species, present at the same place and time.

post-breeding dispersal Dispersal that occurs at or between successive sites of reproduction; also known as "breeding dispersal."

postjuvenile molt A molt that starts soon after weaning.

precocial Born in a relatively well-developed condition (eyes open, fully furred, and able to move immediately) and requiring minimal parental care, as, for example, in snowshoe hares, deer, porcupines, and many bovids; as opposed to altricial.

preference The likelihood that an animal will select a resource if it is offered on an equal basis with other resources.

prehensile Possessing digits or tail able to grasp branches and other objects.

premolars Cheekteeth that are anterior to the molars and posterior to the canines. Unlike molars, there are both deciduous and permanent premolars.

preputial glands Modified sebaceous glands that in males of some species contribute to the formation of the semen and in others secrete a scent used for marking.

presaturation dispersal Dispersal that occurs when young leave the maternal home range even when population density is low, often observed in small mammals. Young may be evicted by parents or leave because of some innate behavior.

priming pheromones Chemical communication substances that produce generalized internal physiological responses, such as the production and release of hormones.

prions Small, modified proteins thought to be the disease agents in spongiform encephalopathies, including "mad cow" disease.

procumbent Projecting forward more or less horizontally, as in teeth in shrews, horses, and prosimian primates.

proestrus The beginning stage of the estrous cycle when nucleated cells are present in a vaginal smear and when estrogen, progesterone, and lutenizing hormone levels reach their peak.

progesterone A steroid hormone produced in small quantities by the follicle and in larger quantities by the corpus luteum; promotes growth of the uterine lining and makes possible the implantation of the fertilized egg.

prolactin (PRL) A hormone produced by the anterior pituitary gland, which has many actions relating to reproduction and water balance in mammals. For example, PRL promotes corpus luteum function in ovaries and stimulates milk production.

promiscuity A mating system in which there is no prolonged association between the sexes and in which multiple matings by both sexes occurs.

propatagium The anterior portion of a bat's wing, which extends from the shoulder to the wrist.

prostaglandins Lipid-based hormones that communicate between cells over a short distance; involved in several aspects of reproductive function such as increased contractions of the uterus.

prostate gland A mass of muscle and glandular tissue surrounding the base of the urethra in male mammals; at the moment of sperm release it secretes an alkaline fluid that has a stimulating effect on the action of the sperm.

protein electrophoresis A method that uses the characteristic migration distance of various proteins in an electric field to identify and compare individuals; sometimes called "allozyme analysis."

protein immunology The cross-reactivity of the homologous (original) antigen (protein) and a heterologous antigen (protein from a different, related species) to provide an estimate of the degree of genetic relationship between the two species.

protocone The primary cusp in a tribosphenic molar at the apex of the trigon. It is lingual in upper molars and labial in lower molars (where it is called the "protoconid").

protrusible Capable of being turned inside out; bulging or jutting out.

provincialism The phenomenon in which areas of endemism for a large number of species overlap, resulting in biogeographic provinces

pseudopregnancy Any period when there is a functional corpus luteum and buildup of the endometrial uterine layer in the absence of pregnancy; synonymous with "luteal phase."

pterygoideus One of three main masticatory muscles of mammals that function to close the mouth by raising the mandible; important in stabilizing and controlling the movement of the jaw.

pulp cavity The part of the tooth below the gumline that contains nerves and blood vessels to maintain the dentine.

Q

quadrate bone A bone in the posterior part of the mandible of lower vertebrates; becomes the incus in modern mammals.

quadritubercular (quadrituberculate) Describing a square or rectangular cheektooth with four major cusps: protocone, paracone, metacone, and hypocone.

R

radiation Energy transmitted as electromagnetic waves (e.g., ultraviolet, visible, and infrared).

radioimmunoassay (RIA) A method for assessing hormone levels on small blood samples involving a radioactively labeled antibody mixed with blood samples

from an animal in a competitive binding assay.

radiotelemetry A method for determining the location and movements of an animal by using a transmitter affixed to the individual, the signals from which are monitored with an antenna and a receiver from known points in the study area.

random amplified polymorphic DNA (RAPDs) Involves the use of restriction enzymes with short primers in conjunction with PCR. The resulting DNA fragments are 200 to 2,000 base pairs long and appear as a series of bands on a gel. The primers are not locus-specific, and thus the amplified loci are said to be anonymous.

ranging Movements that include forays outside the home range, usually in search of suitable habitat or mating opportunities.

Rapoport's rule The "rule" that latitudinal breadth of species ranges tends to be larger for species at higher latitudes than for species at lower latitudes.

realized niche The range of conditions and resources in which the species can maintain a viable population when in the presence of competitors or predators. Compare to **fundamental niche**.

reciprocal altruism The trading of altruistic acts by individuals at different times; that is, the payback to the altruist occurs some time after the receipt of the act.

reciprocal monophyly A pattern of genealogical relationship among haplotypes sampled from two distinct groups, such that all haplotypes from each group are more closely related to one another than to any haplotype from the other group.

refugia Small geographical areas that preserve ancestral biodiversity during periods of envirnomental change.

regionalization The scientific process of identifying biogeographic provinces.

relaxin A hormone produced by the corpora lutea, which acts to soften the ligaments of the pelvis so it can spread and allow the fetus to pass through the birth canal.

renal corpuscle A unit of the mammalian kidney that is located in the cortical portion of the mammalian kidney and composed of Bowman's capsule and the glomerulus.

renal papillae Narrow apices of the cortex of the mammalian kidney. Because the papillae are composed of long loops of Henle, their prominence gives an indication of the number and length of such loops.

renal pyramids Triangular wedges of the medulla of the mammalian kidney.

reproductive effort The energy expended and risk taken to reproduce, measured in terms of the decrease in ability of the organism to reproduce at a later time.

reproductive skew A measure that compares the proportion of each sex that contributes to reproduction in group-living animals.

reproductive value The sum of an individual's current reproductive output and its expected future output at age x.

reservoir A source that maintains a disease agent in nature.

resource defense polygyny A mating system in which males control access to females indirectly by monopolizing resources needed by females.

resource selection A process by which an animal uses a resource to a greater extent than its availability.

Restriction Fragment-Length Polymorphisms (RFLPs) Fragments of DNA that have been isolated and cut with one or more restriction enzymes. They are placed on a gel for electrophoresis and stained to permit viewing of the fragments sorted by size.

rete mirabile A complex mass of intertwined capillaries specialized for exchange of heat or dissolved substances between countercurrent flowing blood; also called "miraculous net," "marvelous net," "wonderful net."

reticulum The second of the four compartments of the stomach of ruminants; a blind-end sac with honeycomb partitions in its walls.

rhinarium An area of moist, hairless skin surrounding the nostrils.

ribs Bones attached to the thoracic vertebrae on the dorsal surface and, in most cases, to the sternum on the ventral surface. The rib cage, or thoracic basket, surrounds and protects the vital internal organs.

ritualized Describing behavior patterns that have become modified through evolution to serve as communication signals.

rods Retinal receptors for black-and-white vision.

root The portion of a tooth that is below the gum and fills the alveolus.

rorquals Literally, "tube throated"; large baleen whales with longitudinal grooves on their throats that allow for expansion as they fill with water during feeding.

rostrum The anterior portion of the face or cranium.

*r***-selection** Selection favoring rapid rates of reproduction and growth, especially among species that specialize in colonizing short-lived, unstable habitats. Compare to *K***-selection**.

rumen The first and largest compartment of the four-part stomach of ruminants.

ruminant artiodactyl A member of Order Artiodactyla that "chews its cud," or ruminates (e.g., cervids, bovids, antilocaprids, giraffids).

ruminant cetartiodactyls Terrestrial ungulates within the Order Cetartiodactyla that ruminate; they have a three- or four-chambered stomach that digests vegetation more efficiently than nonruminant herbivores.

ruminate (rumination) To chew the cud; see **foregut fermentation.**

runaway selection Selection for ornaments (usually in males) that happens due to the genetic correlation and the resulting positive feedback relationship between the trait and the preference for the trait.

rut The mating season in cervids and other artiodactyls.

S

sacculated A stomach with more than one chamber and symbiotic microorganisms for cellulose digestion present in the first chamber(s). The stomach of certain herbivores, whales, and marsupials is sacculated.

sacral (vertebrae) In most mammals, vertebrae that are fused to form the **os sacrum**, to which the pelvic girdle attaches.

sagittal crest The bony midline ridge on the top of the cranium formed by the temporal ridges.

salivary amylase A potent digestive enzyme produced by the salivary glands.

saltatorial locomotion Jumping and ricocheting. Jumping involves the use of all

four feet; ricocheting involves propulsion provided only by the two hind limbs.

sanguinivorous (sanguinivory) Feeding on a diet of blood (e.g., vampire bats).

saturation dispersal Dispersal that is density dependent and occurs when the population reaches a threshold density resulting from food limitation. This form of dispersal is often observed in large mammals.

scaling Structural and functional consequences of a change in size or in scale among animals.

scan sampling The recording of the current activity of all or selected members of a group at predetermined intervals.

scansorial Adapted for climbing.

scapula A part of the pectoral girdle; the shoulder blade.

scent glands Modified sweat or sebaceous glands that produce substances used for a wide variety of functions in mammals.

schizodactylous Grasping digits in which the first two most medial oppose the remaining three.

sciurognathous Describing the mandible in certain rodents; in ventral view. The angular process is in line with the alveolus of the incisor (as opposed to being hystricognathous).

sciuromorph Rodents in which the infraorbital foramen is relatively small.

scramble polygyny A mating system in which males actively search for mates without overt competition.

scrotum A bag or pouch of skin in the pelvic region of many male mammals that contains the testicles.

seasonal molt The change of the pelage more than once each year.

sebaceous glands Structures associated with hair follicles, which secrete oils to keep the hair moist and waterproof.

sectorial Cutting or shearing teeth.

selenodont A cusp pattern in molariform teeth of goats, sheep, cows, and deer in which the lophs form cresent-shaped ridges, or "half-moons," on the grinding surface.

sella A median projection of the nose leaf of horseshoe bats in Subfamily Rhinolophinae.

semantic Of or relating to the meaning of signals; specifically used to denote the use of different alarm signals to warn about different predators.

semelparity (semelparous) The production of offspring by an organism once in its life. Compare to **iteroparity (iteroparous)**.

semen A product of the male reproductive system that includes sperm and the secretions of various glands associated with the reproductive tract; also called "seminal fluid."

semibrachiators An animal that moves by swinging from branch to branch.

seminal vesicles The swollen portion of a male reproductive duct in which sperm are stored and that secretes a fluid useful in the transmission of sperm during copulation; also called "vesicular glands."

seminiferous tubules The long, convoluted tubules of vertebrate testes in which sperm cells are produced and where they undergo various stages of maturation, or spermatogenesis.

senescence The gradual deterioration of function in an organism with age, leading to increased probability of death.

sensory channels The physical modality used for signaling; for example, odor or vision.

Sertoli cells Cells that line the seminiferous tubules and that surround the developing sperm, which they nourish.

set point A "reference" temperature in the hypothalamus; analogous to a thermostatic control.

sexual dichromatism The presence of distinctly different pelage colors in males and females.

sexual dimorphism A difference in the sexes in form, such as size; males are often larger than females, although the opposite occurs in some species.

sexually dimorphic Sexes of a species evolve to look and behave differently.

sexual selection Selection in relation to mating; composed of competition among members of one sex (usually males) for access to the other sex and choice of members of one sex by members of the other sex (usually females).

shaft The central structure of a hair, comprised of the inner medulla, surrounded by the cortex, and covered by a thin outer cuticle.

signal The physical form (behavior or morphology) in which a message is coded for transmission through the en-

vironment, with the condition that it has evolved for that purpose.

signaling pheromones Airborne chemical signals that produce an immediate motor response, such as the initiation of a mounting sequence.

simplex A type of uterus in eutherian mammals in which all separation between the uterine horns is lacking; the single uterus opens into the vagina through one cervix (found in some bats, higher primates, and xenarthrans).

sister groups Two monophyletic groups that are each other's closest relatives.

smooth muscle An involuntary muscle.

social learning The process of acquiring knowledge by observing or interacting with another individual, usually of the same species.

society A group of individuals belonging to the same species and organized in a cooperative manner; usually assumed to extend beyond sexual behavior and parental care of offspring.

somatic muscle Muscle derived from embryonic somites; somatic muscles orient the body in the external environment.

sound window The use of frequencies for communication. These are transmitted through the environment with little loss of strength (attenuation).

source-sink dynamics High-quality habitats that support source populations where birth rates exceed death rates and individuals from those habitats disperse to lower quality or sink habitats where death rates exceed birth rates.

speciation The evolutionary process by which new species are derived from ancestral species.

species-area relationship The equation describing the increase in number of species as a function of the area sampled.

species dispersal The extension of a species range into a previously unoccupied area.

species range The geographic area over which individuals of a particular species occur at a given point in time.

species richness The number of species in an area.

spermaceti An organ found in the head of certain species of toothed whales. It contains a waxy liquid that may function in diving physiology and echolocation.

spermatogenesis A series of cell divisions and chromosome and cytoplasmic

changes involved in the production of functional spermatozoa, beginning with the undifferentiated germinal epithelium.

sperm competition Competition among sperm from different males to fertilize eggs when a female copulates with more than one male.

spines Stiff, enlarged guard hairs that exhibit definitive growth.

spirit specimens Museum specimens that consist of carcasses, or portions of carcasses, preserved in alcohol. Many spirit specimens are initially fixed in formalin.

spontaneous ovulation Ovulation that occurs without copulation.

stable isotopes Variants of chemical elements that have different numbers of neutrons but do not undergo radioactive decay (in contrast to radioisotopes).

stapes Also called the "stirrup"; the last of the three middle ear bones (ossicles) found in mammals. In other vertebrates, this is the only ossicle (the columella) in the middle ear.

static life table A life table generated from a cross section of the population at a specific time. Compare to **cohort life table**.

station-keeping Local movements of an animal within its home range, as it acquires resources or marks and defends its territory.

stem lineages Extinct clades that share a more recent common ancestor with one particular crown group than with another; for example, nonmarsupial metatherians are stem lineages to Marsupialia.

sternum A series of bony elements along the midventral line of the thoracic region, which articulate with the ribs and (in some species) the clavicle; a part of the axial skeleton.

stopover Habitat patches along a migration route where animals pause for a short period of time to rest and forage to renew energy reserves prior to resuming migration.

striated muscle A voluntary or skeletal muscle.

study skin A museum specimen that consists of the preserved integument of an individual mammal. Study skins of small mammals are usually stuffed with cotton and dried in a flattened, linear pose.

subspecies A taxonomic category below the level of species. Subspecies are usually named to recognize discrete poly-morphism across the geographic range of a species.

subterranean Living underground for all activities.

subunguis The lower or ventral portion of the claw, which is continuous with the pad at the end of the digit.

supernumerary An additional tooth (or teeth) in a position where it does not normally occur in a species.

survivorship curve (l_x) The proportion of newborn individuals alive at age **x**, plotted against age.

sweat glands Epidermal glands that lie deep in the dermis but are connected to the surface of the skin by a coiled tube. They produce a watery secretion (sweat).

sweepstakes route A dispersal route in which some unusual occurrence carries an organism or group of organisms across a dispersal barrier into a previously unoccupied area.

symbiosis Two species living together in which one benefits and the other may benefit (mutualism), be unaffected (commensalism), or harmed (parasitism).

Symmetrodonta An early order of therian mammals with tribosphenic teeth, which includes small carnivores or insectivores from the late Triassic period.

sympatric Occurring in the same place; usually referring to areas of overlap in species distributions. Compare to allopatric.

synapomorphy A sharing of a derived trait by two or more taxa.

Synapsida One of two major clades within Amniota, characterized by a single temporal opening on the skull; includes pelycosaurs, therapsids, cynodonts, and mammals.

syndactylous Having digits in which the skeletal elements of the second and third toes are fused and share a common skin sheath, as in the marsupial Orders Peramelemorphia and Diprotodontia; as opposed to didactylous.

syndesmochorial placenta The arrangement of the chorioallantoic placenta that possesses one less layer than the epitheliochorial condition.

syntax The information provided by the sequence in which signals are transmitted.

synteny The localization of homologous genes on the same chromosome in different species.

syntopic Being present at the same time and place.

T

talonid The basin or heel in lower molariform teeth posterior to the trigonid that occludes with the protocone of the upper molar.

tapetum lucidum A reflective layer lying outside the receptor layer of the retina that causes the eye to shine when light strikes the retina at night. This structure aids in night vision by reflecting light that has passed through the receptor layer back toward the retina.

taxon A group of organisms that has been recognized and named in a formal classification.

taxonomic key An arrangement of the traits of a group of organisms into a series of hierarchical, dichotomous choices.

taxonomic ranks Levels such as domain, kingdom, phylum, class, and so on in a hierarchical classification, as distinct from the taxa themselves (e.g., Animalia, Chordata, Mammalia).

taxonomic revision A redefinition of species boundaries within a group of closely related species, usually based on a consideration of all or most of the available specimens (and perhaps genetic data) representing the group.

taxonomy A description of species and the process of classifying them into groups that reflect their phylogenetic history.

taxon sampling The rationale for choosing which species to include in a phylogenetic study.

telescoped skulls Compressed posterior bones and elongated anterior bones in the cranium of modern whales, with associated movement of the nares to the top of the skull.

temporalis One of three main masticatory muscles of mammals, which functions to close the mouth by raising the mandible. Pronounced in carnivorous mammals, the temporalis assists in holding the jaws closed and aids in the vertical chewing action.

territoriality Resource area is defended from conspecific competitors.

territory An area exclusively occupied and defended by an animal or group of animals.

testes Oval glands in males, often in the scrotum, that produce sperm.

testosterone A steroid hormone secreted by the testes, especially in higher vertebrates; responsible for the development and maintenance of sexual characteristics and the normal production of sperm.

Therapsida One of two orders within the reptilian Subclass Synapsida. These mammal-like amniotes eventually gave rise to mammals.

Theriodontia One of two suborders within Order Therapsida, the mammal-like amniotes. Primarily carnivorous, theriodonts encompassed several diverse lineages.

thermal conductance The heat loss from the skin to the outside environment.

thermal windows Bare or sparsely furred areas of certain mammals that reside in regions characterized by intense solar radiation and high air temperatures (e.g., guanacos and many desert antelopes). They function as sites through which some of the heat gained from solar radiation can be lost by convection and conduction.

thermogenin A mitochondrial protein responsible for heat production by brown adipose tissue due to uncoupling oxidative phosphorylation.

thermoneutral zone A range in environmental temperatures within which the metabolic rate of an animal is minimal.

thoracic (vertebrae) Articulating with the ribs; from 12 to 15 pairs in mammals.

threatened species Those that are likely to become endangered in the near future (some listings use the term "vulnerable" instead).

tine A point or projection on an antler.

torpor A form of adaptive hypothermia or dormancy in which body temperature, heart rate, and respiration are not lowered as drastically as in hibernation.

total metabolic rate The total quantity of energy necessary to meet energy demands of an animal.

tradition A behavior pattern that is passed from one generation to the next through the process of learning.

tragus A projection from the lower margin of the pinnae of many microchiropteran bats and functions in echolocation.

transpirational water loss The mechanism by which water is lost by diffusion through the skin and from the surfaces of the respiratory tract; also called "insensible water loss."

tribosphenic Molars with three main cusps (the trigon) arranged in a triangular pattern. Cusp patterns of many modern mammalian groups are derived from this pattern.

Triconodonta An order of small, carnivorous mammals characterized by molars that had three cusps in a row. The lineage extended for 120 million years until the Late Cretaceous.

trigon(id) The three cusps (protocone, paracone, and metacone) of a tribosphenic molar. The suffix "-id" is applied to the mandibular dentition; main cusps are the protoconid, paraconid, and metaconid.

Tritylodonts A lineage of rodent-like reptiles that existed for about 50 million years from the Late Triassic to the Mid-Jurassic.

trophic Pertaining to food or nutrition.

trophic cascade Indirect effects of predators on plant biomass. Also referred to as "top-down effects."

trophoblast The outer layer of the blastocyst in mammals; attaches the ovum to the uterine wall and supplies nutrition to the embryo as part of the placenta.

truth in advertising In sexual selection, the hypothesis that a male's ornaments or behavior are reliable indicators of his overall genetic fitness.

turbinal (turbinate) bones Structures found within the nasal area, which increase the surface area for reception of chemical cues and secrete mucus to aid in filtering small particles from incoming air.

tympanoperiotic The auditory bullae and middle-ear apparatus of whales; not fused to the skull so that the direction of incoming sound waves can be determined.

tympanum A membrane (eardrum) at the interior end of the external auditory meatus; connects to the ossicles of the middle ear.

type specimens One or more specimens, usually part of a systematic collection, that constitute the type of a species; under the International Code of Zoological Nomenclature, the type is the "name-bearing" specimen associated with a particular species.

U

ultradian rhythms Activity rhythms with a period of less than 24 hours.

ultrasound Sound frequencies greater than 20,000 kHzzz.

underfur Fine, short hairs that occur beneath guard hairs in the pelage of a mammal.

unguiculate Having nails or claws instead of hooves.

unguis The upper or dorsal portion of the claw, which is a scale-like plate that surrounds the subunguis.

ungulates Mammals with hooves; perissodactyls and artiodactyls.

unguligrade A running locomotion with only the hooves (tips of the digits) on the ground; characteristic of ungulates.

unicuspid Teeth with a single cusp. Canine teeth are unicuspid, as are premolars in many species.

upper critical temperature The temperature at which an animal must dissipate heat to maintain a stable internal temperature.

ureters Ducts within the mammalian kidney that drain the renal pelvis.

urethra The tube through which urine is expelled from the urinary bladder.

urinary bladder The organ that stores urine in mammals.

urogenital sinus A common chamber for the reception of products from the reproductive and urinary systems. In mammals, it is found in monotremes and marsupials.

uropatagium The membrane between the hind legs of bats, which encloses the tail; also called the "interfemoral membrane."

uteri In female mammals a muscular expansion of the reproductive tract in which the embryo and fetus develop; opens externally through the vagina (sing., **uterus**).

V

vagina The part of the female reproductive tract that receives the male penis during copulation.

vaginal smear technique A procedure for monitoring different stages of the estrous cycle by observing changes in the types of cells lining the vaginal canal.

valvular Describing nostrils or ears that can be closed when an animal is under water.

variable number tandem repeats (VNTRs) Individual loci where alleles

are composed of tandem repeats that vary in terms of the number of core units.

vectors Any agent or carrier that transmits a disease organism.

velli Very short, fine hairs, sometimes referred to as "down" or "fuzz."

velvet Haired and highly vascularized skin covering growing antlers.

vertebrae A series of bony elements that form the spinal column of the axial skeleton, stretching from the base of the skull to the tail.

vestigial Reduced; remnant; atrophied.

viable population analysis Determination of the number of animals needed in a population to prevent it from going extinct within a given time period (often 1,000 years).

vibrissae Long, stiff hairs with extensive enervation at the base of the follicle, which are found on all mammals except humans.

vicariance The splitting of an ancestral species range into two or more smaller ranges by the development of a dispersal barrier, resulting in interrupted gene flow, genetic differentiation, and perhaps speciation of isolated populations.

villi Finger-like projections of capillaries from the outermost embryonic membrane, which penetrate the endometrium; increases exchange between maternal and fetal systems (same as chorionic villi).

viviparous Able to give birth to live young. Therian mammals are viviparous; prototherians are oviparous.

volant Having powered flight.

vomeronasal organ A secondary chemosensory system located between the nasal passages and the mouth of the mouth in most mammals. This system detects primarily nonvolatile chemical compounds often contained in liquids, including pheromones.

voucher specimen A museum specimen (e.g., study skin, skull) that serves permanently to identify the source of a tissue, protein, or DNA sample.

W

warm-blooded Characterized by having a constant body temperature, independent of environmental temperature. Typified by birds and mammals only; endothermy, homeothermy.

wavelength The distance from one peak to the next in a sound (or light) wave.

white adipose tissue In mammals, the major fatty tissue that functions in body insulation, mechanical support, and buoyancy and as an energy reserve.

wing loading In bats (and birds), the body mass divided by the total surface area of the wings.

winter lethargy A period of winter dormancy in which body temperature of the animal decreases only about 5 to 6°C from euthermy, as in black bears (*Ursus americanus*).

wool Underhair that is long, soft, and usually curly.

X

xanthophylls Pigments that produce mixtures of red and yellow (pheomelanin).

Z

zalambdodont Tooth cusps that form a V-shape.

Zeitgeber "Time giver"; environmental cues that serve to set and adjust biological clocks.

zona pellucida A noncellular layer surrounding the zygote.

zonary placenta The type of chorioallantoic placenta in which the villi occupy a girdle-like band about the middle of the chorionic sac.

zoogeography The study of distributions of animals, including mammals.

zoonoses Diseases transmitted from vertebrate animals (nonhuman mammals) to people.

zooplankton Animal material including both plankton and necton fed on by baleen whales.

zygomatic arch Bony structure that surrounds and protects the eye and serves as a place of attachment for jaw muscles.

zygote A diploid cell resulting from the union of the male and female gametes.

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Note: Page numbers followed by f and t indicate figures and tables, respectively.

Equivalent Weights and Measures

Length

Unit	Abbreviation	Equivalent
meter	m	approximately 39 in
centimeter	cm	10^{-2} m
millimeter	mm	10^{-3} m
micrometer	μm	10^{-6} m
nanometer	nm	10^{-9} m

Volume

Unit	Abbreviation	Equivalent
liter	L	approximately 1.06 qt
milliliter	mL	10^{-3} L (1 mL = 1 cm^3 = 1 cc)
microliter	μL	10^{-6} L

Mass

Unit	Abbreviation	Equivalent
kilogram	kg	10^3 g (approximately 2.2 lb)
gram	g	approximately 0.035 oz
milligram	mg	10^{-3} g
microgram	μg	10^{-6} g
nanogram	ng	10^{-9} g
picogram	pg	10^{-12} g

Common Prefixes

Prefix	Equivalent	Examples
kilo	1000	a kilogram is 1000 grams
centi	0.01	a centimeter is 0.01 meter
milli	0.001	a milliliter is 0.001 liter
micro (μ)	one-millionth	a micrometer is 0.000001 (one-millionth) of a meter
nano (n)	one-billionth	a nanogram is 10^{-9} (one-billionth) of a gram
pico (p)	one-trillionth	a picogram is 10^{-12} (one-trillionth) of a gram

Conversion Chart

Length Conversions

1 in = 2.5 cm	1 mm = 0.039 in
1 ft = 30 cm	1 cm = 0.39 in
yd = 0.9 m	1 m = 39 in
1 mi = 1.6 km	1 m = 1.094 yd
1 km = 0.6 mi	

To convert	Multiply by	To obtain
inches	2.54	centimeters
feet	30	centimeters
centimeters	0.39	inches
millimeters	0.039	inches

Volume Conversions

1 tsp = 5 mL	1 mL = 0.03 fl oz
1 tbsp = 15 mL	1 L = 2.1 pt
1 fl oz = 30 mL	1 L = 1.06 qt
1 cup = 0.24 L	1 L = 0.26 gal
1 pt = 0.47 L	
1 qt = 0.95 L	
1 gal = 3.79 L	

To convert	Multiply by	To obtain
fluid ounces	30	milliliters
quart	0.95	liters
milliliters	0.03	fluid ounces
liters	1.06	quarts

Mass Conversions

1 oz = 28.3 g	1 g = 0.035 oz
1 lb = 453.6 g	1 kg = 2.2 lb
1 lb = 0.45 kg	

To convert	Multiply by	To obtain
ounces	28.3	grams
pounds	453.6	grams
pounds	0.45	kilograms
grams	0.035	ounces
kilograms	2.2	grams

Energy Conversions

calorie (cal) = energy required to raise the temperature of 1 g of water (at 16°C) by 1°C

1 calorie = 4.184 joules

1 kilocalorie (kcal) = 1000 cal

1 joule = 0.24 cal

1 kilocalorie = 4.184 kJ

Temperature Conversions

Celsius (Centigrade) $\quad °C = \dfrac{(°F - 32) \times 5}{9}$

Fahrenheit $\quad °F = \dfrac{°C \times 9}{5} + 32$

Kelvin $\quad K = °C + 273$

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