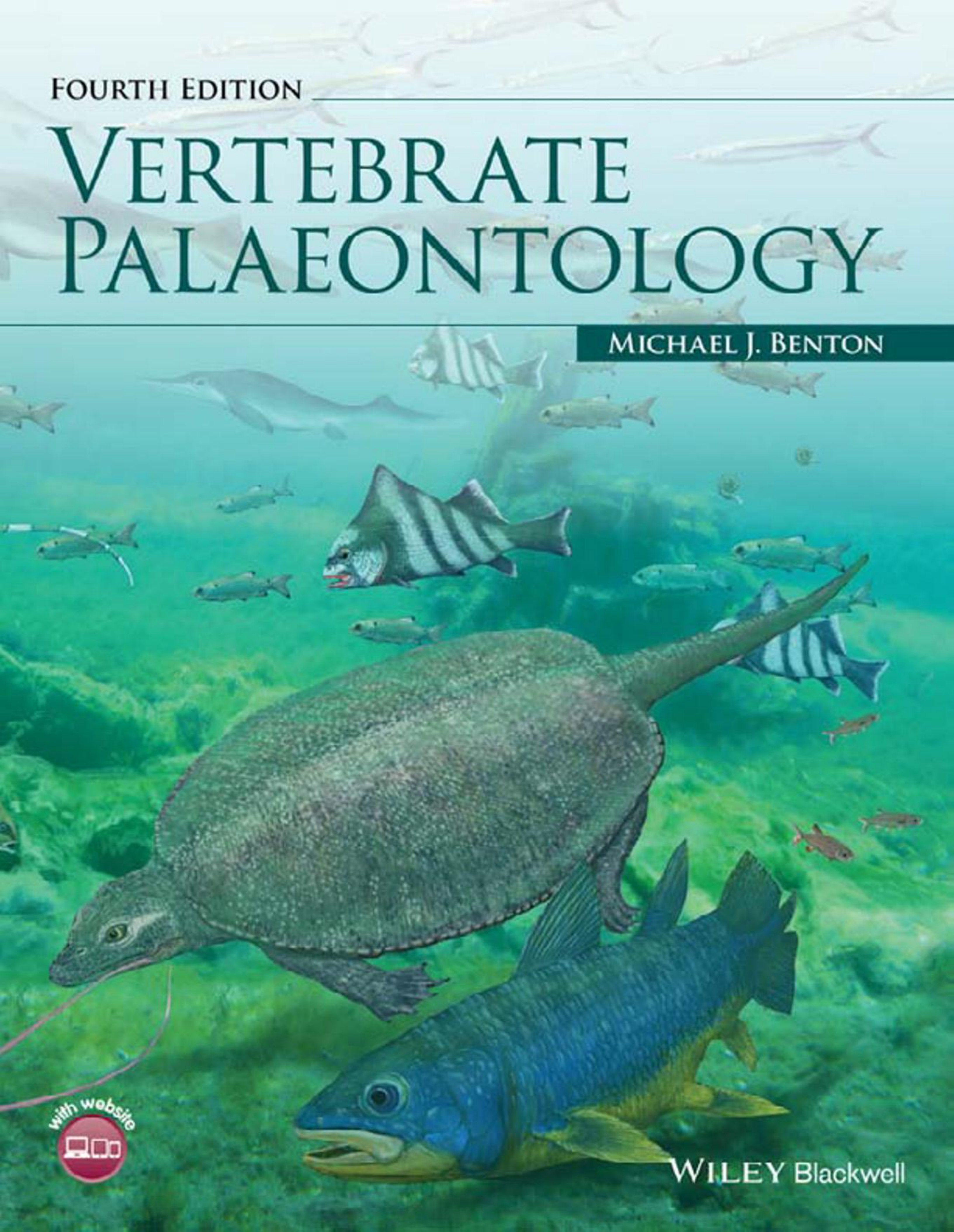
FOURTH EDITION

VERTEBRATE PALAEONTOLOGY

MICHAEL J. BENTON



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VERTEBRATE PALAEONTOLOGY

Dedicated to Mary, Philippa and Donald for their forebearance while I wrote this book.

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Fourth edition

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WILEY Blackwell

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Cover image: Lobster lunch of Luoping; over a muddy seabed during the Middle Triassic (Ansian) at the future site of Luoping County, Yunnan. In the foreground, an early rock lobster (*Yunnanopalinura schrami*) attracts the unwanted attention of the coelacanth *Luopingcoelacanthus eurylacrimalis* and the armoured reptile *Sinosaurosphargis yunguiensis*. Behind them cruise other aquatic reptiles: the ichthyosaurs *Mixosaurus* cf. *panxianensis* and the little pachypleurosaur *Dianopachysaurus dingi*. Swarming around is a diverse community of actinopterygians: ubiquitous *Sangiorgioichthys sui* (numerous fish with black-tipped fins), sleek *Sinosaurichthys longimedialis* (thin with a long snout), tiny *Marcopoloichthys ani* (very small with red-spotted fins), scaleless *Gymnoichthys inopinatus* (blue with a yellow back) and the deep-bodied *Kyphosichthys grandei* (brown and yellow) and *Luoxiongichthys hyperdorsalis* (black and white). Painting by Brian Choo © 2013.

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Contents

The colour plate section can be found between pp. 244–245

Preface

To many, palaeontology in general, and vertebrate palaeontology in particular, might be seen as devoted to discovering new fossils. After all, we read lavish press reports of each new species of dinosaur, fossil bird, or early human fossil that is recorded in the scientific literature. Discoveries from all continents attract attention, and none moreso than the continuing rich haul of remarkable new fossils from China. Our understanding of fossil vertebrate evolution has been much enriched by continuing discoveries of basal chordates from the Chengjiang and associated exceptional faunas of South China, as well as the feathered birds and dinosaurs from the Jehol assemblages in North China. But, as any young palaeobiologist knows, the discovery of new species is a minor concern. Much more exciting has been the blossoming of new numerical techniques that extend the reach of studies in macroevolution and palaeobiology further than might have been imagined even ten years ago.

When I wrote the first edition of this book in 1989, I felt that there was a need for an up-to-date account of what is known about the history of vertebrates, but also for a thorough phylogenetic framework throughout, then something of a novelty. The first edition was published in 1990. The second edition, substantially modified, appeared in 1997, and the third, further extensively rewritten in 2005. These new editions offered extensive coverage of new discoveries and new interpretations through the previous 15 years. Between 1990 and 2005, the book hopped from publisher to publisher: it was commissioned by Unwin Hyman, who were soon after acquired by Harper Collins, and their science list was in turn acquired by Chapman & Hall, so the first edition appeared under three publishers' logos, in 1990, 1991 and 1995. The second edition appeared with Chapman & Hall, but they were then taken over by Kluwer, and this book was marketed by their Stanley Thornes subsidiary for a while, before passing to Blackwell Science in 2000, which is now part of the larger John Wiley & Sons consortium. I hope these wandering days are now over.

The first edition appeared in Spanish in 1995 (*Paleontología y evolución de los vertebrados*, Edition Perfils, Lleida), the second in Italian in 2000 (*Paleontologia dei Vertebrati*, Franco Lucisano Editore, Milano), and the third in German in 2007 (*Paläontologie der Wirbeltiere*, Dr Friedrich Pfeil, München). This is a measure of the international appeal of vertebrate palaeontology and the demand from students and instructors for up-to-date information.

The story of the evolution of the vertebrates, the animals with backbones, is fascinating. There is currently an explosion of new research ideas in the field concerning all the major evolutionary transitions, the origin of the vertebrates, dramatic new fish specimens unlike anything now living, adaptations to life on land, the origin and radiation of dinosaurs and Mesozoic marine reptiles, the evolution and palaeobiology of dinosaurs, the role of mass extinctions in vertebrate evolution, the origin and diversification of birds, the earliest mammals, ecology and mammalian diversification, the Paleogene radiation of modern mammalian clades, reconciling morphological and molecular evidence on bird and mammal evolution,and the origins and evolution of human beings.

I have five aims in writing this book. First, I want to present **a readable narrative of the history of the vertebrates** that is accessible to everyone, with either a professional or an amateur interest in the subject. The book broadly follows the time-sequence of major events in the sea and on land, so that it can be read as a continuous narrative, or individual chapters may be read on their own. I have tried to show the adaptations of all major extinct groups, both in words and in images.

The second aim is to highlight **major evolutionary anatomical changes** among vertebrate groups. This book is not a classic anatomy text and there is no space to give a complete account of all aspects of the hard-part and soft-part anatomy of the major groups. However, I have selected certain evolutionary anatomical topics, such as the vertebrate brain, tetrapod vertebral evolution, posture and gait in archosaurs, and endothermy in mammals, to present an overview of current thinking, including evolutionary and developmental aspects, where appropriate.

The third aim is to show **how palaeobiological information is obtained**. It is important to understand the methods and debates, and not simply to assume that all knowledge is fixed and immutable. Further, science is about testing hypotheses against evidence, not about who shouts loudest, and it is important to realize that even historical sciences such as palaeontology, can work through hypothesis testing. Science is not all mathematics or chemistry! To do this, I summarize in Chapter 2 the methods used by vertebrate palaeontologists in collecting and preparing the fossils, in using them to learn about ancient environments, biomechanics and palaeobiology, and as evidence for discovering parts of the great evolutionary tree of life. Then, throughout the text, I present box features that are divided into three categories: tree of life controversies (deuterostome relationships, jawless fishes, osteichthyans, sarcopterygians, basal tetrapods, amniotes, dinosaurs and the origin of birds, molecular information on mammalian phylogeny, hominin relationships), exceptional fossils or faunas (new exceptionally preserved basal chordates from China, a rich fossil deposit of early tetrapods, exceptional fishes and marine reptiles from the Triassic of China, dramatic new discoveries of Cretaceous birds, fossil mammals with hair, new basal humans from Africa, the Flores 'hobbit') and palaeobiology of selected unusual ancient vertebrates (limb mechanics of the first tetrapods, jaw action and diet of dicynodonts, archosaur locomotion, hadrosaur chewing adaptations, locomotion of the largest pterosaurs, giant penguins, horse-eating birds, rodents as large as rhinos).

The fourth aim is to survey **the present state of discovery of the tree of life of vertebrates**. The cladograms are set apart from the body of the text and comprehensive lists of the key diagnostic characters are given. In some cases, there are controversies among palaeontologists, or between the morphological and the molecular results, and these are explored. In many cases it was a difficult task to represent current views fairly, yet incisively. Some parts of the tree appear to have been relatively stable for ten years or more, whereas others are changing rapidly – these aspects are indicated. The cladograms throughout the book may be linked to provide an overview of the vertebrate tree of life, and this is replicated in the classification (Appendix 1).

The fifth aim, which has always been embedded in earlier editions, is to highlight **career development for aspiring palaeontologists**. This is done partly by the emphasis on method: the young palaeontologist, progressing through Bachelors, Masters, and Doctoral degrees, must keep an open and enquiring mind. Learning in detail about the occurrence, anatomy, systematics, and function of a particular group of sharks, dinosaurs, or rodents is clearly crucial, as ever, but now the enthusiastic student must also master reasonably advanced numerical protocols in phylogenetic, macroevolutionary, palaeoecological, taphonomic, or biomechanical analysis. Interdisciplinarity is key. The message about career development is stressed also by the choice of current research highlights in the box features: many of these are based on recent publications by young researchers.

I am indebted to many people. I thank †Roger Jones and Clem Earle of Unwin Hyman who commissioned the first edition 25 years ago, Ward Cooper of Chapman & Hall who steered the second edition through, and Ian Francis and Delia Sandford who worked hard on the third edition. The following people read parts of the first, second, and third editions, or made other valuable contributions: Dick Aldridge, Peter Andrews, Kenneth Angielczyk, David Archibald, Chris Beard, David Berman, Derek Briggs, Henri Cappetta, Bob Carroll, Luis Chiappe, Jenny Clack, Mike Coates, Liz Cook, Joel Cracraft, Eric Delson, David Dineley, Phil Donoghue, Gareth Dyke, Andrzej Elzanowski, Susan Evans, Jens Franzen, Nick Fraser, Brian Gardiner, Alan Gentry, David Gower, Lance Grande, †Bev Halstead, †Jim Hopson, Axel Hungerbühler, Christine Janis, Philippe Janvier, Dick Jefferies, Tom Kemp, Zofia Kielan-Jaworowska, Gillian King, Jürgen Kriwet, Adrian Lister, Liz Loeffler, Luo Zhe-Xi, John Maisey, Andrew Milner, Sean Modesto, Kevin Padian, †Alec Panchen, Mike Parrish, †Colin Patterson, Kevin Peterson, Mark Purnell, Jeremy Rayner, Robert Reisz, Olivier Rieppel, Bruce Rubidge, †Bob Savage, Paul Sereno, Glen Storrs, Chris Stringer, Pascal Tassy, Mike Taylor, Nigel Trewin, David Unwin, †Cyril Walker, Peter Wellnhofer, Bernard Wood, and Adam Yates. For the fourth edition, I thank Phil Anderson, Chris Beard, Roger Benson, Donald Benton, Martin Brazeau, Steve Brusatte, Richard Butler, Brian Choo, Jenny Clack, Ted Daeschler, Brian Davis, Phil Donoghue, Greg Edgecombe, Susan Evans, Valentin Fischer, Matt Friedman, Jörg Fröbisch, Keqin Gao, David Hone, Christine Janis, Gerald Mayr, Johannes Müller, Jingmai O'Connor, Davide Pisani, Emily Rayfield, Lauren Sallan, Rob Sansom, Rainer Schoch, Koen Stein, Ian Tattersall, Jakob Vinther, Feiziang Wu, and Xu Xing, who read and commented on individual chapters.

My special thanks go to three artists, Libby Mulqueeny (Belfast) who drew most of the diagrams for the first edition of the book in a frenzy of work, John Sibbick (Bath) who prepared the chapter openers, and Debbie Maizels (Surrey) for the new computer-generated artwork. I also thank those people, who are acknowledged separately throughout the book, who supplied photographs and drawings. Finally, thanks to Ian Francis and Delia Sandford at Wiley Blackwell for commissioning the revision, and Kelvin Matthews and Helen Harvey for their careful work on the text.

Michael J. Benton

NOTE CONCERNING THE REFERENCES

Throughout the book, I refer readers to relevant papers. Most of these are recent, but I include a few older, classic works. There are so many papers on some themes, such as the phylogenetic relationships of particular groups or the biomechanics of dinosaurs, that it is impossible to give a comprehensive, or even a fair listing. I have chosen by preference, short and well illustrated papers and reviews that should be accessible to students. Indeed, I have tried to favour work by young researchers, especially in the box features – this has the additional purpose of showing students how their contemporaries and near-contemporaries are using their skill and enthusiasm to forge professional careers for themselves around the world.

Note. I would appreciate any corrections (fax -44-117-925-3385 or e-mail to mike.benton@bristol.ac.uk). More details at http://www.palaeo.bris.ac.uk/

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† Deceased

List of Boxes

TREE OF LIFE BOXES

EXCEPTIONAL FAUNAS AND PALAEOGEOGRAPHY BOXES

BIOMECHANICS AND BEHAVIOUR BOXES

About the Companion Website

This book is accompanied by a companion website:

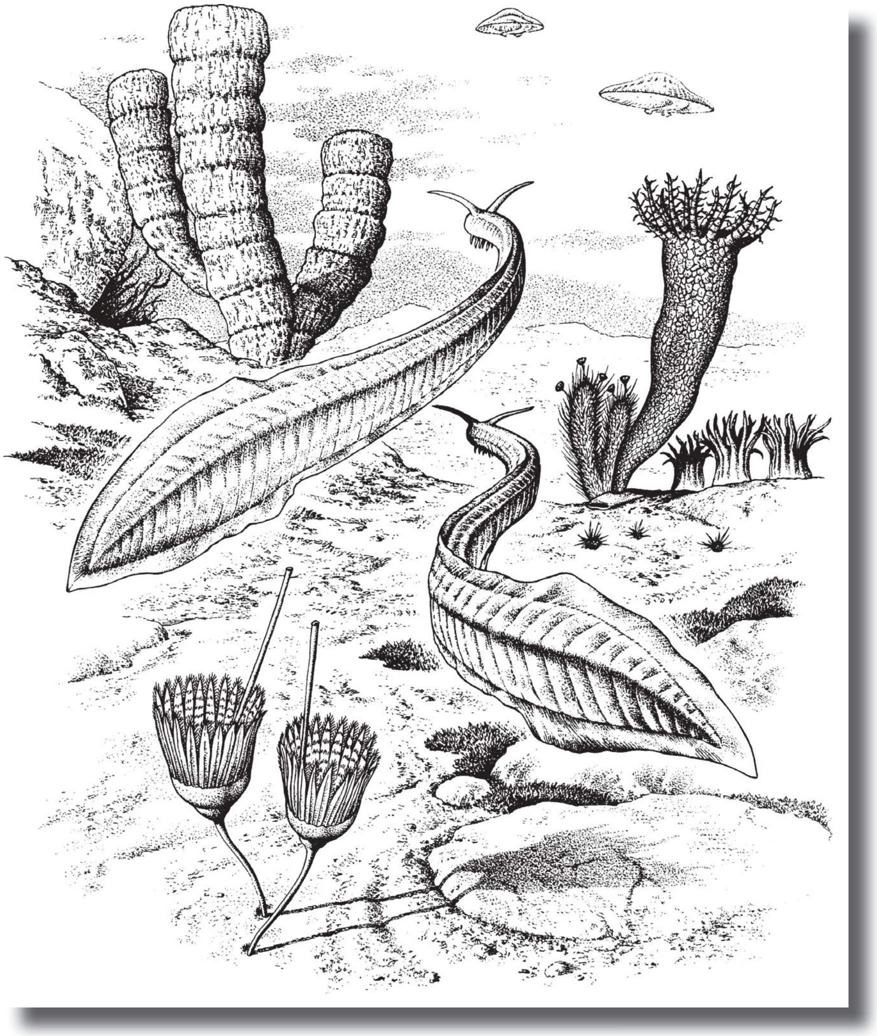
www.wiley.com/go/benton/vertebratepalaeontology

The website includes:

- PowerPoints of all figures from the book for downloading

CHAPTER 1

Vertebrates Originate



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KEY QUESTIONS IN THIS CHAPTER

1 What are the closest living relatives of vertebrates?
2 When did deuterostomes and chordates originate?
3 What are the key characters of chordates?
4 How do embryology and morphology, combined with new phylogenomic studies, inform us about the evolution of animals and the origin of vertebrates?
5 How do extraordinary new fossil discoveries from China help us understand the ancestry of vertebrates?

INTRODUCTION

Vertebrates are the animals with backbones, the fishes, amphibians, reptiles, birds, and mammals. We have always been especially interested in vertebrates because this is the animal group that includes humans. The efforts of generations of vertebrate palaeontologists have been repaid by the discovery of countless spectacular fossils: heavily armoured fishes of the Ordovician and Devonian, seven- and eight-toed land animals, sail-backed mammal-like reptiles, early birds and dinosaurs with feathers, giant rhinoceroses, rodents with horns, horse-eating flightless birds, and sabre-toothed cats. These fossils tell us where the living vertebrates have come from, and they show us glimpses of different worlds that seem so bizarre that they would defy the imagination of a science fiction writer. Despite all this information that has accumulated over the past 200 years, the origin of vertebrates is hotly debated.

One thing is clear from the biology of living animals. Vertebrates are members of a larger group, termed the Phylum Chordata, which also includes their closest living relatives, marine animals such as the sea squirts and amphioxus (see below). These creatures do not have a skeleton, but they share other features, such as a **notochord**, a flexible, tough rod that runs along the length of the body down the back. The notochord in living chordates is generally made from an outer sheath of collagen, a tough fibrous connective tissue that encloses turgid, fluid-filled spaces. Invertebrate chordates also have V-shaped muscle blocks (**myomeres**) along the length of their body. The question about the origin of vertebrates then broadens out to include the origin of chordates.

Looked at more widely, vertebrates are a minor twig in the 'Tree of Life' (Figure 1.1). It is common to think of the major divisions of life as being animals, plants, protists, and simple organisms classed broadly as bacteria and viruses. However, molecular studies since the 1990s (e.g. Woese, 2000; Wolf *et al.*, 2002) have shown that the fundamental splits were between Bacteria, Archaea, and Eukaryota. The familiar plants, animals and fungi are members of Eukaryota, all diagnosed by complex cells with a membrane-bound nucleus and the primitive presence of mitochondria. Within Eukaryota are various protist groups, as well as plants, fungi, and animals, and of course vertebrates are animals. Among animals, it has always been assumed that chordates are closely related to hemichordates (acorn worms and pterobranch worms) and echinoderms (starfish, sea lilies, and sea urchins), and this is now widely confirmed, based on morphological, developmental and molecular evidence.

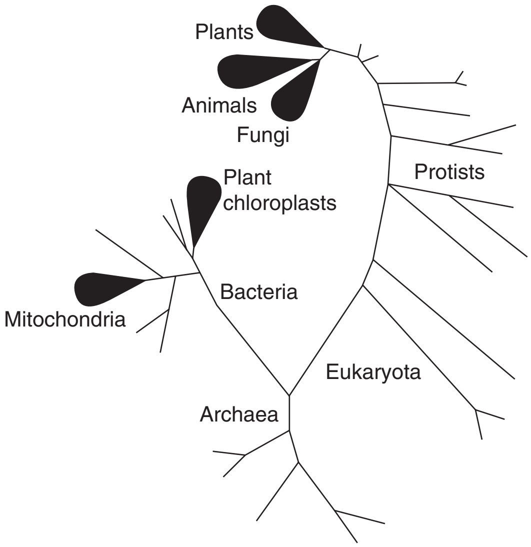


Figure 1.1 The 'Tree of Life', the commonly accepted view of the relationships of all organisms. Note the location of 'Animals', a minor twig in the tree, close to plants and Fungi. Source: Adapted from various sources.

The purpose of this chapter is to explore the various lines of evidence that can be used to reconstruct the origin of the vertebrates: the study of modern animals that are vertebrate-like in some features, the study of molecular relationships, and fossils.

1.1 SEA SQUIRTS AND THE LANCELET

There are two key groups of living non-vertebrate chordates, the sea squirts and the cephalochordates (amphioxus). The amphioxus certainly looks superficially fish-like, but adult sea squirts look like rubbery bottles, and so would hardly seem to be sensible candidates for close relatives of the vertebrates!

1.1.1 Urochordata: sea squirts

A typical sea squirt, or tunicate, is *Ciona* (Figure 1.2(a)), which lives attached to rocks in seas around the world. It is a 100–150 mm tall bag-shaped organism with a translucent outer skin (the tunic) and two openings, or siphons, at the top. The body is firmly fixed to a hard substrate.

The internal structure is fairly complex (Figure 1.2(b)). A large **pharynx** fills most of the internal space, and its walls are perforated by hundreds of gill slits, each of which bears a fringe of **cilia**, fine hair-like vibratile structures. Seawater is pumped through the inhalant siphon into the pharynx by beating movements of the cilia, and the water is then passed through a surrounding cavity, the **atrium**, and ejected through the exhalant siphon. The pharynx serves mainly to capture food particles

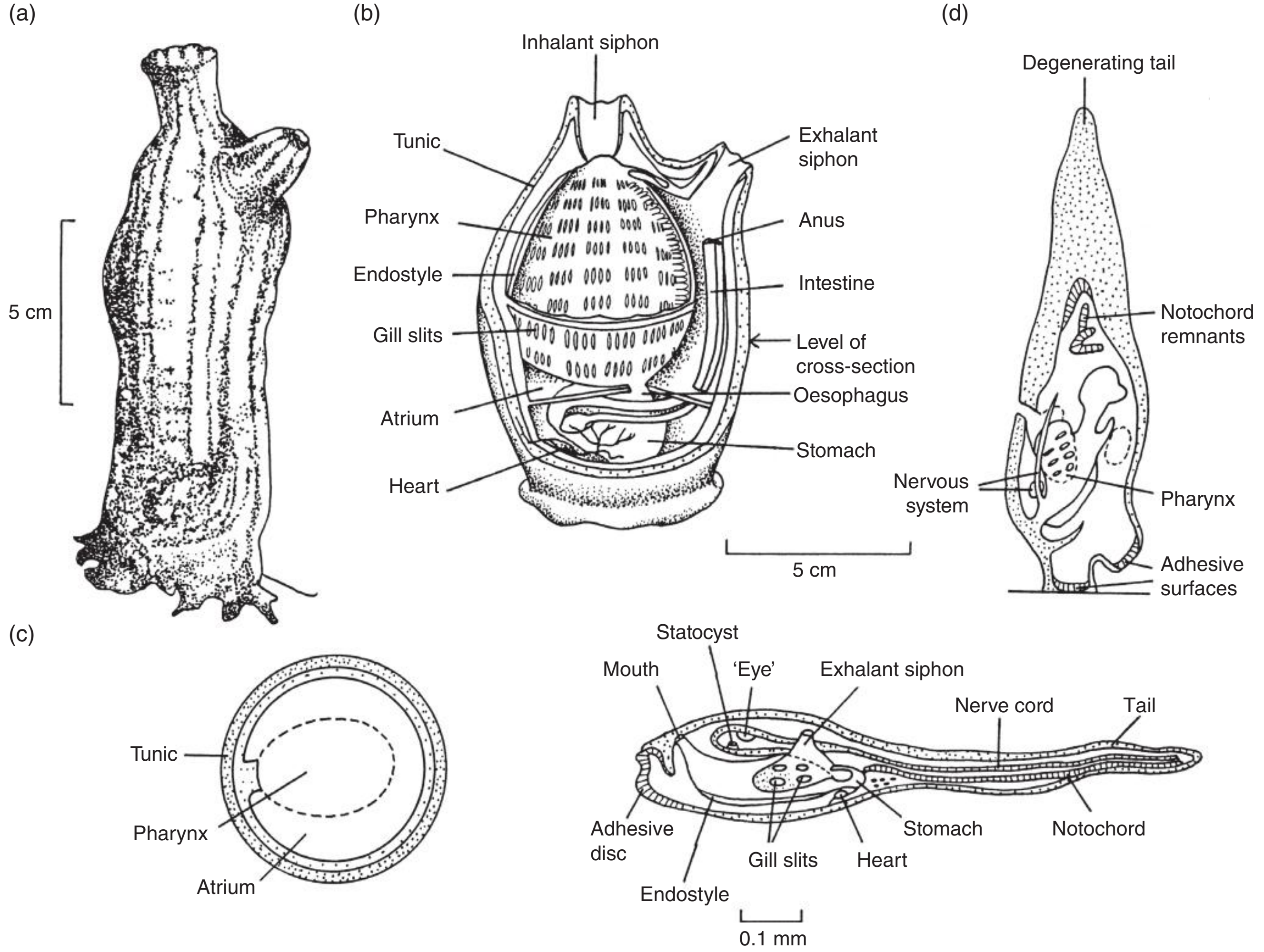


Figure 1.2 The sea squirts: (a) *Ciona*, external view; (b) internal anatomy and cross-section of an adult; (c) swimming larva; (d) metamorphosing form. Source: Adapted from Jefferies (1986) and other sources.

from the stream of seawater that flows through it. The seawater is drawn into a filter bag of mucus, which is produced inside the pharynx by an organ called the **endostyle**. During feeding, the endostyle continuously secretes mucus into the **oesophagus**, together with the food particles that it has filtered from the seawater, and the food is passed to the stomach for digestion. Tunicates also have a heart that pumps the blood around the body; an intriguing aspect is that the heart stops beating every few minutes and the direction of blood flow reverses.

Why is *Ciona* identified as a chordate? The pharynx and other structures are in fact very like those of the cephalochordates and lamprey larvae, but further evidence is to be found in the **larval** stage, when the sea squirt is a tiny free-swimming tadpole-shaped animal with a head and a tail. The larval sea squirt (Figure 1.2(c)) has a notochord that runs along the tail, and this identifies it as a chordate. There are muscles on either side of the notochord that contract alternately, causing the tail to beat from side to side, and this drives the animal forward in the water. The larva has a dorsal nerve cord, running along the tail just above the notochord, and this expands at the front into a very simple brain that includes a light sensor (an 'eye') and a tilt detector.

The larva then settles on a suitable surface. It up-ends onto the tip of its 'snout' and attaches itself by means of adhesive suckers (Figure 1.2(d)). The notochord and tail portion wither away, and the pharynx and gut expand to fill up the body cavity. This extraordinary metamorphosis occurs rapidly to allow the adult to start feeding in its new way as soon as possible.

1.1.2 Cephalochordata: amphioxus

Another chordate generally reckoned to be related closely to the vertebrates is the amphioxus or lancelet, *Branchiostoma*, a representative of the Cephalochordata (or Acraniata). The adult amphioxus is convincingly chordate-like, being a 50 mm long paperknife-shaped animal that looks like a young lamprey or eel, yet lacking a head (Holland, 2010; Bertrand and

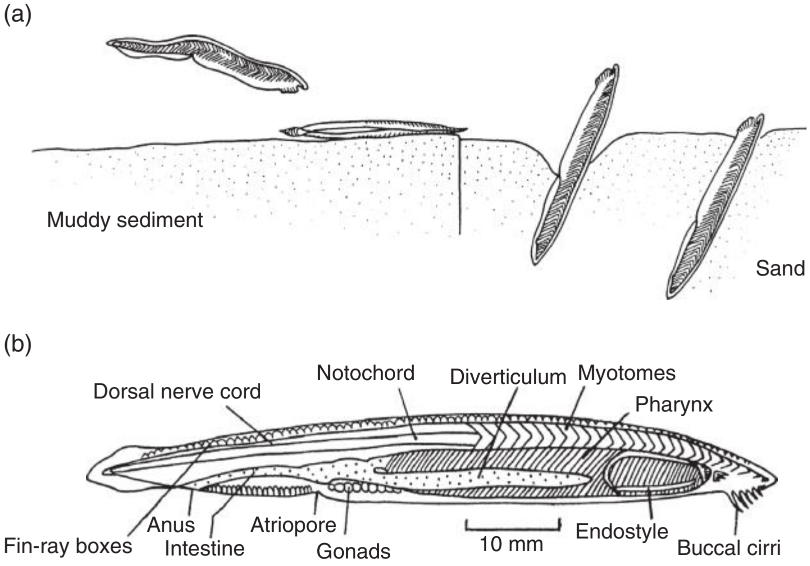


Figure 1.3 Amphioxus, a cephalochordate: (a) modes of life, including swimming and burrowing into sand for protection; (b) internal anatomy. Source: Adapted from Pough *et al*. (2012) and other sources.

Escriva, 2011). Amphioxus swims freely by undulating its whole body from side to side, and it burrows in the sediment on the sea floor (Figure 1.3(a)).

Amphioxus feeds by filtering food particles out of the seawater. Water is pumped into the mouth and through the pharynx by cilia or the gill slits, and food particles are caught up in a bag of mucus produced by the endostyle, the feeding system seen also in tunicates and in the larvae of the lamprey. The mucus with its contained food particles is pulled into the gut for digestion, whereas the seawater passes through the gill slits into the atrium. Oxygen is also extracted, and the waste water then exits through the **atriopore**.

The anatomy of amphioxus, with its pharynx, notochord, dorsal nerve cord, myotomes, and endostyle (Figure 1.3(b)) is typically chordate. Swimming and burrowing are by means of lateral contractions of the myomeres acting against the stiff rod-like notochord.

1.2 AMBULACRARIA: ECHINODERMS AND HEMICHORDATES

Unexpected relatives of chordates are the Ambulacraria, a clade consisting of echinoderms and hemichordates. The living members of these groups do not look much like modern vertebrates, but there is considerable evidence for the relationship (see Box 1.1).

Echinoderms today include such familiar animals as starfish and sea urchins, as well as ophiuroids (brittle stars), crinoids ('sea lilies') and holothurians ('sea cucumbers'). There are some 7000 species of living echinoderms and 13,000 extinct species. Echinoderms all share four key features: (1) a calcite skeleton made from many ossicles, each composed of many aligned small crystals in a somewhat spongy arrangement called stereom; (2) a water vascular system that functions in locomotion, respiration, and feeding; (3) ossicles are linked by mutable collagen, ligaments that are normally rigid, but can be loosened; and (4) pentaradial (five-fold) symmetry. Most of these special features of echinoderms do not show close similarities to other deuterostomes, but the water vascular system may have evolved from simple tentacular systems, such as those of pterobranch hemichordates.

The first putative echinoderms include *Arkarua* from the Vendian of Australia, a disc-shaped organism with radial ridges and a five-pointed central depression, but it has no stereom or evidence of a water vascular system and the identification is inconclusive. The first definitive echinoderms appeared in the Early Cambrian as part of the Cambrian Explosion, and these included some close relatives of living forms, as well as other entirely extinct groups, some of them lacking pentaradial symmetry.

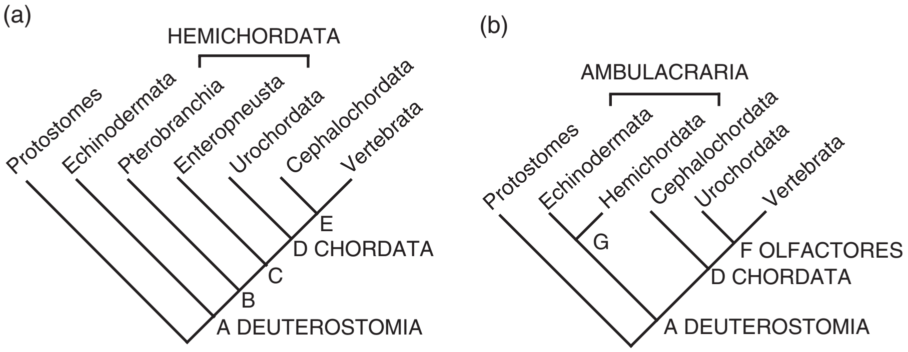
The hemichordates (Röttinger and Lowe, 2012) include two superficially very different kinds of marine animals. The first, the pterobranchs such as *Cephalodiscus* (Figure 1.4(a,b)), are small animals that live in loose colonies on the seabed in the southern hemisphere and in equatorial waters. *Cephalodiscus* has a plate-like head shield, a collar with five to nine pairs of feeding arms, and a sac-like trunk perforated by a pair of gill slits and containing the gut and gonads, and the body ends in a contractile stalk. Cilia on the arms produce a feeding current, and food particles are captured by mucus on the arms, while water passes out of the pharynx through the gill slits. The animal lives in or around a group of horny tubes that the colony has constructed, and it attaches itself inside these tubes by means of a sucker on the end of the stalk.

The second hemichordate group, the acorn worms, or enteropneusts, such as *Saccoglossus*, are worm-like animals varying in length from 20 mm to 2.5 m. They live in burrows low on the shore in Europe and elsewhere. *Saccoglossus* (Figure 1.4(c)) has a long muscular proboscis that fits into a

BOX 1.1 DEUTEROSTOME RELATIONSHIPS

Two substantially different schemes for deuterostome relationships have been proposed. The ‘traditional’ view (e.g. Maisey, 1986; Donoghue *et al.*, 1998; illustration (a)) was to place the hemichordates as basal to chordates since they both share ciliated gill slits and giant nerve cells, as well as other features, which are not seen in echinoderms. Enteropneusts were sometimes said to be closer relatives of chordates since their gill slits are similar, they have a very short dorsal hollow nerve cord, and a number of other features of the gut not seen in pterobranchs. Most authors regarded amphioxus as the closest relative of the Vertebrata on the basis of 10–15 features that are not seen in tunicates.

The second view (illustration (b)) is supported by morphological and molecular data and is now widely accepted (Swalla and Smith, 2008; Edgecombe *et al*., 2011). The first molecular studies, in which the 18S rRNA genes of echinoderms, hemichordates, and chordates were compared were inconclusive, but newer work (e.g. Eernisse and Peterson, 2004; Delsuc *et al*., 2006; Swalla and Smith, 2008; Edgecombe *et al*., 2011; Röttinger and Lowe, 2012; Cannon *et al*., 2013) pairs hemichordates with echinoderms as the clade Ambulacraria, and within the clade Chordata places cephalochordates as the basal clade, and pairs Urochordata and Vertebrata, as clade Olfactores because of shared characters in the olfactory region. See Box 3.1 for phylogeny of Vertebrata.



Cladograms showing the relationships of the main deuterostome groups: (a) the ‘traditional’ model, and (b) molecular model. Synapomorphies: **A DEUTEROSTOMIA**, blastopore becomes anus during development, bipartite mesocoel, mesocoelomic ducts; **B**, stomochord, paired gill slits; **C**, multiple pairs of gill slits, pharyngeal slits U-shaped, dorsal hollow nerve cord, preoral ciliary organ, mouth anterior and ventral and anus posterior and ventral or dorsal, multiciliated cells; **D CHORDATA**, notochord present and not attached to gut, dorsal hollow nerve cord with neural-plate stage in development, endostyle organ, a true tail used in swimming; **E**, digestive caecum, open capillary junctions, somites present, lateral-plate mesoderm, neural tube differentiated into grey and white matter, cerebral vesicle in brain; **F OLFACTORES**, specialized olfactory areas in buccal cavity, hind-tail tripartite, dorsal longitudinal canal connected with notochord; **G AMBULACRARIA**, trimeric arrangement of the adult coelom, axial complex with hydropore, dipleureula larva with neotroch.

fleshy ring or collar behind. The mouth is placed beneath this collar, and seawater and sand are pumped through the gut and expelled through an anus at the posterior end of the body. The long body is pierced by small holes at the front end, homologous with the gill slits of *Cephalodiscus*, sea squirts, amphioxus, and vertebrates, based on morphology and expression of developmental genes (Cannon *et al*., 2013). Developmental genes also indicate homology of the postanal tail regions in *Saccoglossus* and vertebrates.

The fossil record of enteropneusts has been debated. It is widely assumed that the extinct, colonial graptolites were a clade of hemichordates, and particularly allied with pterobranchs, based on similarities in the ultrastructure of their wall structures (Sato *et al*., 2008). However, fossils of the two extant clades have been restricted to rare forms in the Carboniferous and Jurassic until reports (Caron *et al*., 2013; Maletz, 2014) of Cambrian specimens from Chengjiang and the Burgess Shale respectively. The latter example, the worm-like *Spartobranchus*, shows a fibrous tube that might be a precursor of the pterobranch periderm, suggesting that pterobranchs arose from enteropneust-like ancestors.

The phylogeny of hemichordates is actively debated. However, morphological (Smith *et al*., 2004) and molecular (Röttinger and Lowe, 2012; Cannon *et al*., 2013) data now concur that Hemichordata is a valid phylum. Hemichordates do not have a notochord at any stage, but they possess gill slits, as in chordates, and giant nerve cells in the nerve cord of the collar region that are probably equivalent to similar nerve cells in amphioxus and primitive vertebrates. Both pterobranchs and enteropneusts share morphological characters indicating monophyly of the Hemichordata, such as the stomochord (an anterior buccal tube on the dorsal part of the pharynx) and mesocoelomic ducts. Earlier molecular phylogenetic studies suggested that enteropneust worms were either monophyletic (based on 28S rDNA) or not (based on 18S rDNA), but micro-RNAs provide strong evidence for monophyly (Peterson *et al*., 2013).

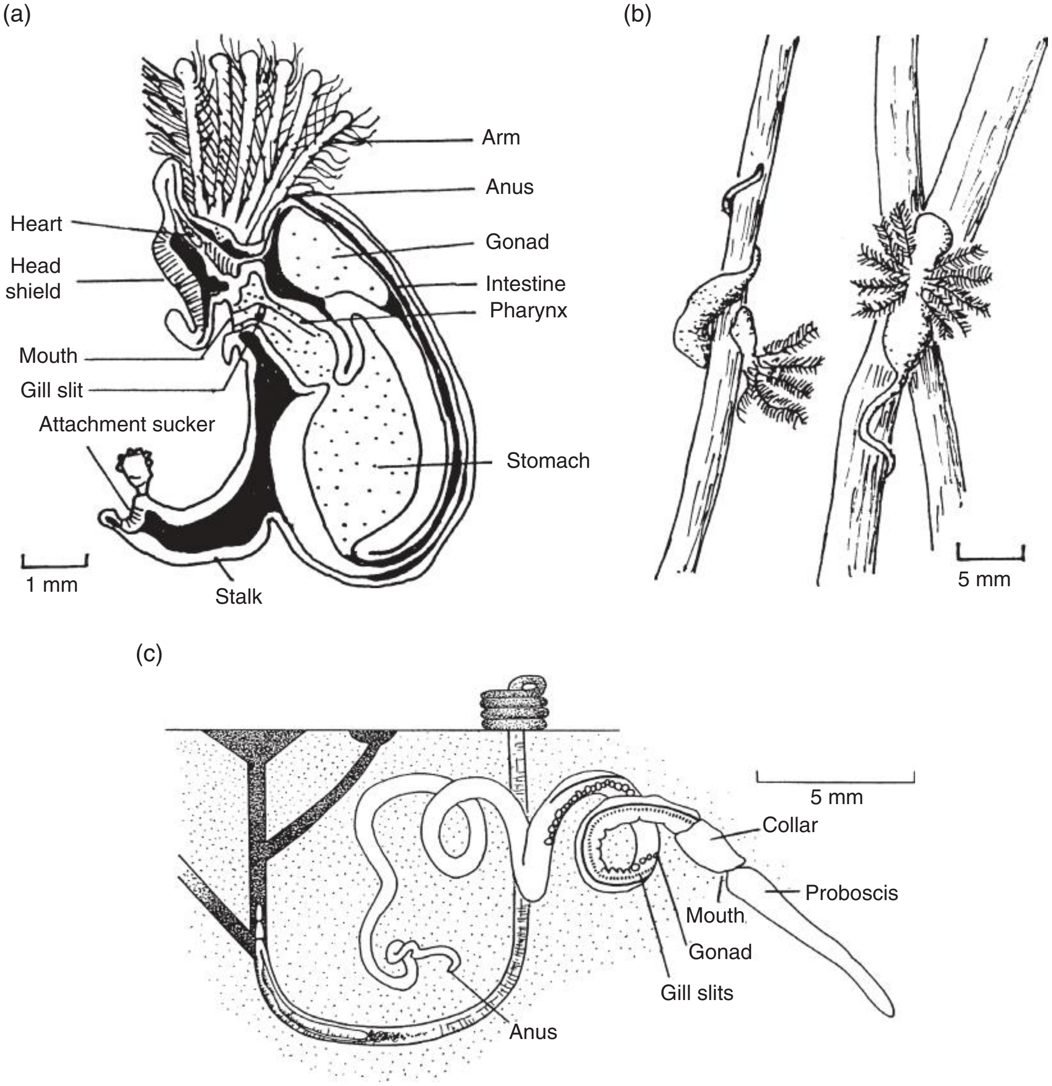


Figure 1.4 Typical hemichordates: (a) the pterobranch *Cephalodiscus*, internal anatomy and (b) mode of life; (c) the enteropneust *Saccoglossus*, mode of life and external anatomy. Source: Adapted from Jefferies (1986) and other sources.

1.3 DEUTEROSTOME RELATIONSHIPS

The relationships of chordates used to be rather problematic, but intensive analyses of molecular data have provided a clearer picture (Eernisse and Peterson, 2004; Swalla and Smith, 2008; Edgecombe *et al.*, 2011). The Phylum Chordata is part of a larger clade, the Deuterostomia, comprising chordates, hemichordates, and echinoderms, which in turn is part of a yet larger clade of all the bilaterally symmetrical animals, the Bilateria, and these in turn fall within Metazoa, the animals. But what exactly diagnoses the Deuterostomia, and how can some of our closest relatives be sea urchins, starfish, and worm-like animals? The clues come from **embryology**, the study of the early phases of development in, and just out of, the egg, and from molecular phylogenetic analysis.

1.3.1 Embryology and the position of the anus

In early development each animal starts as a single cell. Soon this cell begins to divide, first into two cells, then four, then eight, sixteen, and so on (Figure 1.5(a–c)). Eventually a hollow ball of cells is produced, called the **blastula** stage (Figure 1.5(d)). A pocket of cells then moves inwards, forming the precursor of the gut and other internal structures. The opening of this deep pocket is called the **blastopore**. You can imagine pushing in the walls of a hollow rubber squash ball with your thumb to produce a model of this embryonic pattern, known as the **gastrula stage** (Figure 1.5(e–g)).

Embryologists noticed some time ago that animals fall into two large groups depending on the relative orientation of the mouth and anus. The classic story is that in most invertebrates (the **protostomes**), the blastopore becomes the mouth (Figure 1.5(h)),

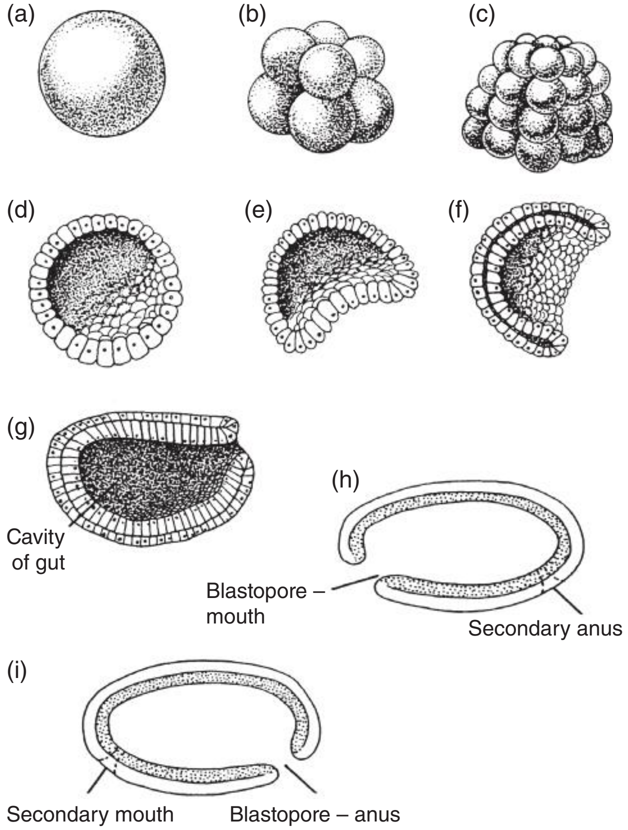


Figure 1.5 Embryonic development: (a–g) sequence of cell division in amphioxus, from the single-cell stage (a), through the blastula stage (d), to the gastrula stage (g). (h) Fate of the blastophore in protostomes, and (i) in deuterostomes. Source: Adapted from Jefferies (1986) and other sources.

whereas in others (the **deuterostomes**), including the chordates, this opening becomes the anus (Figure 1.5(i)), and the mouth is a secondary perforation. Such a dramatic turnaround, a switch from mouth to anus, seems incredible. Note, however, that many protostomes show deuterostomy, and this condition may be primitive and shared by all Bilateria (Eernisse and Peterson, 2004). This peculiarity of embryological development was noted over a century ago, and the group Deuterostomia named in 1908; but does it stand up to the scrutiny of modern molecular phylogenetics?

1.3.2 Animal phylogenomics

Numerous zoologists have contributed over the years to disentangling the relationships of animals. All creatures from sponges and corals to crabs, clams, and birds, are animals, members of the clade Metazoa, diagnosed by a combination of feeding, being motile, lacking rigid cell walls, and passing through the blastula embryonic stage. These characteristics are not all exclusive, however. First, metazoans are distinguished from most plants and algae by being **heterotrophs**, meaning they feed on other organisms to acquire carbon, which is digested in an internal chamber (gut), whereas plants and algae are able to fix carbon from the atmosphere or water. Fungi and many bacteria, however, are also heterotrophs. Secondly, metazoans are **motile**, meaning they use energy to move spontaneously and actively, at least at some stage in their lives (larval stages in 'fixed' forms such as sponges and corals can swim), although some bacteria and protists are also motile, moving by means of a flagellum. Thirdly, animals lack the rigid cell walls seen in plants, fungi, and algae, and fourthly most pass through the blastula embryonic stage (see Section 1.3.1).

Metazoa, Bilateria, and Deuterostomia are **monophyletic** groups, or **clades**. A clade is a group that has a single common ancestor, and that includes all of the descendants of that ancestor (see Section 2.5.1). Before the advent of molecular phylogenetics (see Section 2.5.2), and even after, there has been active debate about the relationships of the various animal clades. It is usually easy to determine membership of these major clades, the phyla (see Box 2.4) – such as arthropods, molluscs, or sponges – but determining how the phyla relate to each other within Metazoa has been difficult. However, by 2010, a consensus about the major outlines of animal relationships had been reached (Figure 1.6).

The fundamental division of Metazoa distinguishes six early-branching clades (including sponges and corals) from the Bilateria, supported by both morphological and molecular evidence (Eernisse and Peterson, 2004; Halanych, 2004; Philippe *et al.*, 2009; Edgecombe *et al.*, 2011; Nielsen, 2012). The Bilateria have bilateral symmetry primitively, and most are **triploblastic**, meaning they have three fundamental body wall tissues that arise from the ectoderm, mesoderm, and endoderm in the embryo. Non-bilaterian metazoans may be diploblastic, lacking the mesoderm, or monoblastic like sponges and placozoans. Within Bilateria, most animals are Nephrozoa, taxa that are characterized by the possession of an excretory system. Finally, Nephrozoa is divided into the two major clades Protostomia and Deuterostomia, long recognized on embryological grounds. Protostomes include the Ecdysozoa (animals that moult, such as nematodes, arthropods, priapulids, and some minor groups) and Spiralia (animals with spiral development, such as bryozoans, annelids, molluscs, brachiopods, rotifers, and other phyla). Most spiralians belong to the clade Lophotrochozoa.

The monophyly of Deuterostomia is confirmed both by morphology and by phylogenomics. All deuterostomes share the posterior blastopore that generally becomes the anus, as well as gill slits (present only in precursors of the echinoderms). Further, most molecular phylogenetic analyses indicate monophyly (e.g. Eernisse and Peterson, 2004; Swalla and Smith, 2008; Edgecombe *et al.*, 2011; Röttinger and Lowe, 2012; Cannon *et al.*, 2013), although this is queried in some studies (e.g. Delsuc *et al.*, 2006; Mallatt *et al.*, 2010). Some recent phylogenomic studies have suggested the addition of two further clades to Deuterostomia, the Xenoturbellida and the Acoelomorpha, simple worms with no through gut and a simple nervous system. However, these assignments are controversial (Edgecombe *et al.*, 2011; Röttinger and Lowe, 2012). Further, there has been some dispute over the interrelationships among these deuterostome taxa (see Box 1.1).

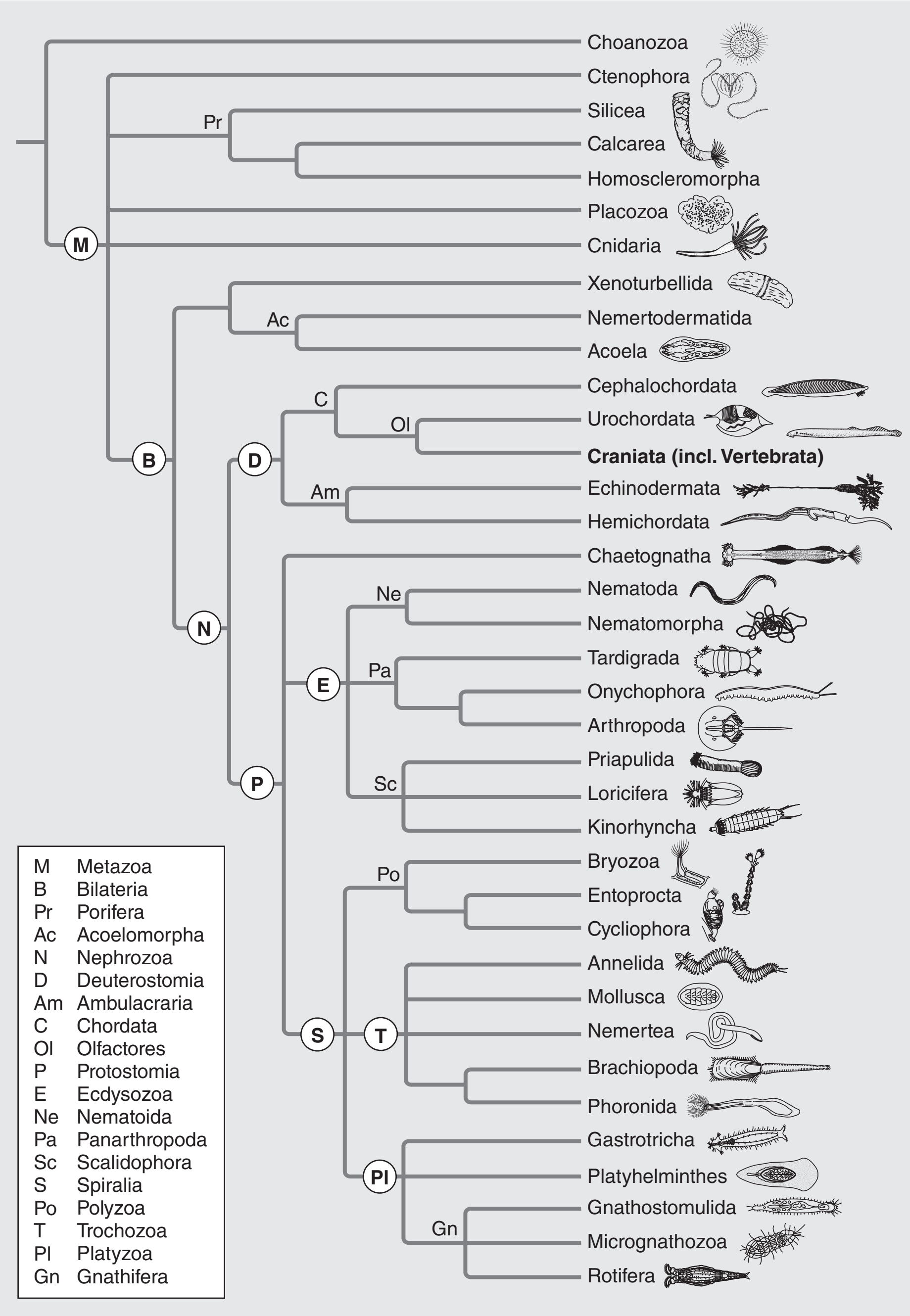


Figure 1.6 Relationships of the major phyla of animals, based on accumulated knowledge from anatomy and embryology, combined with current phylogenomic work. Source: G. Edgecombe, The Natural History Museum, London, UK. Reproduced with permission.

1.4 CHORDATE ORIGINS

Among morphological characters, the chordates all share several unique features such as a notochord, a dorsal hollow nerve cord with a shared developmental pattern, an endostyle organ (equivalent to the thyroid gland of vertebrates), and a tail used for swimming. It is generally accepted that only chordates have true tails. A tail technically may be defined as a distinct region extending behind the visceral cavity, and in particular located entirely behind the anus; hence the term ‘postanal tail’, to be quite precise. Non-chordates, such as insects, worms, molluscs, jellyfish, and sea urchins, do not have tails. What of the fossil evidence?

There are many putative early fossil chordates, and their numbers have grown hugely since 1995, with the announcement of remarkable new finds from the Chengjiang biota of China, an Early Cambrian deposit (see Box 1.2). These new specimens, combined with studies of modern forms, give clues about the

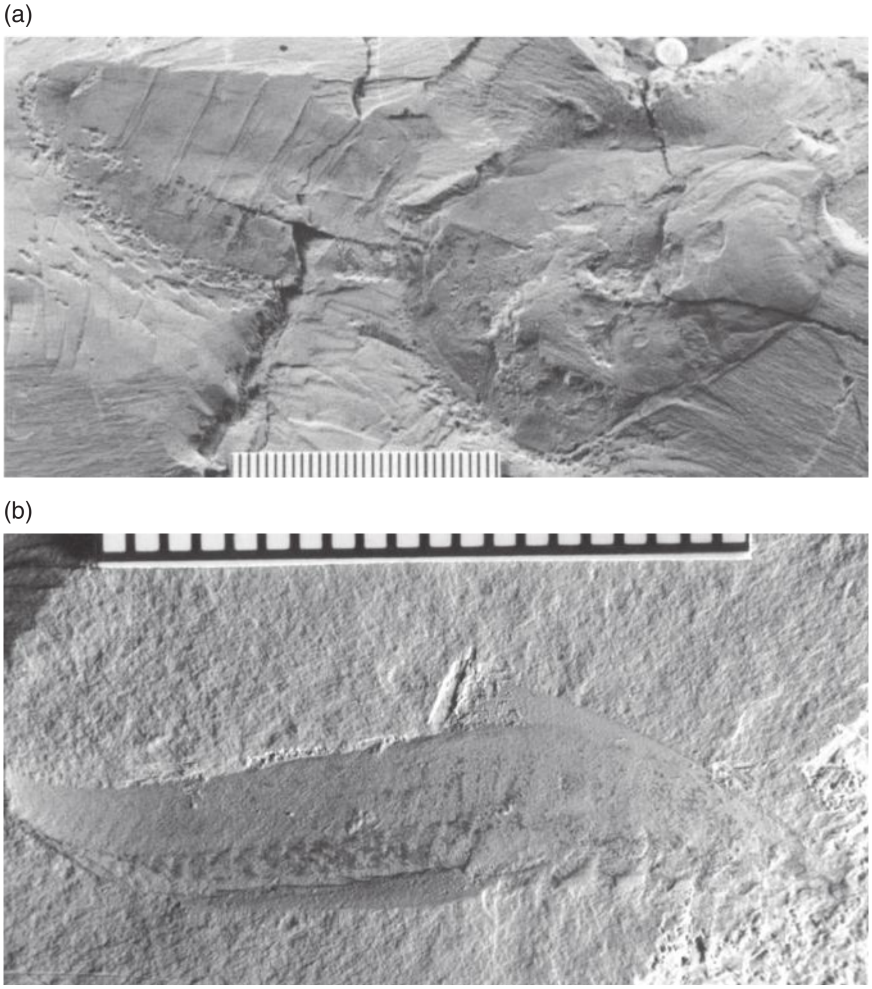
BOX 1.2 THE CHENGJIANG BIOTA

The Chengjiang biota from Yunnan Province, south-west China, is exciting because it is one of the oldest sources of exceptionally preserved organisms, falling early in the great Cambrian radiation of animals in the sea (Hou *et al*., 2004; Shu *et al*., 2010). The fossils come from different levels through several hundred metres of mainly fine-grained sediments, comprising the Maotianshan Shales. When the site was discovered, in 1984, it was thought to correspond to the already well-known Burgess Shale, a Middle Cambrian locality in Canada that has yielded numerous exceptionally preserved arthropods and the putative chordate *Pikaia*. Chengjiang, however, is older, dating from the middle of the Early Cambrian, some 525–520 Myr ago.

The Chengjiang biota is rich, having been collected now from over 30 localities that have produced tens of thousands of specimens. The fauna consists of more than 200 species, mainly of arthropods (trilobites and trilobite-like forms), sponges, brachiopods, worms, and other groups, including possible basal deuterostomes, such as the vetulicolians and yunnanozoons (see Figure 1.7), as well as the first fishes (Zhao *et al*., 2013). Some of the arthropods are like Burgess Shale animals, but others, such as the basal deuterostomes, seem to be unique. Most of the animals lived on the bottom of the seabed, filtering organic matter from the sediment. There were a few floaters and swimmers, and some of the larger arthropods were clearly predators, feeding on the smaller bottom-dwellers.

The Chengjiang beds are grey marine mudstones that preserve soft tissues of many animals in exquisite detail, some replaced by phosphate and others by pyrite. Some soft tissues survive as thin organic films. The grey sediment weathers on contact with the air to a light grey or yellow colour, and the fossils may also be grey, or sometimes reddish, and with internal anatomical details picked out in shades of grey, brown, and black.

Read more at: http://en.wikipedia.org/wiki/List_of_Chengjiang_Biota_species_by_phylum and http://palaeo.gly.bris.ac.uk/Palaeofiles/Lagerstatten/chngjang/index.html.



Typical Chengjiang fossils, the vetulicolian *Xidazoon* (a), facing left, and the basal vertebrate *Myllokunmingia* (b), facing right. Scale bars in millimetres. Compare with interpretive drawings in Figures 1.7 (b) and 3.1(a). Source: D. Shu, Northwest University, Xi'an, China. Reproduced with permission.

early evolution of chordates, but there are many debates (Donoghue and Purnell, 2009).

1.4.1 Diverse early chordates

There are three main categories of possible early chordates: possible urochordates, possible cephalochordates, and vetulicolians. At one time, conodonts, represented in the fossil record generally only by their tooth elements, were treated as dubious chordates. Conodonts are now placed firmly within the Vertebrata, as jawless fishes, as are some of the basal chordate taxa from Chengjiang, such as *Haikouichthys* (see Chapter 3).

Urochordates have a patchy fossil record. Isolated impressions of sac-like bodies, and **trace fossils**, markings made in or on the sediment by the activities of animals, have been ascribed to tunicates. The best fossils are small sac-like specimens from Chengjiang, *Shankouclava*, which shows a large perforated branchial basket, branchial slits, and an elongate endostyle (Chen *et al*., 2003). There is also a possible degenerating tail, suggesting this might be a larva that had just settled (cf. Figure 1.2(d)).

The fossil record of cephalochordates is not much better. The Chengjiang biota includes a superficially amphioxus-like cephalochordate, *Cathaymyrus*, as well as the yunnanozoons, which have also been identified as cephalochordates, although most assign them to other positions among deuterostomes (see below). In the absence of hard tissues such as bone, these non-vertebrate chordates are not often preserved.

1.4.2 Vetulicolians and yunnanozoons

The Vetulicolia are an unusual group, based on about ten species from the Chengjiang Formation, as well as *Banffia*, named in 1911 from the Burgess Shale in Canada, and only later associated with the Chinese fossils, and materials from the Cambrian site, Sirius Passet, in Greenland, and from the United States (Figure 1.7(a,b)). These animals look like sausage balloons, knotted in the middle: the body is in two parts, with bulbous sections in front of, and behind, a flexible connection. There is a large mouth with a strengthened rim, and preserved internal structures include the guts. Both parts of the body appear to be crossed by transverse bands. On the mouth-bearing segment, presumably the front part of the body, are five circular structures in a row that have been interpreted as pharyngeal gill slits.

The vetulicolians were regarded first as unusual arthropods, and then as deuterostomes. In their review and phylogenetic analysis, Aldridge *et al.* (2007) were unable to determine whether vetulicolians were arthropods, deuterostomes, or even kinorhynchs, a clade of segmented ecdysozoans close to priapulids. Most recent authors, however, assign vetulicolians to Deuterostomia, and they have been accorded three positions (Figure 1.8): as basal deuterostomes, as urochordates or as basal chordates (Gee, 2001). Evidence that vetulicolians are deuterostomes are the gill slits and a possible endostyle, although the latter identification has been questioned. They were interpreted as basal deuterostomes by Shu *et al.* (2001, 2010) because they apparently lack an atrium, the internal chamber in cephalochordates and tunicates into which the gill slits and anus open. In vetulicolians, the intestine terminates at the end of the body, and the gill slits presumably opened directly to the outside through openings in the external body wall. Vinther *et al.* (2011) confirmed this, based on new specimens from Greenland that show the lateral pouches that appear to be homologues of gill slits, a large sediment-filled atrium (in opposition to the interpretation by Shu *et al.* (2010)), which they regard as possibly a character of all deuterostomes and not just urochordates, and possible lateral flexure of the tail. Their terminal anus, if the gut is correctly interpreted, means that vetulicolians lack a postanal tail, and so they cannot be regarded as stem-group chordates. Ou *et al.* (2012) confirm this view with their observations of the lateral gill slits in new Chinese material. Others had earlier assigned vetulicolians to Urochordata because of the general resemblance in the bulbous streamlined body shape, as well as the thin external tunic, and the regularly spaced transverse

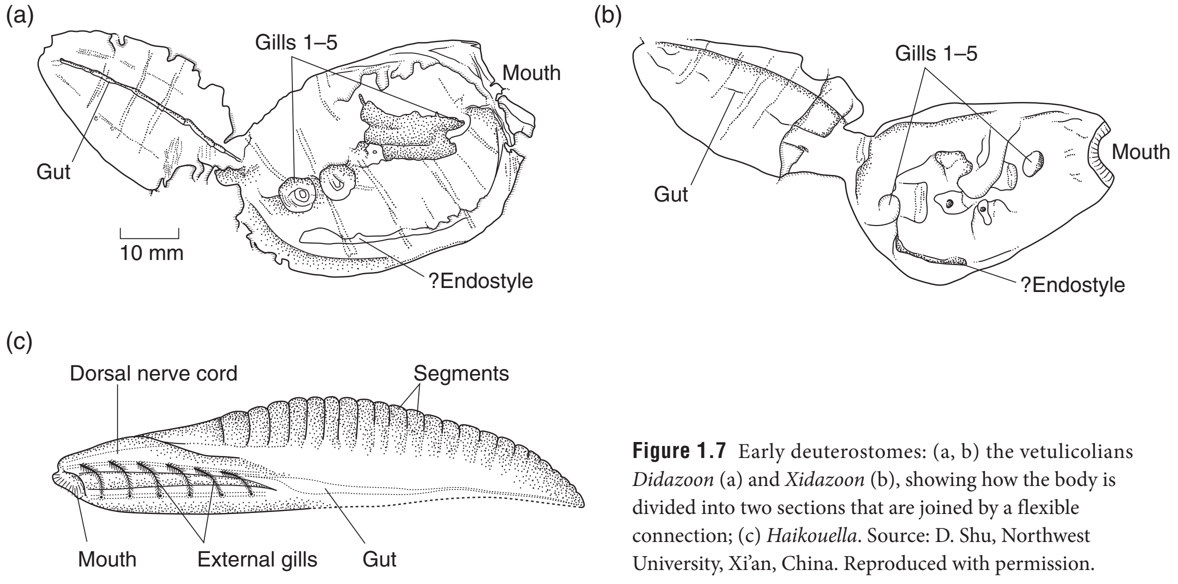


Figure 1.7 Early deuterostomes: (a, b) the vetulicolians *Didazoon* (a) and *Xidazoon* (b), showing how the body is divided into two sections that are joined by a flexible connection; (c) *Haikouella*. Source: D. Shu, Northwest University, Xi'an, China. Reproduced with permission.

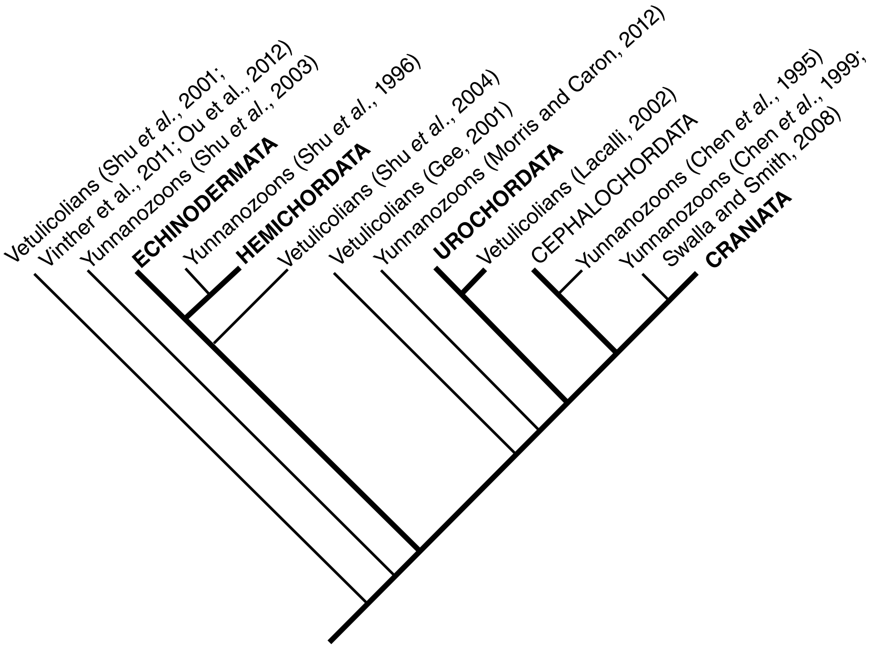


Figure 1.8 Phylogenetic tree of the extant deuterostomes, with suggested locations of the major fossil groups. Source: Adapted from various sources.

bands, which might be muscles that ran round the body in rings (Lacalli, 2002). The absence of a notochord in vetulicolians was said not to be critical, since most adult tunicates also have lost this structure, and Gee (2001) suggested that these unusual fossils are just what would be expected as the ancestral vertebrate, long predicted to have emerged from a sac-like animal that is all guts (like a tunicate), which then became surrounded by musculature, nerves, and sensory systems to enable locomotion.

The yunnanozoons, also from Chengjiang, such as *Yunnanozoon* and *Haikouella* (Figure 1.7(c)) look like much more convincing basal chordates, perhaps even close to vertebrates, with their fish-like form, dorsal fin, postanal tail, notochord, gill slits, and even some head structures. Nonetheless, they have been interpreted as occupying many different positions in deuterostome phylogeny (Figure 1.8) by rival researchers. One team identified these animals first as possible cephalochordates (Chen *et al.*, 1995), and then upwards as vertebrates (Chen *et al.*, 1999; Holland and Chen, 2001; Mallatt and Chen, 2003). The other team preferred to regard the yunnanozoons first as hemichordates (Shu *et al.*, 1996), and then downwards as basal deuterostomes allied to the vetulicolians (Shu *et al.*, 2003b). The problems revolve around different interpretations of coloured blobs, lines, and squiggles in the fossils. There are plenty of fossils – literally thousands – but anatomical interpretation is critical (Donoghue and Purnell, 2009).

Haikouella and *Yunnanozoon* are 25–40 mm long, and preserved as flattened bluish-grey to black films on the rock. Chen *et al.* (1995) were able to see a notochord, a filter-feeding pharynx with an endostyle, segmented musculature, and branchial arches, all chordate characters. Chen *et al.* (1999) and Mallatt and Chen (2003) went further, identifying an enlarged, possibly three-part, brain and paired lateral eyes in *Haikouella*, hence indicating it might have had a distinctive, enlarged head, a key feature of vertebrates. Shu *et al.* (1996) argued, however, that there is no notochord, and that this tubular structure is actually the gut. In addition, they suggested that the segmented musculature was wrongly identified. In contrast, they claimed to see key hemichordate features in *Yunnanozoon*, and especially that the body is divided into three parts from front to back, a proboscis, a collar, and a trunk that is divided into a branchial and a gut region, just as in the living acorn worm (see Figure 1.4(c)). Shu *et al.* (2003, 2010) subsequently noted similarities between the yunnanozoons and the vetulicolians, and moved them down from the hemichordates to a basal position among deuterostomes (Figure 1.8): they could see no evidence of a notochord, segmented muscles, a large brain, lateral eyes, or any of the other chordate features previously reported.

Figure 1.9 The early chordate *Pikaia* from the Burgess Shale, Canada. Source: J-B. Caron, Smithsonian Institution, Washington , DC, USA. Reproduced with permission.

The final early chordate to consider is *Pikaia* from the Burgess Shale in Canada, named in 1911 as an annelid, but subsequently widely regarded as a basal chordate or even basal vertebrate (Figure 1.9). In a thorough redescription of 114 specimens, Conway Morris and Caron (2012) highlight its chordate characteristics: a laterally compressed, hydrodynamic body with about 100 myomeres, a thin dorsal fin, a small bilobed head with tentacles but no eyes, possible pharyngeal pores, a pharyngeal cavity, an almost terminal mouth, a probable terminal anus (and hence no postanal tail), a dorsal nerve cord, a possible notochord, and a blood vascular system. As with the yunnanozoons, however, determining the phylogenetic position of *Pikaia* is problematic. It is a chordate because of the sigmoidal (S-curved) myomeres and the putative notochord. Some would classify it as a chordate, or even a vertebrate, on the basis of the head and putative sensory organs, but Conway Morris and Caron (2012) see it as allied with yunnanozoons, at the base of Chordata (see Figure 1.8). In a revision of the new morphological data, Mallatt and Holland (2013) cannot resolve the phylogenetic position of *Pikaia*, but find it located higher in the tree, either as sister group to Chordata or to Vertebrata.

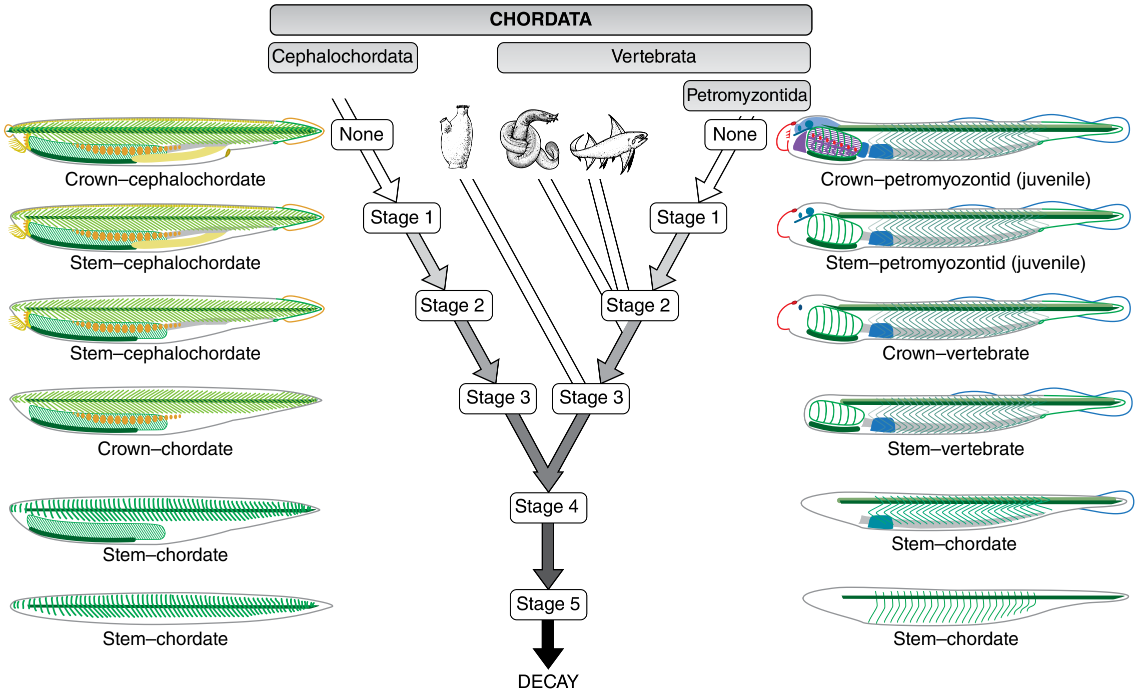
An important note of caution about the interpretation of *Pikaia* and the other early deuterostome fossils is that their phylogenetic placement depends on the identification of key diagnostic characters of the various subclades, such as ambulacrarians, cephalochordates, urochordates, and chordates, and yet taphonomic experiments (see Box 1.3) suggest the need for extreme caution.

BOX 1.3 ROTTING BIAS

When an organism dies its carcass decays, and information is lost. Until recently, such loss of information was assumed to be random, but taphonomic experiments on modern amphioxus and lampreys (Sansom *et al.*, 2010) show that the first tissues to rot away take with them key diagnostic characters. In fact, through the process of decay over a few weeks, tissues are lost in such a way that the specimens become more and more primitive in appearance.

The rather smelly experiments on lamprey and amphioxus juveniles were run for up to 200 days, with dead specimens decaying in normal seawater and at reasonable temperatures. Tissues began to be lost quickly. In the case of amphioxus, the eye spot was lost after 11 days, the atriopore after 15, the anterior bulb after 21, and the midgut caecum and storage organ after 28. Most resilient to decay were the myomeres and the notochord, and before those the endostyle, pharyngeal arches, and gonads. Sansom *et al.* (2010) noted that these last tissues are those most commonly seen in exceptionally preserved basal chordate and deuterostome fossils from the Chengjiang and Burgess Shale biotas.

The initial suite of characters that disappeared in the decaying amphioxus specimens were those diagnostic of Cephalochordata, and the myomeres and notochord are the most general chordate characters. Normal decay processes then favour preservation of primitive characters, and phylogenetic analysis of chordate fossils will position the fossils in a more basal position than is correct. These decay experiments strongly suggest that the fossil record of non-vertebrate chordates is affected by a systematic bias of stem-ward slippage down the cladogram, and that some Cambrian chordate fossils are placed too deep in the phylogeny. These experiments partly explain why palaeontologists have had such a hard time in finding the diagnostic characters that would help them to identify the true phylogenetic positions of vetulicolians, yunnanozoons, *Pikaia*, and early vertebrates such as *Haikouichthys* (see Chapter 3).



Morphological decay stages of amphioxus (left) and larval lamprey (right) and the phylogenetic position of each stage if interpreted as a fossil. Rectangles on branches of the phylogeny are morphological characters, their shade indicating the order of loss (white, early; dark, late). As each organism decays, its phylogenetic position moves down the tree; this is evidence for taphonomic bias in the identification of fossil chordates. Characters are colour coded according to the hierarchical level for which they are informative (green, chordate; yellow, cephalochordate; blue, vertebrate; purple, cyclostome and vertebrate; red, petromyzontid – see Colour plate 1.1). Source: Sansom *et al*. (2010). Reproduced with permission from Nature Publishing Group.

1.4.3 Development and vertebrate origins

The **development** of living vertebrates and other chordates indicates a great deal about their ancestry. Traditionally, embryos are sliced thinly on a microtome, rather like a mini salami-slicer, and three-dimensional reconstructions are made from scans of the thin-sections. In addition, and most importantly, studies of the **genome** allow developmental biologists to relate specific anatomical structures to genes. In many cases, they have found that genes that code for particular organs or functions are shared among widely different species that may have had enormously long independent histories. So, hypotheses of **homology** between organs can be tested by identifying shared genes, and recent work on amphioxus has been remarkably informative (see Box 1.4).

These recent studies shed light on an older theory for the origin of vertebrates, which proposes that we arose ultimately from the sea squirt tadpole. In the 1920s, the distinguished zoologist Walter Garstang noted the similarities between the larval sea squirt (see Figure 1.2(c)), adult amphioxus (see Figure 1.3(b)) and vertebrates. The sea squirt tail seemed to him to be a transient appendage that evolved as an outgrowth from the body to ensure wide dispersal of the larvae before they settled. Garstang (1928) proposed that the evolutionary link between the sea squirts and all higher chordates is through a process termed **paedomorphosis**, the full development of the gonads and

BOX 1.4 GENES AND BRAINS

New work on amphioxus has given clues about the origin of vertebrate characters, particularly the head. Amphioxus, the classic cephalochordate (see Figure 1.3), looks superficially like a rather simple fish, but it lacks the vertebrate hallmarks of a true head with well-defined sensory organs and the three-part brain (see Section 1.5). So how could the head and the sense organs and the three-part brain have arisen from the first chordates?

Anatomists have for a long time sought evidence for homologies between the cerebral vesicle of amphioxus and the three-part brain of vertebrates, the frontal eye of amphioxus and the paired eyes of vertebrates and other such structures. New studies by three developmental biologists, who rather confusingly share the homologous surname of Holland – Linda Holland and Nicholas Holland (both at the Scripps Institute of Oceanography, San Diego) and Peter Holland (at the University of Oxford) – have revealed amphioxus homologues of developmental genes on the basis of amino acid sequences of conserved regions (Holland and Chen, 2001; Holland and Holland, 2001; Holland *et al*., 2001; Koop and Holland, 2008; Holland *et al.*, 2008a, 2008b; Holland, 2009, 2013; Holland, 2010; Holland and Onai, 2011). It turns out that developmental genes show remarkable conservation across a wide range of animal phyla – in sequence, expression and in function. In other words, when the Hollands sequence particular segments of the chromosomes of amphioxus and of vertebrates, they find the same developmental genes (genes that regulate fundamental aspects of an animal's orientation and key organs), and these genes express themselves in comparable parts of the body, hence pointing to potential homologies.

Of particular interest is that, despite over 500 Myr of independent evolution, the amphioxus genome contains a basic set of chordate genes involved in development and cell signalling, including a fifteenth *Hox* gene (Holland *et al*., 2008b). It turns out that, in places where amphioxus has a single gene, vertebrates often have two, three, or four equivalent genes as a result of two intervening whole-genome duplication events. As examples of homologous genes and functions, the expression patterns of amphioxus homologues of the genes called *Dlx*, *Otx, Hox-1* and *Hox-3* indicate that the amphioxus nerve cord, which has no obvious divisions except for a slight anterior swelling, has counterparts in the vertebrate forebrain and hindbrain. Further, expression of the genes *Pax-1*, *Pax-2/5/8* and *Brachyury* homologues support homologies of amphioxus and vertebrate gill slits and notochord.

So even though amphioxus adults have a very simple brain, and simple sense organs (the 'eye spot'), the genes are shared, and phylogenetic precursors of vertebrate brain regions, eyes, and other organs, are there in amphioxus. Even that most typical of vertebrate organ systems, the skeleton, has its gene and morphological precursors in amphioxus.

It had been argued that amphioxus shares the fundamentals of the vertebrate **neural crest**, and this was supported by discovery of shared gene expression. However, this is now regarded as over-interpretation (Donoghue *et al*., 2008). First, the neural crest has been regarded as a unique feature of vertebrates, and indeed it is a developmental precursor of virtually all the distinctive vertebrate characters. The neural crest starts as a group of cells that forms on either side of the developing spinal cord and migrates to all areas of the body, providing the starting point for much of the head and face, and contributes to many other parts of the body such as the skin, nervous system and limbs, producing the cranial nerves, the fin rays, the pharyngeal gill skeleton, and other key vertebrate characters. The neural crest is preceded in development by the **neural plate**, a feature that occurs in the embryos of all bilaterians: this forms as a thickening of the embryonic ectodermal cells, and the borders push up as the neural folds on either side to form an elongate neural tube, precursor of the brain and spinal cord. All aspects of this process are guided by particular developmental genes shared among all bilaterians (Donoghue *et al*., 2008). Genomic studies do not show that amphioxus and vertebrates share unique neural crest specifiers, although some, such as the SoxE family of transcription factors were co-opted to the neural plate and act to specify development of some neural crest derivatives in the lamprey.

Read more about neural crest development, with movies, at: http://php.med.unsw.edu.au/embryology/index.php?title=Neural_Crest_Development, developmental (homeobox) genes at: http://ghr.nlm.nih.gov/geneFamily/homeobox and http://www.nature.com/scitable/topicpage/hox-genes-in-development-the-hox-code-41402, and the song 'It's a long way to amphioxus', sung to the tune of 'It's a long way to Tipperary', with audio performance, at: http://evolution.gs.washington.edu/amphioxus/amphioxus.html.

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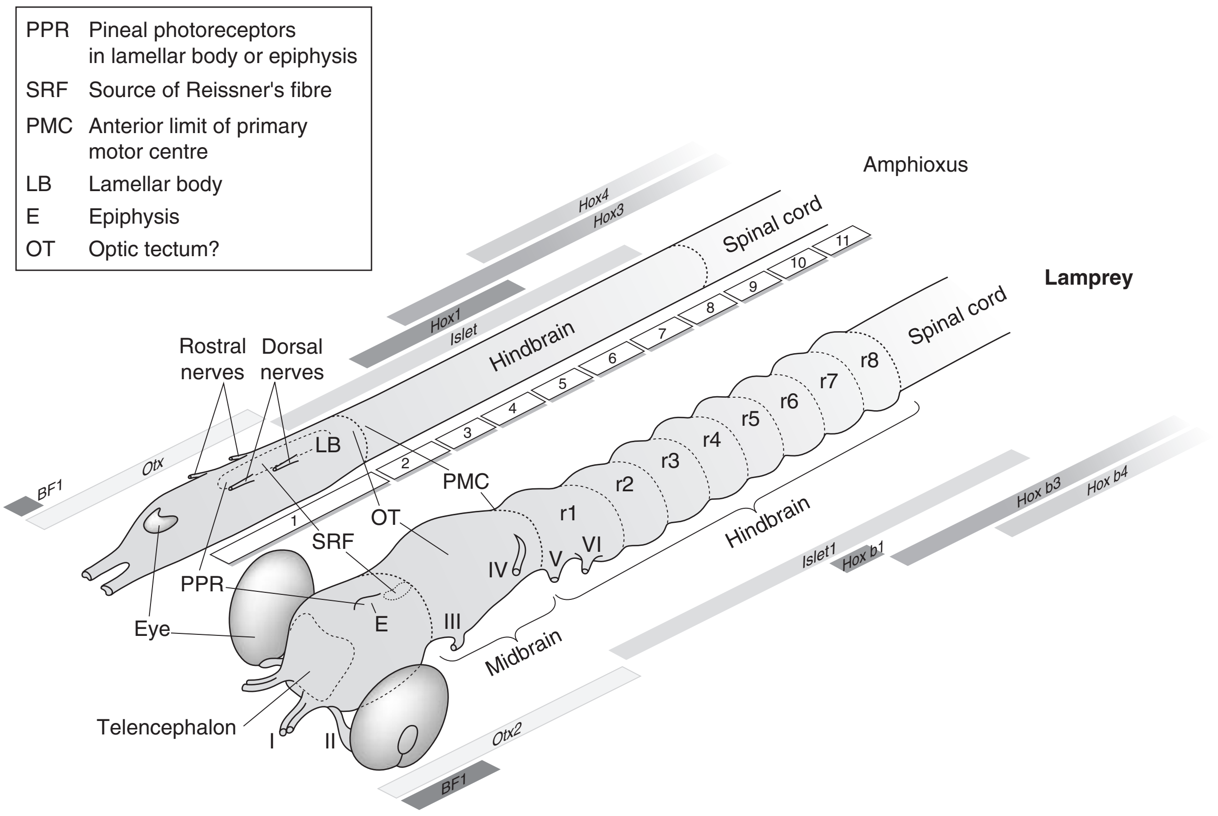

The front part of the developing nerve cords of amphioxus (left) and a vertebrate (right), viewed from above. In amphioxus, the cerebral vesicle, the brain region, is stippled and the numbered rectangles represent the muscular segmentation. Key features of the head and brain of the vertebrate are labelled, and possible homologies with amphioxus are indicated. The zones of expression of developmental genes are indicated to the side, confirming that amphioxus has morphological homologues of the three-part vertebrate brain (forebrain, midbrain, hindbrain), and a segmental structure to the hindbrain, which is composed of eight segments in each case. Source: Adapted from Holland and Chen (200) and Holland and Holland (1999).

reproductive abilities in an essentially juvenile body. According to his view, an ancient sea squirt larva failed to metamorphose and became adult (i.e. reproductively mature) as a swimming larval form. This elegant theory, however, is rejected by recent molecular phylogenies of tunicates that suggest their developmental characters are unique and did not give rise to the vertebrates.

1.5 VERTEBRATES AND THE HEAD

The vertebrates, the major group of chordates, form the subject of this book. They have sometimes been termed craniates since all forms, including the hagfishes and lampreys, have specialized head features (the **cranium,** the skull). The term vertebrate is better known, so will be used here, following recommendations by Donoghue *et al.* (1998).

The basic vertebrate body plan (Figure 1.10) shows all of the chordate characters so far described – notochord, dorsal nerve cord, pharyngeal gill slits, postanal tail, myomeres, and so on. The additional synapomorphies of vertebrates include a range of features that make up a true head: well-defined sensory organs (nose, eye, ear) with the necessary nervous connections, the **cranial nerves**, and the olfactory, optic, and auditory (otic) regions that make up a true brain. Larval sea squirts and amphioxus have an expansion of the nerve cord at the front end and all the vertebrate cell and sensory organ systems, as we have seen, but these are not developed to the same level as in vertebrates. Also, as we have seen, palaeontologists continue to debate whether Cambrian fossils such as the yunnanozoons and *Pikaia* did or did not have a true head with sensory organs.

1.6 FURTHER READING

You can read more about the palaeontological, embryological, and molecular debates concerning the origins of chordates and vertebrates in Gee (1996). Jefferies (1986) provides the fullest

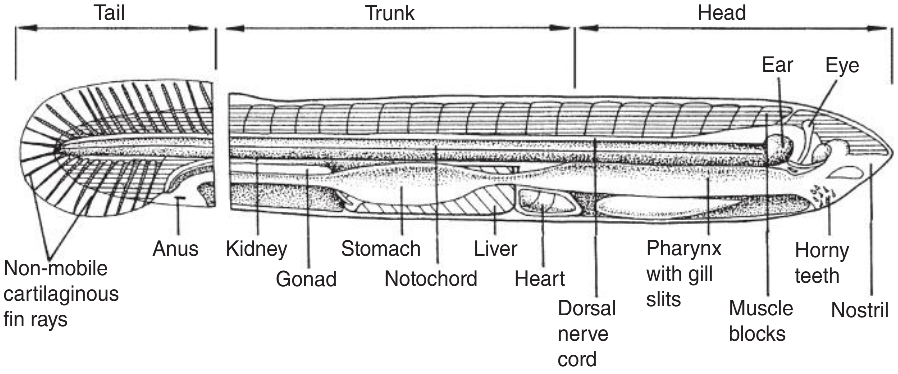

Figure 1.10 The hypothetical 'basic' vertebrate body plan, shown in longitudinal section. Source: Adapted from Jefferies (1986).

account of basal chordate anatomy, and makes an impassioned case for the generally rejected role of carpoids in linking echinoderms and chordates. Edgecombe *et al.* (2011) provide a thorough overview of current evidence on metazoan relationships, and the current position and debates over Cambrian deuterostome fossils are presented in excellent review papers by Holland and Chen (2001), Halanych (2004), Chen (2008), Swalla and Smith (2008), and Shu *et al.* (2010). You can find out more about modern invertebrates, and in particular those classified as deuterostomes in Barnes *et al.* (2001), Brusca and Brusca (2003), and Nielsen (2012). The embryology and anatomy of modern vertebrates is covered by many zoology texts, such as the classic by Romer and Parsons (1986), and more recent textbooks such as Hildebrand and Goslow (2001), Liem *et al.* (2001), Kardong (2011), and Pough *et al.* (2012). Waegele *et al.* (2014) provides review papers on all aspects of current metazoan phylogenomics.

Useful web sites include the interactive Tree of Life pages at: http://tolweb.org/Animals/2374, the Berkeley phylogeny pages at: http://www.ucmp.berkeley.edu/exhibit/phylogeny.html, an interactive tree at: http://www.onezoom.org/, and the Encyclopedia of Life, a summary of all named species, at: http://eol.org/.

QUESTIONS FOR FUTURE RESEARCH

1 What are the closest relatives of chordates among other animal groups?
2 When did the first chordates and the first vertebrates arise?
3 Are there ways to improve interpretation of soft-tissue characters in Cambrian deuterostome fossils from Chengjiang, the Burgess Shales, and other fossil lagerstätten?
4 How does the anatomy and physiology of living deuterostomes inform us about early deuterostome and chordate adaptations?
5 Can different phylogenomic analyses be rationalized, for example to understand why different phylogenetic conclusions may emerge from studies of whole mitochondrial genomes, collections of nuclear genes, and micro-RNAs?

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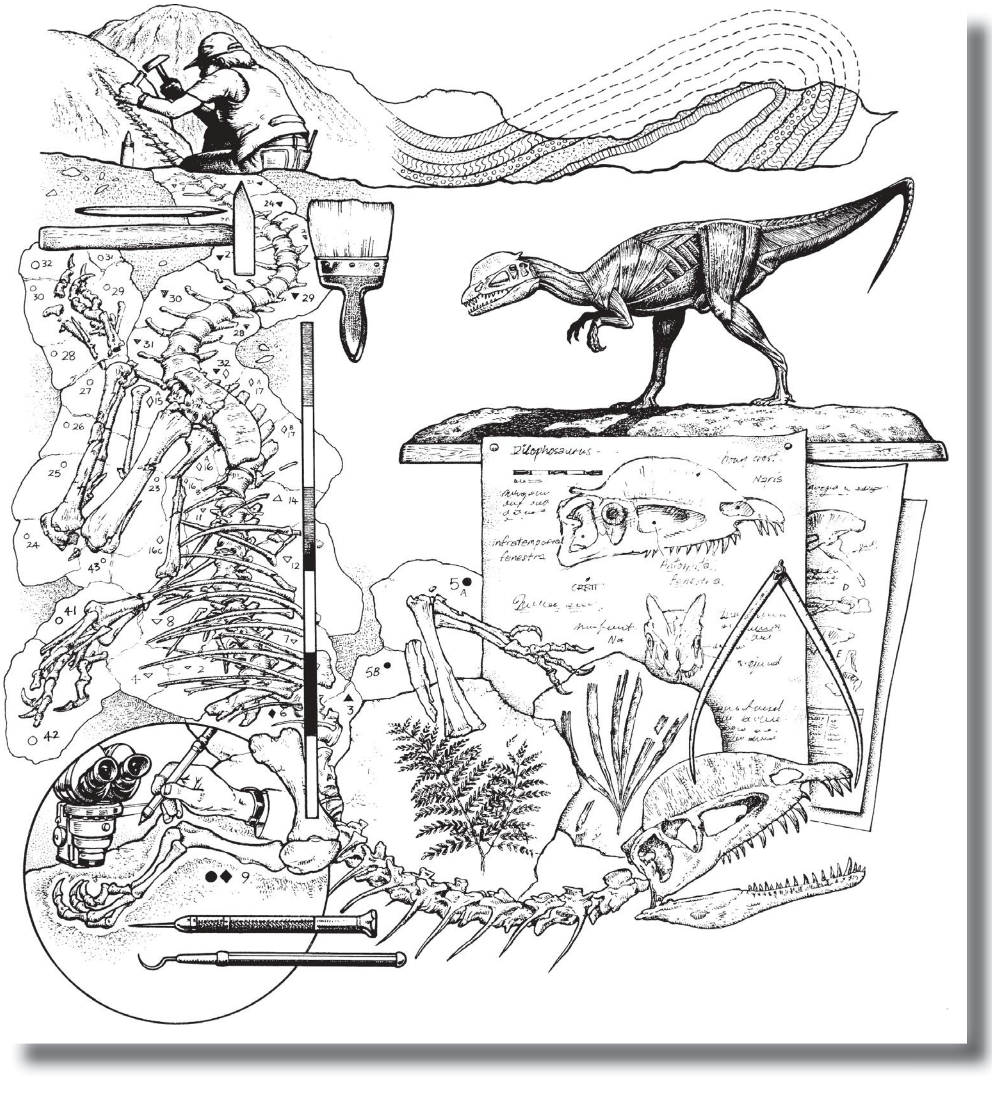
CHAPTER 2

How to Study Fossil Vertebrates



Vertebrate Palaeontology, Fourth Edition. Michael J. Benton.

Companion Website: www.wiley.com/go/benton/vertebratepalaeontology

KEY QUESTIONS IN THIS CHAPTER

1 How do you dig up a dinosaur?
2 What do you do with the bones when you have them back in the laboratory?
3 How do vertebrate palaeontologists reconstruct life modes and ancient ecosystems from fossilized bones and teeth?
4 How do palaeontologists write scientific papers, and how can a young person make a career and get a job?
5 How can you use clues from ancient bones and teeth to work out what happened between the death of an animal and burial in the rock?
6 How can palaeontologists work out the function and biomechanics of the feeding and locomotion of ancient animals?
7 How are organisms classified, and how do fossils help us work out the shape of the tree of life?
8 How can palaeobiologists establish patterns of macroevolution from the vertebrate fossil record?

INTRODUCTION

Most people are introduced to vertebrate palaeontology at an early age when they see dinosaurs in a movie, in a colourful book, or at a museum. Children are familiar with the principles of vertebrate palaeontology because some of the practical skills are well documented. They know that the bones are preserved in the rocks, and that teams of enthusiasts dig up the skeletons, clean them up, and string them together in a museum. They know that skilled artists work with palaeontologists to produce lifelike paintings and animations of life as it was millions of years ago. They may also know a little about how palaeontologists study the phylogenetic relationships of the exotic menagerie of the past, how the rocks are dated, how we know that the continents used to be distributed across the globe, and how the functions of extinct organisms may be inferred.

Obviously the fun part of vertebrate palaeontology is to work in exotic, and sometimes dangerous, territory, removing bones from the rock and shipping them home – all these processes in field collection, transport, fossil preparation, and skeleton restoration are presented in this chapter. In addition, the geological topics of taphonomy, time, continental drift, and palaeoclimates are outlined, and modern, numerical methods of phylogeny reconstruction, macroevolution, and functional morphology are introduced.

2.1 DIGGING UP BONES

Everyone has seen a dinosaur dig on television, even if they have never participated in one. It would be easy to assume that the enthusiasts who dig up dinosaurs and later study them are media stars who are paid handsomely by their museums or universities. This is rarely the case.

2.1.1 Collecting fossil vertebrates

The bones of fossil vertebrates have been collected from many sites around the world. New localities are occasionally discovered by chance, but most excavation is now carried out in places that are already well known for their fossils. Collectors focus on rocks of the right age and of the right type. If they are seeking dinosaurs, they will choose to investigate rocks dated from Late Triassic to Late Cretaceous in age. They will, of course, search only in **sedimentary rocks**, and in particular in rocks deposited in ancient lakes, rivers, or deserts, for example. If their interest is in fossil sharks, they will usually investigate sediments laid down in ancient seas.

Large fossil bones are generally located by prospecting. The collector walks back and forwards over likely areas of rock that are being eroded away by water or wind, either in 'badland' areas or on coasts. Erosion is necessary to expose fresh remains. Once the collectors find broken and disturbed pieces of bone (Figure 2.1(a)), usually small fragments, they follow them back uphill to their source. There may be a portion of limb bone or a rib poking out of the side of the slope. Then the collectors must try to assess the nature and size of the specimen and how it is lying, so that they can plan the excavation.

Excavation of large vertebrate skeletons is a laborious and expensive process. Earlier collectors, such as the dinosaur and mammal bone hunters of the 'heroic' period, from 1880–1910, in North America, employed hordes of labourers who extracted huge bones at incredible speed, but with little regard for their context. Excavators usually take more care now. The rock overlying the skeleton, the overburden, is stripped off using mechanical diggers, power drills, picks and hammers, or even explosives and bulldozers. Once a level just above the skeleton has been reached, the excavators switch to smaller power drills, hammers, and picks (Figure 2.1(b)). The skeleton is exposed from the top and the bones are cleaned up with needles and brushes, and protected with soluble hardening compounds.

Throughout the excavation, the diggers note the arrangement of the bones, and any other associated fossils. The whole dig is often recorded on film. It is also useful to have a geologist present who can interpret the sedimentary context of the skeleton. Once the skeleton is exposed, it is mapped in detail (Figure 2.1(c)).

The bones must somehow be removed safely from the site. The excavators first isolate each bone, or group of bones, on an island of sediment around which they dig trenches. Each block is covered with wet paper or foil, to act as a separator, and then capped with several layers of sackcloth (burlap) soaked in plaster (Figure 2.2(a)). Large blocks are strengthened with wooden beams. The excavators burrow underneath the plaster-capped mounds, and attempt to break through the pedestals beneath them, but well below the bones. They then clear out the sediment from behind the bones, and plaster over the base. Each bone, or group of bones, is now entirely enclosed in a plaster shell, and the blocks can be moved safely. Plastered blocks may weigh several tonnes, and they have to be hauled out of the site,

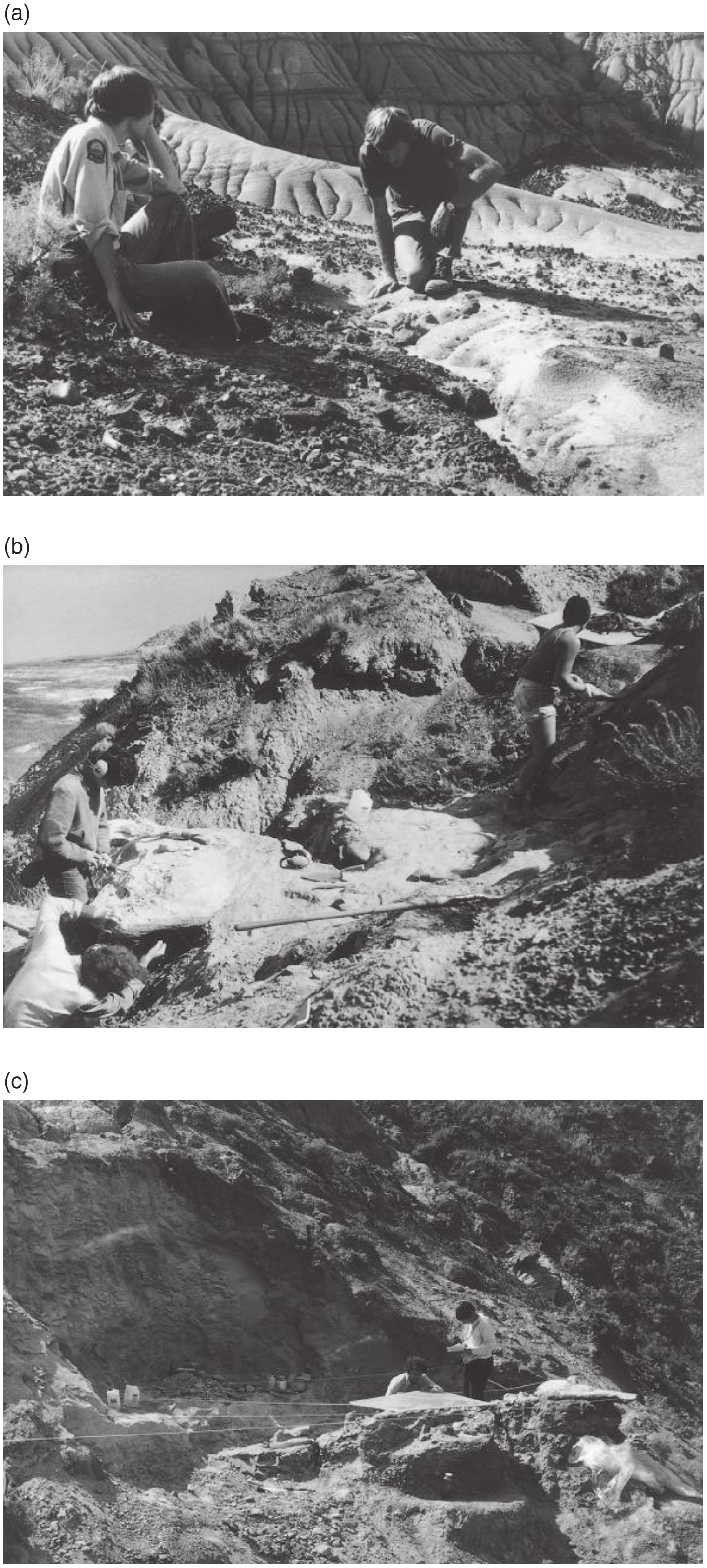


Figure 2.1 Dinosaur digging in the Late Cretaceous of Alberta, Canada: (a) Phil Currie (right) and a park ranger inspect a rich dinosaur bonebed at Sandy Point (all the irregular blocks are dinosaur bones); (b) digging away the overburden, and clearing the rock with pneumatic drills; (c) mapping the distribution of bones. Source: M.J. Benton, University of Bristol, UK. Reproduced with permission.

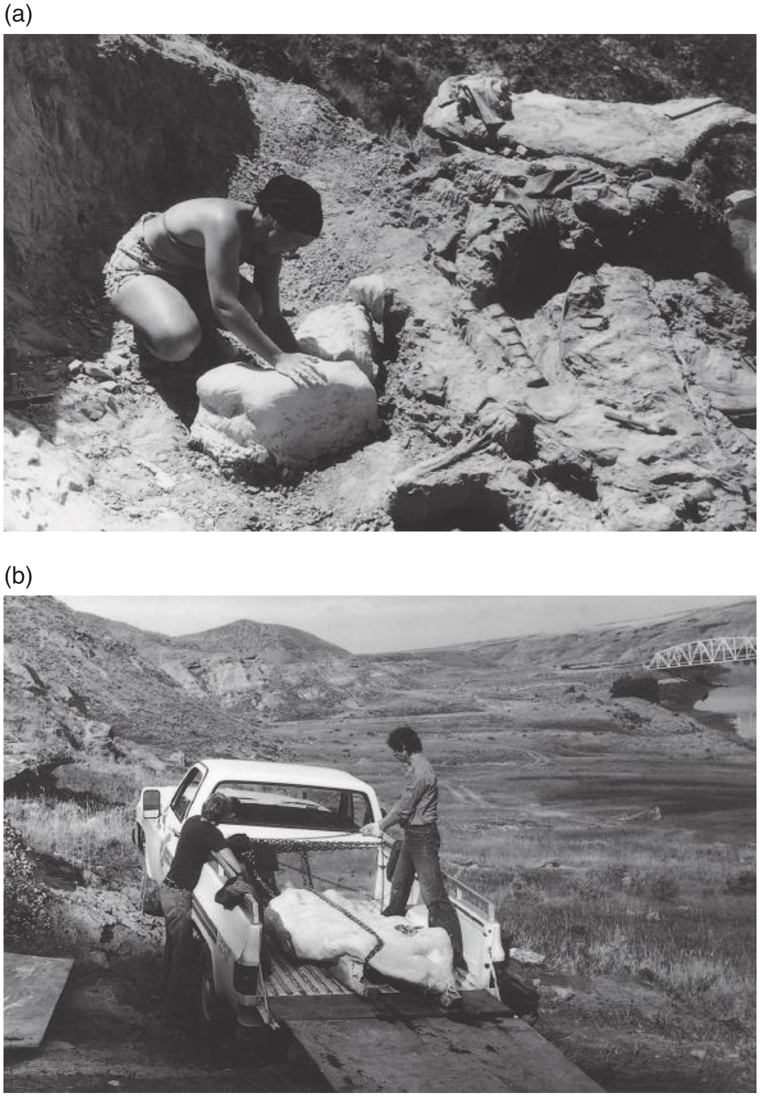


Figure 2.2 Excavating dinosaurs in the Late Cretaceous of Alberta, Canada: (a) Linda Strong protects some hadrosaur bones with bandages soaked in plaster (note the tail segment and the dorsal vertebral column at the right); (b) shifting the blocks for transport back to the laboratory. Source: M.J. Benton, University of Bristol, UK. Reproduced with permission.

often by hand, until they can be loaded on vehicles for transport to the museum (Figure 2.2(b)).

Fossil vertebrates are collected in many other ways. For example, fish specimens are often preserved on well-bedded rocks that were laid down in ancient lakes or seas. The rocks may be fine-grained, and they may break into large slabs. Collecting in these cases consists simply of splitting slabs, and saving those that contain bones. The Early Cretaceous Jehol Beds in China preserved numerous spectacular fossil vertebrates in thin muddy limestones deposited in ancient lakes. Specimens are flattened on thin layers, and they are collected as part and counterpart, representing both sides of the fossil.

Many small fossil vertebrates are found only as isolated bones and teeth. In certain sedimentary settings, skeletons are tumbled together and broken up. The bones and teeth may be concentrated at particular levels, often in small channel-like pockets. In cases such as these, palaeontologists dig out the whole bone-bearing layer, and they may sieve it on the spot, picking out the identifiable bones and teeth, or they may transport sacks of bone-rich sediment back to the laboratory for processing.

2.1.2 Preparation and conservation of bones

The key work follows in the laboratory, where the fossils are made ready for study or for exhibition. There are now many professional palaeontology preparators and conservators, and the techniques available have advanced enormously. The important point to remember is that information is lost at every stage in the process of excavation and preparation, and the good technician seeks to minimize that loss.

Back in the laboratory, the plaster jackets are cut off the large bones, and the difficult job of preparation begins. The general idea of preparation is to remove the sediment from the bones so that they may be studied. Conservation includes the treatments applied to bones so that they may be handled and stored without fear of damage. A variety of hand-held chisels, needles, mechanical drills, and brushes may be used to remove the sediment (Figure 2.3(a)). An airbrasive machine may be used, a system that blows fine abrasives in a focused blast of air at the specimen and removes the matrix grain by grain. If the bones are contained in limestone, then the blocks may be soaked in dilute, buffered acetic or formic acid to remove the sediment. This technique can produce spectacular results, as there is no risk of mechanical damage to the bones, although there is a risk that mineralized traces of other, non-skeletal, tissues may be etched away.

In the preparation laboratory, exposed bones are generally strengthened by coatings of synthetic compounds, such as Paraloid or Butvar, which are readily soluble in acetone or alcohol. These consolidants have replaced the rather crude glues and varnishes that were used in the past, all of which suffer from problems of decay, and which cannot be removed readily to allow further cleaning and preparation. Much of the work in a museum laboratory is also concerned with conserving the fossils that were collected long ago, and that fall apart as a result of chemical changes in the bone and sediment.

Specimens of fossil vertebrates preserved on slabs are usually prepared mechanically, and the skeleton may be left on the slab, as the sediments provide a stable support. Sediment with microvertebrate remains, small bones and teeth, is processed in the laboratory in various ways to extract the fossils. If the enclosing sediment is limestone, then acid treatment is effective. If the sediment is unconsolidated, then simple washing and sieving may be enough to extract the bones (Figure 2.3(b)).

(a)

(b)

Figure 2.3 In the laboratory: (a) preparation of dinosaur specimens at the Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada, using a dental drill to remove rock matrix from the bones; (b) Rachael Walker adjusts an automated sieving machine for processing sediment containing microvertebrate remains, designed by David J. Ward, in the Palaeontology Laboratory, University of Bristol, UK. Source: M.J. Benton, University of Bristol, UK. Reproduced with permission.

2.1.3 Display and study

Bones of spectacular new species of fossil vertebrates, or unusually complete specimens, may be prepared for display. The bones are strung together on metal frameworks, or more frequently, casts are mounted with internal supports. Casts are made in tough lightweight materials, such as fibreglass, from moulds of the original specimens (Figure 2.4(a)). Most fossil vertebrates, however, are never displayed, but are reserved solely for study. The specimens may be studied by the scientists who collected them, or they may be kept in the museum collections for later work. In any case, museums have a duty to conserve their specimens in perfect condition, and to maintain full documentation about their holdings. Palaeontologists find out about the locations of museum specimens from published descriptions of fossils and from online and printed catalogues.

In studying a new fossil vertebrate, the palaeontologist tries to reconstruct the skull and the rest of the skeleton in as much detail as possible. This may be a difficult job. If there is a relatively complete and undamaged specimen, the fit of the bones may be tested directly. It may be possible to slot together the bones of the skull like a three-dimensional jigsaw, and to test the stance of the limbs, to some extent, by fitting the bones together end to end. More normally, the palaeontologist must use information from several specimens in order to reconstruct the original appearance of an undamaged skeleton. In matching up bones, allowances must be made for differently sized animals, and in difficult cases, scale models of missing bones may be made. Extensive reconstruction is possible because vertebrate skeletons are bilaterally symmetrical, and because many bones, such as vertebrae and ribs, occur in repeating or gradually changing series, and so it is not necessary to find every bone in order to make a reasonably accurate reconstruction of a skeleton.

Most fossil skeletons have been compressed or broken up, either before being buried (physical damage, scavenging), or after being buried (compression of the rocks, chemical effects). The palaeontologist must recognize these kinds of damage, and try to correct for it by reconstructing missing parts of bones and making careful measured drawings and models to remove the effects of distortion.

Accurate skeletal reconstructions are essential for further study. If the specimen represents a new species, the palaeontologist may publish a detailed description of all the bones that are available, and gives a reconstruction of part, or all, of the skeleton. Clearly, illustrations are important, and published descriptions are accompanied by drawings (Figure 2.4(b)) and photographs. These then form the basis for artistic restorations

Figure 2.4 Further techniques for studying fossil vertebrates: (a) casting some dinosaur vertebrae; (b) drawing the posterior view of a dinosaur braincase. Source: M.J. Benton, University of Bristol, UK. Reproduced with permission.

of the animal in life, either as pen sketches (look at the examples by John Sibbick in this book), as colour paintings, as static and moving models, and as animations. Dinosaur animation is familiar to everybody now, following early successes such as the Hollywood movie *Jurassic Park* (1993) and the BBC documentary series *Walking with Dinosaurs* (1999). Such computer-generated imagery (CGI) represents an enormous advance over earlier attempts at making dinosaurs come to life.

2.2 PUBLICATION AND PROFESSIONALISM

Students of any subject in science quickly become aware of the published scientific papers in their field, sometimes called generally 'the literature'. At first, these scientific papers may seem hard to understand, and there are so many of them that it might seem to be impossible to know which ones to read. However, it is important to master the literature for several reasons, (1) to know about the latest discoveries, (2) to become aware of the current viewpoint in different fields, (3) to learn how scientists marshal their evidence and argue a case, and (4) to see how professional scientists operate.

It is especially important to master the literature if you, as reader of this book, have plans to enter the profession of palaeontology at some point. The literature then is a key element of your career plan: you not only have to read the latest professional papers to be aware of current discoveries and debates, but also as a potential contributor, to see how papers are constructed and to plan how to make your own published contributions of the very highest quality.

In this section, we shall explore how the scientific literature works, both for the reader or consumer, but importantly also for the producer. This leads to a consideration of career pathways into paid professional work in palaeontology.

2.2.1 The scientific literature

The first thing discovered by a student is the vast magnitude of the scientific literature. Even in a field like vertebrate palaeontology that might be considered quite marginal or low-impact, thousands of new papers are published every year. Indeed, with the wide availability of materials online, it is now many orders of magnitude easier to find papers than it was only ten years ago. How is a newcomer to find their way through this mass of literature, to know what to read and how to read it?

The scientific literature is structured. There is no central committee or organizer, no committee of gate keepers, or other mechanism to regulate who publishes and what they publish. However, there are some core principles, and scientists around the world adhere to these general 'rules'. The literature is structured to reflect the basic principles of science as well as a desire for quality and honesty throughout.

Science is about testing hypotheses. This is not the place to present a detailed insight into the **scientific method**; this can be explored elsewhere (Ziman, 2000; Okasha, 2002; Franklin, 2009). The basics are that in science all research is based around hypotheses, which are explanations of how Nature works. Your hypothesis might concern a large question (Why did the dinosaurs die out?) or a small one (Is there one species or two species of this fossil mammal in Wyoming?). In framing the hypothesis, the question is presented, and the **null expectation** set out. The null expectation is the common-sense conclusion, or guess, that you frame before looking closely at the evidence: 'dinosaurs were killed following an asteroid impact'; 'there are two sets of measurements, so I think there are two species'. Then the null expectation is tested, preferably numerically, but certainly with **evidence**. It is important to realize that scientific debates are not decided by assertion or by bullying or by seniority (*that* might work in politics and some other fields). Testing hypotheses is core, and evidence is core. If a palaeontologist asserts that birds evolved from among the dinosaurs, then evidence is required in the form of shared derived characters and a thorough cladistic analysis (see below). Linking the extinction of the dinosaurs to the asteroid impact requires strong evidence from independent rock dating that the two events happened at exactly the same time, plus of course much more. Evidence that you have two species, and not one, requires at least some statistical analysis (like a t-test) to demonstrate two clusters or peaks in certain key measurements. Sometimes, students believe that science is like politics, and it might seem like that if you go to a scientific meeting, where famous names in the field may get red in the face and angry about defending their viewpoint or attacking another viewpoint, but evidence is always needed.

The second key principle is that science is about perfect honesty. When a scientist is discovered to have faked their results or stolen ideas from someone else (**plagiarism**), they are exposed publicly and it is a great scandal. Such cheating can lead to court cases and almost always the loss of your job. The focus on exposing trickery and fakery is stronger in science than in many other careers because, as Charles Darwin said, 'False facts are highly injurious to the progress of science, for they often endure long; but false views, if supported by some evidence, do little harm, for every one takes a salutary pleasure in proving their falseness.'

This is why your professor makes such a big deal out of the iniquities of plagiarism at all levels – copying sentences and ideas without correct attribution can lead to worse forms of cheating, and so is not tolerated in academic circles.

A second principle is that the doors are open to all. You don't have to be old, or famous, or male, or rich, or a professor at a famous university, or have a PhD in order to publish. Indeed, many of the best new papers come from students working for their Masters or doctoral degrees. All contributions pass through the same review process, and all are equally likely to be accepted or rejected based on the process of **peer review**, that is, review by your peers, or equals. This is discussed below (see Section 2.2.2).

There are three kinds of scientific literature, primary, secondary, and tertiary. The **primary** literature consists of all the journals that publish original observations and ideas. There are hundreds of thousands of scientific journals, some of them very old, and dating back hundreds of years. Scientific journals were founded first by scientific societies in different countries as a place for their members, the professors of those days, to publish ideas and observations. Debates and discussions about topics such as the interpretation of fossils, ancient mammoth bones, and the reality (or not) of extinction were published by naturalists in the early scientific journals of the 1600s and 1700s.

In vertebrate palaeontology, scientists publish in specialist journals, such as *Journal of Vertebrate Paleontology*, published by the Society of Vertebrate Paleontology in the United States, *Palaeontology*, published jointly by the Palaeontological Association and John Wiley & Sons in the United Kingdom, and *Journal of Systematic Palaeontology*, published jointly by the Natural History Museum and Taylor & Francis in London. However, if a vertebrate palaeontologist has made a really important discovery, they may try to publish their paper in *Nature* (London) or *Science* (Washington) or, failing those, *Proceedings of the National Academy of Sciences, USA* (Washington), *Proceedings of the Royal Society B* (London), or *PLoS ONE* (San Francisco). These journals range hugely in age, from 1665 for the *Philosophical Transactions of the Royal Society of London* to 2003 for *PLoS ONE*.

The **secondary** literature consists of review articles and specialist textbooks written by practising scientists, in journals such as *Trends in Ecology & Evolution* or *Annual Review of Ecology, and Systematics*. Here, the writer presents an overview of current primary literature on a particular topic, often a ‘hot’ debate, about a topic such as the macroevolution of dinosaurian origins, or the impact of the end of the Ice Ages on large mammals, and tries to make a strong argument and perhaps set out a research agenda that helps other researchers to focus their efforts. The **tertiary** literature is everything else – news reports, general textbooks, web sites, museum pamphlets, even museum exhibits. As a student beginning to read scientific papers, you work your way up from the tertiary to the secondary, and finally the primary literature. Often, news reports and web sites are easy to read and everything is clearly explained for the non-expert, but they are ‘second-hand’ and written by people who are not themselves engaged in the research.

2.2.2 How to write a scientific paper

So, you are completing your Masters project, or the first year of your PhD work, and you feel you have made an interesting discovery. How do you set about sharing it with the world? The answer is of course that you write a scientific paper. Your supervisor or mentor ought to be encouraging, and indeed may be pressing you to do this. The key here is that you must prepare carefully to make sure your ambition does not fall flat.

There are two practical ways to make sure you give yourself the best chance of success: read and discuss. You cannot hope to write a good paper if you do not read like a mad person. You must read every paper in your subject area, and especially focus on reading papers in the journal or journals you might wish to submit your paper to. Avid reading of the primary literature gives you a feeling for the key scientific questions of course, but also about how to construct a paper. You must pay attention to the writing style, the way illustrations are used, and how the subject is introduced and discussed. This means that when you begin writing you have a model of exactly what your paper ought to look like, and it should save a great deal of wasted time, writing pages of nonsense or preparing low-quality illustrations.

Secondly, you must discuss your ideas with fellow students and your professors, and you definitely must give posters and papers at scientific meetings. The keen student never misses a chance to go to a lecture or conference on their subject, and to present. You must not be passive, and just vaguely listen to others; you must show your work, and be prepared for discussion and criticism. Preparing posters and talks makes you identify the key points, and it makes you sharpen your arguments. Make sure you allow plenty of time before the conference, and have lots of people check over your poster. Run your talk five or six times. It’s amazing how many students think they can prepare a talk or poster the day before the meeting and somehow everything will be all right. These tasks certainly become easier with practise, but for your first talk you must allow several days of preparation time ideally spread through the month before the meeting. Practise the talk as many times as you can, in a lecture hall, and in front of people – until you drive your friends crazy. This will root out all the obvious mistakes (too many slides; writing too small; mumbling; poor explanation), and give you added confidence when you are wheeled out on stage in front of 200 professors at the meeting. They will listen carefully and appreciatively if you have done them the courtesy of preparing properly; they will fall asleep or ignore you at the bar afterwards if you have wasted their time.

The poster/ paper process is essential for gathering feedback, but also for gathering your own thoughts. No scientist ever writes a paper without careful planning. The process of summarising, talking, and discussion helps you to focus on the key ‘story’ you wish to convey. It may seem strange to suggest that scientific papers have a story line, but they do. Today, no scientific journal will publish the kinds of papers that might have been produced in 1850, ‘Observations on ichthyosaurs, and some speculations on the Jurassic of southern England’. There must be a single theme that forms the backbone of the paper, and that theme is emphasized throughout, in the title, abstract, introduction, results, discussion, and illustrations. Have a look at any published scientific paper.

Scientific papers are constructed for ease of rapid reading. First, as a consumer, and second, as a writer, you must appreciate this structure. Most importantly, the title and abstract work together as the means of gathering readers. Often these parts of the paper are set in large print or bold type. Also, they are reproduced everywhere, in scientific search engines, blogs, and other places. Perhaps one hundred times as many people read the title and abstract of a new paper as will actually read the whole paper.

So, the title should be crisp and clear, and the abstract must be self-contained and short. [Too many first authors write long-winded, rambling abstracts. They should not.]

The remainder of the paper follows a standard pattern that has been honed over the centuries: Introduction, Materials and methods, Results, Discussion, Conclusion, References, Appendix. This structure works to separate observations from interpretations ('fact from fiction'), and leads the reader through a logical structure of explanation, evidence, and argument. In writing a scientific paper, the order of approach should be:

1 Materials and methods.
2 Results.
3 Supplementary data.
4 Introduction and discussion.
5 References.
6 Title and abstract.

The student should of course begin writing the paper on the day they begin their study, not at the end. This is how professional scientists work. It is best to write 'Materials and methods' as you make the observations – whether you are describing a locality and its geology (do this during the field work) or explaining some laboratory or numerical-computing procedures (write these up while you do the analyses). Writing 'Materials and methods' a year later is a waste of time, and is risky.

The remainder of the paper has to wait until the work is complete and has been discussed and the key impacts thought through. However, a good strategy, especially if the paper is likely to be data-heavy, is to compile a detailed 'laboratory report' kind of Results section, with all the graphs, tables of data, or cladograms in logical sequence, and terse explanatory text. This will eventually become the **electronic data supplement**, and it allows you to consider which graphs, tables, or cladograms are really important and should go in the main paper. You certainly cannot include them all! If your paper focuses on the description of a new fossil, then the description (which comprises the 'Results' section) is the core.

Many published papers are complete in themselves, whereas others, especially if they involve numerical calculations, may also be associated with a substantial data supplement that is published online. This may include all the raw data, calculations, graphs, and explanations that support the core conclusions in the paper. The supplement, in the form of raw data, might also be lodged with a recognized data repository such as Dryad.

You normally complete and arrange your **illustrations** at this stage. Illustrations may be a mix of digital photographs and drawings. They must share the same style throughout (for example, the same sizes and fonts of lettering, the same scale bars). It is important to save them in editable (vector- or object-mapped) formats so you, and the journal editors, can open them readily and move elements around or change the lettering. For review purposes, the journal may require small versions of the figures, but always keep the editable versions carefully. In broader terms, the illustrations in a scientific paper are of huge importance, and care in planning and design can reap enormous benefits. It is often said that one well-designed illustration can save a thousand words. It can also massively aid understanding, and good images may then find their way into blogs, web sites, and even textbooks, such as this one.

Students usually struggle to write the 'Introduction' of their paper first. Professionals write it last. Experience shows that readers do not wish to read pages of tedious literature review or vague observations. They require a short and direct 'Introduction' that explains in one paragraph the big question, surveys the key recent papers (including some pithy recent reviews), and then sets out in a third paragraph the aims of the paper. That's all. The 'Discussion' is written at the same time, and it ought to reflect the key points from the 'Introduction'. The beginner often misunderstands the role of the 'Discussion', and sometimes uses this portion of the paper to repeat everything just presented in the 'Results', with a few low-level personal reflections. This is boring and pointless. The 'Discussion' should be about the *implications* and *limitations* of the study in general terms, and it can even be divided up with subheadings, such as 'The oldest fossil sharks?', 'Implications for molecular tree calibration', 'Problems with dating of the Smith Formation' – this for an imaginary paper presenting what might be the oldest fossil crown chondrichthyan.

As noted earlier, the Title and Abstract come next. You will have had ideas of a title for your paper, and may have sketched an Abstract. These require care and wide discussion: make sure lots of people read and criticise these portions of the paper. You are aiming for maximum understanding by the widest range of people, including non-experts (and even students). Write and rewrite the Abstract many times, always aiming for directness and clarity. Keep it short. There should be no references, technical terms, or side lines.

The final jobs are tidying up tasks, such as making sure you write the Acknowledgements of everyone who has helped or advised, sources of funding, people who provided permissions and equipment, and people who reviewed the manuscript (MS). The References must be precise and accurate (especially those in languages you do not speak), and they must match the text. These can be compiled by hand or by various referencing programs. Make sure they match exactly the requirements of the target journal.

This is just the beginning! The next task is to fight through the **review process**. As you began writing, you will have considered your target journal, and you will have formatted the paper throughout to match the required style. Journals publish 'Author guides', but it is often easier to look at a recent paper and make sure you copy all aspects of the format. Students often struggle with accuracy here. However, journals require exact adherence to their styles, in terms of spelling (UK or US), sub-titles (numbered or not, capitals or not), paragraphing (indent or not), referencing (author date; or author, date; or superscript number, the so-called Harvard and Vancouver systems), reference style, and so on. It is best to fix these formats correctly when writing, and this saves a day or so of close checking later.

You choose your journal by looking at the kinds of papers recently published in your target journals. Every ambitious scientist would like to publish exclusively in *Nature* or *Science*, because those journals are very widely read and very highly regarded. Indeed one or two papers in those journals can ensure professional tenure. However, this high standard is matched by a high rejection rate, over 90%. More specialist palaeontological journals are not so widely read, but their standards are just as high in terms of science and writing, but their rejection rate may be 50%, giving you a better chance to see your paper published there.

The aspiring palaeontologist must be ready for rejection and criticism, and be ready to take advice throughout. Once your paper is prepared, checked, read and re-read by fellow students and advisers, you upload it into the journal web site, following all the instructions closely. It then passes through three or four stages of scrutiny. A Technical editor may check for style and length. If there are problems with presentation, it may come right back to you, with instructions to correct your errors and pay attention to the Instructions to authors. Next, the Editorial Board (usually senior scientists) will take a look, and decide whether the paper fits the requirements of the journal. They might well return it a week later, and say 'Too specialized for us' or 'Too local interest'. Reformat it and send it somewhere else; don't dither about feeling miserable.

If the paper passes these two filters, it goes out for review. You may have been asked to recommend some reviewers. They must be from other institutions or other countries, and of course knowledgeable about the subject. Some reviewers may be professors, but others may be graduate students. They are not paid, and yet they give several hours of their own time to read your MS and make suggestions for improvement. Some reviewers will mark up corrections on every line of the MS; others will provide a list of general points – explain this better, improve that illustration. After a month or so, the reviews are emailed back to the Editor (sometimes after some gentle e-mail prodding), and the Editor must review the comments and decide whether to encourage the author to revise and resubmit the paper, or to reject it.

Sometimes students are upset when they receive the letter back from the Editor. They have waited perhaps two or three months, and finally the letter comes: 'We regret that we cannot publish this paper, because the reviewers found many problems…' But, read on. The letter may end with a grudging phrase such as, 'If you feel you can answer all the serious criticisms of the reviewers, we might be able to consider your paper…' Don't expect the Editor to write, 'This is an amazing paper, and I congratulate you on your wisdom and amazing skills.' Even Charles Darwin never received such a letter.

Persistence and hard work. Avoid the temptation to fight the reviewers. As far as possible, do what they ask, and provide a detailed 'Response to reviewers' document, in which you list all the criticisms and suggestions, and your response. Best to say 'These changes have all been made.' This makes it easy for the Editor to accept your paper. Sometimes of course reviewers make mistakes or ask for the impossible: 'The author describes one specimen; I would like to see 100 specimens', and such suggestions can be answered, gently, with an explanation like this, 'Regrettably the locality was covered over and I cannot find any more material,' or 'The reviewer asks for substantial additional calculations, but these are impossible because…'

It is important not to be feeble. Don't imagine the reviewers say critical things because they hate you personally. Don't wipe the MS from your hard drive, and decide to give up science. The peer review process is there to maintain high standards in what is published. It is far from perfect, but the extra effort of revising your paper thoroughly, or restructuring it for another journal is the norm, and you must get used to the process if you wish to make a career as a scientist.

2.2.3 Careers in vertebrate palaeontology

Comments here will be brief, as it is impossible to explain a fool-proof route to a successful career. Palaeontologists follow many career paths, and there are many kinds of jobs. But competition is intense. Vertebrate palaeontology is a minority discipline despite its high public profile, and no country can afford unlimited posts. The key jobs are in universities and museums, and these institutions employ research scientists, professors, instructors, education experts, laboratory staff (preparators, conservators, scientific artists), and curators (who care for collections). Some palaeontology enthusiasts dream of a quiet job, where they can spend their days handling fossils and keeping out of the limelight; such jobs do not exist. Museum curators are dragged out to speak to parties of visiting school children, preparators attend conferences and their laboratory may be open to public view like a goldfish bowl, professors have to raise substantial grant funds and manage large groups of graduate students. Palaeontologists, like all other professionals, have to earn their keep.

The obvious career pathway these days for any kind of professional career is to study science to a good standard at school (especially biology, mathematics, chemistry, and physics), to complete a Bachelors degree (or equivalent) in Geology, Earth Sciences, Biology, or Palaeontology, and then to follow with a Masters degree in Palaeobiology, Systematics, Phylogenomics, or Museum studies, or a PhD. Doctoral studies typically last for 3–4 years, but entry is highly competitive, and the student has to take ownership of their topic and work hard and with great flair. This is the crucial time when the student makes their mark, gives papers and posters at conferences, and publishes their first scientific papers. If you grasp these opportunities with enthusiasm, you can perhaps proceed to a postdoctoral position or a research fellowship, or even a tenure-track position that might end in a permanent job.

Rather than proceed further with generalities and platitudes, the best information comes from people who have made it recently (see Box 2.1).

BOX 2.1 VERTEBRATE PALAEONTOLOGY CAREERS

Every year, dozens of vertebrate palaeontologists get jobs, and there are many career pathways. Here we feature three young palaeontologists who have gone through the education process, and now have jobs. They tell their own stories, and these examples may help young readers to plan their own careers.

Karen Moreno, currently Professor, Universidad Austral de Chile, since 2012. Former studies in Chile, UK, Australia, and France (website: http://dinohuella2.free.fr/index.htm).

My current job is dynamic and requires multitasking: to come out with new ideas for research, to search for new techniques, to mentor students, to present the general public with amazing scientific facts and travel to many interesting places. Definitely, there is no time to get bored. I am independent, and do not take orders from a boss. The worst thing though is that the job is highly competitive and it consumes a lot of time, periodically interfering with the time that should be dedicated to family life. But then, no mother has an easy life regardless of the type of work.

I decided to be a professional paleontologist by the end of high school because I found that palaeontology was not developed enough in my country. Key questions that interest me now are about mechanics and palaeobiology of dinosaurs and other fossil creatures. My best advice to a young student would be to try to be as independent as you can, and have no shame in asking for help when needed. It usually works very well!

Steve Brusatte, currently Chancellor's Fellow at the University of Edinburgh, Scotland. Former studies in Chicago, New York, and the UK (website: https://sites.google.com/site/brusatte/).

My job is diverse and allows me to be creative. On any given day I may be teaching, advising student research projects, writing research papers or grants, doing fieldwork, giving lectures, or planning projects with colleagues. Science really is a creative enterprise, and it's very satisfying to be able to wake up every morning knowing that, today, I could discover something new about the world. The worst thing is that science sometimes can become all-consuming and creep into every aspect of my life. It's impossible to stop thinking about research questions when I go home after work. Evenings and weekends are never really free. Sometimes when I travel to do fieldwork or go to conferences I am away from my wife for quite a long time. So science does put demands on our personal lives.

Three young vertebrate palaeontologists: (a) Karen Moreno, now working in Chile; (b) Steve Brusatte, now working in Scotland; (c) Lindsay Zanno, now working in North Carolina, USA. Source: (a) K. Moreno, Universidad Austral de Chile, Valdivia, Chile. (b) S. Brusatte, University of Edinburgh, Edinburgh, UK. (c) L. Zanno, North Carolina Museum of Natural Sciences, Raleigh, NC, USA. Reproduced with permission.

I wasn't very interested in dinosaurs or fossils as a young kid. But I became absolutely enamoured with palaeontology and evolution when I was about 14–15 years old. I saw palaeontology as detective work in deep time, and fossils as a unique gateway for understanding how evolution works and how our world has changed over the course of its multi-billion year history. To me, there is nothing more fascinating! I'd like to better understand what allows some groups of organisms to become very successful, whereas other groups stagnate. And a related question: why are some groups able to endure mass extinctions but others succumb? Answering these questions will give important insight into how evolution actually operates, and may help us better understand what to expect as our own world is rapidly changing due to rising temperatures and environmental degradation. My advice to a young student is to be persistent, driven, and outgoing. Have a collaborative state of mind and always respect fellow students and scientists, because most good science isn't done by solitary individuals sitting in their labs. Take all opportunities to travel, work with other scientists, and learn new techniques. And always be curious—never stop asking questions, never stop exploring.

Lindsay Zanno, currently Director, of the Paleontology & Geology Research Laboratory, North Carolina Museum of Natural Sciences. Former studies in New Mexico and Utah (website: http://naturalsciences.org/nature-research-center/directors/lindsay-zanno).

A growing number of young scientists recognize that the relationship between science and society is at a pivot point. I see a vibrant movement to portray our relationship with the community for what it really is—a mutualism where both sides are striving to improve the future of humanity by means of innovation, objectivity, and knowledge. One of the most frustrating aspects of my career is no doubt the same as for all women, residual inequality. I am often told that I am a role model for girls, which is a great honour. But I relish the day when a woman is perceived as a role model for any sex, race, and gender, not just her own.

Early on I was drawn to science. Put simply, scientists are people who can't quell their curiosity about the world. I tried a variety of scientific disciplines as a college student: genomics, medicine, anthropology. But the very first time I uncovered the fossilized bones of an extinct animal in the desert of New Mexico, I was hooked. Palaeontology became a primal fascination for me; it offered me a way to satiate a love for adventure and discovery while contributing to a broader understanding of how life has evolved on our planet, and why. My advice to a young scientist would be that every once in a while, you should wake up in the morning and question everything you think you know, even the basics. Has anyone actually tested that concept? Science is a process of continuous evaluation; you may stand on the shoulders of giants, but don't forget to rerun their data.

2.3 GEOLOGY AND FOSSIL VERTEBRATES

Fossil vertebrates are found in rocks, and those rocks can offer a great deal of information about the death and burial of organisms and on the environments they inhabited, their age, and their former geographical location. These are all aspects of geology.

2.3.1 Taphonomy

The mode of burial and preservation of fossils, their **taphonomy**, is important in their interpretation. Taphonomy is the study of all the processes that occur between the death of an organism and its final state in the rock. In most cases, these processes ensure that the dead animal is not preserved, but is eaten or rots away. When a fossil is preserved, it has usually passed through a series of stages (Figure 2.5): (1) decay of the soft tissues; (2) transport and breakage of hard tissues; and (3) burial and modification of the hard tissues. Vertebrates are reasonably well represented in the fossil record because they have hard parts, bones and teeth, made from apatite, a form of calcium phosphate. In rare cases, when decay is prevented, soft parts may be preserved.

After death, a vertebrate carcass may lie exposed in the air, or it may be covered by water. In either case, the carcass may be scavenged, that is, eaten by other large animals. In terrestrial settings, carcasses today may be picked over by large scavengers such as hyaenas and vultures, and when they have had their fill, smaller animals, such as meat-eating beetles, may move in. Similar processes occur under water.

At the same time as the carcass is scavenged, it also begins to decay, a set of processes in which microbes transform and digest the tissues. The style of decay depends on a variety of chemical conditions, particularly the supply of oxygen, the pH, the temperature, and the nature of the organic carbon in the carcass. Decay may be slowed down in the absence of oxygen, for example on the deep seafloor, or in a stinking black pond. In such conditions, whole fishes and other animals may be preserved relatively intact. Acid conditions, as are found in peat bogs for example, may also prevent decay. Well-known examples of vertebrates preserved by acid conditions are the famous 'bog bodies' of northern Europe, human remains that are preserved in their entirety, even if the bones may have dissolved and the flesh is somewhat leathery. Most soft tissues are made of highly **volatile** forms of carbon, in other words materials that decay readily. Less volatile forms of carbon may survive for longer.

Certain vertebrates are found in situations of exceptional fossilization, where early mineralization has preserved even the soft tissues. Typically, the soft tissues are replaced by pyrite, phosphate, or calcite. More unusual examples include preservation in amber, in ice, or in asphalt. Examples of exceptional preservations are described later in the book (see Boxes 1.2, 6.2, 7.5, 9.4, 10.8).

In more normal situations, where scavenging and decay have taken place, the surviving hard parts are usually transported by water or wind to their final resting place. Transport processes (Figure 2.5) generally **disarticulate** skeletons, that is, break them up. Further transport frequently causes fragmentation or breakage and **abrasion**, when angles and sharp projections are worn down by physical processes (Figure 2.6).

After transport, the specimen may be buried. Further damage may then occur, such as compaction by the weight of

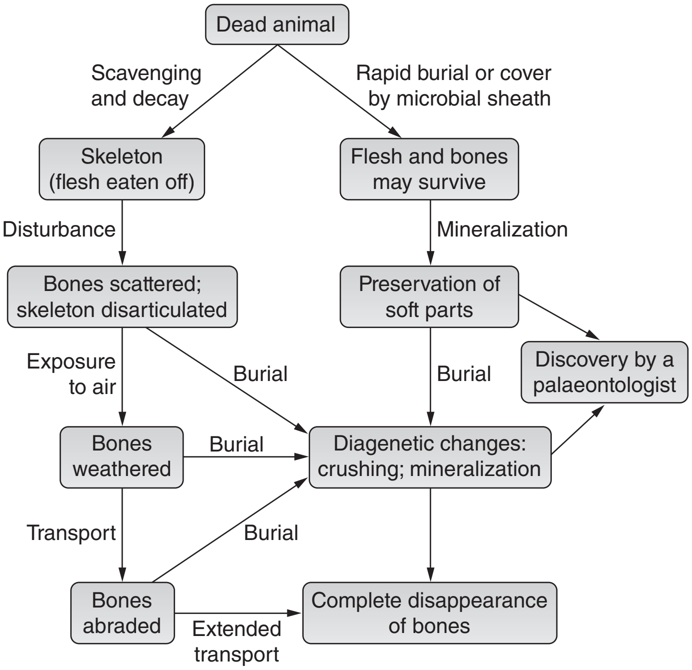


Figure 2.5 Taphonomic processes affecting a fossil vertebrate, from death, through scavenging and decay, and through transport and burial, to eventual discovery by a palaeontologist. Source: M.J. Benton, University of Bristol, UK. Reproduced with permission.

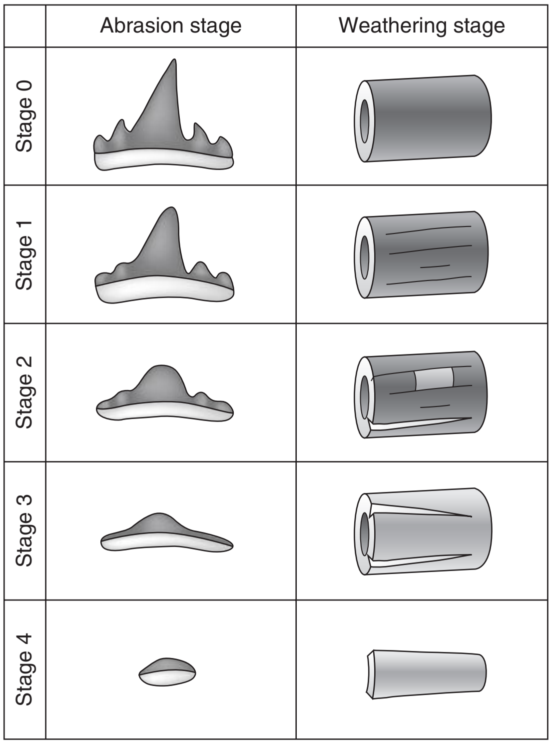


Figure 2.6 Abrasion stages of a bone depend upon the amount of transport and physical battering. Sharp edges and processes are lost, the surface is polished, and the bone eventually becomes a bone pebble (Stage 4). Weathering progressively cracks the surface layers of bone off. Source: E. Cook, BBC, Bristol, UK. Reproduced with permission.

overlying sediment. Hollow parts may collapse, and complex elements will be distorted. After burial and collapse, the organism may be affected by chemical changes, involving the transport of chemicals in solution within the buried sediment. Minerals tend to crystallize out in cavities within bones, and complex sequences of such infilling minerals may be observed in cut sections of fossil bone. Compaction during uplift or folding of the rocks may further distort or compress fossils. These are examples of **diagenesis**, the physical and chemical processes that occur after burial, within sediment or rock.

2.3.2 Continental drift

One of the most dramatic changes that has taken place through geological time (see Box 2.2) is **continental drift**, the movement of continents and oceans relative to each other. The idea that the present layout of continents has not always been the same was suggested in the 19th century, when geographers noted how the Atlantic coasts of South America and Africa could be fitted together like giant jigsaw pieces.

In 1912, Alfred Wegener marshalled a great deal of geological and palaeontological evidence in favour of continental movements. He focused in particular on an ancient supercontinent called Gondwana (Figure 2.7). Palaeontologists had found similar fossil plants, members of the *Glossopteris* Flora, and reptiles, such as the dicynodont *Lystrosaurus*, in rocks of Permian and Triassic age in Africa, South America, India, and Australia. The small freshwater reptile *Mesosaurus* from the Early Permian was known only from a limited area on the coasts of Brazil and west Africa. The normal explanation at the time was that these plants and animals had been able to travel great distances between

BOX 2.2 GEOLOGICAL TIME

Earth is immensely ancient, and yet the history of the Earth and the history of life have been punctuated by so many crises and dramatic changes that it is possible to find markers that are the same worldwide. This means that geologists can **correlate** rocks, and establish an agreed chronology of events through time. Geologists began to realize this 200 years ago. At first they saw that particular assemblages of fossils were always found together; they were not scattered randomly through the rocks in different associations. These principles of **relative dating**, (1) the recognition of repeated fossil assemblages, and (2) their identification as characteristic of particular time units, gave a basis for the standard international geological time scale.

In 1911, numerical or **absolute dating** was attempted for the first time using the newly discovered property of radioactivity. Some chemical elements exist in an unstable radioactive condition. This means that they decay over time, emitting radioactivity and changing from one elemental form to another. The decay process, in which the parent element changes into the daughter element, may last for a matter of hours, for thousands of years, or for billions of years. It is possible to assess when half the parent has decayed, and the time this takes is called the **half-life**. Geologists compare the relative amounts of parent and daughter element in particular **igneous** rocks, rocks formed by crystallization at high temperatures, and they compare the ratios to the known half-lives to establish the absolute, or exact, age in millions of years.

The longest stretch of geological time is the Precambrian, representing most of the history of Earth, from its origin, through its cooling, the origin and early history of life. The last major segment of geological time is the Phanerozoic ('abundant life') Eon, the time during which fossils are abundant and document the well-known history of major modern groups, including the vertebrates. The Phanerozoic is subdivided into three eras, the Palaeozoic ('ancient life'), Mesozoic ('middle life'), and Cenozoic ('recent life'), and these in turn are divided into periods, such as Cambrian, Ordovician, and Silurian, and epochs, such as Paleocene, Eocene, and Oligocene. The epochs are further divided into ages and zones, based on the distributions of single fossils, or specific assemblages, and zones may represent time intervals of as little as 100,000 years. In practice, rocks are dated in the field by means of fossils, and then numerical ages can be added here and there where there is an appropriate igneous rock band, for example, a layer of volcanic lava.

The current geological time scale is based on a massive research effort, combining fieldwork, studies of fossils, radiometric dating, and many other methods. From time to time, a revised version is compiled by international agreement, and the inputs of many researchers (Gradstein *et al*., 2012).

Eon	Era	Period	Epoch	Date at beginning (Myr)
Phanerozoic Eon				
	Cenozoic Era			
		Quaternary Period		
			Holocene Epoch	0.01
			Pleistocene Epoch	2.6
		Tertiary Period		
			Pliocene Epoch	5.3
			Miocene Epoch	23
			Oligocene Epoch	34
			Eocene Epoch	56
			Paleocene Epoch	66
	Mesozoic Era			
		Cretaceous Period		145
		Jurassic Period		201
		Triassic Period		252
	Palaeozoic Era			
		Permian Period		299
		Carboniferous Period		359
		Devonian Period		419
		Silurian Period		444
		Ordovician Period		485
		Cambrian Period		541
Precambrian				4567

The geological time scale, showing the main divisions of geological time, and current numerical age dates, based on the International Geological Times Scale 2012. Source: Adapted from: http://www.stratigraphy.org/; https://engineering.purdue.edu/Stratigraphy/index.html; http://www.geosociety.org/science/timescale/timescl.pdf; http://www.nhm2.uio.no/norges/GTS_2012.pdf; http://www.geosociety.org/science/timescale/timescl.pdf.

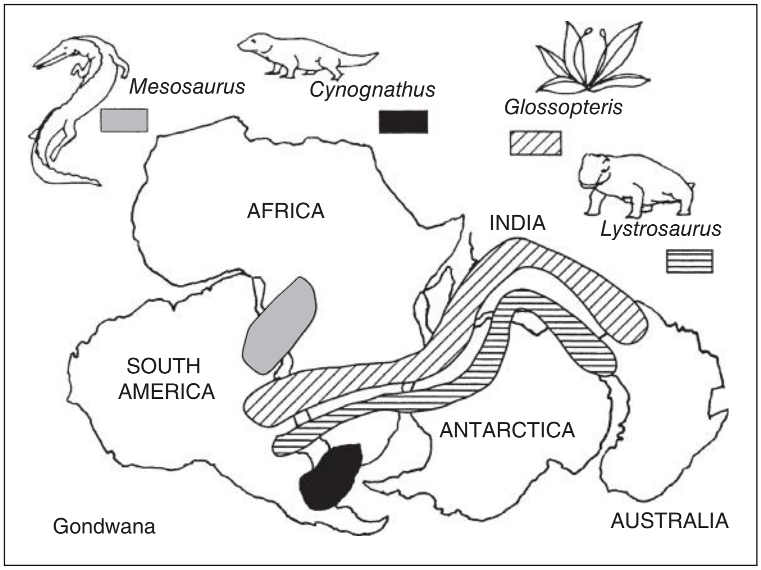


Figure 2.7 Reconstruction of Gondwana as it was from the Late Carboniferous to the Late Triassic, based on the work of Alfred Wegener, showing how this arrangement of continents makes sense of the distributions of Permian reptiles such as *Mesosaurus*, Permian plants such as *Glossopteris*, and Triassic reptiles such as *Lystrosaurus* and *Cynognathus*. Source: M.J. Benton, University of Bristol, UK. Reproduced with permission.

those southern parts of the world. More difficult to explain was how the Late Permian *Glossopteris* Flora could exist both in the southern hemisphere and across the equator in India.

Wegener argued that the southern continents had once been united, and the Permo-Triassic plants and animals had more limited geographical ranges. He recognized a northern supercontinent called Laurasia, and he showed that Gondwana and Laurasia together formed a single global supercontinent, Pangaea, which lasted from the Late Carboniferous to the Late Triassic.

Wegener's ideas were not welcomed by all scientists at the time because the driving force for continental drift could not be identified. The motor was discovered about 1960, however, as a result of geological investigations of deep ocean floors. Fresh oceanic crust was found to form from molten rock along the mid-ocean ridges, and the ocean floor was moving apart slowly and evenly away from these ridges. Earth's crust is divided into a number of plates, some major ones corresponding to the continents and oceans, and many minor ones.

The mechanism driving continental drift is **plate tectonics**. Molten rock, **magma**, circulates in great gyres beneath Earth's solid crust, moving upwards and leaking out through the mid-ocean ridges, and then moving sideways away from the ridges, tending to pull the thin oceanic plates apart. The magma circulates downwards close to the thicker continental crust. The circulation is driven by convection of heat from the centre of Earth. Where oceanic crust meets continental margins, the sideways movements may continue, hence opening the ocean further, or the oceanic plate may dive down beneath the continental plate, forcing up mountain ranges, such as the Andes. Where continental plates collide, they may move past each other jerkily, as along the San Andreas fault, or they may force into each other, as with the Himalayas, raised by India's continuous movement northwards into the main Asiatic land mass.

Continental drift is crucial in the history of the vertebrates. The geography of Earth has never been stable, and it seems that, through time, the continents have amalgamated and divided several times. Most is known about the break-up of Pangaea since the Triassic, but it is possible to make good estimates of continental reconstructions for more ancient times. Continental drift has affected animal and plant distributions: biogeographic ranges are sundered at times, and brought together in unpredictable ways. Dinosaurs evolved in a world on one supercontinent, and they could move freely all over Pangaea. By the Cretaceous, however, their movements became restricted, and local, or **endemic**, faunas are found in South America, Africa, and India. During most of the Cenozoic, South America was an island, but 3 million years ago, the Isthmus of Panama was formed, and a great exchange of land animals took place, with profound effects both north and south (see Section 10.6.6).

Sea level change has been just as important as the continuing dance of the continents. At times in the past, sea levels have been as much as 200 m higher than they are now, caused either by melting of the polar ice caps or massive mid-ocean ridge activity. Upwelling magmas have raised ocean floors at times, such as in the mid-Cretaceous, and this causes a **transgression**, when ocean waters flood the land. Such flooding episodes provide increased habitats for organisms that live in shallow oceans, but they can also restrict land areas, and create islands.

2.3.3 Ancient climates

Climates of the past were very different from those of today, and continental drift has played a major part. For example, parts of north-west Europe and North America that are now temperate lay south of the equator in the early Palaeozoic, moved across the equator in the Devonian and Carboniferous, and finally moved out of tropical latitudes after the Triassic. The plants and animals, as well as the rocks, show the major changes in climate that resulted from these plate movements. On land, there were times when abundant amphibians and reptiles lived in lush tropical rain forests. At other times, vast deserts covered those areas, and vegetation was sparse. Coral reefs ringed the continents, and exotic fishes swam in the shallow waters.

The evidence for ancient climates comes from detailed study of rocks and fossils, as well as isotope measurements (especially oxygen and carbon) and climate models. Many sedimentary rocks are excellent indicators of climate. For example, beds of coal indicate the former existence of lush, humid forests. Red-coloured sandstones and mudstones, showing cycles of dramatic flooding and then mudcracked surfaces, suggest that there were monsoonal climates. Irregular limestone bodies in ancient soils, termed **calcretes**, also indicate dramatic seasonal rainfall and rapid evaporation, as a result of monsoons. Freezing conditions are indicated by ice scratches on rocks, and by glacial **tills**, faceted and striated rocks and dust ground up by moving glaciers.

The positions of the continents affected ancient climates in more dramatic ways. At times when there was no land at the poles, climates seem to have been rather uniform worldwide. The reasoning is that land at the poles is covered with snow and ice in winter. The white colour of the ice reflects sunlight, and makes the land surface even colder, so the ice survives through the polar summer, and in fact grows progressively. The process does not begin if there is only salt water near the poles. This was the case during the Triassic and Jurassic at least, and it seems that the temperature difference from the equator to the poles was much less than it is today. This meant that dinosaurs were free to wander over a wide band of latitudes, and they seemingly did, because dinosaurs have been found within both the Arctic and Antarctic circles. During the Cenozoic, temperatures worldwide became progressively cooler, distinctive climatic belts developed from the Equator to the poles, and most plants and animals became restricted in the zones they can occupy.

2.4 BIOLOGY AND FOSSIL VERTEBRATES

It is great fun to speculate about how ancient animals lived. It is important though to temper this urge to speculate with the application of method, wherever possible, so that other scientists may repeat and test functional hypotheses. There are now a number of analytical techniques for studying functional morphology and palaeoecology (Benton, 2010).

2.4.1 Functional morphology

The first question that people ask about any fossil vertebrate is 'what did it do?' How did the heavily armoured Devonian placoderms use their jaws? Why did some synapsids have massively thick skull roofs? What did *Stegosaurus* use its dorsal plates for? Why did sabre-toothed cats have such massive fangs?

These are all questions of functional morphology, the interpretation of function from **morphology**, the shape and form of an animal. The main assumption behind this approach is that structures are adapted in some way, and that they have evolved to be reasonably efficient at doing something. So, an elephant's trunk has evolved to act as a grasping and sucking organ to allow the huge animal to reach food and drink at ground level. Giraffes have long necks so they can feed higher in trees than other mammals (and reach the ground to drink), and they may also be sexually selected in that females may choose male giraffes with the longest necks. Tunas have more red muscle than most other fishes so they can swim faster and further.

The bones of fossil vertebrates can provide a great deal of information about function. The bones show directly how much movement was possible at each joint, and this can be critical in trying to reconstruct how particular vertebrates could walk, swim or fly. The maximum amount of rotation and hinging at each joint can be assessed because this depends on the shapes of the ends of the limb bones. There may be **muscle scars** on the surface of the bone, and particular knobs and ridges (**processes**) that show where the muscles attached, and how big they were. Muscle size is an indicator of strength, and this kind of observation can show how an animal moved.

There are several approaches to the study of functional morphology (Figure 2.8). First is comparison with living animals. If the extinct animal belongs to a modern group, perhaps a Miocene elephant, then this exercise can be very useful, if applied with care. The palaeontologist can compare the bones of the fossil species with those of a modern elephant to work out the size and weight of the extinct animal, whether it had a trunk or not, how it used its teeth, and how fast it could move.

If there are no close living relatives, or if the living relatives are very different from the fossil species, then it might seem to be impossible to identify a reasonable living analogue for the extinct species. The **extant phylogenetic bracket** (EPB; Witmer, 1997) may help. The concept of the EPB is simple: even if a fossil is distant from living species, it will be bracketed in the phylogenetic tree by some living organisms. So, it would be wrong to interpret all dinosaurs simply in terms of their descendants, the birds, but in the evolutionary tree dinosaurs are bracketed by birds and crocodiles. So, any character shared by both crocodiles and birds, such as air sacs in the head region, is likely to have been present in dinosaurs, even if air sacs have never been seen in a fossil. In comparing a Miocene elephant with modern elephants the EPB highlights one problem: it cannot be assumed that Miocene elephants had all the characters of modern forms, as some characters may have been acquired between the Miocene and the present day.

In some cases, of course, the fossil forms are entirely different from modern animals and have no obvious relatives that are close enough phylogenetically. Examples are the giant marine reptiles called pliosaurs (see Section 8.10.1) that lived in Jurassic and Cretaceous seas. These animals (Figure 2.8(a)) had massive heads and short necks, and long, wing-like paddles. They do not have any close living relatives, but comparison with modern marine predators, such as killer whales, which feed on seals, fish, and squid, suggests that pliosaurs fed on their contemporary equivalents, namely smaller marine reptiles, as well as fishes and **ammonites**, coiled swimming molluscs.

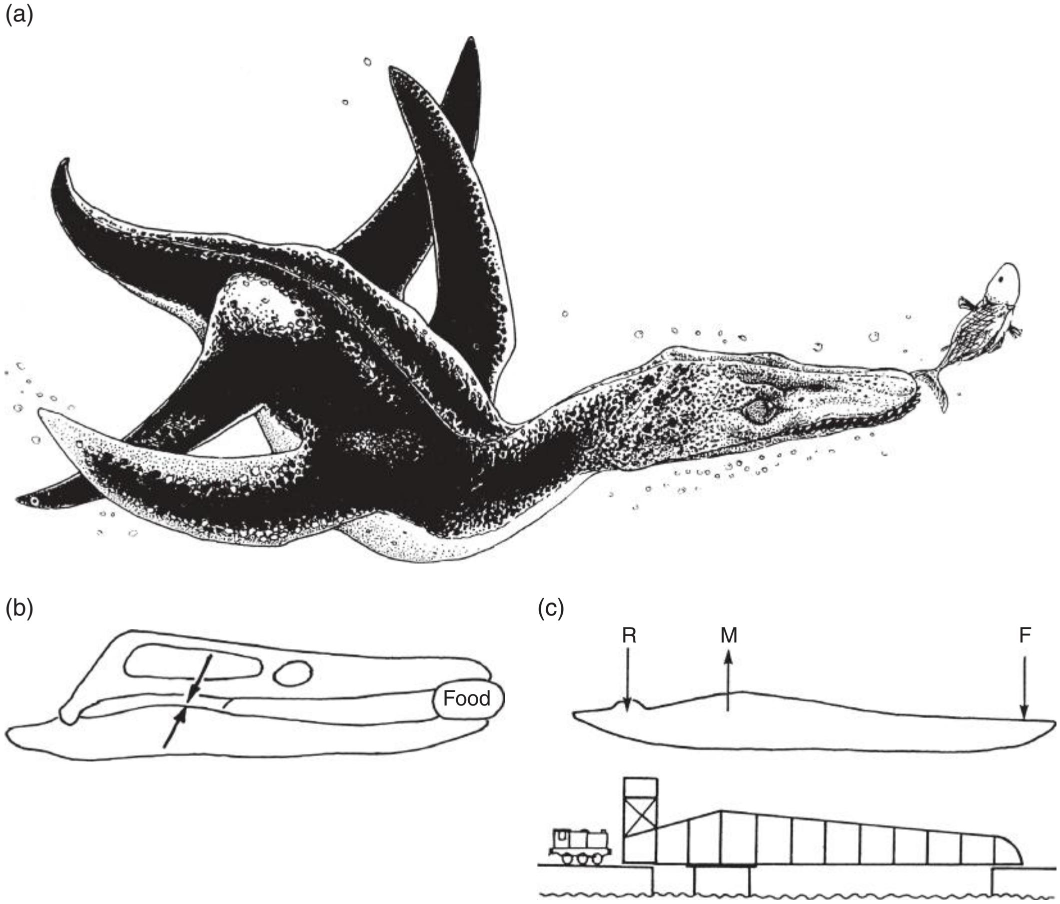


Figure 2.8 Interpretations of the functional morphology of the Early Jurassic pliosaur, *Rhomaleosaurus*: (a) the pliosaur in life, shown chasing a fish; (b) the head in static equilibrium, gripping a piece of food at the front of the jaws; (c) the lower jaw modelled as an asymmetrical swing bridge, with major muscular forces (M), reactions from the food at the bite point (F), and reactions at the jaw joint (R). Source: (a) J. Martin, formerly, Museum and Art Gallery, Leicester, UK. Reproduced with permission. (b,c) Adapted from Taylor (1992).

The pliosaur skull may be interpreted by means of the second approach in functional morphology, which is to use mechanical models (Taylor, 1992). The jaw (Figure 2.8(b)) may be compared to a lever, and calculations made of the forces acting to close the jaw. Changes in the shapes of jaws in ancient herbivores and carnivores can often then be understood in terms of adaptations to achieve a stronger bite at the front of the mouth, or perhaps to evolve an efficient grinding and chewing system further back in the mouth. In pliosaurs, the jaw was designed to clamp shut with huge force, and to prevent the prey struggling free.

The shape of the pliosaur jaw, with an elevated coronoid eminence near one end has been compared to an asymmetrical swing bridge (Figure 2.8(c)) that is loaded by its own weight when it is open. Similarly, the layout of bones in the skull may be interpreted in terms of the stresses acting in different directions in a hypothetical model of a box with holes. The skull and jaw structure suggests that pliosaurs used their heads to bite their prey firmly, but whether they used twisting movements to tear off flesh (Taylor, 1992) is unclear (Foffa *et al*., 2014). These kinds of **biomechanical** studies are much enhanced by the application of simple mathematical models.

Conclusions in functional morphology may be checked by the use of information from the context of a fossil. Pliosaurs, for example, are always found in marine sediments, associated with other smaller marine reptiles and fishes. Their skeletons often lie in deep-sea sediments that apparently lacked oxygen, so the carcasses clearly fell from higher, oxygenated, waters. This confirms that pliosaurs were free-swimming predators, and the associated fossils show some possible elements of their diet. Some skeletons preserve remnants of stomach contents, and fossil dung, **coprolites**, and supposed ichthyosaur vomit (? vomitite) are also known. There are even some specimens of plesiosaur bones bearing tooth marks that precisely match those of some pliosaurs.

This example illustrates the classic approach to functional interpretation of fossils, a combination of **empirical** (=observational) evidence, such as fossils, and comparison with modern analogues to find plausible modes of life and functions. The weakness of these kinds of functional studies, however, is that they are not repeatable, a core requirement in experimental science, even though they may be quantifiable. However, one new approach offers a more objective, experimental approach to the function of extinct organisms, and this is by testing engineering models.

Most successful has been **finite element analysis**, a method that provides graphic and testable evidence for hypotheses in skeletal function, including feeding and locomotion (Rayfield, 2007). The method is applied to three-dimensional digital images, usually constructed from CT (computed tomography) images, made from serial X-ray scans of a bone or skull, for example. The complex 3D structure is divided into pyramidal, tetrahedral, or cuboid cells, or 'elements', which can be thought of as a kind of mesh. The critical point is that material properties are assigned to each element in the 3D mesh, and these are taken from studies of modern bone and comparisons with sectioned fossil bone. There would be no point in carrying out such experimental studies on a physical model because it would be made from clay or plastic, for example, nor on a fossil because it has been much modified and turned into rock. We are interested in the physical properties of the skull or bone in life. Once the material properties are assigned, the computerized model can be subjected to forces to assess stress (force per area) and strain (deformation due to stress) under normal and abnormal loads, to test the jaws during feeding or the limbs during locomotion. One of the most spectacular studies so far has been an exact calculation of the maximum bite force of the dinosaur *Tyrannosaurus rex* (see Box 2.3).

2.4.2 Palaeoecology

Fossil vertebrates lived in communities in which some animals ate others, some specialized in eating particular plants, and others suffered from particular parasites. Some fossil vertebrates lived in damp tropical forests, whereas others preferred to burrow in temperate soils, or to swim in deep cold seas. Just as today, organisms have always interacted in different ways with other organisms, and with the physical environment. The study of ancient modes of life and interactions is **palaeoecology**, and the focus of study may be a single animal or a whole community.

Unlike an ecologist who works on modern plants and animals, a palaeontologist has to work with one hand tied behind the back. It is obvious that specimens of any particular species will be incomplete, and palaeontologists can never see the animal in action. Also, the collection of fossil plants and animals from any particular site is likely to be incomplete, and biased: the relative numbers of fossil specimens of different species are unlikely to reflect their true abundances in life.

Nevertheless, much can be done. The modes of life of individual species of fossil vertebrate can be deduced from their bones and teeth. If there are enough specimens of any particular species, detailed measurements may show **sexual dimorphism**, that is, two sets of adult individuals, one presumably female, and the other male. Sometimes, juveniles are found, and these can

BOX 2.3 ENGINEERING THE SKULL OF *T. REX*

Tyrannosaurus rex is probably the most famous fossil vertebrate because of its huge size and fearsome reputation. A common question is 'how strong was its bite force?' Experts have speculated about whether *T. rex* could snap a car in half, although such a feat would presumably have conferred little survival value in the Late Cretaceous. Nonetheless, having the power to bite another dinosaur in half would be a spectacular property for an acknowledged huge predator. In a smart application of empirical evidence, Erickson *et al*. (1996) estimated a bite force of 6410–13400 Newtons, based on tooth impressions. They worked with a pelvis of the herbivore *Triceratops* that bore 58 tooth marks. On making casts, they identified these puncture marks as matching the teeth of *T. rex*, and then estimated from the depth of the puncture, up to 37 mm, and experiments with steel teeth and modern cow bones, the possible forces required to penetrate so deep.

This was a single calculation based on a single event, and ought to be generalized. **Finite element analysis (FEA)**, an engineering technique, provides scientific, testable models. Emily Rayfield noted a paradox in the construction of the *T. rex* skull; while *T. rex* is assumed to have been capable of producing extremely powerful bite forces, the skull bones are quite loosely articulated. Does this mean that the skull would have expanded and distorted if its owner bit too hard into a *Triceratops* carcass, or did *T. rex* have to control its bloodthirsty efforts? Rayfield (2004) studied all the available skulls and constructed a mesh of triangular elements, small triangular or cuboid cells that define the 3D shape in preparation for engineering analysis. In her FEA model of the *T. rex* skull, Erickson *et al.*'s (1996) bite forces of around 31,000 N* (equivalent to 78,060 N along all the teeth in a single jaw, and 156,120 N for both jaws together) were applied to individual teeth, and the distortion of the element mesh was observed. Rayfield's (2004) results show that the skull is equally adapted to resist biting or tearing forces and therefore the classic 'puncture-pull' feeding hypothesis, in which *T. rex* bites into flesh and tears back, is well supported. Major stresses of biting acted through the pillar-like parts of the skull and the nasal bones on top of the snout, and the loose connections between the bones in the cheek region allowed small movements during the bite, acting as 'shock absorbers' to protect other skull structures. In reality, all teeth would almost certainly not be operating at their maximum possible force together, so Rayfield (2004) estimates a maximum single-tooth bite force of 31,000 N, equivalent to 3 tonnes, twice the value for the maximum bite force of the great white shark, at a modest 18,216 N – our most fearsome chomper today.

Even higher bite forces of 35,000–57,000 N at a single posterior tooth were calculated by Bates and Falkingham (2012) using multi-body dynamics, methods that model machines or organisms as solid bodies, or links, that are connected to each other by joints that restrict their relative motion. The method requires reconstruction of the major jaw muscles in terms of their mass, maximum contraction velocity, muscle fibre length, and pennation angle (the angle at which the muscle attaches to the terminal tendon), and it would be interesting to determine how these high bite forces are accommodated by further FEA study of the *T. rex* skull.

*N = Newton, the SI unit of force, equivalent to the force required to accelerate a mass of 1 kg at a rate of 1 m per second per second.

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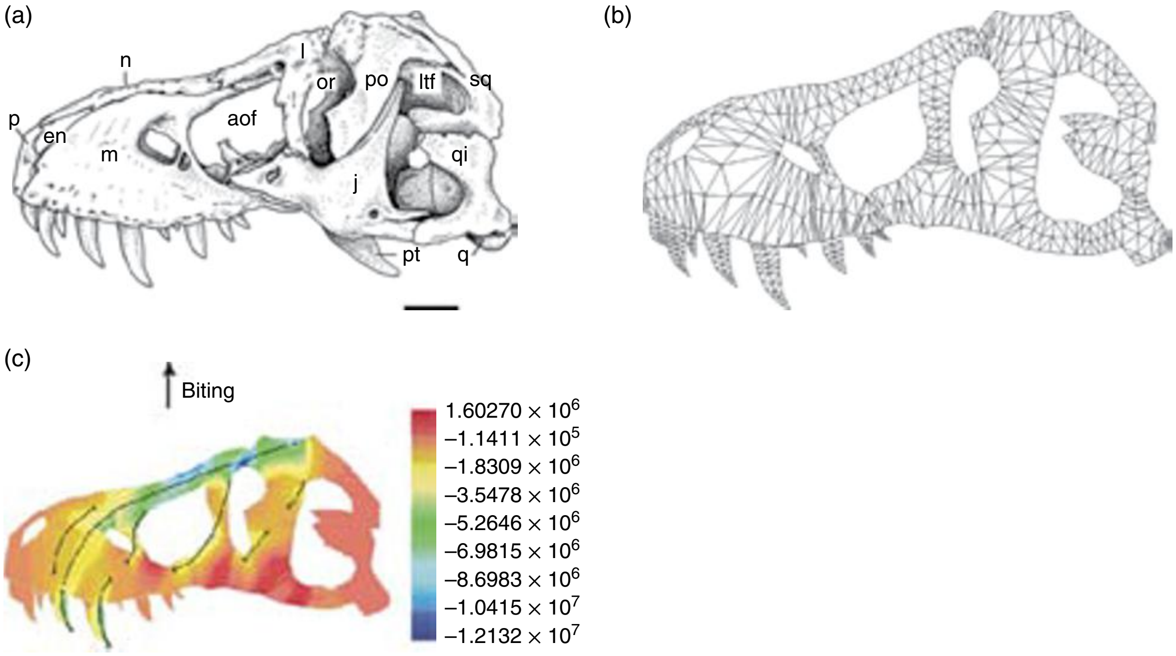

The skull of *Tyrannosaurus rex* as an engineering model. First, the skull (a) is scanned to produce a digital model. Then (b), a mesh of individual elements is constructed to represent the major distinguishable components of the skull; two directions of bite force are indicated, for inserting teeth into the prey vertically, and for tearing backwards, horizontally. Each cell is assigned material properties for bone of the appropriate structure, and forces are applied (c). Grey indicates highest stress, and light grey lowest. At intense biting forces, the greatest stresses are along the top of the snout, and just behind the tooth row in the jugal. Source: E. Rayfield, University of Bristol, Bristol, UK. Reproduced with permission.

show how the animal's form changed as it grew up. If several species are found together, it may be possible to work out which ate what, and to draw up a food web (see Box 4.4). The food web should include plants, insects, and other animals, as well as the vertebrates. The whole assemblage of organisms that lived together in one place at one time, the **community**, can be compared in detail with communities from other localities of the same age, and with similar communities through time. Some communities remain fairly constant, although different species may take the key roles at different times. In other cases, new communities arise, or communities can become more complex, for example, with the evolution of new modes of life such as tree-climbing, flight, burrowing, or mollusc-eating.

2.5 DISCOVERING PHYLOGENY

The basis of all studies in palaeontology is the tree of life. All organisms, living and extinct, are linked by a single great branching tree, or **phylogeny**. Living organisms, from viruses and slime moulds to humans and oak trees, and all known fossil species, are related to each other. This means that they can be traced back through numerous ancestors, to a single **common ancestor** of all life. The fossil evidence suggests that life originated at least 3500 million years ago, and that is probably when the common ancestor lived.

It is clearly impossible to discover the entire phylogeny of life because so many fossil species are probably missing, and indeed so many living species have not yet been studied (perhaps only 15–20% of living species have been named). Palaeontologists and biologists concentrate on disentangling parts of the tree of life, and this has now become a major research theme. There are two principal analytical techniques for establishing the relationships of vertebrates and their relatives, **cladistic** analysis of **morphological** data and cladistic, and other, approaches to **molecular phylogeny** reconstruction. The purpose of the following account is to introduce some general concepts and terminology, not to provide a primer of how to generate phylogenies. That is covered elsewhere (see Section 2.7).

2.5.1 Cladistic analysis of morphological characters

Cladistic analysis of morphological characters is the main technique used to determine the relationships of living and fossil vertebrates. The result of a cladistic analysis is a **cladogram**, such as those in Figure 1.8. A cladogram is a branching diagram that links all the species, living and fossil, that are under investigation, and the branching points, or **nodes**, mark points at which shared characters arose. A cladogram is not an evolutionary tree because there is no *absolute* time-scale, although the *relative* order of nodes is shown. The cladogram shows the closeness of relationship, or recency of a common ancestor shared by two species, by the arrangement of the groups – the closer they are to each other, the closer is the postulated relationship.

A cladogram is constructed after an assessment of **characters**. It is important to find shared derived characters (**synapomorphies**), features that are shared by two or more species, but nothing else. Synapomorphies are distinguished from primitive characters, which may be widespread outside the group under study. Among basal deuterostomes, for example, debates have focused on whether characters such as the endostyle, the postanal tail, and the cranium are synapomorphies of vertebrates, chordates, or even deuterostomes as a whole (see Chapter 1).

The key to distinguishing synapomorphies, characters that are potentially useful in cladistic analysis, from primitive characters is **outgroup comparison**. The outgroup consists of everything that lies outside the group under study (the 'ingroup'). In the analyses of deuterostome relationships, the outgroup consists of all non-deuterostomes, anything from banana trees to clams, worms to viruses. For practical purposes, the outgroup is usually selected from among the organisms that are closely related to the ingroup, so that meaningful comparisons can be made. The tail and the notochord are synapomorphies within Deuterostomia, because other animals lack these characters. Other features shared by all deuterostomes, such as a gut and a nervous system, are useless in reconstructing their phylogeny as members of the outgroup (e.g. worms, arthropods, molluscs) also have these characters.

Character discovery and analysis is a complex and time-consuming business. The analyst studies the anatomy of all the organisms of interest in detail, identifying unique and shared characters. There are no objective rules about what is and is not a character. Some are fairly uncontroversial, such as the presence or absence of a particular element, such as the fused clavicles (=furcula/ wishbone) in birds and near-relatives: the fusion of two bones can probably be seen as a single event in evolution, and so this feature is either present (coded 1) or absent (coded 0). Others may be harder to determine. For example, in looking at theropod dinosaurs and basal birds, some specimens have feathers and others do not. Experts debate whether to code feathers as a single character (feathers present or absent), or as many characters that describe feather anatomy in much more detail, so that full flight feathers are distinguished from other types of feather, such as wispy down 'hairs'. Character states (coded 0, 1, 2…) are listed in a **data matrix**, a table of species/specimens versus characters. Well-established computer programs, such as TNT, PAUP, NONA, MacClade, and others, are used to process the data matrices and extract patterns of relationships that are expressed as trees. Relationship is determined by shared synapomorphies, and taxa are organized hierarchically to reflect a continuum from most to least proportions of shared synapomorphies.

Derived characters indicate whether a group is **monophyletic**, that is, it arose from a single ancestor and includes all living and fossil descendants of that ancestor (Figure 2.9(a)). Most familiar named groups of animals are monophyletic groups (also termed **clades**): examples are the Phylum Chordata, the Subphylum Vertebrata, the Family Canidae (dogs), and so on (see Box 2.4). All members of the clade share at least one derived character.

Traditional classifications of vertebrates and other groups often include non-monophyletic groups, although these should be avoided wherever possible. The commonest examples are **paraphyletic** groups, which include only the most primitive descendants of a common ancestor, but exclude some advanced descendants (Figure 2.9(b)). A well-known paraphyletic group is the 'Dinosauria', as traditionally understood, which almost certainly arose from a single ancestor, but which excludes most of the descendants, namely the birds. All members of the paraphyletic group share one or more derived characters, but other organisms, excluded from the paraphyletic group, do too, although they may have acquired other features. So, for example, all dinosaurs have vertical hindlimbs with a hinge-like ankle, but so too do birds. The upper bound of 'Dinosauria' is defined only by the absence of characters such as powered flight and wings, and so it is an arbitrary construct.

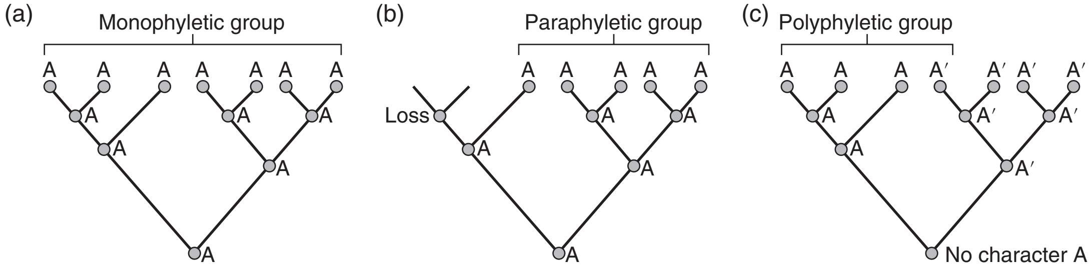

Figure 2.9 Cladograms showing: (a) a monophyletic group, (b) a paraphyletic group, and (c) a polyphyletic group, and the presence and absence of hypothetical characters A and A′ (character A′ is convergent on [very similar to] character A). In the monophyletic group (a), all species have character A, a synapomorphy of the clade. In the paraphyletic group (b), some species have lost the synapomorphy A by transformation (e.g. the keratinous scale of reptiles is transformed into feathers or hair). In the polyphyletic group (c), the apparent shared characters (A, A′) are convergences and the ultimate common ancestor of the two clades lacks that feature. Source: M.J. Benton, University of Bristol, UK. Reproduced with permission.

BOX 2.4 CLASSIFICATION

Animals are classified according to a system established by Carolus Linnaeus (or Linné) in 1758. Each distinguishable form is given a genus (plural, genera) and species name, such as *Homo sapiens*, *Tyrannosaurus rex*, and *Canis familiaris*. The generic name is first, and it has a capital letter. The specific name is second, and it has a lower case letter. Generic and specific names are always shown in italics, or underlined.

Living species are defined according to the **biological species concept**, as all the members of different populations that naturally interbreed, and produce viable (i.e. fertile) offspring. In practice, of course, taxonomists do not carry out breeding experiments, and they apply the **morphological species concept**, which defines a species in terms of unique characters. This is close to the **phylogenetic species concept**, that a species is a small clade of diagnosable forms of the same basic kind, and sharing particular characters. Palaeontologists use the morphological and phylogenetic species concepts.

Species are grouped together in genera, and each genus may contain one or more species. Genera are then grouped in families, families in orders, and so on. This pattern of inclusive hierarchical grouping reflects the splitting pattern of evolution, and the way that evolution is represented in a cladogram. The basic traditional classification of humans is:

Species	*sapiens*
Genus	*Homo*
Family	Hominidae
Order	Primates
Class	Mammalia
Subphylum	Vertebrata
Phylum	Chordata
'Superphylum'	Deuterostomia
Kingdom	Animalia

The other kind of non-monophyletic groups are **polyphyletic**, those that arose from several ancestors, and that are diagnosed by a convergent feature (Figure 2.9(c)). Two examples of polyphyletic groups of vertebrates are 'Natantia', a classical grouping together of fishes and whales based on their similarity in shape and in swimming in the sea, or the 'pachyderms', a group of thick-skinned, greyish mammals such as elephants, hippos and rhinos.

The sorting of characters in cladistics into primitive and derived is an exercise in determining character **polarity**, in other words, the direction of evolution. The polarity should be made clear by outgroup comparison, and polarity can reverse, depending on the context. For example, in the analysis of deuterostome relationships, absence of a tail is the primitive character state, and possession of a tail is the derived state. In the context of human relationships, however, loss of the tail is one of the synapomorphies of the Family Hominidae (apes and humans).

There are often problems in distinguishing just what are shared derived characters (synapomorphies), and what are not: the classic evolutionary dilemma of separating **homologies** from **analogies**. A homology is a feature seen in different organisms that is the same in each – it is anatomically and generally functionally equivalent, and shows evidence of derivation from a single source – while an analogy is a feature that may look or act in a broadly similar way in different organisms, but which gives evidence of separate origins. An example of a homology is the wing of a robin and the wing of an ostrich. Although the ostrich wing is not used in flight, its location in the body and its detailed structure show that it is a direct equivalent to the robin wing, and the latest common ancestor of robins and ostriches would have had such a wing. The wing of a robin and the wing of a fly are analogies because their detailed structures show that they arose independently, even though they perform similar functions. Homologies, then, are synapomorphies, the clues that indicate common ancestry.

2.5.2 Molecular phylogeny reconstruction

There is a second, largely independent, approach to discovering phylogeny. Molecules record evolution, and molecular biologists have sought to discover relationships by comparing molecules from different organisms. In many methods, it is assumed that the amount of similarity between homologous molecules in different organisms is proportional to their degree of relationship, or the time since they diverged, and this in turn is based on the assumption of a **molecular clock**, the suggestion that the rate of evolutionary change of any particular protein or nucleic acid was approximately constant over time and over different lineages. Other molecular phylogenetic methods seek out particular genes, or portions of sequences, as synapomorphies and apply cladistic assumptions.

There are several techniques for converting comparisons of molecules into phylogenies, and these are applied generally to comparisons of sequences of the **nucleic acids**, such as RNA and DNA (e.g. Box 1.1(b)). Once the molecules have been sequenced, they are recorded as strings of the letter codes for the component nucleotides (adenine, cytosine, guanine, thymine, uracil), such as …AGGCUAAGUUCAAAGCC… Individual **genes** are identified and then compared from organism to organism. **Alignments** may be made by hand or by the use of software such as Clustal. Once the genes have been aligned, the amount of difference may be assessed and particular sites where changes occur identified.

A molecular tree of relationships may be produced from the aligned gene or protein sequences by a variety of methods. Several techniques use the computed distances between the different species under consideration – the sequences of closely related species are similar and hence distances between them are short, whereas unrelated species are separated by great distances. **Distance methods** seek a tree that summarizes best all the relative distance information among all species in the analysis. Three distance methods are commonly used.

1 UPGMA (unweighted pair group method with arithmetic means) produces a tree in which all the tips are equidistant from the root of the tree, which is equivalent to assuming a molecular clock.

2 Neighbour joining (NJ) techniques pair off apparently similar species, and then make links between ever more distantly related clades until the tree is complete; the method is quick, but not necessarily very accurate.

3 Minimum evolution (ME) methods seek to minimize the sum of the lengths of all the branches in the tree.

Distance methods are widely used in molecular phylogeny reconstruction because they are well established and often quick, and they give just one tree. They have been criticised, however, for losing information (using distances ignores the evolution of gene characters or types of site), for producing branch lengths that are hard to interpret (are they computed means or are they biologically meaningful?), and for being **phenetic** (estimating trees in a purely mathematical way, but without reference to synapomorphies).

As alternatives to the distance methods, molecular trees may also be constructed from **discrete methods,** which operate directly on the sequences, or functions derived from the sequences. Two techniques are commonly used.

1 Maximum parsimony (MP) is analogous to the tree-finding techniques generally used with morphological data (see Section 2.4.1). The method seeks to find the tree that implies the fewest evolutionary changes.

2 Maximum likelihood (ML) techniques choose the tree, or trees, that are most likely to have produced the observed data. The method requires the input of a model of evolution that expresses assumptions of rates of evolutionary change and relative probability of certain base-pair changes, before a tree can be selected to fit.

A criticism of parsimony, as a method applied to molecular or morphological data, is that there is no evidence that evolution is parsimonious. In some cases, the calculated tree may be spurious, especially with molecular data, if there has been a long period of evolution on two or more of the branches. Likelihood methods are criticized because the most likely tree depends on the model that was fed in at the start: change the model and the tree may change.

The most widespread methods of molecular tree selection now are Bayesian, based on a system of statistics that assesses the likelihood that a set of results reflects the wider reality; as further observations are made, the likelihood of the predictions are updated. In phylogenetics, Bayesian methods begin with a *prior* assumption of a phylogenetic tree and a model of evolution, and generate a *posterior* distribution, composed of the prior for that parameter and the likelihood of the data. Commonly used programs for Bayesian inference in phylogeny include MrBayes and BEAST.

Molecular phylogenies have been calculated since the 1960s, and the field expanded rapidly after 1985 with the invention of the polymerase chain reaction (PCR) technique for cloning small samples of nucleic acids to generate large enough quantities for analysis. In addition, advances in the speed and efficiency of tree-finding programs and computers allow investigators to analyse data matrices that would once have been considered far too large. Even so, it may take days or weeks of run time to calculate some trees if a data matrix is large or has a great deal of missing data. The exciting prospect for palaeontologists and systematists is that there are two approaches to reconstructing the tree of life (morphological and molecular), and their results may be continually cross-compared in reconstructing ever-larger portions of the tree of life.

2.6 THE QUALITY OF THE FOSSIL RECORD

A key question palaeontologists always ask is whether the fossil record is good enough to tell the history of life or whether it is hopelessly riddled with error. Opinions have wavered back and forwards over the years, but it is important to be aware of the context. The fossil record is neither good nor bad in general; the question is better framed in terms of its *adequacy* to answer any particular question. This then brings questions about fossil record quality into the realm of normal observational science, where error is assessed and accounted for as part of a numerical study.

The broadest context is in documenting the history of life in general. Figures 2.10 and 2.11 show the pattern of the evolution of vertebrates based on current information about their relationships, the geological occurrence of members of each of the groups, and their relative diversity through time. The information is shown in two ways, as a ‘spindle diagram’ (Figure 2.10), and as a pair of diversity plots (Figure 2.11) that highlight times of rapid diversification (increases in numbers) and times of extinction (declines in numbers). Major extinction events are highlighted.

But are these diagrams in any way accurate, or are there so many gaps in the fossil record that they are misleading? In recent debates about the quality of the vertebrate fossil record, many authors (e.g. Barrett *et al*., 2009; Benson and Butler, 2011; Mannion *et al*., 2013) have identified evidence for so-called ‘megabias’ in the close covariation of rock record and fossil record time series (e.g. Figure 2.12). Their analyses have suggested that many of the rises and falls in global palaeodiversity curves result directly from bias, and especially from differential amounts of rock. The argument of the *bias hypothesis* (Smith, 2007) is that as rock volume rises and falls, palaeontologists may find more and fewer fossils, and so the apparent diversity curves in Figures 2.11 and 2.12 are largely records of rock availability rather than ancient biodiversity.

The bias hypothesis may seem self-evident. However, there are two alternative explanations, the *common cause hypothesis* (Peters, 2005) and the *redundancy hypothesis* (Benton *et al*., 2011, 2013). The common cause hypothesis is that both records,

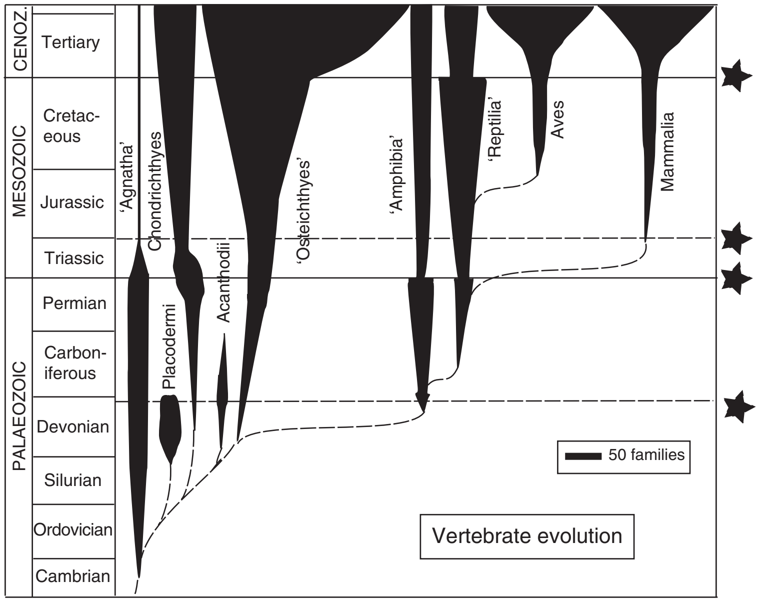

Figure 2.10 The pattern of evolution of the vertebrates, showing the relative diversity of the major groups through time and mass extinction events (marked with stars). This is a ‘spindle diagram’, in which the vertical axis represents time, and the horizontal axis represents the diversity of the group. In this case, the horizontal dimension is proportional to the number of families of each group, based on data compiled by various authors in Benton (1993). Dashed lines indicate hypothesized relationships. “Agnatha” includes conodonts (see Chapter 3). Source: Adapted from Benton (1993).

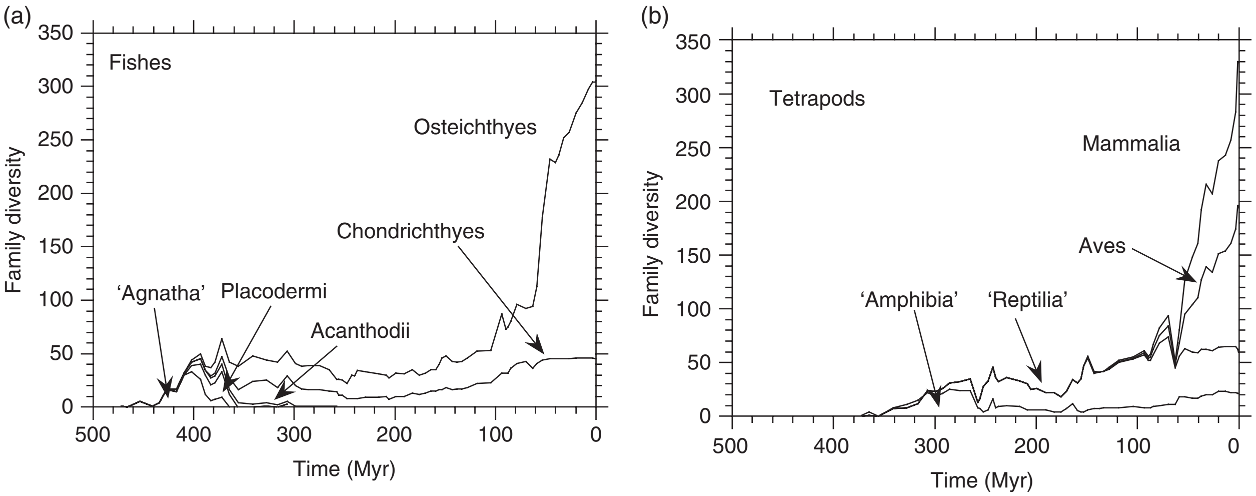

Figure 2.11 The diversification of fishes (a) and tetrapods (b), based on the numbers of families of each group through time. Mass extinction events are highlighted. Source: Adapted from Benton (1993).

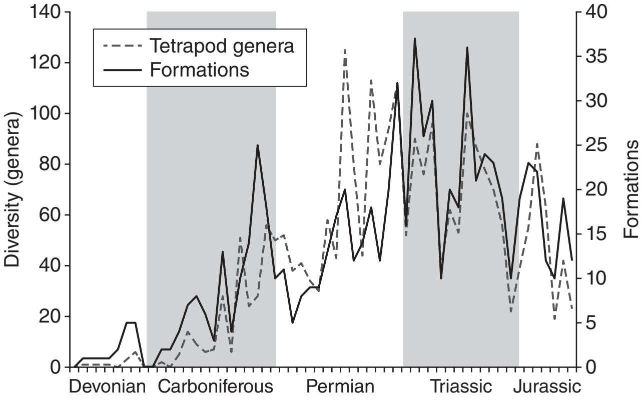

Figure 2.12 Diversity of early tetrapods through the first half of their evolution, from the Middle Devonian (Givetian, 380 Myr ago) to Early Jurassic (Toarcian, 190 Myr ago), compared to a proposed sampling proxy, tetrapod-bearing formation count. The apparently close covariation between these rock and fossil signals, especially in the Triassic, has been taken as strong evidence for megabias, the bias hypothesis. However, it is likely that both signals are somewhat interdependent, and so neither can be used to test the accuracy of the other. Source: Benton *et al.* (2013). Reproduced with permission from Elsevier.

the rock and fossil time series, owe their covariation to a third factor, such as sea level change: as shallow seas expand, they deposit more sediment and are also inhabited by more life, so rock volume and palaeodiversity increase together. Such a common cause hypothesis works well for shallow seas (Peters, 2005; Benson and Butler, 2011), but is harder to formulate, or imagine, for life on land, where so many environmental factors may influence biodiversity. The third hypothesis is that the covariation of global rock and fossil records might often be the result of redundancy. This is especially true when the rock record proxy is 'number of formations containing fossils of X'. For example, the diversity of genera of dinosaurs through time correlates closely with counts of dinosaur-bearing geological formations (e.g. Barrett *et al*., 2009) because the two metrics are more or less equivalent: new dinosaur species or genera are found in new geological formations, and the two records grow in tandem as palaeontologists explore the world. It is no wonder then that the two are correlated because they are largely redundant with each other (Benton *et al*., 2011, 2013). Sampling metrics often correlate with each other at global scale for different terrestrial vertebrate clades in the Cretaceous, but tetrapod sampling proxies from different continental areas do not, and this suggests that there is no unified 'global' sampling signal for terrestrial tetrapods (Benson *et al*., 2013).

This debate continues, but it must not be forgotten that broad patterns of the evolution of life (e.g. Figures 2.10, 2.11) do not change much with new discoveries. Further, molecular and morphological phylogenies more often agree than disagree. In a direct test of congruence between phylogenies and the fossil record, Norell and Novacek (1992) compared geological evidence about the order of appearance of different groups of mammals with evidence from cladograms about the order of nodes. In most cases, they found a good match of age and clade order. Indeed, it turns out that the fossil record of land vertebrates is as good as that of echinoderms, a group that is usually assumed to have a good fossil record, and fishes and **tetrapods** (literally 'four feet'), the land vertebrates, have equally good fossil records (Benton and Hitchin, 1996). At family level, the fossil record does not deteriorate the further back in time one goes (Benton *et al.*, 2000).

Perhaps palaeontologists have been overly apologetic about the quality of their data, and they are now moving to incorporate an expectation of error into their numerical analyses. Further, much of the debate has focused on a single kind of study, the production of global-scale palaeodiversity curves (e.g. Figures 2.11, 2.12). For regional-scale studies, analyses of ecosystems, and studies of function and morphological variation, questions of error and confidence are entirely different.

2.7 MACROEVOLUTION

Phylogenetic trees (see Section 2.4) provide an ideal basis for studying **macroevolution**, the evolution of life above the species level. Broad-scale patterns of diversification and extinction events may be discerned and their effects analysed, and patterns of character (=trait) evolution determined. Until recently, many such studies used palaeodiversity time series as a basis for analysis, seeking to identify the magnitude of extinction events, whether they were selective or not (do the survivors have any special characters compared to the victims?), whether there were major macroecological patterns such as latitudinal diversity or size gradients (more species and smaller species at the Equator than the poles), or whether there were major temporal patterns such as Cope's Rule (species become larger through time). A problem with all such studies is that species are not independent of each other, and phylogenetic relationships among the species should be taken into account.

Many macroevolutionary studies are conducted using **phylogenetic comparative methods**, in which diversity and trait data are mapped onto a phylogeny. At the very least, the data are corrected for phylogenetic signal by methods such as independent contrasts, or, more informatively, rates and timings of evolution are explored across phylogenetic trees. For example, bursts of lineage splitting, *diversification shifts*, may be sought. In such cases, the rate of lineage diversification is compared to the expectations of an equal-rates model, and any substantial deviations noted. In other cases, measures of evolutionary rates, usually rates of change of a particular character such as body size, are compared to the statistical null model, that evolution is random (Brownian motion or random walk models), and any rates that exceed the expectations of such a random pattern can be identified as *trends*, patterns of change that are *driven*, in evolutionary terms.

A key physiological character is body size. Dinosaurs famously grew to large and very large size, and they have been cited as classic examples of Cope's Rule. In a study of body size increase in archosaurs through the Triassic, Sookias *et al.* (2012)

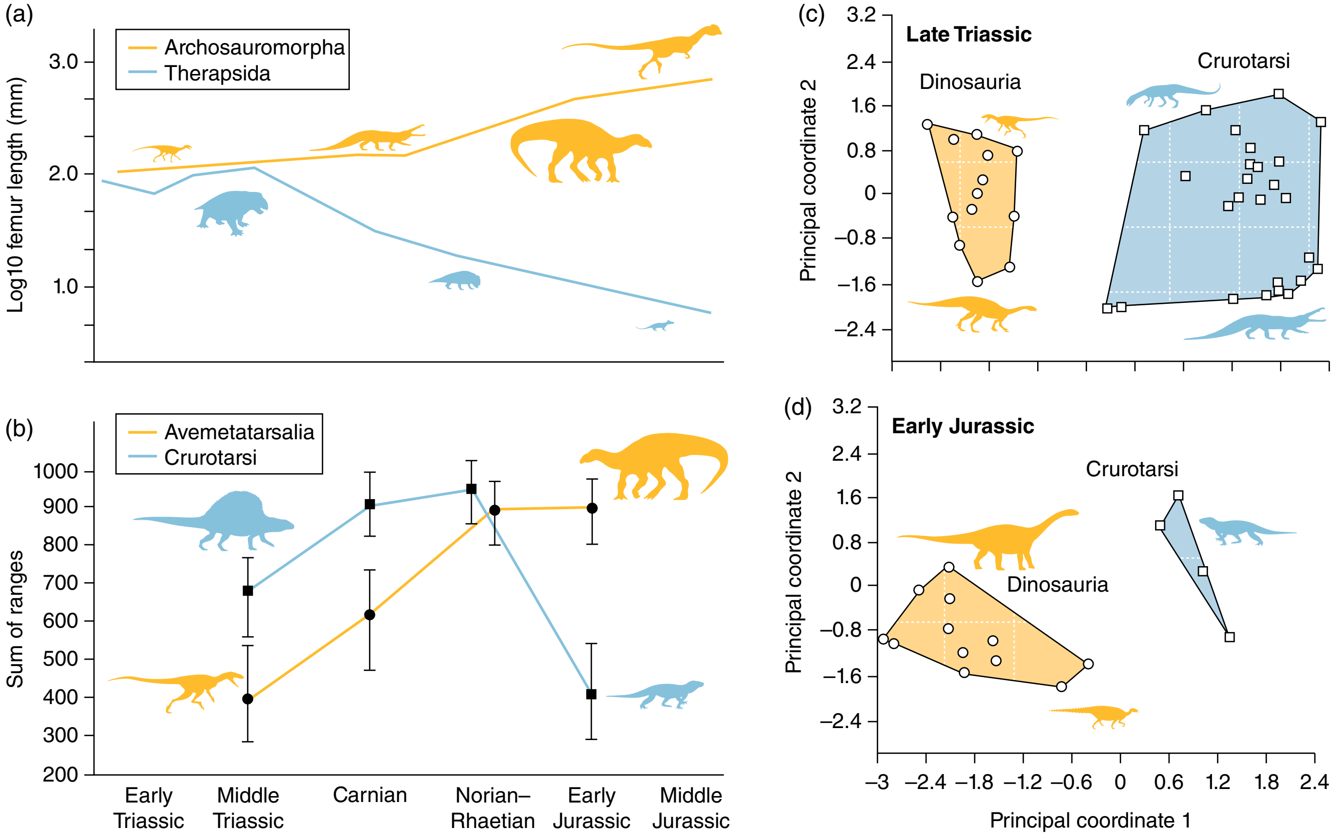

Figure 2.13 Macroevolution of tetrapods and the origins of dinosaurs. (a) The relative fates of therapsids (derived synapsids) and archosauromorphs (archosaurs and close relatives) through the Triassic and the early part of the Jurassic, showing a long-term diminution of mean body size (indicated by femur lengths) of therapsids and increase in mean body size of archosauromorphs. Model fitting indicates these trends were random (Brownian motion model). (b) Changing evolutionary rates of Avemetatarsalia (dinosaurs and immediate relatives) and Crurotarsi (crocodile-line archosaurs) through the Middle Triassic to Early Jurassic, showing parallel changes in disparity (measured by sum of ranges) in the Triassic, and decline in crurotarsan rates through the end-Triassic mass extinction. (c,d) Changing relative morphospace occupied by Dinosauria and Crurotarsi in the Late Triassic and Early Jurassic, suggesting a lack of impact of early dinosaurian evolution on crurotarsan morphospace in the Late Triassic, and a modest response by Dinosauria following substantial extinction of Crurotarsi through the end-Triassic mass extinction. See Colour plate 2.1. Source: (a) Adapted from Sookias *et al.* (2012). (b) Adapted from Brusatte *et al.* (2008).

used maximum-likelihood methods to seek examples of Cope's Rule, and they found it was extremely rare, despite substantial changes in body size. In comparisons of archosauromorphs and synapsids (Figure 2.13(a)), they found that size increased in both clades, but only according to passive evolutionary models (Brownian motion model; stasis model) in which overall variance increases (more small and more large animals), but there was not a driven trend in which *all* species became larger. The study shows that dinosaurs diversified and became larger during the Late Triassic and Early Jurassic in a passive way, without evidence for any long-term drive, and that the dinosaurs did not necessarily outcompete earlier ecologically dominant clades of synapsids (see Chapter 7). In an independent study, Turner and Nesbitt (2013), on the other hand, found evidence for an active trend in body size evolution in archosauriforms through the Triassic, and it is not yet clear why the results differ.

In studies of macroevolution, it is useful to think of ways to quantify morphological evolution, and this can be done in terms of *evolutionary rates* and *disparity*. An evolutionary rate is a measure of how fast anatomical features (traits) evolved over time or across a phylogeny. **Disparity** is a measure of morphological variation, and it can be used to compare the variability of one group with another, or one time period with to another. Disparity can be measured from overall shape characters, sometimes based on landmark studies of parts or whole organisms, or from discrete characters, such as cladistic apomorphies. Brusatte *et al.* (2008) compared evolutionary rates and disparity of basal dinosaurs and coeval archosaurs in order to explore how the rise of dinosaurs had, or had not, affected postulated competitors such as the crurotarsan archosaurs. The study was based on some 500 features of the skull and skeleton, and evolutionary rates were calculated by mapping characters onto the phylogenetic tree, which was converted into a time tree by using the geological age of each species. This meant that the amount of change in the ensemble of characters could be assessed from one time bin to the next, so providing a measure of the rate of evolution.

Perhaps surprisingly, dinosaurs and crurotarsans were evolving at nearly identical rates during the Late Triassic (Figure 12.13(b)). Neither group was outperforming the other, and they kept pace over their 30 Myr of shared history.

Comparisons of *disparity* also showed rather surprising results (Brusatte *et* al., 2008). The sum of character states provides a measure of 'novelty', although the method combines apomorphies and plesiomorphies. It was found that crurotarsans were twice as disparate as dinosaurs in the Late Triassic (Figure 12.13(c)). Even after the extinction of major crurotarsan clades at the end of the Triassic, the dinosaurs did not expand their morphological variance substantially or rapidly (Figure 12.13(d)): it was more a slow step-wise acquisition of new morphologies.

The numerical, phylogenetic study of macroevolution is developing fast, as palaeontologists apply new mathematical methods to their phylogenies (Benton *et al*., 2014). At last, such work has moved from the 'narrative phase', where assumptions, methods, and conclusions were weak, to an analytical phase, where models may be tested.

2.8 FURTHER READING

There are many useful books that cover basic palaeontological, geological, and palaeobiological principles. Briggs and Crowther (2001) is an excellent compendium of short articles on all aspects of palaeobiology, and Benton and Harper (2009) is a useful introduction to all aspects of palaeontology, including methods, taphonomy, and palaeoecology. Buffetaut (1987), Colbert (1968), and Cadbury (2010) are highly readable accounts about the history of vertebrate palaeontology, especially the heroic big-bone expeditions of the past.

There are many manuals of laboratory practice in palaeontology, including Leiggi and May (1994, 2004) on vertebrates. Allison and Bottjer (2010) and Lyman (1994) are good introductions to taphonomy, and you can read more about Earth history in Stanley and Luczaj (2014). The methods of cladistics are presented by Kitching *et al.* (1998), and Page and Holmes (2004), Lemey *et al*. (2009), and DeSalle and Rosenfeld (2013) give good overviews of molecular phylogeny methods. Smith (1994) gives an excellent account of cladistics in palaeontology, and he touches on questions of the quality of the fossil record, a theme developed more fully by authors in McGowan and Smith (2011). Good introductions to numerical methods in palaeontology are Hammer and Harper (2006) and Foote and Miller (2007). Sutton *et al*. (2014) is an introduction to the remarkable outcomes of CT scanning, or 'virtual palaeontology'.

Useful web sites include: http://www.nhm.ac.uk/paleonet/Index.html and http://www.paleoportal.org/, which have links to societies, information pages, journals, jobs, and more; http://www.vertpaleo.org/, the premier international society for vertebrate palaeontologists; http://evolution.berkeley.edu/, for educational materials on evolution; http://www.earth4567.com/, for educational materials on earth sciences; http://animals.nationalgeographic.co.uk/animals/prehistoric/, palaeontological work sponsored by the Society; http://www.bbc.co.uk/nature/life/Dinosaur, the BBC dinosaur and palaeontological pages; http://www.amnh.org/apps/dinosaurs, dinosaurs at the AMNH; and http://www.scotese.com/, the Paleomap Project web site. An excellent resource for professional fossil preparators in the American Museum of Natural History guide (http://preparation.paleo.amnh.org/1/home), and other useful sites include: http://paleobiology.si.edu/FossiLab/preparation.html, http://www.fossilprep.org/, and http://www.jpaleontologicaltechniques.org/, a free, online journal of rel1evant articles.

Online primers in cladistics and phylogenomics include: http://www.learner.org/courses/biology/textbook/compev/compev_3.html, http://www.ucmp.berkeley.edu/exhibit/phylogeny.html, and http://www.palass.org/modules.php?name=palaeo&page=19&sec=newsletter. A summary of commonly used phylogenetics software is given here: http://evolution.gs.washington.edu/phylip/software.html, and an online TNT application is http://www.phylogeny.fr.

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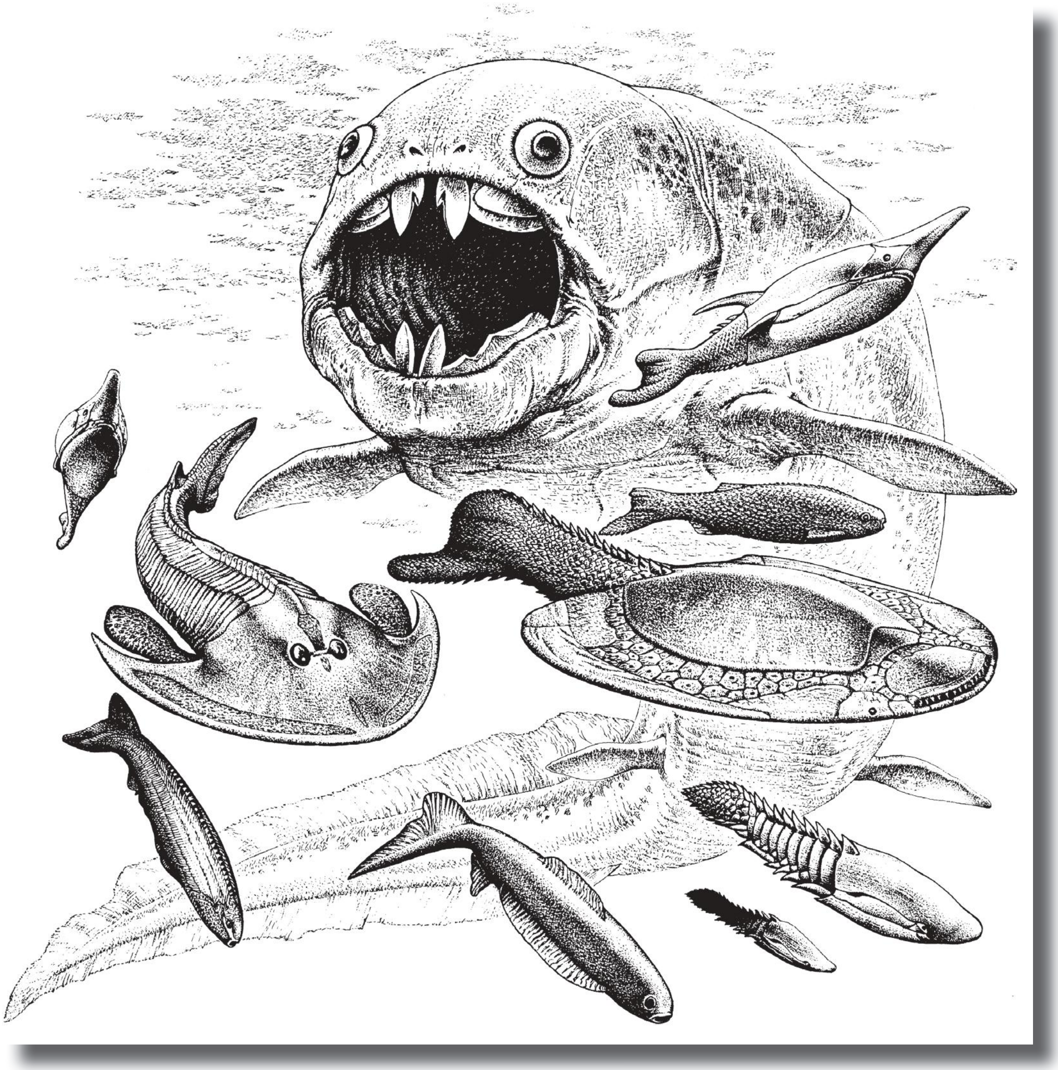
CHAPTER 3

Early Palaeozoic Fishes



Vertebrate Palaeontology, Fourth Edition. Michael J. Benton.

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KEY QUESTIONS IN THIS CHAPTER

1 When did fishes arise, and where did they come from?
2 What are the different kinds of bone and when did bones and teeth evolve?
3 Where do the conodonts and other Palaeozoic jawless fishes fit in the scheme of things?
4 How did jaws originate?
5 Why were so many Silurian and Devonian fishes so heavily armoured?
6 Why are so many Old Red Sandstone fishes so well preserved?
7 How did the lobe-finned fishes evolve, and which group is closest to tetrapods?
8 Why was there a major switch from armoured and lobe-finned to 'modern' fish types at the end of the Devonian?

INTRODUCTION

Vertebrate fossils have not been reported from the Precambrian (4567–541 Myr), and indeed the clade may have originated early in the Cambrian (541–485 Myr) as part of the 'Cambrian Explosion' (Erwin and Valentine, 2013). This was the time when abundant and diverse skeletonized animals, such as sponges, trilobites, brachiopods, and echinoderms, appeared in the fossil record, and it has been debated whether this explosion of fossil abundance and diversity reflects the actual time of origin of the groups, or merely their appearance as fossils. In either case, fascinating fishy fossils are first known from the early Cambrian, but these early vertebrates were poorly armoured or not armoured.

There is then a gap in time until the Ordovician (485–444 Myr), when a very few fish fossils are known, and further groups emerged in the Silurian (444–419 Myr), but specimens became abundant only in the Devonian (419–359 Myr). These Ordovician, Silurian, and Devonian fishes were mostly covered with armour plates. In the Late Devonian, these armoured groups disappeared, and sharks and modern-style bony fishes replaced them; at the same time, fishes gave rise to land vertebrates, the tetrapods (see Chapter 4). The terms Osteichthyes and Sarcopterygii refer to clades that include tetrapods, but the less formal terms 'fishes', 'bony fishes', or 'lobe-finned fishes' will be used here to refer only to the paraphyletic groups that exclude tetrapods.

3.1 CAMBRIAN VERTEBRATES

Until recently, the oldest putative vertebrates were isolated fragments of **dermal** armour from the Late Cambrian of North America, Greenland, and Spitsbergen, and arguably also the superficially amphioxus-like *Pikaia* from the Burgess Shale of Canada and the yunnanozoons from Chengjiang in South China (see Box 1.2), but these may be basal chordates or basal deuterostomes (see Chapter 1). Other specimens from Chengjiang are, however, widely interpreted as stem vertebrates, and these extend the record of the clade back to the Early Cambrian; three genera of these myllokunmingiids have been named, *Myllokunmingia*, *Haikouichthys*, and *Zhongjianichthys*, although there is debate about how many are truly distinct (Shu *et al.*, 1999, 2003; Shu, 2003; Zhang and Hou, 2004; Shu *et al.*, 2014).

Myllokunmingia, 28 mm long, is streamlined in shape (Figure 3.1(a). The head is poorly defined, but a possible mouth is seen at the anterior end. Behind this are five or six gill pouches. Up to 25 double-V-shaped myomeres extend along most of the length of the body. Other internal organs include a possible notochord, a heart cavity, and a broad gut. There is a low dorsal fin along the anterior two-thirds of the length of the body, and possibly a ventro-lateral fin along the posterior two-thirds.

Haikouichthys, now known from over 500 specimens (Shu *et al.*, 1999, 2003), is a slender, streamlined animal, about 25 mm long (Figure 3.1(b)). The head bears eyes and a small paired nasal capsule, there is a brain surrounded by cartilaginous protective tissues, and six pharyngeal gill arches extending about one-third of the length of the body. There is a notochord, and some specimens show up to ten separate squarish elements lying across the notochord, putative vertebrae that may have been made from cartilage in life. The posterior half tapers to a slightly rounded end, and it is marked by a series of obvious, W-shaped myomeres (muscle blocks). There are traces also of structures interpreted as the heart, gut and a series of **gonads** (egg- or sperm-producing organs).

Phylogenetically, both *Myllokunmingia* and *Haikouichthys* are placed low in the tree of vertebrates (see Box 3.1). *Myllokunmingia* was described (Shu *et al.*, 1999) on the basis of a single specimen, and a second specimen suggested to Zhang and Hou (2004) that in fact *Myllokunmingia* and *Haikouichthys* are a single species. A third taxon, *Zhongjianichthys* (Shu, 2003), is a small eel-like animal with possible vertebral arches, two obvious eyes and possible nasal sacs. Shu (2003) groups these three Chengjiang fishes in the Myllokunmingiida.

The earliest vertebrates with hard tissues are known from the late Cambrian – conodonts (see Section 3.3.2) and isolated pieces of dermal armour, most notably *Anatolepis* from Wyoming and Greenland (Figure 3.2), both assumed to have come from jawless fishes. The tiny *Anatolepis* specimens have a knobbly surface ornament that could represent scales of some kind, when viewed under the microscope. These fossils are important as they are composed of the mineral **apatite** (calcium phosphate), the mineralized constituent of bone (see Section 3.2), a characteristic of most vertebrates, and not seen in the non-vertebrate chordates, or in the early and mid-Cambrian vertebrates. The exoskeletal fragments of *Anatolepis* are composed largely of a dentine-like tissue around a pulp cavity, and they are somewhat tooth-like (Smith *et al.*, 1996; Friedman and Sallan, 2012). These specimens show that bone evolved some time after the origin of the vertebrates, and that the apatitic tissues of vertebrates may be complex.

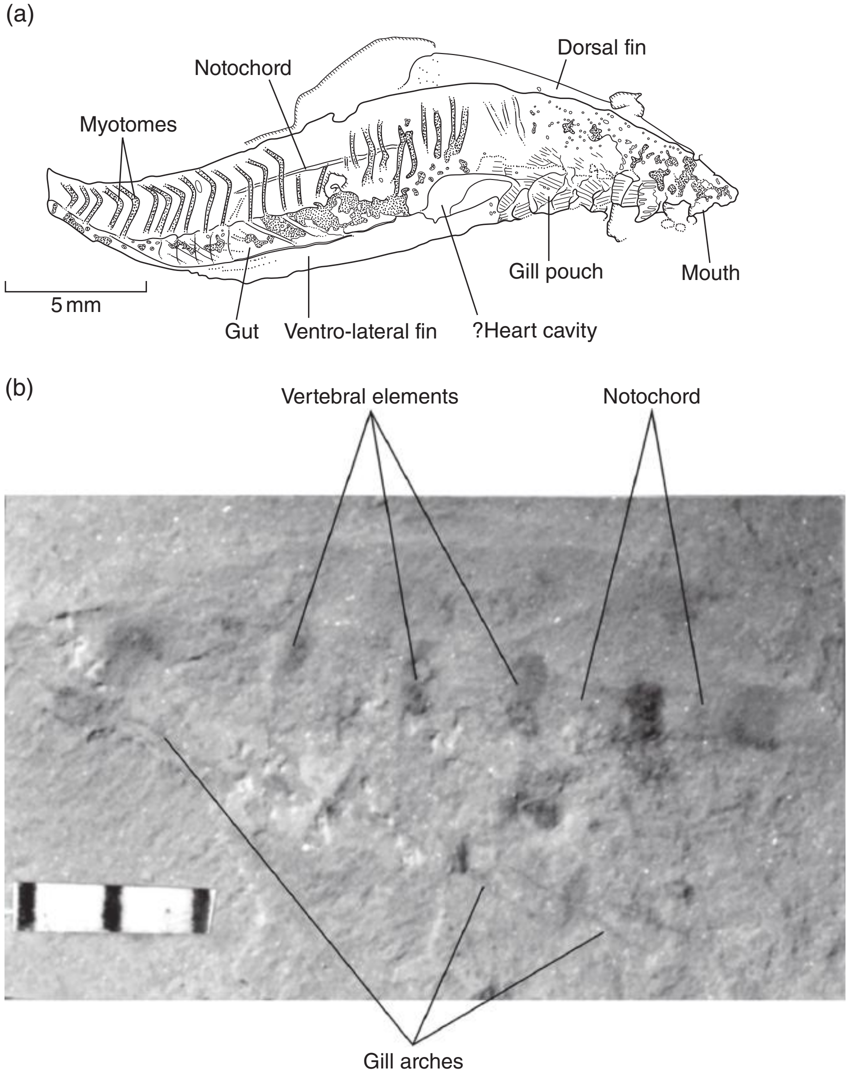


Figure 3.1 The Early Cambrian vertebrates *Myllokunmingia* (a) and *Haikouichthys* (b) from the Early Cambrian Chengjiang locality in China. In (b), showing the anterior half of the animal, the key chordate feature of a notochord is indicated, as well as the key vertebrate character of possible cartilaginous vertebrae surrounding it.
Source: D. Shu, Northwest University, Xi'an, China. Reproduced with permission.

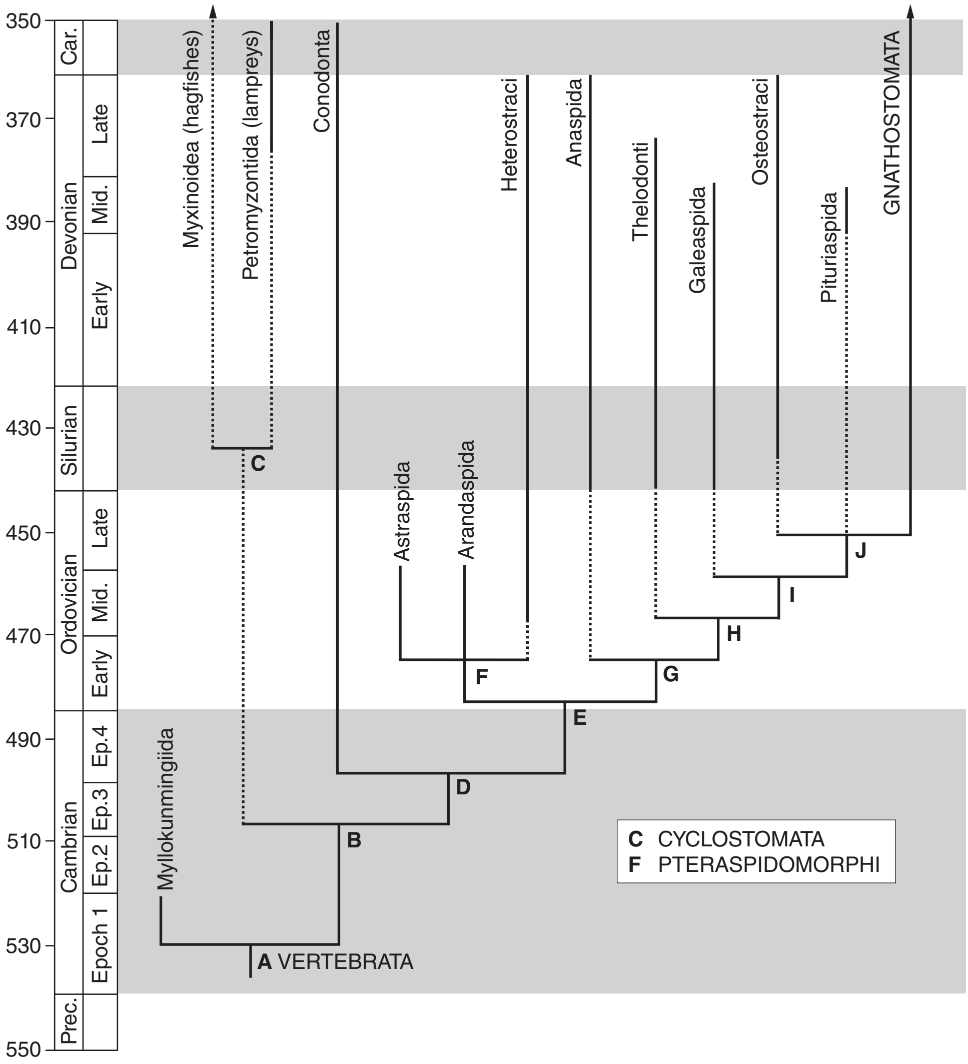
BOX 3.1 EARLY VERTEBRATE RELATIONSHIPS

The relationships of the fundamental vertebrate groups to each other have been controversial. For a long time, zoologists grouped the living lampreys and hagfishes together as Cyclostomata. The first cladistic studies (e.g. Maisey, 1986; Forey and Janvier, 1993), however, broke up Cyclostomata, and generally separated hagfishes as basal and paired lampreys with gnathostomes (jawed vertebrates). Molecular phylogenetic studies generally pair the two clades as Cyclostomata (reviewed, Kuraku *et al*., 2009), but Near (2009) argued that this was largely a methodological issue, and he argued for the (hagfishes (lampreys + gnathostomes)) phylogeny. This was flatly rejected by a study of microRNAs (Heimberg *et al*., 2010) that identified four unique microRNA families shared by hagfishes and lampreys, and so resuscitated Cyclostomata. Nonetheless, these authors found that a reanalysis of morphological characters did not strongly resolve the question. miRNAs are said to trump other molecular approaches because these are highly conserved, noncoding genes that can be treated in datasets as presence/absence characters, and they are rarely lost in evolution. In addition, miRNAs are regulatory genes that are strongly involved in cell differentiation during early development, so they have a fundamental role in determining vertebrate complexity. If miRNAs are as stable and fundamental as claimed (e.g. Heimberg *et al*., 2010) – but this is queried by some (reviewed, Telford and Copley, 2011) – they then provide a guaranteed way to resolve phylogenetic conflicts. Regardless, morphological data is equivocal, whereas molecular studies all suggest monophyly of Cyclostomata.

Recent cladistic analyses (Donoghue *et al.*, 2000; Janvier, 2008; Heimberg *et al*., 2010; see illustration), confirms that myllokunmingids are the basal vertebrates, followed by cyclostomes (myxiniforms + petromyzontiforms), and then conodonts. The pteraspidomorphs (astraspids,

Continued

arandaspids and heterostracans) come next, then the anaspids, thelodonts, a clade of forms with a heavy head shield (osteostracans, galeaspids and pituriaspids), and then the gnathostomes. The cladistic analysis highlights many morphological characters that are shared between lampreys and gnathostomes and that are absent in hagfishes.



Cladogram showing the postulated relationships of the jawless fishes and the Gnathostomata (jawed fishes) based on morphological characters. See Box 1.1 for context of Vertebrata; see Box 3.7 for phylogeny of Gnathostomata. Selected synapomorphies from Donoghue *et al*. (2000) and other sources: **A/B VERTEBRATA**, neural crest, brain, optic tectum in the brain, paired olfactory capsules, at least one set of semicircular canals, arcualia (embryonic precursors of vertebrae), unpaired fin ray supports closely set; **C CYCLOSTOMATA**, mouth armed with retractable horny teeth; **D**, calcified dermal skeleton, extrinsic eye musculature, sexual dimorphism, olfactory tract, cerebellum, pretrematic branches of branchial nerves, flattened spinal cord, vertical semicircular canals; **E**, cerebellum, vertical semicircular canals forming loops well separate from the utricle, trunk dermal skeleton, diamond-shaped scales, dermal head covering, sensory line-system with neuromasts, electroreceptive cells, gills symmetrical, open blood system, braincase with lateral walls; **F PTERASPIDOMORPHI**, paired nasal openings, three-layered exoskeleton, oak-leaf-shaped tubercles, oral plates; cancellar layer in exoskeleton, rod-shaped scales, large unpaired dorsal and ventral dermal plates on head; **G**, externally open endolymphatic ducts, paired fins or fin folds [reversed in Galeaspida]; **H**, sensory line enclosed in canals [shared with Heterostraci], opercular flaps associated with gill openings [reversed in Gnathostomata and Galeaspida], dorsal fin [shared with Petromyzontiformes]; **I**, large lateral head vein, neurocranium entirely closed dorsally and covering the brain, occiput enclosing cranial nerves IX and X, cellular perichondral bone, globular calcified cartilage, three-layered exoskeleton; **J**, gill openings and mouth ventral, oral plates, massive endoskeletal head shield covering the gills dorsally, paired pectoral appendages, paired pelvic appendages, slit-shaped gill openings, a dorsally elongated tail fin, sclerotic ring and ossified sclera. Abbreviations: Car, Carboniferous; Ep, Epoch; Mid, Middle.

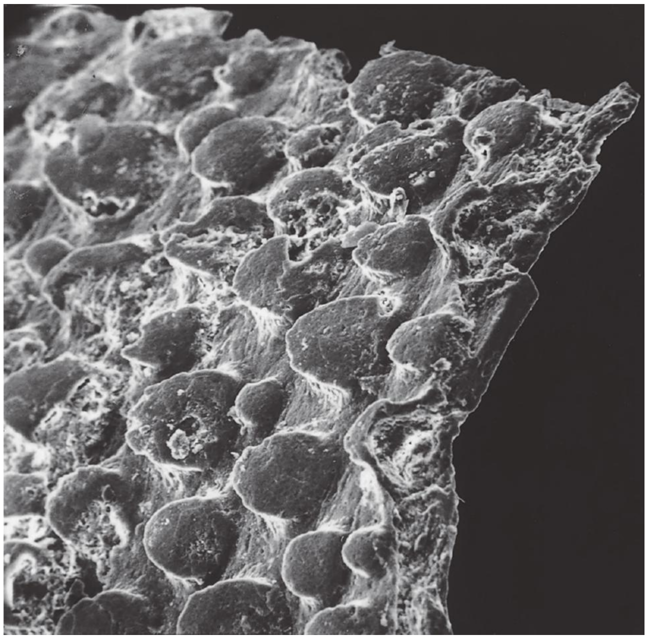


Figure 3.2 The armour of *Anatolepis*, one of the first vertebrates with bone, from the Late Cambrian of Crook County, Wyoming, USA. The scale-like tubercles are composed of dentine around a pulp cavity. Photograph ×200. Source: J. E. Repetski, US Geological Survey, Reston, VA, USA. Reproduced with permission.

3.2 VERTEBRATE HARD TISSUES

Bone is a key feature of vertebrates. There are different kinds of bone, and other bone-like hard tissues, and it is important for palaeontologists to understand these, especially when they are trying to classify isolated phosphatic scales and teeth. Bone is made from mineral and protein components. Living bone tissue consists of fibres of the protein **collagen** on which are deposited tiny hexagonal-prismatic crystals of apatite.

Cellular bone is a living tissue. Typical bone contains channels for blood vessels that pass through the structure, and carry calcium phosphate in solution both to and from the bone. The cells that control bone formation, the **osteocytes**, are generally encapsulated in the bone as it mineralizes. Vertebrate skeletons clearly have functions in support and protection (if they are partially external, like the shell of a turtle or the head skeleton of an early fish). The bulk of our skeleton, the internal skeleton is the **endoskeleton**, and external features, like the shell of a turtle or the bony head shields of early fishes, are parts of an external skeleton, sometimes called the **exoskeleton**. As the animal grows, the bones constantly reshape themselves. Bones also act as stores of calcium and phosphorus, and these elements can be mobilized by erosion of the bone, and they can be carried to other parts of the body where they are required for growth and energy transfer.

Vertebrates display a variety of hard tissues made from apatite. **Dentine**, which forms the main volume of our teeth, is very like bone, but it grows in such a way that cells are rarely encapsulated within the mineralizing tissue. Dentine contains narrow tubules in a zone between the centre of the tooth, the **pulp cavity**, and the surface, just below the enamel. **Enamel** is another hard tissue that forms the outer thin layer of our teeth and the outer layer of early armour and scales. It is largely inert crystalline apatite with some structural proteins, but with no collagen or blood vessels in the structure. Early fishes had **enameloid** in their scales, a heavily mineralized tissue based around an organic scaffold of proteins that also covers the teeth in many sharks and bony fishes.

The vertebrate skeleton is composed of bones that develop from different parts of the early embryo. During early development of most animals (see Figure 1.5; Section 1.3.2), three germ layers emerge, the ectoderm on the outside of the developing gastrula, the endoderm inside the cavity, and the mesoderm between. Skeletons are made up from five parts, each of which has a different developmental origin, the **splanchnocranium** (primary palate and jaws, branchial elements) from the endoderm, the **neurocranium** (braincase), **axial skeleton** (backbone and ribs), and **appendicular skeleton** (pectoral and pelvic fins or limbs and girdles) all from the mesoderm, and the **dermal skeleton** (external portions of the skull, teeth, armour plates, clavicle, patella) from the ectoderm.

The dermal skeleton in early vertebrates (Figure 3.2) had scales made from bone dentine, containing dentine tubules, capped with enamel (Figure 3.3(a); Donoghue and Sansom, 2002), whereas the tooth-like elements of conodonts had enamel and dentine. These astonishing observations suggested that the dermal plates of early vertebrates apparently had more in common with our teeth than with endoskeletal bone. One view, the ‘inside-out’ hypothesis, was that the teeth-like structures in the dermal skeleton and teeth in jaws, evolved independently and convergently. The other, the ‘outside-in’ hypothesis, was that a tooth developmental module, the **odontode**, appeared first in the dermal skeleton, and later expanded into the mouth area, where it was appropriated to produce teeth associated with jaws and the branchial arches. Close study of the anatomy of the earliest conodonts shows that their tooth-like structure evolved independently of gnathostome teeth and so they have no bearing on the evolution of the vertebrate skeleton and teeth in particular. The ‘outside-in’ hypothesis best fits the data, with the odontodes of early vertebrates later taken over as precursors of true teeth (Murdock *et al*., 2013).

The tubercles on a dermal plate of *Anatolepis* are like individual teeth, made from dentine, and with a pulp cavity inside each of them (Figure 3.3(b)). Incremental growth lines can be seen within the dentine, showing how the tissue was laid down as the animal grew larger. Between these tooth-like tubercles is a lamellar, or layered, hard tissue containing pore canals, perhaps containing nerves for sensing movements of predators or prey in the water.

Later vertebrates also had dentine tubercles on the outer surface of their dermal bone, but deeper layers were more complex than in *Anatolepis*. Beneath the dentine tubercles lay a thick middle layer of spongy bone, and beneath that a laminated layer of compact bone. Both layers are **acellular**: they lack internal spaces for osteocytes. Tooth-like outer bone coverings are found in many fossil fish groups, and sharks today have pointed scales made from dentine and enameloid all over their bodies. Certain early armoured fishes had a complex bone of this kind called **aspidin** (Figure 3.3(c)).

The earliest vertebrates had unmineralized internal skeletons, perhaps made from **cartilage**, a flexible material consisting mainly of collagen. The cartilage of these earliest vertebrates though was not composed of collagen (Donoghue and Sansom, 2002; Sire *et al.*, 2009), unlike in modern vertebrates. Cartilage makes up most of your nose and ears; the cartilaginous fishes, sharks and rays, have an internal skeleton made from cartilage covered with a mineralized rind, prismatic calcified cartilage, which is a synapomorphy of the clade. Bone began to appear in internal skeletons at different times, when vertebral centra and skeletal arches arose in various lineages. **Perichondral** bone forms by crystallization of apatite to form acellular bone around soft tissues such as nerves that pass through cartilage, for example, in the braincase. It is also found in the girdle bones that support the fins of fishes. Endochondral bone forms as a more substantial replacement of cartilage. **Endochondral** bone is unique to Osteichthyes, contributing to the skeleton of bony fishes and forming most of the skeleton of land vertebrates, which require additional internal support. In human babies, large parts of the limb bones are made from cartilage, and during growth these **ossify**, or are replaced by endochondral bone by the deposition of apatite. The fontanelle, the diamond-shaped opening on the top of a baby's skull, is a cartilaginous zone that ossifies as the parietal and frontal bones fuse.

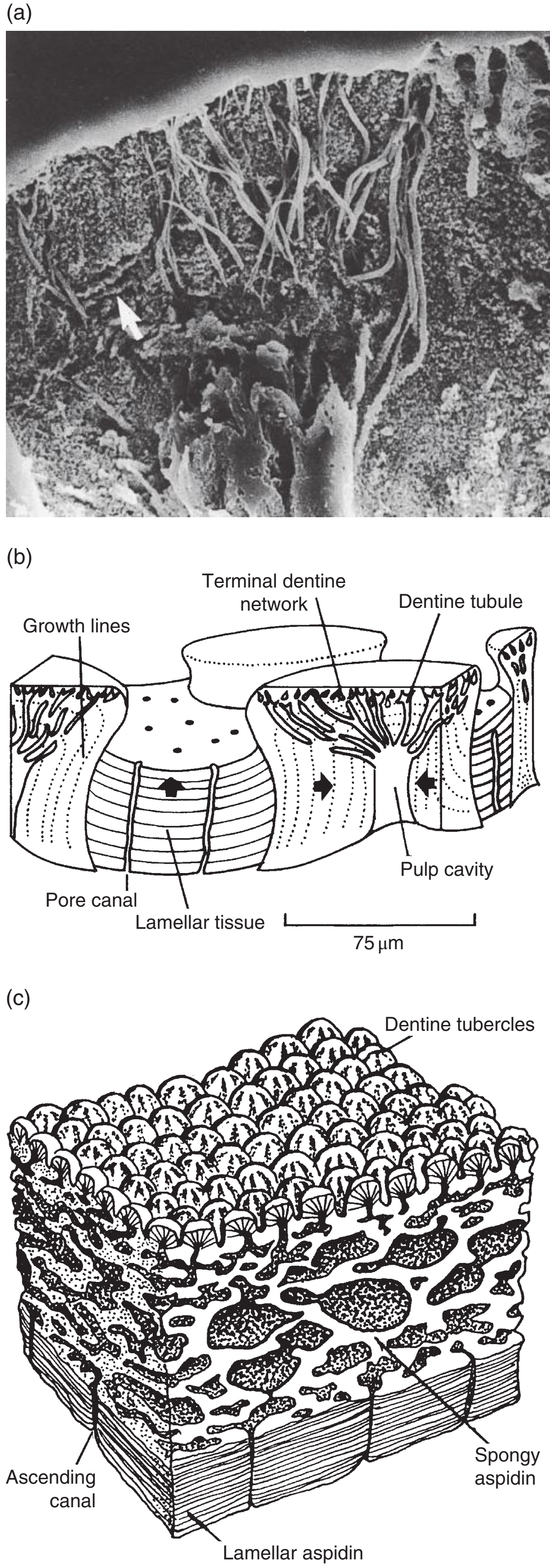


Figure 3.3 The structure of vertebrate hard tissues. (a) Dentine in a dermal tubercle in one of the presumed oldest vertebrates with a dermal skeleton, *Anatolepis* from the Late Cambrian of the USA, showing dentine tubules running from the pulp cavity (bottom) to the outer surface (top). Lamellar tissue curves up to the base of the tubercle (arrowed). Photograph × 1500. (b) Block reconstruction of the hard tissues of *Anatolepis*. (c) Block reconstruction of the hard tissues (aspidin) of a heterostracan. Source: P. Smith, University of Oxford, Oxford, UK. Reproduced with permission.

3.3 THE JAWLESS FISHES

The earliest fishes are sometimes included in the paraphyletic group 'Agnatha' (literally, 'no jaw'), and they achieved a great diversity of forms and sizes in the Cambrian to Devonian periods. The main groups of jawless fishes, in order of acquisition of key characters (see Box 3.1) are the living Petromyzontiformes (lampreys) and Myxiniformes (hagfishes), the Conodonta, the Pteraspidomorphi (comprising the Ordovician Arandaspida and Astraspida, and the heavily armoured Heterostraci), the Anaspida, the small-scaled Thelodonti, and the armoured Osteostraci, Galeaspida and Pituriaspida, which are collectively close outgroups of Gnathostomata, the jawed fishes. The armoured jawless fishes from the early Palaeozoic are sometimes referred to as '**ostracoderms**' ('armour skins'), a term that does not refer to a clade but to a collection of clades of jawless vertebrates on the gnathostome stem.

3.3.1 Living jawless fishes

Among living fishes, lampreys (Petromyzontiformes) and hagfishes (Myxiniformes) lack jaws, interpreted as retention of a primitive character (Shimeld and Donoghue, 2012). Lampreys and hagfishes are very different from many of the extinct jawless fishes, but they are unique in perhaps showing us something of the early Palaeozoic world, before jaws existed. Both groups have elongated bodies, no bony armour, no jaws and no paired fins. They used to be seen as successive outgroups to Gnathostomata, but growing evidence links them as a clade Cyclostomata (see Box 3.1).

The 39 species of lampreys range from 13–100 cm in length, and they all spend some of their life in freshwaters where they breed. Most are parasitic, and they feed by attaching themselves to other fishes with their sucker-like mouths (Figure 3.4(a)), and rasping at the flesh. The mouth and oesophagus are within a deep funnel, which is lined with small pointed unmineralized teeth that permit firm attachment to the prey. There is a fleshy protrusible 'tongue', which also bears teeth and which is used in rasping at the flesh. Lampreys (Figure 3.4(b)) have a single nasal opening on top of the head that runs into a pouch beneath the brain, large eyes and two vertical **semicircular canals** in the internal ears on each side. There is an internal skeleton consisting of a notochord, vertebra-like structures, an attached cartilaginous skull and gill arches, and fin rays.

The 77 species of marine hagfishes (Figure 3.4(c)) look superficially like lampreys, ranging from 18 cm to 1.2 m in length, but they live in burrows in soft sediments, feeding on invertebrates and decaying carcasses on the seabed, and also actively preying on live teleost fishes. Hagfishes have a single nasal opening at the very front that connects directly to the pharynx (Figure 3.4(d)), quite unlike the lamprey nostril. The eyes are reduced and often covered with thick skin and muscle, and there is only one semicircular canal on each side. The mouth is ringed with six strong tentacles, and inside it are two pairs of horny plates bearing numerous small keratin toothlets that can be protruded with the mouth lining. This

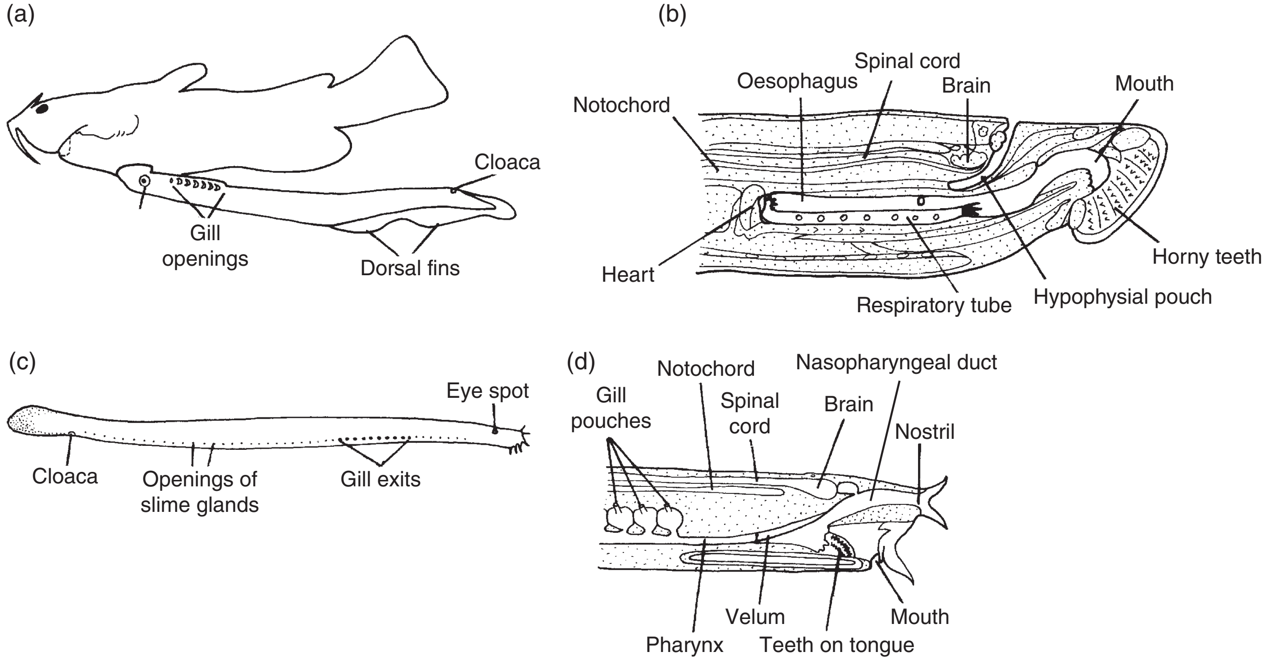


Figure 3.4 Living jawless fishes: (a) lamprey, feeding by attachment to a bony fish, and (b) longitudinal section of anterior end of body; (c) Pacific hagfish, external lateral view of body, and (d) longitudinal section of anterior end of body. Source: Adapted from Young (1981) and other sources.

apparatus can be turned in and out, producing a pinching action with which the hagfishes can grasp the flesh of a dead or dying animal. They remove a large lump of flesh by holding it in a firm grasp, and then they force it off by tying a knot in the tail, passing it forwards towards the head, and bracing against the side of their prey. Hagfishes lack true vertebrae and it was debated whether these structures had been lost; it turns out (Ota *et al.*, 2011), however, that they have arcualia, developmental precursors of vertebrae.

Cyclostomes have a limited fossil record. There is a single putative hagfish fossil from the Carboniferous, *Myxineidus*, which might actually be a lamprey (Germain *et al.*, 2014), and a few lamprey fossils, the oldest being Devonian in age (Gess *et al.*, 2006) and others are Carboniferous and Cretaceous.

3.3.2 Conodonta

Some of the longest-lived early vertebrates, the conodonts, were identified with certainty as fishes only in 1983. Conodont elements, small (0.25–2 mm) tooth-like structures made from apatite, have been known since 1856, and they are so abundant in many marine rocks from the Late Cambrian to the end of the Triassic, that they are used for stratigraphic dating. Particular conodont species, and groups of species, are characteristic of certain **stratigraphic** zones, and they form the basis of a worldwide international standard of relative dating. Over the years, these small phosphatic fossils have been assigned to many groups: annelid or nemertean worms, chaetognaths (arrow worms), molluscs, representatives of a separate phylum, or even plants.

The enigma was solved in a brilliant story of luck and bold interpretation when the first complete conodont, *Clydagnathus*, was reported from the Early Carboniferous of Edinburgh (Briggs *et al.,* 1983), and since then nine further specimens have been located in the Edinburgh rocks (Aldridge *et al.,* 1993; Donoghue *et al.*, 2000), as well as different conodont taxa from the Late Ordovician of South Africa and the Early Silurian of Wisconsin, USA. The first Edinburgh specimen (Figure 3.5(a)) is a 40.5 mm long eel-like creature that appears to show several chordate synapomorphies: a head with eyes, a notochord and myomeres. Specimen 5 (Figure 3.5(b)) provides additional evidence of the large eyes, including cartilages that supported the eyeballs themselves. Behind the eyes in specimen 1 are possible remnants of the otic capsules, structures associated with hearing and balance, and traces of what may be branchial bars. The phosphatic conodont elements lie beneath the head region, in the oral cavity on the pharynx.

Conodont elements had occasionally been found in associations of several types, usually arranged in a particular way. These conodont apparatuses (Figure 3.6(a)) were interpreted as the jaw or filter-feeding structures of some unknown animal, and the 1983 find proved that they were indeed complex feeding baskets. More recent work has revealed microwear patterns on different conodont elements, which demonstrates that they functioned in feeding, in seizing prey and chopping it into pieces (Purnell, 1995). The backwardly directed teeth helped the conodont stuff food into its mouth, and perhaps prevent any live prey from escaping. A mystery had been how the conodonts could have used their tiny teeth effectively when they lacked jaws: biomechanical analysis (Jones *et al.*, 2012) shows that they overcame size limitations through developing dental tools of extraordinary sharpness that maximized the pressure they could apply to their prey.

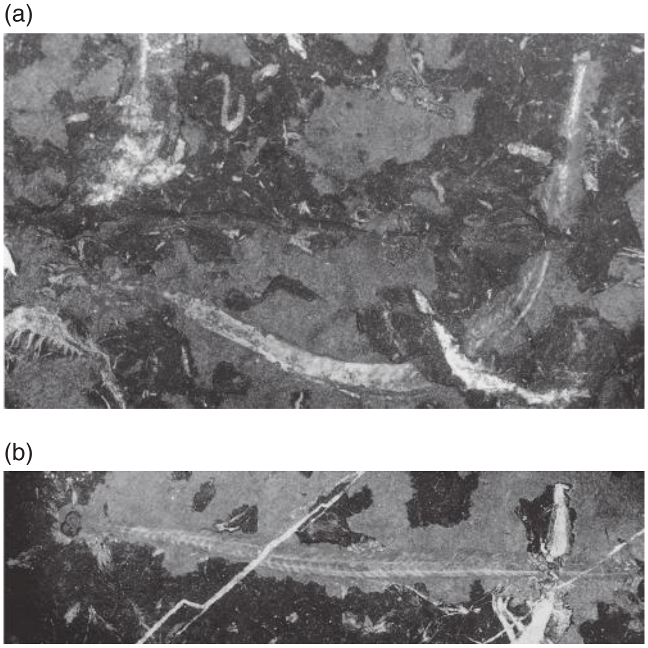


Figure 3.5 The conodont animal *Clydagnathus* from the Early Carboniferous Granton Shrimp Bed of Edinburgh, Scotland: (a) specimen 1; (b) specimen 5. In places, fossil shrimps lie across the conodont bodies. The animal is 40 mm long. Source: R. Aldridge, University of Leicester, Leicester, UK. Reproduced with permission.

The body region of the Edinburgh conodont animals shows a clear midline structure (see Figure 3.5) that has been interpreted as the notochord. Some specimens show traces of a possible dorsal nerve cord above the notochord. The other obvious feature of the body is its division into V-shaped tissue blocks, or myomeres (see Figure 3.5), muscle units that contracted on alternate sides to provide a powerful eel-like swimming motion. Conodonts had narrow tail fins, as shown by tissue traces on either side in some specimens (see Figure 3.5(a)). Overall, the conodont animal looked very like a small lamprey (Figure 3.6(b)).

The affinities of conodonts have long been debated, and the new whole-body specimens did not at first resolve the issue. The consensus now is that conodonts are vertebrates, and closely related to jawed fishes, as they share bone-like calcified tissue with other vertebrates, and there are at least two types, dentine and the enamel-like crown tissue (Murdock *et al.*, 2013; see Box 3.1). Chordate synapomorphies are the notochord,

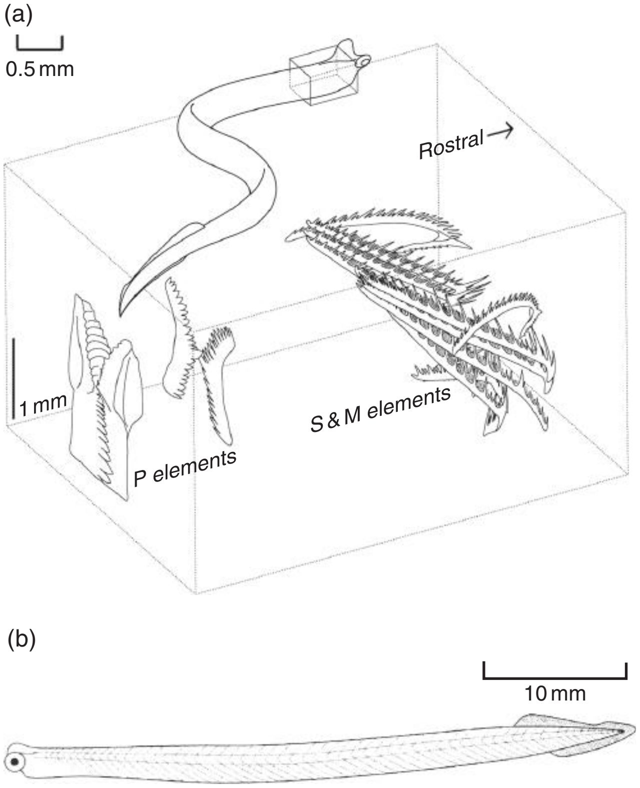


Figure 3.6 The conodont animal: (a) a complete conodont apparatus of the type possessed by *Clydagnathus*, showing different tooth elements (P, S, and M types), and location of the apparatus; (b) restoration of *Clydagnathus* in life, showing the eyes and the eel-like body. Source: M. Purnell, University of Leicester, Leicester, UK. Reproduced with permission.

the dorsal nerve cord, the myomeres, the tail and the midline tail fin. Vertebrate synapomorphies are the cranium in front of the notochord, the paired sense organs, the extrinsic eye musculature (absent in hagfishes) and the caudal fin with radial supports. The dentine and enamel of conodonts, as well as the eyes, with their sclerotic eye capsule, presumably developed from neural crest tissues of the early embryo, a clear vertebrate feature (see Section 1.4.4; Donoghue *et al.*, 2000).

3.3.3 Ordovician jawless fishes

After the Cambrian radiation of vertebrates, with and without skeletons, including the conodonts, a diversity of groups of fishes appeared in the Ordovician, but most are represented only by dermal elements. Two 'agnathan' clades, the Astraspida and Arandaspida are known, however, from more complete specimens in the Late Ordovician (Sansom *et al.*, 2001, 2005).

Astraspids and arandaspids are small fishes, about 200 mm long. They have a mobile tail covered with small protruding pointed plates, and a massive bony head shield made from several large plates that cover the head and most of the body.

Astraspis from North America (Sansom *et al.*, 1997) has an extensive head shield composed of a complex of separate bony plates that surround large eyes on either side, and a series of eight separate gill openings in a row (Figure 3.7(a)). The body is oval in cross section, and covered with broad overlapping scales, but the tip of the tail is unclear. The bony plates are composed of aspidin (see Section 3.2) covered by tubercles composed of dentine capped with enameloid. The tubercles are typically star-shaped over much of the body, hence the name *Astraspis* ('star shield').

Sacabambaspis from Bolivia (Sansom *et al.*, 2005) has a head shield (Figure 3.7(b)) made from a large **dorsal** (upper) plate that rose to a slight ridge in the midline, and a deep curved **ventral** (lower) plate. Narrow **branchial plates** link these two along the sides, and cover the gill area. Long, strap-like scales cover the rest of the body behind the head shield. The eyes are far forward and between them are possibly two small nostrils, and the mouth is armed with very thin plates.

The fossils of *Sacabambaspis* and *Astraspis* show clear evidence of a sensory structure that is peculiar to all fishes – the **lateral line** system. This is a line of open pores within each of which are open nerve endings that can detect slight movements in the water, produced for example by predators. The arrangement of these organs in regular lines allows the fish to detect the direction and distance from which the disturbance is coming. Genomic investigation confirms that these sensory systems of the earliest fishes are homologous with our inner ear hairs and other elements of our hearing system.

3.3.4 Heterostraci

The heterostracans, a large group of some 300 species, radiated extensively in the Silurian and Early Devonian (Janvier, 1996). All were armoured, with a substantial head shield, and they varied in shape from the bullet-like pteraspids to the flattened drepanaspids. Heterostracans all have in common a broad ornamented shield dorsally, one or more plates on either side of this, and a large bony element covering the underside. These agnathans form the clade Pteraspidomorphi, together with Astraspida and Arandaspida, as all share the synapomorphy of aspidin in their dermal armour plates (Donoghue *et al.*, 2000; see Box 3.1). Heterostracans are distinguished from astraspids and arandaspids by having a single exhalant opening on each side into which the gills open.

There were four main groups of heterostracans, the cyathaspids, amphiaspids, pteraspids and psammosteids. The cyathaspids (Lundgren and Blom, 2013), such as *Anglaspis* (Figure 3.8(a)), are completely encased in bony plates and scales. The dorsal, ventral and branchial plates (or shields) are broadly similar in shape to those of *Sacabambaspis*, and they bear an ornament of narrow parallel ridges. The body portion is covered with large bony scales that overlap backwards like the slates on the roof of a house. There is no sign of paired fins or paddles, so heterostracans must have steered by making lateral movements of the tail, a rather clumsy method.

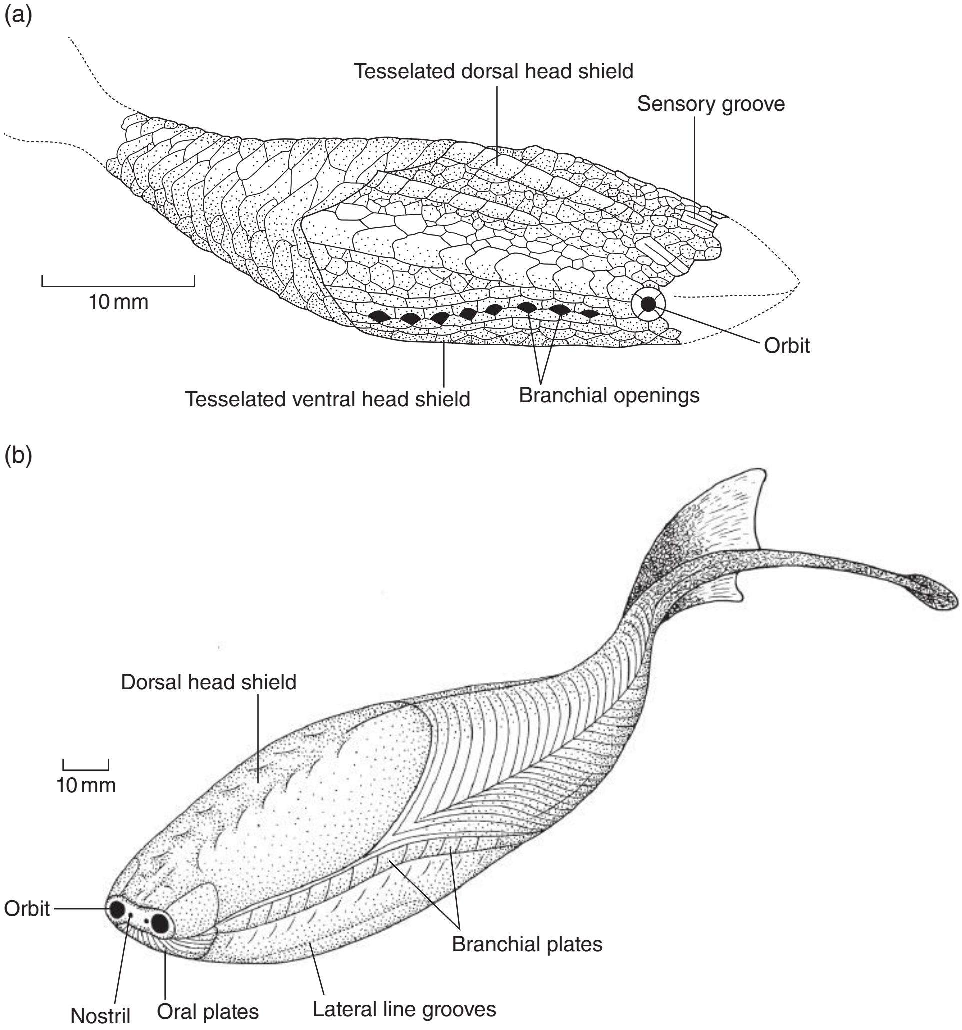


Figure 3.7 Ordovician jawless fishes: reconstructions of (a) *Astraspis* from the Ordovician of North America, in dorsal view, and (b) *Sacabambaspis*, from the Ordovician of Bolivia, in side view, showing the full anatomy with the formerly missing tail restored in place. Source: (a) Adapted from Sansom *et al.* (1997). (b) I. J. Sansom, University of Birmingham, Birmingham, UK. Reproduced with permission.

The amphiaspids show complete fusion of the head shield along the sides to form a single carapace, and the eyes are reduced. It has been suggested that amphiaspids lived partially buried in the mud where sight was not required: some forms, such as *Eglonaspis* (Figure 3.8(b)), have a long tube at the front of the carapace with the mouth opening at the end, possibly used as a kind of 'snorkel' when burrowing.

The pteraspids of the Early and Mid-Devonian are much better known, with more than 25 genera, which show considerable variation in the shape of the head shield (Pernègre and Elliott, 2008). In *Errivaspis* (Figure 3.8(c)) there are large dorsal and ventral plates, the linking branchial plate, as well as a **cornual plate** at the side, an **orbital plate** around the eye, a **rostral plate** forming a pointed 'snout', several small plates around the mouth, and a dorsal spine pointing backwards. The rest of the body is covered with small scales that look more like modern fish scales than the bony plates of earlier forms. The tail is fan-shaped.

The psammosteids are much larger than other heterostracans, sometimes 1.5 m in width, and they are flattened (Figure 3.8(d)). They have several rows of small scale-plates called **tesserae** lying between the main shields. The flattening of the body has pushed the eyes well apart and turned the mouth upwards. *Drepanaspis* looks like a pteraspid that has outgrown its armour – all the major plates are the same, but they have moved apart, and are linked by skin covered in smaller bone plates.

Feeding in heterostracans has been controversial: did they snap up largish prey items, or did they plough through the seabed mud? Heterostracans have numerous overlapping bony **oral** plates in the base of the mouth, but these do not show wear at the tips, so they could not have been used for ploughing. The oral plates are also covered with tiny pointed **denticles** that point outwards, and this would prevent larger food particles entering the mouth. Purnell (2002) suggests that most heterostracans swam above the seabed, taking in small prey items floating or swimming in the water.

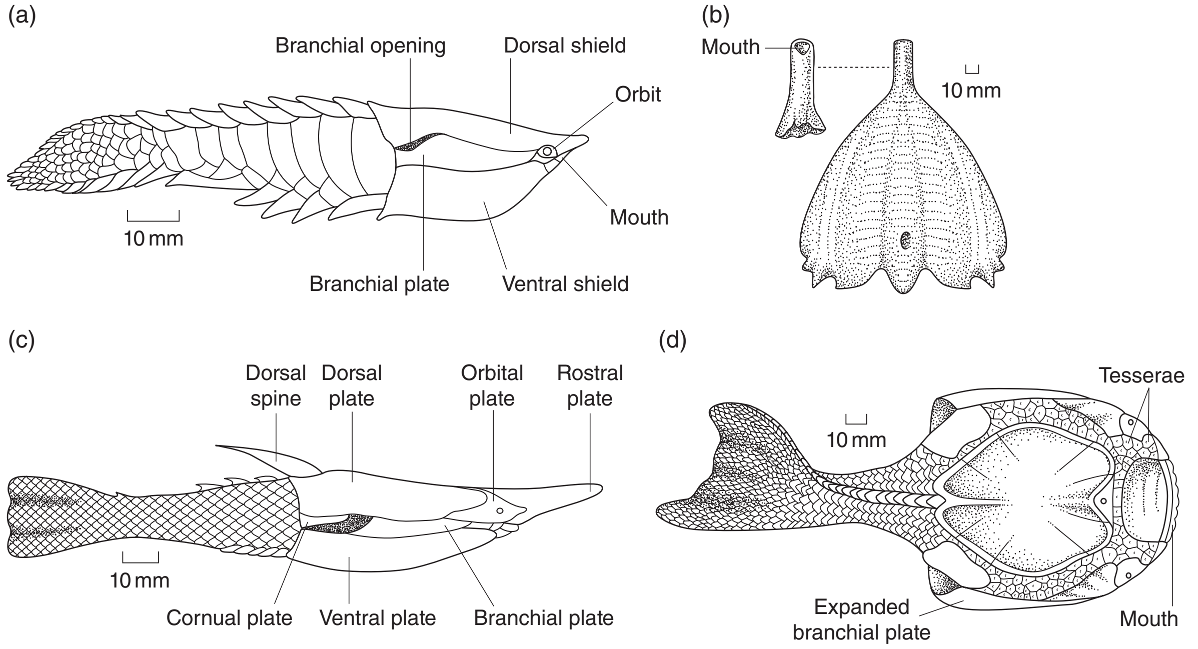


Figure 3.8 Heterostracans: (a) *Anglaspis*; (b) *Eglonaspis*, dorsal view of head shield and underside of mouth tube; (c) *Errivaspis*; and, (d) *Drepanaspis*. Source: Adapted from Moy-Thomas and Miles (1971).

3.3.5 Anaspida and Thelodonti

The anaspids and thelodonts were modest in size, had limited armour, and their affinities are unclear. In recent cladistic analyses (Donoghue *et al.*, 2000; Donoghue and Smith, 2001), anaspids and (some) thelodonts were successive outgroups to osteostracans, galeaspids and gnathostomes (see Box 3.1). Some other small, slender Silurian and Devonian fishes, sometimes exceptionally preserved and showing eyes, notochords, myotomes, guts, and skin, also appear to fall phylogenetically close to anapsids and thelodonts in the cladogram, and these include much-studied taxa such as *Euphanerops* (Janvier and Arsenault, 2007; Sansom *et al.*, 2013) and *Jamoytius* (Sansom *et al.*, 2010).

Anaspids are known from some 20 species from the Silurian and Devonian (Blom *et al.*, 2002; Blom, 2012). *Pharyngolepis* (Figure 3.9(a)) is a cigar-shaped animal 200 mm long, with a terminal mouth, small eyes, a single dorsal nostril and a covering of irregular scales and plates in the head region. The body scales are long and regular, and arranged in several rows. There is a **pectoral** spine and two paired fins beneath, and a tail fin on top of the downwardly bent tail.

Thelodonts are known mainly from isolated scales in the Ordovician, and abundant scales and rarer whole specimens in Upper Silurian and Lower Devonian rocks of various parts of the world (Donoghue and Smith, 2001; Märss *et al.*, 2007; Žigaitė *et al.*, 2013). *Phlebolepis* (Figure 3.9(b,c); Wilson and Märss, 2012) is 70 mm long, with a slightly flattened body, a broad snout, an eye at each side and a wide mouth. There are lateral fins behind the eyes, low dorsal and anal fins, and a long ventral tail fin. The body is completely covered with small scales, and there is no sign of bone shields in the head region at all. In certain thelodonts, there are eight small gill openings beneath the lateral fins.

Some thelodonts from the Early Devonian of northern Canada (Wilson and Caldwell, 1998) had a deep, laterally compressed body shape (Figure 3.9(d)). The tail is deep and symmetrical, with an upper and lower fleshy lobe. The body surface bears several different kinds of scales, and ten gill openings extend in an oblique line behind the eye. The fossils are well enough preserved to show that these thelodonts had a large stomach, seen also in *Turinia* (Donoghue and Smith, 2001), and this suggests that some thelodonts at least were deposit-feeders.

The scales (Figure 3.9(e)) are lozenge-shaped, concave beneath, and they rise to a point above. The shapes of scales and arrangements of spines and nodules are used to identify thelodont species from isolated specimens. In cross section (Figure 3.9(f)), the thelodont scale is composed of dentine around an open pulp cavity, as in a tooth, although it lacks enamel and it shows the typical composition of scales and tubercles of many early vertebrates.

3.3.6 Osteostraci and relatives

Three clades of jawless fishes that lie close to the origin of jawed vertebrates (see Box 3.1) all have a massive head shield that covered the gills dorsally and ventrally-opening gills, as well as a mineralized braincase welded to the underside of the dermal skeleton, all features that are convergent with placoderms (see Section 3.5). Of these, the Galeaspida appear to have branched off earlier than the Osteostraci, which are probably the closest

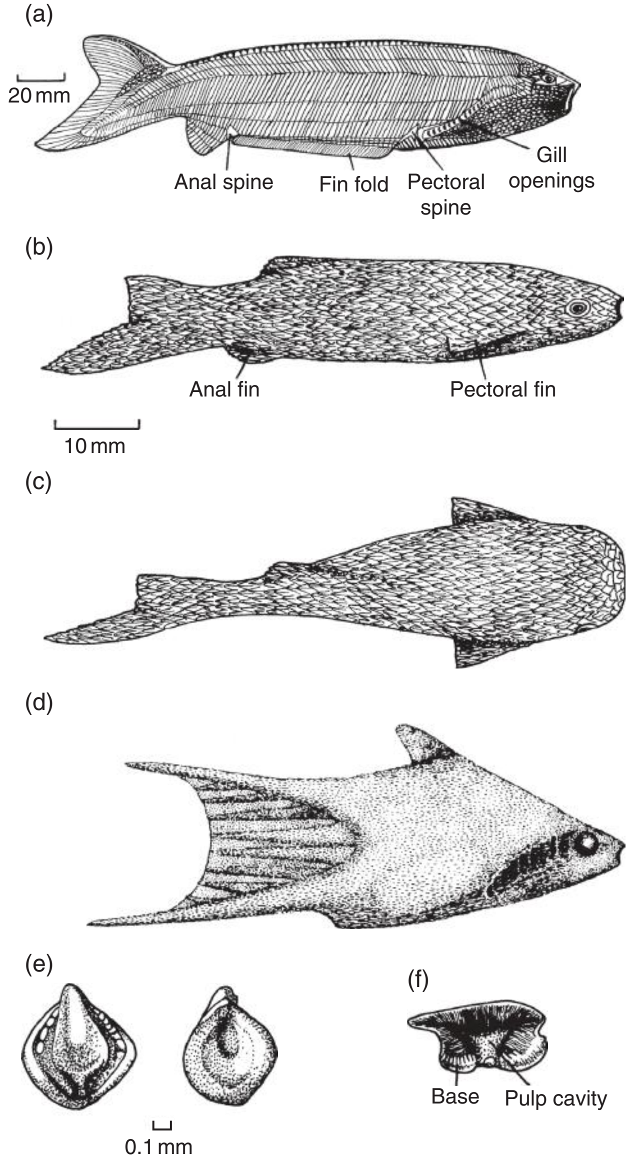


Figure 3.9 Anaspids (a) and thelodonts (b–f): (a) the anaspid *Pharyngolepis*; (b,c) whole-body restoration of *Phlebolepis*, in (b) lateral and (c) dorsal views; (d) whole-body restoration of the fork-tailed thelodont *Furcacauda*; (e) scales of *Logania* in dorsal (left) and ventral (right) views; and (f) scales of *Thelodus* in cross-section. Source: (a,e,f) Adapted from Moy-Thomas and Miles (1971). (b,c) Adapted from Wilson and Märss (2012). (d) M. Wilson, University of Alberta, Edmonton, Alberta, Canada. Reproduced with permission.

outgroup to Gnathostomata, and the Pituriaspida are of uncertain phylogenetic position (see Box 3.1).

The galeaspids are a group of some 75 species from the Silurian and Devonian of China and Vietnam (Janvier, 1996; Zhu and Gai, 2007). Many have broad head shields, but others show an impressive array of processes (Figure 3.10(a)): curved cornua pointing backwards, a ‘hammer-head’ rostral spine, and pointed snout spines that are longer than the head shield itself. Some forms also have very long lateral spines that may have acted like the wings of a glider during swimming, to maintain a stable body position. Galeaspids have their mouth just beneath the head shield, and they have a single nostril at the tip of the snout that may be a transverse slit, a broad oval, a heart shape, or a longitudinal slit. The internal anatomy of the head shield sheds remarkable light on key transformations that relate to the origin of jaws (see Box 3.2). Some galeaspids have up to 45 gill pouches, the largest number in any vertebrate. Galeaspids lack paired fins.

The Osteostraci, comprising some 200 species, arose in the Ordovician, and radiated in the Late Silurian and Early Devonian (Janvier, 1996; Sansom, 2008). These were the first vertebrates with paired fins. They are heavily armoured in the head region, and most have a flattened, curved semicircular head shield shaped rather like the toe of a boot. *Hemicyclaspis* from the Late Silurian of Europe and Canada has a solid **carapace** made from a single bony plate that enclosed the head region (Figure 3.10(b)). Behind the head plate is a pair of pectoral fins covered with small scales, and these could presumably have been used in swimming. *Tremataspis* and relatives lack pectoral fins. The body and tail are covered with broad scales on the side and beneath, and narrower ones on top that form a dorsal ridge and a dorsal fin. These osteostracan pectoral fins had endoskeletons and are likely homologous with our arms, so forelimbs evolved in vertebrates before jaws (Janvier, 1996).

In the course of their evolution, the head shield of osteostracans adopted a variety of shapes, ranging from rectangular and hexagonal forms, some with backward-pointing spines, or cornua, and some even with a long rostral spine in front (Figure 3.10(c)), to an elongate bullet shape in some later forms.

The head shield is remarkably well preserved in certain cephalaspids. In dorsal view (Figure 3.10(d)), it shows two oval openings for the eyes, the orbits and a narrow keyhole-like slit in front of them in the midline, the **nasohypophyseal opening**. Behind it, and still in the midline, is a tiny **pineal opening**, associated with the pineal gland in the brain that might have been light sensitive. In addition, there are three depressions, the dorsal field in the midline behind the orbits, and the two lateral fields. They might have had a sensory function, perhaps in detecting movements nearby, either by physical disturbance of the water, or by weak electrical fields. The underside of the cephalaspid head shield (Figure 3.10(e)) shows a large mouth at the front with a broad area of small ventral scales behind. Around the edges of this scale field are eight to ten gill openings on each side.

Most remarkable is the internal anatomy; the mineralized braincase enclosed much of the brain and sensory organs, as well as parts of the blood circulatory system and digestive system (Figure 3.10(f)). Even the semicircular canals of the inner ear, the organs of balance, can be seen. The brainstem is located in the midline, and it comprised the three main portions seen in living fishes and tetrapod embryos, the **medulla** at the back which leads into the spinal cord, the **pons** in the middle, and the **telencephalon** (forebrain) in front with an elongate **hypophyseal sac** running forwards from it. The cranial nerves III (eye movement), V2 (mouth and lip region), VII (facial), IX (tongue and pharynx) and X (gill slits and anterior body) have been

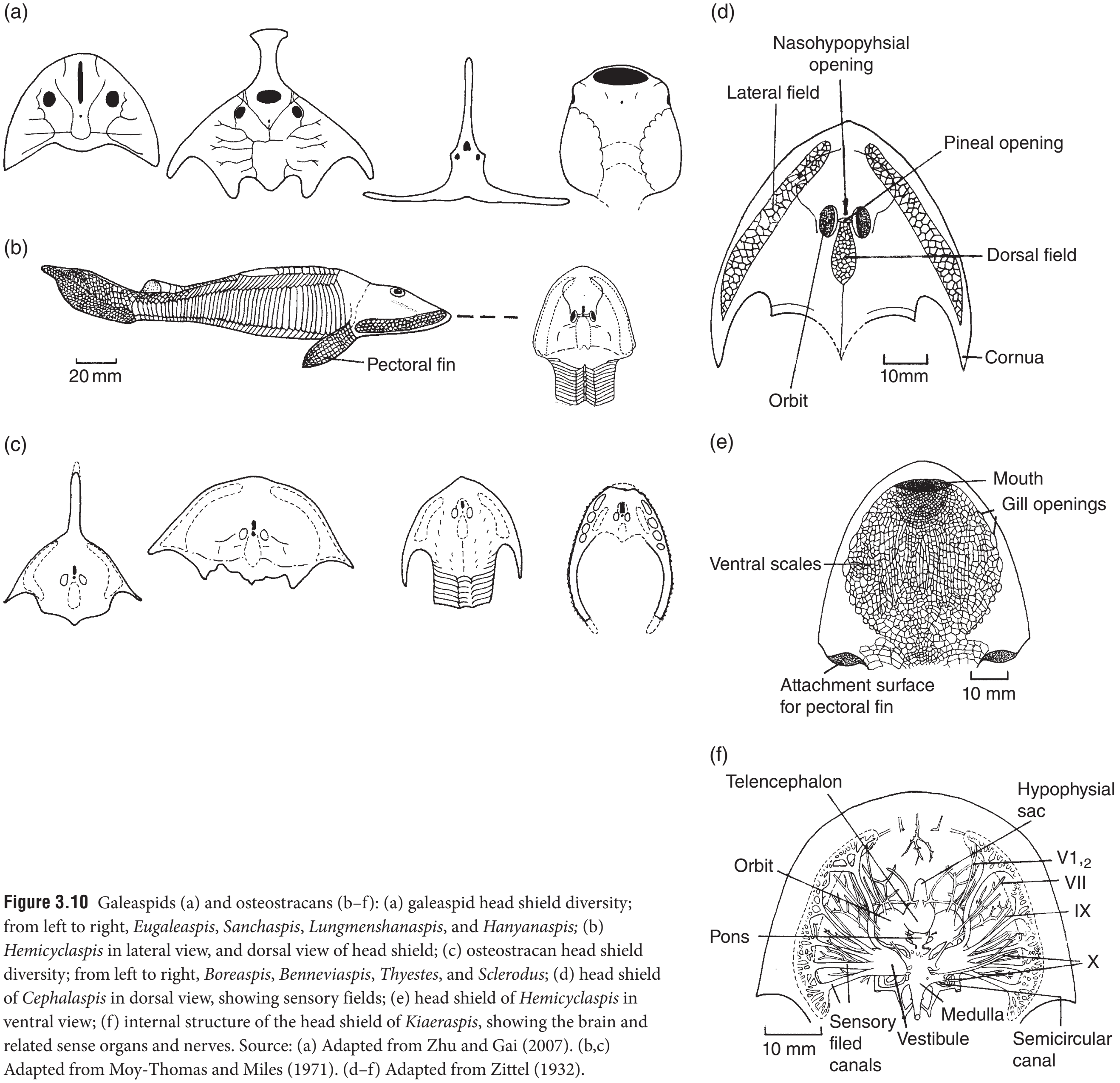


Figure 3.10 Galeaspids (a) and osteostracans (b–f): (a) galeaspid head shield diversity; from left to right, *Eugaleaspis*, *Sanchaspis*, *Lungmenshanaspis*, and *Hanyanaspis;* (b) *Hemicyclaspis* in lateral view, and dorsal view of head shield; (c) osteostracan head shield diversity; from left to right, *Boreaspis*, *Benneviaspis*, *Thyestes*, and *Sclerodus*; (d) head shield of *Cephalaspis* in dorsal view, showing sensory fields; (e) head shield of *Hemicyclaspis* in ventral view; (f) internal structure of the head shield of *Kiaeraspis*, showing the brain and related sense organs and nerves. Source: (a) Adapted from Zhu and Gai (2007). (b,c) Adapted from Moy-Thomas and Miles (1971). (d–f) Adapted from Zittel (1932).

BOX 3.2 SCANNING GALEASPID HEADS

New technology has provided some unexpected opportunities for understanding early vertebrate anatomy. Already, Erik Stensiö, the legendary Swedish anatomist, had reconstructed the internal anatomy of cephalaspid head shields in astonishing detail (see Figure 3.10(f)) in the 1920s. But he had to destroy his specimens to extract the anatomical detail: his method was serial grinding, in which he ground down the fossil, a millimetre at a time, took detailed tracings, and then continued until the specimen was a pile of dust. He then modelled his tracings in wax, at magnified scale, to reveal the intricacies of blood vessels and nerves encased in the bone.

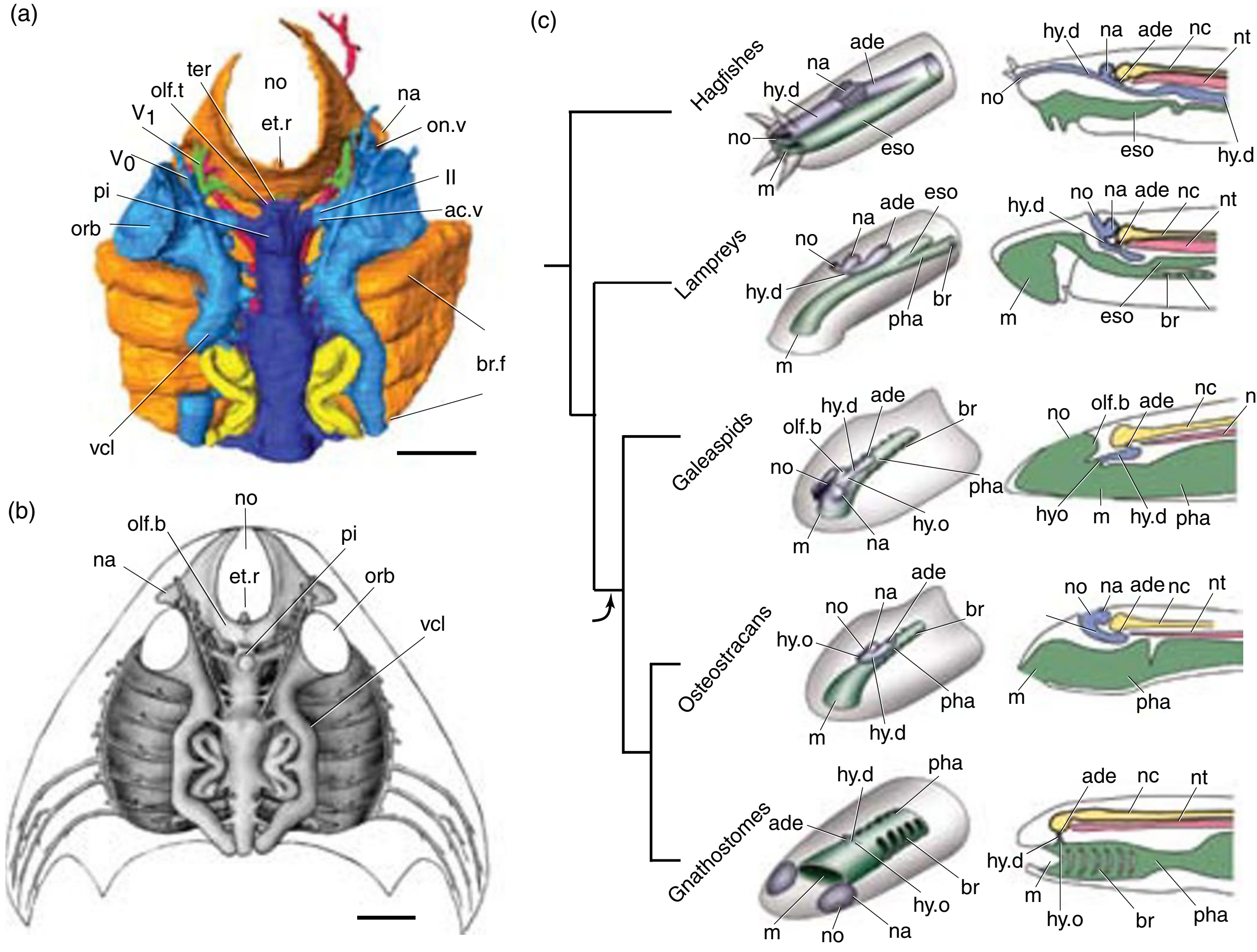
None of this is necessary now. Palaeontologists use micro-computed tomography (micro-CT) to reveal most of the details Stensiö could see, but the specimens are not damaged. In a typical study, Zhikun Gai of the University of Bristol and the Institute of Vertebrate Paleontology and

Continued

Paleoanthropology in Beijing, was able to reconstruct the internal anatomy of the galeaspid *Shuyu* (Gai *et al*., 2011). He scanned specimens at the Swiss Light Source in Zürich, producing closely-spaced X-ray slices, reconstructed these as 3D images, and was able to determine details of the arrangement of the brain and sensory structures that shed light on the origin of jawed vertebrates.

The reconstructed internal organs (illustrations (a,b)) show the orbits (eye sockets) on either side of, and behind, the single, median nostril. This nostril served both as an olfactory organ, and also as the main water intake. The brain and sensory organs lie above a substantial oro-branchial chamber, comprising the mouth, pharynx, and gill slits. Behind the single nostril are the tiny olfactory bulbs, and these connect to the brain via the olfactory tracts. The nasal sacs are located to the sides, and they connect to the olfactory bulbs via narrow spaces that would have housed the olfactory nerve. Beneath these, the hypophyseal duct opens anteriorly into the mouth cavity, but it does not extend to the external nostril. The separation of the nasal sacs, to right and left, and the hypophyseal duct in the roof of the mouth was unexpected. The primitive condition, seen in living cyclostomes (lampreys, hagfishes), is to have a nasohypophyseal duct connecting the nostril to the mouth cavity, through which water flows. In jawed vertebrates, including humans, the hypophyseal is modified to form a pouch in the roof of the mouth during early development, and this then migrates towards the brain and forms part of the pituitary gland.

The switch from a single nasohypophyseal canal, as seen in living cyclostomes, to the separated hypophysis and nasal sacs approaches the gnathostome condition (Janvier, 2012). Jawed vertebrates have two nostrils, each associated with a nasal sac, a later anatomical change in gnathostomes. Importantly, the severing of the nasohypophyseal tract allowed the embryological precursors of jaws to grow forwards into the snout region, and so the galeaspid head anatomy shows changes that were necessary before jaws could evolve (see Section 3.4).



Internal anatomy of the head region of the Silurian galeaspid *Shuyu zhejiangensis*. (a) Virtual endocast, reconstructed from micro-CT scans; (b) reconstruction of external morphology; (c) evolution of the nasohypophyseal complex in craniates, shown in oblique view (left) and midline section (right). The disassociation of the nasohypophyseal complex, an evolutionary prerequisite for the origin of jaws, happened at least in the common ancestor of galeaspids, osteostracans and gnathostomes (arrow). The condition of osteostracans probably converged with that of lampreys. See Colour plate 3.1. Abbreviations: ac.v, anterior cerebral vein; ade, adenohypophysis; br, branchial duct or slit; eso, oesophagus; et.r, ethmoid rod; hy.d, hypophyseal duct; hy.o, hypophyseal opening; m, mouth; na, nasal sac; nc, neural cord; no, nostril; nt, notochord; olf.b, olfactory bulb; olf.t, olfactory tract; orb, orbit; pha, pharynx; pi, pineal organ; ter, terminal nerve;vc, lateral head vein or dorsal jugular vein; II, V_0, V_1, cranial nerves II, V (superficial ophthalmic; profundus). Source: Gai *et al*. (2011). Reproduced with permission from Nature Publishing Group.

identified by comparison with living vertebrates. The five broad canals running from the lateral sensory fields to the vestibule of the inner ear also show clearly.

The pituriaspids, represented by limited material from the Middle Devonian of Australia, could be close relatives of the osteostracans. They share a heavy, bony head shield with osteostracans and galeaspids, and they have unusual, large openings immediately below the eyes. They also have a pair of openings on the trunk, just behind the branchial chamber wall that were most likely apertures for paired pectoral fins.

3.4 ORIGIN OF JAWS AND GNATHOSTOME RELATIONSHIPS

The Gnathostomata, the jawed vertebrates (all fishes and tetrapods other than 'agnathans'), all have jaws, and these permit a wide range of diets and food-handling techniques that are not available to jawless vertebrates. Jaws enable gnathostomes to be actively processing predators: only jaws can grip a prey item firmly, and allow it to be manipulated, cut cleanly, and ground up. They also allow feeding on really tough food (**durophagy**) and efficient suction feeding. Jaws could only evolve after the subdivision of the nasohypophyseal canal that linked the single cyclostome nostril with the roof of the mouth, and this depended on fundamental developmental changes (see Box 3.2).

How did jaws evolve? There are three models, the so-called classic theory that jaws arose from anterior gill arches, the ventilation theory that jaws evolved first for breathing, and the heterotopy theory that suggests a relative shift developmentally in the position of the agnathan and gnathostome mouths.

3.4.1 Jaws

The 'classic theory' for the origin of jaws is that they formed from modified anterior gill arches (Figure 3.11). In jawless fishes, the gill slits are separated by bony or cartilaginous arches. A hypothetical ancestral vertebrate with eight gill slits and nine gill arches evolves into an early gnathostome by the loss of four gill slits, and the fusion and modification of the anterior three gill arches. The most anterior may form parts of the floor of the braincase. The second gill arch might have been modified to form the **palatoquadrate**, the main part of the upper jaw, and **Meckel's cartilage**, the core of the lower jaw (**mandible**). The third gill arch was then supposedly modified in part to provide a skull bone and a mandible bone that formed part of the jaw joint, the **hyomandibular** in the skull and the **ceratohyal** in the lower jaw. All these modifications affect the splanchnocranium, the gill arch and oral portion of the skull derived embryologically from the neural crest.

The 'ventilation theory' (Mallatt, 2008) suggests that jaws evolved first for breathing: the mandibular branchial arch in the pre-gnathostome enlarged first to improve the intake of oxygenated water. Only later, with the evolution of suction feeding, did the jaws take on a feeding function. Evidence is that the gill lamellae in lampreys develop medially to the supporting skeleton, whereas the gills of gnathostomes develop laterally to the skeleton, so there must have been a transition from internal to external gill arches before the jaws evolved.

Finally, the 'heterotopy theory' (Shitegani *et al*., 2002; Kuratani *et al*., 2013) is founded on developmental genetic evidence that different parts of the cephalic ectomesenchyme, the embryonic precursor tissues of the palate and jaws, give rise to the upper and lower margins of the mouth between these two animal groups. In other words, lamprey lips are not the same as gnathostome lips, and it is wrong to assume that jaws arose by encircling the existing basal vertebrate mouth. In gnathostomes, the jaws develop from cells that arose initially from the neural crest (see Section 1.4.4), and similar cells are seen early in development of the lamprey. In the lamprey, however, these cells go on to develop into the upper lip and velum, whereas in gnathostomes they become the precursor of the jaw. There is evidence for a major repatterning process during development, and this implies that it is wrong to expect to see precursors of jaws in the adults of jawless vertebrates.

The developmental genes that trigger the anterior to posterior patterning of the lips (*Fgf8*, *Bmp2/4*, *Dlx1*, and *Msx*) are the same in cyclostomes and gnathostomes, but anatomical elements and genes act differently in both. For example, whereas lampreys express *Dlx* genes in their upper and lower lips, gnathostomes do so only in the mandibular (lower) arch. The lips in lampreys comprise portions of tissue that arise from postoptic and mandibular arch neural crest domains, whereas in gnathostomes the entire mouth is formed from mandibular arch tissue, and the postoptic cells become parts of the anterior snout skeleton.

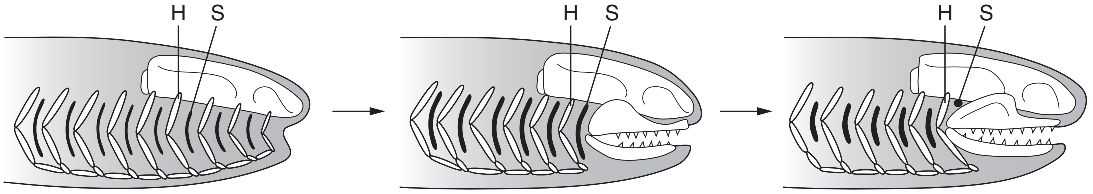


Figure 3.11 The evolution of jaws: the 'classic' theory for the evolution of jaws from the anterior two or three gill arches of a jawless form (left) to the fully equipped gnathostome (right); gill openings in black; H, hyomandibular; S, spiracular gill opening. Source: Adapted from Romer (1933).

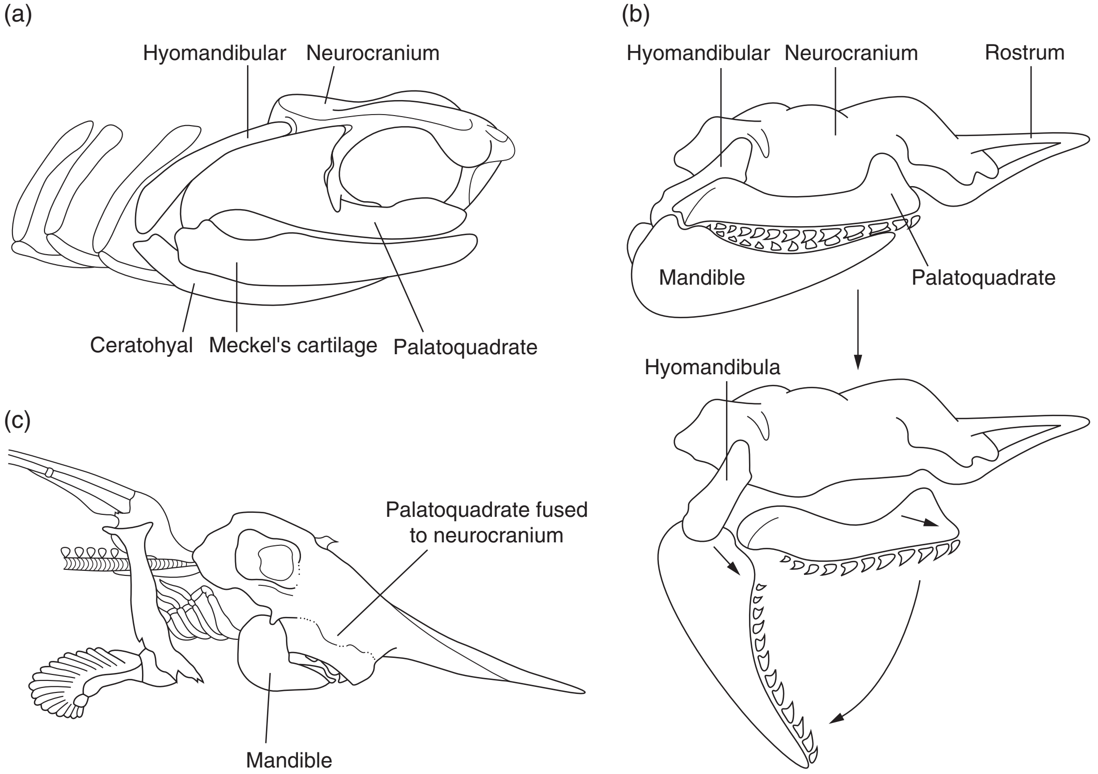


Figure 3.12 Jaw suspension in sharks. (a) The braincase, jaws, and gill supports of the Carboniferous shark *Cobelodus*, to show the amphistylic system of jaw attachment to the neurocranium; (b) braincase and jaws of the modern shark *Carcharhinus*, with the jaws closed (top) and open (bottom), to show the hyostylic system of jaw support and the highly mobile palatoquadrate; (c) head of a chimaerid chondrichthyan, to show the autostylic, or fused, system of jaw attachment. Source: (a) Adapted from Zangerl and Williams (1975). (b) Adapted from Wilga *et al.* (2000) and other sources. (c) Adapted from various sources.

3.4.2 Jaw attachments and gnathostome relationships

The palatoquadrate in gnathostomes is generally attached to the **neurocranium**, the main portion of the skull that enclosed the brain and sensory organs, in various ways. In early sharks, such as *Cobelodus* from the Late Carboniferous of North America (Figure 3.12(a)), there is a double attachment with links fore and aft, the **amphistylic** condition.

The amphistylic pattern has been modified in two main ways. In most modern fishes, the palatoquadrate contacts the neurocranium at the front only, and the jaw joint is entirely braced by the hyomandibular. On opening the jaw, the palatoquadrate can slide forwards, which increases the gape (Wilga *et al.*, 2000). This is the hyostylic jaw suspension condition (Figure 3.12(b)). The second modification has been to exclude the hyomandibular from support of the jaw, and to fuse the palatoquadrate firmly to the neurocranium, the autostylic condition. This is typical of certain fish groups, the chimaeras (Figure 3.12(c)) and lungfishes, as well as the tetrapods.

Living gnathostomes are grouped into the clades Chondrichthyes and Osteichthyes (bony fishes and tetrapods), and two extinct traditional groups are the Acanthodii of the Ordovician to Permian, and the Placodermi of the Silurian and Devonian. The placoderms and the acanthodians, long difficult to position phylogenetically, both appear to represent evolutionary grades that include a mix of stem gnathostomes and stem chondrichthyans (see Section 3.7).

3.5 PLACODERMS: ARMOUR-PLATED MONSTERS

The osteostracans and heterostracans (see above) were not the only heavily armoured fishes in Silurian and Devonian seas. The placoderms bore similar bony carapaces over the regions of their heads and shoulders, but in all cases these shields were mobile. There was a special neck joint that allowed the anterior portion of the head shield to be lifted. Placoderms include the first vertebrates to have paired pelvic fins. In all, there were nearly 350 genera of placoderms, known from the Early Silurian to the end of the Devonian (Janvier, 1996; Young, 2010; Johanson and Trinajstic, 2014).

The placoderms include seven clades, listed in phylogenetic sequence from most basal to most derived: Acanthothoraci, Rhenanida, Antiarchi, Petalichthyida, Ptyctodontida, Phyllolepida, and Arthrodira. The arthrodires form the largest group, and they will be described first and in most detail. It is currently debated whether placoderms form a clade (Young, 2008, 2010) or a grade, a series of stem lineages to crown gnathostomes (Johanson, 2002; Brazeau, 2009; Davis *et al.*, 2012; Johanson and Trinajstic, 2014). Brazeau (2009) showed, for example, that petalichthyids and some acanthothoracids have braincases with orbital morphologies and jaw/hyoid attachments that quite closely resemble those in osteostracans (and to a lesser extent, galeaspids). So, it is likely that the various placoderm subclades may distribute themselves along the phylogenetic tree, internesting with acanthodians, between ostracoderms and along the osteichthyan stem (see Box 3.4).

3.5.1 Arthrodira

The arthrodires, some 200 genera, make up more than half of all known placoderms, and new taxa are still being found. The Middle Devonian form *Coccosteus* (Miles and Westoll, 1968) has a trunk shield that covers only part of the dorsal surface, and it extends back as far as the shoulder region below (Figure 3.13(a)). There are paired pectoral and pelvic fins, both supported by limb girdles, but much smaller than in sharks. The tail is heterocercal, and there is a long dorsal fin. The posterior part of the body is covered with small scales, but these are rarely preserved. It is likely that *Coccosteus* was a powerful swimmer, achieving speed by lateral sweeps of its tail and posterior trunk. Its flattened shape suggests, however, that it probably lived near the bottom of seas or lakes.

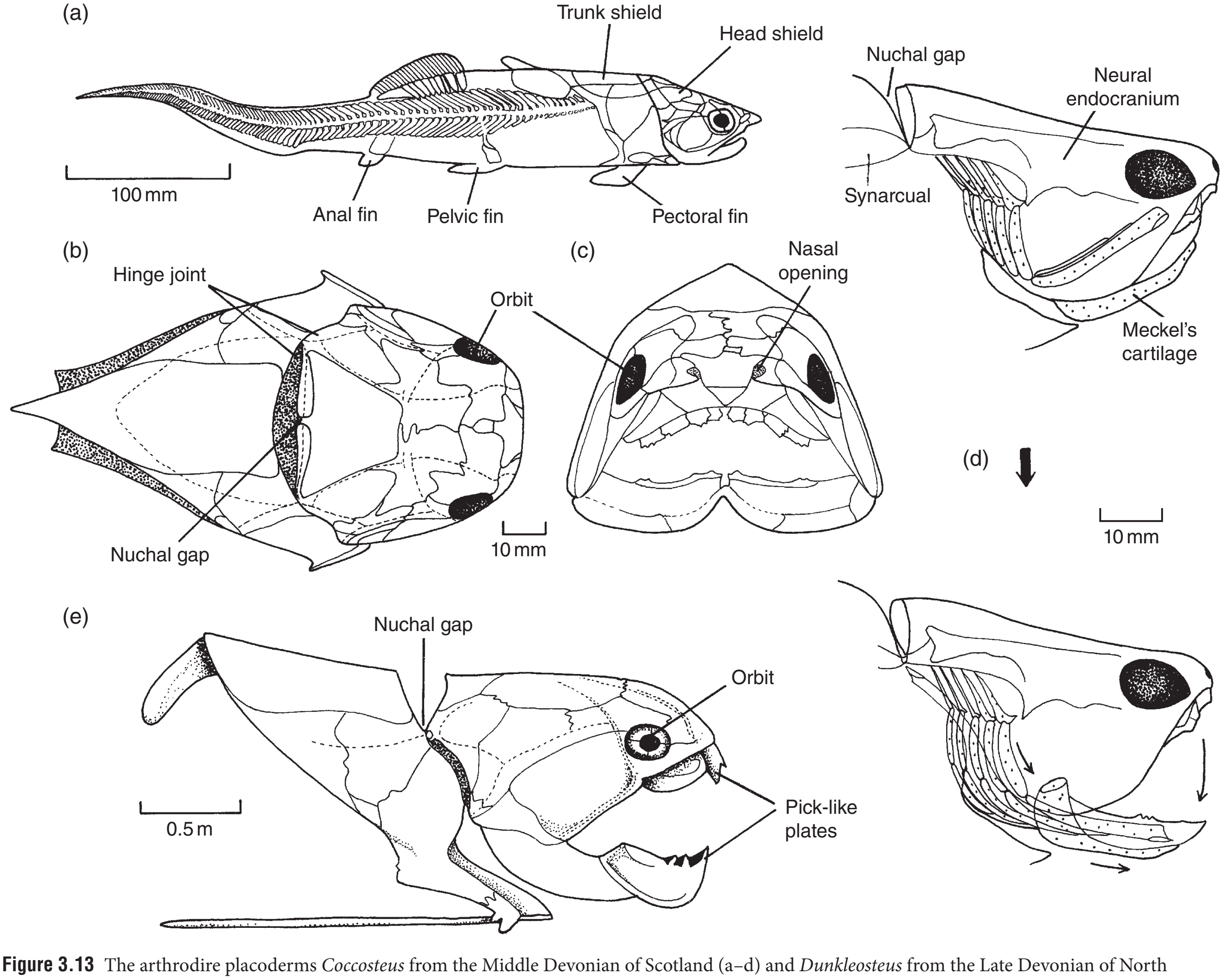


Figure 3.13 The arthrodire placoderms *Coccosteus* from the Middle Devonian of Scotland (a–d) and *Dunkleosteus* from the Late Devonian of North America (e): (a) whole body in lateral view, (b) head shield in dorsal and (c) anterior views, and (d) jaw opening movements showing the position of the head and visceral and branchial skeletons, with the jaws closed (left) and open (right); (e) lateral view of armour shield. Source: (a,e) Adapted from Moy-Thomas and Miles (1971). (b,c) Adapted from Miles and Westoll (1968). (d) Adapted from Miles (1969).

The head and trunk shields (Figure 3.13(b,c)) consist of several plates, and there is a gap (the **nuchal gap**) between the head and trunk shields at the line of hinging. The jaws open (Figure 3.13(d)) by an upwards swing of the skull and dropping of the lower jaw. The skull hinges about the ball and socket joints within the lateral margins of the dorsal part of the head shield, and the size of the gape is limited by the width of the nuchal gap. It has been suggested that placoderms used a head-lifting form of jaw opening in feeding on the bottom of the sea and lakes. It would have been easier to capture prey by driving the lower jaw forwards in the bottom mud and lifting the head, than by attempting to drop the lower jaw.

Later arthrodires have even more reduced armour than *Coccosteus*, often only a very limited trunk shield. Two Late Devonian families, the Dinichthyidae and the Titanichthyidae of North America and northern Africa, achieved giant size, as much as 6–7 m in length. *Dunkleosteus* (Figure 3.13(e)) was the largest predator in Devonian seas, and the largest vertebrate yet to evolve; it was the Devonian 'Jaws' (see Box 3.3).

Some placoderms at least produced live young and practised internal fertilization. Tiny embryos have been reported (Long *et al.*, 2009; Johanson and Trinajstic, 2014) within the skeletons of the ptyctodont *Materpiscis* and the arthrodire *Incisoscutum* from the Late Devonian Gogo Formation of Western Australia. **Viviparity** (live birth) is common across all vertebrates, and has arisen convergently many times among sharks, bony fishes, frogs, lizards, snakes, and mammals. Among living sharks, about 55% of species give birth to live young, and the placoderm embryos prove the antiquity of this adaptation. Like sharks, apparently the male *Incisoscutum* had claspers, elongate, articulated structures behind the pelvic girdle that were used during internal fertilization to hold both individuals steady.

3.5.2 Placoderm jaws and teeth

The bone of the lower jaw margin in arthrodires and most other placoderms is worn to a sharp edge against a series of eight small plates in the upper jaw. These wear into sharp beak-like plates that would have been capable of an effective cutting, puncturing and crushing action.

BOX 3.3 DEVONIAN JAWS!

Soon after the origin of jaws in the Late Silurian and Devonian, some placoderms evolved massively powerful bite forces. In a world of gently slurping and mumbling seabed foragers, such extremes of carnivory might seem out of place. Nonetheless, *Dunkleosteus* (see Figure 3.13(e)) from the Late Devonian of North America, and with species from Europe and North Africa, was a massive predator, 6–7 m long and weighing 3–4 tonnes. It was probably a slow swimmer.

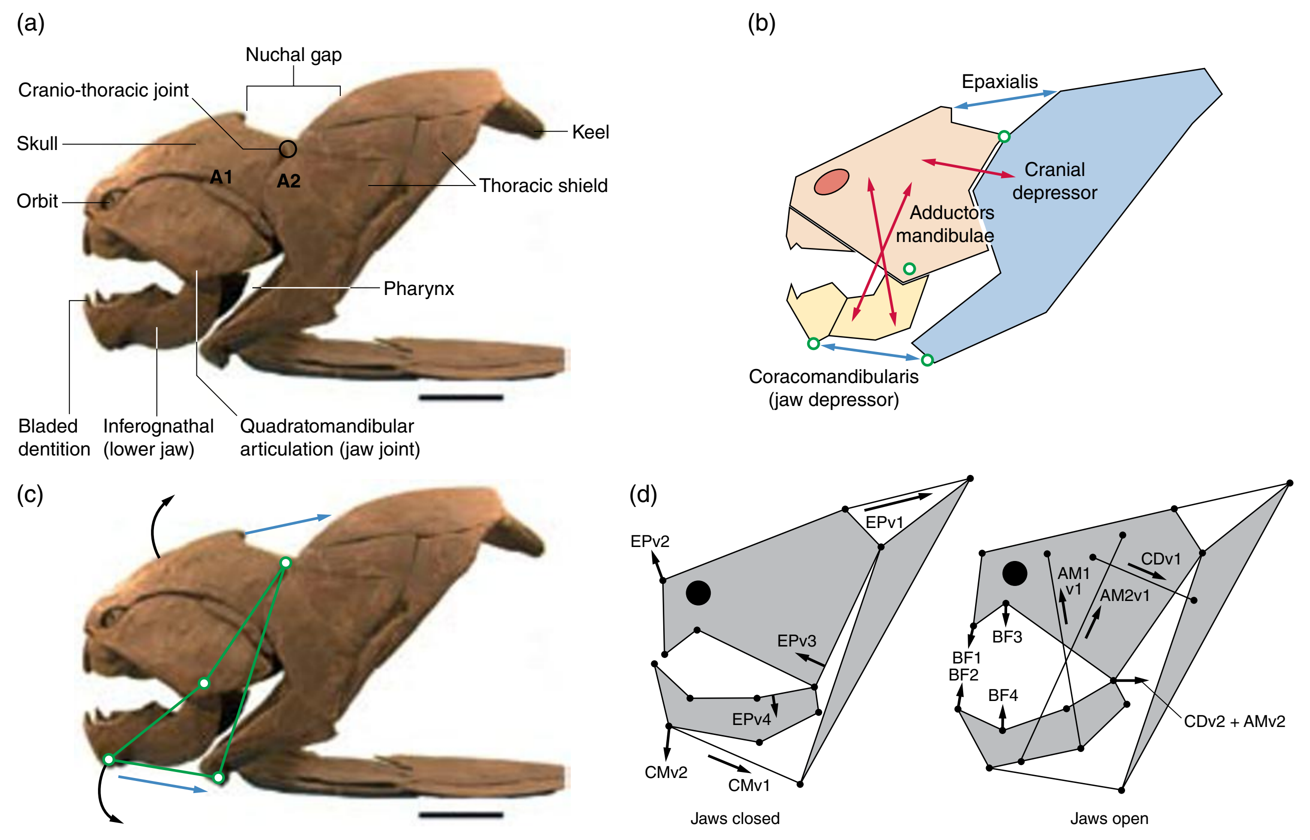
Palaeontologists have always realized *Dunkleosteus* was a powerful carnivore. Its jaws are edged with sharp bony plates that were used in shearing, one blade sliding past the other, as in a pair of scissors, and self-sharpening during normal feeding actions. In a biomechanical study, Anderson and Westneat (2007, 2009) have explored the skull and jaw motions used in feeding, and calculated the *Dunkleosteus* bite force. They were able to take advantage of the fact that many *Dunkleosteus* specimens are very well preserved in three dimensions.

This study, which formed part of Phil Anderson's PhD at the University of Chicago (supervised by Mark Westneat), used materials in the Cleveland Museum of Natural History. Anderson and Westneat experimented with a number of lever models to represent the most probable skull mechanics, and they discovered that the best fit was a four-bar linkage mechanism (see illustration). A four-bar linkage is a mechanical system composed on four rigid beams or 'cranks' connected at four rotation points. Two of the pivot points are the jaw joint, between quadrate and mandible (of course), but also the nuchal articulation, placed high and located between the cranial and thoracic portions of the head shield system. The main muscles involved in the jaw action are the mandibular adductors, running from skull to lower jaw, as in all vertebrates. In addition, to power the cranio-thoracic movement, are cranial depressor muscles that drop the head when they contract, and opposed by dorsally located epaxial muscles from the top of the head to the top of the thoracic/ shoulder shield. Ventrally were jaw depressor (=lowering) muscles running from the base of the lower jaw to the lower angle of the thoracic shield. These muscles would act as a rigid crank when under tension and facilitated an additional pair of rotational junctions in the four-bar linkage model at the front of the mandible and at the front of the ventral thoracic shield.

Anderson and Westneat then designed a computer simulation that reflected exact measurements of each of the four crank elements and the four pivot points. In this way, they had reduced a three-dimensional problem to a two-dimensional simulation. They modelled muscle contractions in increments of 0.5% up to 10% to explore relative movements of each portion of the head shield system, and then they modelled the forces that would be applied to an item of prey held between the shearing tooth plates.

They found that the jaws opened very fast, in a fraction a second, and this would have produced a rapid expansion phase similar to modern fishes that use suction during prey capture. On the other hand, the jaw closing muscles powered an extraordinarily strong bite, with an estimated maximal bite force of over 4400 N at the jaw tip and more than 5300 N at the rear dental plates, for a large individual (6 m in total length). This bite force capability is among the most powerful bites in animals (see Box 2.2), and it suggests placoderms were adapted to crack open any armoured vertebrate of the Devonian with forensic ease.

See a movie of *Dunkleosteus* at: http://animal.discovery.com/tv-shows/other/videos/animal-armageddon-dunkleosteus.htm.



Anatomy and biomechanical model of the armoured skull and thoracic region of *Dunkleosteus terrelli*. (a) Anatomy of *Dunkleosteus terrelli*. (b) Drawing of (a) showing the four rotational joints (open circles) forming the four-bar linkage that mediates skull and mandibular rotation. The lines of action of four muscles are shown, including two jaw openers (epaxialis and coracomandibularis) and two jaw closers (cranial depressor and two alternate reconstructions of the adductor mandibulae). (c) Four-bar linkage motion during opening driven by EP and CM muscles. (d) Vector diagrams of the biomechanics of feeding, showing jaw opening (right) and jaw closing (left). During jaw opening, the muscle input force vectors (epaxialis vector 1- EPv1) and coracomandibularis vector 1 (CMv1) cause cranial elevation (EPv2) and lower jaw depression (EPv3–4 via the linkage). Jaw closing mechanics are driven by force vectors of the cranial depressor (CDv1) and the adductor mandibulae, reconstructed in two configurations (AM1v1, AM2v1). Bite force is exerted by both lever and linkage force vectors if a prey item is caught between the anterior fangs (BF1 and BF2) or between the rear dental blades (BF3 and BF4). Scale, 20 cm. Specimen no. CM6090. Cleveland Museum of Natural History, Cleveland. See Colour plate 3.2. Source: Anderson and Westneat (2009). Reproduced with permission from The Paleontological Society.

Placoderms have figured in debates about the origins of teeth, whether this happened early or late in gnathostome evolution. For a long time, it was assumed that placoderms had no teeth, but when Smith and Johanson (2003) reported teeth, they claimed a separate origin of teeth in this clade and in the other gnathostomes. Arthrodire teeth are located inside the mouth, behind the main shearing bone plates at the edges of the jaws. Micro-CT study of the arthrodire *Compagopiscis* (Rücklin *et al.*, 2012) shows that its teeth were composed of dentine and bone and that there is a pulp cavity. Development of these teeth in the jaws differs from the structure and development of tooth-like structures on the dermal plates in *Compagopiscis* and other placoderms, but suggests nonetheless a single origin of teeth among gnathostomes, soon after the origin of jaws (on the assumption that placoderms are paraphyletic).

The new placoderm *Entelognathus*, from the Late Silurian of Yunnan, China (Zhu *et al.*, 2013) has suggested a major overhaul of our understanding of gnathostome phylogeny. It is classified as a basal gnathostome, but shows characters previously thought to have been unique to Osteichthyes, namely large dermal bones around the mouth (premaxilla, maxilla, dentary). In their phylogenetic analysis, Zhu *et al.* (2013) confirm that placoderms are a paraphyletic assemblage and that acanthodians are all on the stem to Chondrichthyes (see Boxes 3.4, 3.7).

3.5.3 Diverse placoderms

Acanthothoracids have a head shield rather like that of some early arthrodires. The plates were separate in juveniles, but appear to have fused in the adults.

Rhenanids have a body covering of small tesserae instead of the more typical large plates. *Gemuendina* from the Early Devonian of Germany (Figure 3.14(a)) looks superficially like a ray with its very flattened body, broad pectoral fins, and narrow whip-like tail, and it may have swum by wave-like undulations

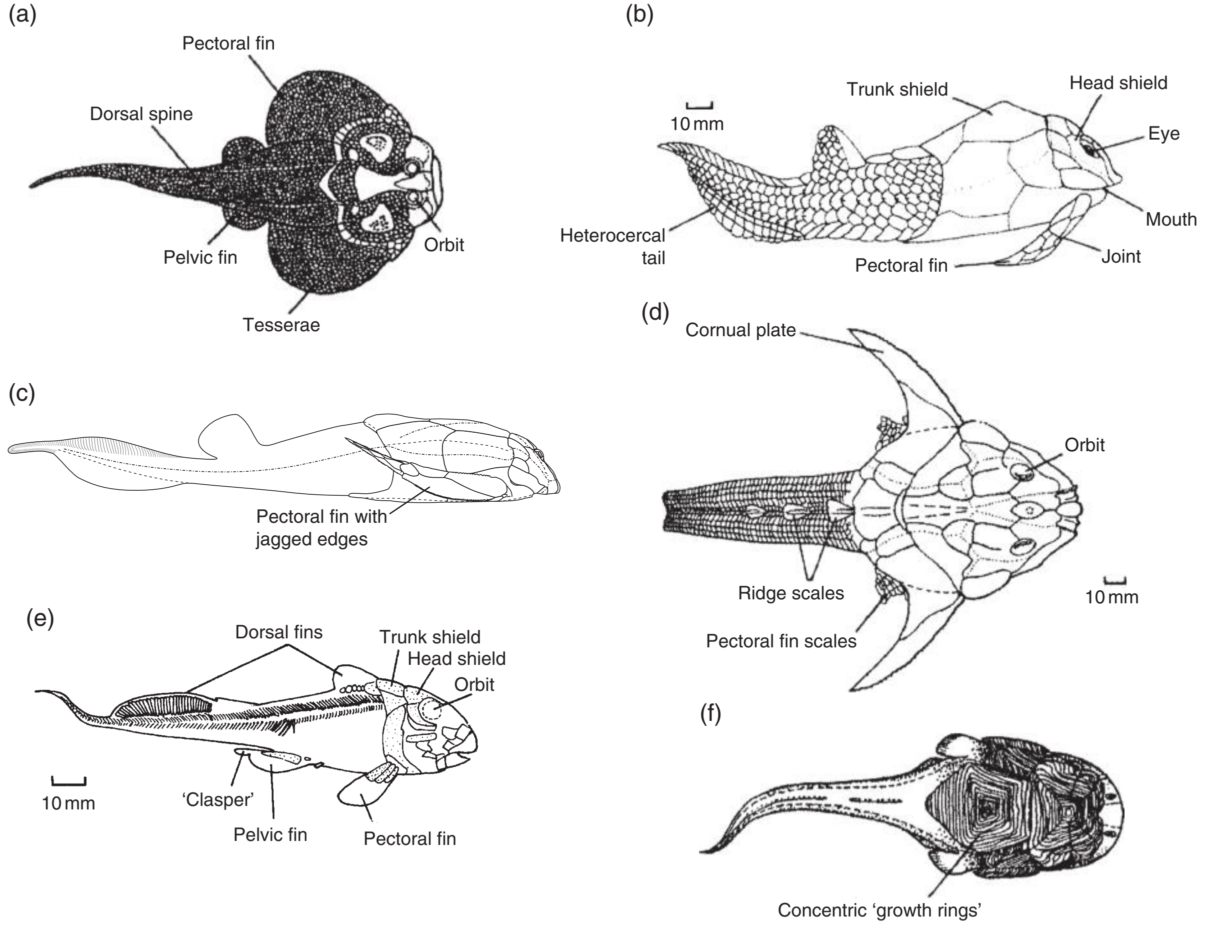


Figure 3.14 Diverse placoderms: (a) the rhenanid *Gemuendina* in dorsal view; (b, c) the antiarchs *Pterichthyodes* (b) and *Bothriolepis* (c) in lateral view; (d) the petalichthyid *Lunaspis* in dorsal view; (e) the ptyctodont *Ctenurella* in lateral view; (f) the phyllolepid *Phyllolepis* in dorsal view. Source: (a,d–f) Adapted from Moy-Thomas and Miles (1971). (b) Adapted from Hemmings (1978). (c) Adapted from Béchard *et al*. (2013).

of the pectoral fins. There are large bone plates in the midline, around the eyes, nostrils and mouth, and on the sides of the head, which are divided by a mosaic of small plates that extends on to the trunk and pectoral fins.

Antiarchs were a diverse group from the Silurian to Late Devonian that retained a heavy armour covering, and specialized in a bottom-dwelling mode of life, feeding by swallowing mud and extracting organic matter. *Pterichthyodes*, an early form (Figure 3.14(b)), has a high domed trunk shield made from a small number of large plates. The pectoral fin is entirely enclosed in bone, and it was movable against the trunk shield by a complex joint. There is also a second joint about halfway along the fin. This fin was probably of little use in swimming, and it may have served to shovel sand over the back of the animal so that it could bury itself.

The most successful placoderm was the antiarch *Bothriolepis* (Figure 3.14(c)), which diversified into more than 100 species in the Middle and Late Devonian of all parts of the world. *Bothriolepis* (Béchard *et al*., 2013) is a slender placoderm, with a lightly scaled tail region, bearing paired pelvic fins. The pectoral fins are slender and covered with armour plates, some of them with jagged tooth-like edges. Several specimens show evidence for lungs preserved inside the dermal armour. *Bothriolepis* probably grubbed in the mud for organic detritus, and it may have been able to survive in stagnant ponds by breathing air.

Petalichthyids are another small group of bottom-dwelling forms. *Lunaspis* from the Early Devonian of Europe (Figure 3.14(d)) is flattened, with a short trunk shield and long cornual plates. The anterior part of the head shield, around the eyes and nostrils, is covered by numerous tiny scales, as is the long trunk, and it appears to lack pelvic fins.

Ptyctodonts have reduced armour plating. They are generally small, usually less than 200 mm in length, with long whip-like tails, a long posterior dorsal fin, and a high anterior dorsal fin supported by a spine on the trunk shield. *Ctenurella* from the Late Devonian of Australia and elsewhere (Figure 3.14(e)) has much reduced armour. Some ptyctodonts have **claspers**, elongate elements associated with the pelvic fins that are assumed to have been involved with the process of internal fertilization. Claspers are seen in male chondrichthyans, but the structure of the ptyctodont clasper is different from that of a shark.

Finally, the phyllolepids (Long and Daeschler, 2013) have large bony heads and trunk shields made from plates with a very clear ornament of concentric ridges. *Phyllolepis* (Figure 3.14(f)) has a flattened body with a rounded snout and a long, narrow tail portion, although this is not well known from fossils.

3.6 CHONDRICHTHYES: THE FIRST SHARKS

The first chondrichthyans ('cartilaginous fishes'), distant ancestors of modern sharks and rays, may be indicated by isolated scales and teeth from the Late Ordovician and Silurian (Sansom *et al.*, 2001). The first definitive remains containing prismatic calcified cartilage (see below) date from the Early Devonian. The most extraordinary of these is *Doliodus* from Canada, previously known from only isolated remains and variously classified as an acanthodian or a chondrichthyan. More complete specimens (Miller *et al.*, 2003; Maisey *et al.*, 2014) show that *Doliodus* is indeed an early chondrichthyan, but it has paired pectoral fin-spines, previously unknown in cartilaginous fishes. This was early evidence that many acanthodians might be closely related to Chondrichthyes (see Box 3.4).

A later shark, *Cladoselache* from the Late Devonian of Ohio (Figure 3.15), reached a length of 2 m. The skin does not seem to have borne scales, although small multicusped tooth-like scales have been found on the edges of the fins, in the mouth cavity, and around the eye. Externally the tail fin is nearly symmetrical, but internally the notochord bends upwards into the dorsal lobe only (the **heterocercal** tail condition). There are two dorsal fins, one behind the head, and the other halfway down the body, and the anterior dorsal fin has a spine in front. There are two sets of paired fins, the pectoral and **pelvic** fins, each set approximately beneath one of the dorsal fins, and each associated with girdle elements of the skeleton.

Cladoselache was probably a fast swimmer, using sideways sweeps of its broad tail as the source of power, and its pectoral fins for steering and stabilization. As in modern sharks, the skeleton of *Cladoselache* is made from **calcified cartilage**, in other words, cartilage invested with some calcium phosphate, but not true bone. Calcified cartilage is known also in placoderms and several agnathans, but chondrichthyans appear to be unique in having **prismatic** calcified cartilage, arranged as small platelets or prisms. At one time, it was argued that chondrichthyans were 'primitive' because they had only cartilaginous skeletons, and that the bony dermal skeleton of osteichthyans evolved later. The discovery of the Silurian *Entelognathus* (see Section 3.5.2) confirms that extensive dermal ossification of the skull was likely the basal gnathostome condition, and that Chondrichthyes lost their dermal skull bones subsequently.

The major chondrichthyan lineages arose in the Devonian, but radiated in the subsequent Carboniferous Period, so this later history is discussed in more detail in Chapter 7.

3.7 ACANTHODIANS: THE 'SPINY SKINS'

Acanthodians (Denison, 1979) were generally small fishes, mostly less than 200 mm long. The first acanthodians date from the Late Ordovician, but they became abundant only in the Devonian. A few lines survived through the Carboniferous and only one into the Early Permian. Although long regarded as a clade, it is clear that 'acanthodians' form a grade, with various taxa initially (Brazeau, 2009; Davis *et al.*, 2012) distributed around the gnathostome phylogeny as stem gnathostomes, stem chondrichthyans, and stem osteichthyans, but now (Zhu *et al.*, 2013) seen as exclusively members of the stem lineage to Chondrichthyes: they are thus crucial in our understanding of the origins of the major jawed vertebrate clades (see Box 3.4).

Most acanthodians have slender bodies with one or two dorsal fins, an anal fin, and a heterocercal tail fin (Figure 3.16(a, b)). The pectoral and pelvic fins bear substantial spines along their anterior margins, and there may be as many as six pairs of spines along the belly of early forms. The other fins just noted (except the anal fin) are supported by a spine on the leading edge. The name 'acanthodian' refers to these liberal arrays of spines (*akanthos* = spine). The internal skeleton is rarely seen.

The acanthodian head is large (Figure 3.16(c)) and covered with light bony plates. Acanthodians have large eyes supported by a number of **sclerotic plates**, and many species have sensory canals running through the surfaces of the cranial bones. The shoulder girdle, or **scapulocoracoid**, is ossified in some forms, and is separate from the skull (Figure 3.16(c)), as in all

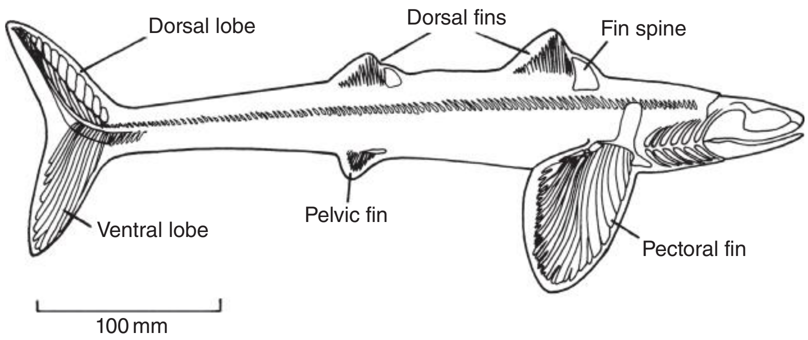


Figure 3.15 *Cladoselache*, one of the first sharks. Source: Adapted from Zittel (1932).

BOX 3.4 ACANTHODIANS AND GNATHOSTOME ORIGINS

Acanthodian fishes occupied Devonian to Early Permian seas, sometimes flitting in large shoals, and evading capture by virtue of their spiny coverings. They have long been classed as a single clade, partly because they all share the synapomorphy of an anal fin spine, but probably also because they were not placoderms, and could not be conveniently fitted into the clades Chondrichthyes and Osteichthyes. However, everything has changed thanks to recent discoveries and new phylogenetic studies.

The first concerns emerged thanks to discoveries from a remote locality in the Canadian Arctic, the so-called MOTH (= 'Man on the Hill') locality in North West Territories. Acanthodian and other Devonian fishes had been found there in the 1970s, but restudy has shown that taxa such as *Kathemacanthus*, *Obtusacanthus*, and *Lupopsyrus* have chondrichthyan-like scales (Hanke and David, 2012).

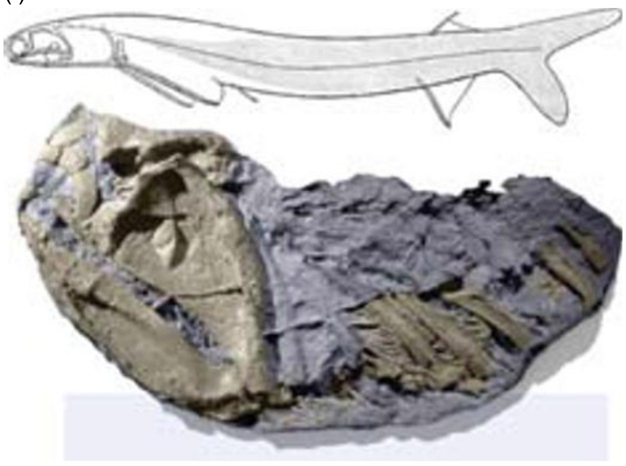
New phylogenetic studies (Brazeau, 2009; Davis *et al.*, 2012) initially revealed a much more complex story: two groups, the diplacanthids and climatiids were identified as stem gnathostomes; a series of genera from the Early Devonian of Canada were classed as stem chondrichthyans; and the acanthodids and ischnacanthids were retained as stem osteichthyans. The clade Acanthodii no longer exists!

Brazeau (2009) showed that palaeontologists had focused too much on the braincase of *Acanthodes*, which is very osteichthyan-like, but that the braincase of *Ptomacanthus* is radically different from either *Acanthodes* or any osteichthyan. So, there has either been massive convergence between different acanthodians and other taxa, or acanthodians are not a clade.

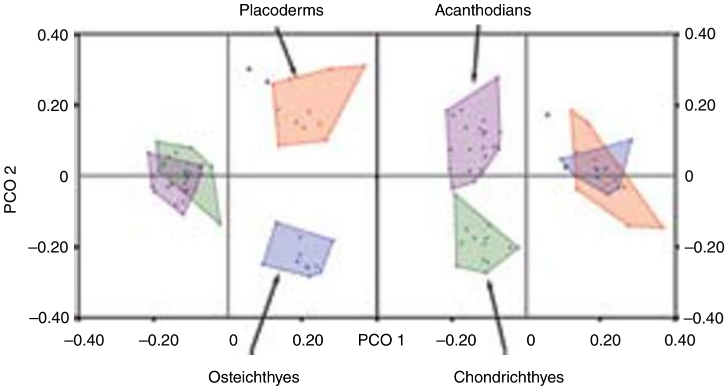
Davis *et al.* (2012) also showed that some acanthodians share resemblances with early sharks. Indeed, a principal coordinates analysis (illustration II) shows that, in terms of overall morphology, acanthodians form a coherent group, with acanthodians more similar to one another than to other gnathostome groups. However, cladistic analysis, focusing on new anatomical studies of the skull and braincase in particular, shows that these appearances are deceptive.

In the revised phylogenetic tree (illustration III), *Acanthodes* is a stem osteichthyan on the basis of some shared characters, notably a number of features of the shared narrow-based braincase, a deeply angled ventral margin on the scapula, a subcircular scapular process, and absence of prepectoral fin spines and of fin spines with nodes. The cladistic analyses are weakly supported (Davis *et al*., 2012), and indeed within a year, Zhu *et al*. (2013) had shown that it is most likely that **all** acanthodians lie on the stem to Chondrichthyes, forming a series of outgroups.

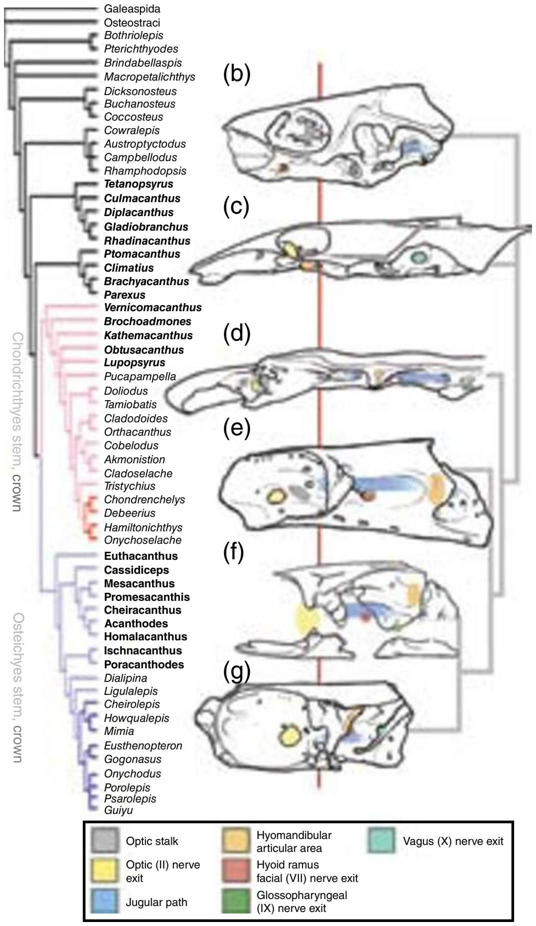
(I)



(II)



(III) (a)



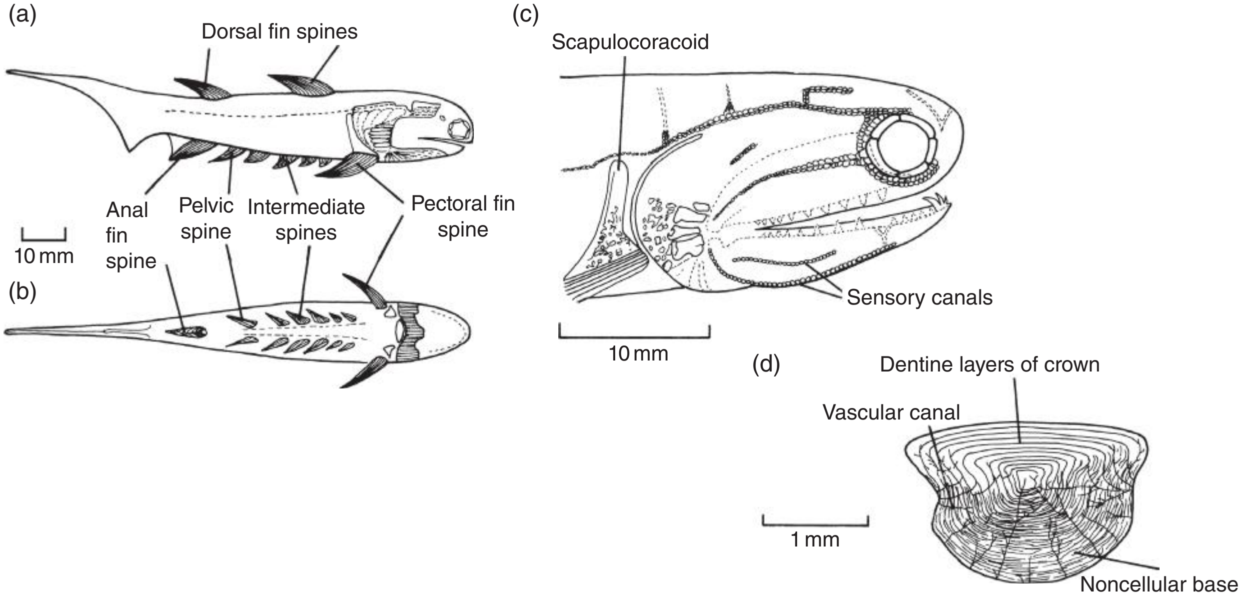


Figure 3.16 Acanthodian diversity and anatomy: (a) *Climatius* in lateral view; (b) *Euthacanthus* in ventral view, showing the fin spines; (c) head region of *Ischnacanthus* in lateral view; (d) single scale of *Acanthodes*. Source: Adapted from Moy-Thomas and Miles (1971).

gnathostomes, thus allowing greater freedom of movement than in some ostracoderms.

The body is covered with small closely fitting scales that are made from bone and dentine (Figure 3.16(d)). These show concentric lines that record the growth of the scale. It seems that young acanthodians had a fixed number of scales over most of the body, and each scale grew by addition of bone and dentine at the margins as the animal grew larger.

There is a great diversity of tooth types within acanthodians, including tooth whorls, placoderm-like dentitions, and series of tooth files that look similar to those of early chondrichthyans. Most acanthodiiforms lack teeth. This suggests a broad range of feeding modes in the different acanthodian subclades. Toothless forms probably fed on small food particles filtered from the water, whereas toothed forms may have taken larger prey. They had a wide gape and **gill rakers**, sharpened spikes in the throat region that are attached to the hyoid and branchial arches. One specimen has been found with a bony fish in its body cavity, presumably swallowed whole. The large eyes of acanthodians suggest that they lived in open deep water. Different groups occupied marine and fresh waters in the Devonian, and Carboniferous forms were predominantly freshwater. The fin spines and other spines may have had a primarily defensive function in making acanthodians unpleasant for larger fishes to swallow. Later forms, such as *Acanthodes*, seem to have been able to erect their pectoral spines, which would have caused them to stick in the gullet of a would-be predator. Perhaps this was a useful defensive measure, as seen in modern sticklebacks.

3.8 DEVONIAN ENVIRONMENTS

The early Palaeozoic world was very different from today, largely because of an entirely different continental layout. Oceans have come and gone, and continents have drifted from tropical regions to the north and south. Precise details of former continental positions (see Chapter 2) are less certain for the Palaeozoic than they are for the Mesozoic and Cenozoic, so **palaeogeographical** maps of the Silurian and Devonian worlds are controversial in some respects.

Understanding the acanthodians. (I) Whole-body reconstruction and specimen of *Acanthodes* (Natural History Museum, P4997), a peel from a natural mould of the anterior end, braincase, jaws, hyoid arch and gill arches, gill rays and rakers, and overlying skin with denticles. The extended array of gill apparatus behind the jaws and braincase looks particularly shark-like. (II) Principal coordinates analysis (PCO) of early gnathostome character data. PCO 1 (17.5% explained variance) is plotted on the horizontal axis and PCO 2 (13.7%; left) and PCO 3 (10.1%; right) on the vertical axes. The four traditionally named groups (placoderms in green, acanthodians in red, osteichthyans in blue, chondrichthyans in purple) cluster in distinct and non-overlapping regions on the first three PCO dimensions. The two black points represent outgroups, the Galeaspida and Osteostraci. (III) Results of phylogenetic analysis, and early gnathostome braincases preceding conditions in modern jawed vertebrates. a, Strict consensus of the 512 shortest cladograms; bold font signifies acanthodian genera; black branches indicate the gnathostome stem group; coloured branches indicate the crown clades. b–g, Braincases in lateral view, anterior to right; simplified cladogram (grey) on left summarizes interrelationships of illustrated taxa; vertical bar aligns braincases at level of pituitary vein canal. b–d, Placoderm-grade taxa: b, *Brindabellaspis*; c, *Macropetalichthys*; d, *Dicksonosteus*. e–g, Crown group gnathostomes: e, *Cladodoides* (Chondrichthyes); f, *Acanthodes* (stem Osteichthyes); g, *Mimia* (crown Osteichthyes). Source: Adapted from Davis *et al*. (2012).

3.8.1 Siluro-Devonian faunal provinces

It is possible to distinguish **faunal provinces** among early fishes (Žigaitė and Blieck, 2013). For example, there were as many as eight distinctive fish assemblages in the Silurian (Figure 3.17(a)). These are located around the margins of the supercontinent that straddled the Equator, and they show distinctive sets of genera and species. The geographic separation between the Canadian and Siberian provinces, on the northern margins of the supercontinent from the Appalachian to Russian provinces on the south are clear. Only one province, from South China, is identified in the southern landmass, a precursor of Gondwana (see Section 2.3.2).

The Silurian fish faunas were kept apart by barriers to mixing, major land masses and wide oceans. Many of these barriers disappeared in the Early Devonian, and a single thelodont assemblage, for example, the *Turinia* fauna, occurs nearly worldwide (Figure 3.17(b)). Most Early Devonian faunal provinces were still equatorial in distribution, except for a far southern, South American, province, located in colder waters. One remarkable change was the emergence of a North Atlantic Province in the Devonian, with shared genera of agnathans and placoderms from North America to western Europe. This followed complete closure of the Iapetus Ocean, which had separated a northern landmass incorporating Canada, Scotland and Baltic regions from a southern landmass comprising the United States, England and Wales, and central Europe.

A major trend in Devonian fish evolution was a move from regional or endemic faunas in the Early Devonian to more or less worldwide occurrence by the Late Devonian. Some still showed geographic endemism, for example the galeaspids, which are found only in Vietnam and South China, and the camuropiscid arthrodires and others, which are restricted to Australia.

3.8.2 Siluro-Devonian environments

Silurian and Devonian seas and fresh waters were warm, and fish fossil localities are clustered in the equatorial and tropical belt (Figure 3.17). Important environmental changes took place

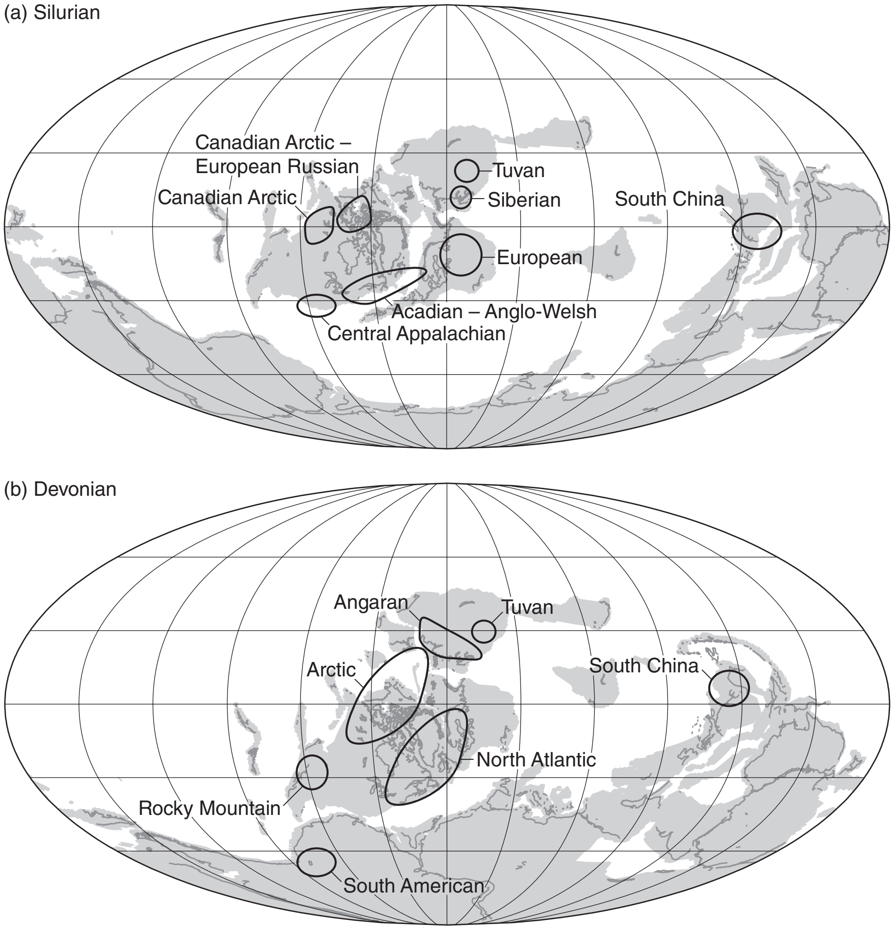


Figure 3.17 Distributions of vertebrates in the Silurian and Early Devonian. (a) Silurian base map, showing locations of major continents, and eight faunal provinces of fishes. (b) Early Devonian base map, showing agnathan vertebrate provinces. Source: Adapted from Scotese (2002), Alroy (2013), and Žigaitė and Blieck (2013).

on land during the Silurian and Devonian, and these affected vertebrate evolution. The first land plants appeared in the Middle to Late Silurian. They were small and reed-like, and probably grew around ponds and lakes with their tuberous roots partly in the water. There are some exceptional fossil localities of Late Silurian and Early Devonian age that provide windows into the first terrestrial land plants and animals, but such localities are rare. It was only by the Middle and Late Devonian that large horsetails and scale trees (lycopods) became quite common.

The first land animals (Garwood and Edgecombe, 2011) were scorpions, millipedes and spider-like arthropods, all of which could live in water and on land. They first appeared in the Late Silurian, and they crept ashore presumably to exploit the new green plants around the waters' edge. In the Early Devonian, fossils of spiders, mites and wingless insects have been found, and the diversity of insects increased in the Late Devonian. These plants and animals provided new sources of food for animals that could exploit the shallow waters of the lakes and the land around the edges.

Early fish evolution has been studied most on the Euramerican continent, sometimes called the Old Red Sandstone continent (ORC), because the Devonian rocks of Scotland, first studied in the 1820s (see Box 3.5), were termed the Old Red Sandstone. This continent was a large tropical landmass, characterized by hot, arid climates in its core, and monsoonal climates around the edges. The land surface was probably bare rock with limited soil cover, as very few plants ventured far from the watersides. Periodic rainfall would have eroded the interior of the ORC at a prodigious rate, and transported the debris down rivers in flash floods to the margins. Fishes are found in rivers, freshwater lakes and marine lagoons around the margins of the ORC, and there is some uncertainty about how much of early fish evolution took place in the sea, and how much in fresh waters.

BOX 3.5 OLD RED SANDSTONE FISHES OF SCOTLAND

Some of the most prolific collections of Devonian jawless fishes, placoderms, acanthodians and lobe-finned fishes, have come from the Old Red Sandstone (ORS) of the Orcadian Lake, a large subtropical lake in the north of Scotland that covered much of Caithness, the Moray Firth, Orkney and Shetland. This lake lay on the southern margins of the Old Red Continent, and sediment was fed in by erosion of the uplands round about (see illustration I). The region was affected also by annual seasons of dramatic rainfall.

Lake levels rose and fell as a result of the seasonal wet and dry climatic conditions, some following annual cycles, others longer-term Milankovitch cycles of 20,000 and 100,000 years. The fluctuations in lake level affected the oxygen content and salinity of the water. The sediments frequently occur in repeated cycles that occupy thicknesses of about 10 m of the rock column, and repeat through a total thickness of 2–4 km of rock (Trewin and Davidson, 1999; Stephenson *et al*., 2006). In places, annual varves, generally less than 1 mm thick, may be detected.

There has been some debate about whether these Old Red lakes were permanent or ephemeral. Aeolian (wind-blown) layers are found at points through the ORS cycle, indicating dry sand blown across the lakes. Rogers and Astin (2009) have argued that aeolian sands dominate, and that the Old Red lakes should be compared with Lake Eyre in Australia today, an ephemeral lake that fills and dries out at intervals, and may be dry for 90% of the time. This radical suggestion requires reinterpretation of sedimentary structures, and traditionalists argue that the abundance of ORS fish beds is hard to square with lake systems that are dry for most of the year.

Fossil fishes occur in the Scottish ORS both as scattered fragments and in great concentrations within 'fish beds'. Mortality horizons, single layers containing high concentrations of fish carcasses, formed during deoxygenation events that may have occurred every 10 years or so when the lake was deepest. These repeated mortality events probably relate to algal blooms, when decaying algae removed oxygen from the water (Stephenson *et al*., 2006). Other explanations have been that severe storms stirred up deep anoxic waters to the surface, rapid changes in salinity and cold shock. The carcasses floated for some time near the surface, buoyed up by gases of decay. After a few days the gas escaped, possibly by rupturing the body walls, and the carcasses fell to the anoxic lake-floor where they were buried by fine sediments. This process yields extensive beds of fish remains representing several species, and the carcasses are often in good condition (see illustration II) because they have not been scavenged, and because of the low-energy bottom conditions.

The ORS food chains are based on lakeside plants (mosses, reedy horsetails and scale trees) and phytoplankton, which were eaten by shrimps and molluscs, which in turn were eaten by lobefins such as *Dipterus* (see Figure 3.20) and *Osteolepis* (see Figure 3.23(b,c)). There is also evidence for small arthropods around the lake margins, and these may have been a source of food for these fishes as well. The smaller fishes were preyed on by carnivorous forms such as *Coccosteus* (see Figure 3.13) and the bony fish *Cheirolepis* (see Figure 3.19) that have been found with remains of acanthodians and of *Dipterus* in their stomachs. The heavier placoderms such as *Pterichthyodes* (see Figure 3.14(b)) scavenged for organic matter – decaying plant and animal remains – on the shallower oxygenated parts of the lake bed. The top carnivore was the lobefin *Glyptolepis,* which reached lengths of over 1 m. It may have been a lurking predator like the modern pike, hiding among water plants and launching itself rapidly at passing prey.

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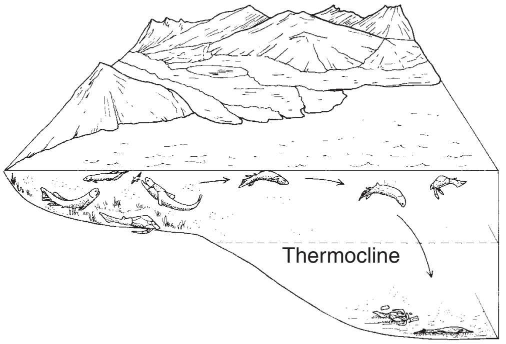
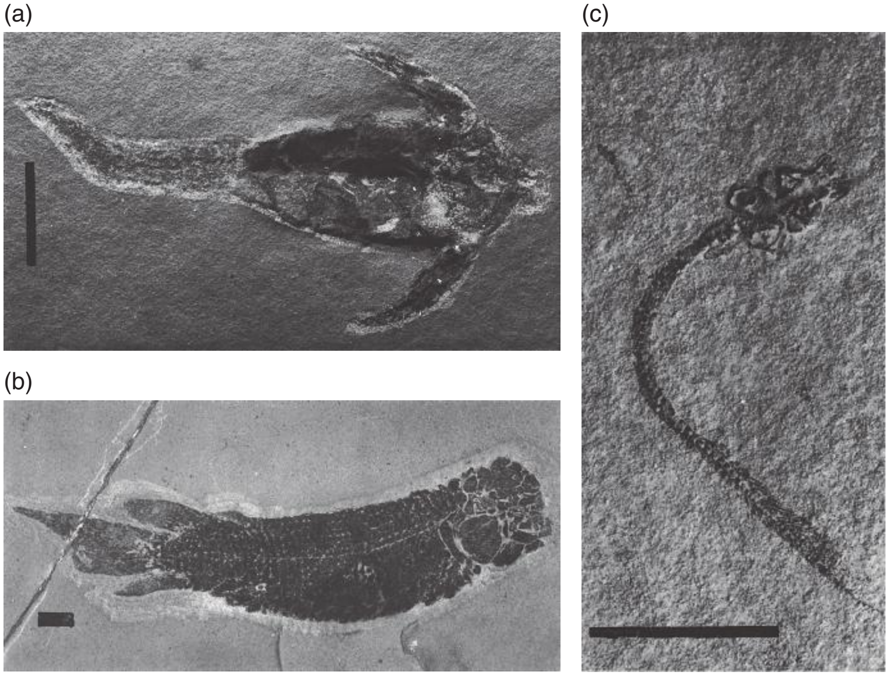


(I) The Old Red Sandstone lakes of the north of Scotland: topographic sketch showing sediment source from alluvial fans and plains derived from erosion of the uplands, and the cycle of life, death, and fossilization of the fish fauna; from left to right: fishes living in shallow areas of the lake, carcasses float out to the middle of the lake, and sink into the cold anoxic conditions beneath the thermocline where they are preserved in laminated muds on the deep lake-floor. Source: Adapted from Trewin (1985).



(II) Typical ORS fishes from Achanarras Quarry, Caithness: (a) juvenile *Pterichthyodes*; (b) *Dipterus*, showing slight separation of head elements on fossilization; (c) *Palaeospondylus*, a possible larval lungfish. Scales: 100 mm rulers in (a) and (b); scale bars are 10 mm in (c). Source: N. Trewin, formerly, University of Aberdeen, Aberdeen, UK. Reproduced with permission.

3.9 OSTEICHTHYES: THE BONY FISHES

Bony fishes, Osteichthyes, are distinguished from all other vertebrates so far considered by a number of characters (Friedman and Brazeau, 2010), including endochondral bone (see Section 3.2), maxillary and dentary tooth-bearing bones with the teeth fused into the bone, gular plates (medial bones between the jaws), a skull roof that consists of large dermal plates, as well as modified body scales with a peg-and-socket articulation.

Osteichthyes is divided into two clades, Actinopterygii and Sarcopterygii. The earliest fossil actinopterygians are Early Devonian, whereas the first sarcopterygians are Late Silurian. These two clades are distinguished readily by their fins (Figure 3.18) – actinopterygians have ‘ray fins’ that are supported by a series of narrow cartilaginous or bony rods called radials, whereas sarcopterygians have fleshy ‘lobe fins’ supported by a single basal bone and with muscles that can modify the posture of the fin. These distinctions were not clear among the first osteichthyans, but new specimens

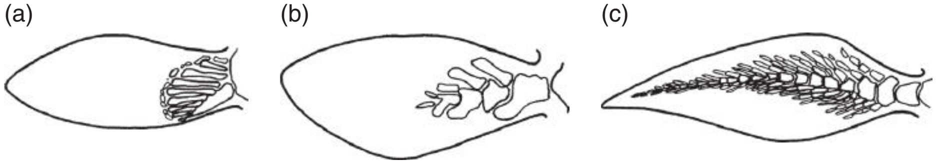


Figure 3.18 The fins of (a) an actinopterygian, *Amia*, to show the simple basal skeleton, (b) the lobefin *Eusthenopteron*, a tristichopterid, and (c) the lobefin *Neoceratodus*, a lungfish, to show the more complex skeleton that supports a muscular lobe in the middle of the fin. Source: Adapted from Zittel (1932).

from China shed some light on the phylogeny of the group (see Box 3.6).

3.9.1 Devonian actinopterygians

The oldest actinopterygians, represented by scales, are Early Devonian in age, but the group began to diversify only in the Late Devonian. An early form is *Cheirolepis* from the Middle Devonian of Scotland, typically 250 mm in length (Pearson and Westoll, 1979). The body is slender and elongate (Figure 3.19(a)), and the tail is strongly heterocercal, although the tail fin beneath makes it nearly symmetrical. There are large triangular dorsal and anal fins and paired pectoral and pelvic fins.

The body is covered with small overlapping lozenge-shaped scales (Figure 3.19(b)) that articulate with each other by means of a peg and socket arrangement in the tail region. The scales are arranged in sweeping diagonal rows that run backwards and downwards. There are larger ridge scales on the dorsal edge of the tail that act as a cutwater. The fin rays (**actinotrichia**) are covered with jointed dermal bones, the **lepidotrichia**. These provide a covering for the fin and they also stiffen it in comparison with sharks, for example, which have only actinotrichia. The scales are composed of layers of bone, dentine, and an enamel-like substance on the outside.

The skull is relatively heavy, with a bony braincase and palatal elements inside, and an outer bony box made from numerous thin dermal bone plates. There is a large eye and two nostrils on each side, and a broad mouth lined with irregularly spaced sharp teeth (Figure 3.19(c–e)). The teeth are borne on three bones around the edges of the mouth, the **maxilla** and **premaxilla** in the skull, and the **dentary** in the lower jaw, and these are the main tooth-bearing elements in subsequent vertebrates. The palatoquadrate is inside the maxilla, and is covered by palatal bones bearing rows of teeth. At the back of the skull are the outer dermal elements of the shoulder girdle, attached to the gill region.

The head skeleton of *Cheirolepis* is **kinetic**, that is, composed of several mobile units that can move against each other (see Figure 3.19(d,e)). When the jaws open, a very wide gape is possible because the five units move apart. The skull roof moves back, the gill region expands and moves back and down, and the shoulder girdle moves downwards.

Cheirolepis was a fast-swimming predator that presumably used its large eyes in hunting in murky water (Pearson and Westoll, 1979). Its great gape would have enabled *Cheirolepis* to engulf prey up to two-thirds of its own length; such prey would include the abundant acanthodians, and small lobefins and placoderms found in the same beds. The sharp teeth of *Cheirolepis* might not seem suitable for cracking open placoderms, but there were denticles on the palatal bones that might have been capable of moderate crushing activity.

Cheirolepis was capable of powerful and prolonged swimming using sideways beats of its tail region to produce thrust. It used its pectoral fins for steering, but these were not highly mobile, and *Cheirolepis* was probably rather clumsy when trying to turn rapidly. The paired fins also functioned to prevent rolling.

Devonian actinopterygians such as *Cheirolepis* are known from all parts of the world, but only some 15 genera have been found so far. The actinopterygians radiated dramatically in the Carboniferous and later, and they are the dominant fishes in the seas today (see Chapter 7).

3.9.2 Dipnomorpha: the lungfishes

The Sarcopterygii were a more diverse group in the Devonian than the Actinopterygii, although sarcopterygian fishes have since become much less diverse (Sarcopterygii of course includes all tetrapods). Sarcopterygians all have muscular, lobed paired fins with bony internal skeletons (Figure 3.18(c)), as well as a highly kinetic skull (see Section 3.9.4). There are two living sarcopterygian clades, the lungfishes (Dipnoi) and coelacanths (Actinistia), as well as numerous extinct clades, the oldest being known from the Late Silurian. Relationships among living and extinct sarcopterygians, and their relationships to early osteichthyans have been controversial (see Box 3.7).

The lungfishes (Bemis *et al.*, 1986; Jørgensen and Joss, 2010) were particularly diverse in the Devonian, but they have dwindled in importance ever since, leaving only three genera still living. Lungfishes more widely, the Dipnomorpha, arose in the Early Devonian, with forms such as *Youngolepis* and *Diabolepis* from China and *Powichthys* from the Canadian Arctic and Spitsbergen. *Dipterus* from the Middle Devonian of Scotland (Figure 3.20) has a long body, as in the tristichopterids, but the fins and skull bones are very different. The fins are pointed, with long central lobes supported, in the paired fins, by a rather symmetrical array of bones. The tail is heterocercal and bears a narrow fin beneath.

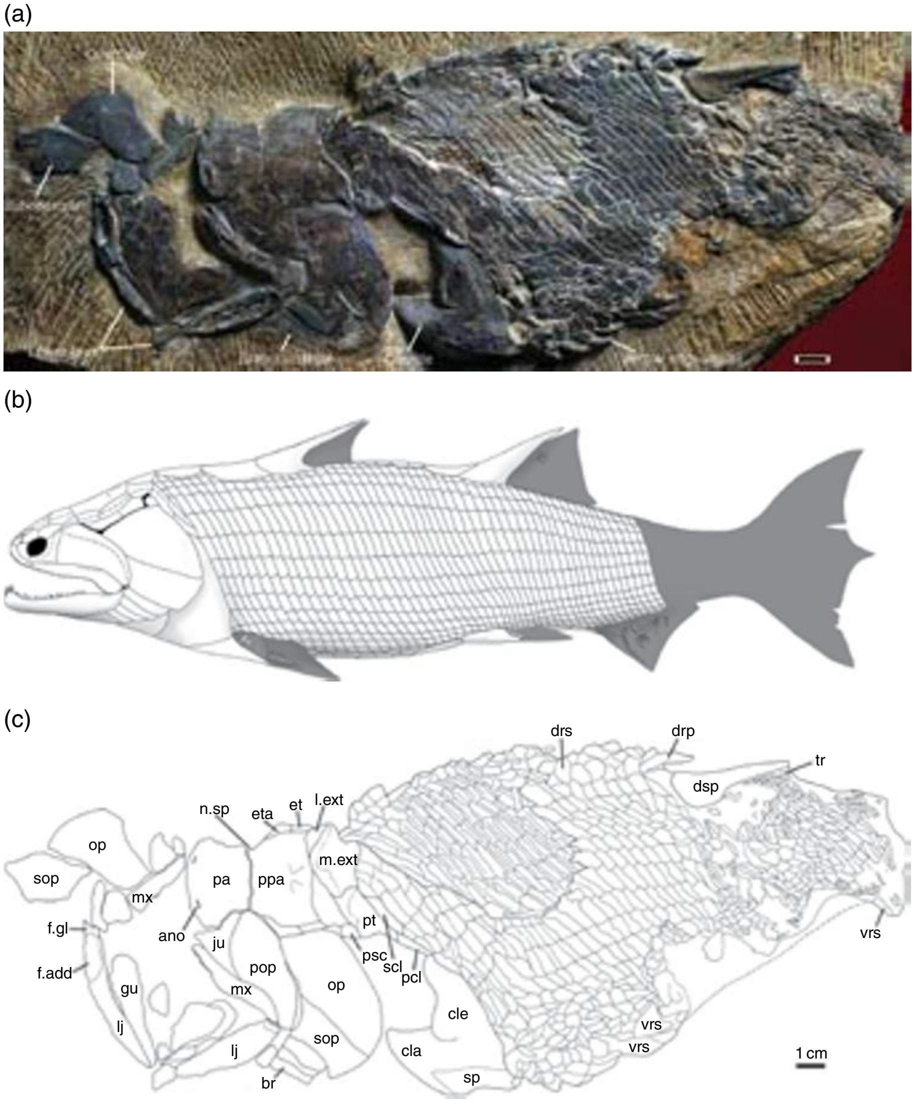
BOX 3.6 *GUIYU* AND THE ORIGIN OF BONY FISHES

Until recently, the actinopterygian and sarcopterygian fishes seemed to be quite distinct clades, but new fossils from the Late Silurian and Early Devonian of China are shedding new light on the basal split between these two clades. *Guiyu* from the Kuanti Formation of Yunnan Province (Zhu *et al.*, 2009) is a remarkable fossil, the first reasonably complete bony fish from the Silurian, a record previously represented mainly by isolated scales and teeth. The new specimen is similar to *Psarolepis*, previously described from the Early Devonian of China, and is classified at the base of Sarcopterygii, even though it shares some apparently actinopterygian-like characters.

This 33-cm-long fish (see illustration) has a braincase divided into separate front and rear units, and like *Psarolepis*, the cheek bones resemble those of early actinopterygians. It has some primitive features not seen before in osteichthyans, such as a single, midline, toothed bone between the premaxillae, perhaps equivalent to the prerostral or premedian plate of placoderms. *Guiyu* has numerous rows of small teeth, as well as some large tusks on the coronoid bones.

There are also some characters that are not seen in later bony fishes: *Guiyu* and *Psarolepis* have a huge pectoral spine extending back from the shoulder girdle, and there is a median spine in the midline behind the head (see illustration). A pectoral spine like this is known in some placoderms and in acanthodians, as well as in one early chondrichthyan, and the median spine is known in sharks and acanthodians, but neither has been seen in later osteichthyans. Beside these primitive features, *Guiyu* has derived forms of scales, showing an anterodorsal process, and this might be a synapomorphy of crown osteichthyans rather than the actinopterygians (Zhu *et al*., 2009).

In earlier studies, it had been hard to determine the phylogenetic position of *Psarolepis*, whether at the base of actinopterygians or sarcopterygians, such was its mosaic of characters. However, the new material of *Guiyu* helps determine that these early bony fishes from China are correctly placed at the base of Sarcopterygii, forming a small subclade from China



The early osteichthyan *Guiyu* from the Late Silurian of China: (a) one of the specimens, showing parts of the skull and body scalation; (b) whole-body restoration; (c) interpretation of the anatomy of the preserved specimen (a). Source: Zhu *et al*. (2009). Reproduced with permission from Nature Publishing Group.

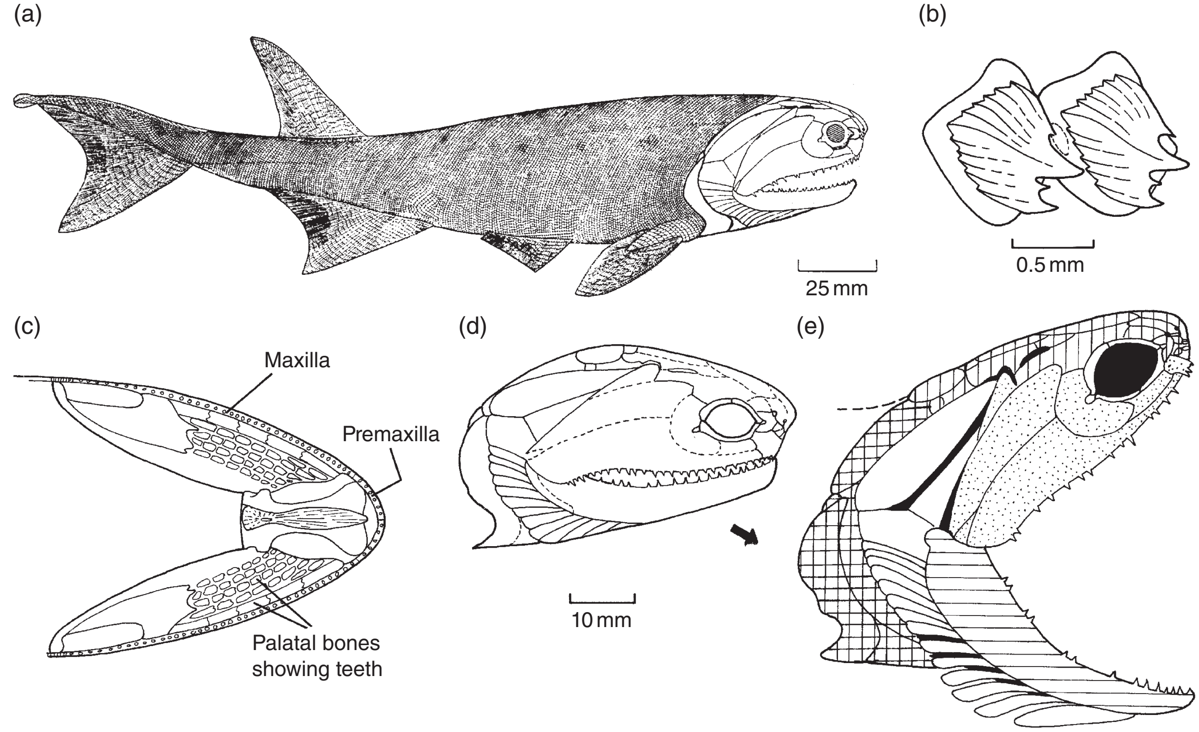


Figure 3.19 The Middle Devonian bony fish *Cheirolepis*: (a) reconstruction of the body in lateral view; (b) two trunk scales; (c) ventral view of the palate showing the teeth; (d, e) opening and closing of the jaws, showing the five major mobile units, as described in the text. Source: Adapted from Pearson and Westoll (1979).

BOX 3.7 EARLY GNATHOSTOME RELATIONSHIPS

Gnathostomes arose early in the Palaeozoic from among the jawless fishes (see Box 3.1). Relationships of clades within Gnathostomes, and especially within Osteichthyes, have long been debated. This is not surprising because Osteichthyes comprise the bulk of modern vertebrates, including all the living fishes except sharks and lampreys, as well as all tetrapods. Molecular phylogenetic studies can go a certain distance in exploring the relationships between actinopterygians, coelacanths, lungfishes, and tetrapods, but of course such studies cannot place the plethora of extinct clades. The expectation is, of course, that the last three group as Sarcopterygii to the exclusion of Actinopterygii, but relationships between coelacanths, lungfishes, and tetrapods are debated.

It has been surprisingly difficult to resolve the three-clade problem within Sarcopterygii. Most analyses support lungfish as a sister group of tetrapods (e.g. Venkatesh *et al*., 2001), but others found a pairing of coelacanths + tetrapods, or even coelacanths + lungfishes. With mitochondrial DNA, the traditional lungfish-tetrapod pairing is generally found with single genes, but the coelacanth-tetrapod pairing was found with 12S and 16S rRNA genes, and the coelacanth-lungfish sister relationship from some single-gene and whole genome analyses (Meyer and Zardoya, 2003). Shan and Gras (2009) found the lungfish-coelacanth pairing in an analysis of 43 nuclear protein-encoding genes. However, a more extensive study (Chen *et al*., 2012), based on Bayesian analysis of transcriptomes, expressed sequence tags, and whole genome sequences, found the traditional pattern of relationships across gnathostomes, namely (coelacanths (lungfishes + tetrapods)), as well as traditional relationships of actinopterygians and chondrichthyans. This is confirmed from study of the whole genome of the coelacanth (Amemiya *et al*., 2013).

Recent phylogenetic analyses of new and older fossil fishes from the Late Silurian and Devonian (e.g. Swartz, 2009; Zhu *et* al., 2009, 2013; Jeffery, 2012; Lu *et al*., 2012) confirm the (coelacanth (lungfish + tetrapods)) phylogenetic pattern, and add considerable detail, especially with new forms from the Late Silurian and Early Devonian of China (see Box 3.6) that provide examples of early, stem actinopterygians and sarcopterygians. The consensus cladogram (see illustration) shows rapid splitting of the major sarcopterygian clades in the Late Silurian and Early Devonian, as long predicted, and the new fossil finds and renewed phylogenetic study has resolved a previously poorly understood part of vertebrate phylogeny on the route to tetrapods (see Box 4.1).

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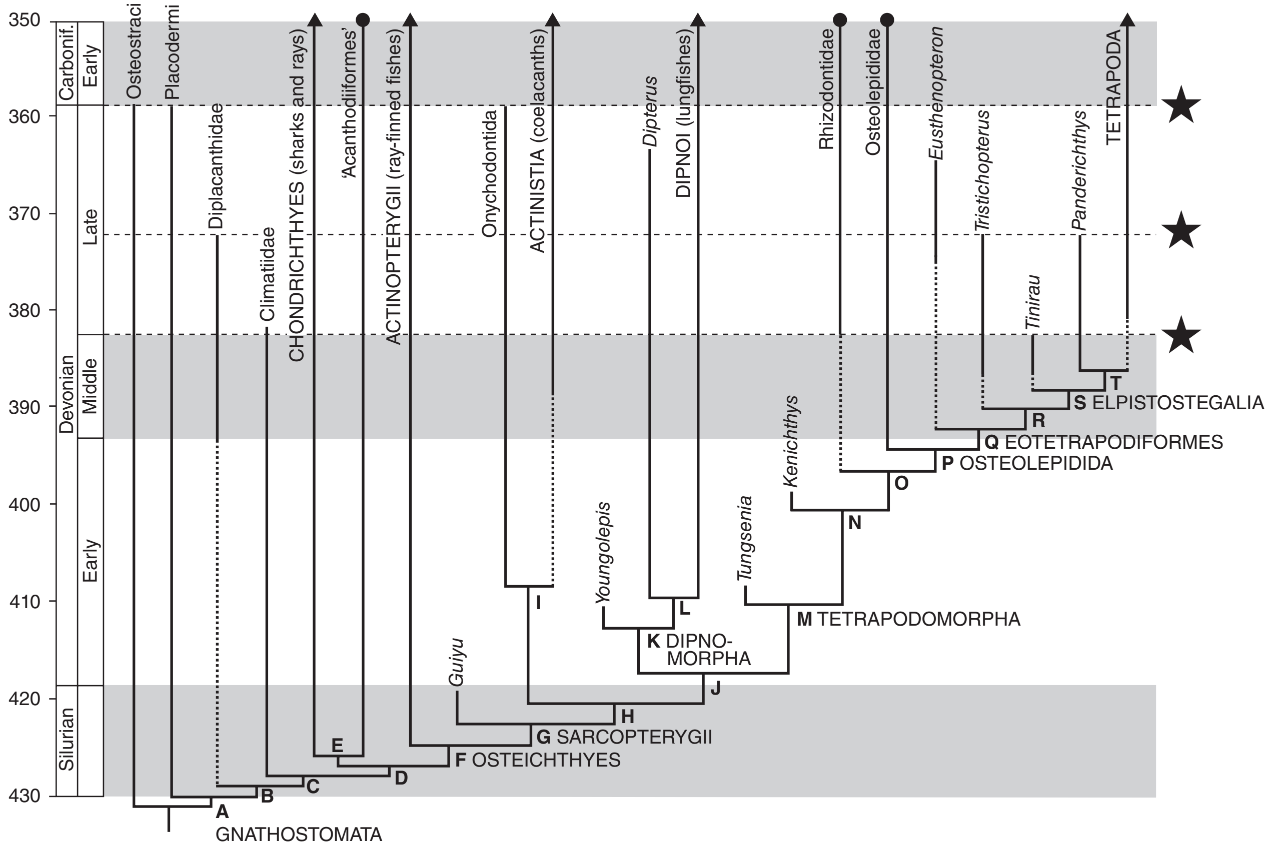

Phylogeny of gnathostomes (jawed vertebrates), concentrating on early forms ('acanthodians') and sarcopterygians. Refer to Box 3.1 for early vertebrates, Box 7.2 for chondrichthyans, Fig. 7.7 for actinopterygians, and Box 4.1 for early tetrapods. Synapomorphies from Maisey, 1986; Donoghue *et al*., 2000; Brazeau, 2009; Davis *et al*., 2012; Swartz, 2012; Zhu *et al*., 2013: **A GNATHOSTOMATA**, jaws composed of a primary upper (palatoquadrate) and lower (Meckel's cartilage) jaw component, supporting hyoid arch (not in placoderms), separate endoskeletal pectoral and pelvic girdles and fin skeletons, basals and radials supporting dorsal and anal fins, horizontal semicircular canal; **B**, flank scales in oblique rows or hexagonal/ rhombic packing, dermal skull roof consists of undifferentiated plates, opercular ossification absent, dermal shoulder girdle forms a complete ring around the trunk, pectoral median dorsal plate, anal fin spine, fin spines with ridges, anal fin; **C**, bony hyoidean gill cover, dermal jaw plates on biting surfaces of jaw cartilages, large otic processes of the palatoquadrate, intermediate fin spines, prepectoral fin spines; **D**, teeth erupt from a dental lamina, fusion of nasal capsule to the rest of the chondrocranium, postorbital connection between palatoquadrate and braincase, internal rectus eye muscle inserts in a posterior position in the orbits, superior and inferior oblique eye muscle with an anterior insertion in the orbit, branchiostegal ossifications narrow and ribbon-like, extended prehypophyseal portion of sphenoid, short otico-occipital region of braincase, procoracoid mineralization; **E**, skull bone reduction; body scales with a neck and bulging base; skull roof comprising undifferentiated plates or tesserae; **F OSTEICHTHYES**, body scales with peg-and-socket articulation, body scale profile flattened, body scales with bulging base absent, dermal skull roof consists of large dermal plates, gular plates, teeth ankylosed in dermal bones, maxillary and dentary tooth-bearing bones, anal fin spine absent, paired fin spines absent; **G SARCOPTERYGII (including Tetrapoda)**, muscular pectoral and pelvic limbs with substantial limb bones, true enamel on teeth, sclerotic ring composed of more than four plates, tectal bone in skull, one or more squamosals, splenial in lower jaw, triradiate scapulocoracoid; **H**, extratemporal present, squamosal present, preopercular does not contact maxilla or postorbital, tusk on vomer, double-headed hyomandibular, single bone (humerus) in pectoral fin contacts girdle, folded enamel and dentine (plicidentine) in teeth; **I**, pineal foramen, coronoid fangs absent, branchiostegal rays absent, median gular absent, interclavicle absent, scales round; **J**, basipterygoid process developed as a broad platform, posterior expansion of maxilla, posterodorsal process of maxilla, infraorbital canal follows premaxillary suture, premaxilla bears no canals, sensory canal or pit line on maxilla, dorsal end of cleithrum broad and rounded, ascending process of clavicle wraps round anterior edge of cleithrum, triradiate scapulocoracoid; **K DIPNOMORPHA**, anterior margin of parietal slightly posterior to orbits, pineal foramen absent, pineal eminence, dermal intracranial joint, parasymphysial dental plate absent, three coronoids, enamel lining of pore canals; **L**, posterior nostril palatal, paired bones anterior to parietals, pterygoids articulate with each other, premaxilla absent, marginal teeth on dentary, ethmoid commissure absent, anterior and middle pitlines in lower jaw; **M TETRAPODOMORPHA**, parasymphysial tooth whorl absent, anterior mandibular (precoronoid) fossa, contact between otic and supraorbital canals; **N**, parasphenoid slender and splint-shaped, lateral sides of parasphenoid converge anteriorly; **O**, one pair of external nostrils, parietals surround a pareital foramen or eminence, premaxilla is canal-bearing, tuberculate ornament, round body scales, loss of cosmine; **P OSTEOLEPIDIDA**, large median postrostral, spiracular notch a narrow groove, exposed anocleithrum, basal lepidotrichial segments not elongate; **Q EOTETRAPODIFORMES**, long posterior process on vomers, overlap of vomers and parasphenoid, posterior margin of tabular level with posterior margin of postparietals, contact margin for clavicle on cleithrum strongly concave; **R**, ethmoid width less than 50% length, ethmosphenoid much longer than otoccipital, posterior coronoid significantly longer than middle coronoid; **S ELPISTOSTEGALIA**, one pair of dentary fangs, posterior coronoid one-third longer than more anterior coronoids, organized tooth row on posterior coronoid, posterodorsal maxillary process weak/absent, pineal foramen posterior to orbits, height/width ratio of glenoid fossa is 40–50%, highly reduced postaxial process on fibula; **T**, prearticular contacts angular edge-to-edge, median postrostral absent, anterior nostril at edge of mouth, jugal-quadratujugal contact, frontal present, scapulocracoid is a large plate pierced by a coracoid foramen, coracoid plate, lateral component to glenoid orientation, rhomboid scales. Abbreviation: Carbonif, Carboniferous. Dashed lines and star symbols indicate extinction events.

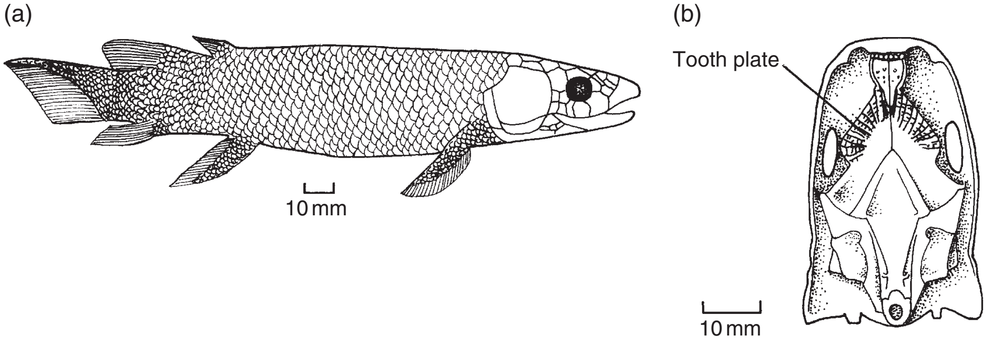

Figure 3.20 The Devonian lungfish *Dipterus*: (a) in lateral view, and (b) ventral view of the palate, showing the tooth plates. Source: Adapted from Moy-Thomas and Miles (1971).

The skull of *Dipterus* has a complex array of small bones around the large eyes and mouth. There are no teeth on the margins of the jaws as in other bony fishes, only a pair of large dentine-covered grinding plates in the middle of the palate (Figure 3.20(b)), and a scattering of smaller tooth-like structures in front. These paired plates are typical of later lungfishes and indicate a crushing function for feeding on tough and hard food.

Several lineages of lungfishes appeared in fresh waters in the Carboniferous, and two continued into the Mesozoic and Cenozoic. Many changes took place over this time: elaboration of the crushing tooth plates, and the development of a special hypermineralized dentine, all of which increased the crushing power of the jaws. The body shape changed too after the Devonian, becoming more symmetrical, and the tail also became symmetrical above and below the body.

The three genera of living lungfishes (Figure 3.21) have reduced the bony parts of their skeletons. The braincase and parts of the backbone remain cartilaginous, and the outer skull bones are reduced in number and weight. The Australian lungfish *Neoceratodus* is deep-bodied and has broad pectoral and pelvic fins, whereas the South American *Lepidosiren* and the African *Protopterus* have stout, muscular, eel-like bodies and very slender, elongate paired fins.

Modern lungfishes, as their name suggests, have lungs as well as gills. However, the name is misleading because all osteichthyans have lungs of some sort, even if these are modified into a swim bladder in most actinopterygians (see Section 7.4.4); presumably many Palaeozoic osteichthyans apart from dipnomorphs could breathe air with their lungs as well. Dipnoans today use the lungs for breathing air when the pools they inhabit become stagnant. Indeed, the lungfishes can haul themselves laboriously overland in search of a fresh pool when conditions become very dry. *Protopterus* can also **aestivate**, meaning that it can survive through the hot summer in a semi-inanimate condition. The lungfish digs a flask-shaped pit in the mud, curls up, and seals itself in with an envelope made from dried mucus. The mucus keeps the body damp, and the fish reduces its metabolic rate during the dry season. When the monsoonal rains fall, the lungfishes come to life again, and creep out of their cocoons. Large fossilized burrows in Permian and Triassic rocks suggest that early lungfishes also aestivated.

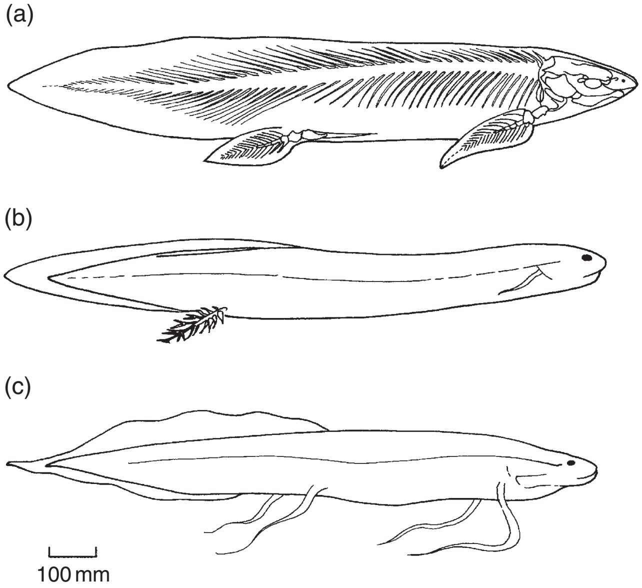

Figure 3.21 (a) The living lungfishes *Neoceratodus* from Australia, (b) *Lepidosiren* from South America and (c) *Protopterus* from Africa. Source: Adapted from various sources.

3.9.3 Actinistia: the coelacanths

Coelacanths arose in the Early Devonian (Friedman and Coates, 2006; Zhu *et al.*, 2012), and are represented by fossils up to the Late Cretaceous, when it was thought they had died out. Typical coelacanths, such as *Diplurus* from the Triassic of eastern North America (Figure 3.22(a)) have short bodies with large dorsal, anal and paired fins, all of which are lobed except for the anterior dorsal. The tail is characteristically divided into three parts – a dorsal and ventral portion separated by a small middle lobe at the end of the notochord. The skull is short overall, although the snout portion is longer than in the tristichopterids.

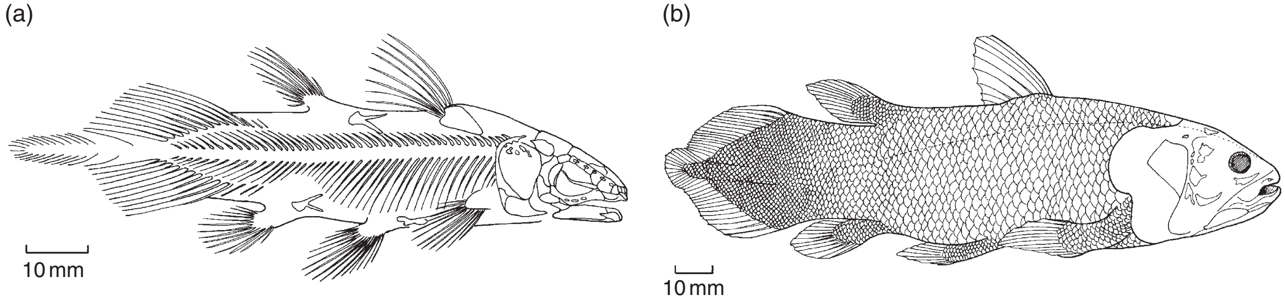

Figure 3.22 Coelacanths fossil (a) and living (b): (a) the Triassic *Diplurus* from North America; (b) the living *Latimeria* from the modern seas of the Indian Ocean. Source: Adapted from Andrews (1973).

Coelacanths are often called **living fossils**. In 1938, an unusual large lobe-finned fish was hauled up in the Indian Ocean, and brought ashore in South Africa. Eventually, the fish was identified as a coelacanth, and named *Latimeria* (see Figure 3.26(b)). *Latimeria* (Forey, 1998; Weinberg, 2011) is often called a living fossil because it belongs to a group that was long thought to be extinct, and its morphology is very like that of its ancestors of more than 100 million years ago. The term 'living fossil' has been disputed (Casane and Laurenti, 2013), and it may not be really helpful: *Latimeria* does not show particularly low genomic substitution rates nor low intra-specific molecular diversity, and the living species are quite distinct morphologically from the fossil forms. At times in the past the clade was more diverse, with up to 20 species known from the Early Triassic (Forey, 1998; Wen *et al.*, 2013).

Since 1938, more than 200 specimens of *Latimeria* have been fished up from the deep oceans off the coast of eastern and southern Africa and the Comoro Islands for the first species, and Sulawesi in Indonesia for the second species. *Latimeria* feeds on fishes, and swims slowly by beating its paired fins in a pattern like the locomotion of a tetrapod, and sculling with its muscular dorsal and anal fins. It can achieve fast thrust by beating its tail, a standard escape response seen in all bony fishes.

For a long time, the breeding mode of modern *Latimeria* was uncertain, and indeed the question had been resolved in the 1920s from Jurassic fossil specimens: coelacanths bear live young instead of laying eggs, **oviparity**, the fundamental mode in vertebrates. This is confirmed from dissection of *Latimeria*, in which the very large eggs (9 cm across) and embryos (up to 33 cm in a 1.6-m-long mother) were identified. Intrauterine embryos, evidence for **ovoviviparity** (bearing live young from retained eggs), are reported from Triassic, Jurassic, and Cretaceous coelacanths. The oldest, in the Middle Triassic *Luopingcoelacanthus*, are two embryos, each 10–14% of the mother's body length, and presumably ready to be born (Wen *et al.*, 2013). Ovoviviparity has arisen some 30 times among fishes, being known in placoderms (see Section 3.5.2) and actinopterygians, as well as probably in all coelacanths, and extensively among chondrichthyans.

3.9.4 Early sarcopterygians: origins of Tetrapodomorpha

In comparison to living sarcopterygians, the clade was diverse in the Devonian. Key sarcopterygian subclades include Porolepiformes, Onychodontida, Rhizodontida, Osteolepidae, Tristichopteridae and Panderichthyida, and these are partly members of the wider clade containing lungfishes, the Dipnomorpha, but most fall on the stem to Tetrapoda, called collectively the clade Tetrapodomorpha (see Box 3.7).

The porolepiforms, represented by *Holoptychius* (Figure 3.23(a)), generally have large rounded scales, and long pointed pectoral fins with more extensive lobed portions than in the tristichopterids. Porolepiforms have deep bodies and a short skull. Their strongly folded teeth are welded into the jaws by a plug of attachment bone inserted into the pulp cavity, and bite marks on contemporary heterostracans, placoderms, and sarcopterygians appear to have been made by hungry porolepiforms (Lebedev *et al.*, 2009).

The onychodontids were a small group of probably predatory fishes with long, hooked teeth at the front of the lower jaw. They ranged in length from 50 mm to over 1 m. There are only five genera, but new specimens from Australia (Johanson *et al.*, 2007) show many features in common with *Guiyu* and other stem-group sarcopterygians (see Box 3.6). Onychodontida are either stem coelacanths or stem sarcopterygians (Zhu et al., 2009; Lu *et al.*, 2012).

Basal tetrapodomorphs, sarcopterygians on the evolutionary branch to tetrapods (see Box 3.7), emerged in the Early Devonian, and are best known from China. *Tungsenia* (Lu *et al.*, 2012) is an extraordinarily early form to show modifications of the brain and lower jaw that were once thought to be unique to tetrapods.

The rhizodontids from the later Devonian and Early Carboniferous were large hunters. One massive rhizodont jaw from Scotland suggests that its owner must have reached a length of 6–7 m, although many rhizodontid species were smaller (Jeffery, 2012). These were fearsome hunters of some of the early tetrapods (see Chapter 4), as well as being a close outgroup of Tetrapoda (Jeffrey, 2012; Lu *et al.*, 2012).

The next tetrapodomorph group, the osteolepids, possibly a grade rather than a clade, had their heyday in the Devonian,

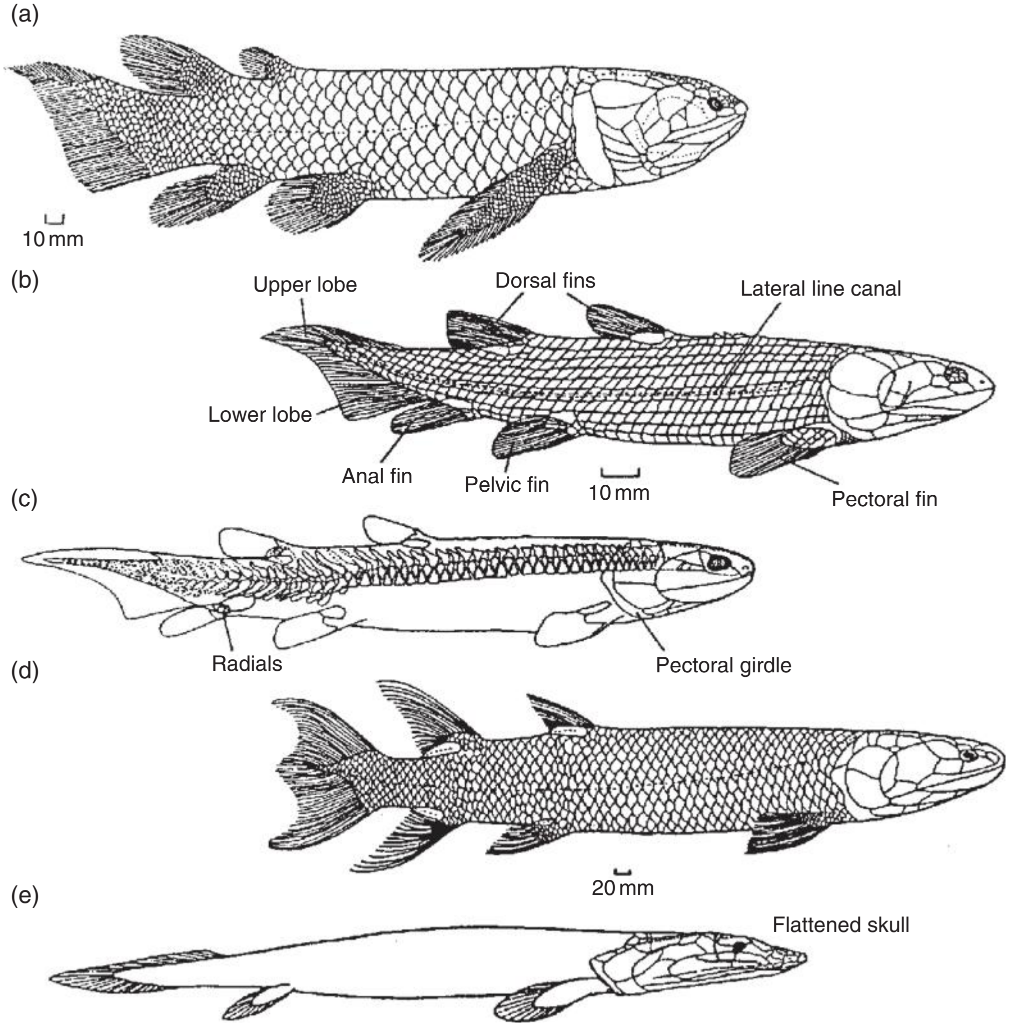

Figure 3.23 Diversity of Devonian sarcopterygians: (a) lateral view of the porolepiform *Holoptychius*, (b,c) lateral views of the osteolepid *Osteolepis*, with and without scales, (d) lateral view of the tristichopterid *Eusthenopteron*, (e) lateral view of the panderichthyid *Panderichthys*. Source: (a) Adapted from Andrews (1973). (b,d) Adapted from Moy-Thomas and Miles (1971). (c) Adapted from Andrews and Westoll (1970a). (e) Adapted from Vorobyeva and Schultze (1991).

although one lineage survived into the Carboniferous. *Osteolepis* from the Middle Devonian of Scotland and elsewhere (Andrews and Westoll, 1970b) has a long slender body with large midline fins (two dorsals, one anal), and lobed, paired fins (pectoral and pelvic). The tail is heterocercal, with fins above and below (Figure 3.23(b,c)). Some Late Devonian sarcopterygians were larger.

Next on the stem lineage to tetrapods (see Box 3.7) are the tristichopterids, such as *Eusthenopteron* from the Late Devonian of Canada (Figures 3.23(d) and 3.24). *Eusthenopteron* reached a length of 1 m, and it has a characteristic three-pointed symmetrical tail. The outer portions of the head, gill region, and attached shoulder girdle are covered by a complex of thin dermal bone plates (Figure 3.24(a,b)). Small teeth are borne on the maxilla, premaxilla and dentary, as well as on several bones of the palate (Figure 3.24(c)). Some of the palatal and lower jaw teeth are large and fang-like, and they have complex, or labyrinthine, internal patterns of infolding (Figure 3.25(E)), the so-called labyrinthodont type of tooth, found also in early tetrapods. The skull is highly kinetic, being jointed in order to allow the mouth to open wide, a synapomorphy of Sarcopteryii. Even the braincase (Figure 3.25(d)), deep within the skull, is jointed in order to permit greater flexibility, a feature retained in *Latimeria*, but otherwise unknown in other living sarcopterygians. The tristichopterids either form a distinctive clade (Swartz, 2012) or are successive outgroups to Elpistostegalia (Lu *et al.*, 2012; see Box 3.7).

The panderichthyids, or elpistostegids, are a series of Middle and Late Devonian taxa very close to the origin of tetrapods with legs. *Panderichthys* from the Late Devonian of Latvia (see Figure 3.23(e)) was an elongate fish with a long snout. The skull is flattened, and the eyes are located partly on top of the head. *Panderichthys* has only the paired pectoral and pelvic fins, as well as a tail fin, and it lacks the midline fins seen above and below the body in more basal tetrapodomorphs. These taxa are very similar to the early tetrapod *Tiktaalik* (see Section 4.2 and Box 4.1).

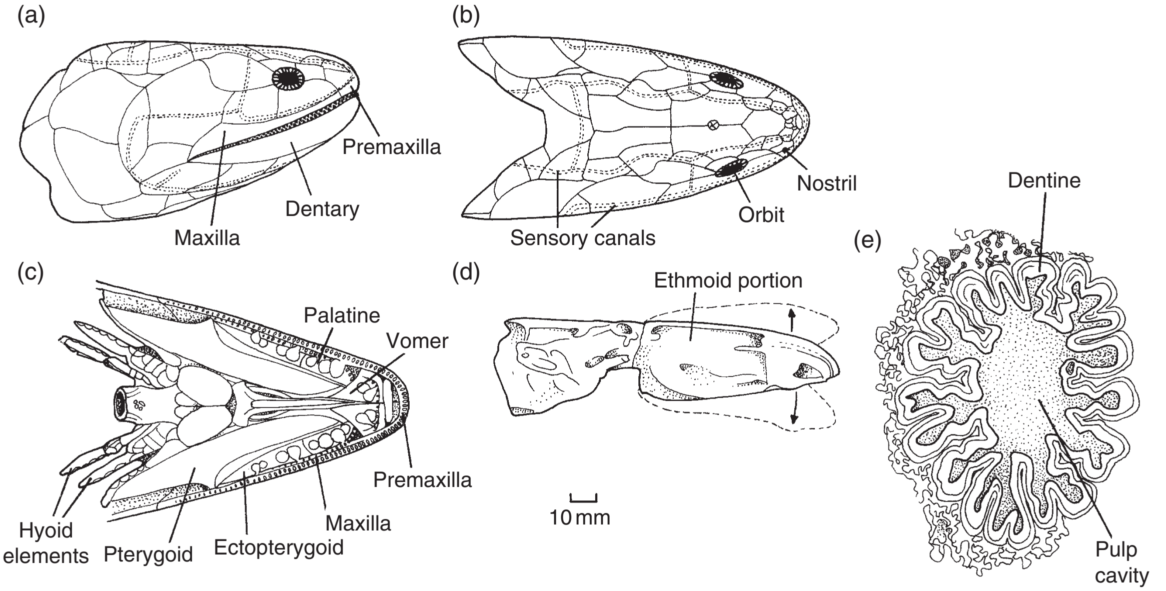

Figure 3.24 The skull of the tristichopterid *Eusthenopteron* in (a) lateral, (b) dorsal, and (c) ventral views; (d) lateral view of the braincase, showing the postulated range of movement about the middle joint; (e) cross-section of a tooth to show the labyrinthine infolding of the enamel (tooth diameter, 5 mm). Source: Adapted from Moy-Thomas and Miles (1971).

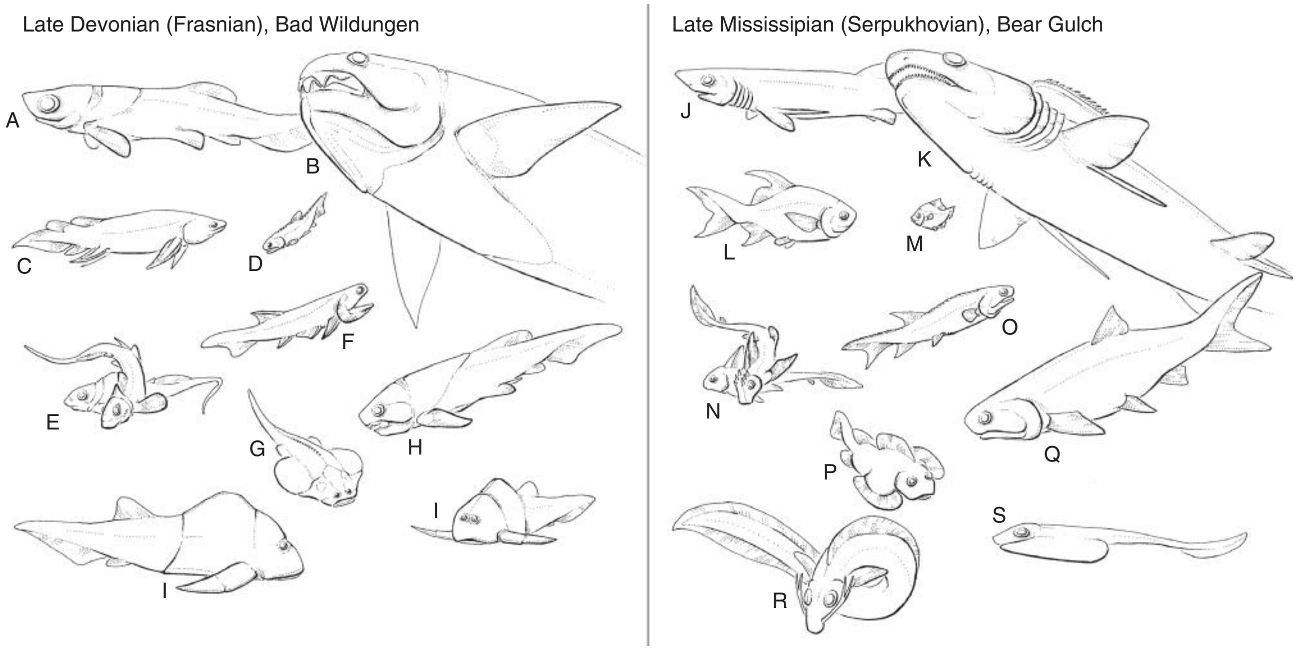

Figure 3.25 Before (left) and after (right) the end-Devonian mass extinction among fishes. The Devonian assemblage is from Frasnian (385–374.5 Ma) deposits at Bad Wildungen, Germany. The Carboniferous assemblage is from Serpukhovian (328–318 Ma) deposits at Bear Gulch, Montana, USA. A, the arthrodire placoderm *Wildungenichthys*; B, the arthrodire placoderm *Erromanosteus*; C, the dipnoan sarcopterygian *Chirodipterus*; D, the actinopterygian *Moythomasia*; E, the ptyctodontid placoderm *Rhynchodus*; F, the acanthodiform acanthodian *Homacanthus*; G, the rhenanid placoderm *Jagorina*; H, the arthrodire placoderm *Coccosteus*; I, the antiarch placoderm *Lepadolepis*; J, the symmoriiform chondrichthyan *Falcatus*; K, the symmoriiform chondrichthyan *Stethacanthus*; L, the actinopterygian *Aesopichthys*; M, the actinopterygian *Discoserra*; N, the holocephalan chondrichthyan *Echinochimaera*; O, the actinopterygian *Kalops*; P, the holocephalan chondrichthyan *Belantsea*; Q, the actinopterygian informally named '*Yogoniscus*;' R, the holocephalan chondrichthyan *Harpagofututor*; S, the elasmobranch chondrichthyan *Squatinactis*. Source: Friedman and Sallan (2012). Reproduced with permission from John Wiley & Sons.

3.10 EARLY FISH EVOLUTION AND MASS EXTINCTION

3.10.1 Diversification of early vertebrates

The narrative of the diversification of vertebrates through the early and middle Palaeozoic is hard to determine accurately because of the patchy occurrence of the earliest fish groups (Friedman and Sallan, 2012; Žigaitė and Blieck, 2013). Fishes arose in the Early Cambrian, at least based on the evidence of the myllokunmingiids, and radiated by the Late Cambrian, as shown by the conodonts and *Anatolepis* (see Box 3.1). The Ordovician once seemed to be almost barren of fish fossils, other than conodonts, until several well preserved Early Ordovician astraspids and arandaspids came to light. Renewed efforts in searching for more isolated remains have turned up evidence of a wide array of Late Ordovician fish groups: thelodonts, shark-like fishes, possible acanthodians, conodonts and osteostracans.

In the Silurian, fishes became more diverse and more abundant (see Boxes 3.1, 3.7), with the radiation of the armoured jawless fishes and the acanthodians. Further, in the Devonian, the seven major placoderm orders arose, as well as the first sharks, and numerous important groups of bony fishes, including their derivatives, the tetrapods.

The rise of life on land and the diversification of gnathostomes in the Late Silurian and Devonian have been explained variously by both intrinsic (=biological) and extrinsic (=physical environmental) factors. The fact that jawed vertebrates rose to significance and jawless forms declined during the Devonian points to the importance of jaws and diversified modes of predation (Anderson *et al*., 2011) rather than simple competition between agnathans and gnathostomes. At the same time, ammonoids and eurypterids (predatory arthropods) were on the rise, and there is considerable evidence that the levels of predatory attacks by these invertebrates, as well as by gnathostomes, were substantially increasing in the Early Devonian (Klug *et al*., 2011).

An alternative explanation for the diversification of vertebrates in the Late Silurian and Devonian is that it was driven by rising atmospheric oxygen levels (Qu *et al*., 2010). Oxygen levels were about 15% in the Middle Ordovician, and rose to modern levels (21%) in the Early Silurian, and then rose further to 25% in the Early Devonian, before falling back to 15% in the Late Devonian. This Siluro-Devonian oxygen peak could have enabled the diversification of certain larger, more active fishes in oceans and fresh waters, and of arthropods on land. On the other hand, there is limited matching between the various peaks in oxygen and clade diversifications among fishes, and the physiological explanation for why rises and falls in atmospheric oxygen would drive originations and extinctions of aquatic vertebrates is not clear (Friedman and Sallan, 2012).

3.10.2 The Late Devonian mass extinctions

The first extinctions of fishes occurred at the end of the Early Devonian, with the loss of cyathaspids, acanthothoracids and others. Further fish groups, including some 'agnathan' and placoderm families, and some acanthodians, disappeared during the Middle Devonian. These were seemingly modest events.

The Late Devonian, on the other hand, has long been identified as one of the 'big five' mass extinctions, times when some 50% of species died out. In fact, the Late Devonian 'event' has rarely been seen as a sudden extinction, but rather as a series of events, sometimes termed the 'Late Devonian Biodiversity Crisis' (Stigall, 2010), that spanned 25 Myr of the late Middle and Late Devonian. Three extinction events have been identified during this time span (McGhee, 2013), the end-Givetian Taghanic event (383 Ma), the end-Frasnian Kellwasser event (372 Ma), during which 60% of marine genera and up to 82% of species died out, and the end-Famennian Hangenberg event (359 Ma).

Among fishes, the Late Devonian has long been seen as the time when armoured fishes disappeared, and modern-style chondrichthyans and actinopterygians, as well as tetrapods, replaced them (Friedman and Sallan, 2012). For example, most of the jawless fishes, including many conodont families, heterostracans, anaspids, osteostracans, as well as the placoderms and most remaining acanthodians and sarcopterygians, died out (see Boxes 3.1, 3.7). Sallan and Coates (2010) identified the complete loss of 44% of major gnathostome clades through the Hangenberg event, marking a striking changeover in fish faunas across the Devonian-Carboniferous boundary (see Figure 3.25), leading to the rise of many new clades in the Carboniferous (see Chapter 7).

3.11 FURTHER READING

You can read more about the Palaeozoic fish groups in Janvier (1996), a comprehensive and beautifully illustrated book, while papers in Ahlberg (2001) present a variety of current views on basal vertebrate and fish phylogeny. Aldridge *et al.* (1993) and Donoghue *et al.* (2000) are excellent overviews of current knowledge about the conodonts and the phylogeny of early vertebrates. Arratia *et al.* (2004) and Elliott *et al.* (2010) are collections of essays in honour of two great palaeoichthyologists, Hans-Peter Schultze and Meeman Chang; both volumes contain papers primarily about early Palaeozoic vertebrates. Forey (1998) gives a full account of coelacanths and the living *Latimeria*, and the full story of its discovery is told by Weinberg (2011). Bemis *et al.* (1986) and Jørgensen and Joss (2010) contain a number of papers about living and fossil lungfishes. There are good reviews of the relationships of sarcopterygians in Ahlberg (2001) and Clack (2002).

QUESTIONS FOR FUTURE RESEARCH

1 What is the true diversity of myllokunmingiids, and how much of their soft tissue anatomy can be discerned with confidence?
2 Why do microRNAs and other phylogenomic data sources give different answers in some cases, for example on the monophyly, or otherwise, of Cyclostomata?
3 Can we identify more, and more complete ostracoderms (armoured jawless stem gnathostomes) from the early Palaeozoic?
4 To what extent was early vertebrate evolution dependent on palaeogeography and palaeoclimate?
5 How did early fishes respond to the physiological challenges of living in marine and fresh waters?
6 What were the feeding and swimming modes of the armoured fishes of the Silurian and Devonian?
7 What are the phylogenetic positions of the various taxa of placoderms and acanthodians, and what does this tell us about the origins of typical chondrichthyan and osteichthyan characters?
8 How did the Devonian sarcopterygians evolve, and how do they relate to the three extant sarcopterygian clades, Actinistia, Dipnomorpha, and Tetrapoda?
9 How and why did some tetrapodomorph sarcopterygians make the move from dominantly living in water to dominantly living on land?

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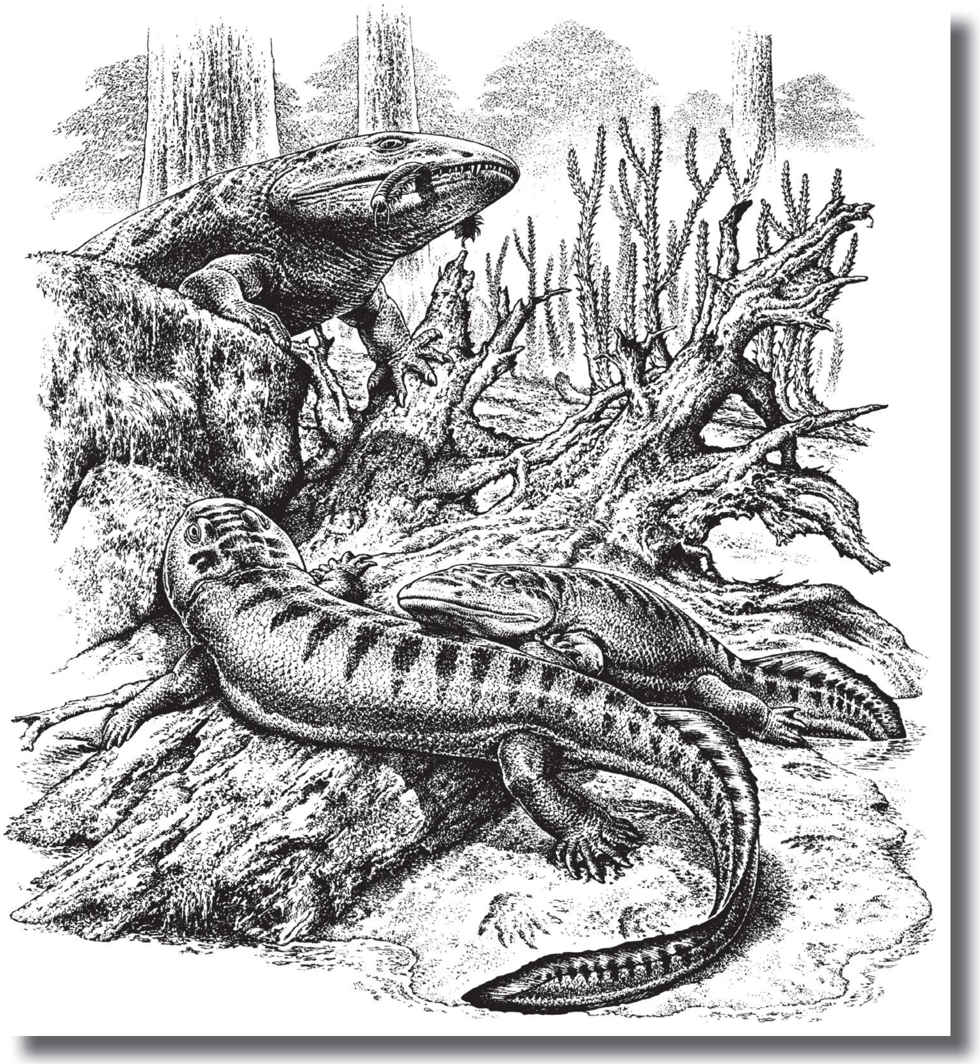
CHAPTER 4

Early Tetrapods and Amphibians



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KEY QUESTIONS IN THIS CHAPTER

1 What were the key challenges facing vertebrates when they moved onto land?
2 How did terrestrial locomotion evolve if the first tetrapods were still aquatic?
3 If the first tetrapods had seven or eight fingers and toes, why are five fingers so widespread, and how are the fingers coded genetically?
4 How did tetrapods diversify in the Carboniferous?
5 How did early tetrapods adapt the larva-to-adult transition in response to environmental stimuli?
6 How did the early tetrapods evolve towards modern amphibians and reptiles?

INTRODUCTION

Vertebrates made a significant evolutionary move in the Devonian when the first **tetrapods** developed features that would allow the first steps onto land. Our understanding of this transition from fish to tetrapod has been improved enormously by new fossil finds, new methods of visualizing the specimens, and new approaches in phylogenetics, developmental evolutionary biology (Coates *et al.*, 2008; Laurin, 2010), and biomechanics (Pierce *et al.*, 2012, 2013a,b). After the origin of limbs, tetrapods diversified extensively during the Carboniferous and Early Permian, some as small semi-aquatic forms, but many as larger animals that fed on fishes and other tetrapods, and that could, in some cases, live fully terrestrial lives.

The basal tetrapods are often termed 'amphibians', a term also applied to the living forms, frogs, salamanders and caecilians. The name amphibian ('both life') refers to the fact that the modern forms live both in the water and on land, and it is assumed that many of the extinct basal tetrapods had similar double lifestyles. The Class Amphibia used to include all the Palaeozoic basal tetrapods, and so was paraphyletic, because it excludes many descendant groups, the reptiles, birds and mammals. The term Amphibia can be redefined to include only the modern groups, the Lissamphibia, or it can be extended to equate to Batrachomorpha, including also their stem taxa, the temnospondyls to the point at which they split from Reptiliomorpha (see Box 4.5).

In this chapter, the major anatomical and physiological changes that were necessary during the transition from lobefin fish to early tetrapods are reviewed, and the evolution and biology of the extinct and living forms is described.

4.1 PROBLEMS OF LIFE ON LAND

The first tetrapods faced major problems in moving from the water onto the land (Zimmer, 1998; Laurin, 2010; Clack, 2012a). Air breathing was not in fact the major problem, but rather weight and structural support. New modes of locomotion had to evolve, as well as new ways of feeding, of sensing prey and predators, of water balance and of reproduction.

When all these problems of life on land are considered, it may seem surprising that vertebrates ever left the protection of the water. However, suggestions for why tetrapods made this momentous step include escape from excessive competition in the water, exploration of new ecological opportunities, or even as a means of returning to the water. The last, classic theory (Romer, 1966) was that fishes evolved the ability to move over land in order to escape from drying pools. The Devonian was a time of seasonal droughts on the Old Red Sandstone continent (see Section 3.8.2), and the freshwater fishes probably often found themselves in stagnant and dwindling pools. The conclusion of this viewpoint is that terrestrial locomotion evolved as a means of staying in the water!

New research suggests that this classic model is flawed; fully functioning limbs with digits evolved *before* tetrapods moved onto land (Pierce *et al.*, 2012, 2013a,b), and it is now intriguing to determine why aquatic animals needed arms and legs. Further, when and why did they use these limbs at a later time to support their body weight in true terrestrial locomotion? The move onto land was presumably because there was a rich and untapped supply of food there. Waterside plants and terrestrial invertebrates diversified in the Late Silurian and Devonian, and it was inevitable that various organisms would exploit them sooner or later.

4.1.1 Support

Fishes are generally neutrally buoyant, meaning they are supported in the water, and their mass is effectively zero. On land, however, a tetrapod holds its body up on its limbs, and the skeleton and all of the internal organs have to become structurally modified in order to cope with the new downwards pull of gravity. The backbone of a fish is adapted for the stresses of lateral stretching and bending during swimming, but the main force affecting a tetrapod is gravity. The vertebrae and the muscles around the backbone have to become modified to prevent the body from sagging between the limbs. Further, the internal organs must themselves be strengthened to avoid collapse, but also held in place so they do not fall out of the rib cage of a walking tetrapod. Such adaptations are costly, and they may be lost by secondarily aquatic animals, such as whales, which effectively collapse and suffocate when they are washed up on land.

4.1.2 Locomotion

Tetrapods move in a very different way from fishes. Instead of a smooth gliding motion, the limbs have to operate in a jerky fashion producing steps to propel the body forwards. The paired fins of sarcopterygian fishes already had internal bones and muscles that produced a form of 'walking', although different in detail from tetrapod walking. But profound modifications had to occur in the lobed fin before it became a moderately effective land limb.

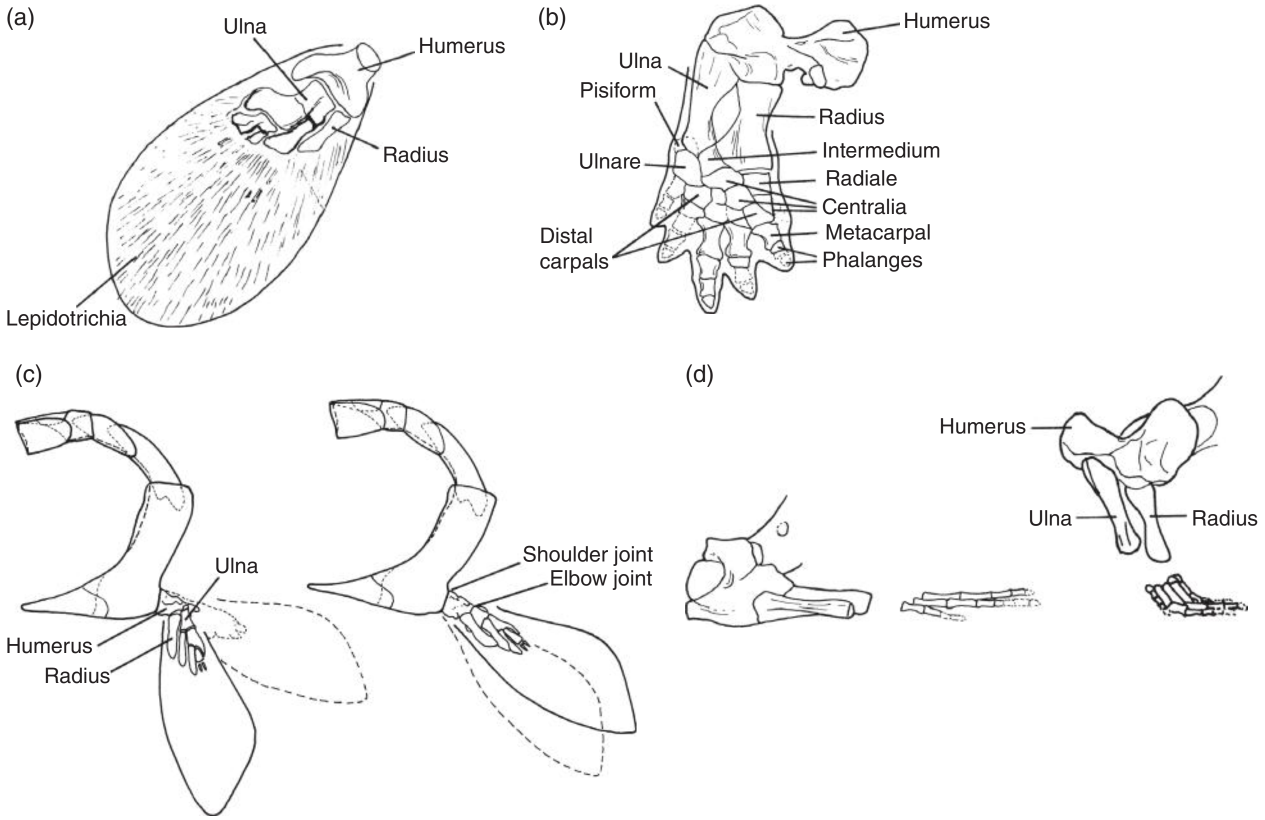


Figure 4.1 The origin of tetrapod limbs and land locomotion: (a) pectoral fin of the tristichopterid fish *Eusthenopteron* showing interpreted identities of the bones; (b) equivalent forelimb of the basal tetrapod *Eryops*; (c) possible movements of the forelimb of *Eusthenopteron*; (d) step cycle of the forelimb of the basal tetrapod *Proterogyrinus*. Source: (a,b) Various sources. (c) Adapted from Andrews and Westoll (1970). (d) Adapted from Holmes (1984).

The pectoral fin of the tristichopterid *Eusthenopteron* (Figure 4.1(a)) contains the major proximal bones of a tetrapod limb (Figure 4.1(b)): the single upper arm bone, the **humerus**, the two forearm bones, the **radius** and **ulna**. The tetrapod has additional elements in the wrist, the **ulnare**, the **radiale** and **intermedium**, and the **centralia** (singular, centrale), distal **carpals** 1–5, sometimes an additional bone at the side, the **pisiform**, and the four or five fingers, which are composed of **metacarpals** and **phalanges**. The fin bones of *Eusthenopteron* are to be found in early tetrapods, and indeed most of them are still present in our arms, although it is speculative to attempt to draw homologies for all of the bones of the hand and wrist. The tristichopterid pelvic fin also contains the basic tetrapod bones of the hindlimb, the thigh bone (**femur**), the lower leg bones (**tibia**, **fibula**), but the tetrapod ankle bones (**fibulare**, **intermedium**) and digits cannot be identified. Although close anatomical similarities exist, there were major functional differences: *Eusthenopteron* could not have walked properly on land on its fins.

How can we compare the locomotor abilities of a tristichopterid and an early tetrapod? In *Eusthenopteron*, the fins point backwards and a little sideways, and the fin skeleton could swing back and forwards through only 20–25° (Andrews and Westoll, 1970). The main motion was at the shoulder joint, with a very slight elbow bend (humerus-ulna/radius hinge). The lepidotrichia of the remainder of the fin were flexible, and they might have increased the size of the swing, but only slightly (Figure 4.1(c)).

In evolving the ability to walk, the tetrapod limb had to alter considerably both in structure and in orientation, when compared with the tristichopterid fin (Holmes, 2003). New bones appeared, and the elbow and wrist joints became more clearly defined. The humerus lengthened and the shoulder joint swung round so that the humerus pointed partly sideways as well as backwards. The elbow joint became more of a right angle and the lower part of the limb was directed downwards. The wrist acted as a hinge, and the new bones in the hand allowed it to spread out widely and fulfil its role as a weight-supporting surface. In walking (Figure 4.1(d)), the humerus swung back and forwards in a horizontal plane. During a stride, it also twisted so that the radius and ulna were swung down from a near-horizontal orientation.

The limb girdles became heavily modified with the change in limb function. The pectoral girdle of most fishes is effectively part of the skull (Figure 4.2(a,b)) as the outer elements are attached to the gill and throat bones. When the first tetrapod used its pectoral fins in walking, additional forces were applied. At every step, the pectoral girdle takes up the impact of the weight of the front part of the body as each hand hits the ground. In a fish-like arrangement, these impacts would be transmitted from the pectoral girdle directly to the skull, and the whole head would reverberate in

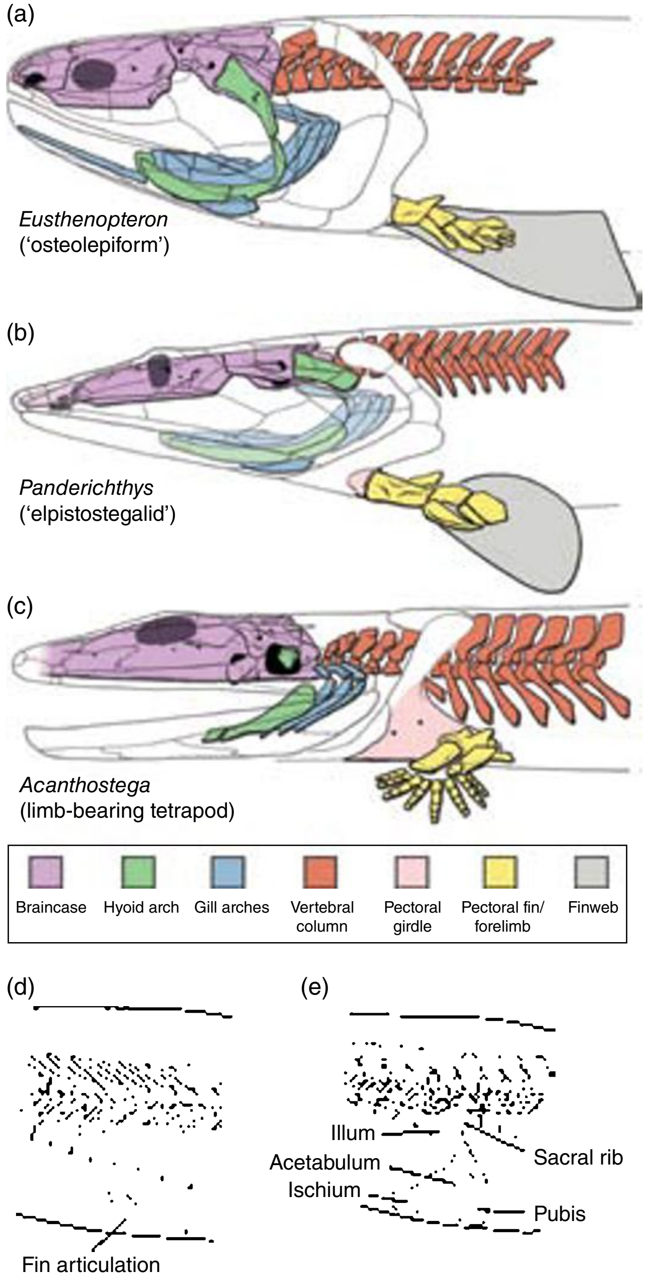


Figure 4.2 The transition from tristichopterid fish (a) and (d), through panderichthyid (b), to basal tetrapod (c) and (e): (a–c) the separation of the skull from the shoulder girdle; (d) and (e) the enlargement of the pelvic girdle and its firm attachment to the vertebral column via the ilium and sacral rib. See Colour plate 4.1. Source: (a–c) M. Coates, University of Chicago, IL, USA. Reproduced with permission. (d,e) Adapted from various sources.

time to the walking steps. In addition, more flexibility is needed in the neck by tetrapods so they can snap at prey without twisting their entire body. The pectoral girdle became separated from the skull in the earliest tetrapods (Figure 4.2(c)).

The pelvic girdle was also much modified. Whereas in fishes it is a small unit that is embedded within the body wall (Figure 4.2(d)), it eventually became grossly enlarged and firmly attached to the vertebral column in terrestrial tetrapods (Figure 4.2(e)). This is because of the additional forces imposed by the role of the hindlimb in walking. A terrestrial tetrapod is rather like a wheelbarrow, as the main driving forces in walking come from the hindlimbs, and the sacrum and pelvis had to become rigid to allow more effective transmission of thrust. The suspension is at the front, in order to keep the chest off the ground and permit expansion of the lungs.

4.1.3 Feeding and respiration

The earliest tetrapods had to modify the ways in which they fed and breathed. The skulls of osteolepiforms and tristichopterids were highly kinetic (see Section 3.9.4) but this mobility was largely lost in the early tetrapods. The jaw movements of tetrapods are also much simpler than those of most fishes. The lower jaw hinges at one point at the back of the skull, on a roller joint between the **articular** bone in the lower jaw and the **quadrate** in the skull. The first tetrapods presumably fed on small fishes and the increasing numbers of terrestrial invertebrates – millipedes, spiders, cockroaches, dragonflies and the like.

Air-breathing needs lungs, or some equivalent supported vascular surface, instead of gills. Lungs contain internal folds and pouches lined with heavily vascularized skin and bathed in fluid. Air is drawn in, passed into the fine pouches, and oxygen passes through the moistened walls into the bloodstream. Living lungfishes have functional lungs of course, and the same is assumed for tetrapodomorph fishes and indeed most other early bony fishes. The first tetrapods may have been only marginally better than their fish ancestors at air breathing.

There are two main modes of breathing in tetrapods, (1) **costal ventilation**, where the ribs and costal muscles expand and contract the lungs, and (2) **buccal pumping**, where air is sucked into the mouth and throat, and then rammed into the lungs by raising the floor of the mouth. Amniotes all rely on costal ventilation, but living amphibians use buccal pumping, and it is seen especially in frogs.

It had been assumed that the earliest tetrapods used buccal pumping, but many of them seem to have retained internal gills and so continued to breathe in fish-like fashion (Schoch and Witzmann, 2011). Evidence for internal gills in a range of basal tetrapods is the location of the gill arches and inferred branchial arteries on the ventral side of gill arch elements. Palaeozoic tetrapods retained internal gills in aquatic adults of some taxa, and external gills in larvae of these aquatic forms, as well as in the larvae of terrestrial forms, which resorbed the external gills after the larval phase.

4.1.4 Sensory systems and water balance

Sensory systems had to change too in the first tetrapods. The lateral line system could be used only in the water (it was retained in many aquatic tetrapods). Eyesight was even more

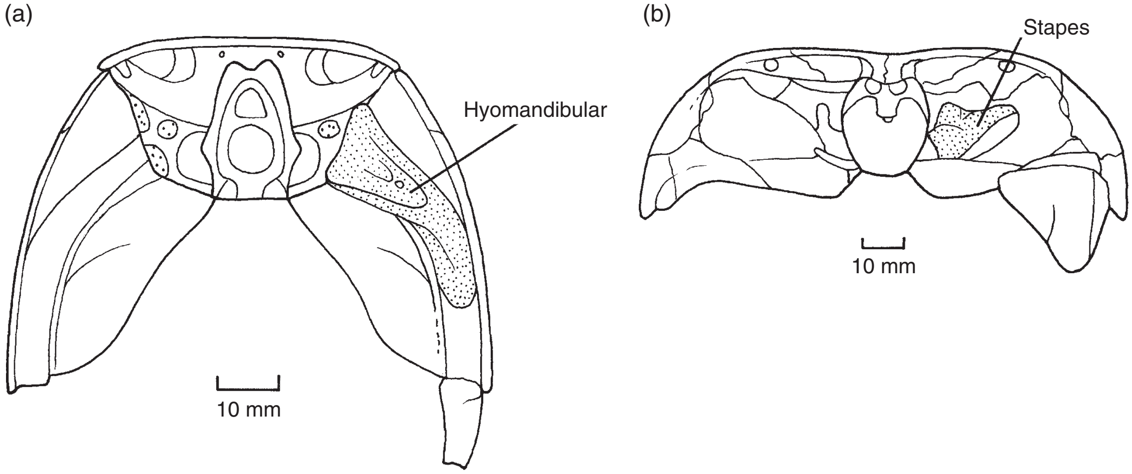


Figure 4.3 Posterior views of the skulls of the sarcopterygian *Eusthenopteron* (a) and the tetrapod *Greererpeton* (b) to show the changing function of the fish hyomandibular, which acted largely as a supporting element, to the tetrapod stapes, which functions in transmitting sound vibrations in air from the tympanum to the brain. Source: Adapted from Smithson (1982).

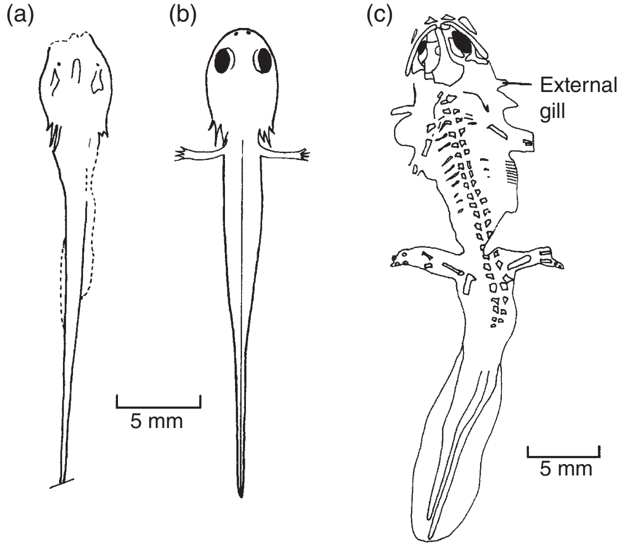


Figure 4.4 Fossil ‘tadpoles’ of Carboniferous and Permian tetrapods; drawings of fossils from (a) France and (c) North America; (b) reconstruction of an intermediate stage. Source: (a,b) Adapted from Boy (1974). (c) Adapted from Milner (1982).

important on land than in shallow ponds (tetrapods have larger eyes than their precursors), and the sense of smell may have improved, but there is no evidence of that in the fossils. Early tetrapods had a poor sense of hearing in air, as did their ancestors. The main bone associated with hearing in modern amphibians and reptiles, the **stapes**, is present in early tetrapods (Figure 4.3), but it is too massive to be effective in hearing high-frequency sound. The stapes is a modified version of the hyomandibular element, which forms part of the jaw-hinging apparatus in most fishes (see Section 3.4.1).

A further physiological problem with life on land is the maintenance of water balance. In the air, water can evaporate through the moist skin of the body, the lining of the mouth, and the nostrils, which means that the early tetrapods risked desiccation. These animals probably remained close to fresh water, which they could drink in order to avoid this problem. Certain forms evolved semi-permeable skin coverings that would have cut down water loss.

4.1.5 Reproduction

Living amphibians betray their ancestry in their mode of reproduction. Most frogs and salamanders, even terrestrially adapted forms, have to lay their eggs in water where the young hatch out as aquatic larvae, often called tadpoles. After some time in the water, breathing through their gills, tadpoles metamorphose into the adult form. Fossil larvae are rare, probably because they are so small and their bones are poorly developed, but sufficient specimens have been found in Carboniferous and Permian rocks to confirm that at least some early tetrapods passed through larval stages similar to those of modern amphibians (Figure 4.4).

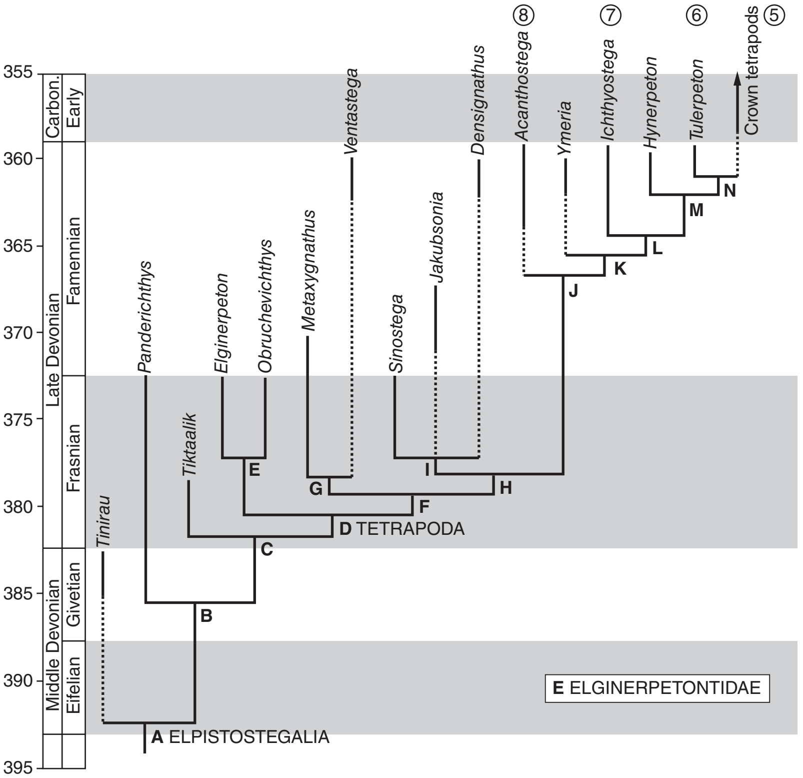
4.2 DEVONIAN TETRAPODS

Knowledge about Devonian tetrapods has increased dramatically since 1990: until that time, there were only three genera, two from Greenland and one from Russia. Since then, the total has grown to more than ten genera, although many are based on incomplete remains (Ahlberg *et al.*, 2005; Blieck *et al.*, 2010; Clack, 2012b). The fossils include possible tetrapod footprints from the early Middle Devonian Poland, which set the origin of the group at least to that time, followed by skeletal remains from the Late Devonian. Among these, are five taxa from the Frasnian (383–372 Myr ago), *Sinostega* from China, *Elginerpeton* from Scotland, *Obruchevichthys* from Latvia, and *Metaxygnathus* from Australia. Then, in the Famennian (372–359 Myr ago) is a single early Famennian form, *Jakubsonia* from Russia, followed by a number of late Famennian taxa, namely *Acanthostega*, *Ichthyostega*, and *Ymeria* from Greenland, *Densignathus* and

BOX 4.1 PHYLOGENY OF THE DEVONIAN TETRAPODS

The relationships of the Late Devonian tetrapods (see cladogram), and their closest fish relatives, are controversial, not least because many of the specimens are incomplete and are currently under study. The finned elpistostegalian *Tiktaalik* seems to be the closest finned sarcopterygian relative of tetrapods, sharing various features of the head and body that are not seen in osteolepiforms and tristichopterids (see Box 3.7). The Tetrapoda, literally those vertebrates with 'four feet' include a number of Late Devonian taxa, such as the well-known *Acanthostega* and *Ichthyostega* from Greenland, higher in the cladogram.

It is hard to determine the relationships of the remaining Late Devonian tetrapods, probably because most of the taxa are founded on incomplete remains. This means that cladistic resolution is hard to establish (Clack, 2012b). In most analyses (e.g. Ruta *et al*., 2003a,b; Coates *et al*., 2008; Clack, 2012b), *Acanthostega* is more basal than *Ichthyostega*, as shown here (see cladogram), whereas others reversed the order. Further, there is considerable movement in the phylogenetic positions of *Elginerpeton*, *Metaxygnathus*, and *Densignathus*, depending on exact character codings (Clack *et al*., 2012b). Therefore, the cladogram shown here is likely to be revised substantially in the future as more materials come to light.



Cladogram showing postulated relationships of the basal tetrapods, based on synapomorphies from Ruta *et al*. (2003a,b), Ahlberg *et al*. (2005), Daeschler *et al*. (2006), and Clack (2012b). See Box 3.7 for context of Tetrapoda; see Box 4.5 for relationships of main post-Devonian tetrapod groups. The number of fingers/toes is indicated, where known. Synapomorphies include: **A ELPISTOSTEGALIA**, one pair of dentary fangs, posterior coronoid one-third longer than more anterior coronoids, organized tooth row on posterior coronoid, posterodorsal maxillary process weak/absent, pineal foramen posterior to orbits, height/width ratio of glenoid fossa is 40–50%, highly reduced postaxial process on fibula; **B**, prearticular contacts angular edge-to-edge, median postrostral absent, anterior nostril at edge of mouth, jugal-quadratojugal contact, frontal present, scapulocoracoid is a large plate pierced by a coracoid foramen, coracoid plate, lateral component to glenoid orientation, rhomboid scale; **C**, wide spiracular tract, absence of opercular, subopercular and extrascapulars, scapulocoracoid expanded dorsally and ventrally, glenoid fossa oriented laterally, pectoral fin with elaborated distal endoskeleton, mobile segmented regions and reduction of lepidotrichia distally; **D TETRAPODA**, large nasal bones, fang pair and tooth row on the parasymphysial plate, anterior coronoid narrow, meckelian bone floors precoronoid fossa, rudimentary sacrum, pre- and postzygapophyses on vertebrae, ilium branches in two; **E ELGINERPETONTIDAE**, deep furrow along dentary-splenial suture, humerus with thin flat entepicondyle continuous with humerus body and narrow tall ectepicondyle, tibia with articulation surfaces for intermedium and tibiale; **F**, cheek with broad jugal–quadratojugal contact, large ornamented interclavicle, carpus, tarsus, up to eight digits, iliac blade extends dorsally and attached to vertebral column by sacral rib; **G**, coronoid fangs in tooth row; **H**, no synapomorphies identified; **I**, no synapomorphies identified; **J**, single pair of nasals meeting in midline, stapes, coronoid fangs absent, well-developed ventrally-directed ribs, pectoral girdle detached from skull, femur with adductor muscle crest, radius and ulna/ tibia and fibula parallel and both articulate with carpus/ tarsus, hand and foot with series of digits; **K**, enlarged anterior dentary teeth; **L**, postsplenial pit line in lower jaw absent, free ventral flange of the splenial absent, only symphysial and articular ends of the Meckelian element ossified, anocleithrum absent, olecranon process present and ulna as long as radius or longer, seven or fewer digits; **M**, distinct cleithrum; **N**, open lateral line system on most or all dermal bones, elongate scapula, six or fewer digits, tail fin absent. Abbreviation: Carbon, Carboniferous.

Hynerpeton from the United States, *Ventastega* from Latvia, and *Tulerpeton* from Russia.

The most completely known Devonian tetrapodomorphs are *Tiktaalik* from Canada (Daeschler *et* al., 2006; Shubin *et* al., 2006; Downs *et al*., 2008) and *Acanthostega* and *Ichthyostega* from the latest Devonian of Greenland (Clack, 1998; Coates and Clack, 1990, 1991; Coates, 1996; Blom, 2005; Pierce *et al*., 2012, 2013a,b). For a long time, attention focused on *Ichthyostega*, but recent finds of tetrapodomorph fishes (see Section 3.9.4) and basal tetrapods has greatly enriched our understanding of the dramatic transition of vertebrates from life in the water to life on land. Nonetheless, despite these new finds, establishing their relationships has been difficult (see Box 4.1).

4.2.1 Anatomy

Here we focus on the three most completely known taxa that are close to the fish-tetrapod (= fin-limb) transition, *Tiktaalik*, *Acanthostega*, and *Ichthyostega*. These three all measure 0.5–1.2 m long, and they were carnivorous, presumably feeding on fishes. They retain a fish body outline with a streamlined head, deep vertebrae and a tail fin. They all have poorly developed wrists and ankles. In *Ichthyostega* the ribs are unusually massive, and they have broad plate-like processes along their posterior margins that overlap considerably and form a near-solid side wall.

The oldest of the three, *Tiktaalik* (Figure 4.5), shares its body scales, fin rays, lower jaw and palate with tetrapodomorph fishes such as *Eusthenopteron* and *Panderichthys*, but has tetrapod-like features such as a shortened skull roof, modified ear region, functional wrist joint, and separation of its skull from the pectoral girdle allowing for a mobile neck (Daeschler *et al*., 2006). This separation was achieved in *Tiktaalik* and in later tetrapods by the loss of three fishy elements that linked the gill region and pectoral girdle, the opercular, subopercular, and extrascapular series. *Tiktaalik* has a spiracle, a remnant of the exhalant system for underwater breathing, as well as powerful gular bones in the floor of the mouth and branchial gill arch bones that may have been used to power buccal pump breathing in the air. The head is flattened and strengthened with consequent modifications in the braincase region (Downs *et al*., 2008). The forelimb skeleton in *Tiktaalik* was particularly interesting (Shubin *et al*., 2006), showing numerous distal endochondral bones and **synovial joints** (joints between the limb elements with facets allowing movement) as in more derived tetrapods. The front fin was capable of a range of postures, including backwards paddle-like thrusts for swimming, and a limb-like stance in which the distal part of the fin sat on the ground and the shoulder and elbow were flexed to support the body weight. The hindlimb and pelvis of *Tiktaalik*, discovered later (Shubin *et al*., 2014) show a similar mix of characters. The pelvis has a substantial ilium and pubis, with a deep acetabulum to house a powerful hindlimb. However, there is no ischium, and the ilium is not firmly fused to the backbone via the sacral ribs. This animal could have walked on land, but probably not for long.

The skulls of *Acanthostega* (Figure 4.7(a)) and *Ichthyostega* look generally like those of the tetrapodomorph fishes

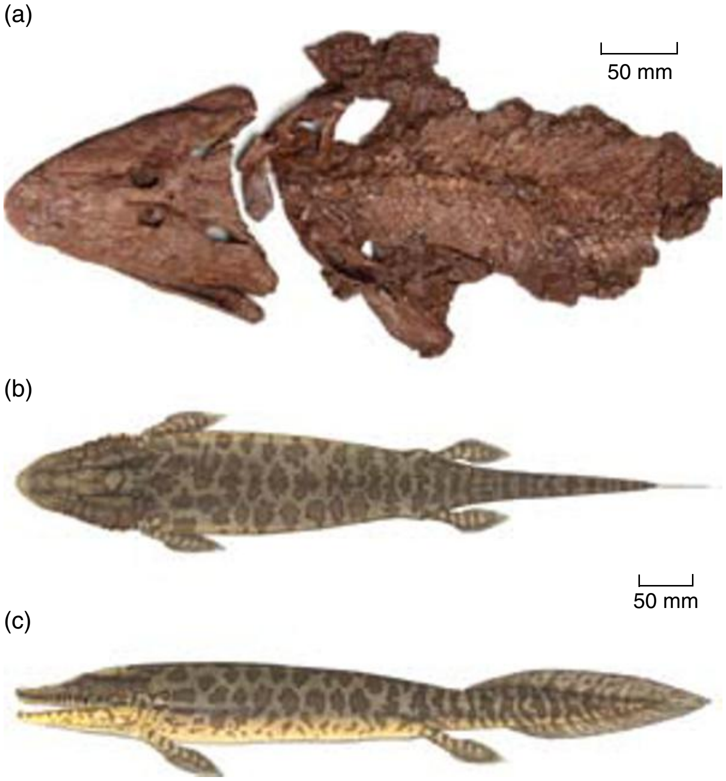


Figure 4.5 The original specimen of *Tiktaalik* from northern Canada, viewed from above (a), and restoration in dorsal (b) and lateral (c) views. Source: (a–c) E. Daeschler and S. Rawlins (artist), Academy of Natural Sciences, Philadelphia, PA, USA. Reproduced with permission.

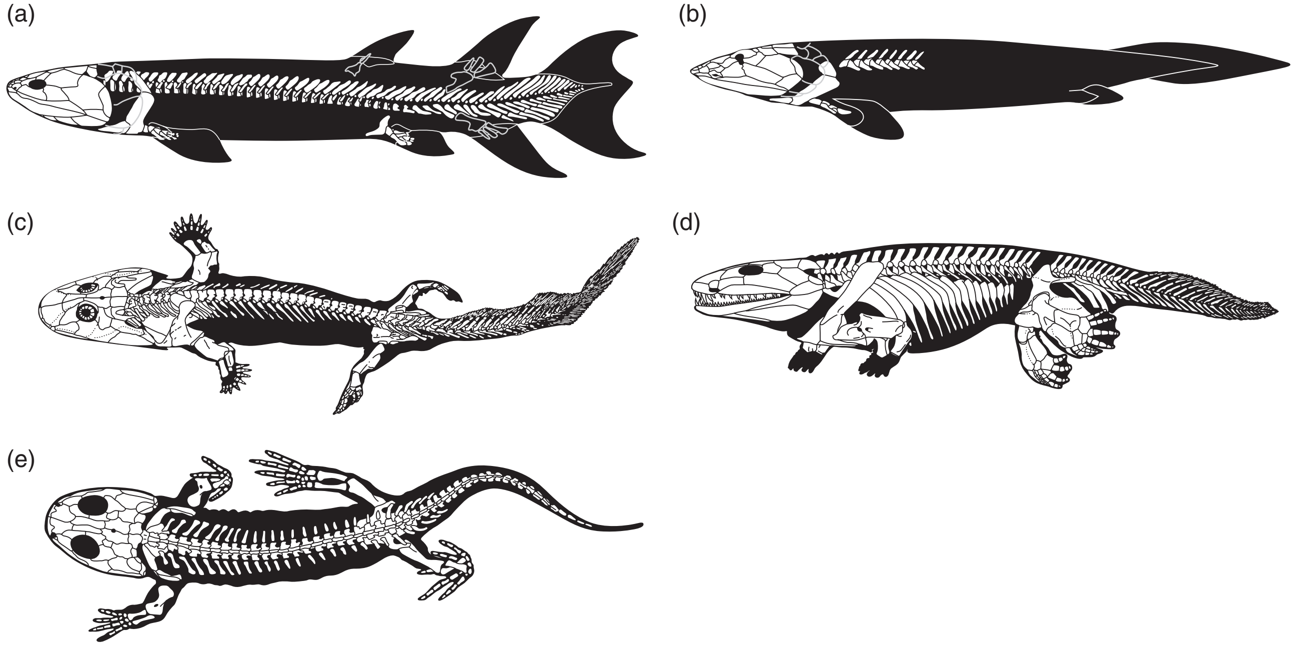


Figure 4.6 Silhouette diagrams of tetrapod outgroups (a,b) and tetrapods (c–e): (a) *Eusthenopteron*; (b) *Panderichthys*; (c) *Acanthostega*; (d) *Ichthyostega*; (e) *Balanerpeton*. Source: M. Coates, University of Chicago, IL, USA. Reproduced with permission.

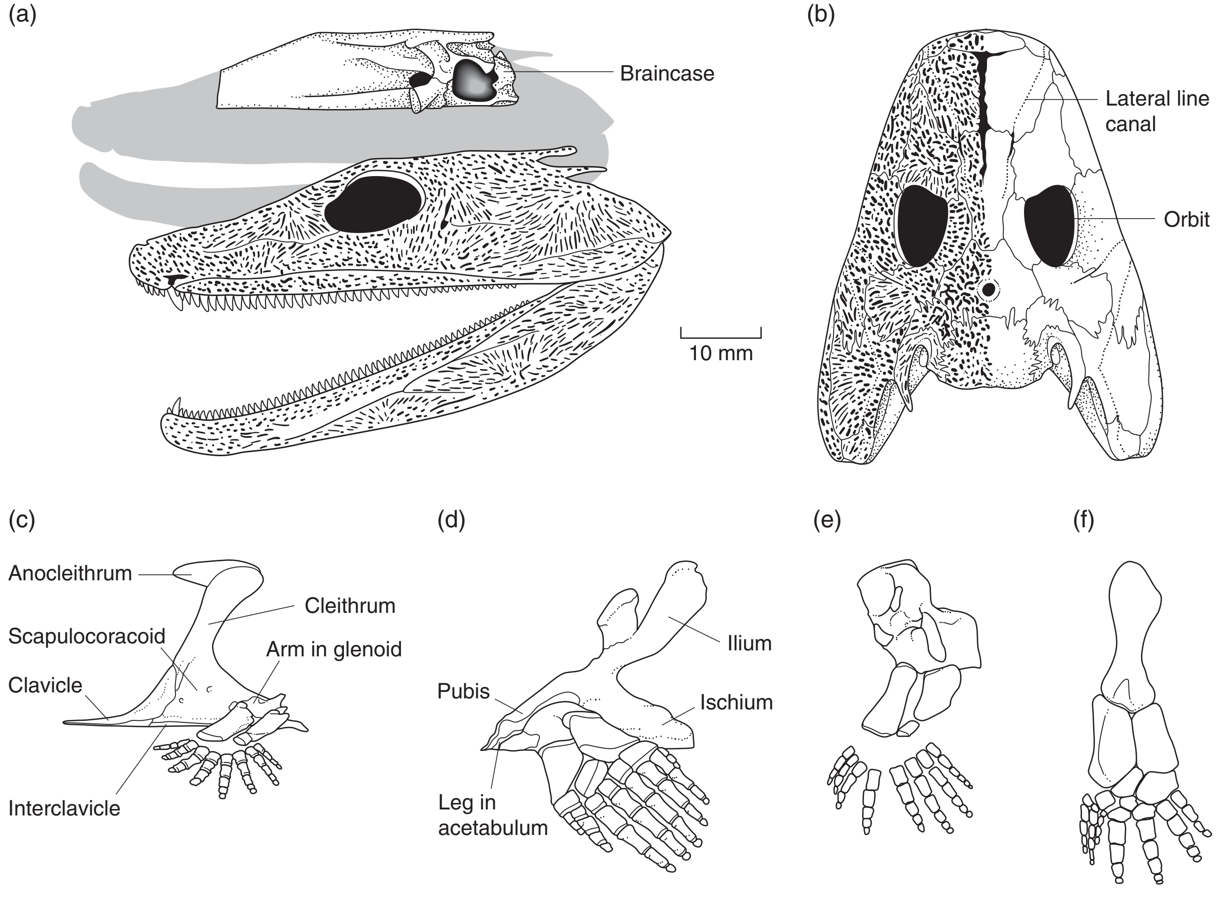


Figure 4.7 The anatomy of *Acanthostega*: (a,b) skull in lateral view, with braincase (a) and dorsal view (b); (c) shoulder girdle and arm in lateral view; (d) pelvic girdle and leg in lateral view; (e) arm and hand in anterior view; (f) leg and foot of *Ichthyostega* in anterior view. Source: (a,b) J. Clack, University of Cambridge, Cambridge, UK. Reproduced with permission. (c–f) M. Coates, University of Chicago, IL, USA. Reproduced with permission.

Eusthenopteron, *Panderichthys* and *Tiktaalik* in side view (Figures 4.6(a–d)), and they retain the buried lateral line canals. As with *Tiktaalik*, both the Greenland tetrapods have lost the posterior skull elements that covered the gill and throat region, and the pectoral girdle is now separate. In dorsal view, it can be seen that *Acanthostega* (Figures 4.6(c), 4.7(b)) has a broader and shorter skull than *Eusthenopteron* (Figure 3.24(b)), with the eyes placed further back. Ventrally, the arrangement of bones and teeth is still as in a basal tetrapodomorph fish.

The pectoral girdle of *Acanthostega* (Figure 4.7(c)) is simplified in some respects when compared to that of a sarcopterygian fish. In *Acanthostega*, there are five main elements: a **cleithrum** above and a **scapulocoracoid** below, the latter bearing the joint surface or **glenoid** for the humerus, and a **clavicle** and **interclavicle** in front of and below the scapulocoracoid respectively. A fifth element is the **anocleithrum**, a thin sheet of bone at the top of the scapulocoracoid, and a primitive structure that links the shoulder girdle to the skull in fishes, but which is lost in most post-Devonian tetrapods. The pelvic girdle (Figure 4.7(d)) is a single plate, showing regions that correspond to the typical paired elements seen in all tetrapods on each side: an **ilium** above, and a **pubis** and **ischium** below, the pubis lying to the front. The joint surface for the head of the femur, the **acetabulum**, is borne in part on all three of these bones. The pelvis is attached to the vertebral column by an elongate rib of the **sacral vertebra,** which meets the inner surface of the ilium on each side. The pubes and ischia also meet their opposite numbers in the midline ventrally, thus making the pelvic girdle a firm all-round basket that holds the acetabula in immovable positions, and supports the posterior part of the trunk and the tail. The glenoid and acetabulum face sideways and backwards, the characteristic of tetrapods, instead of simply backwards as in sarcopterygians.

The limbs of *Acanthostega* and *Ichthyostega* are like those of later tetrapods in most features, but recent work has shown that they are startlingly different in others, especially following the use of modern imaging methods (see Box 4.2). The arm of *Acanthostega*, for example (Figure 4.7(e)), has all the major bones seen in later tetrapods (cf. Figure 4.1(b)), but Coates and Clack (1990) had a surprise when they prepared the hand region of one of their new specimens: they found that it had eight fingers. They then investigated the hindlimb (Figure 4.7(d)), and found that it had eight toes. *Ichthyostega* has seven toes (Figure 4.7(f)), and *Tulerpeton* has six. Again, the remainder of

BOX 4.2 TRANSITIONAL TETRAPOD TOMOGRAPHY

The basal tetrapod *Ichthyostega* from the Late Devonian of East Greenland has been one of the most studied fossil vertebrates. And yet, some aspects of its anatomy remained hidden because of the limitations of regular laboratory preparation techniques. Since the 1930s, specimens have been prepared by skilled technicians in the palaeontology laboratories of Stockholm in Sweden and Cambridge, UK, but the rock is hard and the bones are sometimes incomplete and preserved in rather confused masses.

The application of micro-CT scanning (see Section 2.4.1) has changed all that. Scans made by Stephanie Pierce, in a joint project between the University of Cambridge and the Royal Veterinary College in the UK have begun to generate spectacular results (Pierce *et al*., 2012, 2013a,b). Their model is a composite of 13 specimens, each representing a different portion of the anatomy, but the pectoral girdle and forelimb and the pelvic girdle and hindlimb each come from single individuals, so functional conclusions are not compromised. The resulting model (see illustration) is the result of many months of work, but it is as complete as possible, and has an advantage over the original bones in that the joint mobility can be tested freely, without risk of damage.

The investigators have used their new *Ichthyostega* model for two things so far, to investigate limb motions (Pierce *et al*., 2012) and to establish the homologies of vertebral elements (Pierce *et al*., 2013a). By manipulating the limb bones in the computer models, Pierce *et al*. (2012) showed that the *Ichthyostega* forelimb and hindlimb could move in most ways seen in modern tetrapods, except that there was almost no long-axis rotation of the humerus and femur, meaning that the animal could not turn the hand or foot flat to the ground. This meant *Ichthyostega* could have flopped along on land using its hands and feet like flippers, but it could not have pushed the body off the ground or moved the limbs in an alternating sequence, as in normal tetrapod walking. The main arm and leg motions were an anteroventral to posterodorsal arc, in other words, a sweep from low at the front, to higher at the back, and so more akin to paddle swimming than walking.

Whether *Ichthyostega* was unusual in this aquatic adaptation, as has been suggested before (Coates and Clack, 1995), or whether all Devonian tetrapods were still tied to the water, and had limited ability to haul themselves about on land, has yet to be resolved.

In associated research, Pierce *et al*. (2013a) used their three-dimensional models to explore the nature of the vertebrae in *Ichthyostega*. They found evidence that the pattern of vertebral column evolution was unexpectedly different from the usual assumptions (see Section 4.4.5), with the pleurocentra being fused to the intercentra that directly succeed them, indicating a ‘reverse’ rhachitomous design. (In the rhachitomous pattern, the pleurocentrum sits behind, not in front of, the associated intercentrum.) Examination of other basal tetrapods, including *Acanthostega* from the Late Devonian and *Pederpes* from the Early Carboniferous, shows that reverse rhachitomous vertebrae might be the ancestral condition for tetrapods.

Read more about this research at: http://www.rvc.ac.uk/SML/Projects/TetrapodLimbMotion.cfm, and see movies of the new Cambridge-RVC three-dimensional model of *Ichthyostega* at: http://www.youtube.com/watch?v=GvLlEHQfzBk, movements of the forelimb at: http://www.youtube.com/watch?v=9Ee_qnhldac, and movements of the hindlimb at: http://www.youtube.com/watch?v=zIsvhZAUkic.

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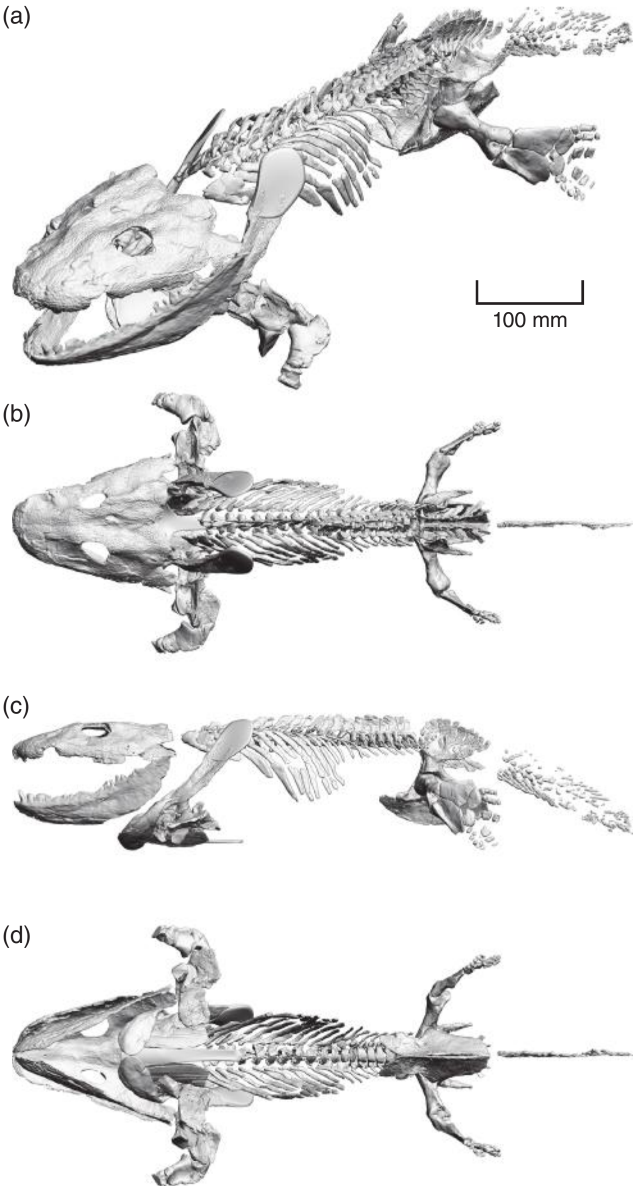


Three-dimensional reconstruction of *Ichthyostega* from micro-CT scan data, in anterolateral (a), dorsal (b), lateral (c), and ventral (d) views. The head is relatively larger than in many previous reconstructions, the pectoral girdle is located more ventrally, and the proportions of parts of the vertebral column are altered (longer trunk, shorter tail). The forelimbs and hindlimbs are shown in their resting pose. Source: Pierce *et al*. (2012). Reproduced with permission from Nature Publishing Group.

the leg shows the standard tetrapod elements, although there are fewer elements in the ankle than in later tetrapods: femur, tibia and fibula in the leg, fibulare, intermedium, **tibiale**, perhaps one centralium, and at least five distal **tarsals** (1–5) in the ankle, and seven toes, each of which has a **metatarsal** and a number of phalanges. Counting outwards from toe 1, equivalent to our 'big toe', but in *Acanthostega* a small toe, the phalanges number 1,2,3,3,3,3,3,2. These observations have profound implications for our understanding of the development of the standard **pentadactyl** ('five-fingered') condition in all later tetrapods.

4.2.2 How many fingers and toes?

For years, everyone had assumed that five fingers and toes was the normal complement for tetrapods. The so-called pentadactyl ('five-digit') limb was a classic synapomorphy of all tetrapods, from salamanders to humans. Our counting system is based on ten, in other words, two handfuls of fingers. The new finds of basal tetrapods with six, seven, or eight digits showed that there is nothing special about five digits, and that each finger or toe is not individually mapped to a single gene.

The tetrapod limb can be divided into three portions that appear in the embryo one after the other, and that appeared in evolutionary history in the same sequence. First came the proximal portion of the limb, the **stylopod** (the upper arm or thigh), equivalent to the root of the fins of Silurian fishes. The middle portion of the limb, the **zeugopod** (the forearm or calf) appears in sarcopterygians in the Devonian, and the distal portion, the **autopod** (the hand and wrist or foot and ankle) appears only in tetrapods in the Late Devonian.

This evolutionary sequence is replicated during development of the embryo (Coates *et al.*, 2008; Clack, 2009; Woltering and Duboule, 2010; Schneider and Shubin, 2013; Suzuki, 2013; Yano and Tamura, 2013). At an early phase, the limb is represented simply by a limb bud, a small lateral outgrowth from the body wall. The tip of the limb bud is the **apical ectodermal ridge (AER)**, a zone of ectoderm that acts as a major signalling centre to ensure proper development of the limb. To one side of the limb bud is the **zone of polarizing activity (ZPA)**, an area of the **mesenchyme** (undifferentiated connective tissue derived mostly from the mesoderm) that contains signals to determine the anterior-posterior axis of the developing limb bud. A key ZPA gene involved in determining the anterior-posterior axis is *Sonic hedgehog* (*Shh*). The proximo-distal axis (shoulder to finger tip) axis is determined by AER signals such as *Fgf8* and *Wnt3a*, and the dorso-ventral axis (top vs. bottom) by AER signals including *Wnt7as* and *En1* (Yano and Tamura, 2013).

Vertebrate fins and limbs develop from proximal to distal, with distinctive developmental zones or domains. In fish fins, these domains separate the proximal sets of bones at the root of the fin from the distal fin rays. In tetrapods, the key skeletal domains are the stylopod, zeugopod, and autopod, probably present already in sarcopterygian fishes, and the limb bud differentiates during development from proximal to distal, under the control of *Shh* and other genes. In fishes, the AER elongates to form an **apical fold** (AF) that gives rise to the dermal fin rays. In tetrapods, the AER never converts to an AF, and fin rays do not develop, but the AER persists until the autopod emerges and digits differentiate. This loss of the AF step and persistence of the AER is critical in the conversion of a fishy fin to a tetrapod limb (Schneider and Shubin, 2013; Yano and Tamura, 2013).

Key to the differentiation of the limb domains are *Hox*, or homeobox, genes. All animals have *Hox* genes, and these function in determining position and orientation of the early embryo, segmentation, and other aspects of the architecture of the body. These genes occur in four replicated sets, or paralogs, and it is the *HoxA* and *HoxD* clusters in particular that control limb development.

Laboratory manipulation of chick and mouse embryos during three phases of development has shown how this works (Figure 4.8(a)). In phase I, the stylopod in the limb bud sprouts, and this is associated with expression of the genes *Hoxd9* and *Hoxd10*. In phase II, the zeugopod sprouts at the end of the limb bud, and the tissues are mapped into five zones from back to front by different nested clusters of all the limb bud genes *Hoxd9* to *Hoxd13*. Finally, in phase III, the distal tip of the lengthening limb bud is divided into three antero-posterior zones, each associated with a different combination of genes *Hoxd10* to *Hoxd13*. Phases I and II have been observed in teleost fish development, but phase III appeared to be unique to tetrapods until experiments with zebra fish embryos showed similar functioning of the *HoxA* and *Hox D* clusters (Woltering *et al.*, 2014). In some sense at least, fish radials are equivalent to tetrapod digits in terms of developmental control.

In the development of vertebrate embryos, there is no fixed plan of every detail of the limb. A developmental axis runs from the side of the body through the limb, and cartilages condense from soft tissues in sequence from the body outwards to the tips of the fingers. In a tetrapodomorph fish (Figure 4.8(b)), the developmental axis presumably ran through the main bony elements, and additional bones, radials, developed in front of the axis (preaxial side). In tetrapods (Figure 4.8(c)), the axis in the leg (arm) runs through the femur (humerus), fibula (ulna), the ankle (wrist), and it swings through the distal carpals (tarsals). Radials condense preaxially at first, as in the sarcopterygian, forming the tibia (radius) and various ankle (wrist) bones. The developmental process then switches sides to sprout digits postaxially (behind the axis). This reversal of limb bud growth direction in the hand/foot is matched by a reversal of the expression of the *Hox* genes. In the zeugopod, *Hoxd9* is expressed in all five zones, *Hoxd10* in the posterior four zones, down to *Hoxd13* only in the posterior of the five. In the autopod, on the other hand, *Hoxd13* is present in all zones, but *Hoxd10* to *Hoxd12* are found only in the posterior zone.

In the Late Devonian tetrapods, six, seven, or eight digits were freely produced, and it was only at the beginning of the Carboniferous that tetrapods seem to have fixed on five digits in hands and feet. Since then, digital reduction has commonly occurred, down to four fingers in the hand (lissamphibians), three (many dinosaurs), two (cows and sheep), or one (horses). In rare cases where there is a sixth digit (some large dogs, pandas), it is a supplementary outgrowth of the wrist or ankle bones.

4.2.3 Modes of life of the first tetrapods

The Late Devonian tetrapods were aquatic, as is shown by the flat, hydrodynamic body outline of the head and body, the retention of a tail fin, a lateral line system and internal gills. The vertebral column was flexible, as in a fish, and the early tetrapods could have swum by powerful sweeps of their tails. In addition, the orientation of the shoulder and pelvic girdles, and the shapes of the limb bones, show that the Late Devonian tetrapods used their limbs more in swimming than walking. The hand and foot, each with its extra digits, were broad and flat, and more use as paddles than feet (Figures 4.6 and 4.7(c, d)). Indeed, it was impossible for *Ichthyostega* to support its weight on its hindlimbs, and these were useful only as swimming paddles (Pierce *et al.*, 2012, 2013a). It could support the weight of its forequarters using its arms, and so *Ichthyostega* moved on land rather like a mudskipper today, crutching forwards in jerky movements, with its tail and hindquarters dragging behind, and stopping frequently

Acanthostega and *Ichthyostega* come from the Britta Dal Formation in East Greenland, from sediments that were deposited

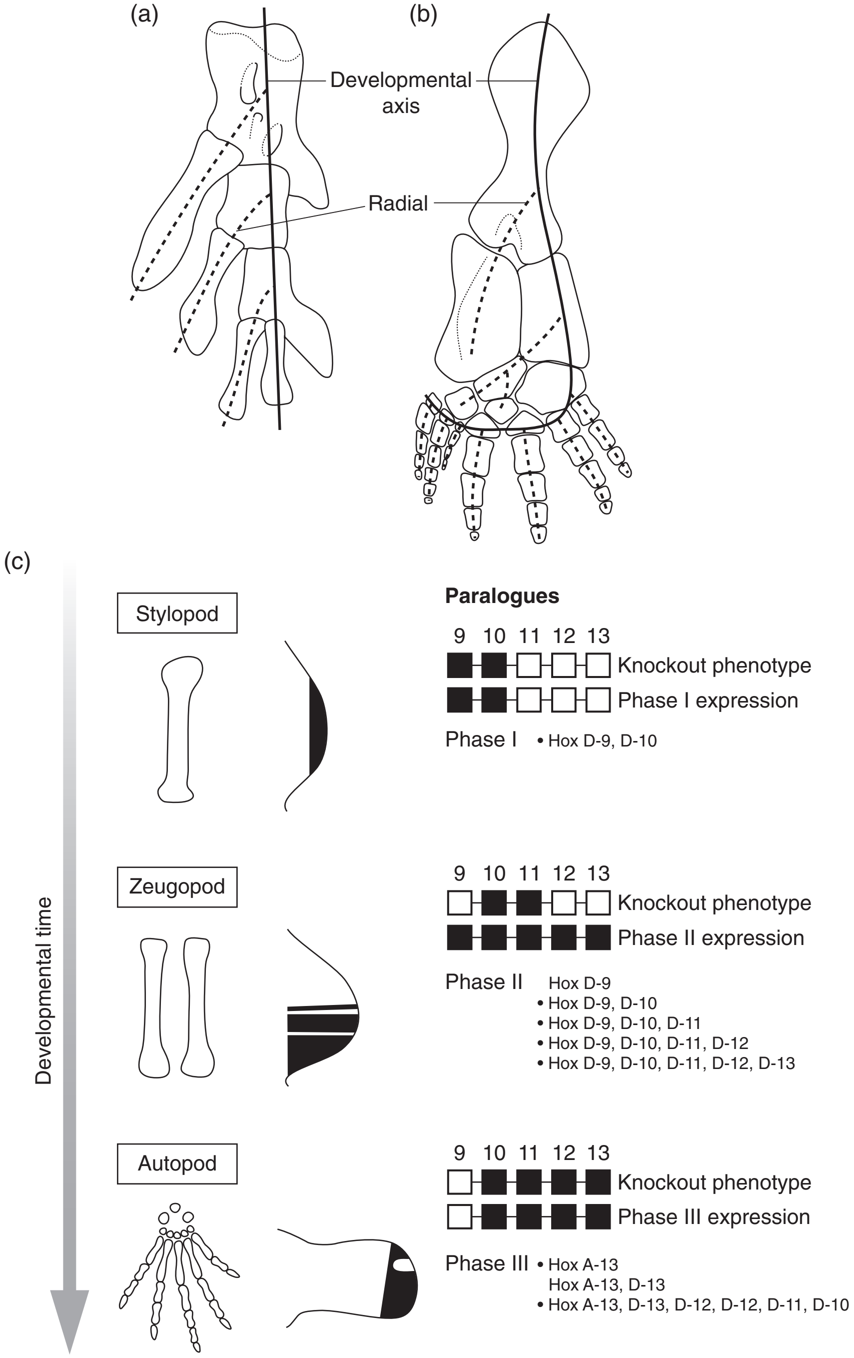


Figure 4.8 Tetrapod limb development. (a) The sequence of growth of a tetrapod limb, reading from top to bottom, showing how the stylopod (humerus, femur), zeugopod (forearm, shin), and autopod (hand, foot) differentiate. The pattern is determined by turning on (filled squares) and off (open squares) of *Hox* genes *Hoxd9* to *Hoxd13*. (b,c) Interpretation of the forelimbs of *Eusthenopteron* (b) and *Acanthostega* (c) in terms of development. The developmental axis (solid line) branches radial elements (dashed lines) in a preaxial (anterior) direction in both forms, and the digits of tetrapods condense in a postaxial direction. Source: (a) Adapted from Shubin *et al.* (1997). (b,c) M. Coates, University of Chicago, IL, USA. Reproduced with permission.

by meandering rivers that flowed through forests of lycopods and low-growing ferns. *Tiktaalik* was found in sediments of the Fram Formation on Ellesmere Island, Nunavut Territory, Canada, also deposited by meandering rivers and streams (Daeschler *et al.*, 2006). In both cases, the climate was monsoonal. These geological units indicate stagnant, vegetation-choked backwaters, from which the tetrapods could emerge in damp conditions, but stay underwater in the dry season, gulping air at the surface. These animals probably walked largely underwater, stepping over vegetation, and kicking themselves along the bottom.

If this is true, it suggests a rather unexpected change in the 'standard' view of why tetrapods grew limbs. Instead of simply stepping out of the water and trotting about on the land, the first tetrapods were still largely aquatic. Coates and Clack (1995) argued that *Acanthostega* and *Ichthyostega* lived in fresh waters, and that *Tulerpeton* lived in the sea. The broad ribs of *Ichthyostega* could have served as a partial support for the internal organs when it ventured on to land, whereas the forelimbs acted as props and the hindlimbs as paddles, rather like a seal. *Acanthostega* and *Ichthyostega* had functioning gills, even as adults (Coates and Clack, 1991), as did *Tiktaalik* (Daeschler *et al*., 2006). Perhaps fully terrestrial tetrapods emerged only 25 Myr later, in the Carboniferous.

4.3 THE CARBONIFEROUS WORLD

Just as there have been debates about **intrinsic** (internal, biological) reasons for *why* the first tetrapods might have ventured onto land in the Devonian (see Section 4.1), researchers have been keen to find correlates with changes in the physical environment. It is common to seek **extrinsic** (external, physical) environmental drivers for major phases in the evolution of life. For example, several authors have speculated that the burst in evolution of gnathostomes in the Late Silurian and Early Devonian was associated with elevated oxygen levels (see Section 3.10.1), and similar explanations have been sought for the rise of tetrapods in the Middle and Late Devonian.

4.3.1 Romer's Gap

It has been suggested that the rise of tetrapods in the Early and Middle Devonian matched a time of generally high temperatures and especially elevated oxygen levels (e.g. Ward *et al*., 2006). The argument is that elevated oxygen levels, for example, enabled fishes and other aquatic animals to breathe air more readily than when atmospheric oxygen levels were low. This would then have provided the boost that was necessary to enable sarcopterygians, as well as air-breathing arthropods, to crawl onto land. Ward *et al*. (2006) in particular argued for close tracking of tetrapod diversity and oxygen levels through the Late Devonian and Carboniferous. They noted that low oxygen levels in the first 14 Myr of the Carboniferous matched the so-called 'Romer's Gap' (Coates and Clack, 1995), a time of sparse tetrapod fossils.

Oxygen as a control on global biodiversity might seem plausible, but calculated levels during Romer's Gap were not particularly lower than through the Late Devonian, when levels were even lower (Ward *et al*., 2006). In fact, such close tracking of global oxygen levels (or indeed any other environmental parameter) and ancient biodiversity might seem improbable. Perhaps high oxygen levels and climatic warming can be said to have encouraged the diversification of early tetrapods, but it is likely they were evolving to exploit new terrestrial food resources (arthropods and plants) in any case, and would have done so whatever the atmospheric conditions (Blieck *et al*., 2010).

Romer's Gap then is likely partly real, a reflection of the substantial faunal turnover between Late Devonian fishes and tetrapods and the new Carboniferous forms, following the Late Devonian mass extinctions (see Section 3.10.2). Biodiversity then might have been kept low by low oxygen levels. It could also be the case that appropriate sedimentary settings in which early tetrapods might be found are also sparse. Combining these factors suggests that Romer's Gap was a combination of low diversity and poor sampling.

4.3.2 The Carboniferous scene

The main phases of early tetrapod evolution took place in the Carboniferous period (359–299 Myr ago). By that time, most of the continents were coalescing into a supercontinent, and land was continuous from Europe to North America, South America and Africa, with no intervening Atlantic Ocean (Figure 4.9).

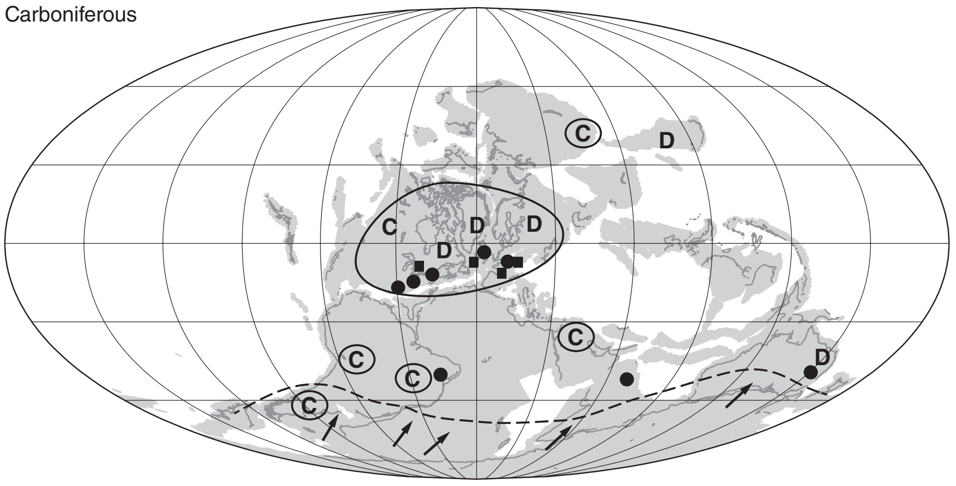


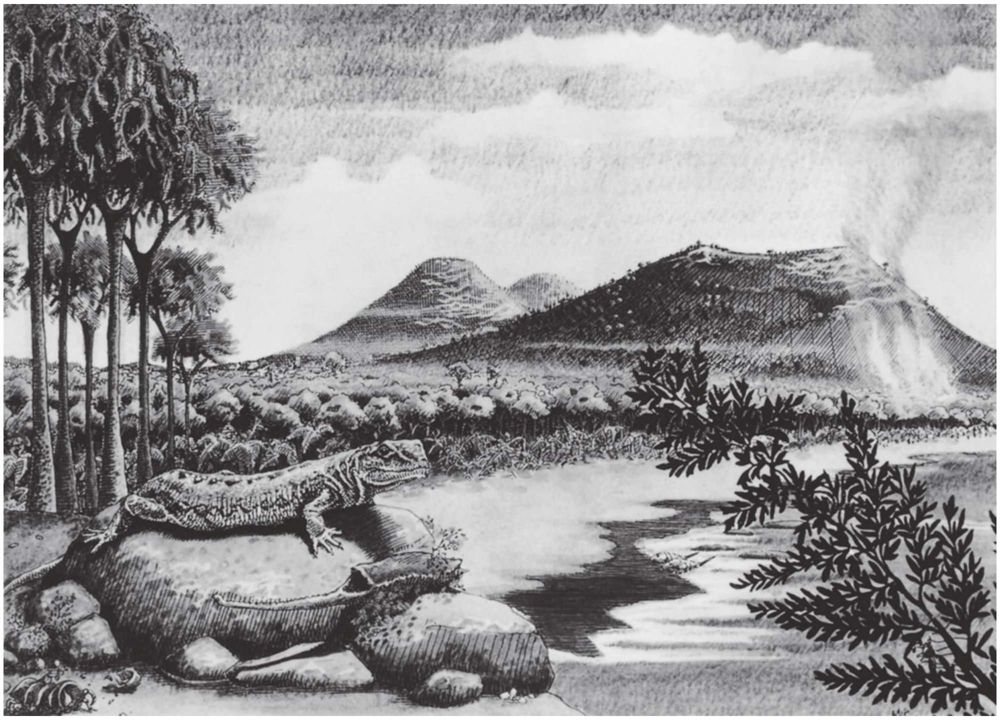
Figure 4.9 Map of the world in Carboniferous times, showing the north (N) and south (S) poles, and the postulated continental positions. Coal forests are circled and marked C, including the extensive coal forests over North America and Europe. The main amphibian localities are shown with symbols as follows: Late Devonian (D), Early Carboniferous (●), and Late Carboniferous (■). The dashed line over South America, southern Africa, India, and Australia shows the known edge of Carboniferous glacial deposits, and the arrows show directions of glacier movement. Source: Alroy (2013) and various sources.

BOX 4.3 TETRAPODS OF THE VOLCANIC SPRINGS

The Midland Valley of Scotland, around Edinburgh and Glasgow, was an important coal-producing area. The coal is associated with richly fossiliferous Carboniferous rocks, and East Kirkton, near Edinburgh, has become one of the most famous sites (Milner *et al.*, 1986; Clarkson *et al.,* 1994; Ruta and Clack, 2006). The rocks consist of volcanic tuffs associated with limestones and unusual layered silica deposits, interpreted as the products of hot springs that were heated by nearby volcanoes.

Fossils were first found at East Kirkton in the 1830s, and the site was rediscovered in 1984 by Stan Wood (1939–2012), a renowned professional fossil collector and preparator. He found tetrapod remains in a dry-stone wall that had been built from rocks taken out of an old quarry. He bought the walls and leased the quarry and re-opened it. After a few years of excavation, he had amassed a huge collection of plants, arthropods (eurypterids, a spider, scorpions, millipedes), fishes (sharks, acanthodians, actinopterygians, a rhizodontid) and tetrapods (see illustration). The tetrapods include a broad-skulled temnospondyl, *Balanerpeton* (see Figure 4.6(e)) and the baphetid *Eucritta*, both of which may have fed on arthropods, a limbless aïstopod, and some embolomeres, *Eldeceeon*, *Silvanerpeton* and *Westlothiana*. *Westlothiana* is close to the ancestry of amniotes and, indeed, was hailed for a time as the world's oldest amniote. The East Kirkton locality is fascinating because of the unusual environmental conditions represented, but it also documents the earliest example of a probable *terrestrial* vertebrate community. The extraordinary diversity of tetrapods contrasts with the very different Late Devonian tetrapod faunas.

In his last years, Stan Wood continued searching in rocks that others might have deemed unpromising. His last major discovery was to identify Tournaisian-age fossils from four localities on the east coast of Scotland between Edinburgh and Berwick (Smithson *et al.*, 2012). The Tournaisian (359–347 Ma) is the first stage of the Carboniferous, corresponding to the bulk of 'Romer's Gap' (see Section 4.3.1), and the new sites provide a glimpse of life immediately after the Late Devonian extinctions. Fossils include arthropods, actinopterygians, rhizodontids, lungfishes, and tetrapods, including a *Crassigyrinus*-like jaw, the basal tetrapod *Pederpes*, and isolated limb and skull remains.



Reconstructed scene at East Kirkton, Scotland, 340 million years ago, during the Early Carboniferous. The reptiliomorph *Westlothiana* sits on a rock contemplating the active volcanoes in the distance, and the steaming hot springs closer by. Fragments of a dead millipede lie at bottom right, and a scorpion fragment is wedged in front of *Westlothiana.* Two eurypterids are testing the water temperature in the middle distance. Source: M. Coates, University of Chicago, IL, USA. Reproduced with permission.

Much of Europe and North America lay around the Carboniferous equator, and tropical conditions prevailed in Carboniferous tetrapod localities.

Damp forests of vast trees and lush undergrowth became widespread. The plants included giant club mosses, 40-m-tall lycopods such as *Lepidodendron*, horsetails up to 15 m tall such as *Calamites*, ferns and seed ferns. As these trees and bushes died, they built up thick layers of decaying trunks, leaves and roots that were buried and eventually turned into coal, the basis of the vast commercial coal deposits of much of Europe and North America today. The trees provided new habitats for flying insects, including some giant forms like dragonflies with the wingspans of pigeons. The decaying plant matter and undergrowth provided even richer habitats for ground-dwelling insects, spiders, scorpions and millipedes (some up to 1.8 m long).

These new habitats opened up great possibilities for the early tetrapods, which diversified extensively. Some forms continued to feed on freshwater fishes by becoming secondarily aquatic, whereas others became adapted to feed on the insects and millipedes. Early Carboniferous tetrapods were poorly known until work on localities in Scotland (see Box 4.3) revealed extensive faunas. Late Carboniferous tetrapods, on the other hand, are well known from Europe and North America in particular.

A major change happened 305 Myr ago, just before the end of the Carboniferous, when the tropical rainforest habitat, the Coal Forests of Europe and North America, collapsed. This was associated with a dramatic climate change across the Euramerican continent from humid to arid, which was itself set off either by a short spell of global warming or by the formation of a south-polar ice cap, which caused sea levels to drop, so increasing continental-scale arid conditions. Coincident with this climate change and the collapse of the lush rainforests, tetrapod biodiversity plunged worldwide, local-scale tetrapod diversity diminished, and **endemism** (regional differentiation of faunas) increased. Sahney *et al.* (2010) suggested that as rainforests fragmented during this time of climatic crisis, tetrapods acquired new feeding strategies, as top predators and as herbivores. Most importantly, the basal tetrapods ('amphibians') that had enjoyed the lush, humid rain forest conditions, declined, and surviving clades, including the amniotes, became more dry-adapted, as a prelude to the Permian world (see Section 5.3).

4.4 DIVERSITY OF CARBONIFEROUS TETRAPODS

Tetrapods radiated into about 40 families in the Carboniferous (Coates *et al.*, 2008). The relationships of Carboniferous and later forms have been debated, but most analysts accept that there were some basal forms before a major split into a batrachomorph ('frog-form') and reptiliomorph ('reptile-form') lineage. Major clades of Carboniferous tetrapods include a series of basal forms, temnospondyls, lepospondyls, and embolomeres. Temnospondyls fall on the batrachomorph line, embolomeres on the reptiliomorph, and lepospondyls have been variously assigned to either of these.

4.4.1 Early Carboniferous tetrapods

The Early Carboniferous used to be a poorly known time interval in tetrapod evolution, but many new species have been described in the past 10 years. Their relationships are still much debated, and many probably fall outside the major clades.

The colosteids, such as *Greererpeton* from the Early Carboniferous of West Virginia, USA (Smithson, 1982), have an elongate body with 40 vertebrae in the trunk and neck, a broad tail and short limbs (Figure 4.10). The eyes are placed well

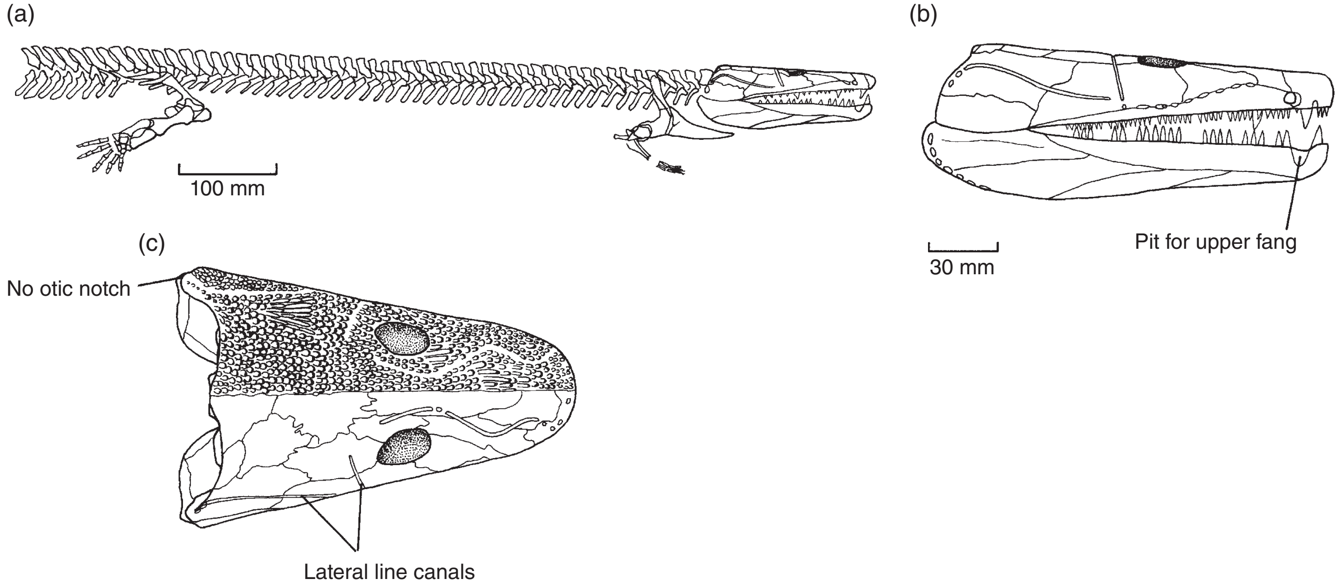


Figure 4.10 The colosteid *Greererpeton*: (a) whole-body restoration; (b,c) skull in lateral and dorsal views, showing the sculpturing of the skull bones on the left side of the dorsal view (c) only. Source: (a) Adapted from Godfrey (1989). (b,c) Adapted from Smithson (1982).

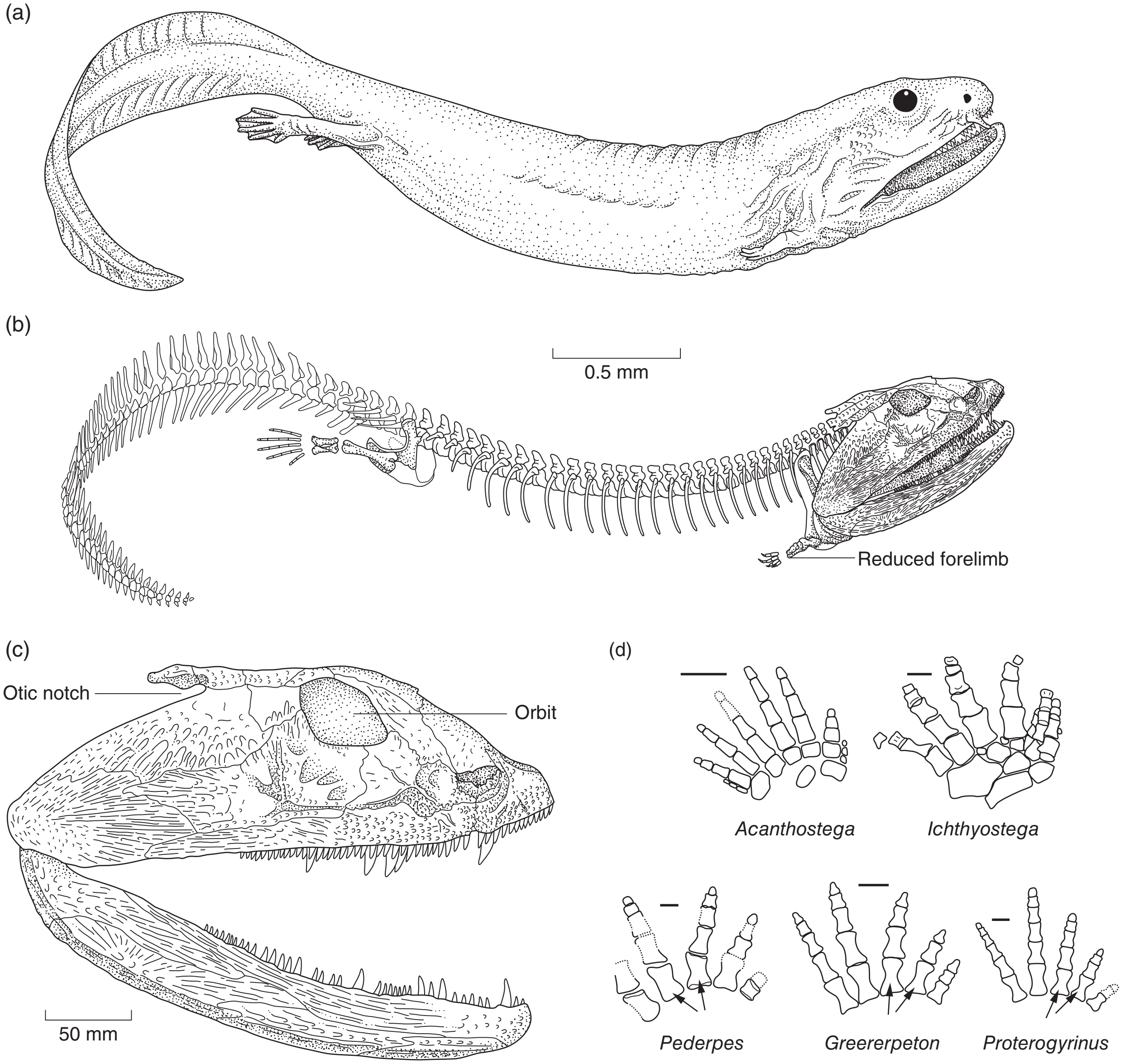


Figure 4.11 Early Carboniferous tetrapods: (a–c) *Crassigyrinus*, whole-body restoration (a), skeleton (b) and skull and lower jaw in side view (c); (d) feet of various early tetrapods, including *Pederpes*. Source: (a,b) M. Coates, University of Chicago, IL, USA. Reproduced with permission. (b,c) J. Clack, University of Cambridge, Cambridge, UK. Reproduced with permission.

forward, the skull and lower jaw are low and flat, and there is no otic notch. The lateral line canals are also well developed, suggesting an aquatic lifestyle.

Crassigyrinus from the Early Carboniferous of Scotland (Clack, 1998; Smithson *et al.*, 2012) was quite different, an elongate Moray eel-like animal with a massive head (Figure 4.11(a–c)). The large skull is covered with heavily sculptured bones. The deep embayments in the side of the skull just behind the eyes are generally called temporal (or otic) notches, and it was once assumed that these accommodated a **tympanum**, or eardrum, which was supposedly linked to the inner ear by the stapes. In basal forms such as *Crassigyrinus*, this space was more likely occupied by a **spiracle**, a remnant of an anterior gill slit still seen today in sharks. With its deep skull and sharp fangs, *Crassigyrinus* was clearly a meat-eater with powerful jaws that could have seized large fishes and resisted their struggles by clamping its jaws shut firmly. *Crassigyrinus* has minute forelimbs, a long narrow body and probably a flattened tail bearing a broad fin.

The Whatcheeriidae are a further distinct clade from the Early Carboniferous, including *Whatcheeria* from Iowa, USA, *Ossinodus* from Australia, and *Pederpes* from Scotland (Clack and Finney, 2005), which were all about 1–2 m long. The lower jaw is deep, and the teeth sharp and slightly **recurved**, indicating that these were predators that presumably fed on large fish, and perhaps other tetrapods. The whatcheeriids show a mix of characters. They retain some fish-like features, such as teeth on the bones of the palate and on the coronoid in the lower jaw, a lateral line enclosed in bone, and a rather primitive ilium, as seen in *Acanthostega*. But, whatcheeriids show derived features: the skull is narrower and taller than that of most sarcopterygians and basal tetrapods, there is a massive tooth on the maxilla, and the skull is lightly sculpted. Most importantly, the foot probably has five toes (Figure 4.11(d)), as in later tetrapods such as *Greererpeton* and *Proterogyrinus,* but the hand might still retain a tiny sixth finger. Functionally, though, these were the first tetrapods adapted more to walking than swimming.

The baphetids, or loxommatids, comprise 11 species from the Carboniferous of the British Isles, the Czech Republic, Nova Scotia, and Ohio (Beaumont, 1977; Milner *et al*., 2009). *Megalocephalus* from the Early Carboniferous (Figure 4.12(a–c)) has a small rounded orbit that extends into an unusual pointed structure in front, which might have housed a gland, or have been a site for muscle attachments. There are traces of lateral line canals. The jaws are lined with short pointed teeth, and there are about six larger ‘fangs’ in the palate. The skull is very low; in fact it is only about as deep as the lower jaw, so that accommodation for the brain was clearly not a priority! Almost nothing is known of the postcranial skeleton of any baphetids.

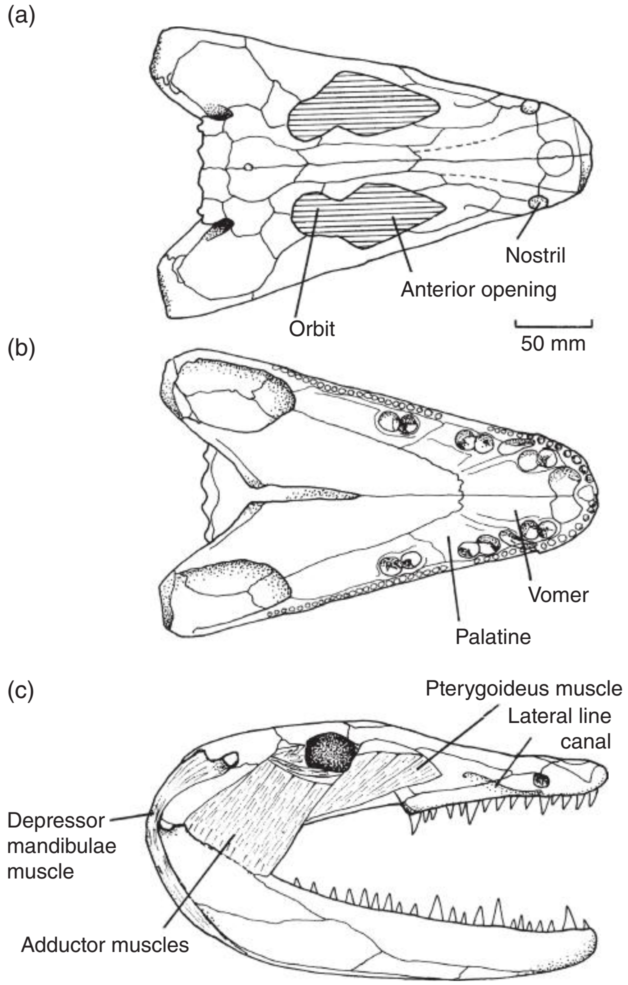


Figure 4.12 The baphetid (loxommatid) *Megalocephalus* : (a,b) skull in dorsal and ventral views; (c) skull in lateral view, with a tentative reconstruction restoration of the main jaw muscles. Source: Adapted from Beaumont (1977).

Large jaw muscles probably ran from the side of the skull to the upper surface of the lower jaw, and these **adductor muscles** acted to close the jaw (Figure 4.12(c)). The jaw opened by means of a smaller jaw **depressor muscle** that ran behind the jaw joint. This is a tetrapod novelty, and represents a further shift from fish-like anatomy in which basibranchial muscles connecting with the shoulder girdle depress the jaw. Muscles can only pull, and the solution of placing a jaw opener *behind* the pivot joint of the jaw is adopted in most tetrapods.

4.4.2 Temnospondyli

The temnospondyls are the main Carboniferous tetrapods, a group that survived in abundance through the Triassic, and with much reduced diversity into the Early Cretaceous, a total span of over 150 Myr. Total numbers of taxa are 300 species and 200 genera (Schoch, 2013). *Balanerpeton* from the Early Carboniferous of Scotland (see Figure 4.6(e)) and *Dendrerpeton* (Figure 4.13) from the Late Carboniferous of Nova Scotia, Canada (Holmes *et al*., 1998) have broad skulls with a rounded front margin, typical of most temnospondyls. The palate of *Dendrerpeton* (Figure 4.13(b)) shows several characteristic temnospondyl features: a broad open space in the middle, an interpterygoid vacuity, which is very small in embolomeres, a long narrow process from the braincase that runs forward across the interpterygoid vacuity, and a pair of broad flat vomers at the front. The arms and legs are stout, the shoulder and hip girdles are strong, and there is a slender sound-conducting stapes, all of which suggest that *Dendrerpeton* was a largely terrestrial animal. Temnospondyls diversified substantially in the Permian (see Section 4.5.1).

4.4.3 Lepospondyli

The lepospondyls are generally small tetrapods that may form a clade (Coates *et al*., 2008), although this has been disputed. They comprise five subclades, of which two, the Lysorophia and Adelospondyli are minor. Lysorophians comprise about ten species of tiny animals form the Late Carboniferous and Early Permian of North America and the British Isles. They are limbless, or have reduced limbs, and about 100 vertebrae, both features being convergent with snakes. Adelospondyls include four species from the mid Carboniferous of the Edinburgh area in Scotland, and they show considerable reduction of skull and limb elements.

The microsaurs, some 30 genera from the Carboniferous and Early Permian (Carroll and Gaskill, 1978), were mainly terrestrial in habits. Cladistic analyses (e.g. Anderson, 2001; Ruta *et al*., 2003a,b; Marjanović and Laurin, 2013) show that the

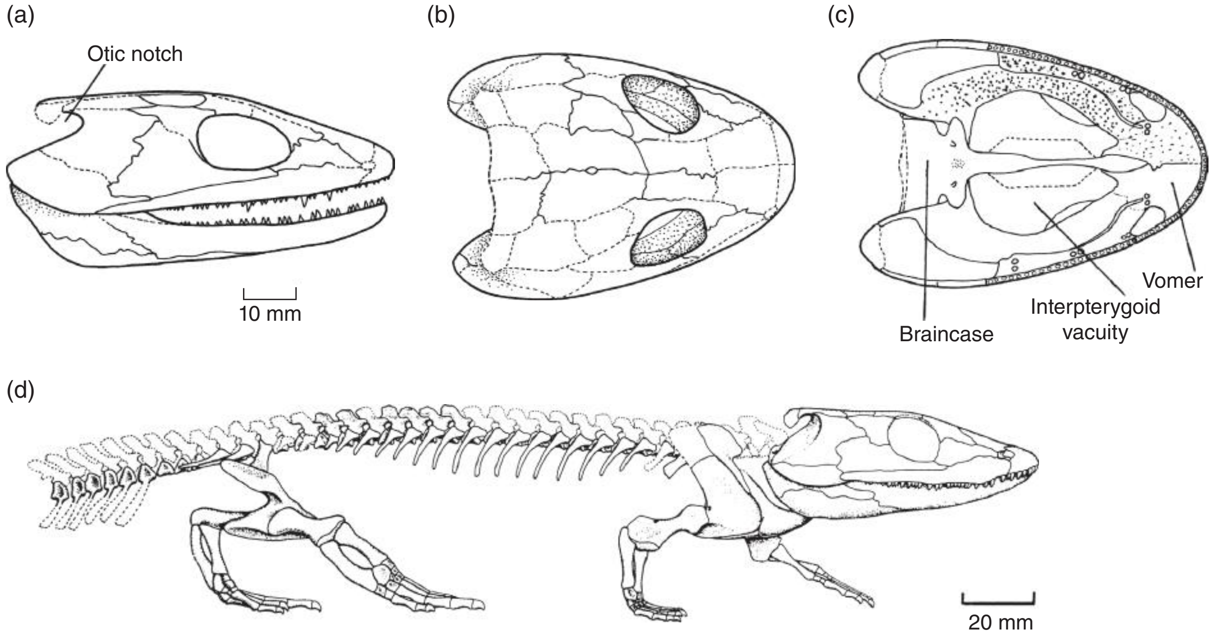


Figure 4.13 The early temnospondyl *Dendrerpeton*: skull in (a) lateral, (b) dorsal and (c) ventral views; (d) lateral view of skeleton. Source: Adapted from Holmes *et al*. (1998).

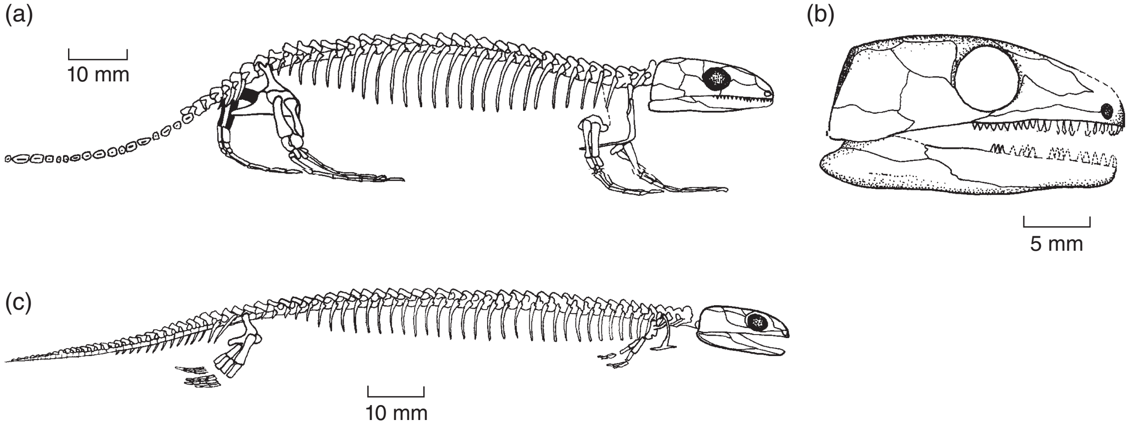


Figure 4.14 Two microsaurs: (a,b) the terrestrial *Tuditanus*; and (c) the aquatic *Microbrachis*. Source: Adapted from Carroll and Gaskill (1978).

Microsauria is not monophyletic, with *Microbrachis* and some other close relatives falling outside the main clade. *Tuditanus*, an early form from the Late Carboniferous of Ohio, USA (Figure 4.14(a,b)), was a highly terrestrial animal, having the proportions of a lizard, with powerful limbs and a strong skull. Its short teeth were adapted for crushing and piercing the tough skins of invertebrates such as insects, spiders and millipedes. Other microsaurs, such as *Microbrachis* (Figure 4.14(c)) from the Late Carboniferous of the Czech Republic, seem to have been secondarily aquatic, with long slender bodies, and reduced limbs and limb girdles. Some microsaur lineages show reduced skull bones, massive occiputs (the posterior part of the skull roof), long bodies, and short legs, which suggest that they were burrowers or leaf-litter foragers.

The nectrideans (Bossy and Milner, 1998) were an aquatic group, known from the Late Carboniferous and Permian. Many, such as *Sauropleura* from the Late Carboniferous of Europe and North America (Figure 4.15(a)), are newt-like in appearance, with very long flattened tails that were presumably used in swimming. The caudal vertebrae of these forms (Figure 4.15(b)) have remarkable ornamented symmetrical spines above and below, part of the deep flat-sided tail that was used for propulsion.

Diplocaulus and *Diploceraspis* from the Late Carboniferous and Early Permian of midwestern USA (Figure 4.15(c–f)) have dramatically expanded skulls marked by enormous ‘horns’ growing out at the sides, which gives the head a boomerang-like appearance. The extensions are formed from massive outgrowths

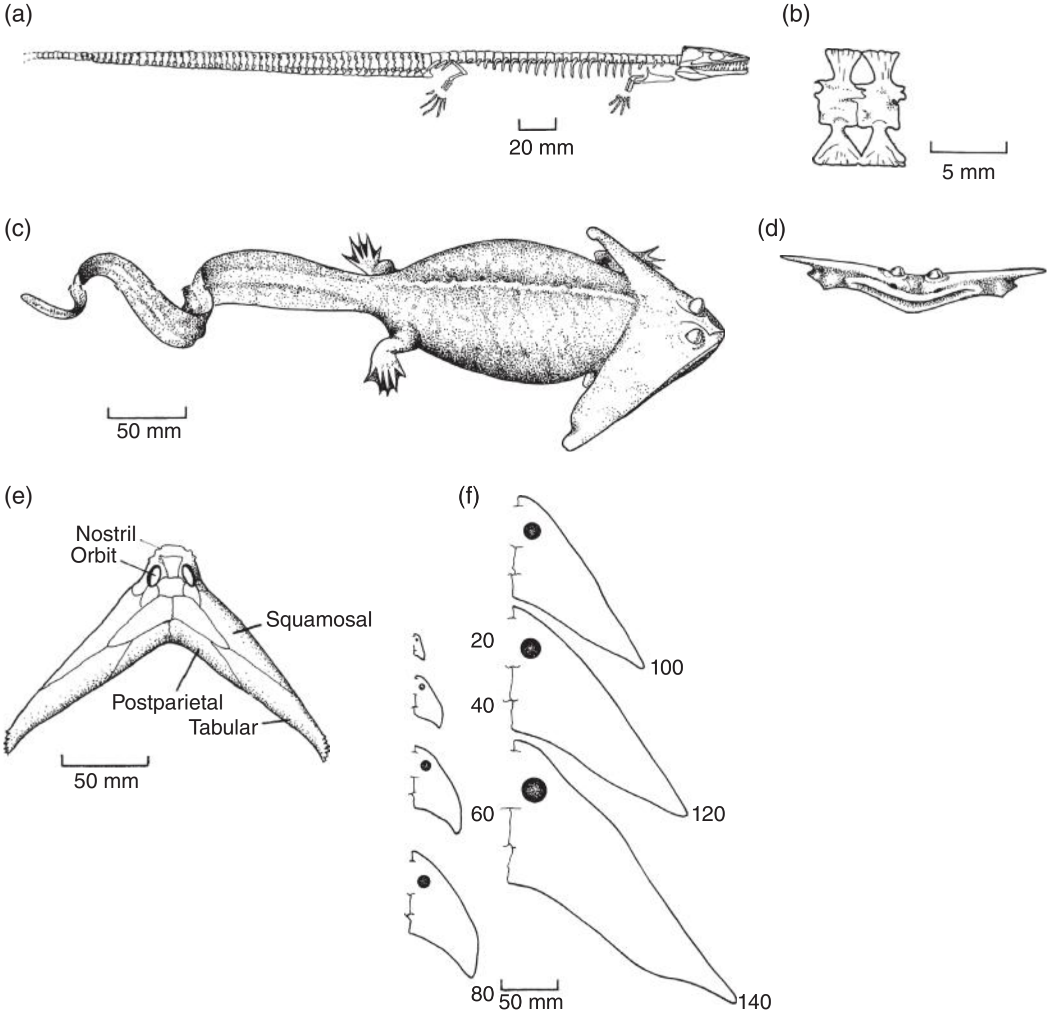


Figure 4.15 Aquatic nectrideans, *Sauropleura*, skeleton (a) and caudal vertebrae in lateral view (b) and *Diplocaulus* (c–f): (c) life restoration; (d) anterior view of head; (e) dorsal view of skull; (f) sequence of growth stages, from juvenile (top left) to adult (bottom right), showing the growth of the projecting ’horns’. The numbers 20, 40, 60, etc., are measurements, in millimetres, of total body lengths. Source: (a,b) Adapted from Bossy and Milner (1998). (c–e) Adapted from Cruickshank and Skews (1980). (f) Adapted from Olson (1951).

of the squamosal and tabular bones, which normally form relatively small parts of the back corners of the tetrapod skull. Juveniles have almost no posterior projections at all, but a study of hundreds of specimens of *Diplocaulus* at all stages of growth (Olson, 1951) shows how they grew out more and more as the animals became older (Figure 4.15(f)). The function of the nectridean ‘horns’ is more of a problem. Biomechanical studies on models of the head of *Diplocaulus* (Cruickshank and Skews, 1980) have shown that its hydrofoil shape provided lift when it was held roughly horizontal, or just tipped up, in even very weak currents. Perhaps *Diplocaulus* and *Diploceraspis* fed on fishes that they caught from a lurking position on the river or lake bottom. They flicked their tails sharply, rushed up from beneath, grabbed a fish, and rapidly sank to the bottom again to enjoy their feast.

The aïstopods, a small group from the Carboniferous and Early Permian of North America and Europe (Carroll, 1998; Anderson, 2002), were snake-like animals, ranging in length from 50 mm to nearly 1 m, with up to 230 vertebrae, and no limbs or limb girdles (Figure 4.16(a)). *Aornerpeton* has a light skull (Figure 4.16(b–d)) with large orbits, and the bones that normally form the back of the skull have been reduced or lost. Because the skull is small, the braincase seems relatively large, and it is exposed in all views. Each vertebra (Figure 4.16(e)) is formed from a single element, unlike those of most other early tetrapods, a condition termed **holospondylous**. The upper portion of the vertebra, the neural arch, which encloses the spinal cord and provides sites for muscle attachment, is fused to the main body of the vertebra, the **centrum**. Similar vertebrae are seen in nectrideans and microsaurs.

The aïstopods are assumed to have lost their limbs secondarily, rather than to have evolved directly from a limbless fish ancestor. Their long trunk and short tail is similar to snakes, and some aïstopods at least may have been able to open their jaws unusually wide because of extra joints in the skull. Perhaps the aïstopods filled terrestrial and semiterrestrial snake-like niches.

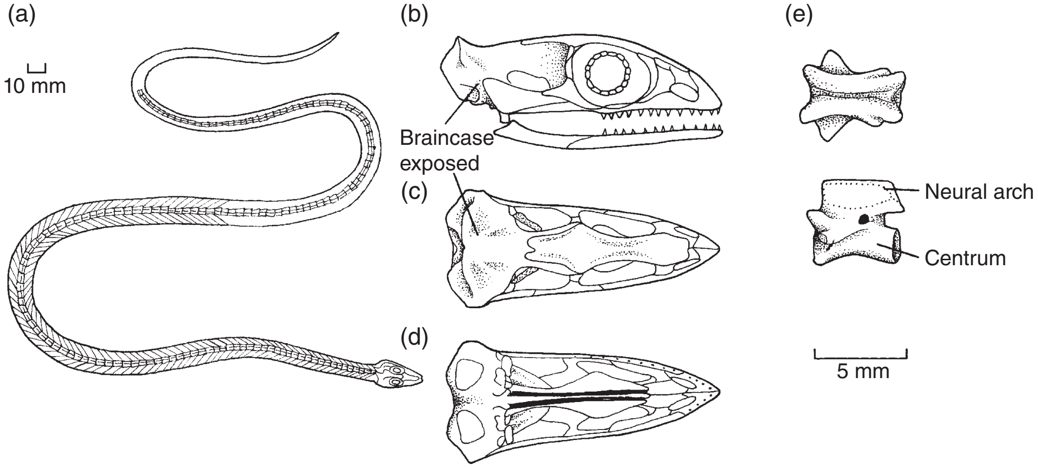


Figure 4.16 The aïstopod *Aornerpeton*: (a) reconstructed skeleton; (b–d) skull in lateral, dorsal and ventral views; (e) trunk vertebra in dorsal (left) and lateral (right) views. Source: Adapted from Gregory (1948).

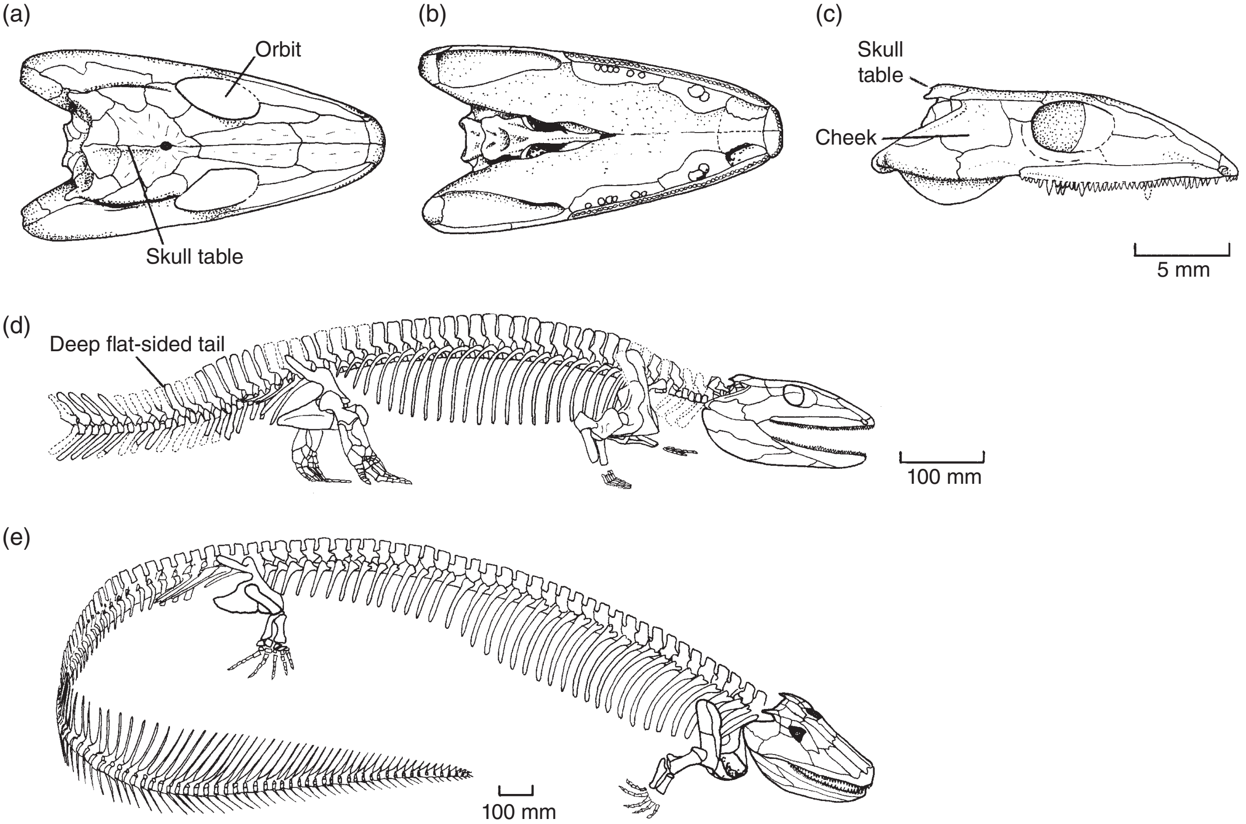


Figure 4.17 The embolomere *Proterogyrinus*: (a–c) skull in lateral, dorsal and ventral views; (d) restoration of the skeleton; (e) the embolomere *Pholiderpeton*. Source: (a–d) Adapted from Holmes (1984). (e) Adapted from Panchen (1972).

4.4.4 Basal Reptiliomorpha: Embolomeri and Gephyrostegidae

The reptiliomorphs, the line that led to amniotes, includes a number of stem amniotes in the Carboniferous and Permian, the aquatic embolomeres and the terrestrial gephyrostegids, seymouriamorphs (see Section 4.5.2) and diadectomorphs (see Section 4.5.3). The basal reptiliomorphs have sometimes been called anthracosaurs, a term that may refer to a group that is similar in content to embolomeres. Embolomeres arose in the Early Carboniferous and include a number of moderate-sized fish-eaters from the Carboniferous and Permian. Some were apparently terrestrial, whereas others became secondarily adapted to life in the water.

Proterogyrinus from the Early Carboniferous of West Virginia, USA (Holmes, 1984) and Scotland, is about 1 m long and has an elongate skull (Figure 4.17(a–d)). The skull table, the square area at the back of the skull (Figure 4.17(a,c)), is set off from the cheek area, and there is a line of weakness between the two units that presumably allowed the skull to flex during jaw opening, as in osteolepiforms. *Proterogyrinus* has large vertebrae, a short neck and a flat-sided tail. The limbs are well developed for moving rapidly on land, but the flattened tail shows that *Proterogyrinus* could swim well. Later embolomeres, such as *Pholiderpeton* from the Late Carboniferous of England (Panchen, 1972), were even more clearly adapted for an aquatic lifestyle, with their long slender bodies, small limbs and deep tail fin (Figure 4.17(e)).

The Gephyrostegidae includes three genera of small Late Carboniferous insect-eaters. These share many features with embolomeres, but also with amniotes, in the palate, shoulder girdle, and tarsus (Ruta *et al*., 2003a,b).

4.4.5 Vertebral evolution

One of the most startling patterns of evolution observed among the basal tetrapods occurs in the backbone. In sarcopterygian fishes, there are three main components of each vertebra, a **pleurocentrum** and an **intercentrum** encompassing the notochord below and a **neural arch** above (Figure 4.18). Then, in the early evolution of tetrapods, the pleurocentrum became the main element of the vertebra in reptiliomorphs, including amniotes (where the pleurocentrum is generally termed simply the 'centrum'), and the intercentrum became the main element in batrachomorphs, including temnospondyls and lissamphibians. The reptiliomorph vertebral condition is sometimes termed 'schizomerous', the temnospondyl 'rhachitomous'.

This split in vertebral evolution among tetrapods is documented in successive fossils. The vertebrae of *Eusthenopteron* and *Acanthostega* are similar in that the intercentrum is the dominant element, a crescent-shaped structure in anterior view, wedge-shaped in lateral view, that is associated with a smaller pleurocentrum, composed of two short elements, one on each side. Close investigation of the vertebrae in *Ichthyostega*, *Acanthostega*, and *Pederpes* by micro-CT scanning (see Box 3.2) showed an unexpected 'reverse-rhachitomous' arrangement, where the substantial intercentrum is fused to the reduced pleurocentrum in front, not behind (Pierce *et al*., 2013b). This discovery may require reconsideration of the condition of vertebrae in later tetrapods. In temnospondyls, the intercentrum expands and the pleurocentrum reduces to a small wedge on either side, the classic 'rhachitomous' condition of the vertebrae seen in the majority of temnospondyls (Schoch, 2013). Among reptiliomorphs, the

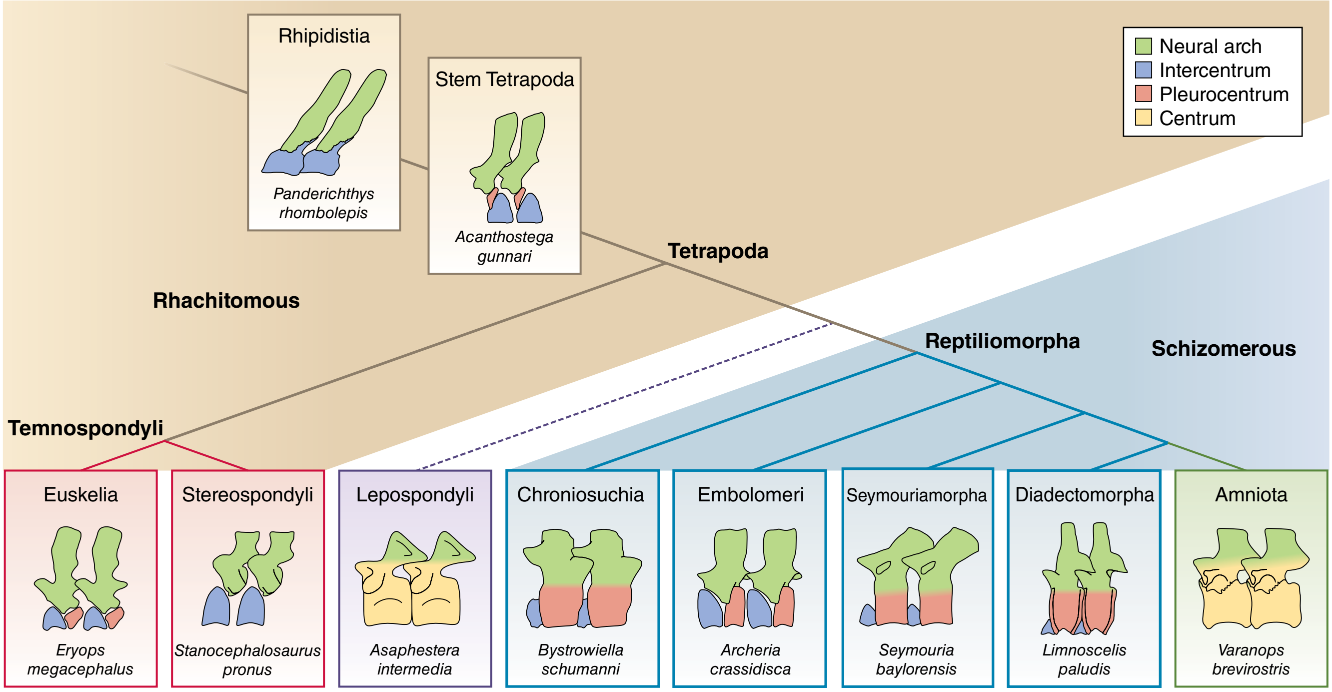


Figure 4.18 Evolution of the basic vertebral structure of tetrapods, showing the classic rhachitomous form to the left (intercentrum dominant) and schizomerous to the right (pleurocentrum dominant). These occur broadly in the Amphibia (Batrachomorpha) and Reptiliomorpha respectively, characterizing modern lissamphibians and amniotes respectively. New work (Pierce *et al*., 2013) has cast doubt on some aspects of this classic model, in demonstrating that the stem tetrapods *Acanthostega* and *Ichthyostega* have a different pattern, in which the intercentrum dominates (like the rhachitomous model), but that the intercentrum is associated, through the pleurocentrum, with the neural arch in front, not behind. See Colour plate 4.2. Source: By Smokeybjb (Own work) [CC-BY-SA-3.0 (http://creativecommons.org/licenses/by-sa/3.0) or GFDL (http://www.gnu.org/copyleft/fdl.html)], via Wikimedia Commons. Adapted with the *Acanthostega* vertebrae modified.

intercentrum and pleurocentrum of embolomeres may be of equal size, and then the intercentrum reduces to a small wedge in seymouriamorphs, and reduces even further in amniotes, becoming either a thin plate or disappearing altogether.

The vertebrae of two groups, the lepospondyls and lissamphibians, have been much debated. Lepospondyls have holospondylous vertebrae (see Section 4.4.3), but is the fused centrum the pleurocentrum or the intercentrum? As expected from their phylogenetic position (see Box 4.5), the centrum of lepospondyls is composed of the pleurocentrum: while this is not clear in nectrideans and aïstopods, many microsaurs have a small intercentrum tucked under the pleurocentrum, and the two elements fuse to form a single centrum. The single centrum in lissamphibians is presumably composed largely of the pleurocentrum, as their closest relatives, the dissorophoids, are unusual among temnospondyls in that the pleurocentrum is much larger than the intercentrum.

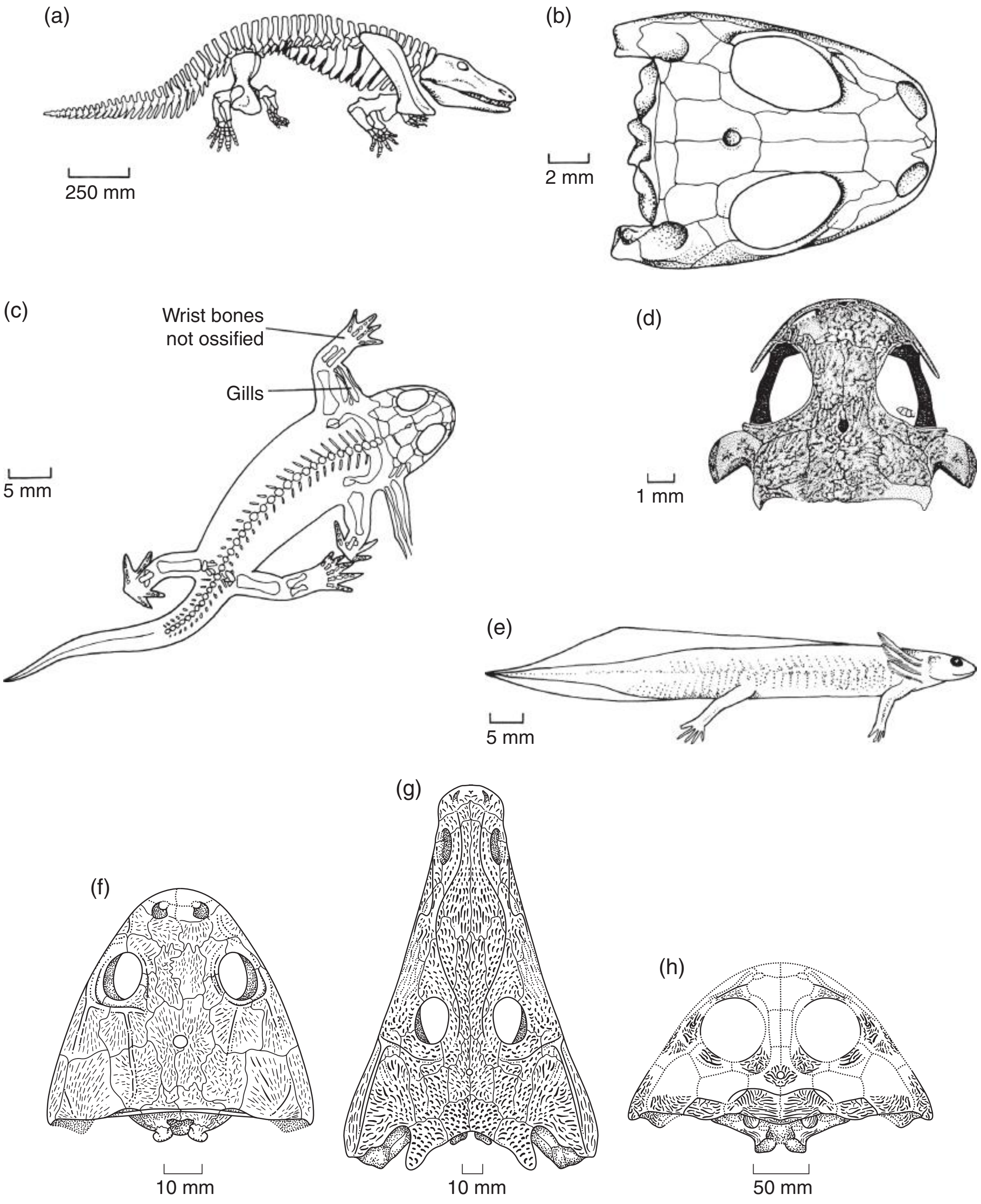


Figure 4.19 Diverse temnospondyls from the Permian (a–e) and Triassic (f–h): (a) *Eryops*; (b) dorsal view of skull of *Doleserpeton*; (c,d) the neotenous branchiosaurid *Apateon*, showing tadpole-like characters, such as gills and poorly ossified bones: (c) reconstructed skeleton; (d) skull in dorsal view; (e) reconstructed branchiosaur; (f) the dvinosaur *Tupilakosaurus*; (g) the capitosaur *Benthosuchus*; (h) the plagiosaur *Plagioscutum*. Source: (a) Adapted from Gregory (1951). (b) Adapted from Bolt (1977). (c,d) Adapted from Boy (1972). (e) Adapted from Milner (1982). (f–h) M. Shishkin, formerly, Paleontological Institute, Moscow, Russia. Reproduced with permission.

4.5 TEMNOSPONDYLS AND REPTILIOMORPHS AFTER THE CARBONIFEROUS

The major environmental upheaval towards the end of the Carboniferous, when humid coal forests were replaced by drier conditions (see Section 4.3.2), marked the end of many basal tetrapods. Those that survived into the Permian (299–252 Myr ago) and beyond include some Embolomeri, Aïstopoda, Nectridea and Microsauria, most of which died out by the end of the Early Permian. Three clades lasted much longer, the Temnospondyli and the reptiliomorph Seymouriamorpha and Diadectomorpha. Among the survivors importantly were the Amniota also (see Chapter 5).

4.5.1 Temnospondyli: Permian to Cretaceous history

Temnospondyls radiated extensively after the Carboniferous (see Section 4.4.2), splitting into some 30 lineages (Yates and Warren, 2000; Schoch, 2013). They are noted for their broad, rather frog-like, skulls that were well adapted for sucking in prey underwater, and also for buccal pumping (see Section 4.1.3).

Among Early Permian temnospondyls were a number of terrestrially-adapted forms. *Eryops* from the Early Permian of North America (Figure 4.19(a)) has heavier limbs and a more massive skeleton than its earlier relatives. This 2-m-long animal was one of the top carnivores of its day, feeding on smaller tetrapods and on fishes. The dissorophid temnospondyls were probably fully terrestrial in habit. They have short skulls (Figure 4.19(b)) with huge orbits and a large ear drum. Other Early Permian temnospondyls, such as archegosaurids, were gharial-like fish-eaters.

The branchiosaurs represent an interesting side-branch in temnospondyl evolution in the Late Carboniferous and Early Permian of central Europe in particular. These small animals, 50–100 mm long, show larval characters (Figure 4.19(c,d)), such as external gills, and **unossified** elements in the wrist and ankle (i.e. they were still cartilaginous and had not turned into bone). At one time, the branchiosaurs were identified as the tadpole larvae of temnospondyls such as *Eryops*, but Boy (1974) concluded that, while some may be larvae (cf. Figure 4.4), most are in fact paedomorphic adults, sexually mature animals with juvenile bodies. The anatomy of the *Branchiosaurus* skull in particular (Figure 4.19(d)) shows so many synapomorphies with the dissorophids (Figure 4.19(b)) that Milner (1982) and Schoch and Milner (2008) have interpreted the branchiosaurs as a paedomorphic sister group.

A remarkable series of lake deposits in the Saar-Nahe basin of Germany document some 20 Myr of the Late Carboniferous and Early Permian, and they have yielded thousands of specimens of fishes and basal tetrapods throughout (Schindler and Heidtke, 2007; Schoch, 2009a,b). Among the rich fossil finds are branchiosaurs and other temnospondyls that show in exquisite detail how their ontogenetic trajectories altered to permit adaptation to climate cycles from wet to dry conditions (Box 4.4).

BOX 4.4 LIFE CYCLES AND CLIMATE IN THE EARLY PERMIAN

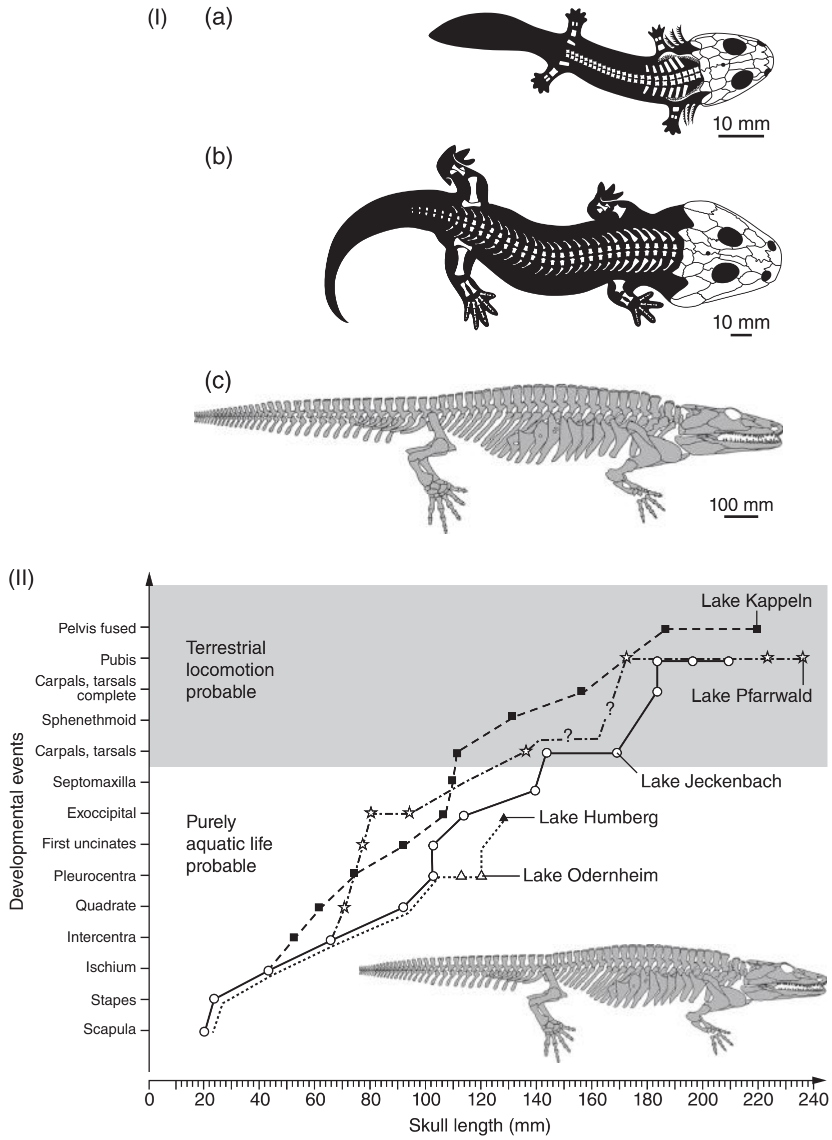
Modern amphibians are well known for their elaborate larval cycles, in which the egg hatches in water as a tadpole, a gill-breathing, aquatic form, and then later metamorphoses into the air-breathing adult. Today, frogs and salamanders can modify this life cycle to take account of changing climatic conditions, with some forms, such as the famous axolotl, suppressing metamorphosis and essentially remaining as an adult tadpole all its life, whereas others shorten the tadpole stage and concentrate on more terrestrial adult forms. These variations on the regular life cycle are termed **heterochrony** (‘different timing’), and they can be a powerful opportunity for major evolutionary change. Well-known examples of heterochrony include **paedomorphosis** (‘child form’), where the adult retains juvenile features and the opposite, **peramorphosis** (‘older form’), where the adult form appears to develop further than is usual.

Some of the best examples of heterochrony in basal tetrapods come from the Carboniferous to Permian Saar-Nahe Basin in Germany, a succession of sediments that documents a series of ancient lakes and surrounding lands. During a span of 1–2 Myr in the earliest Permian, researchers identify a series of four lake systems in stratigraphic levels M6–10: (1) M6, during which a medium-sized water body (Lake Jeckenbach) existed in the northern part (30 km length) and a much smaller one (Lake Niederkirchen) in the southern part (10 km); (2) M8, during which the two subbasins were flooded by a larger lake (Lake Odernheim) that covered almost half of the Saar-Nahe Basin area (40 km); (3) M9, in which a large lake existed in the northern part (Lake Kappeln, 70 km long) and a smaller lake in the southern region (Lake Pfarrwald, 20 km); and (4) M10, during which almost the entire Saar-Nahe Basin was covered by a deep, long-lived water body (Lake Humberg-Lebach) approaching 80 km in length.

Tetrapods are found throughout these successions, and one of the most closely studied is the actinodontid temnospondyl *Sclerocephalus*, the largest aquatic predator in the ecosystem, which fed primarily on the palaeoniscid fish *Paramblypterus*. Over 100 specimens are known, from tiny larvae barely 5 cm long to adults at 1.0–1.7 m, and these have allowed detailed reconstruction of the sequence of ossification of the skull and skeleton, and overall changes in size and proportions (Schoch, 2003, 2009a,b; Schoch and Witzmann, 2009). In early embryos, the skull and shoulder area are well ossified, emphasizing the importance of these regions in feeding and swimming. Later in ontogeny, the vertebral column ossifies back to the pelvis, the limb bones become more substantial, and bones appear in the fingers and toes. Last to be ossified are the wrist, ankle, and caudal vertebrae (see illustration I).

Sclerocephalus was breeding in all six of the Saar-Nahe lakes, and so ontogenetic trajectories in each lake could be reconstructed (Schoch, 2009b). These show subtle differences in the relationship between body length (a rough indication of age) and the timing of ossification events in each of the lakes (see illustration II(a)). At a certain skull length (about 110–140 mm), *Sclerocephalus* adults became primarily terrestrial in habits, based primarily on ossification of the carpus and tarsus, and later of the pelvis. However, in Lake Niederkirchen, adults left the water early, partly to escape the large predatory shark *Orthacanthus*. Further, in Lakes Odernheim and Humberg it seems that *Sclerocephalus* remained aquatic, not exceeding skull lengths of 130 mm, reflecting the rather limited food supplies. The populations in Lakes Odernheim and Humberg show truncation of development, a form of paedomorphosis, because the small adults retained some juvenile characters (lateral line systems; certain skull elements not ossified).

This example shows how complex evolutionary data may be drawn from cases where the fossil record is unusually rich, and where conditions have preserved organisms at a variety of developmental stages. The differences in *Sclerocephalus* life cycles were likely driven by local environmental pressures of the Saar-Nahe lakes (lake extent, depth, climate, prey, predators). However, whether these differences would become locked into the genome, and so become fixed in evolution, is less clear. Organisms generally have wider potential in terms of morphology and adaptation than is expressed because they are limited by other species occupying similar ecospace. Heterochronic shifts may be a way for a species to make a relatively short-term adjustment to changing conditions, or they might eventually become locked in permanently into the genome of the species and so affect its longer-term evolution.



(I) Sequence of developmental stages of *Sclerocephalus* from the earliest Permian of Germany, showing an early larval stage (a) a larger larva (b), showing how portions of the skull and postcranial skeleton become ossified successively. The adult form (c) shows full ossification at considerably larger body size.

(II) Ontogenetic trajectories of the six "populations" of *Sclerocephalus*. Reconstructed trajectories of the best-studied samples from five of the six lakes. Source: Schoch (2013) Reproduced with permission from John Wiley & Sons.

At the end of the Permian, the temnospondyls largely died out, except for three main lineages, *Tupilakosaurus*, and the progenitors of the Capitosauria and the Trematosauria (Schoch and Milner, 2000; Yates and Warren, 2000). *Tupilakosaurus* was a last surviving member of the Dvinosauria, a clade known mainly from Russia, consisting of animals from 0.5 to 1 m long, with broad skulls (Figure 4.19(f)) marked by radiating sculpture and obvious lateral line grooves. The capitosaurs, known only from the Triassic, diversified to include a number of genera of large flat-headed semi-aquatic or completely aquatic animals, some of them 3–4 m long. *Benthosuchus* (Figure 4.19(g)) was common in the Early Triassic of Russia. Capitosaurs dominated the freshwater ponds, lakes and rivers of the Triassic, but they became extinct before the end of the period.

The trematosaurs include a number of lineages, most of them Triassic in age, and most of them aquatic. Among these, the plagiosaurs, such as *Plagioscutum* (Figure 4.19(h)) were most remarkable (Damiani *et al*., 2009). These were like giant, flattened tadpoles, up to 1 m long, and equipped with external branching gills as adults. They had remarkably short, broad skulls and reduced limbs, and they were highly aquatic.

The habitats and feeding modes of temnospondyls changed substantially through time, especially as the different clades adapted to major crises and competitor groups through the Carboniferous, Permian, and Triassic. A functional study of temnospondyl skulls (Fortuny *et al*., 2011) shows that basal temnospondyls, such as edopoids, were able to leave the water and feed on land. In the Early Permian, eryopids were terrestrial feeders, although some members showed a shift to increased aquatic feeding, and archegosaurs especially occupied the aquatic environment. After the end-Permian mass extinction, trematosaurs and capitosaurs returned to the aquatic environment and they became amphibious and fully aquatic feeders, presumably because of competition from synapsids and archosaurs in terrestrial habitats.

Temnospondyls largely disappeared during the end-Triassic mass extinction, but isolated post-Triassic examples are known, all of them trematosaurs. An Early Jurassic chigutisaurid was reported from Australia in 1983, Middle and Late Jurassic brachyopids from China in 1985 and 2005, a Late Jurassic brachyopid from Mongolia in 1991, and finally an Early Cretaceous chigutisaurid, *Koolasuchus*, from Australia (Warren *et al*., 1997). The chigutisaurids and brachyopids seem to have survived very late in Australia and Asia, perhaps in isolated basins that were not invaded by crocodilians.

4.5.2 Seymouriamorpha

The seymouriamorphs are a small group of terrestrial and aquatic reptiliomorphs. *Seymouria* from the Early Permian (Figure 4.20(a)) was a 600-mm-long active terrestrial animal that lived in reasonable abundance in the southern midwestern USA and Germany

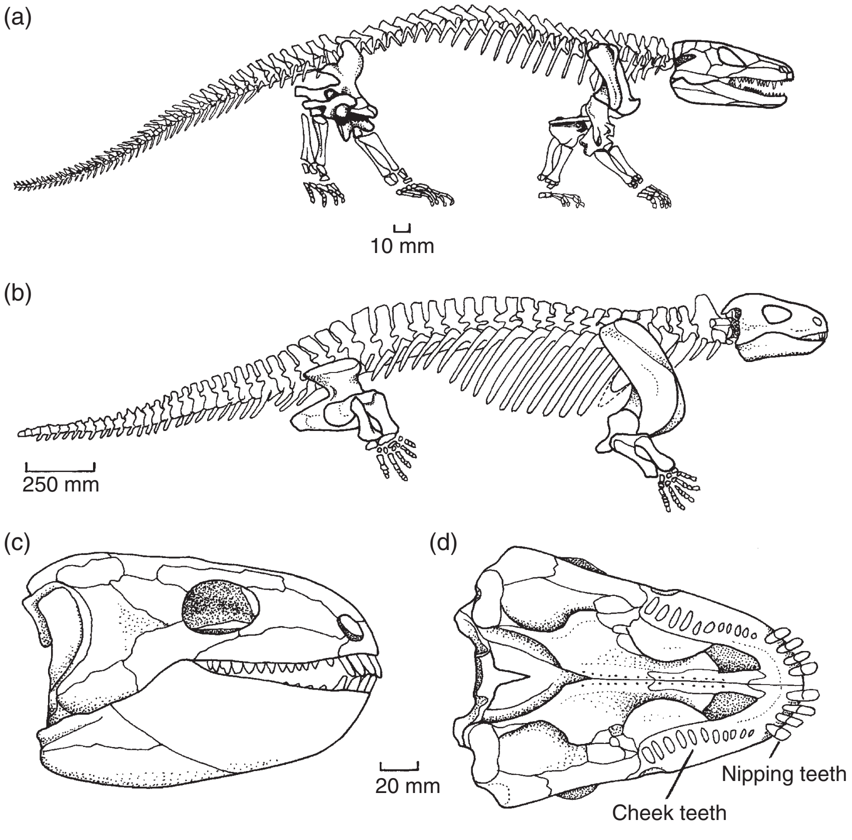


Figure 4.20 Advanced reptiliomorphs: (a) *Seymouria* skeleton; (b–d) *Diadectes*: (b) skeleton; (c) skull in lateral and (d) ventral views, showing the herbivorous adaptations of the dentition. Source: (a) Adapted from White (1939). (b) Adapted from Romer (1944). (c,d) Adapted from Carroll (1969).

(Klembara *et al*., 2005). It had powerful limbs, and the body was held higher off the ground than in most other basal tetrapods.

Seymouriamorphs might have disappeared in the Middle Permian, but several largely aquatic lineages radiated in Russia, and extended their ranges into central Asia and China, and the Germanic Basin at times through the Late Permian to Middle Triassic. The 1–2 m long Late Permian kotlassiids had broad skulls and fed on fishes. The discosauriscids were small, 400 mm long, terrestrial forms from the Permian of Europe and Asia. The chroniosuchians, small to medium-sized, long-snouted animals from the Late Permian to Middle Triassic of Russia and surrounding territories had broad, paired, interlocking bony plates running down the middle of their backs, giving them some protection and support of the torso, as in crocodilians, especially for powerful beating of the tail during swimming (Buchwitz *et al*., 2012). Note that the phylogenetic position of chroniosuchians has long been debated, whether they are basal or derived reptiliomorphs: their braincases, for example, are identical to those of embolomeres (Clack and Klembara, 2009).

4.5.3 Diadectomorpha

The diadectomorphs, Late Carboniferous and Early Permian terrestrial forms, are reptiliomorphs, very close to the origin of the amniotes (Kissel and Reisz, 2004). *Diadectes* from the western USA and Germany (Figure 4.20(b–d)) is rather heavily built, with massive limb girdles, short limbs and heavy vertebrae and ribs (Berman *et al*., 1998). Its key features are, however, seen in the skull. *Diadectes* was one of the first terrestrial vertebrates to adopt a herbivorous diet: there are eight short peg-like teeth at the front of the jaw that were used for nipping off mouthfuls of vegetation, and rows of broad blunt cheek teeth that were used to grind it up. Diadectomorphs have the distinction of featuring close to the origin of Amniota in most phylogenies (see Box 4.5).

4.6 EVOLUTION OF THE MODERN AMPHIBIANS

Modern amphibians, the Lissamphibia, are diverse, being represented by more than 7200 species that fall into four distinctive clades, the extinct albanerpetontids, the anurans (frogs and toads), the urodeles (newts and salamanders), and the gymnophionans (limbless caecilians). The history of each of these will be outlined briefly before a consideration of their origins and relationships.

4.6.1 Albanerpetontidae

The albanerpetontids are a family of some five or six genera, known from the Middle Jurassic to the Pliocene of Europe (Gardner, 2001; McGowan, 2002; Maddin *et al*., 2013), and most widely represented by *Albanerpeton* from North America. *Celtedens*, an early form, about 70 mm long, from the Late Jurassic and Late Cretaceous of Europe (Figure 4.21(a,b)), looks just like a salamander, and it is no wonder that the albanerpetontids

BOX 4.5 RELATIONSHIPS OF THE BASAL TETRAPODS

Cladistic analyses of basal tetrapods show that the Devonian and many Early Carboniferous forms are outgroups, or stem taxa, to a major neotetrapod clade (see Box 4.1). The neotetrapods diverged along two major lines in the Early Carboniferous, one terminating in modern amphibians (Lissamphibia) and one in modern reptiles, birds and mammals (Amniota), forming the clades Batrachomorpha and Reptiliomorpha respectively.

The assignment of the major extinct clades of basal tetrapods – the temnospondyls, lepospondyls, embolomeres, seymouriamorphs, and diadectomorphs – has been controversial. Debate points include whether Lepospondyli is a valid clade or not, and whether it sits within Batrachomorpha or Reptiliomorpha, whether temnospondyls, embolomeres and seymouriamorphs are reptiliomorphs or lie below the split between Batrachomorpha and Reptiliomorpha, and whether the modern amphibians, Lissamphibia, arose from among the temnospondyls or from among the lepospondyls.

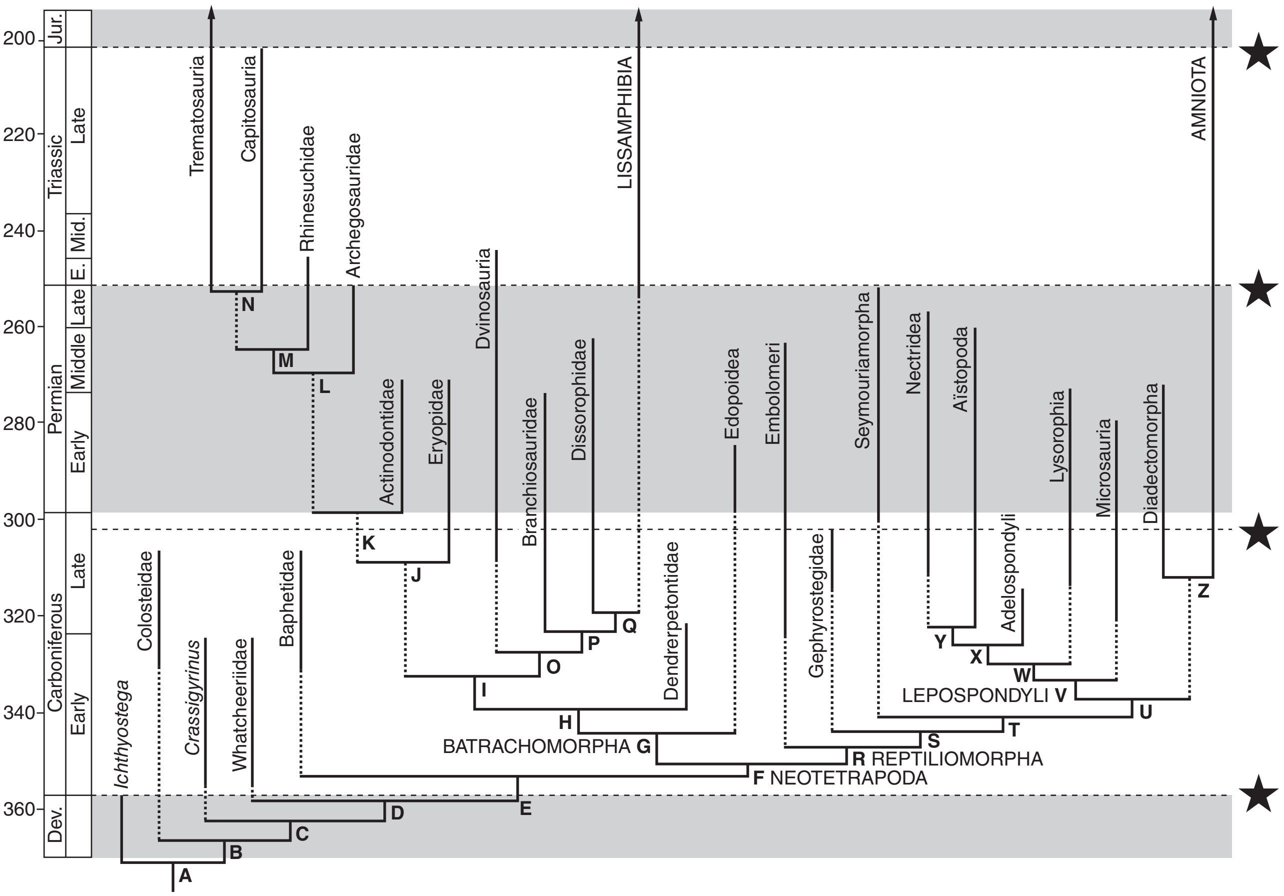
These debates have been rumbling since the 1980s, and it would be fruitless to track through all the to-and-fro of the argument. Marjanović and Laurin (2013) present a thorough summary of the whole debate, focusing on their favoured Lepospondyl Hypothesis (LH), and reasons for seeking the origins of Lissamphibia among Lepospondyli. Their argument rests on numerous shared similarities between various of the lepospondyls (lysorophians, microsaurs, nectideans, and aïstopods) and various of the lissamphibians. Further, these authors note good temporal overlap between lepospondyls (extending arguably to the Late Permian or even Early Triassic), and the first lissamphibians in the Early Triassic. However, the majority view prefers the alternative Temnospondyl Hypothesis (TH).

The TH is that Lissamphibia emerged from among Temnospondyli, the majority view, and supported by Ruta *et al*. (2003a,b), Ruta and Coates (2007), Coates *et al.* (2008), Sigurdsen and Green (2011), and Schoch (2013, 2014). The phylogeny presented here (see illustration) follows these recent results. From the base, there are some stem-group taxa (Colosteidae, *Crassigyrinus*, Whatcheeriidae, Baphetidae), and then a major clade, sometimes termed Neotetrapoda, that divides into a batrachomorph clade, those tetrapods on the line to lissamphibians, and a reptiliomorph clade, those tetrapods on the line to the amniotes.

The Batrachomorpha have a shallow skull and a fused skull roof with no kinesis with the cheek. Batrachomorphs have only four fingers in the hand, representing the permanent loss of one finger. Temnospondyls, as classically defined, are a paraphyletic group, forming a series of outgroups to Lissamphibia.

Continued

The Reptiliomorpha comprises some basal forms (Embolomeri, Gephyrostegidae, Seymouriamorpha), the Lepospondyli (nectrideans, aïstopods, adelospondyls, lysorophians, and microsaurs) and Diadectomorpha + Amniota.



Cladogram showing the relationships of the major groups of basal tetrapods, based on synapomorphies from Ruta *et al*. (2003a) and Coates *et al*. (2008), with divisions of 'Temnospondyli' from Schoch (2013). Only a small selection of temnospondyl families is shown. See Box 4.1 for context of Devonian tetrapods; see Box 5.1 for relationships of Amniota. Synapomorphies include: **A**, see Box 4.1; **B**, five or fewer digits; **C**, orbits neither round nor elliptical, tabular does not contact squamosal, large scapular blade; **D**, anterior palatal vacuity absent, humerus shorter than the length of two and a half mid-trunk vertebrae; **E**, occipital condyles present, notochord excluded from braincase in adult, ectepicondylar foramen in humerus absent; **F NEOTETRAPODA**, lateral line system on skull roof absent, mandibular canal absent, ventral humeral ridge absent; **G BATRACHOMORPHA**, postparietal and exoccipital contact, wide vomer, stapes rod-like, humerus with distinct elongate shaft, four fingers; **H EUTEMNOSPONDYLI**, premaxilla alary process forms posterior hook-like indentation; **I RHACHITOMI**, humerus entepicondylar foramen absent; **J**, internal carotids entered basicranium at posterolateral corner; **K STEREOSPONDYLOMORPHA**, deep ventral ridge on tabular that almost doubles its thickness in occipital view, interclavicle 1.3 times as long as wide; **L**, premaxilla box-like and anteriorly blunt, paired anterior depressions on vomer; **M STEREOSPONDYLI**, otic notch small and rounded and confined to dorsomedial part of squamosal, marginal dentition with transversely oval tooth bases, vertebral transverse processes distally extended and with diapophysis pointing laterally, interclavicle anterior margin smooth; **N**, basicranium has sutural contact, palatine and vomer with medial wing framing the interpterygoid vacuity anteriorly; **O**, prefrontal and postfrontal separated by frontal, *jugal* and lacrimal separated by orbit or palate bones (both homoplasies); **P**, quadrate dorsal process, humerus is a very long rod from early in ontogeny, and an elongate and slender rod in the adult; **Q**, maxilla enters orbit margin, narrow interorbital bar, longest trunk ribs poorly ossified short rods; **R REPTILIOMORPHA**, premaxillae less than half of skull width, vomers taper forwards, phalangeal formula of foot 2.3.4.5.4–5; **S**, reduced dorsal iliac blade; scapulocoracoid extending posteroventrally with respect to the posterior glenoid margin; L-shaped tarsal intermedium; **T BATRACHOSAURIA**, jugal enters ventral margin of skull roof, intetemporal absent, vomer lacks fang pair, palatine lacks fang pair, trunk neural spines fused to centra, neural spines swollen laterally, interclavicle wider than long, humerus with expanded proximal and distal ends; **U**, premaxillae less than two-thirds of skull width, parietal-tabular contact, vomers elongate and strip-like, tarsus with L-shaped proximal element; **V LEPOSPONDYLI**, supratemporal absent, stapedial foramen absent, vertebrae consist of cylindrical pleurocentra only, neural arches and centra fuse indistinguishably early in ontogeny, atlantal intercentrum absent; **W**, postorbital absent; **X**, reduced nasals, elongate frontals and parietals, posterior portion of interclavicle shorter than anterior; **Y HOLOSPONDYLI**, prefrontal less than three times as long as wide, ectopterygoid with tooth row, extra articulations above zygapophyses in at least some trunk and caudal vertebrae, neural and haemal spines rectangular to fan-shaped in side view, haemal spines fused to caudal centra; **Z**, postparietal and tabular entirely in occiput, supraoccipital present, first coronoid absent, sacrum with two vertebrae. Abbreviations: Dev, Devonian; E, Early; Jur, Jurassic; Mid, Middle. Dashed lines and star symbols indicate extinction events.

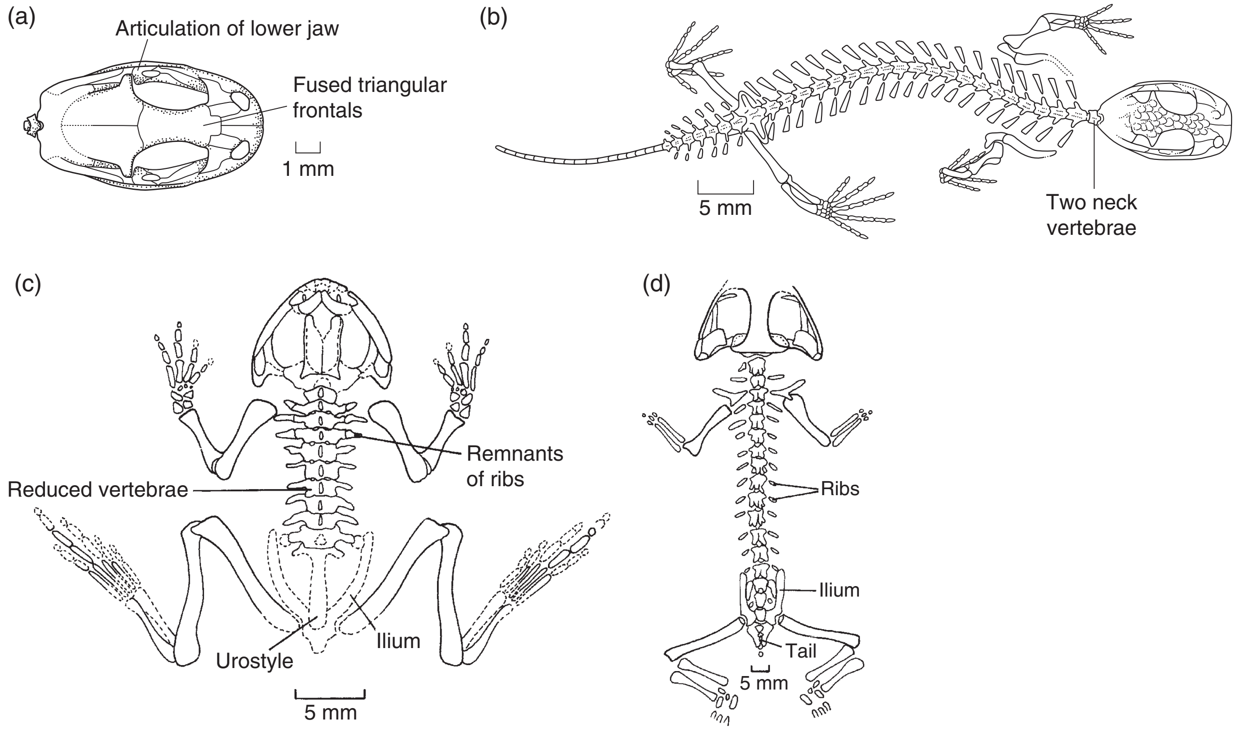


Figure 4.21 Albanerpetontids (a,b) and early frogs (c,d): (a,b) skull and skeleton of the Cretaceous *Celtedens*; (c) the Jurassic *Vieraella*, showing most adaptations of modern frogs; (d) the first frog *Triadobatrachus*. Source: (a,b) J. McGowan, Royal Tyrrell Museum of Palaeontology, Drumheller, Canada. Reproduced with permission. (c,d) Adapted from Estes and Reig (1973).

were long classified simply as salamanders. The body is long and flexible, the ribs are short, the tail tapers rapidly to a thin structure, and the limbs are powerful. Key albanerpetontid characters are seen in the skull (Figure 4.21(b)): the frontals are fused together as one triangular element, and there is a prominent process pointing forwards and contacting the premaxilla, nasal and lacrimal, and the articulation of the lower jaw and the skull is nearly vertical. In addition, the cervical vertebrae are most unusual (Figure 4.21(b)) – there are effectively two of them, the atlas and axis, and these contact the first vertebra of the trunk. Other lissamphibians retain only one cervical vertebra, the atlas, so the possession of two provided albanerpetontids with some additional neck flexibility.

4.6.2 Anura (Salientia)

The 6300 species of modern frogs and toads are so distinctive in their anatomy that they are immediately recognizable. The skeleton (Figure 4.21(c)) is highly modified for their jumping mode of locomotion: the hindlimb is extremely long, with the addition of a flexible pelvis and elongate ankle bones giving it a ‘five-crank’ hindlimb; the ilia run far forwards and the posterior vertebrae are fused into a rod called a **urostyle**, making a strong pelvic basket; the forelimbs and pectoral girdle are impact absorbers for when the frog lands; and there are usually no ribs and a short stiffened vertebral column with only four to nine vertebrae in the trunk. The head is short and flat, and the upper jaw is usually lined with small gripping teeth for processing insects or other prey.

The specialized characters of the frog skeleton can be detected even in one of the earliest forms, *Vieraella* from the Early Jurassic of South America (Figure 4.21(c)), which has elongate hindlimbs, reduced numbers of vertebrae, and a flattened skull. It is primitive in having more vertebrae than in most modern frogs (nine), small traces of ribs, and slightly heavier limb bones, but it offers few guides to ancestry. *Prosalirus*, another Early Jurassic frog, from the south-west USA (Jenkins and Shubin, 1998) has more elongate hindlimbs, and it was clearly the first jumping frog.

Some of the 33 modern families of frogs may be traced back as far as the Jurassic or Cretaceous, but most have very short fossil records, or none at all (Estes and Reig, 1973; Sanchíz, 1998). The oldest proto-frogs date from the Early Triassic, *Triadobatrachus* from Madagascar (Figure 4.21(d)) and *Czatkobatrachus* from Poland (Evans and Borsuk-Białynicka, 2009): they already have a reduced number of vertebrae, reduced ribs, elongate ilia and frog-like skulls, and likely had some modest jumping ability. Most fossil frogs are represented by isolated bones from relatively small animals; only rarely are anuran experts astonished by larger specimens (see Box 4.6).

4.6.3 Urodela (Caudata)

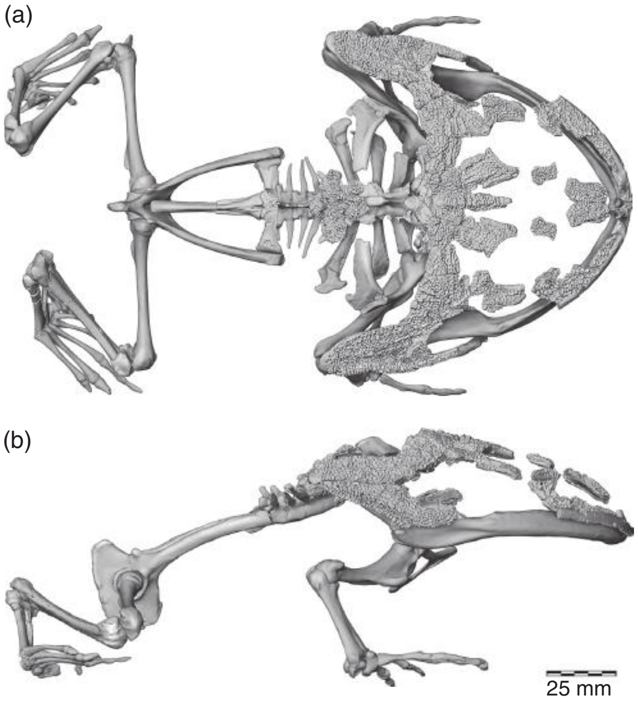
The 650 species of modern newts and salamanders show far fewer obvious specializations than frogs. The body is elongate, and there are generally four short walking limbs and a flattened swimming tail in aquatic forms. The fossil record of salamanders, like that of frogs, is patchy (Estes, 1981),

BOX 4.6 THE DEVIL TOAD FROM MADAGASCAR

It is hard to imagine frogs and dinosaurs living together, but this clearly happened. An example is the large frog, *Beelzebufo* (up to 23 cm long), which lived in the Late Cretaceous of Madagascar, side by side with armoured crocodiles (see Section 8.8.3) and diverse dinosaurs (see Box 8.2). Today's largest anuran, the Goliath frog, is 32 cm long [length measurements mean snout to vent length and do not include the outstretched hindlegs]. The *Beelzebufo* fossils consist of isolated skull elements, vertebrae, and limb bones (Evans *et al*., 2008, 2014), and they were found in the Maevarano Formation, source of dinosaurs such as *Majungasaurus*, *Masiakasaurus*, and *Rahonavis*.

The skull of *Beelzebufo*, meaning 'devil toad', was up to 15 cm broad at the back, but relatively short and with the usual rounded front margin. The skull roof bones bear a marked sculpture. The vertebrae are powerful, with expanded and sculptured arches, and the hindlimb short and probably more adapted for walking than jumping.

The key importance of this find, apart from its size and possible habits, is palaeobiogeographical. Based on characters of the skull, phylogenetic analysis places *Beelzebufo* in the Ceratophryidae, a clade previously known only from South America. Modern ceratophryids, or 'common horned frogs', can grow quite large, up to 17 cm long. They are all carnivorous and may be either terrestrial or semi-aquatic. The occurrence of the oldest fossil ceratophryid in Madagascar proves somewhat problematic. It could be said to confirm a land link between South America and Madagascar, which had been suggested before based on dinosaur faunas (see Box 8.2). In the Triassic and Jurassic, Gondwana consisted of the southern continents, South America, Africa, Antarctica, India, and Australia (see Section 2.3.2). As the South Atlantic opened during the Cretaceous, South America and Africa moved apart. However, Madagascar had separated from other landmasses by 120 Myr ago, and yet *Beelzebufo* is about 66 Myr old, so if the attribution is correct it must have been part of a long-lived ceratophryid lineage that remained in the area for 50 Myr, or somehow rafted in from elsewhere. Further, molecular analyses of ceratophryid phylogeny suggest the clade originated much more recently. This fossil poses more questions at present than it answers.



Three-dimensional digital reconstruction of skeleton of *Beelzebufo ampinga*. (a) dorsal view; and (b) right lateral view (with left limbs removed for visual clarity. Source: Evans *et al.* (2014). Reproduced with permission.

but modern families are now known from the Middle Jurassic onwards (Gao and Shubin, 2003, 2012). One of the oldest stem-salamanders, *Karaurus* from the Late Jurassic of Kazakhstan (Figure 4.22(a)), has a broad flattened skull with large orbits and rows of small teeth around the jaws. The skull roof is covered with heavily ornamented bone. The skull of a modern salamander (Figure 4.22(b)) shows many changes; the bones are generally lighter, and the braincase has become fused with the parietal bones and is partially exposed on the skull roof.

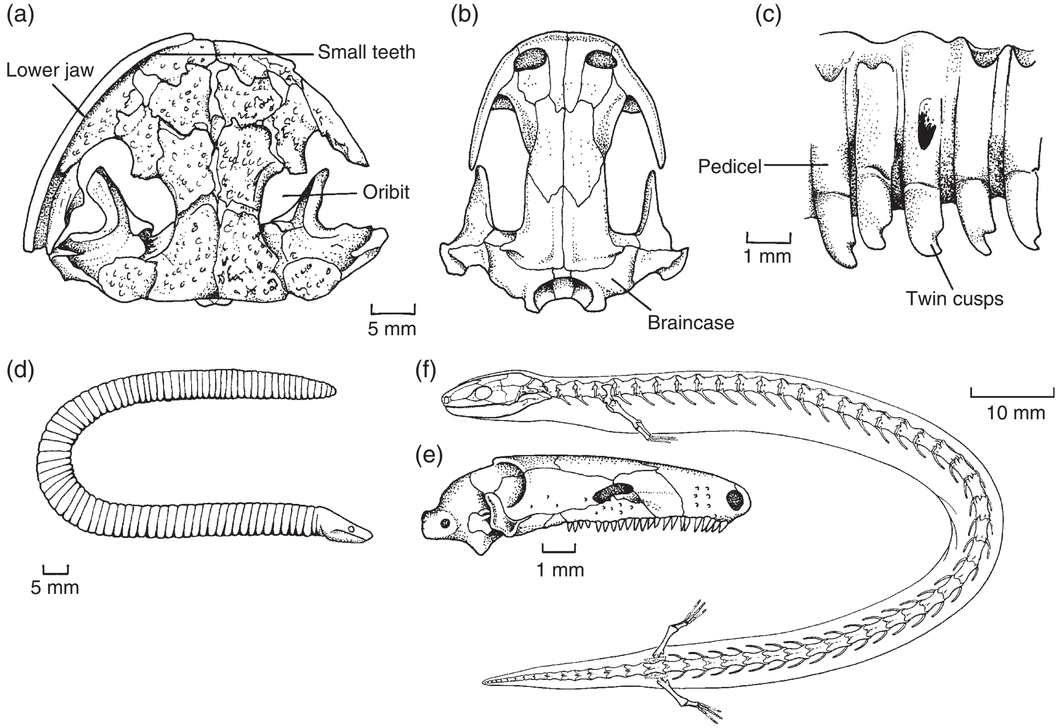


Figure 4.22 Salamanders and caecilians: (a) dorsal view of the skull of the Jurassic salamander, *Karaurus*; (b) similar view of a modern salamander skull; (c) pedicellate teeth of the salamander *Amphiuma*; (d) a typical modern caecilian; (e) skull of the modern caecilian *Grandisonia*; (f) reconstructed skeleton of the oldest caecilian, *Eocaecilia*. Source: (a) Adapted from Ivanhnenko (1978). (b,c) Adapted from Romer and Parsons (1986). (d,e) Adapted from Pough *et al.* (2012). (f) F. Jenkins, Jr, deceased; formerly, Harvard University, Cambridge, MA, USA. Reproduced with permission.

4.6.4 Gymnophiona (Apoda)

The nearly 200 species of modern gymnophionans, or caecilians, are strange little amphibians that look like earthworms (Figure 4.22(d)). They have lost their legs, hence their alternative name Apoda (literally 'no feet'), and they live by burrowing in leaf litter or soil, or swimming in ponds, in tropical parts of the world. They produce live young, having presumably suppressed the larval stage seen in frogs and salamanders. The skull is solidly built, and can be used for burrowing by battering the soil with the snout (Figure 4.22(e)). There may be as many as 200 vertebrae in the trunk region, but the tail is generally short.

The caecilian fossil record is meagre. For a long time, only isolated vertebrae had been reported from the Palaeocene of South America. The record was extended dramatically by the discovery of several Early Jurassic specimens in Arizona, USA, named *Eocaecilia* (Jenkins *et al.*, 2007), and later by isolated remains from the Cretaceous of Morocco and Sudan. *Eocaecilia* (Figure 4.22(f)) shows typical caecilian features in the skull and its long body, but it has much reduced legs, confirming the origin of the group from limbed lissamphibian ancestors.

4.6.5 Origin of the modern amphibians

There is debate on three issues concerning the modern amphibians, whether they form a clade, how the three subclades relate to each other (and to the extinct albanerpetontids), and where the modern amphibians arose from among extinct forms.

On the first question, most biologists regard the three modern amphibian groups as members of a clade Lissamphibia, based on morphological and molecular phylogenetic analyses (Ruta *et al.*, 2003a,b; Zhang *et al.*, 2005; Frost et al., 2006; Ruta and Coates, 2007; Pyron, 2011; Pyron and Wiens, 2011; Sigurdsen and Green, 2011; Marjanović and Laurin, 2013), although some molecular (e.g. Fong *et al.*, 2012) and palaeontological (e.g. Anderson, 2008) studies suggest that frogs and salamanders had distinct points of origin from among the Palaeozoic basal tetrapods. Morphological evidence for monophyly of Lissamphibia is that all modern amphibians share bicuspid (two-cusped) teeth that are **pedicellate** teeth (Figure 4.22(c)), in other words, the base and crown are separated by a zone of fibrous tissue.

The relationships of clades within Lissamphibia have also been controversial. Generally, frogs and salamanders are paired as sister groups, together termed the Batrachia, with gymnophionans as outgroup (Ruta *et al.*, 2003a; Ruta and Coates, 2007; Sigurdsen and Green, 2011). Hitherto, the albanerpetontids had been regarded as rather odd salamanders, but they are now (Gardner, 2001; McGowan, 2002; Ruta *et al.*, 2003a) identified as an outgroup to Batrachia, but their position relative to Gymnophiona is harder to resolve. The Batrachia clade (Anura + Caudata) is found by most molecular and combined morphological-molecular analyses (e.g. Zardoya and Meyer, 2001; Zhang *et al.*, 2005; Anderson, 2008; Pyron, 2011; Pyron and Wiens, 2011; Marjanović and Laurin, 2013), although an alternative pairing of Caudata and Gymnophiona, the putative clade Procera, has been found by others (Feller and Hedges, 1998; Fong *et al*., 2012).

The third debate, concerning the origin of Lissamphibia divides into the Temnospondyl Hypothesis (TH) and the Lepospondyl Hypothesis (LH). These two views generally assume a monophyletic Lissamphibia, but the LH can involve variants that suggest modern amphibians arose from different subclades among the lepospondyls (Anderson, 2008). These two hypotheses can be distinguished only on the basis of fossil evidence, and the difficulty has always been to distinguish convergence from apomorphy. In other words, many lissamphibians and lepospondyls share characters associated with miniaturization and their varied terrestrial and aquatic lifestyles, and the problem is to determine whether these are convergences, and so of no value in reconstructing phylogeny (Ruta and Coates, 2007), or true shared derived characters (Marjanović and Laurin, 2013). The LH has its vocal supporters (reviewed, Marjanović and Laurin, 2013), but the TH is the majority view (Ruta *et al*, 2003a,b; Ruta and Coates, 2007; Coates *et al*., 2008; Sigurdsen and Green, 2011; Schoch, 2013, 2014), and it is represented here (see Box 4.5).

4.7 FURTHER READING

The biology of modern amphibians is outlined in textbooks by Duellman and Trueb (1994) and Vitt and Caldwell (2013), and the evolution of amphibians by Carroll (2004). Zimmer (1998), Laurin (2010), and Clack (2012a) give thorough and clear accounts of all the recent work on Devonian and Carboniferous basal tetrapods, and the new evidence about the transition on to land.

The best web site on modern amphibians is: http://amphibiaweb.org/, which lists all 7000+ species, and provides daily updates on systematic and conservation research. Searchable listings are also provided by: http://research.amnh.org/vz/herpetology/amphibia/, a companion to the Frost *et al*. (2006) paper.

QUESTIONS FOR FUTURE RESEARCH

1 Search for Middle, and even Lower, Devonian tetrapod skeletons to show more of the fin to limb transition.
2 Further exploration of genomic controls of tetrapod characters in the skull, limbs, lungs, and skeleton.
3 Exploration of the role of external environmental drivers (e.g. temperature, oxygen, humidity) on early tetrapod evolution (terrestrialisation, Romer's Gap, Carboniferous-Permian transition).
4 Resolution of dispute over the timing of lissamphibian origins and identity of their closest sister groups.
5 Better understanding of the spike in temnospondyl diversity after the Permo-Triassic mass extinction, and the later, Mesozoic evolution of temnospondyls.

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CHAPTER 5

Evolution of Early Amniotes

Vertebrate Palaeontology, Fourth Edition. Michael J. Benton.

Companion Website: www.wiley.com/go/benton/vertebratepalaeontology

KEY QUESTIONS IN THIS CHAPTER

1 How did tetrapods adapt to the arid conditions of the Permian?
2 What were the first amniotes ('reptiles') like?
3 How do we know that Carboniferous amniotes laid eggs when the oldest confirmed eggs are Triassic in age?
4 How did amniotes diversify in the Carboniferous and Permian?
5 What were the adaptations of the key Permian synapsids?
6 Are turtles diapsids or parareptiles, and why has it been hard to determine their true relationships?
7 How did the tetrapods fare in the Permo-Triassic mass extinction, when as many as 90% of species were wiped out?

INTRODUCTION

During the Late Carboniferous, temnospondyls and reptiliomorphs dominated most terrestrial landscapes, especially the damp forests. Small lizard-sized tetrapods were also in existence, creeping in and out of the vegetation, in search of insects and worms. They laid eggs that did not have to hatch in water. These were the first **amniotes**, a group that rose in significance after a major climate shift from humid to dry near the end of the Carboniferous, and into the subsequent Permian Period. Amniota divided early on into two major subclades, the Synapsida (mammal-like reptiles and mammals) and the Reptilia (extinct forms, leading to turtles, lizards, crocodiles, and birds). This re-alignment of the term Reptilia is different from its traditional usage, to include a broader, paraphyletic group of all amniotes other than birds and mammals.

In this chapter, the early amniotes will be described, and key biological problems of living a life completely divorced from the water will be explored. The radiation of amniote groups in the Late Carboniferous and Permian built up complex ecosystems that were to be destroyed by the huge end-Permian mass extinction. But among these Permian amniotes were the ancestors of the animals that rose to importance during the later age of dinosaurs and age of mammals.

5.1 *HYLONOMUS AND PALEOTHYRIS* – BIOLOGY OF THE FIRST AMNIOTES

The oldest amniotes are *Hylonomus* and *Paleothyris* from the mid-Carboniferous of Nova Scotia (Carroll, 1964, 1969). The body (Figure 5.1(a)) is slender, and is about 200 mm long, including the tail. Unlike many basal tetrapods, the head is relatively small, being about one-fifth of the trunk length rather than one-third to one-quarter. The skull of *Hylonomus* is incompletely known, with uncertainty about the posterior view and the palate, but *Paleothyris* is represented by better skull remains (Figure 5.1(b–f)).

5.1.1 The amniote skull

The tetrapod skull consists of a thin outer covering of dermal roofing bones with a modest-sized braincase, loosely attached, inside. There are two major openings on each side of the dermal skull, a large orbit, located about halfway along, and a nostril near the anterior tip of the snout. The bones in the skull of *Paleothyris* are similar to those of advanced reptiliomorphs (cf. Figure 4.20), but it has no otic notch, and the bones at the back of the skull table (supratemporal, tabular, postparietal) are very much reduced and seen mainly in the posterior view of the skull on the occiput (Figure 5.1(e)). The skull and jaw bones may be divided into five main sets, which relate to the following standard views.

1 *Cheek* (Figure 5.1(b)): from the front, the side of the skull shows the following bones: **premaxilla** and **maxilla**, both bearing teeth, **lacrimal** and **prefrontal** in front of the **orbit**, and **postfrontal**, **postorbital** and **jugal** behind. The **squamosal**, **quadratojugal** and **quadrate** make up the posterior angles of the skull.

2 *Skull table* (Figure 5.1(c)): paired **nasals**, **frontals** and **parietals** form the dorsal surface of the skull, with the nasals lying between the nostrils, and the frontals between the orbits. Many early tetrapods have a large **parietal foramen** lying in the midline between the parietals (e.g. Figures 5.1(c), 5.6(c), 5.8(e)), a feature that was lost in most Mesozoic descendants. This foramen is often associated with the 'pineal organ', a part of the brain that serves a light-detecting function in some vertebrates.

3 *Palate* (Figure 5.1(d)): paired **vomers** lie behind the palatal portions of the premaxillae, and behind them the **pterygoids**, which run back and sideways to meet the quadrates. The pterygoids are attached to the maxillae and jugals at the side by the **palatines** and **ectopterygoids**. The main ventral element of the braincase, the **parasphenoid**, lies behind and between the pterygoids, and it sends a long process forwards in the midline in the interpterygoid vacuity. Several of the palatal bones (palatine, pterygoid, parasphenoid) bear teeth, and these teeth tend to be lost in the course of amniote evolution.

4 *Occiput* (Figure 5.1(e)): the view of the back of the skull shows how the braincase fits inside the cranium: the **postparietals**, **tabulars** and **supratemporals** of the skull table form the dorsal margin and are attached to the **supraoccipital**, the dorsal braincase element. The other elements of the braincase, the **opisthotics** and **exoccipitals**, support the semicircular canals of the inner ear, and the exoccipitals lie on either side of the **foramen magnum**, the broad passage through which the spinal cord passes back from the brain. The opisthotic also runs sideways towards the squamosal, quadratojugal, and quadrate of the cheek region, and a robust stapes makes a link to the quadrate. The lower margin of the braincase is formed by the **basioccipital**, which also provides a ball-like **occipital condyle** that articulates with the first vertebra in the neck.

5 *Lower jaw (mandible)* (Figure 5.1(b,g)): the main lower jaw element in lateral (outside) view (Figure 5.1(b)) is the dentary at the front that bears the teeth. Behind it are the **surangular** above and the **angular** below. In medial (inside) view (Figure 5.1(g)), it can be seen that the angular wraps round under the jaw, and the main bones are the **splenial** in front and the **prearticular** behind, with a small **coronoid** between and forming a peak in the jaw margin. The jaw joint lies on the **articular** bone, a small complex element at the back.

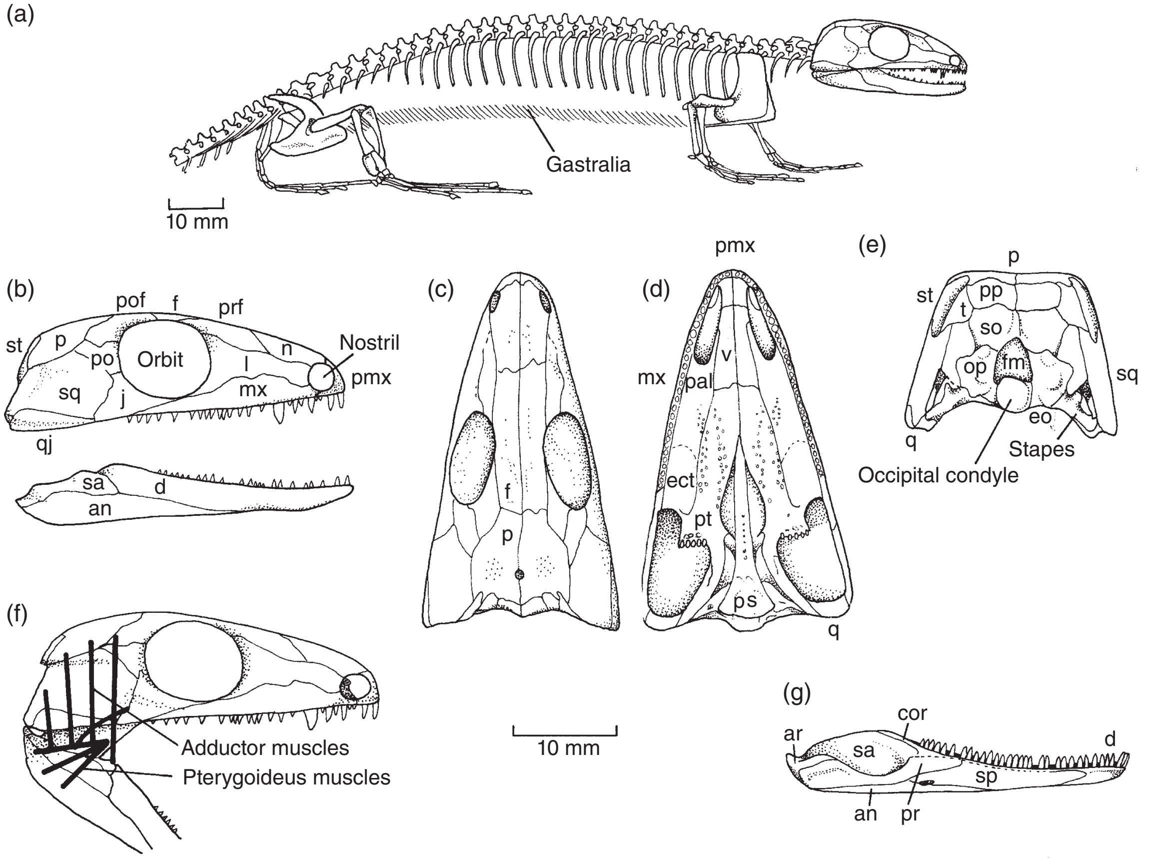


Figure 5.1 The earliest amniote, *Paleothyris*: (a) skeleton in side view; (b–e) skull in lateral (b), dorsal (c), ventral (d), and occipital (e) views; (f) restoration of the main jaw closing muscles; (g) lower jaw. Abbreviations: an, angular; ar, articular; cor, coronoid; d, dentary; ect, ectopterygoid; eo, exoccipital; f, frontal; fm, foramen magnum; j, jugal; l, lacrimal; max, maxilla; n, nasal; op, opisthotic; p, parietal; pal, palatine; pmx, premaxilla; po, postorbital; pof, postfrontal; pp, postparietal; pr, prearticular; prf, prefrontal; ps, parasphenoid; pt, pterygoid; q, quadrate; qj, quadratojugal; sa, surangular; so, supraoccipital; sp, splenial; sq, squamosal; st, supra-temporal; t, tabular; v, vomer. Source: (a) Adapted from Carroll and Baird (1972). (b–g) Adapted from Carroll (1969).

5.1.2 The amniote skeleton

The skeleton of *Hylonomus* (Figure 5.1(a)) and *Paleothyris* is lightly built. The vertebrae consist of spool-like pleurocentra with small crescent-shaped intercentra between. The first two **cervical** vertebrae (Figure 5.2(a)), the vertebrae of the neck, are highly modified to make the junction with the occipital condyle of the skull. Vertebra 1, the **atlas**, consists of six separate elements, the intercentrum, which fits beneath the occipital condyle, the pleurocentrum behind it, and a paired **proatlas** and atlas arch, one on each side above the occipital condyle. Vertebra 2, the **axis**, is a large element with the pleurocentrum and neural arch fused to each other, and a small intercentrum in front. The atlas accommodates the ball-like occipital condyle of the skull and allows rotary movements of the head, whereas the atlas is locked in place and permits broadly up-and-down movements. The remaining three or four cervical vertebrae follow a similar pattern, but they have rather smaller neural arches than the axis.

The dorsal vertebrae, those lying in the trunk region, number about 21 in *Hylonomus* and 28 in *Paleothyris*, making totals of 26 and 32 **presacral** vertebrae (cervicals + dorsals) respectively. The cervicals bear short ribs, whereas the dorsal ribs are longer and form a rib cage. Behind the presacral vertebrae are two sacrals in the hip region that are attached to the ilia by specialized ribs, and then an unknown, but large, number of **caudal** vertebrae in the tail.

The limbs and limb girdles are basically the same as in the Carboniferous basal tetrapods (cf. Figures 4.1(b) and 4.7(c–f)). The pectoral girdle (Figure 5.2(b)) is dominated by a large fused scapulocoracoid (composed of a scapula and two coracoids) that bears a screw-shaped glenoid for the head of the humerus. The cleithrum and clavicle are reduced to thin strips of bone in front of the scapulocoracoid, and the interclavicle is a long T-shaped element beneath. The arm is short (see Figure 5.1(a)), and the hand (Figure 5.2(c)) long and slender. It shows all the wrist bones seen in *Eryops* (see Figure 4.1b), and the phalangeal formula of the hand is 2-3-4-5-3 – a typical value for early reptiliomorphs and amniotes.

The pelvis (Figure 5.2(d)) consists of a narrow ilium, and a heavy pubis and ischium beneath, which meet each other in the midline as in basal tetrapods (cf. Figure 4.7(d)). The hindlimb and foot are longer than the forelimb and hand (Figure 5.2(e)). The ankle bones have changed in one respect from those of

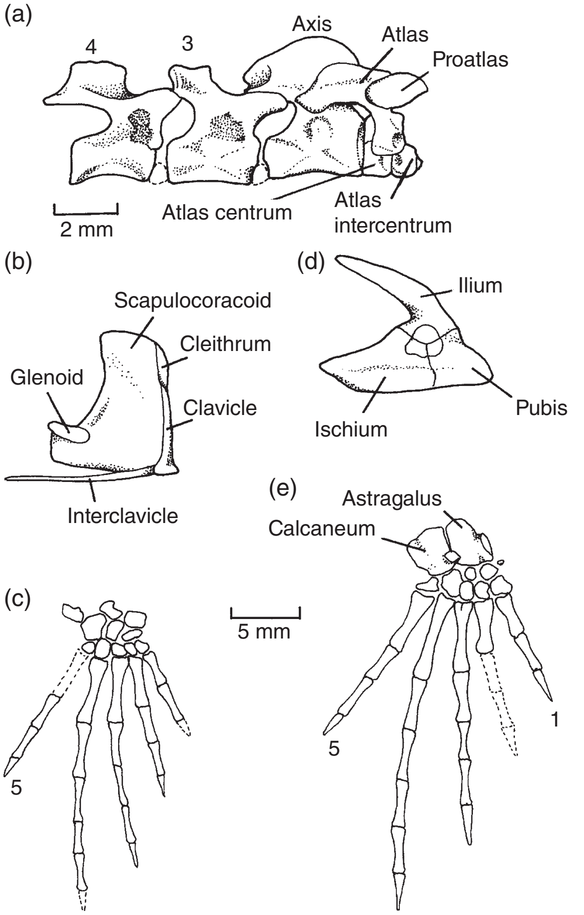


Figure 5.2 Vertebrae and limbs of the earliest amniotes (a–c,e) *Paleothyris* and (d) *Hylonomus*: (a) cervical vertebrae 1–4; (b) pectoral girdle; (c) hand; (d) pelvic girdle; (e) foot. Source: Adapted from Carroll (1969).

Acanthostega (see Figure 4.7(f)), apart from becoming more slender. The tibiale, intermedium and a centrale of basal tetrapods have fused into a larger element termed the **astragalus**; this is supported by the observation of three components separated by sutures in the astragalus of *Hylonomus* (Meyer and Anderson, 2013). The fibulare is also larger, and is termed the calcaneum. The phalangeal formula of the foot is 2-3-4-5-4.

There are no bony scales in the skin of *Hylonomus* or *Paleothyris*, but these animals have chevron-like **gastralia**, or abdominal 'ribs', closely spaced in the belly region (see Figure 5.1(a)).

5.1.3 Palaeobiology of the first amniotes

The light construction of the skull, and the small sharp teeth, suggest that *Hylonomus* and *Paleothyris* fed on invertebrates such as insects and millipedes. The teeth could readily pierce the tough cuticle to reach the flesh inside.

One of the key features of the skull of *Paleothyris* that relates to feeding is an increase in the strength of the jaws when compared with basal tetrapods, sufficient to nip through the toughest arthropod cuticle. A major muscle group, the pterygoideus, supplements the adductors in pulling the jaw up and forwards (see Figure 5.1(g)). The palatal teeth in *Paleothyris* are smaller than those on the premaxilla and maxilla, and they presumably played a less important role, probably in holding the food and in further crushing it after it had been cut up. The tongue was probably toughened on its upper surface, and worked against the palatal teeth.

The stapes in *Paleothyris* is heavy, as in the basal tetrapods, and it probably had a limited function in hearing. Low-frequency sounds could be transmitted as vibrations from the throat region through the stapes to the braincase. It is unlikely that *Paleothyris* had a tympanum as there is no otic notch.

Restorations of the life appearance of *Hylonomus* and *Paleothyris* (Figure 5.3) show that they probably looked like modern terrestrial insectivorous lizards. Both are lightly built, so it is remarkable how well their remains have been fossilized. This may be explained by the unique conditions of preservation: both *Hylonomus* and *Paleothyris* have been found in fossilized tree trunks.

Hylonomus remains have been found in mudstones, sandstones and coals, deposited in shallow freshwater lakes and rivers of the Cumberland Group of Joggins, Nova Scotia (Carroll, 1970; Falcon-Lang *et al.*, 2006). In the 1840s, geologists discovered abundant upright tree stumps of the lycopods (club mosses) *Sigillaria* and *Lepidodendron*. The first fossil vertebrates were collected there in 1852, and since then over 30 productive tree stumps have been discovered, and the contained bones removed for study. The total haul included skeletons of dozens of basal tetrapods (six species of microsaurs, one temnospondyl, and one embolomere) as well as two amniote species, *Hylonomus* and the basal synapsid, *Protoclepsydrops*.

It seems that in mid-Carboniferous times the Joggins area was covered with lush forests of *Sigillaria* and *Lepidodendron*, up to 30 m tall. Occasionally, there were major fires that destroyed the forests, and at times the lakes flooded and the forests were inundated with sediment. The trees died and fell, leaving only their roots and buried lower trunks in place. As new forests became established above, the centres of the lycopod tree trunks rotted, and millipedes, snails and small tetrapods crawled in seeking food or shelter (Figure 5.3). These animals lived for some time in the tree trunks as the tetrapods fed on the invertebrates and left faecal remains, but eventually they died or were inundated by further floods. The tetrapods may have crept in, seeking food, or they may have used the hollow tree trunks as dens, keeping them safe from harm. The bottoms of the tree trunks then provide a concentration of the small terrestrial animals of the time.

5.2 AMNIOTE EVOLUTION

The amniotes of the Late Carboniferous include about 25 genera of small- and medium-sized insect-eaters. Then, following a major climatic shift from humid to dry some 305 Ma

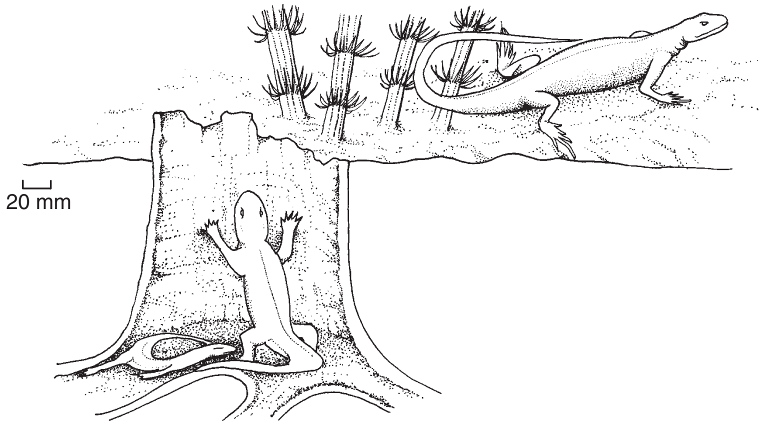


Figure 5.3 The mode of preservation of the early amniotes *Hylonomus* and *Paleothyris*, which were trapped in hollow tree stumps in the mid-Carboniferous of Nova Scotia. Source: Adapted from Carroll (1970) and other sources.

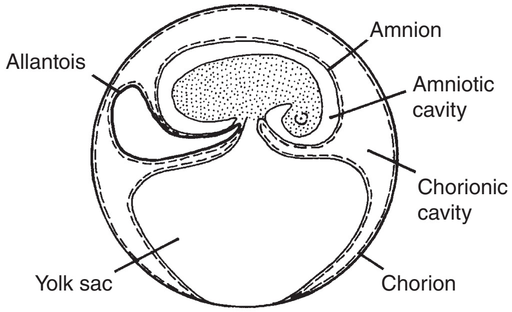


Figure 5.4 The cleidoic egg, showing the semipermeable shell and the extraembryonic membranes.

(see Section 4.3.2), amniote diversity expanded enormously, and the main lines are documented later in this chapter. But what was it that set amniotes apart from the other basal tetrapods? The key features are to be seen in their eggs and their skulls.

5.2.1 The cleidoic egg – a private pond

Modern amniotes are distinguished from the basal tetrapods primarily by the fact that they lay eggs that have semipermeable shells and that contain sufficient fluid and food for the embryo to develop fully into a terrestrial hatchling. The eggs are not laid in water, and there is no aquatic larval stage, such as a tadpole. Amniotes generally lay far fewer eggs than do amphibians or fishes because more reproductive energy has to be invested in each egg, and because the young are protected from predation to a much later stage in development. Reproduction also takes place on dry land, so that internal fertilization is essential.

The egg of amniotes, called the **amniotic** or **cleidoic** (literally 'closed') egg (Figure 5.4) has two key features.

1 A semipermeable shell, usually calcareous, but leathery in snakes, some lizards, and some turtles, which allows gases to pass in (oxygen) or out (waste carbon dioxide), but keeps the fluids inside.

2 Extraembryonic membranes, specialized membranes that lie 'outside' the embryo, the chorion, amnion and allantois. The **chorion** surrounds the embryo and yolk sac, whereas the **amnion** surrounds the embryo with water. Both function in protection and gas transfer. The **allantois** forms a sac that is involved in respiration and stores waste materials. As the embryo develops, the yolk sac, full of highly proteinaceous food, dwindles and the allantois fills up.

Fossil eggs are rare. The oldest examples are from the Triassic, much younger than the time of origin of the amniotes. In the absence of Carboniferous eggs, how can we identify *Hylonomus* and *Paleothyris* as the oldest amniotes? The argument is phylogenetic. The key features of the cleidoic egg of all living amniotes develop in the same way (compare the eggs of a turtle, lizard, crocodile, bird, and monotreme mammal), and hence it is most likely that the cleidoic egg is an apomorphy of Amniota, a feature that arose once only in the common ancestor of reptiles, birds and mammals. *Hylonomus* and *Paleothyris* already lie on one of the major amniote lineages, above the initial split among the ancestors of turtles, lizards and mammals (see Box 5.1) so the amniotic egg must have arisen at a point in the cladogram *below* those two early amniotes.

5.2.2 Amniote phylogeny and temporal fenestrae

Fundamental early splits in amniote evolution are documented in their **temporal fenestrae** – openings behind the orbit that probably function in reducing the weight of the skull and in conserving calcium. The argument is that bone is costly to produce and maintain, as well as being heavy, and it can be advantageous to dispense with it where it is not required. Much of a skull is under stress from the movements of the jaws and neck muscles, but some spots, in the cheek region and palate, are under very little stress, and openings may appear, and the skull becomes an engineering marvel of struts and braces without reducing the effectiveness of the skull. Fenestrae also provide additional attachment edges for specific jaw muscles, and they allow jaw muscles inside the skull to bulge out.

There are four amniote skull types (Figure 5.5(a–d)).

1 **Anapsid**: amniotes with no temporal fenestrae, a condition that is also plesiomorphic for tetrapods. Might include early forms such as *Hylonomus* and *Paleothyris*, as well as several lineages of parareptiles in the Permian and Triassic, and the turtles. Some of these were once grouped in the clade Anapsida, but they are now considered paraphyletic with respect to diapsids, and the phylogenetic position of turtles is so debated, and may lie within Diapsida, that the term Anapsida is rarely used now, except as an adjective ('anapsid') to describe the skull type.

2 **Synapsid**: amniotes with one lower temporal fenestra, surrounded by the postorbital, jugal and squamosal. The clade Synapsida includes the extinct synapsids and the mammals.

3 **Diapsid**: amniotes with two temporal fenestrae, a lower one as in synapsids, and an upper one surrounded by the postorbital, squamosal and parietal. The clade Diapsida includes the lizards, snakes, crocodilians and birds, as well as numerous extinct groups such as the dinosaurs and pterosaurs. The turtles might also belong within Diapsida, and this would suggest that they once had a diapsid skull, and then lost the temporal fenestrae to become anapsid secondarily.

4 **Euryapsid**: present in a broad range of later amniotes, especially the marine nothosaurs, plesiosaurs and ichthyosaurs of the Mesozoic. In the euryapsid condition, there is one upper temporal fenestra, surrounded by the postorbital, squamosal and parietal. This pattern probably evolved from the diapsid by the loss of the lower temporal bar, as evidenced by the presence of a lower embayment in some basal forms of these clades.

Whereas, at one time, it was thought that each of these four skull types indicated an independent and distinct line of evolution, both the anapsid pattern in turtles and the euryapsid pattern in various marine reptile groups may have evolved from the diapsid pattern. Moreover, random smaller skull fenestrations are known in parareptiles.

The fundamental split in amniote evolution (see Box 5.1) took place in the Middle Carboniferous, into two great clades, the Synapsida, leading eventually to mammals, and the Reptilia, including Parareptilia and Eureptilia (which includes Diapsida), which led to turtles, lizards, snakes, crocodilians and birds.

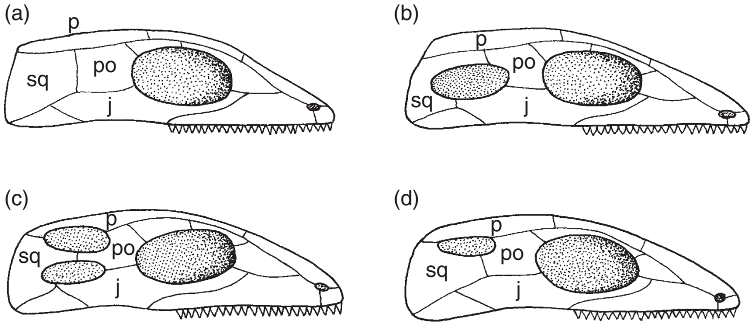


Figure 5.5 The four main patterns of temporal fenestrae in amniote skulls: (a) anapsid; (b) synapsid; (c) diapsid; (d) euryapsid. Abbreviations: j, jugal; p, parietal; po, postorbital, sq, squamosal.

BOX 5.1 RELATIONSHIPS OF EARLY AMNIOTES

The clade Amniota falls into three main subclades: Synapsida, Parareptilia, and Eureptilia (=Diapsida plus stem forms). These clades have long been recognized in one form or another, but there has been much debate about their exact contents and their correct names. At one time it was thought that the temporal fenestrae in the skull were the key to amniote phylogeny (see Section 5.2.2), and indeed amniotes with synapsid and diapsid skulls more or less map onto Synapsida and Diapsida. However, the anapsid skull pattern, lacking temporal fenestrae, is plesiomorphic for tetrapods and seen among amniotes in Parareptilia and turtles (likely members of Diapsida), and the euryapsid skull pattern evidently derived from the diapsid perhaps several times independently.

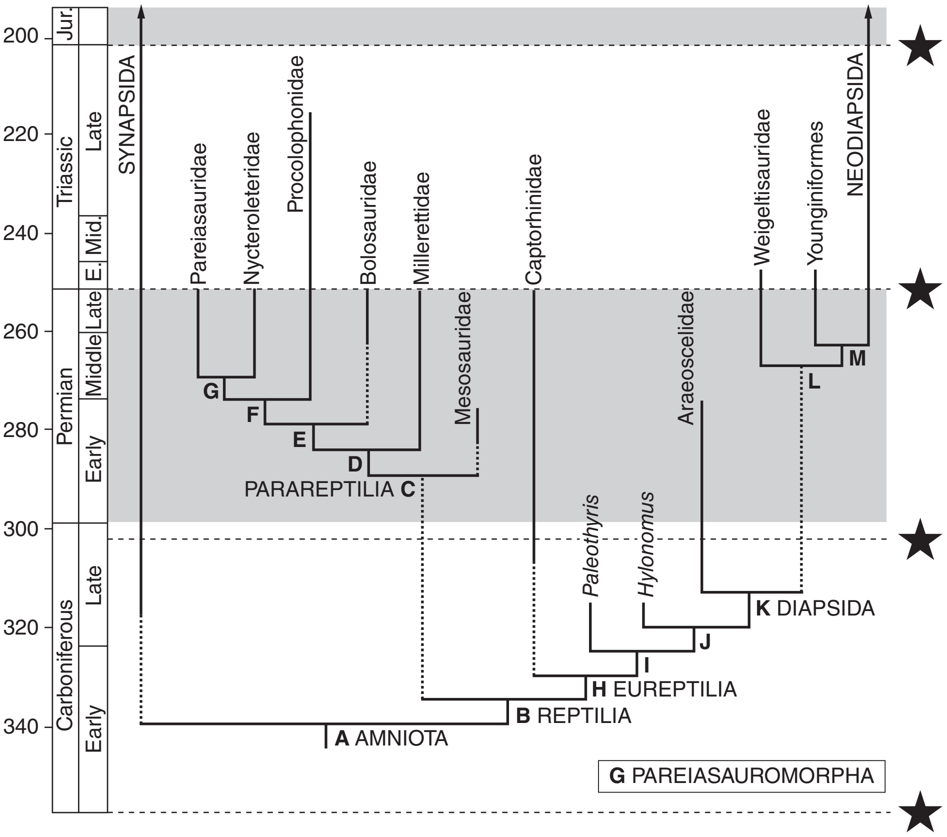
The outline phylogeny of Amniota (see illustration) has been worked out through a long serious of large-scale cladistic analyses. For example, Gauthier *et al.* (1988) discovered the basal split into Synapsida and Reptilia (Parareptilia + Eureptilia). The phylogeny of Synapsida is explored further in Box 5.3. The clades Parareptilia and Eureptilia are widely identified as a clade, generally termed Reptilia (formerly, sometimes Sauropsida).

The Parareptilia, comprising Mesosauridae, Millerettidae, Bolosauridae, Procolophonidae, Nycteroleteridae, and Pareiasauridae, has been confirmed in many studies (Laurin and Reisz, 1995; Tsuji, 2006; Tsuji and Müller, 2009). For a time, turtles were included in Parareptilia, either as sister taxon of Procolophonidae (Laurin and Reisz, 1995) or Pareiasauridae (Lee, 1995). It is true that turtles share many features with both groups, but these are generally now thought to be convergences, in light of alternative morphological, and especially molecular, evidence that turtles are members of Diapsida.

The Eureptilia comprises the Diapsida and some outgroups, the Captorhinidae, *Paleothyris* and *Hylonomus*, on the stem to Diapsida. Within Diapsida, there are some Carboniferous and Permian clades, Araeoscelidae, Weigeltisauridae, and Younginiformes, which lie on the stem to the derived diapsids, the Neodiapsida, and these divided in the Middle Permian into two major lineages, Lepidosauromorpha and Archosauromorpha (see Box 6.1). The broad pattern of eureptilian and diapsid phylogeny has been established through a series of detailed studies (e.g. Benton, 1985; Laurin and Reisz, 1995; Müller and Reisz, 2006; Reisz *et al*. 2007).

Continued

Molecular phylogenetic analyses of modern Amniota largely support the pattern discovered from morphological study of the fossils (e.g. Hedges and Poling, 1999; Lee, 2001), with distinct Synapsida and Diapsida, and the Diapsida divided into Lepidosauromorpha (lizards, snakes, tuatara) and Archosauromorpha (crocodilians, birds). Nearly every molecular study, based on a broad range of genes, point to a placement of turtles among diapsids, and specifically within Archosauromorpha (e.g. Hedges and Poling, 1999; Shen *et al*., 2011; Tzika *et al*., 2011; Chiari *et al*., 2012; Crawford *et al*., 2012). Unexpectedly, micro-RNAs indicate a definite pairing of turtles and lepidosauromorphs (Lyson *et al*., 2012), a difficult issue to resolve at present. There is no molecular evidence that pairs Synapsida and Diapsida, with turtles as outgroup, as would have been expected from the traditional morphological phylogeny. Some morphological analyses (e.g. deBraga and Rieppel, 1997) support the placement of turtles among the diapsids, and specifically in the lepidosauromorph clade, supporting the micro-RNA result. The majority view then is that turtles are within Diapsida, and probably branching near the base of Archosauromorpha, outside Archosauria proper, but the alternative placement within Lepidosauromorpha cannot be ruled out. Further, re-analyses of morphological data sets sometimes still find a result with turtles in something like the traditional position, outside Diapsida (Lyson *et al*., 2010).



Cladogram showing the postulated relationships of the major groups of amniotes, with synapomorphies from Laurin and Reisz (1995), Lee (1995), Müller and Reisz (2006), Tsuji (2006), and Tsuji and Müller (2009). See Box 4.5 for context of Amniota; see Box 5.3 for relationships of Synapsida and Box 6.1 for relationships of Neodiapsida. Synapomorphies: **A AMNIOTA**, frontal contacts orbit, rounded occipital condyle, three ossifications in scapulocoracoid, astragalus; **B REPTILIA**, maxilla separated from quadratojugal by jugal, tabular small or absent, parasphenoid wings absent, supraoccipital narrow in posterior view, large post-temporal fenestra, suborbital foramen in palate, single coronoid, femoral shaft long and slender, single centrale in ankle; **C PARAREPTILIA**, caniniform maxillary tooth absent, caudal haemal arches attached to anterior centrum, supraglenoid foramen absent, femoral shaft long and slender; **D**, large lateral foramen on maxilla, quadratojugal expanded dorsally, temporal emargination bordered by quadratojugal and squamosal, jaw articulation in front of occiput, ectopterygoid small and lacks teeth, ectepicondylar groove and foramen in humerus, iliac blade expanded dorsally; **E**, 'anchor-shaped' interclavicle; **F**, enlarged quadratojugal, pineal foramen near frontoparietal suture, tabular absent, sacral ribs with narrow distal contact, T-shaped interclavicle, astragalus and calcaneum sutured or fused, fifth distal tarsal absent, dorsal dermal ossifications; **G PAREIASAUROMORPHA**, ornamented quadratojugal, basicranial articulation sutured and/ or immobile, lateral flange of exoccipital present; **H EUREPTILIA**, bilaterally embayed posterior skull margin, small supratemporal, absence of a supratemporal/ postorbital contact, strong ventrolateral constriction of the dorsal centra, narrow iliac blade; **J**, Uncertain; **K DIAPSIDA**, upper and lower temporal fenestrae, suborbital fenestra, ossified sternum, complex tibio-astragalar joint, first metatarsal less than half the length of the fourth metatarsal; **L**, lacrimal reduced, caniniform maxillary teeth absent, quadratojugal reduced; **M**, anterior process of squamosal narrow, trunk ribs mostly single-headed, ends of humerus robust. Abbreviations: **E**, early; Jur, Jurassic; Mid, middle. Dashed lines and star symbols indicate extinction events.

5.3 THE PERMIAN WORLD

During the Permian, the continents moved into even closer contact than in the Carboniferous (see Figure 4.9), and the supercontinent Pangaea (literally 'whole world') came fully into being (Figure 5.6). As Gondwana drove northwards into Laurasia, a great mountain chain, as high as the Himalayas, formed roughly along the line of the palaeoequator. A southern ice-cap developed over Gondwana (South America, Africa, India, Australia and Antarctica) in the Late Carboniferous (see Figure 4.9), and disappeared in the Early Permian as Gondwana drifted north.

In the northern hemisphere, following the collision of the supercontinents, Early Permian climates became hot and arid, with the development of extensive evaporite deposits in North America and Europe. Major floral changes took place as a result of these climatic changes. The lush damp tropical Carboniferous forests of club mosses and horsetails were replaced by seed-bearing plants of rather more modern type, conifers in the northern hemisphere, and glossopterids in the south. The replacement of basal tetrapods by amniotes as the dominant terrestrial tetrapods during the latest Carboniferous and Permian was probably triggered by this wholesale switch from humid to arid conditions (see Section 4.3.2).

Most finds of Late Carboniferous and Early Permian tetrapods are from the northern hemisphere, perhaps because the southern continents were experiencing cold and temperate climates. By the Middle and Late Permian, however, rich deposits of fossil tetrapods are known from South Africa and Russia in particular (Figure 5.6), with rarer findings from Argentina, Brazil, East Africa, India, and China. Most unexpected are the extensive finds of fossilized footprints from the Middle and Late Permian in particular, often occurring in wind-blown sandstones of ancient desert dunes (Lucas and Hunt, 2006). These animals doubtless walked over the dune fields, but were able to feed in moist, vegetated areas between. In addition, Permian tetrapod skeletons are known from arid zones (Figure 5.6) in Europe, with rare skeletons from Scotland, and more recently from Niger, in the southern hemisphere arid belt (Sidor *et al.*, 2005). The major split in tetrapod faunas north and south, and with only rare specimens in desert regions, opens questions about how the different faunas intermixed – because, for example, there are many shared taxa between Russia and South Africa.

There was once said to be a major temporal gap in the Permian tetrapod fossil record between the rich Early Permian fossils from the United States, and the equally rich Middle and Late Permian records of Russia and South Africa. This was termed Olson's Gap, after Everett C. Olson, a distinguished vertebrate palaeontologist who in the 1950s and 1960s had sought to correlate the Early Permian redbeds of the southwestern United States with emerging knowledge of the Middle and Late Permian in Russia. Ironically, he did not see a gap, and substantial redating of the Permian fossil beds, as well as new finds, have closed the gap (Benton, 2012). For example, recent finds have confirmed that three basal synapsid clades, the Varanopidae, Caseidae, and Sphenacodontidae, once thought to be exclusively Late Carboniferous and Early Permian in age, all existed into the Middle Permian (see Box 5.3). Further, the classic Russian and South African terrestrial fossiliferous series (see Boxes 5.2, 5.5) extend much deeper than had been thought, to the beginning of the Middle Permian.

5.4 THE PARAREPTILES

The Amniota diverged into two subclades, the Synapsida and Reptilia in the Late Carboniferous, and the latter split further into Parareptilia and Eureptilia (see Box 5.1). Here we shall consider the history of the Parareptilia through the Carboniferous, Permian, and Triassic, in approximate branching order, the aquatic mesosaurs, and the terrestrial millerettids, bolosaurids, procolophonids, nycteroleterids, and pareiasaurs.

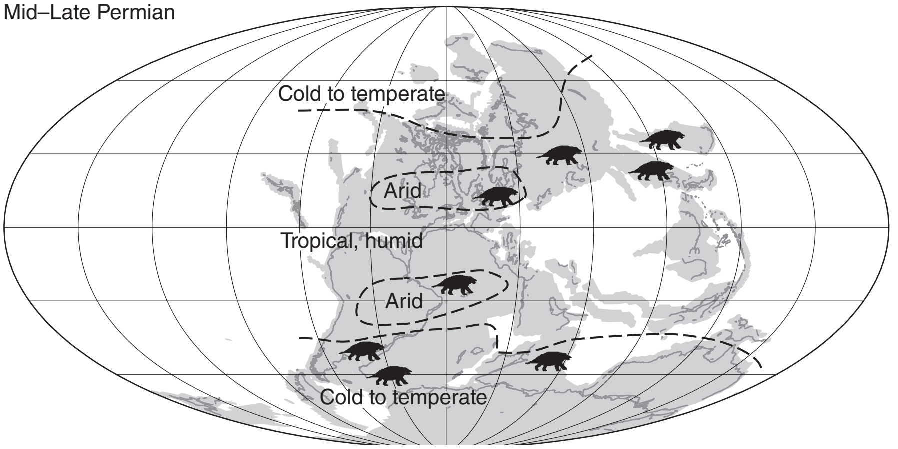


Figure 5.6 Palaeogeographic map of the world in the Middle to Late Permian, showing major climatic belts, and especially the extent of tropical humid and arid conditions. Most tetrapods are found in the cool to temperate zones, with rarer skeletons and footprints in arid zones in the UK, Germany, and Niger. Source: Alroy (2013) and various sources.

5.4.1 Mesosauridae

Mesosaurs (Modesto, 2006, 2010) are the first-known fully aquatic amniotes, represented by abundant small skeletons, up to 1 m long, from the Early Permian of South America and southern Africa, areas that were in contact at the time. They were used by Alfred Wegener as key evidence for the existence of Gondwana (see Section 2.3.2) The body (Figure 5.7(a)) is elongate, with a long neck and an especially long flat-sided tail that was used in swimming. The long thin jaws are lined with needle-like teeth that intermesh as the jaws close. They provide a kind of straining device that allowed *Mesosaurus* to take a mouthful of small arthropods or fish and strain the water out before swallowing.

Unborn embryos have been reported (Piñeiro *et al*., 2012) from a *Mesosaurus* specimen from Uruguay. The evidence is a single small skeleton, about one-tenth the size of the adult, contained within the rib cage of the presumed pregnant female. The small skeleton is unlikely to have been eaten by the adult because it does not show evidence of tooth damage or attack by stomach acids. There is no sign of an eggshell around the supposed embryo. If this is an embryo retained to the point of hatching, then this discovery proves that amniotes in the Early Permian laid eggs (as expected, see Section 5.2.1). Further, this finding shows that in the aquatic mesosaurs, viviparity had evolved, as it had done in coelacanths and sharks (see Section 3.9.3), presumably as a means of protecting the young in their early stages of development.

5.4.2 Millerettidae

The millerettids from the Late Permian of South Africa show some superficially lizard-like features in the skull (Figure 5.7(b,c)). There is usually a temporal fenestra, but its lower bar is often incomplete, and the squamosal, quadrate and quadratojugal may have been mobile. *Millerosaurus* was a small active insectivore with a 50 mm skull, and it probably lived rather like a modern lizard.

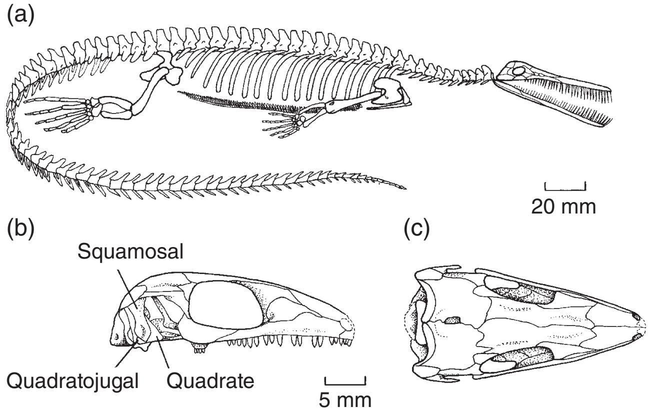


Figure 5.7 Small Permian parareptiles: (a) the mesosaur *Mesosaurus*; (b,c) the millerettid *Millerosaurus*, skull in lateral and dorsal views. Source: Adapted from Gregory (1951).

5.4.3 Bolosauridae

The bolosaurids are an enigmatic group of six or seven species from the Early Permian of North America and Europe, and the Middle Permian of Russia (Reisz *et al*., 2007). Bolosaurids have **heterodont** teeth, meaning teeth of several shapes, unusual for a reptile (but common in mammals, of course). In *Belebey* from the Middle Permian of Russia, there are four long teeth on the premaxillae that protrude forwards, and 9–10 broad teeth on each maxilla that had sharp edges, all suggesting a diet of tough plants. Another bolosaurid, *Eudibamus* from the Early Permian of Germany (Berman *et al*., 2000), was a slender reptile, some 250 mm long, and most unexpectedly, the first facultatively bipedal tetrapod. Its hindlimbs are twice as long as the forelimbs, and its feet are long, so that it probably ran up on its toes when moving at high speed (Figure 5.8). The tail is as long as the body, and was probably used for balancing.

5.4.4 Procolophonidae

The procolophonids are a clade of some 40 species that arose in the Late Permian and lived for about 50 Myr to the end of the Triassic, becoming rather diverse in the Triassic (Cisneros, 2008; Cisneros and Ruta, 2010). *Procolophon* from the Early Triassic of South Africa and Antarctica (deBraga, 2003) is 300–400 mm long, and has a stocky body and a relatively large broad skull. The large orbits include a posterior portion that was associated with the jaw adductor muscles, and the quadratojugal is expanded into a 'horn'. Later procolophonids often had several horn-like projections on the quadratojugal, possible defensive structures. The cheek teeth are blunt and peg-like, present only in small numbers, and they met during occlusion. They suggest a diet of fibrous plant material, and possibly arthropods with tough cuticles.

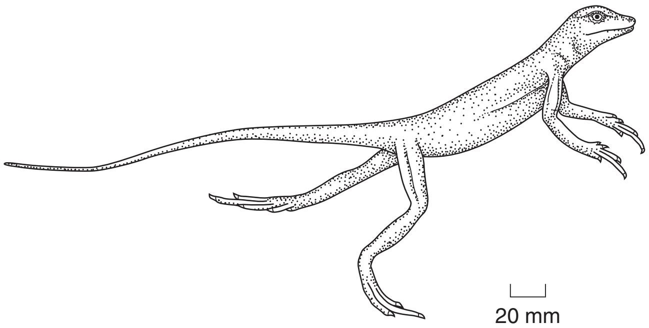


Figure 5.8 The bolosaurid *Eudibamus* running at speed. Source: D. Scott and D. Berman, Carnegie Museum of Natural History, Pittsburg, PA, USA. Reproduced with permission.

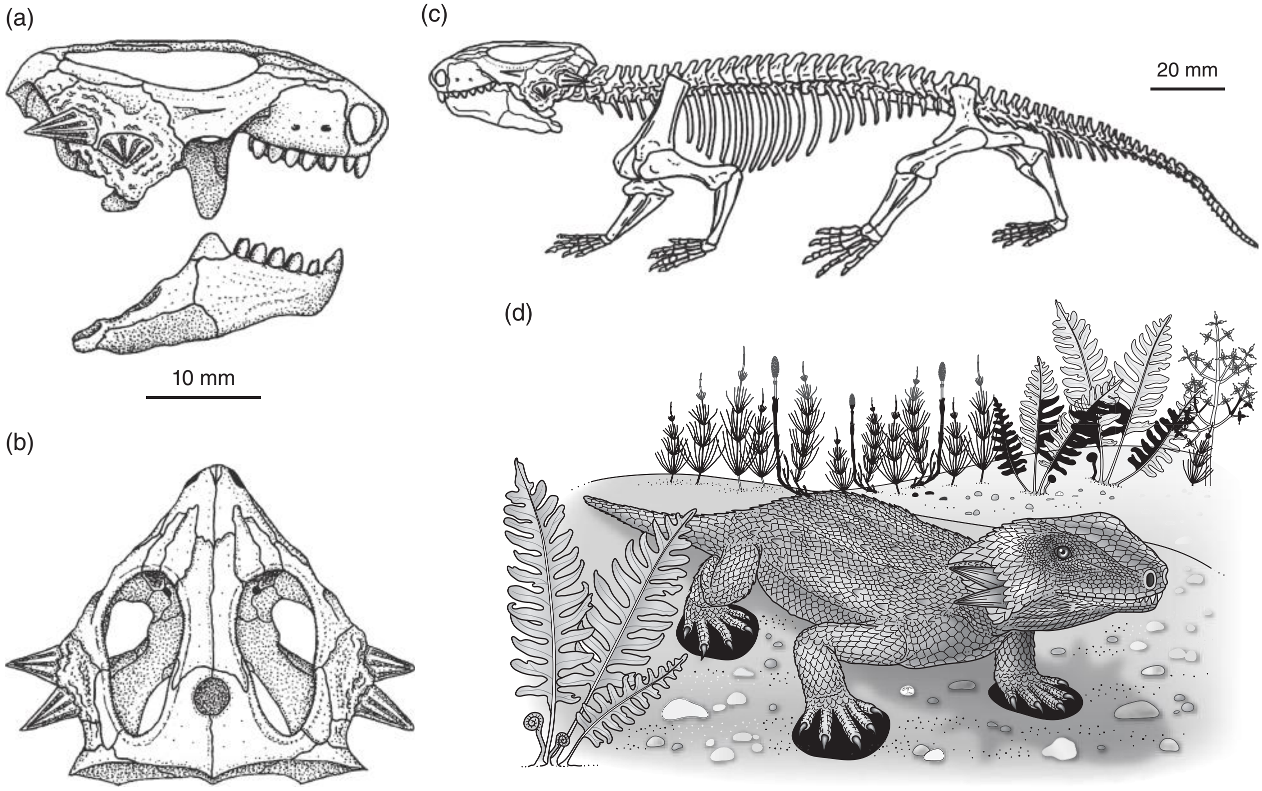


Figure 5.9 The procolophonid *Leptopleuron* from the Late Triassic, skull in lateral and dorsal views (a,b), skeleton (c), and restoration (d). Source: Säilä (2010). Reproduced with permission from the Royal Society of Edinburgh.

Some later procolophonids, such as *Leptopleuron* from the Late Triassic of Scotland (Säilä, 2010), evolved remarkable triangular projections on the posterior skull bones, giving their skulls an appearance like a modern horned lizard (Figure 5.9). These 'horns' were presumably more for show than physical function, and may have helped make the animal appear larger or more threatening to its many predators. Procolophonids may have been burrowers, using their broad hands and curved claws to shift sand fast (deBraga, 2003; Säilä, 2010). Some burrows in the South African Karoo (see Box 5.5) have been attributed to procolophonids.

5.4.5 Pareiasauromorpha: nycteroleters and pareiasaurs

Nycteroleterids were a somewhat obscure clade, known mostly from the Middle and Late Permian of Russia, and their relationships have only recently been established (Tsuji *et al.*, 2012) as being close to the pareiasaurs, forming a clade Pareiasauromorpha (see Box 5.1). Nycteroleterids are generally tiny animals, with skulls 50–100 mm long, and rows of small, pointed teeth (Figure 5.10(a–d)), evidently adapted to a diet of insects and other small invertebrates. The group is not restricted to Russia, with one taxon, *Macroleter*, reported from both Russia and North America, and other taxa from South Africa. The last nycteroleterid, *Emeroleter*, was more lightly built than its earlier relatives, and may have been a nippy little animal; it comes from the astonishing Russian locality of Kotel'nich, source of an extraordinary array of Late Permian amniotes (see Box 5.2).

The pareiasaurs (Lee, 2000; Tsuji, 2013) are restricted in time to the Late Permian, and they are known especially from Russia and South Africa, but also from China, Niger, Brazil, and Scotland. Most are large, typically 1–3 m long and heavily built. The Russian *Deltavjatia* from Kotel'nich (see Box 5.2) is a medium-sized form, with a small, heavily sculpted skull. The later *Scutosaurus* (Figure 5.10(e–g)) has massive elephantine limbs with short feet, and a muscle 'hump' over the shoulders associated with massive neck muscles. The skull is broad and heavy and covered with thickened knobs and incised sculpture, and a broad lateral frill that descends below the jaw line. The angular bone of the lower jaw is expanded to form a ventral boss. The teeth suggest that pareiasaurs were plant-eaters that fed on soft vegetation. Pareiasaurs are highly derived parareptiles, closest phylogenetically to nycteroleterids (see Box 5.1), and they were key components of the latest Permian ecosystems, right up to the end-Permian mass extinction (see Section 5.7).

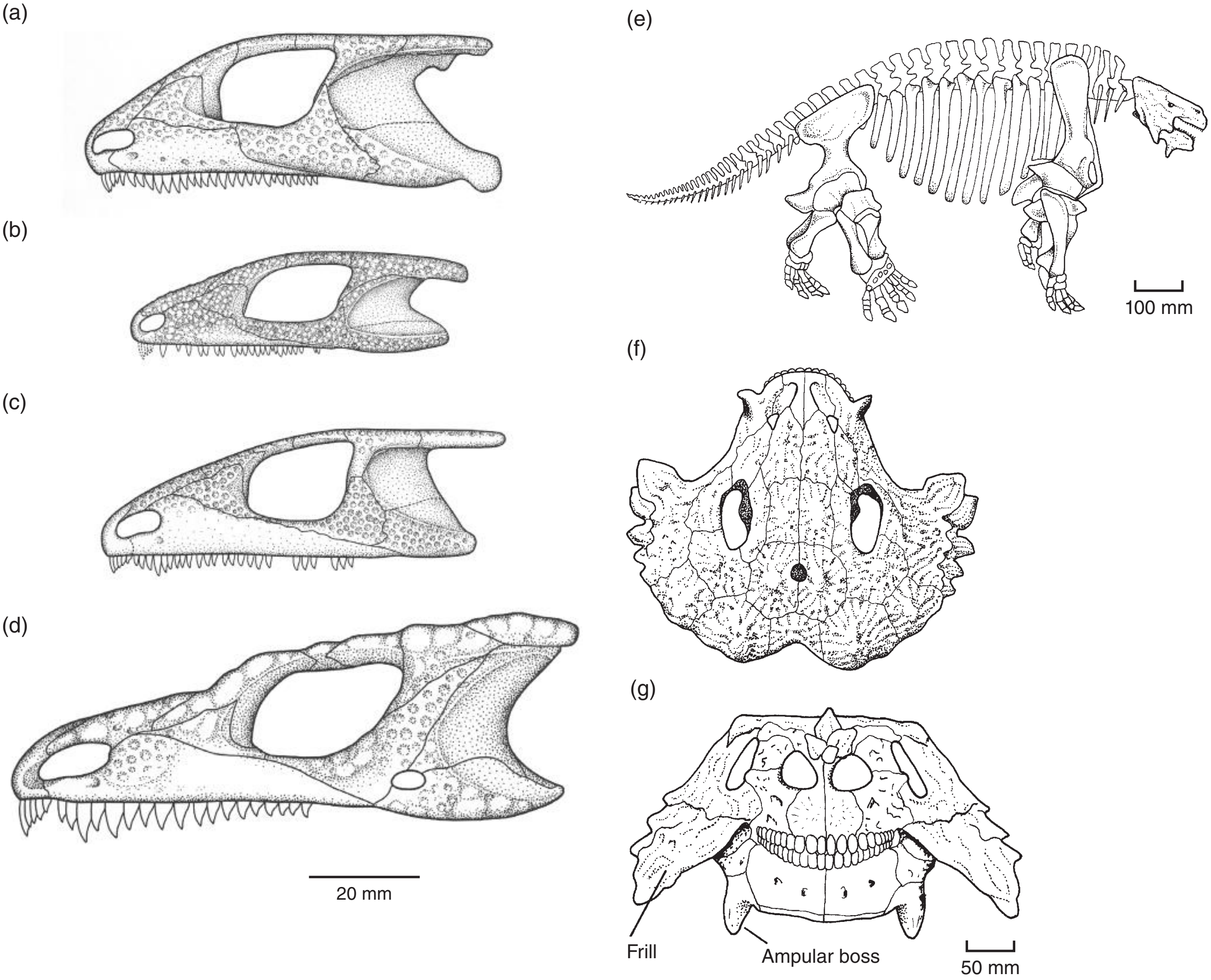


Figure 5.10 Permian pareiasauromorphs: (a–d) skulls of the nycteroleterids *Emeroleter* (a), *'Bashkyroleter' bashkyricus* (b), *Nycteroleter* (c), and *Macroleter* (d); (e–g) the pareiasaur *Scutosaurus*, skeleton and skull in lateral and ventral views. Source: (a–d) L. Tsuji, University of Washington, Seattle, WA, USA. Reproduced with permission. (e–g) Adapted from Kuhn (1969).

5.5 THE EUREPTILES

Of the two reptilian subclades, the Eureptilia was much more long-lived than the extinct Parareptilia, comprising some early stem-group clades and the Diapsida, represented today by lizards, snakes, crocodilians, and birds. The Carboniferous and Permian eureptilian subclades are introduced here in phylogenetic sequence: captorhinids, *Paleothyris*, and *Hylonomus*, and the early Diapsida, the araeoscelidians, weigeltisaurids, younginiforms, and *Protorosaurus*.

5.5.1 Captorhinidae

The captorhinids are known from the Early Permian of North America primarily, with late survivors in the Late Permian of North America, Africa and Eurasia. *Captorhinus* (Figure 5.11(a–c)) is a small animal, about 400 mm long, but with a relatively large heart-shaped head (Heaton and Reisz, 1986; Reisz *et al.*, 2011). The skull is heavy and bears surface sculpture. The proportions are similar to the earlier amniotes, but the skull is much broader at the back. The main pecularities of captorhinids are seen in the dentition. The peg-like teeth are often present in multiple rows (Figure 5.11(b,c)) that seem to slope diagonally across the width of the jaw, and five or six rows may be distinguished in one jaw bone.

Ricqlès and Bolt (1983) argued that the teeth of captorhinids were budded off from a dental lamina, the medially-placed gum tissue that produces teeth. As the animal grew in size, the maxilla added bony tissue plus teeth from the inside, and bone was removed and teeth worn on the outside. Thus, over time, the inner teeth in each row will come into wear at the jaw edge as older teeth are lost. This complex system of tooth replacement is

BOX 5.2 ON THE BANKS OF THE MIGHTY VYATKA

Some fossil vertebrate localities have a romantic aspect, probably because they are located in rather remote areas. Permian tetrapods from Russia were first collected in the 1850s, and occasional specimens were sent back from the copper mines around the southern Urals to be studied by scientists in St Petersburg, Moscow, and western Europe. Then, from 1895 onwards, Vladimir Amalitskii (1860–1917) began collecting specimens from northern parts of European Russia, and he made especially impressive collections of large amniotes from along the shores of the North Dvina River. At that time, travelling by river boat was much easier in remote parts of Russia than using the rudimentary roads (Ochev and Surkov, 2000).

For such a huge land area, the numbers of vertebrate palaeontologists operating in Russia was always small. Ivan Efremov (1907–1972) was the next great name, and he fostered widespread collecting from his base at the new Palaeontological Institute in Moscow. Fossiliferous Permo-Triassic sediments extend from Vladimir, east of Moscow to the Ural Mountains, and some 2000 km from the Arctic shores southwards to Orenburg and the border with Kazakhstan. Efremov and colleagues were able to show that the Russian Permo-Triassic yielded a succession of faunas, now known to range in age from the very end of the Early Permian to the end of the Middle Triassic, a span of 35 Myr. One of the key localities was along the west bank of the Vyatka River, south of the city of Kotel'nich.

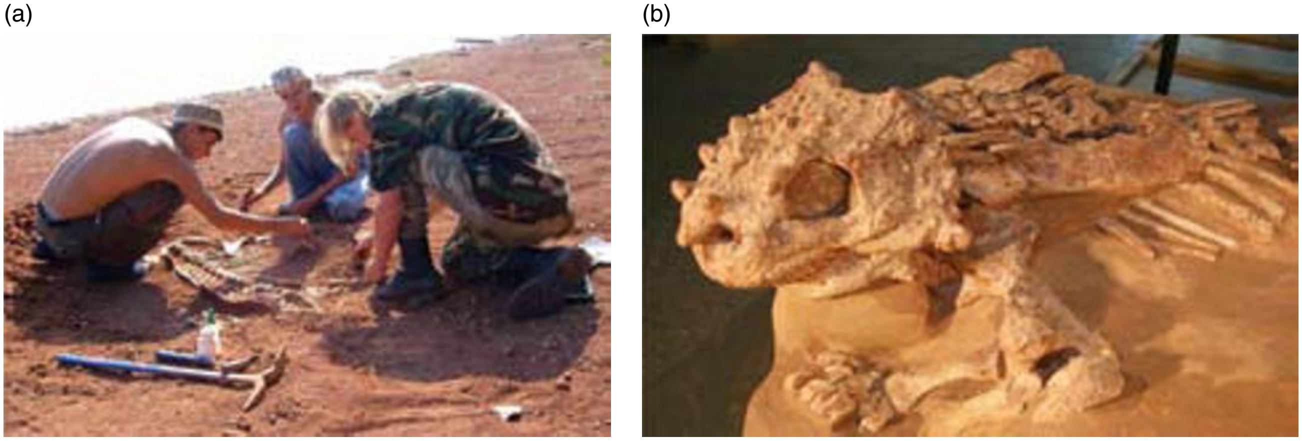
Since 1935, several large-scale expeditions to the Kotel'nich shores have yielded dozens of skeletons of the pareiasaur *Deltavjatia*, together with rarer remains of small amniotes including the parareptile *Emeroleter* (a nycteroleterid) and the agile, tree-climbing anomodont *Suminia* (see Figure 5.20). Excavations continue (illustration (a)), and by far the commonest fossils are skeletons of *Deltavjatia*, which are nearly always complete, and preserved at a single horizon in the Vanyushonki Member along the banks of the mighty Vyatka River. In some cases, it almost looks as if the animal is in a hollow in the mud, with its arms up, as if trying to escape (illustration (b)).

There has been much speculation about why pareiasaur skeletons are so common in the Kotel'nich section, and how they were buried. In interpreting the taphonomy of these specimens, several points are worth noting (Benton *et al*. 2012): (1) the skeletons all sit in hollows scoured into a palaeosol surface; (2) there is usually just one – sometimes two - skeletons per hollow; (3) the skeletons are remarkably complete and articulated; (4) the skeletons are almost never belly-up; (5) the bones sometimes show evidence of exposure; (6) the animals are of uniform size, and small; and (7) pareiasaurs were terrestrial herbivores.

The taphonomy of these strikingly complete skeletons has been interpreted in eight ways, as: (1) stuck in the mud of deep lakes; (2) killed by desertification events; (3) buried under sand dunes; (4) trapped in burrows, perhaps following hibernation; (5) carcasses dumped in fluviatile scours; (6) animals caught in hollows while digging for water; (7) animals trapped in shallow wallows; or (8) animals mired when weakened by an arid season.

The last of these models is most likely, that the pareiasaurs had become trapped in boggy muds, and were preserved more or less *in situ*. The evidence is the posture of most of the skeletons, with the dorsal side facing up and the limbs down, as if they had died standing, as well as the excellent quality of preservation. Late Permian climates (see Section 5.3) were hot, and possibly monsoonal in this area. Perhaps the animals all died at the same time during a particularly devastating aridification event. In the wet season, herds of pareiasaurs lumbered over the plains, feeding on waterside plants. As conditions became worse at the onset of the dry season, the pareiasaurs congregated around remaining ponds, and smaller and weaker animals died. As the ponds dried out completely, soils were formed, and the carcasses were not scavenged or broken up, but were covered by gentle deposition of lake sediments during the following wet season.

Read more at: http://palaeo.gly.bris.ac.uk/Russia/Kotelnich.html, and in the pages of the Vyatka Palaeontological Museum, which continues excavations along the banks of the Vyatka, at: http://suminia.com/index.php?page=home.



The Late Permian sediments and fossils of the Kotel'nich section. (a) Expedition of the Vyatka Palaeontological Museum: from left to right, Maxim Kovalyov, Alexey Toropov, and Il'ya Shumov remove sediment from a complete pareiasaur specimen near Boroviki, with the Vyatka River at top left. (b) Skeleton of *Deltavjatia vjatkensis* seen from the front, as preserved. See Colour plate 5.1. Source: A. Yu Khlyupin, Vyatka Paleontological Museum, Kotel'nich, Russia. Reproduced with permission.

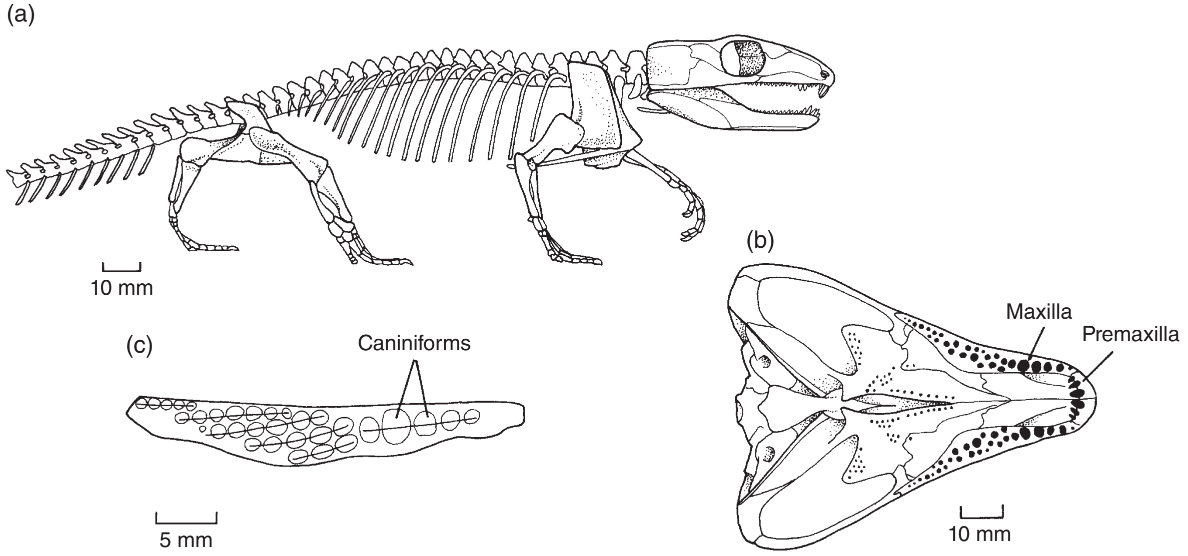


Figure 5.11 The captorhinid *Captorhinus*: (a) skeleton in walking posture; (b) ventral view of the palate; (c) ventral view of the maxilla, showing the multiple rows of teeth. Source: (a) Adapted from Heaton and Reisz (1986). (b,c) Adapted from Ricqlès and Bolt (1983).

interpreted as an adaptation for piercing or grinding tough plant material or hard-shelled invertebrates.

5.5.2 *Paleothyris* and *Hylonomus*

Early eureptiles include animals such as *Hylonomus* and *Paleothyris* (see Figures 5.1–5.3) and six other genera from the Late Carboniferous and Early Permian of North America and Czechoslovakia that were formerly assigned to the Protorothyrididae (Carroll and Baird, 1972). It is now known that all these 'protorothyridids' are basal eureptiles (see Box 5.1; Laurin and Reisz, 1995). *Paleothyris* and *Hylonomus* were agile insectivores, rather like modern lizards in their ecology.

5.5.3 Araeoscelidia

Diapsids are rare in the Carboniferous, being known from only two taxa from the Late Carboniferous of Kansas, USA. One of these, *Spinoaequalis*, was possibly aquatic and the other, *Petrolacosaurus* (Reisz, 1981), retained terrestrial adaptations. *Petrolacosaurus*, a slender 400-mm-long animal, has a body (Figure 5.12(a)) similar in proportions to *Hylonomus*, but with a relatively smaller head, less than one-fifth of the body length, a longer neck and longer limbs. The skull (Figure 5.12(b–d)) is also similar, but with larger orbits, two temporal fenestrae, and more small teeth on the palatal bones. The teeth are small and sharp and clearly indicate a diet of insects and other small animals. In addition to the **choana**, or internal nostril, of all tetrapods, through which the air passages from the nasal cavity pass into the mouth, there is an extra opening in the palate, the **suborbital fenestra** (Figure 5.12(d)). These two taxa, as well as *Araeoscelis* from the Early Permian of North America, comprise a basal diapsid clade, the Araeoscelidia, diagnosed by shared features of the vertebrae and limbs.

5.5.4 Permian diapsids

The diapsids remained at low diversity during the Early Permian, and radiated in the Late Permian. The most unusual were the gliding weigeltisaurids of Europe and Madagascar (Evans and Haubold, 1987). These small animals have elongated bony rod-like ribs that stick out sideways forming horizontal 'wings' (Figure 5.13(a)), but could be folded back when the animal was running about. The ribs were presumably covered with skin, and *Coelurosauravus* could have glided from tree to tree as the living lizard *Draco* does. The skull (Figure 5.13(b)) is diapsid (the lower temporal bar is incomplete), and the squamosal and supratemporal have striking 'toothed' margins at the back.

The other Late Permian diapsids were less exotic. They include forms such as *Protorosaurus* (Figure 5.13(c)), a slender long-necked animal from the Late Permian of Germany (Gottmann-Quesada and Sander, 2009), the first representative of the Neodiapsida, and the Archosauromorpha (see Section 6.2). *Youngina* (Figure 5.13(d)), only 350–400 mm long (Gardner *et al.*, 2010), was probably an active lizard-like insectivore and carnivore. The skull is similar to that of *Petrolacosaurus* (cf. Figure 5.12), but with rather larger temporal fenestrae. The neck is short and the limbs are long. *Youngina* is part of a wider clade Younginiformes that includes other Late Permian and Early Triassic terrestrial and aquatic relatives, some of the latter with deep flattened tails and paddle-like feet.

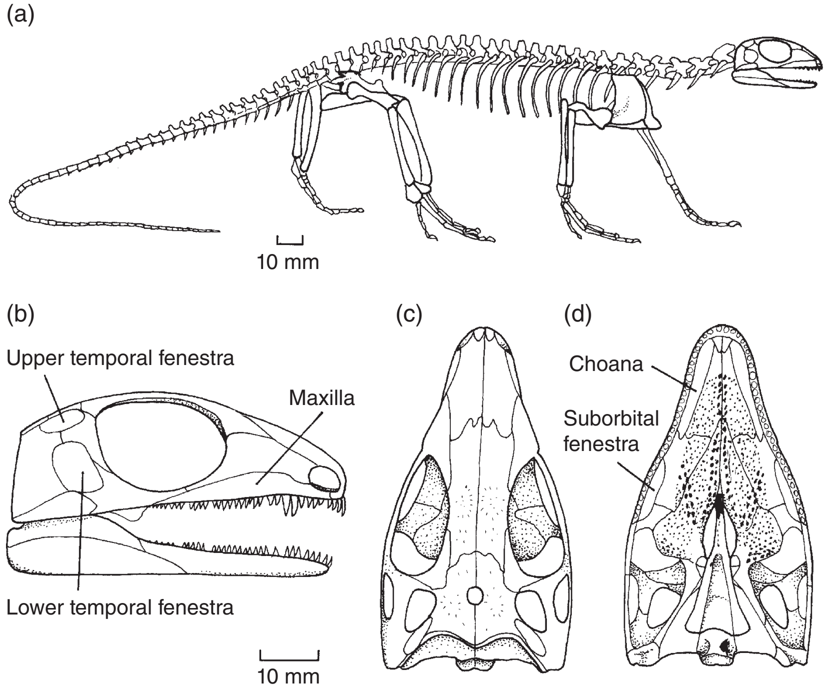


Figure 5.12 The first diapsid, *Petrolacosaurus*: (a) skeleton; (b–d) skull in lateral, dorsal, and ventral views. Source: Adapted from Reisz (1981).

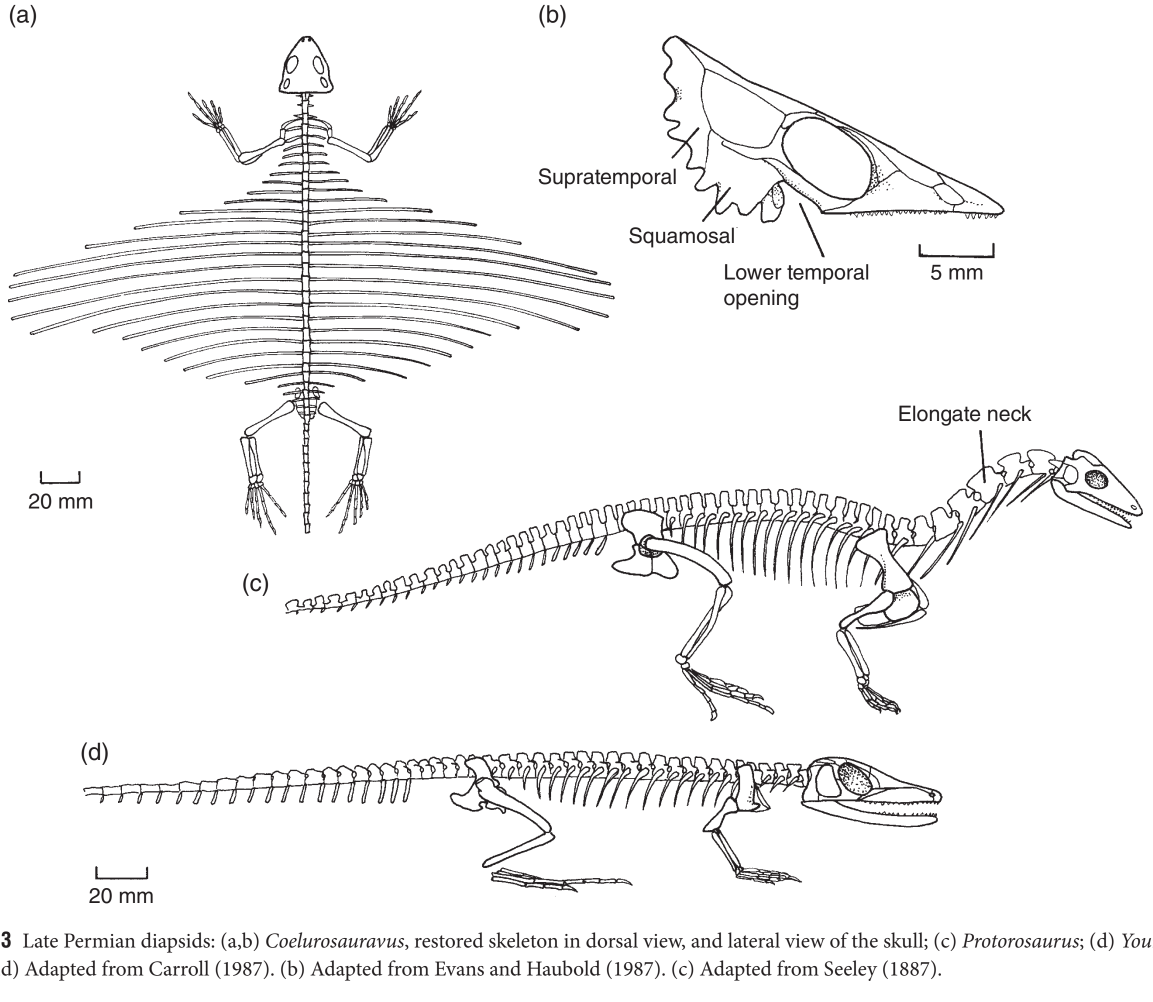


Figure 5.13 Late Permian diapsids: (a,b) *Coelurosauravus*, restored skeleton in dorsal view, and lateral view of the skull; (c) *Protorosaurus*; (d) *Youngina*. Source: (a,d) Adapted from Carroll (1987). (b) Adapted from Evans and Haubold (1987). (c) Adapted from Seeley (1887).

5.6 BASAL SYNAPSID EVOLUTION

The Synapsida are the sister group of the Reptilia (Parareptilia + Eureptilia) with an evolutionary history reaching as far back as the Late Carboniferous, and they diversified enormously during the Permian, becoming the dominant land animals (Kammerer *et al.*, 2014). The clade is generally divided into two groups. The 'pelycosaurs' (Romer and Price, 1940; Reisz, 1986; Benson, 2012; Brocklehurst *et al.*, 2013) are a paraphyletic group of six families of basal synapsids that were particularly important in the Early Permian. These were succeeded in the Middle Permian by the Therapsida, a diverse clade of small to large plant- and flesh-eaters (see Box 5.3).

5.6.1 Carboniferous and Early Permian synapsids

The Ophiacodontidae, a group of six or seven genera, arose in the Late Carboniferous and survived into the Early Permian. The first ophiacodont, *Archaeothyris* from the Morien Group of Nova Scotia, which also yielded *Paleothyris*, is incompletely known, being represented by only a backbone, pelvis and partial skull (Figure 5.14(a)). Its relative *Ophiacodon*, from the Late Carboniferous and Early Permian of New Mexico (Romer and Price, 1940; Reisz, 1986), is larger than the amniotes so far described, being 1.5–3 m in length (Figure 5.14(b–d)). The skull is relatively very large. It has a long, high narrow snout region that makes up three-fifths of the total length, and the orbit and temporal fenestra are small and placed high. The limb bones are massive. *Ophiacodon* was a meat-eater, and it may have fed on fishes and tetrapods rather than mainly on insects.

The varanopids comprise eleven genera of small carnivores from the Late Carboniferous and Early Permian of North America, as well as from the Middle Permian of Russia and South Africa (Campione and Reisz, 2010). The limbs are long and the skeleton lightly built, so that they are interpreted as active and agile in their habits. *Varanops* (Figure 5.15(a,b)) has a long low skull, with the dentition extending unusually far back to lie below the temporal fenestra.

The eothyridid *Eothyris*, a small animal from the Early Permian of Texas (Figure 5.15(c)), has a low skull with a much shorter and broader snout than that of *Ophiacodon*. The two caniniform teeth are very large, and *Eothyris* was clearly a powerful predator.

The caseids, herbivorous pelycosaurs from the Early and Middle Permian of North America, Russia, Italy, and France (Maddin *et al.*, 2008), include small and large forms. *Cotylorhynchus* from Texas and Oklahoma (Figure 5.15(d–f)) is the largest basal synapsid, at a length of 3 m, but its disproportionately small skull looks as if it comes from an animal one-quarter of the size. The key caseid characters are seen in the skull (Figure 5.15(d,f)): greatly enlarged nostrils, a pointed snout that extends well in front of the tooth rows, reduced numbers of teeth with no caniniforms, and a very large parietal (pineal) opening. There are several indications that *Cotylorhynchus* was a herbivore: the teeth are spatulate in shape rather than pointed, and they have crinkled edges, the jaw joint is placed *below* the level of the tooth rows, an adaptation that shifts the maximum bite force to the cheek teeth, the jaw could probably have been moved fore-and-aft, and the barrel-shaped ribcage presumably contained massive guts that were necessary for digesting large quantities of rough plant food.

5.6.2 The sail-backed synapsids

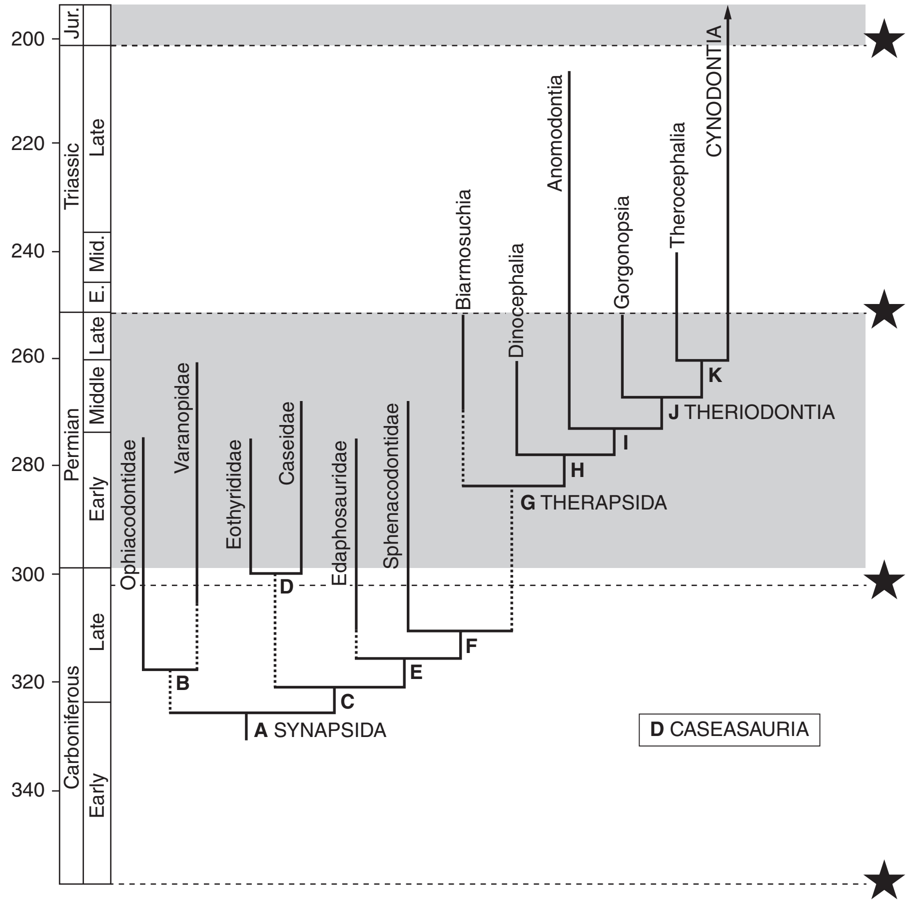
Two groups of Early Permian synapsids, the edaphosaurids and the sphenacodontids, include genera that had massive 'sails' on their backs. The edaphosaurids, such as *Edaphosaurus* from the Late Carboniferous and Early Permian of New Mexico and Texas (Figure 5.16) were herbivores. They have enormously elongated neural spines of the cervical and dorsal vertebrae, which were probably covered by skin. The skull of *Edaphosaurus* (Modesto, 1995) is relatively small in comparison with the body size, and it shows several adaptations to herbivory: peg-like teeth, a deep lower jaw, a sliding jaw joint to allow **propalinal** (back-and-forwards) jaw movements, and extensive palatal teeth (Figure 5.16(d)) that are large and form a broad crushing surface, and occlude against a similar battery on the coronoids and prearticular of the lower jaw.

The sphenacodontids (Reisz, 1986), were medium- to large-sized carnivores from the Late Carboniferous and Early and early Middle Permian of North America and Europe. *Dimetrodon* from the Early Permian of Texas and neighbouring states, as well as Germany, has a large sail, and it reaches a length of about 3 m. It has a large skull, with a small orbit and a high temporal fenestra (Figure 5.17). The powerful jaw muscles of *Dimetrodon* have been reconstructed (Figure 5.17(c)): the **adductors** were attached to the inside of the lower jaw and pulled the jaws shut, whereas the **pterygoideus** ran from the pterygoid to the outer face of the angular and provided a backwards jaw movement.

The pelycosaur sail has long been a puzzle. The neural spines in *Dimetrodon* have grooves at the base that were probably occupied by blood vessels. Further, when fossil skeletons are excavated, the neural spines generally lie in a neat fence-like array, which suggests that they were held together by a tough covering of skin in life. The 'sail' then was probably composed of heavily vascularized skin, and its function seems to have been thermoregulatory (Haack, 1986). The idea is that, early in the morning, when *Dimetrodon* was cold and sluggish, it would stand with its sail fully facing the sun, and would then absorb heat rapidly. This would have given it a head start over its sail-less prey. Later in the day, if it became overheated, *Dimetrodon* could stand in the shade and radiate heat from the sail. The weakness of this argument is that most pelycosaurs, and their contemporaries, lacked sails, and yet seemed to have survived perfectly well.

BOX 5.3 RELATIONSHIPS OF THE SYNAPSID GROUPS

Synapsida comprises two phases of diversification, a series of basal branches in the Late Carboniferous and Early Permian, referred to informally as 'pelycosaurs', and Therapsida, a clade that emerged at the beginning of the Middle Permian, and includes many Permian and Triassic taxa, as well as, ultimately, mammals. Both groups together were formerly sometimes called 'mammal-like reptiles', although it should be noted that they neither are nor derive from reptiles. The 'pelycosaurs' form a sequence of outgroups to Therapsida, with the sphenacodontids being the most derived (Reisz, 1986; Benson, 2012), although the ordering of the more basal subclades is unstable. The Biarmosuchia are the most basal therapsids. The dinocephalians, dicynodonts and gorgonopsians follow next (Hopson and Barghusen, 1986; Sidor and Hopson, 1998). The dicynodont branch is more extensive, i.e. the Anomodontia proper, consisting of basal taxa such as the venyukovioids from Russia and relatives from South Africa, Brazil, and China (Modesto and Rybczynski, 2000). The therocephalians are a sister group of the cynodonts, which include the mammals.



Cladogram showing the postulated relationships of the main groups of synapsids, with synapomorphies from Hopson and Barghusen (1986), Reisz (1986), Sidor and Hopson (1998), and Benson (2012). See Box 5.1 for context of Synapsida, and Figure 10.1 for relationships of Cynodontia. Synapomorphies: **A SYNAPSIDA**, maxilla contacts quadratojugal, caniniform maxillary teeth, lower temporal fenestra, paroccipital process contacts tabular and squamosal, trunk neural arches narrow; **B**, more than 25 maxillary teeth, long slender mandible, splenial does not contribute to mandibular symphysis; **C**, supratemporal has prominent lateral processes, pterygoid toothless, presacral and sacral intercentra absent, three or more sacral vertebrae, iliac blade tall and prominent anterior process; **D CASEASAURIA**, quadratojugal extends far forward to meet maxilla, pineal foramen large, parasphenoid toothless; **E**, postorbital narrow, parietal foramen well in front of occiput, stapes with blade-like shaft, ilium expanded in front and with horizontal dorsal margin; **F**, buttress in maxilla at root of caniniform tooth, premaxillary teeth in deep sockets; **G THERAPSIDA**, septomaxilla facial exposure extensive, contact between maxilla and prefrontal, external acoustic meatus in squamosal, basipterygoid articulation absent, jaw joint in line with occiput, anterior coronoid absent, serrations on teeth, 12 or fewer teeth behind caniniform, ectopterygoid teeth absent, vertebral notochordal canal absent in adult, anterior dorsal intercentra absent, cleithrum and clavicle separated, ossified sternum, acetabulum deep; **H**, posterior skull roof narrow, temporal fossa expanded laterally; **I**, pineal foramen opens flush with skull roof, lateral palatal foramen, coronoid process present and formed by dentary or dentary and surangular; **J THERIODONTIA**, zygomatic arch flares laterally, coronoid process on dentary, dentary masseteric fossa, postdentary bones reduced in height, atlas and axis pleurocentra fused, calcaneal tuber; **K**, temporal roof eliminated and temporal fossae meet in midline sagittal crest, postorbital reduced, postfrontal reduced, secondary palate on maxilla and palatine, teeth absent on palatine bone, dentary extends below angular. Abbreviations: **E**, early; Jur, Jurassic; Mid, middle. Dashed lines and star symbols indicate extinction events.

5.6.3 Biarmosuchia: the basal therapsids

The Therapsida are a substantial clade, diagnosed by numerous characters not seen in the basal synapsids, including an enlarged temporal fenestra, loss of the supratemporal bone, a deeply notched reflected lamina on the angular bone (Figure 5.18(c)), an anterior position of the jaw joint, reduction of the palatal teeth, as well as modifications of the shoulder and pelvic girdles and of the hindlimb (Hopson and Barghusen, 1986; Sidor and Hopson, 1998; see Box 5.3).

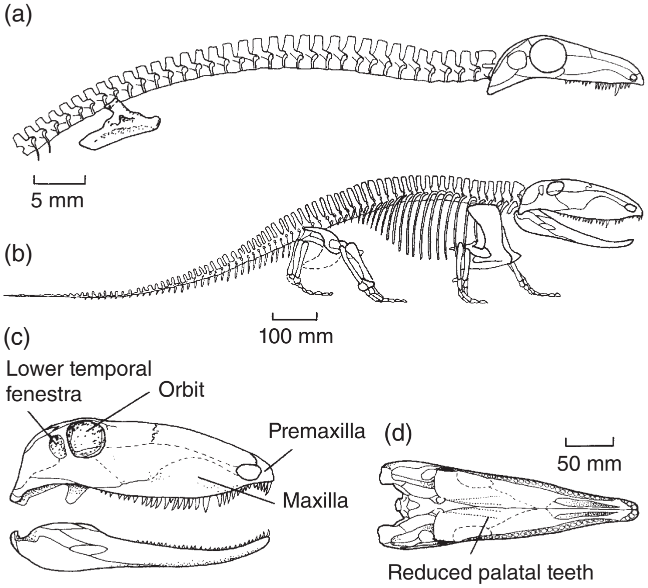


Figure 5.14 The ophiacodonts (a) *Archaeothyris* and (b–d) *Ophiacodon*: (a) partial skull and skeleton in lateral view; (b) skeleton; (c,d) skull in lateral and ventral views. Source: Adapted from Romer and Price (1940) and Reisz (1989).

A synapsid from the Early Permian of Texas, USA, *Tetraceratops* (Figure 5.18(a,b)) may be the oldest known therapsid (Laurin and Reisz, 1996). In many features, it seems to be intermediate between sphenacodontids and later therapsids, but it shows an enlarged temporal fenestra and some reduction in the palatal teeth. Its phylogenetic position was queried by Liu *et al.* (2009), but Amson and Laurin (2011) confirmed that *Tetraceratops* is the most basal therapsid.

The Biarmosuchia comprises some ten species from the Middle and Late Permian of Russia primarily, as well as South Africa and China (Battail and Surkov, 2000; Liu *et al.*, 2009). *Biarmosuchus* (Figure 5.18(c,d)), for example, was a small carnivore that resembled the sphenacodontids in most respects. The occiput slopes back rather than forwards, however, and the supratemporal bone is absent. The numbers of teeth are reduced and there is a prominent single canine, as well as a few small palatal teeth. An additional element, the septomaxilla, present within the nostril of earlier synapsids, is now exposed on the side of the skull.

5.6.4 Dinocephalia

The dinocephalians include 40 genera of synapsids from the Middle Permian of Russia and South Africa predominantly, with rare examples from China and Brazil, and there are both

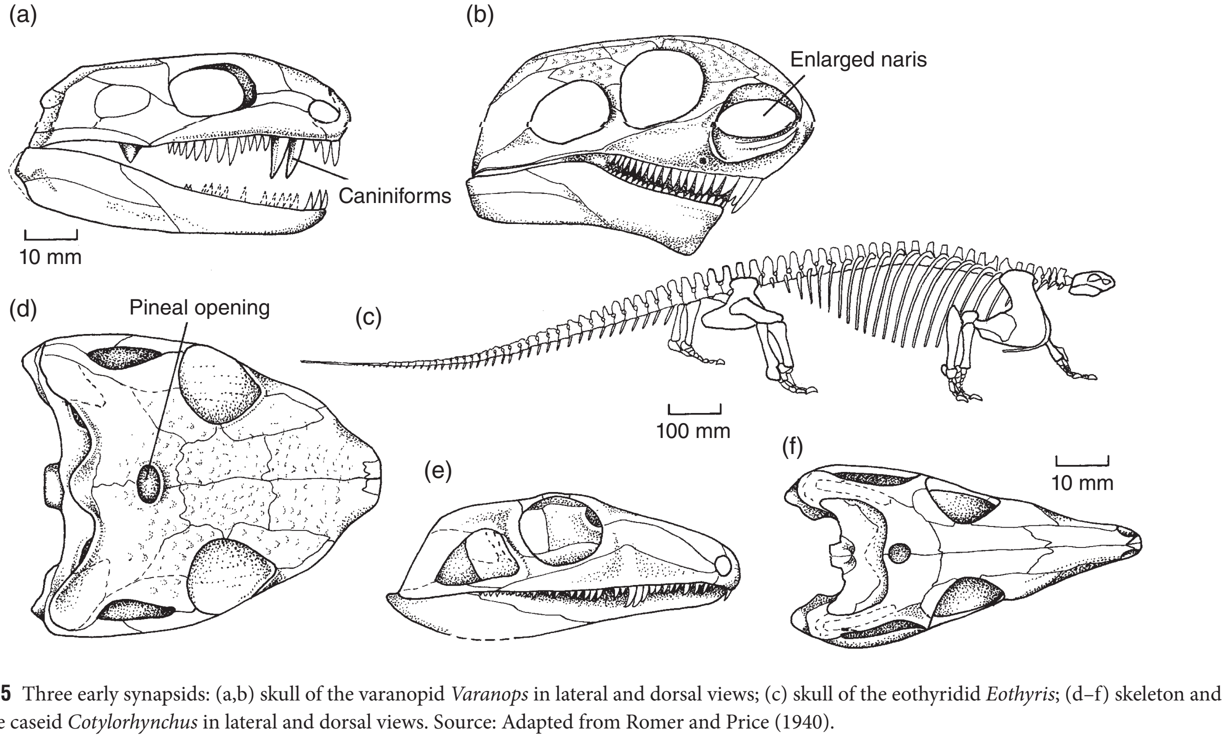


Figure 5.15 Three early synapsids: (a,b) skull of the varanopid *Varanops* in lateral and dorsal views; (c) skull of the eothyridid *Eothyris*; (d–f) skeleton and skull of the caseid *Cotylorhynchus* in lateral and dorsal views. Source: Adapted from Romer and Price (1940).

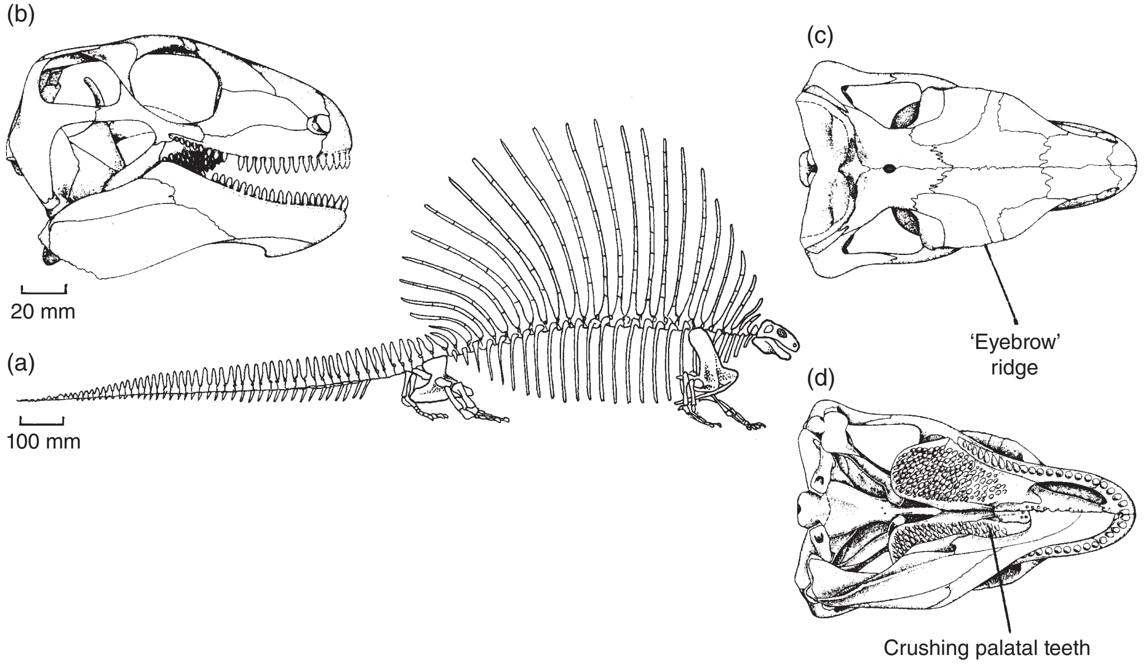


Figure 5.16 The herbivorous edaphosaurid *Edaphosaurus*: (a) skeleton; (b–d) skull in lateral, dorsal, and ventral views. Source: (a) Adapted from Romer and Price (1940). (b–d) S. Modesto, Cape Breton University, Sydney, Nova Scotia, Canada. Reproduced with permission.

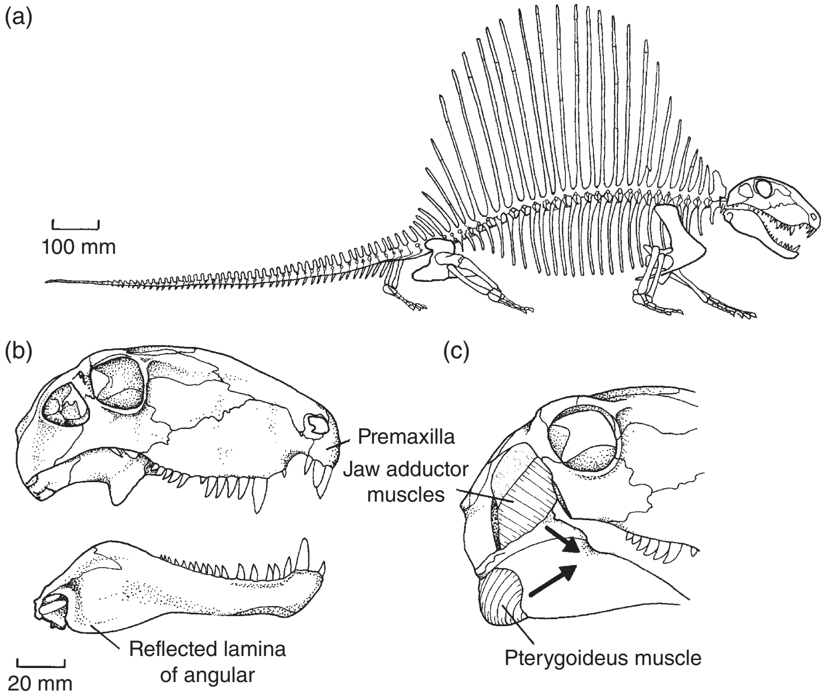


Figure 5.17 The carnivorous sphenacodontid *Dimetrodon*: (a) skeleton; (b) skull in lateral view; (c) major jaw muscles reconstructed, in lateral view. Source: Adapted from Romer and Price (1940).

carnivorous and herbivorous lineages (Battail and Surkov, 2000; Kammerer, 2011; Cisneros *et al.*, 2012). Dinocephalians were major components of their ecosystems, but disappeared at the end of the Middle Permian, to be replaced by gorgonopsians and dicynodonts. The carnivorous forms, the Anteosauria (Kammerer, 2011), include *Titanophoneus* from the Middle Permian of Russia (Figure 5.18(e)), a large animal with short limbs and a heavy skull. The incisors and canines are well developed, and presumably they were used for grasping and piercing prey.

The herbivorous dinocephalians, the Tapinocephalidae, include a range of herbivorous forms, some quite bizarre in appearance. *Moschops* from South Africa (Figure 5.18(f)) is a large animal about 5 m long with a massive ribcage and heavy

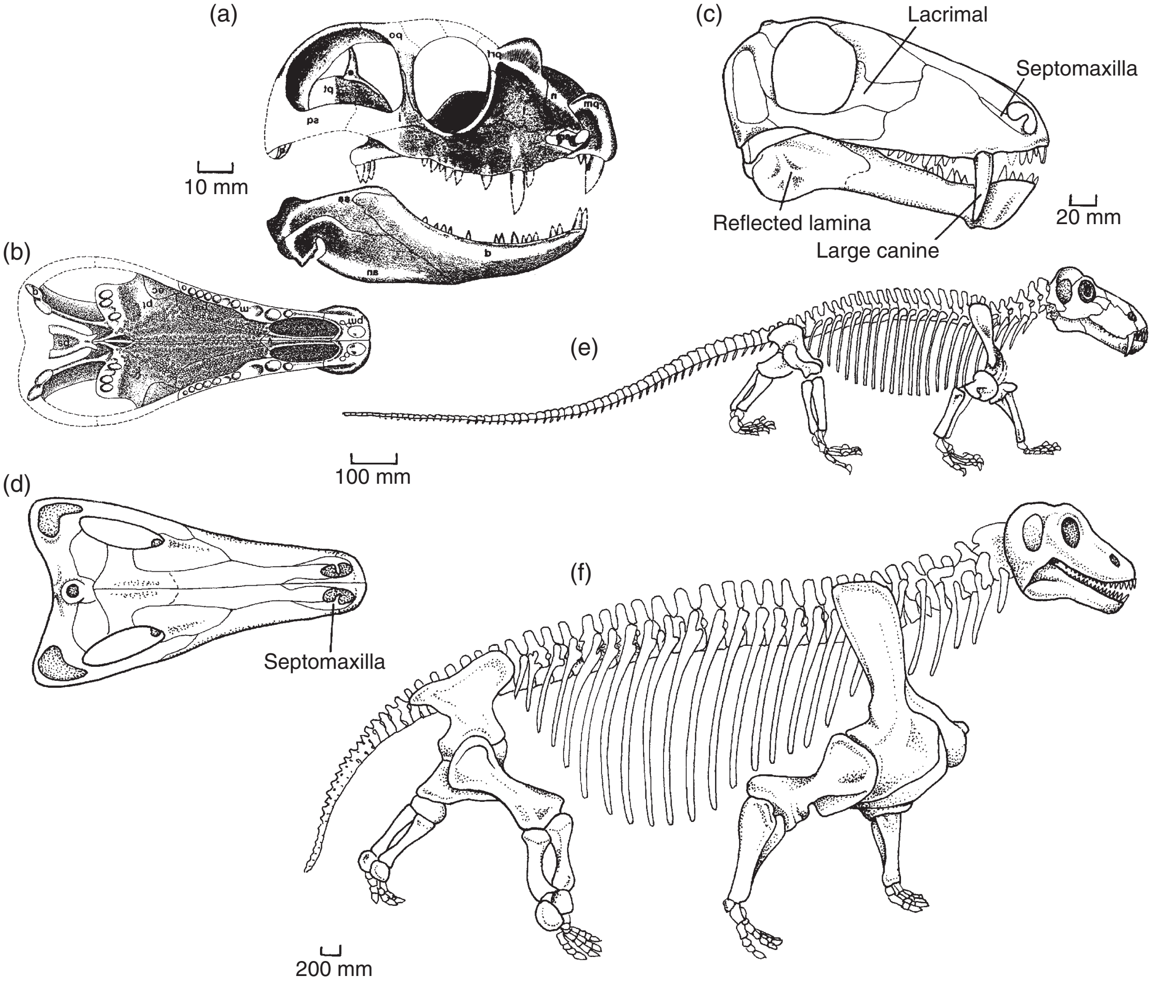


Figure 5.18 Early therapsids: (a,b) skull of *Tetraceratops* in lateral and ventral views; (c,d) skull of *Biarmosuchus* in lateral and dorsal views; (e) carnivorous dinocephalian *Titanophoneus*; (f) herbivorous dinocephalian *Moschops*. Source: (a,b) Adapted from Laurin and Reisz (1996). (c,d) Adapted from Battail and Surkov (2000). (e,f) Adapted from Gregory (1951).

limbs, but tiny feet. The hindlimbs were held close under the body in a more or less erect posture, whereas the forelimbs still stuck out sideways in a sprawling posture. The head is also relatively small compared with the body, reminiscent of the herbivorous basal synapsids (cf. Figures 5.15(c) and 5.16(a)). The skull of *Moschops* has a rounded snout, but the posterior part is elevated in a broad, square heavily built structure. What was its function? The roofing bones of the cranium are extraordinarily thick (up to 100 mm), and it has been suggested (Barghusen, 1975) that this was an adaptation for head butting, as is observed today among sheep and goats (Figure 5.19). The main force of the butt hit the thickened dorsal shield of the skull, and was transmitted round the sides to the occipital condyle. The occiput was also thickened and placed well beneath the skull, and the occipital condyle lay in direct line with the butting point. The impact was then transmitted down the thick vertebral column of the neck to the massive shoulder region.

5.6.5 Anomodontia

Anomodonts include about ten basal taxa, and the major clade, Dicynodontia. The basal forms include some medium-sized animals from the Middle and early Late Permian of Russia, South Africa, Brazil, and China that experimented with different means of consuming plant food. One of the most unusual is *Suminia* from the Late Permian of Kotel'nich, Russia (see Box 5.2), which appears to have been a tree-climber (Fröbisch and Reisz, 2009, 2011). *Suminia* has the short snout and differentiated teeth of other early anomodonts, but its limbs are unusually long, and the hands and feet appear to have been adapted to grasping (Figure 5.20). Another early anomodont, *Tiarajudens* from Brazil (Cisneros *et al*., 2011), has a massively elongate canine tooth, an unusual feature in a herbivore and perhaps used in sexual combat, as in the muntjac deer today.

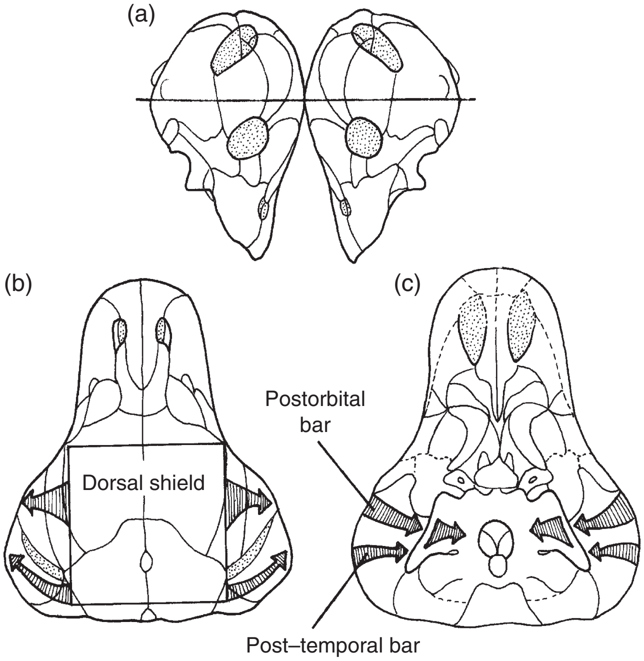


Figure 5.19 Head-butting behaviour in *Moschops*: (a) lateral view of the skulls of two butting individuals showing the line of transmission of the impact through the occipital condyle; (b,c) dorsal and ventral views of the skull showing the broad thickened dorsal shield, and transmission of forces from it through the postorbital and post-temporal bars to the occipital condyle. Source: Adapted from Barghusen (1975).

Figure 5.20 Restoration of the skeleton and body outline of *Suminia*, the world's first tree-climbing tetrapod, an herbivorous basal anomodont from the Late Permian of Russia. Source: Fröbisch and Reisz (2011). Reproduced with permission from John Wiley & Sons.

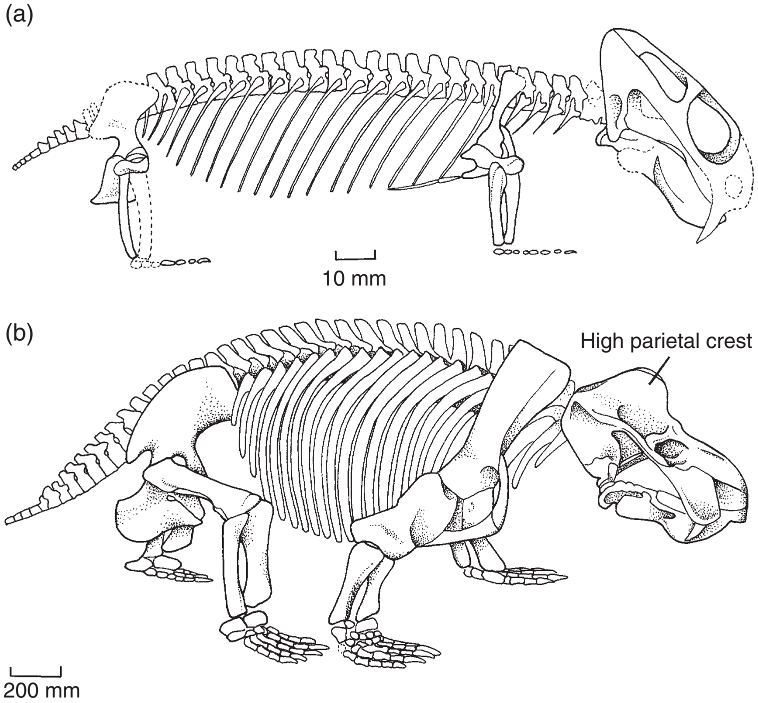


Figure 5.21 Skeletons of dicynodonts: (a) *Robertia* from the Late Permian; (b) *Kannemeyeria* from the Middle Triassic. Source: Adapted from King (1988).

BOX 5.4 DICYNODONT DIETS

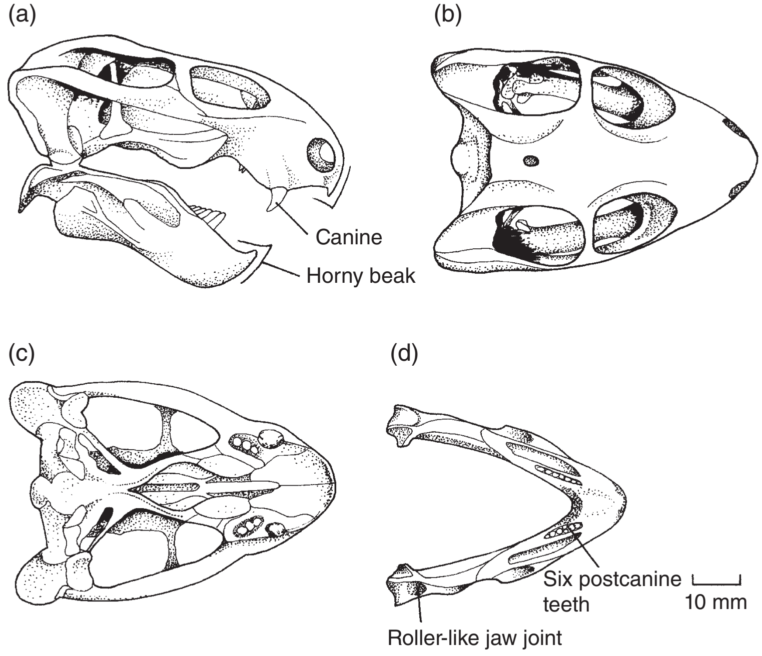
In the Late Permian, dicynodonts such as *Pristerodon* made up 80–90% of species in typical faunas (Fröbisch, 2009). Often, five or six dicynodont species of different sizes were present in a fauna, and they were preyed on by carnivorous dinocephalians or gorgonopsians. The shapes of dicynodont skulls and necks, and the inferred neck muscles, suggest that dicynodonts divide into three feeding categories according to the height of vegetation they could address: low, medium and high (Surkov and Benton, 2008). Such ecological distinctions among closely similar herbivores are seen today among mammals. Further, some dicynodonts such as *Lystrosaurus*, had specialized, foreshortened skulls and, based on FEA studies (see Box 2.1), may have used a snapping bite to cope with particularly tough vegetation (Jasinoski *et al.*, 2009). The huge success of these Late Permian dicynodonts may relate to their specialized jaw apparatus.

Pristerodon, a small dicynodont from the Late Permian of South Africa, has a skull 40–60 mm long with a particularly short snout (see illustration I(a–d)). *Pristerodon*, unlike many dicynodonts, retains a few teeth in addition to the canines, about six postcanines in the maxilla and in the dentary. These small sets of teeth worked against each other, and they are worn to form a single grinding surface. The rest of the jaw margins are made of sharp bone, presumably covered by a horny beak in life.

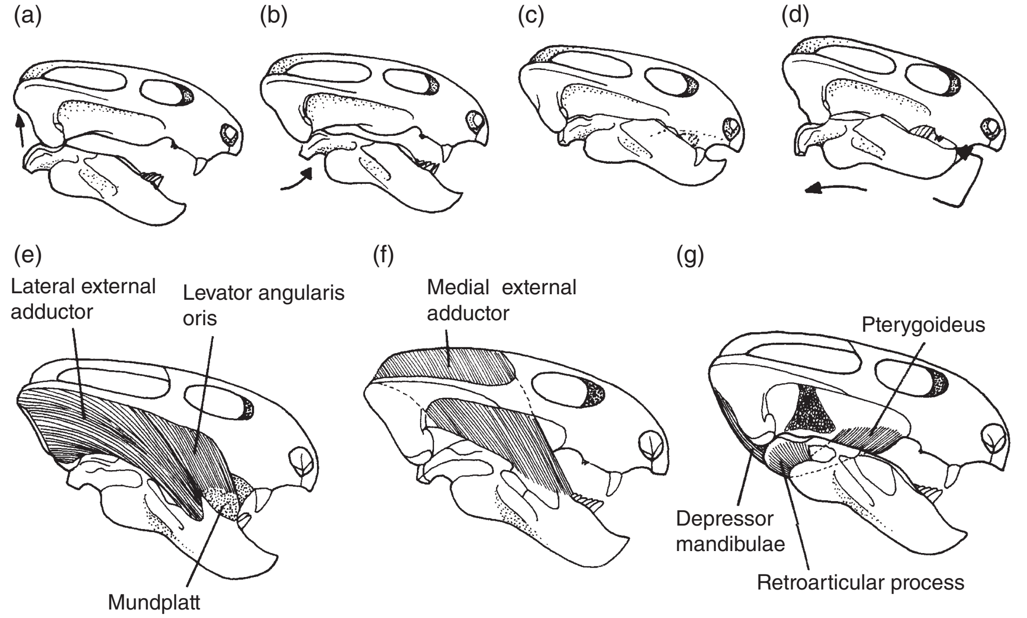
Pristerodon had a highly mobile jaw joint. The articulating surface of the articular is nearly twice as long as that of the quadrate, so that the lower jaw could slide some distance back and forwards during a jaw opening cycle. Crompton and Hotton (1967) reconstructed the jaw actions of *Pristerodon* using a complete and undistorted skull. By manipulating the jaws and studying patterns of tooth wear, they were able to work out with some confidence how *Pristerodon* seized and processed food (see illustration II(a–d)). Firstly, the jaw opened fully, then moved forwards by sliding at the joint. The food was taken in between the tips of the jaws as the lower jaw closed completely, and was then pulled back firmly with the jaw joint sliding back. This last **retraction** phase was the most powerful and had the effect of tearing the food at the front of the mouth and slicing any food that was between the cheek teeth.

The jaw muscles of *Pristerodon* were also reconstructed (illustration II(e–g)) by an analysis of the shape of the jaw bones and patterns of the surface. Most of the jaw adductors ran nearly horizontally, and their contraction would have powered the retraction phase of the jaw action. These key muscles include a major lateral external adductor that ran from the outside of the squamosal and quadratojugal to a long ridge on the side of the dentary (illustration II(e)), a medial external adductor that ran inside the zygomatic arch from the parietal and postorbital to the top of the dentary (illustration II(f)). Other features include a flexible sheet of tissue in the cheek region, the Mundplatte, which limited the jaw opening, and was kept taut by the levator angularis oris muscle (illustration II(e)), a small pterygoideus muscle that pulled the jaw forward, and the jaw opening muscle, the depressor mandibulae (illustration II(g)), that ran from the back of the squamosal to the **retroarticular process**, the part of the lower jaw behind the jaw pivot.

Pristerodon fed on vegetation that it snipped off with its horny beak and passed back, probably with a muscular tongue, to the cheek region for grinding and crushing before it was swallowed. The tusks of certain dicynodonts show wear striations when they are examined under high magnification, which suggests that they were used for scraping in the soil for plant material, and the diet may have consisted of roots, horsetail stems, club mosses and ferns. Dicynodont tusks may also show wear on the inside surfaces, confirming the prolapinal (back-and-forwards) jaw movements. Their tough diet generated copious excrement, and a supposed dicynodont communal latrine has been reported from the Middle Triassic of Argentina (Fiorelli *et al*., 2013).



(I) The skull of the dicynodont *Pristerodon* in (a) lateral, (b) dorsal, and (c) ventral views, and (d) the mandible in dorsal view. Source: Adapted from Crompton and Hotton (1967).



(II) (a–d) A single chewing cycle of *Pristerodon*, (a) as it lowers its jaw and moves it back, (b) moves it forward, (c) up for the bite, (d) and backwards to tear the food; (e–g) restoration of the jaw muscles of *Pristerodon*, drawn as if at progressively deeper levels, from (e) to (g). Source: Adapted from Crompton and Hotton (1967).

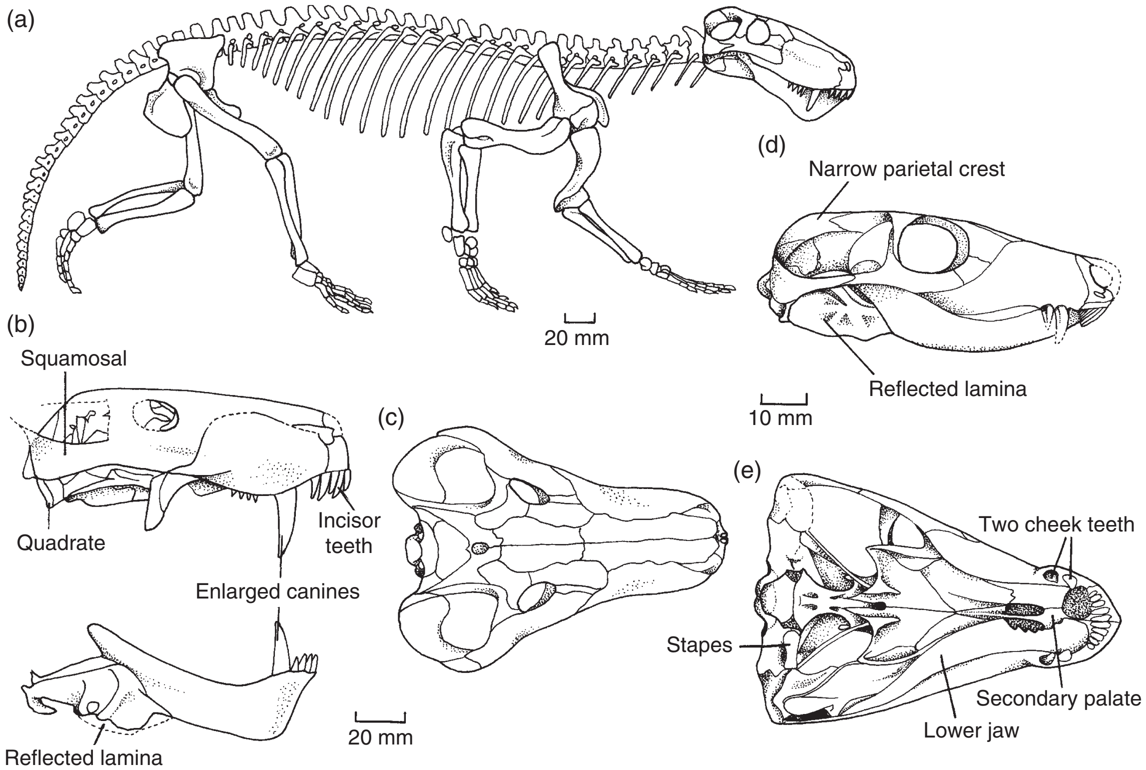


Figure 5.22 The gorgonopsians (a) *Lycaenops*, (b) *Arctognathus*, and (c) *Leontocephalus*; (d,e) the therocephalian *Theriognathus*. Source: (a) Adapted from Broom (1932). (b,c) Adapted from Kemp (1969). (d,e) Adapted from Brink (1956).

The dicynodonts, a group of over 60 genera, were dominant herbivores in the Late Permian (Fröbisch, 2009; Kammerer and Angielczyk, 2009; Angielczyk and Rubidge, 2010; Kammerer *et al.*, 2011). Some, such as *Diictodon*, were burrowers, occasionally found preserved in burrows, whereas others such as *Cistecephalus* and *Kawingasaurus* were diggers that rooted in the sediment for plant food. Nearly all dicynodonts died out at the end of the Permian. Late Permian dicynodonts, such as *Robertia*, were generally medium-sized pig-shaped animals with barrel-shaped bodies and unsatisfactory tails (Figure 5.21(a)). Dimensions ranged from rat- to hippo-sized. Dicynodonts were hit hard by the end-Permian mass extinction (see Section 5.7), and they passed through a ‘bottleneck’, when nearly all species died out (Ruta *et al.*, 2013). The suriving dicynodonts radiated in the Triassic, and some were large, being 3 m or so long. These must have had an ecological role similar to large modern browsing mammals. The Triassic *Kannemeyeria* (Figure 5.21(b)) has a narrow pointed snout and the parietals form a high crest. The ribcage is vast and the limbs and girdles powerfully built. Dicynodont feeding has been studied in some detail (see Box 5.4).

5.6.6 Gorgonopsia

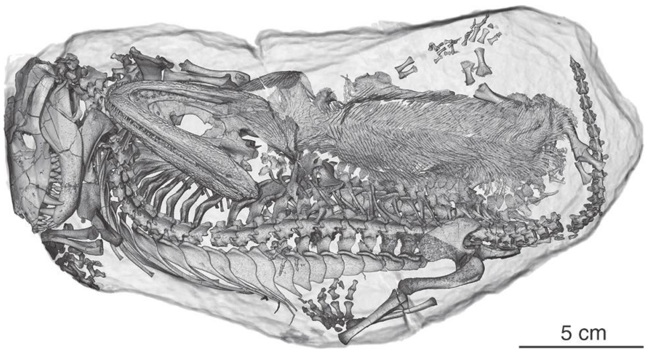
The dominant carnivores in the Late Permian were the gorgonopsians (Figure 5.22(a,b)), a group of some 35 genera from southern Africa, Russia and China. Their anatomy is remarkably conservative, most forms being about 1 m long and with a skull superficially like that of the earlier carnivorous therapsids. A typical form, *Arctognathus*, could have opened its jaws with a gape of 90° or so in order to clear its vast canines. The jaws then accelerated shut on to the prey animal, and the large fangs passed each other but did not touch, thus effectively piercing the skin and flesh, and disabling its victim. The jaw then shifted forwards and the incisors met, thus removing bite-sized chunks of flesh (Kemp,

BOX 5.5 THERAPSIDS OF THE KAROO

Middle and Late Permian therapsids are best known from the Karoo basin of South Africa, and the southern Urals region of Russia. The first records of these extraordinary animals came from South Africa in the 1850s, and since then, many thousands of skulls and skeletons have been collected (Nicolas and Rubidge, 2010; Rubidge, 2013; Rubidge *et al*., 2013). The Karoo basin covers a huge area, some 600,000 km^2, more than half the area of South Africa, and the sequences of Permian to Jurassic sediments total 12 km in thickness (Smith and Botha-Brink, 2014). During the Late Permian, sediments were fed into the Karoo basin from a ring of mountains that girdled southern Gondwanaland, partly located on what is now South America and Antarctica.

The Middle Permian to Middle Triassic sediments of the Karoo basin belong to the Beaufort Group, which is subdivided into eight biozones, based on the distributions of tetrapod taxa. Each biozone is 250–450 m thick. In all, the Beaufort Group has yielded about 100 therapsid genera, belonging to all major groups, as well as parareptiles (pareiasaurs, procolophonids, millerettids), diapsids (*Youngina*), temnospondyls and palaeoniscid fishes. The fossil amniotes are found in association with mudstones and sandstones that were deposited by meandering rivers on a broad floodplain, and soil horizons that developed after flooding episodes. Skeletons are preserved most often in a partly disarticulated condition in mudstones that were laid down between the river channels.

Spectacular recent discoveries include excellently preserved skeletons in burrows of all shapes and sizes. The most unexpected was the finding (Fernandez *et al*., 2013) of a therapsid and amphibian fitting snugly together at the end of a burrow in Early Triassic sediments (see illustration). The therapsid, *Thrinaxodon*, is interpreted as being the main burrow occupant: it had dug the burrow into damp mud at the side of a river or pond, and was aestivating. The injured temnospondyl amphibian, *Broomistega*, crept in, seeking cool conditions, and then both died.



The odd couple: two species in an Early Triassic burrow form the Karoo. The therapsid *Thrinaxodon* (lower) was apparently there first, and an injured temnospondyl, *Broomistega*, entered later, and then both died together. This is an upper side 3D rendering of CT scans of the specimen. See Colour plate 5.2. Source: Fernandez *et al*. (2013). Reproduced with permission.

1969). The gorgonopsians are reminiscent of sabre-toothed cats, which arose much later on and had similar enlarged canines and vast gapes (see Section 10.11.1). The gorgonopsians may have owed their success to the ability to prey on large thick-skinned dinocephalians and dicynodonts, and when these groups dwindled at the end of the Permian, so too did their predators.

5.6.7 Therocephalia

The therocephalians, a group of some 25 genera of carnivorous therapsids, are known from the Middle Permian to early Middle Triassic (Huttenlocker, 2009). They ranged in size from small insectivores to large carnivores, and also include some herbivores in the Early Triassic. *Theriognathus*, a small carnivorous form from the Late Permian of South Africa (see Box 5.5), has a skull 75 mm long (Figure 5.22(c,d)) with large orbits and temporal fenestrae. It shows several derived characters in comparison with the gorgonopsians (see Box 5.3): a reflected lamina placed near the back of the jaw, a vaulted palate made from vomer, premaxilla, maxilla and palatine (Figure 5.22(d)), and a narrow parietal crest that was extensively covered with the jaw adductor muscles.

Several lineages of therocephalians survived into the Triassic, and one group, represented by *Bauria* from the Early Triassic of South Africa (Figure 5.23(e,f)), became successful herbivores. The teeth of *Bauria* are generally robust, and there is a solid battery of broad cheek teeth for cutting up fibrous plant material. Between these teeth, the palate is vaulted over with bone to form a secondary palate. This is like the secondary palate of mammals. *Bauria* also has another superficially mammalian character in the loss of the bar of bone between the orbit and temporal fenestra.

5.6.8 Cynodontia

The clade Cynodontia includes mammals (see Box 5.3). Cynodonts arose at the end of the Permian and radiated mainly in the Triassic. The Permian forms are described here, and later cynodont evolution will be considered in Chapter 10, as a prelude to the origin of the mammals.

Among the six or seven cynodonts from the Late Permian of South Africa and Russia (Botha *et al.*, 2007), *Procynosuchus* from southern Africa is best known (Kemp, 1979). It has a long-snouted skull with an expanded temporal region (Figure 5.23(a–d)). *Procynosuchus* shows a large number of features that are generally mammalian in character (Hopson and Barghusen, 1986): the wide lateral flaring of the zygomatic arches that allowed an increased mass of jaw adductor muscles; a depression, the adductor fossa, for expanding jaw muscles on the upper part of the dentary behind the tooth row; an enlarged coronoid process of the dentary making up more than three-quarters of the length of the lower jaw; an enlarged nasal bone; the frontal excluded from the margin of the orbit; a double occipital condyle (Figure 5.23(d)); and the beginnings of a secondary palate composed largely of the maxillae and palatines (Figure 5.23(c)), rather than the vomers and maxillae, as in therocephalians. The size of *Procynosuchus* and the shape of its teeth suggest that it ate insects or small tetrapods.

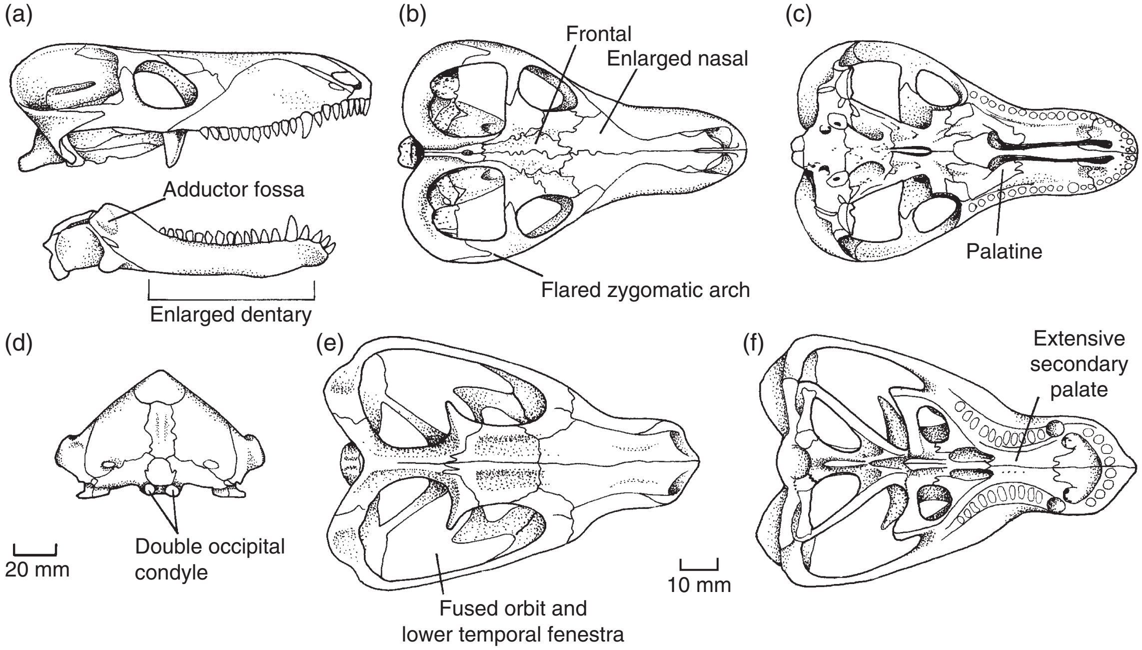


Figure 5.23 The early cynodont *Procynosuchus*, skull in (a) lateral, (b) dorsal, (c) ventral, and (d) occipital views; (e, f) the herbivorous therocephalian *Bauria*, skull in dorsal and ventral views. Source: (a–d) Adapted from Kemp (1979). (e,f) Adapted from Carroll (1987).

5.7 THE PERMO-TRIASSIC MASS EXTINCTION

The greatest mass extinction of all time, the Permo-Triassic mass extinction (Benton, 2003; Erwin, 2006), took place 252 Myr ago and it had a devastating effect on tetrapods. Complex latest Permian ecosystems that were dominated by herbivorous pareiasaurs and dicynodonts and carnivorous gorgonopsians, were replaced by new clades of archosaurs (crurotarsans, dinosauromorphs) and synapsids (cynodonts). Current estimates (Benton *et al*., 2013) are that four out of 11 families of amphibians (36%) and 17 out of 32 families of amniotes (53%) became extinct at the end of the Changhsingian, the final stratigraphic stage of the Permian. This represents an overall loss at family level of 49% of tetrapods through the Permo-Triassic mass extinction. It is important to note that 11 of the 22 familial lineages (50%) that survived through the Permo-Triassic mass extinction were extinct by the end of the Induan, the first stage of the Triassic, so the mass extinction had long-lasting repercussions. A loss of 49% of families would scale up to the extinction of as many as 80–90% of species because each family contains many species, and the surviving families were actually hugely depleted.

The Permo-Triassic mass extinction comprised several pulses of extinction, with the main event rather rapid, and dated at just before 252.28 Ma, based on high-resolution uranium-lead dating at various Permian-Triassic boundary (PTB) sections in south China (Shen *et al*., 2011). The extinction lasted for about 180,000 years, and this span actually resolves into two pulses of extinction in the marine record of south China (Song *et al*., 2013), the first in the latest Permian which was marked by the extinction of 57% of species, namely all plankton and some benthic groups, including algae, rugose corals, and fusulinids. The second phase occurred in the earliest Triassic, and resulted in the extinction of 71% of the remaining species. As both extinction pulses affected different groups of organisms, and so may have had distinct causes. It is not possible at present to discriminate these two phases of extinction on land, but the well documented sections in the red beds of South Africa and Russia show major losses of taxa at the PTB (Benton *et al*., 2004; Benton and Newell, 2014; Smith and Botha-Brink, 2014).

The bulk of evidence indicates that this largest-of-all mass extinctions was triggered by massive volcanic eruptions in Siberia which produced gases that led to global warming, acid rain, and ocean stagnation (Figure 5.24). There is currently no evidence for the impact of an asteroid or comet, a core trigger for the well-known end-Cretaceous mass extinction of dinosaurs (see Section 8.11). The Siberian Traps represent massive volumes of basalt lava, erupted in several bursts through a span of perhaps 0.6 Myr, and accumulating 3 million km^3 of lava over a vast area. The eruption released huge volumes of gases such as CO_2 and SO_2, and the CO_2, a greenhouse gas, caused flash heating of the atmosphere (Wignall, 2001; Algeo *et al*., 2011; Retallack, 2013; Benton and Newell, 2014). On land, it seems that acid rain was a consequence

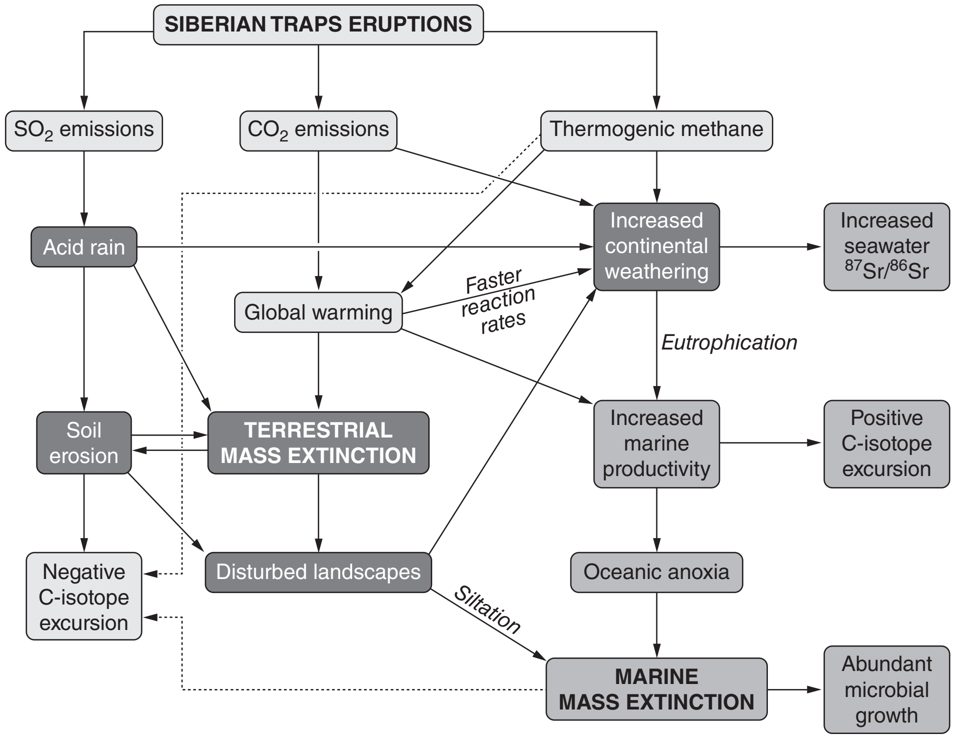


Figure 5.24 Model of likely environmental consequences of the Siberian Traps eruptions, showing the flows of consequences of global warming and acid rain. Causal links are indicated by solid arrows, and possible second-order controls on the negative carbonate C-isotope excursion at the Permo-Triassic mass extinction are indicated by dashed lines. Source: T. Algeo, University of Cincinnati, Cincinnati, OH, USA, adapted from Wignall (2001). Reproduced with permission.

of the huge influx of gases into the atmosphere, and this killed trees, and plants in general. Without their stabilizing root systems, soil was massively removed from the land and washed into the sea, and this is indicated by major changes in fluvial systems in redbed sequences across the PTB, from gentle, meandering streams in the latest Permian to rapid-flowing braided streams and alluvial fans in the earliest Triassic (Smith and Ward, 2001). In addition, trees, wood, and coals disappear from the rock record through the first 10 Myr or so of the Triassic (the 'coal gap'; Retallack, 2013) and there is an influx of terrestrially derived organic matter and sand into the sea in the earliest Triassic (Algeo *et al*., 2011).

In the sea, the masses of sand and mud doubtless killed shallow-water filter feeders. More importantly, the heating of the surface waters probably slowed down ocean circulations in which cold polar waters skim along the sea bed and rise at the equator, where they pick up oxygen, and bring it back down to the seabed. Geologists have identified a worldwide anoxic episode at the beginning of the Triassic, where sediments are all black, full of carbon, and often associated with sulphur minerals such as iron pyrites. This all indicates absence of oxygen, and indeed the earliest Triassic marine sediments are often virtually empty of life: in the many sections that span the PTB, life appears to have been rich and diverse immediately before the event, and then the burrowers, the seabed dwellers, the reef-builders, and the animals that swam above the sea floor are all gone.

The Permo-Triassic mass extinction was a dramatic punctuation mark, separating the Palaeozoic faunas from those of the Mesozoic. The complex multi-tier Late Permian ecosystems on land were destroyed. These changes can be tracked in South Africa and in Russia (Smith and Ward, 2001; Benton *et al*., 2004; Smith and Botha-Brink, 2014). Where there had once been some 40–50 tetrapods in a fauna, ranging from tiny insect-eaters to giant sabre-toothed gorgonopsians that preyed on the thick-skinned pareiasaurs and dicynodonts, only two or three tetrapod taxa survived. Most famous of the survivors was the dicynodont *Lystrosaurus*, which spread worldwide in the earliest Triassic. Such dominance by a single taxon, making up perhaps 75% of the post-extinction faunas, is a sure indication that a major crisis has happened. Other survivors included two or three temnospondyl lines (see Section 4.5.1), some procolophonids, some basal archosaurs and lepidosauromorphs (see Chapter 6), four species lineages of dicynodonts, and some therocephalians and cynodonts (see Section 10.1).

5.8 FURTHER READING

You can read more about the phylogeny of early amniotes in Chinsamy-Turan (2011) and Steyer (2012). Two older accounts of Permo-Triassic synapsids are Kemp (1982) and Hopson and Barghusen (1986), and a more recent collection of papers is Kammerer *et al*. (2014). An overview of the stratigraphy and faunas from the Permo-Triassic of Russia is given in Benton *et al*. (2000). Benton (2003) and Erwin (2006) provide accounts of the current understanding of the Permo-Triassic mass extinction.

QUESTIONS FOR FUTURE RESEARCH

1 More search of Late Carboniferous tetrapod sites for amniote specimens to aid understanding of the initial phylogenetic splitting of major groups, and the adaptations of the earliest forms.
2 More exploration of early Middle Permian localities to enhance knowledge at the transition between basal synapsids and therapsids.
3 More biomechanical studies of feeding and locomotion in the diverse and successful Middle and Late Permian therapsids.
4 Study of climate change through the Middle and Late Permian, and whether there was an extinction event at the end of the Middle Permian.
5 Fine-scale investigations of the nature of the Permo-Triassic mass extinction among tetrapods and links to environmental changes.

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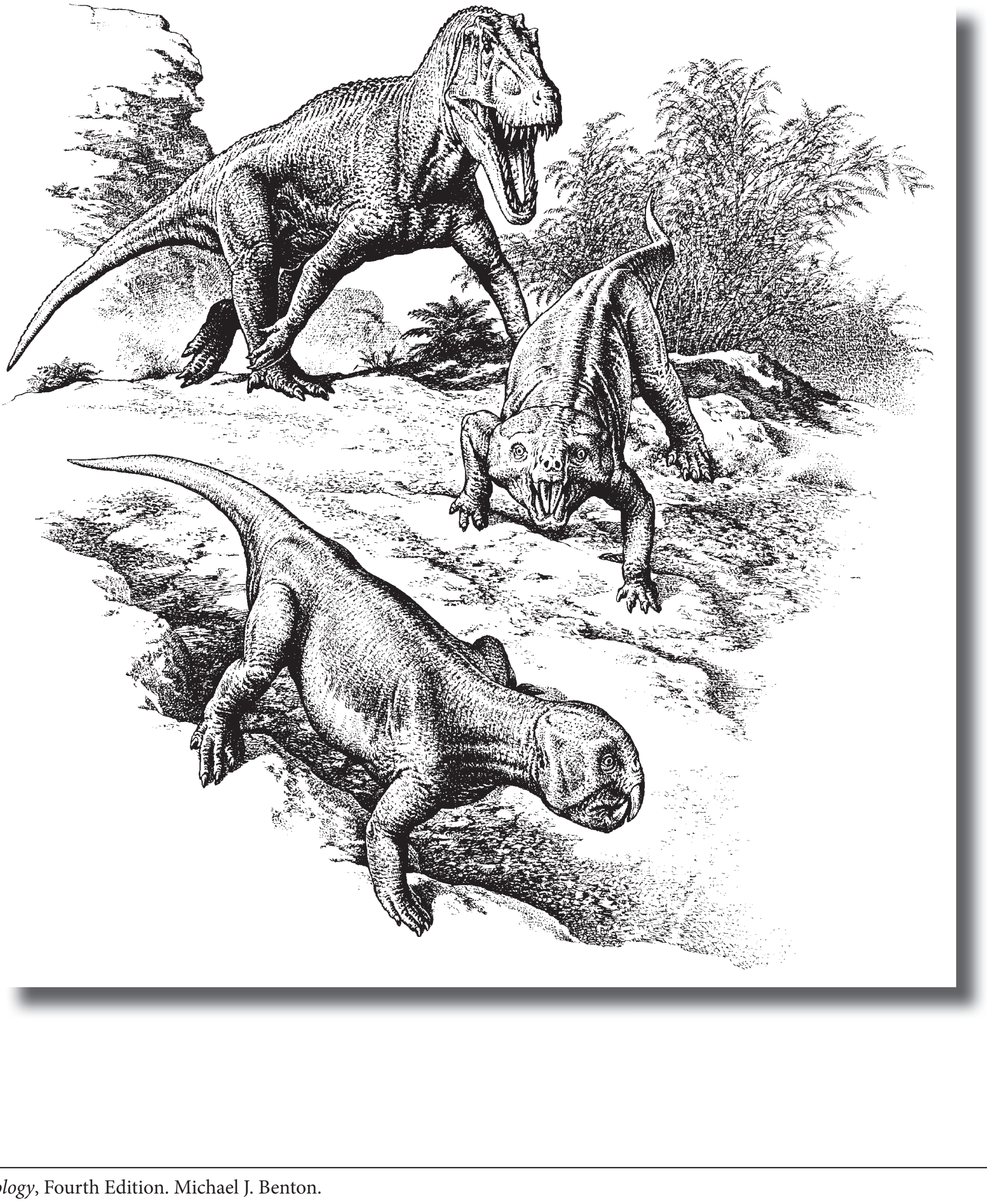
CHAPTER 6

Bounceback: Tetrapods of the Triassic



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KEY QUESTIONS IN THIS CHAPTER

1 How did tetrapods recover from the devastation of the Permo-Triassic mass extinction?
2 How did marine reptiles diversify during the Triassic?
3 What is the full range of carnivore and herbivore ecological roles occupied by archosaurs during the Triassic?
4 What do studies of the posture and locomotion of early archosaurs tell us about the major differences between crocodilians and birds?
5 How did other diapsid groups diversify on land and in the sea during the Triassic?
6 What is the oldest dinosaur?
7 How did dinosaurs take over the world in the Late Triassic?

INTRODUCTION

The Triassic (252–201 Myr ago) was an extraordinary time in vertebrate evolution. The Permo-Triassic mass extinction (see Section 5.7) was so serious, and so many major fish and tetrapod groups had disappeared, that the nature of the recovery could not be predicted from the few survivors. Following any smaller extinction event in which fewer species disappeared, the recovery might consist of refilling empty spaces within ecosystems. However, in the Early Triassic, all major ecological groups had been devastated, and the survivors entered a very empty and unpredictable world.

The scale of the Triassic recovery is evident from the fact that major new clades of fishes and tetrapods emerged. Indeed, it has been suggested that the Permo-Triassic crisis triggered the origins of modern ecosystems in the sea and on land. Certainly, by the Late Triassic, the ancestors of modern lissamphibians (see Section 4.6), turtles, crocodilians, lizards (see Chapter 8), and mammals (see Chapter 10) had arisen. The dinosaurs too appeared during the Triassic, perhaps earlier than had been thought, and dinosaurs included the ancestors of birds. In the sea, marine reptiles emerged for the first time – placodonts, pachypleurosaurs, nothosaurs, ichthyosaurs, and thalattosaurs – and new groups of chondrichthyan and actinopterygian fishes (see Chapter 7) also radiated. In this chapter, we explore the turbulent times of the Triassic.

6.1 THE TRIASSIC WORLD AND ITS EFFECT ON THE RECOVERY OF LIFE

The Triassic world was similar in many ways to that of the Permian. All continents remained united as the supercontinent Pangaea (Figure 6.1), with the equatorial Tethys Ocean partially separating northern continents (Laurasia) from southern continents (Gondwana). The remainder of the global ocean is the Panthalassa Ocean. The single major landmass, Pangaea, remained together throughout most of the Triassic, with some islands comprising parts of south-eastern Asia in the north of the Tethys Ocean. Towards the end of the Triassic, the North Atlantic began to open up, first by the unzipping of land between Morocco in northwest Africa and the eastern United States. Initial rifting along this line opened up the long, narrow rift lakes that were filled by sediments of the Newark Supergroup, from the Late Triassic to Early Jurassic, down the North American coast, from Nova Scotia in the north to North Carolina in the south (see Section 7.3.3).

For the first 6 Myr of the Triassic, spanning the entire Early Triassic and the earliest Middle Triassic, there were poor environmental conditions on Earth. This is shown by the sedimentology of the rocks, where there is repeated evidence for anoxic (oxygen-poor) conditions in the oceans, and especially by the carbon isotope record (Figure 6.2). The Permian-Triassic boundary is marked by a sharp carbon spike, indicating a massive shift to lighter carbon isotopes in atmospheres and oceans.

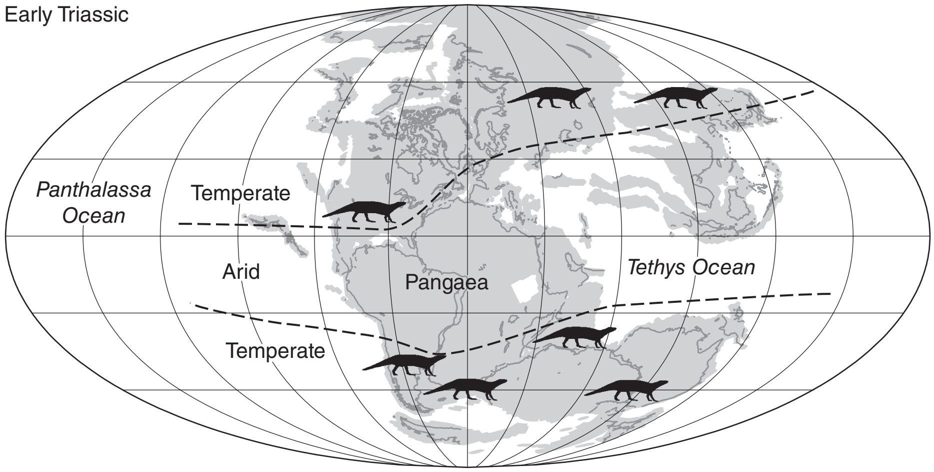


Figure 6.1 Palaeogeographic map of the world in the Triassic, showing major climatic belts, and especially the extent of the tropical arid belt, a 'dead zone' in the Early Triassic. Most tetrapods are found in the temperate zones, with. Source: Adapted from Alroy (2013) and various sources.

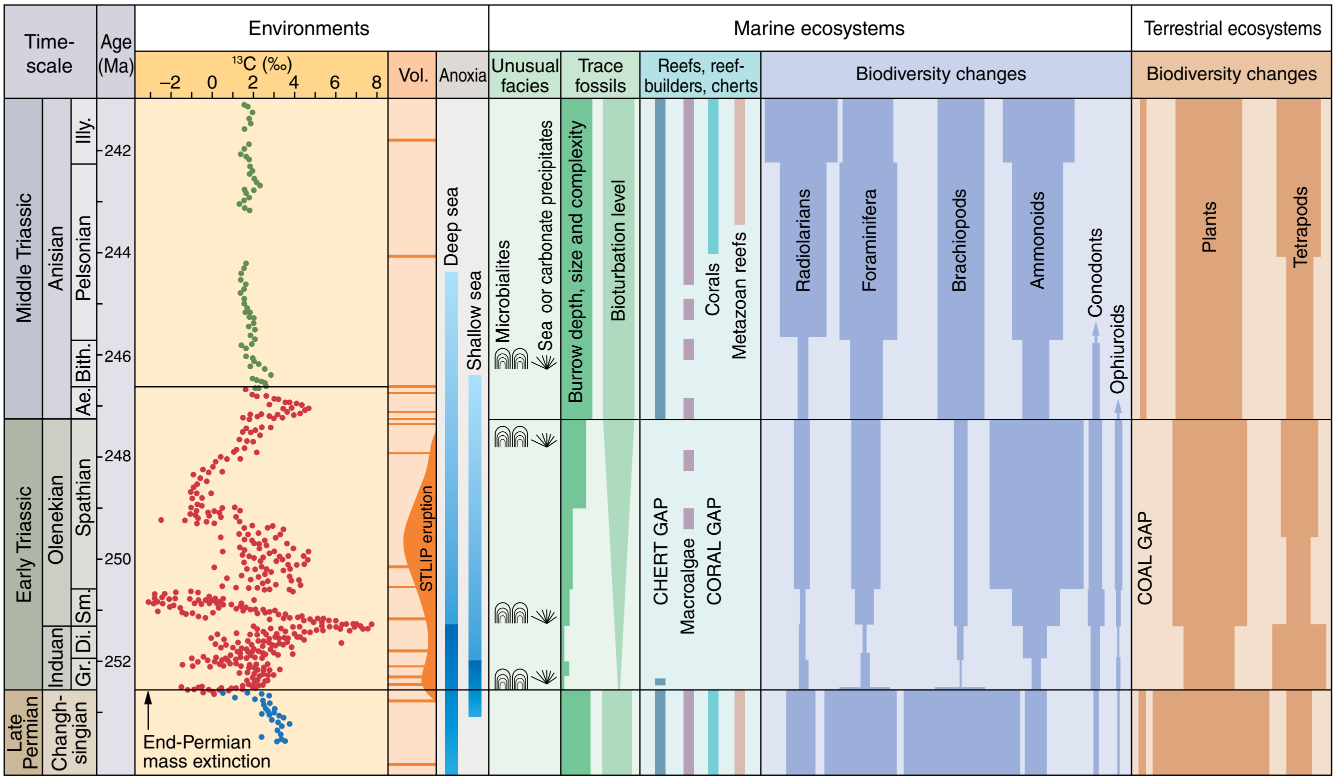


Figure 6.2 The recovery of life in the sea and on land during the Early and Middle Triassic, showing environmental changes and biodiversity variations. Carbon isotope fluctuations, Siberian Traps large igneous province (STLIP) eruption, anoxia ranges, trace fossil data, and reef, reef builder, chert and coal gap data from many sources. See Colour plate 6.1. Abbreviations: Ae, Aegean; Bith, Bithynian; Di, Dienerian; Gr, Griesbachian; Illy, Illyrian; Sm, Smithian; Vol, volcanism. Source: Chen and Benton (2012). Reproduced with permission from Nature Publishing Group.

This was interpreted (Wignall, 2001; Benton and Twitchett, 2003; Algeo *et al.*, 2011) as evidence that flash global warming had caused massive burial of light carbon from dead organisms, coal, volcanic carbon dioxide, and even methane hydrates, the carbon residues of plankton frozen on polar ocean floors (see Section 5.7). Evidence from carbon and oxygen isotopes shows that conditions remained perturbed for 6 Myr, with several sharp carbon spikes, either caused by repeat volcanism, burning of coals traversed by lava, or even resulting from the boom-and-bust cycles of recovering life and repeat extinction and burial of organic carbon (Irmis and Whiteside, 2012). Whatever their cause, these Early Triassic carbon spikes indicate episodes of global warming during the Early Triassic, when temperatures rose up to 10 °C (Figure 6.2; Payne *et al.*, 2004; Sun *et al.*, 2012). These times of exceptional warming seem to be associated with the absence of vertebrates – fishes, marine reptiles, and terrestrial tetrapods – from a broad equatorial band (see Figure 6.1).

Such repeated episodes of flash warming affected the recovery of all life in the Triassic. Certainly, tetrapods on land would have suffered from the long-term absence of trees (the 'coal gap' of some 10 Myr; Retallack, 2013), perhaps associated with acid rain and mass erosion of sediment from the land associated with the global warming. The exclusion of tetrapods from the tropics reflects the harsh effects of aridity and prolonged heat on land animals, and on vertebrates in particular (Benton and Newell, 2014). Although much debated, the recovery of life in the Triassic took nearly 10 Myr (Payne *et al.* 2004; Chen and Benton, 2012). Certainly, some taxa such as foraminifera, ammonites, fishes, and temnospondyls diversified within the first 1–2 Myr of the Early Triassic, but the long durations of the coral gap and chert gap in the sea (no reefs, no deep-sea silicates) and the coal gap on land, amounting to 10–15 Myr, suggests that ecosystems were far from normal for a very long time.

Triassic climates continued warm throughout, with much less variation from the poles to the equator than today. There is no evidence for polar ice caps, and the north and south poles both lay over oceans at the time. However, climates were not uniform: coastal belts were wet, often with evidence for monsoonal seasonality, and Pangaean interiors were most arid. During the Late Triassic, there was a broad climatic shift, at least in terms of the reptile-bearing rock formations, from warm and moist (the Carnian pluvial episode; Simms and Ruffell, 1990) to hot and dry. The Late Triassic climatic change caused a major turnover in floras. During the earlier part of the Triassic, floras in the southern hemisphere were dominated by the seed fern *Dicroidium*, a shrubby plant with broad leaves. These floras disappeared in the Late Triassic, and were replaced by northern-style conifer-dominated floras, better adapted to dry climatic conditions. The floral turnover was matched by a major faunal turnover, and the dominant herbivores died out, to be replaced in time by the first herbivorous dinosaurs (see Section 6.5). We explore the remarkable Triassic marine tetrapods first, and then the recovery of life on land.

6.2 TRIASSIC MARINE REPTILES

There were five main groups of reptiles in Triassic seas (McGowan and Motani, 2003; Rieppel, 2000a; Benton *et al*., 2013), the placodonts, pachypleurosaurs, and nothosaurs, all members of Sauropterygia, as well as ichthyosaurs and thalattosaurs, all of which have the euryapsid skull pattern (see Section 5.2.2), with one (upper) temporal fenestra. Each has very different aquatic adaptations and they represent a major radiation of marine predators, probably from two or three independent sources among the early diapsids (see Box 6.1). Triassic marine reptiles have long been known from Europe, as well as from western Canada, the western United States, Spitsbergen, and South China.

6.2.1 Placodontia

The placodonts were most abundant in the Middle Triassic of central Europe, some Mediterranean areas and southern China, and disappeared at the end of the Triassic. *Placodus* (Figure 6.3(a)) looks at first like a heavily built land animal, but its remains are found in shallow marine beds. The tail is not deep, as might be expected if it were used in propulsion, and the limbs are not modified as paddles. The limb girdles, although heavier than in the nothosaurs, are not as firmly attached to the sides of the body as one would expect in a terrestrial form. The heavy array of gastralia covering the belly region is a feature shared with pachypleurosaurs and nothosaurs. Some placodonts carried massive armour shields over their backs, composed of polygonal bony plates.

The skull of *Placodus* (Figure 6.3(b,c)) shows all of the remarkable features of this group (Rieppel, 2000b; Neenan *et al*., 2013). The teeth consist of three spatulate incisors on each premaxilla, four heavy teeth on each maxilla, three on each palatine and three or four on each dentary. These palatal teeth are broad, flattened and covered with heavy enamel. They were clearly used in crushing some hard-shelled prey, most probably molluscs and brachiopods, which were levered off the rocks in shallow coastal seas with the incisors, smashed between the massive palatal and posterior dentary teeth and the flesh extracted. The broad triangular skull is of such a shape that the maximum biting force occurs just in the region of the largest teeth on the palatine and dentary, and the extended squamosal probably bore powerful jaw adductor muscles that ran forwards to the high process of the dentary. These muscles then ran nearly horizontally and they would have provided a powerful backwards, grinding pull to the lower jaw.

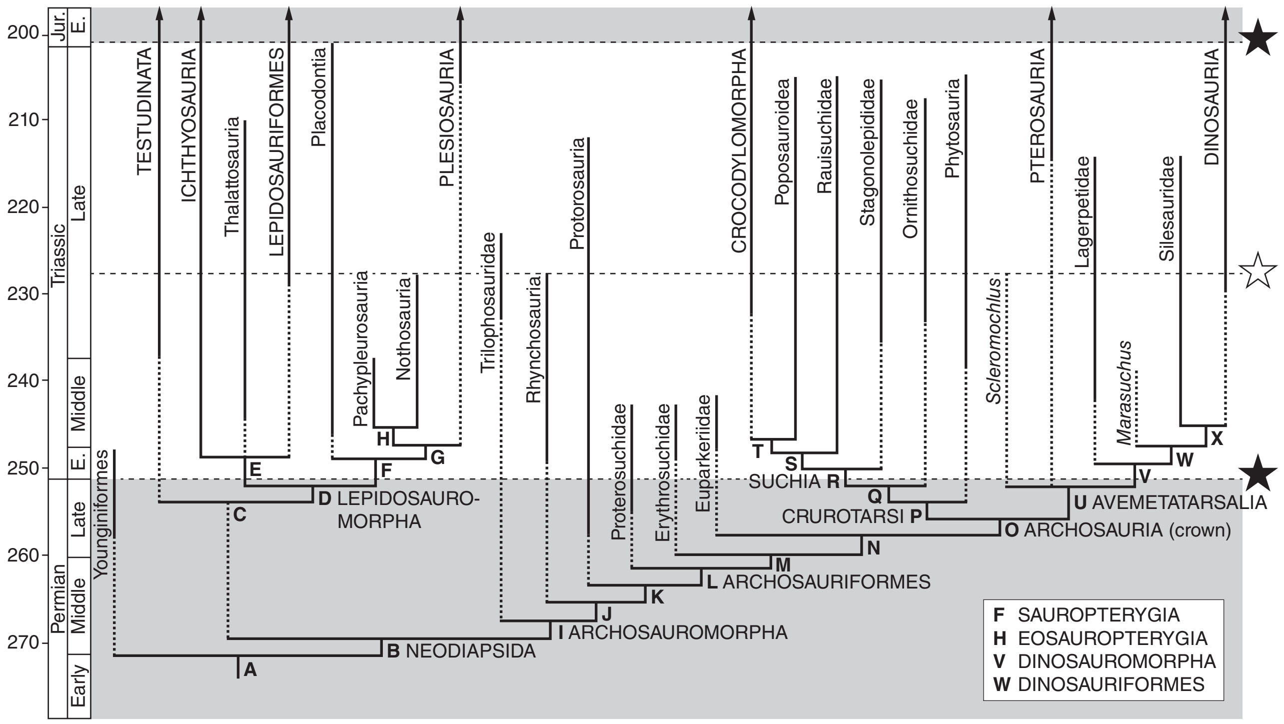
BOX 6.1 DIAPSID DIVERSIFICATION

The Diapsida was the key group of Triassic tetrapods. Whereas, diapsids had been modest contributors to Carboniferous and Permian ecosystems (see Box 5.1), the clade expanded substantially in the Triassic, presumably triggered by the opportunities provided by the Permo-Triassic mass extinction. The cladogram (see illustration) is based on a mix of older and newer work. Some elements, such as the split into Lepidosauromorpha and Archosauromorpha, and the outgroups to Archosauria, were established early on (e.g. Benton, 1985; Gauthier, 1986). The position of Testudines (turtles) is debated, but here we show the assumed consensus view from current molecular analyses (see Box 5.1).

Within Lepidosauromorpha, the inclusion of the various marine reptile clades (Ichthyosauria, Thalattosauria, Sauropterygia) is somewhat controversial. Earlier cladistic analyses of Diapsida showed this as the most parsimonious position, although the positions are not phylogenetically very robust (e.g. Rieppel, 1993; de Braga and Rieppel, 1997; Evans and Jones, 2010), and indeed the marine reptiles may fall outside Lepidosauromorpha, as basal Neodiapsida (Neenan *et al*., 2013). By Late Triassic times, Lepidosauriformes had arisen, the clade including sphenodontids, lizards, and snakes, as well as their immediate outgroups (see Box 8.8).

The phylogeny of Archosauromorpha has been heavily studied (e.g. Benton, 1985; Gauthier, 1986; Dilkes, 1998) and many aspects appear to be relatively stable. The initial splitting of Trilophosauridae, Rhynchosauria, and Protorosauria in sequence from the Archosauriformes is widely found, and provides a basal date for the clade founded on *Protorosaurus* from the Late Permian (see Section 5.5.4). Within Archosauriformes, Proterosuchidae, Erythrosuchidae, Proterochampsidae, and Euparkeriidae have generally formed outgroups to crown Archosauria (e.g. Benton, 1985; Gauthier, 1986; Benton and Clark, 1988; Sereno, 1991; Brusatte *et al*., 2010a; Nesbitt, 2011). The fundamental split of crown Archosauria (called also Avesuchia) into the ‘crocodile line’ (Crurotarsi) and the ‘bird line’ (Avemetatarsalia) was discovered early on and has been confirmed many times since. The composition of Crurotarsi is generally reconstructed as shown here, but Brusatte *et al*. (2010a) found a pairing of Stagonolepididae and Crocodylomorpha, and Nesbitt (2011) found Phytosauria as outgroup to crown Archosauria.

Thanks to many new discoveries, and intense re-study of the Avemetatarsalia (e.g. Benton, 1999; Langer and Benton, 2006; Brusatte *et al*., 2010a; Nesbitt, 2011; Nesbitt *et al*., 2010, 2013a), their relationships are broadly agreed. There is uncertainty about whether *Scleromochlus* is the basal avemetatarsalian or a close sister group of Pterosauria, and some (e.g. Bennett, 2012) have proposed that pterosaurs might not be avemetatarsalians, but basal archosauriforms, but relationships within Dinosauromorpha and Dinosauriformes are more or less established.



Cladogram showing the relationships of the Triassic diapsids, with synapomorphies from Benton (1985), Gauthier (1986), Benton and Clark (1988), Sereno (1991), Rieppel (1993), de Braga and Rieppel (1997), Benton (1999), Langer and Benton (2006), Brusatte *et al*. (2010a), Nesbitt *et al*. (2010, 2013a), Nesbitt (2011), Neenan *et al*. (2013), and others. See Box 5.1 for the context of Diapsida, Box 8.5 for relationships of Dinosauria and Box 8.8 for more detail on turtle, lepidosaur, crocodylomorph and pterosaur relationships. Synapomorphies: **A**, anterior process of squamosal narrow, trunk ribs mostly single-headed, ends of humerus robust; **B NEODIAPSIDA**, anterior process of squamosal narrow, trunk ribs mostly single-headed, ends of humerus robust; **C**, prootic-parietal contact, hooked fifth metatarsal; **D LEPIDOSAUROMORPHA**, external nares close to the midline, sphenethmoid absent, presacral intercentra absent, entepicondylar foramen in humerus absent, radius as long as ulna, fifth distal tarsal absent; **E**, external nares close to the midline, sphenethmoid absent, presacral intercentra absent, entepicondylar foramen in humerus absent, radius as long as ulna, fifth distal tarsal absent; **F SAUROPTERYGIA**, premaxilla large, lacrimal absent, upper temporal fenestra larger than orbit, lower temporal fenestra open ventrally, anterior premaxillary and dentary teeth procumbent (slope forward), cervical intercentra absent, three or more sacral ribs, clavicles positioned anteroventrally to interclavicle and meet medial surface of scapula, humerus curved, humerus with reduced epicondyles, radius and ulna of equal length, fifth metatarsal long and slender, straight fifth metatarsal; **G**, zygosphene-zygantrum articulation, pedicels of neural arch received on ‘butterfly’-shaped platform on centrum, clavicles with anterolaterally expanded corners, scapula constricted in the middle, entepicondylar foramen, three tarsal ossifications; **H EOSAUROPTERYGIA**, quadratojugal without anterior process, occiput plate-like, clavicles broad medially, coracoid strongly waisted; **I ARCHOSAUROMORPHA**, posterodorsal process on premaxilla, sagittal crest, slender and tapering cervical ribs, notch on anterior margin of interclavicle, small anterior process and larger posterior process on iliac blade, medial centrale in carpus absent; **J**, ectopterygoid expanded posteriorly, upturned retroarticular process, second sacral rib bifurcates and posterior process truncated sharply, anterior apron of pubis; **K**, long snout and narrow skull, nasals longer than frontals, recurved teeth, extensive partricipation of parasphenoid/ basisphenoid in lateral wall of braincase, long thin tapering cervical ribs with two or three heads and an anterior process; **L ARCHOSAURIFORMES**, parietal foramen absent, jugal-quadratojugal contact, antorbital fenestra in snout wall between nostril and orbit, ossified laterosphenoid in braincase, lateral mandibular fenestra in posterior lower jaw bones, tooth serrations, **M**, antorbital fossa surrounding the fenestra, pubis and ilium elongated, anterior process on iliac blade; canal between astragalus and calcaneum absent, distal tarsals 1 and 2 not ossified, metatarsal 3 longer than 4; **N**, distal ends of cervical and dorsal neural spines expanded laterally, osteoderms (bony plates) running along the back, fourth trochanter on femur, fibula with rounded proximal end and asymmetrical distal end, calcaneal tuber shaft broader than tall; **O ARCHOSAURIA (crown group)**, palatal processes of maxilla meet in the midline, antorbital fossa on the lacrimal and maxilla, posteroventral portion of the coracoid has ‘swollen’ tuber, femur has anteromedial tuber on the proximal end, tibial facet of astragalus divided into posteromedial and anterolateral basins, calcaneal tuber oriented at 50–90° posteriorly; **P CRUROTARSI**, teeth absent on palatal process of pterygoid, cervical ribs short and stout, scapulocoracoid notch at anterior junction of scapula and coracoid, ventral astragalocalcaneal articular facet large, astragalar tibial facet flexed, calcaneal tuber distal end rounded, hemicylindrical calcaneal condyle, osteoderm sculpture; **Q**, pubic acetabular margin posterior portion recessed, calcaneal tuber distal end with dorsoventrally aligned median depression; **R SUCHIA**, longitudinal ridge on jugal rounded and broad, separate articular facets for fibula and astragalus on the calcaenum, calcaneal tuber has shaft nearly twice width of fibular facet, articular surface for fibula on calcaneum convex and hemicylindrical; **S**, extensive medial contact between the ischia but dorsal margins are separated, rounded or elliptical outline of the distal portion of the ischium, ischium expanded relative to ischial shaft, ischium elongate, dorsal osteoderms arranged in staggered pattern; **T**, pubis distal boot expanded (convergent in saurischian dinosaurs), metatarsal IV subequal or shorter than metatarsal II; **U AVEMETATARSALIA**, forelimb/hindlimb ratio less than 0.55, pubis longer than ischium, tibia/ femur ratio more than 1.0, distal tarsal 4 subequal in transverse width to distal tarsal 3, compact metatarsus with metatarsals I–IV tightly appressed, metatarsals II–IV more than 50% tibial length, absence of dorsal body osteoderms; **V DINOSAUROMORPHA**, subrectangular and distinctly offset femoral head, astragalar ascending flange on anterior face of tibia, astragalar anteromedial corner acute, calcaneal distal articular face less than 35% of that of astragalus, articular facet for metatarsal V less than half of lateral surface of distal tarsal 4, midshaft diameters of metatarsals I and V less than II–IV, metatarsal V has no ’hooked’ proximal end and articular face for distal tarsal 4 is subparallel to shaft axis; **W DINOSAURIFORMES**, parallelogram-shaped cervical centra, acetabular antitrochanter, articular surface on the femur that extends under the proximal head, weakly developed lesser (anterior) trochanter on the femur; **X**, elongate pubis, extensive medial contact of ischia, distally tapering fibula. Abbreviations: **E**, early; Jur, Jurassic. Dashed lines and star symbolsindicate extinction events.

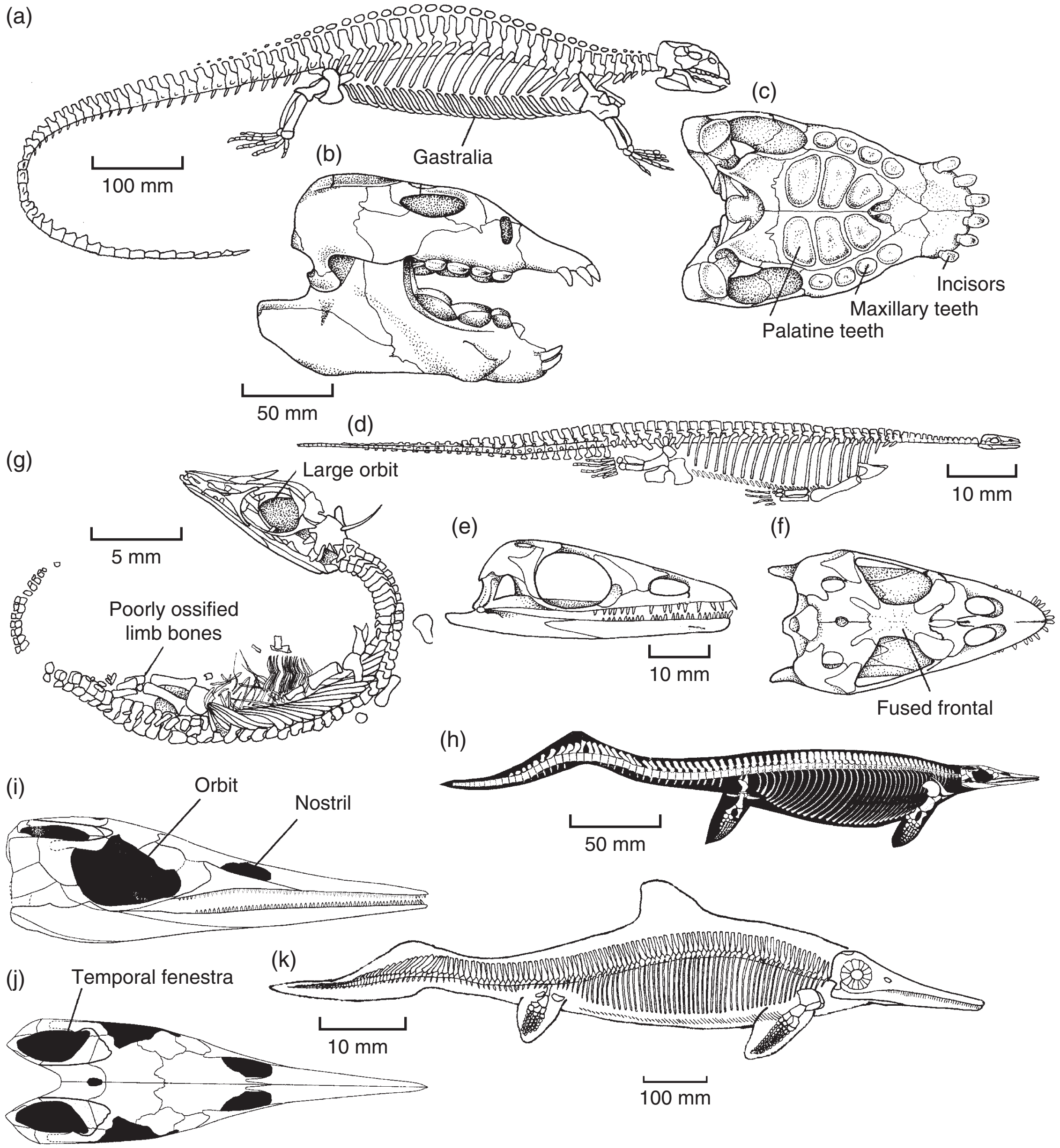


Figure 6.3 The marine reptiles of the Triassic: (a–c) the placodont *Placodus*: (a) skeleton in walking pose; (b,c) skull in lateral and ventral views; (d–f) the pachypleurosaur *Pachypleurosaurus*: (d) skeleton; (e,f) skull in lateral and dorsal views; (g) putative embryo pachypleurosaur; (h–j) the ichthyosaur *Utatsusaurus*, skeleton and skull in lateral and dorsal views; (k) the ichthyosaur *Mixosaurus*. Source: (a) Adapted from Peyer (1950). (b,c) Adapted from Peyer and Kuhn-Schnyder (1955). (d–f) Adapted from Carroll and Gaskill (1985). (g) Adapted from Sander (1988). (h–j) R. Motani, University of California, Davis, CA, USA. Reproduced with permission. (k) Adapted from Kuhn-Schnyder (1963).

6.2.2 Eosauropterygia: Pachypleurosauria and Nothosauria

The eosauropterygians include two subclades, the pachypleurosaurs and nothosaurs. Pachypleurosaurs are elongate animals with small heads, long necks and tails and paddle-like limbs (Figure 6.3(d)). They are best known from the Middle Triassic of central Europe where animals such as *Pachypleurosaurus* have been found abundantly in marine sediments (Carroll and Gaskill, 1985; Liu *et al.*, 2011). These 0.2–1.0 m-long animals were clearly mainly aquatic in adaptations, using wide sweeps of their deep tails to produce swimming thrust. The forelimbs may also have been used to some extent for thrust and steering. The hindlimbs were probably held along the sides of the body most of the time in order to reduce drag. The limb girdles are very much reduced and they are only lightly attached to the sides of the body, so that they could not have supported the animal's weight on land.

The skull of pachypleurosaurs is long and lightly built with a very large orbit and nostril, but a small temporal fenestra (Figure 6.3(e,f)). The pointed peg-like teeth are spaced fairly widely and project at the front of the jaws. They suggest a diet of fishes that the agile pachypleurosaurs could have chased and snapped up with darts of their long necks.

Pachypleurosaurs could presumably have moved, perhaps clumsily, on land, but they bred entirely at sea. Among the abundant remains of pachypleurosaurs from Switzerland, Sander (1988) found a specimen of a young animal, less than 50 mm in length (Figure 6.3(g)). The specimen shows two key features that prove it is a juvenile: the orbit is relatively large and the limb bones are poorly ossified. Subsequently, the discovery of pregnant females of the pachypleurosaur *Keichousaurus* from Xingyi in south China (Cheng *et al*., 2004) confirms that these earliest of marine reptiles already gave birth to live young rather than laying eggs on shore.

The larger nothosaurs (Rieppel, 1998, 2000a), 1–4 m long, had elongate heads and large temporal fenestrae, but were otherwise similar to pachypleurosaurs in their adaptations. These early sauropterygians apparently used their forelimbs in paddling in pursuit of their prey, and in one rare case at least, regular series of paddle marks show they may have disturbed the seabed mud to flush out lurking lobsters and fishes (Zhang *et al*., 2014). Nothosaurs are related to a smaller group, generally called the pistosauroids, which are known from limited remains from the latest Early Triassic and Middle Triassic of North America and China (Sato *et al*., 2013). Pistosauroids are probably a paraphyletic assemblage, but they include outgroups of the large clade Plesiosauria, which is known from limited remains in the Late Triassic, and radiated dramatically in the Jurassic and Cretaceous (see Section 8.10.1).

6.2.3 Ichthyosauria

The ichthyosaurs (literally 'fish lizards') were the most obviously aquatic reptiles of all with their dolphin-like bodies – no neck, streamlined form, paddles and fish-like tail. They arose in the Early Triassic and continued throughout the Mesozoic Era with essentially the same body form. The oldest ichthyosaurs include *Utatsusaurus* from Japan (Cuthbertson *et al*., 2013), a 3-m-long basal form (Figure 6.3(h–j). It shows typical ichthyosaurian characters of about 40 cylindrical presacral vertebrae, and limbs and girdles shortened and broadened to act as paddles. In the skull (Figure 6.3(i,j)) the orbit is large, the nostril is placed well back from the tip of the snout and there is a single high temporal fenestra. The jaws are long and narrow and lined with uniform peg-like teeth. Primitive features, hinting at the land-living ancestry of ichthyosaurs, are that there are two sacral ribs and the hindlimb and forelimb are of roughly equal size. In later ichthyosaurs, there are no sacral ribs (the hip joint is completely separated from the vertebral column) and the front paddle is larger than the hind. In later forms too the snout became longer, the teeth more pointed, the orbit larger and the bones at the back of the skull more 'crowded' backwards.

The ichthyosaurs radiated in the Middle and Late Triassic of central Europe, Nevada, Spitsbergen, China, and Japan (McGowan and Motani, 2003). *Mixosaurus* (Figure 6.3(k)) has derived paddles with short limb bones and an excess number of phalanges. Giant ichthyosaurs up to 8 m long had already appeared in the Middle Triassic (Fröbisch *et al*., 2013), and the shastasaurids reached the same lengths in the Late Triassic. They had long bullet-shaped heads, teeth only at the front of the snout, a vast rib cage and tremendously elongated limbs, and they are interpreted (Sander *et al*., 2011) as suction feeders, like the modern beaked whales and some dolphins that open their mouths rapidly close up to their selected prey, often fish or squid, and effectively suck them in. The later ichthyosaurs (see Section 8.10.2) were important in Jurassic and Cretaceous seas, but never reached this huge size.

6.2.4 Thalattosauria

Thalattosaurs were large marine reptiles, up to 4 m long, that shared some superficial similarities in skull and paddle shape with ichthyosaurs. They existed only in the Middle and early Late Triassic, and were top predators in marine ecosystems in North America, Europe and South China (Müller, 2005; Liu *et al*., 2013). These were long, slender reptiles with deep, flat-sided tails, presumably used in swimming (Figure 6.4). The skull is short relative to the length of the body, but the jaws are nonetheless long and deep, and the orbit is large. The ribs are massive and the paddles

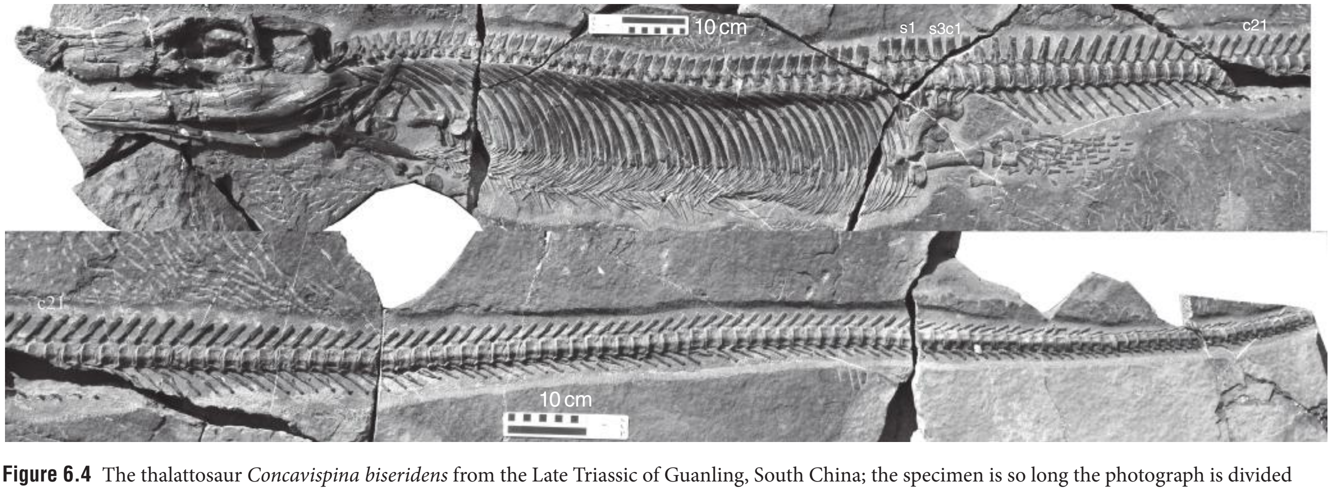


Figure 6.4 The thalattosaur *Concavispina biseridens* from the Late Triassic of Guanling, South China; the specimen is so long the photograph is divided in two. Abbreviations: c1⁄4caudal vertebra; s1⁄4sacral vertebra. Scale bars are 10 cm. Source: Liu *et al*. (2013). Reproduced with permission from The Paleontological Society.

relatively small, perhaps primarily used in manoeuvring. In overall shape, thalattosaurs come closest to the mythical sea dragons!

Thalattosaurs are especially well known from South China, where dozens of specimens have been recovered from exceptionally preserved faunas of fishes and marine reptiles particularly in Yunnan and Guizhou provinces (Benton *et al*., 2013); the best known of these is the Guanling fauna (see Box 6.2).

BOX 6.2 AMONG THE SEA LILY FIELDS OF GUANLING

The marine Triassic of South China is famous for four remarkable faunas of vertebrates, the Luoping (see Box 7.5), Panxian, and Xingyi biotas of the Middle Triassic, and the Guanling biota of the Late Triassic (Xiaowa Formation; early Carnian). These exceptional faunas comprise dozens of species represented by thousands of specimens, and some exceptionally preserved soft tissues (Chen and Benton, 2012; Benton *et al*., 2013). The first three comprise a mix of benthic (sea bed crawlers and burrowers) and pelagic (mid-water swimmers) forms, but the Guanling biota (Wang *et al*., 2008) is entirely different, being dominated by pelagic forms such as large floating crinoids attached to logs, very large ichthyosaurs and thalattosaurs, and pseudoplanktonic bivalves, with no benthos and no burrowing.

The reconstructed Guanling scene (see illustration) emphasizes the crinoids. These huge echinoderms, some with stems up to 5 m long, attached as larvae to floating logs, and they grew to form massive dangling, trailing net-like structures that captured organic particles that were then directed towards their mouths. The floating crinoid colonies provided homes also for other invertebrates, as well as a feeding ground for many of the fishes, including actinopterygians and coelacanths. The crinoids probably also helped shield the fishes from the depredations of the marine reptiles.

The Guanling marine reptiles include two ichthyosaurs, *Qianichthyosaurus zhoui*, ranging in length from 0.5 to 2 m, and *Shastasaurus liangae*, from 5–10 m long, and very closely related to *Shastasaurus* species from North America (Sander *et al*., 2011). The thalattosaurs *Anshunsaurus*, *Xinpusaurus* and *Miodentosaurus* are 1.4–2.4 m long, and appear superficially ichthyosaur-like, with their long, narrow snouts, but their heads are relatively small and their bodies somewhat serpentine, when compared to the ichthyosaurs. They were mainly ambush predators that snatched their prey, rather than pursuing it. Guanling sauropterygians are unusually rare, with only one taxon, the placodont *Sinocyamodus xinpuensis*, with durophagous dentition and a carapace. The pachypleurosaurs and nothosaurs, so typical of the Middle Triassic faunas are absent.

One of the most remarkable finds from Guanling was the world's oldest turtle, *Odontochelys semitestacea*, which predates the previously oldest forms by some 5–10 Myr (Li *et al.*, 2008). *Odontochelys* has a fully developed ventral plastron, but the dorsal carapace consists of neural plates only. The dorsal ribs are expanded, and osteoderms are absent. The *Odontochelys* specimen shows that the plastron evolved before the carapace and that the first step of carapace formation is the ossification of the neural plates coupled with a broadening of the ribs (see Section 8.7).

Among the floating lily fields of Guanling, original artwork by Brian Choo (http://gogosardina.deviantart.com/). The giant pseudopelagic crinoids *Traumatocrinus hsui* form massive curtains hanging below floating logs. From the top, the ichthyosaurs *Shastasaurus*/ *Guanlingsaurus liangae* and *Qianichthyosaurus zhoui* swim past the thalattosaurs *Xinpusaurus bamaolinensis* and *Miodentosaurus brevis.* Foraging among the giant sea-lillies are smaller armoured reptiles, the turtle-like placodont *Psephochelys polyosteoderma* (left foreground) and the early genuine turtle *Odontochelys semitestacea* (right foreground). Flitting around them are coiled ammonoids (*Trachyceras multituberculatus*) and a variety of fishes, including large predators (hybodont shark, *Guizhoucoelacanthus guanlingensis, Birgeria sp*.), the slender shoaling *Pholidopleurus xiaowaensis,* pursued by *Miodentosaurus* in the background, and the diminutive *Peltopleurus brachycephalus.* See Colour plate 6.2. Source: B. Choo, Institute for Vertebrate Paleontology and Paleoanthropology, Beijing, China and Flinders University, Australia.

6.3 EVOLUTION OF THE ARCHOSAUROMORPHS

The key terrestrial tetrapods to benefit from the Permo-Triassic mass extinction was the Archosauromorpha, a major subclade of Diapsida (see Box 5.1). Archosauromorphs include several groups, the trilophosaurids, rhynchosaurs, protorosaurs, and archosauriforms. The first two are known only from the Triassic, but protorosaurs had arisen in the Late Permian, and archosauriforms in the latest Permian. The most important of the archosauromorph groups is the Archosauriformes, and their subclade the Archosauria, whose evolution in the Triassic was critical for the later history of vertebrate life on land: here were laid the foundations of the radiatsion of the dinosaurs, pterosaurs and crocodiles, and ultimately of the birds. These later stages of archosaur evolution are described in Chapters 8 and 9.

6.3.1 Diverse archosauromorphs

Trilophosaurus from the Late Triassic of the south-western United States (Gregory, 1945; Heckert *et al*., 2006) has an unusual heavily built skull (Figure 6.5(a,b) with broad flattened teeth that were used for shearing tough plant food. The trilophosaurids are unusual diapsids as they have lost the lower temporal opening. On the basis of numerous other characters, it has to be concluded that the lower temporal opening closed secondarily.

Rhynchosaurs have been found in many Triassic faunas where they were often the dominant herbivores, representing 40–60% of all skeletons found. Early forms (Dilkes, 1998) were small, but Late Triassic rhynchosaurs such as *Hyperodapedon* (Benton, 1983b; Montefeltro *et al*., 2011) were up to 2 m long. *Hyperodapedon* has a deep cheek region composed mainly from the jugal and maxilla, and the premaxillae extend forwards and downwards as rounded and pointed elements (Figure 6.5(c)). The lower jaw is also deep and the dentary bears two rows of teeth, one on the crest and the other lower down on the inside (Figure 6.5(d)). The skull is triangular in plan view (Figure 6.5(e)). The back of the skull is broader than the total length, and this

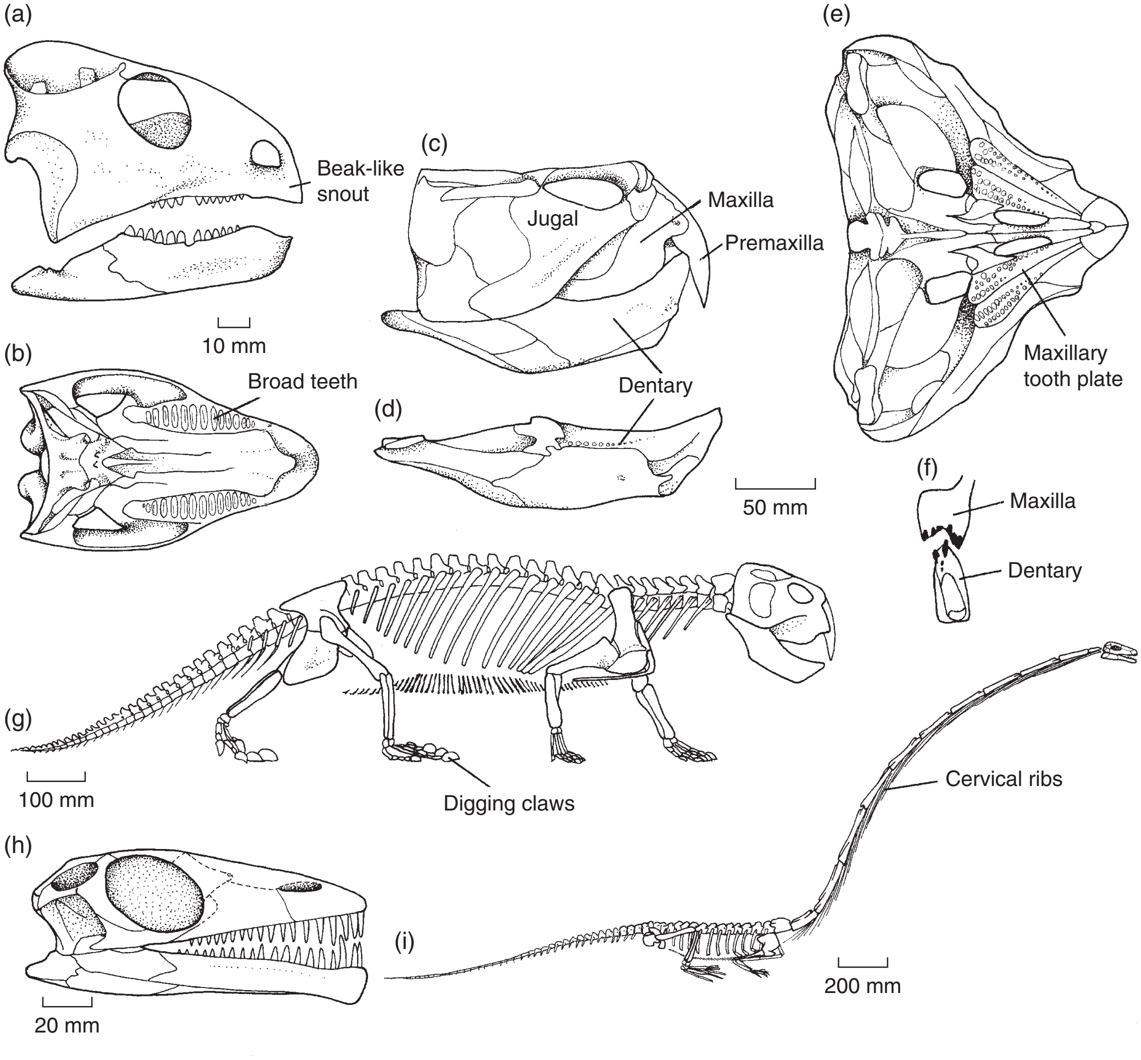


Figure 6.5 Archosauromorphs of the Triassic: (a,b) the trilophosaurid *Trilophosaurus*, skull in lateral and ventral views; (c–g) the rhynchosaur *Hyperodapedon*: (c) skull in lateral view, (d) lower jaw in medial view, (e) skull in ventral view, (f) vertical cross-section through the tooth-bearing bones of the skull (maxilla) and lower jaw (dentary) to show the precise fit, (g) skeleton; (h,i) the protorosaur *Tanystropheus*: (h) skull, (i) skeleton of a large species, showing the enormously elongated neck. Source: (a,b) Adapted from Gregory (1945). (c–g) Adapted from Benton (1983b). (h,i) Adapted from Wild (1973).

vast width seems to have provided space for strong jaw-closing muscles. There are broad tooth plates on the maxillae in the palatal region that bear several rows of teeth on either side of a midline groove. The lower jaw clamped firmly into the groove on the maxilla, just like the blade of a penknife closing into its handle (Figure 6.5(f)). This kind of jaw action, with no sliding back and forwards, or from side to side, is the precision-shear system, just like a pair of scissors. Rhynchosaurs were herbivores that fed on tough plants, possibly seed-ferns. *Hyperodapedon* has massive high claws on its feet (Figure 6.5(g)) that were probably used for uncovering succulent tubers and roots by backwards scratching.

The third group of archosauromorphs, the protorosaurs, had appeared first in the Late Permian, represented by *Protorosaurus* (see Section 5.5.4), and they radiated in the Triassic. Most of the Triassic forms probably looked like lizards, but by the Middle Triassic, one of the most unusual reptilian lineages had arisen within this clade. Protorosaurs are characterized by long necks, but that of *Tanystropheus* from Central Europe (Wild, 1973; Nosotti, 2007) and China was extraordinary, being more than twice the length of the trunk (Figure 6.5(i)). The neck was not greatly flexible as it is composed of only 9–12 cervical vertebrae. Each of these bears long thin cervical ribs that run back beneath the backbone and may have provided attachments for powerful neck muscles. Juveniles of *Tanystropheus* have relatively short necks and, as they grew larger, the neck sprouted at a remarkable rate. Its function is a mystery. The sharp teeth (Figure 6.5(h)) suggest that *Tanystropheus* fed on meat (fishes and cephalopod hooklets are known as stomach contents), whereas the limbs and other features may indicate a life in the water. Indeed, many of the specimens are found in marine sediments, and Wild (1973) and Nosotti (2007) reconstruct *Tanystropheus* as a slow, coastal swimmer that fed on small fishes that it caught by darting its head about.

6.3.2 Basal archosauriforms

During the Triassic the archosauriforms radiated into several groups. Some clades branched in the Early Triassic, outgroups to the large clade Archosauria, amongst others and in sequence, the Proterosuchidae, Erythrosuchidae, Proterochampsidae, and Euparkeriidae.

The Early Triassic proterosuchids (Ezcurra *et al*., 2013) were slender, long-snouted fish- and meat-eaters. *Proterosuchus* (Figure 6.6(a,b)) from South Africa (Cruickshank, 1972) shows

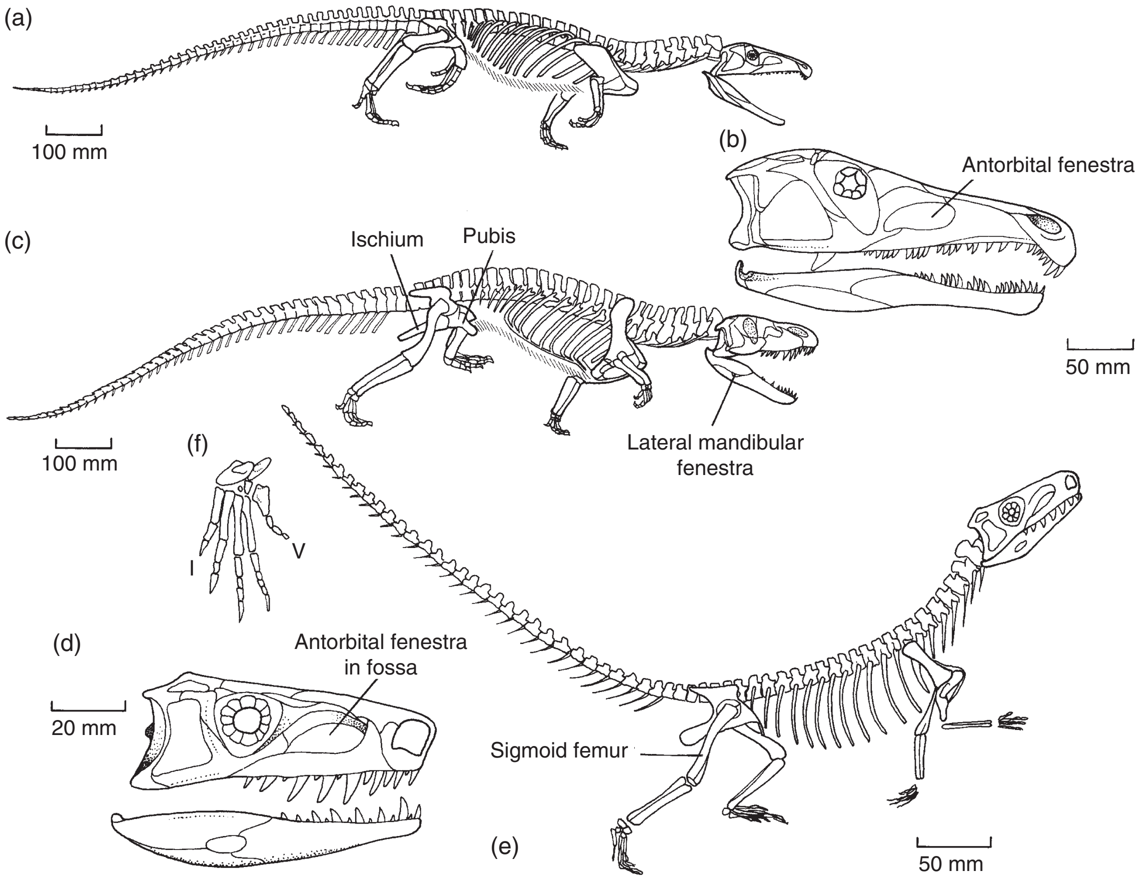


Figure 6.6 Early Triassic archosauriforms: (a,b) the proterosuchid *Proterosuchus*, skeleton in running posture and skull; (c) the erythrosuchid *Vjushkovia*, skeleton in running posture; (d–f) the agile *Euparkeria*, skull in lateral view, skeleton and foot. Source: (a,c) Adapted from G. Paul in Parrish (1986). (b) Adapted from Cruickshank (1972). (d–f) Adapted from Ewer (1965).

four archosauriform hallmarks: an **antorbital fenestra** (an opening in the side of the skull between the nostril and the eye socket that housed an air sinus), an ossified **laterosphenoid** (a midline structure in front of the braincase), a **lateral mandibular fenestra** (an opening in the side of the lower jaw) and flattened (instead of rounded) teeth bearing serrations on the anterior and posterior edges. *Proterosuchus* is a slender animal 1.5 m long that probably preyed on small and medium-sized synapsids (therocephalians, dicynodonts) and procolophonids. It has short limbs and adopted a sprawling posture, as in most Permian synapsids and living lizards and salamanders.

In the Early and Middle Triassic, further basal archosaur lineages flourished for a short while. The erythrosuchids (Ezcurra *et al*., 2013), such as *Garjainia* from Russia (Figure 6.6(c)) and *Erythrosuchus* from South Africa, reached very large size, up to 5 m long. These powerful animals were top predators, capable of feeding on the bulky dicynodonts and other herbivores. Typical archosaur characters that are seen in erythrosuchids and later archosaurs, but not proterosuchids, include a three-pronged ilium with an elongate preacetabular process, and metatarsal 3 longer than 4.

Two final archosauriform groups preceded the origin of the major clade Archosauria. The proterochampsids were long-snouted forms known only from the Middle and Late Triassic of South America (Trotteyn *et al*., 2013). They had **osteoderms**, or bony dermal plates down the middle of the back, a feature of all later archosauriforms. The euparkeriids are represented primarily by *Euparkeria* (Ewer, 1965; Sookias and Butler, 2013) from the early Middle Triassic of South Africa. This animal was only 1 m or so in length (Figure 6.6(d–f)), may have been capable of walking both on all fours and bipedally. It has a short, high-snouted skull with a large antorbital fenestra set in a pit, and large orbits and temporal fenestrae. It shows features in the skeleton such as an S-shaped femur and a knob-like muscle attachment on the femur termed the **fourth trochanter**, that place it close to the common ancestry of crocodilians and birds (see Box 6.1).

6.3.3 Crurotarsi: Middle and Late Triassic archosaur diversity

The crurotarsans (sometimes called pseudosuchians), members of the 'crocodilian line' of archosaurian evolution, are diagnosed by an ankle joint that allows rotation between the astragalus and calcaneum (Sereno, 1991). The basal crurotarsans, the phytosaurs (but see Box 6.1), are known mainly from the Late Triassic of Germany (Stocker and Butler, 2013) and North America. *Parasuchus* from India (Chatterjee, 1978) is 2.5 m long and exhibits crocodilian-like adaptations to fish eating (Figure 6.7(a,b)). The long narrow jaws are lined with sharp teeth that interlock in such a way that *Parasuchus* could seize a rapidly darting fish and pierce it with the long teeth, and then hold it firm while it expelled water from the sides of its mouth before swallowing. The nostrils of *Parasuchus* are raised on a mound of bone just in front of the eyes (not at the tip of the snout as in crocodilians), so it could have lain just below the surface of the water with only its nostril-mound showing. *Parasuchus*, like many modern crocodilians, did not only hunt fishes in the water. Two specimens of *Parasuchus* have been found with stomach contents of small tetrapods – the bony remains of protorosaurs and a small rhynchosaur – that may have been seized on the river bank and dragged into the water. Phytosaurs fed on larger prey too: isolated teeth have been found around skeletons of prosauropod dinosaurs on which they may have been scavenging (Hungerbühler, 1998).

The ornithosuchids are known from the Late Triassic of Scotland and South America (Baczko and Ezcurra, 2013). They include forms such as *Ornithosuchus* (Walker, 1964), which ranged in length from 0.5 to 3.0 m (Figure 6.7(c)). It has a slender build and long hindlimbs that were probably adapted for both quadrupedal and bipedal progression. Superficially, *Ornithosuchus* looks dinosaur-like, but it is a crurotarsan (see Box 6.1). The Ornithosuchidae are characterized by a unique arrangement of the jaws and teeth, with the premaxilla downturned and a substantial **diastema**, or gap, between premaxillary and maxillary teeth. The orbit has a sharp V-shaped ventral margin. Further, they possess a unique ankle joint, sometimes called 'crocodile-reversed', in which the calcaneum has a projection that fits into a concavity on the astragalus (in other crurotarsans, the peg is on the astragalus and the socket on the calcaneum).

The aetosaurs (Aetosauria or Stagonolepididae) were the first herbivorous archosaurs, and they radiated nearly worldwide in the Late Triassic (Parker, 2007; Sulej, 2010; Desojo *et al*., 2013). *Stagonolepis* from Scotland (Walker, 1961) is up to 2.7 m long with a small head, a powerful heavy tail and short stout legs (Figure 6.7(d,e)). The snout is blunt and upturned and it may have been used to dig around in the soil for edible tubers and roots. The body is encased in an extensive armour of heavy bony plates that are set into the skin, a necessary defence against the major carnivores of that time, the rauisuchians.

The rauisuchians are large Middle and Late Triassic carnivores, some quadrupedal and some possibly bipedal, referred to subclades such as the Rauisuchidae, Poposauroidea, Ctenosauriscidae, and Shuvosauridae. Relationships among these forms are unclear: Brusatte *et al*. (2010a) recovered a monophyletic Rauisuchia, whereas others (e.g. Benton and Clark, 1988; Sereno, 1991; Nesbitt, 2011; Nesbitt *et al*., 2013b) find that Rauischia is a paraphyletic group that includes outgroups to Crocodylomorpha. The rauisuchid *Postosuchus* (Figure 6.7(f)), a 2- to 5-m-long carnivore from Texas, USA (Long and Murry, 1995; Weinbaum, 2013), was a top predator, with a high skull and deep jaws lined with long recurved teeth. The skull is narrow from side to side, and in many ways it is superficially similar to the skull of a carnivorous theropod dinosaur (see Section 8.3).

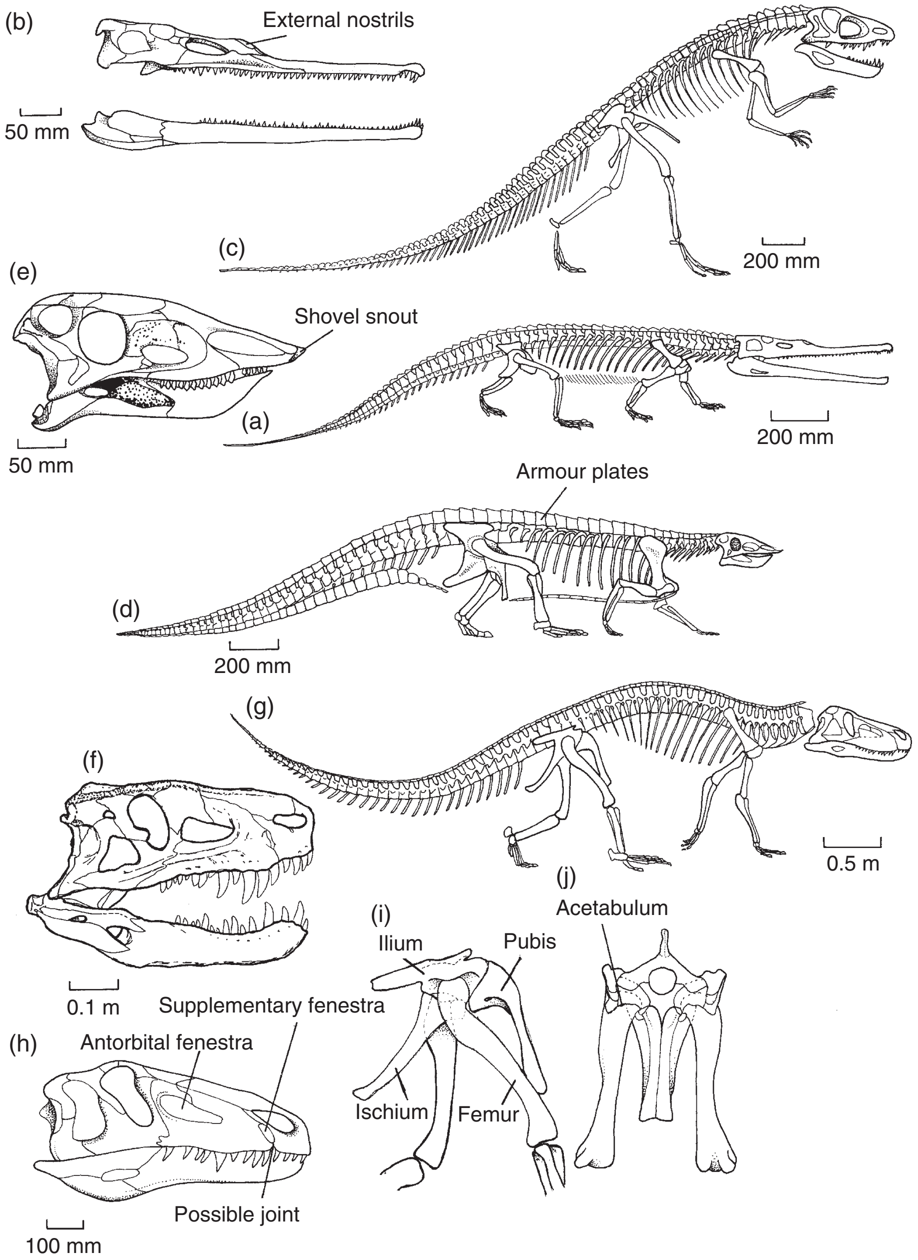


Figure 6.7 Crurotarsan archosaurs: (a,b) the phytosaur *Parasuchus*, skeleton and skull in lateral view; (c) the ornithosuchid *Ornithosuchus*, skeleton in lateral view; (d,e) the aetosaur *Stagonolepis*: skeleton in lateral view, showing part of the armour, but most armour missing to show skeleton and skull in lateral view; (f) the rauisuchian *Postosuchus*, skull in lateral view; (g–j) the rauisuchid *Saurosuchus*, skeleton in walking pose (g), skull in lateral view (h), pelvic girdle and hindlimbs in lateral (i) and anterior (j) views to show the 'pillar erect' gait. Source: (a,b) Adapted from Chatterjee (1978). (c) Adapted from Walker (1964). (d,e) Adapted from Walker (1961). (f) Adapted from Long and Murray (1995). (g,h) Adapted from Bonaparte (1981).

Saurosuchus, a rauisuchid from Argentina (Bonaparte, 1981), is one of the largest rauisuchians, reaching 6 or 7 m in length (Figure 6.7(g)). The skull (Figure 6.7(h)) shows a specialized slit-like opening just behind the nostril, and a possible joint just below. In addition, the hip bones are preserved in three dimensions, and Bonaparte (1981) was able to show how highly modified *Saurosuchus* was for a specialized erect gait (see Box 6.3) in which the femur remained vertical, the pillar-erect posture (Figure 6.7(i,j)). The ilium has a very low blade and it was oriented almost as much horizontally as vertically, which meant that the socket for the femur (the acetabulum) faced downwards rather than sideways.

The poposauroids are a relatively well-defined clade of rauisuchians that include the facultatively bipedal *Poposaurus* from the Late Triassic of North America, the ctenosauriscids and shuvosaurids. The ctenosauriscids, such as *Arizonasaurus* from the Middle Triassic of North America (Figure 6.8(a)) all had substantial sails supported by elongate neural spines on their posterior cervical, dorsal, sacral, and anterior caudal vertebrae (Nesbitt, 2003; Butler *et al*., 2011; Nesbitt *et al*., 2013b). The shuvosaurids, such as *Effigia* from the Late Triassic of North America (Figure 6.8(b)) are most unusual, sporting toothless jaws, a large orbit, and a huge mandibular fenestra that is larger than half the length of the lower jaw. They have tiny arms and hands and were almost certainly bipedal. Shuvosaurids had long been mysterious and hard to classify, sometimes confused with dinosaurs, but new specimens, and new studies (e.g. Nesbitt, 2007) show that these are crurotarsans, close to Crocodylomorpha. An unusual form with toothless jaws and a large dorsal sail, *Lotosaurus* from the Middle Triassic of China, may be a close relative of Shuvosauridae.

6.3.4 Crocodylomorpha: origin of the crocodilians

Crocodilians arose in the Early Jurassic (see Section 8.8), but there were a number of close relatives in the Late Triassic. Some of the Late Triassic crocodylomorphs seem most uncrocodilian at first sight (Irmis *et al*., 2013). An example is *Terrestrisuchus*

BOX 6.3 ARCHOSAUR HINDLIMB EVOLUTION AND POSTURE

Archosaurs showed dramatic changes in their posture, and these are reflected in the two living groups. Crocodilians are essentially, though secondarily, like their sprawling Triassic ancestors, whereas birds stand fully upright, or erect (illustration). The key changes happened largely in the Triassic.

Early Triassic archosauriforms such as *Proterosuchus* were apparently sprawlers. **Sprawling** is the standard reptilian posture, in which the proximal bones of the limbs (femur, humerus) are directed sideways and the body is held only a little way off the ground. Some later archosauriforms, such as *Euparkeria*, probably had a semi-erect posture, in which the body could be hoisted clear of the ground during walking. The fully **erect** posture, in which the limbs are tucked beneath the body and the whole length of the limb operates to produce a stride in the vertical plane, appeared in different Late Triassic archosaur groups: ornithosuchids, aetosaurs, rauisuchians, early crocodylomorphs, pterosaurs and dinosauromorphs. The posture shift could have evolved several times, or more likely once, at the base of Archosauria, and was then lost by phytosaurs. The erect posture also arose independently during the Triassic in the cynodonts (see Section 10.1) and it is seen in their descendants, the mammals.

Why the change? Advantages of an erect posture are that more of the limb is used in walking or running and stride length is increased. Also, having the limbs tucked beneath the body means that erect animals can more readily support their body weight. When a sprawler lifts its belly from the ground, its elbows and knees are subject to intense bending stresses. An erect animal, such as an ostrich or an elephant, can support its body weight with much less stress as the upper and lower elements of the limb are more in line.

In the switch from sprawling to an erect posture (illustration (a,b)), muscle forces changed and these can be seen in a comparison of living crocodilians and birds, and in the fossils (Hutchinson and Gatesy, 2000). When a sprawler is standing still, its body is liable to collapse. This forces the knee joint up (abduction) as the body goes down and the tendency is opposed by the adductor muscles that lie beneath the limb, running from the pubis and ischium to the underside of the femur. In erect animals, on the other hand, the tendency is for the femur to move in towards the midline (adduction), so this is opposed by muscles above the limb, the iliotrochanteric (iliofemoralis) muscles, which extend from the posterior part of the blade of the ilium to the dorsal surface of the femur, attaching on the fourth trochanter.

In walking, sprawlers swing the femur through a wide arc and the retraction ('backwards pull') phase of the stride is powered by the large caudifemoralis muscle, which attaches all down the side of the tail and runs to the posterior margin of the femur. Birds, on the other hand, have tiny tails, a somewhat reduced caudifemoralis muscle and most of their stride is composed from rotation of the femur along its long axis and movements at the knee powered by 'hamstring' muscles that run from femur to tibia and below.

These changes in muscle function may be seen in the evolution of early archosaurs and various dinosaur groups on the way to birds. The iliofemoralis (IF) muscle divided its functions during archosaur evolution, and the anterior part, the iliotrochanteric muscle (ITC), moved more anteriorly on the iliac blade (illustration (c), 1b), whereas the posterior part stayed in place above the acetabulum. This move was paralleled by a similar split in the site of insertion on the head of the femur: the ITC inserted on the so-called lesser trochanter, which separated from the head of the femur and moved inward and forward. This forwards and inwards move of the ITC was necessary in erect archosaurs to oppose the tendency to adduction and to rotate the femur. The location of the puboischiofemoralis internus (PIFI) muscle (illustration (c), 2) does not move much, although its function changed from protraction of the limb in basal archosaurs to rotation of the femur in birds. The puboischiofemoralis externus (PIFE) muscle did move substantially (illustration (c), 3). First, in dinosauromorphs, the insertion on the head of the femur moved laterally as the femoral head curved more and more inwards, and so the PIFE became more involved in lateral rotation of the femur. Then in birds and close relatives, the pubis moved back dramatically, also moving the origin of the PIFE backwards. This cut out the muscle's function in protraction of the femur and allowed it only to produce retraction and rotation of the femur.

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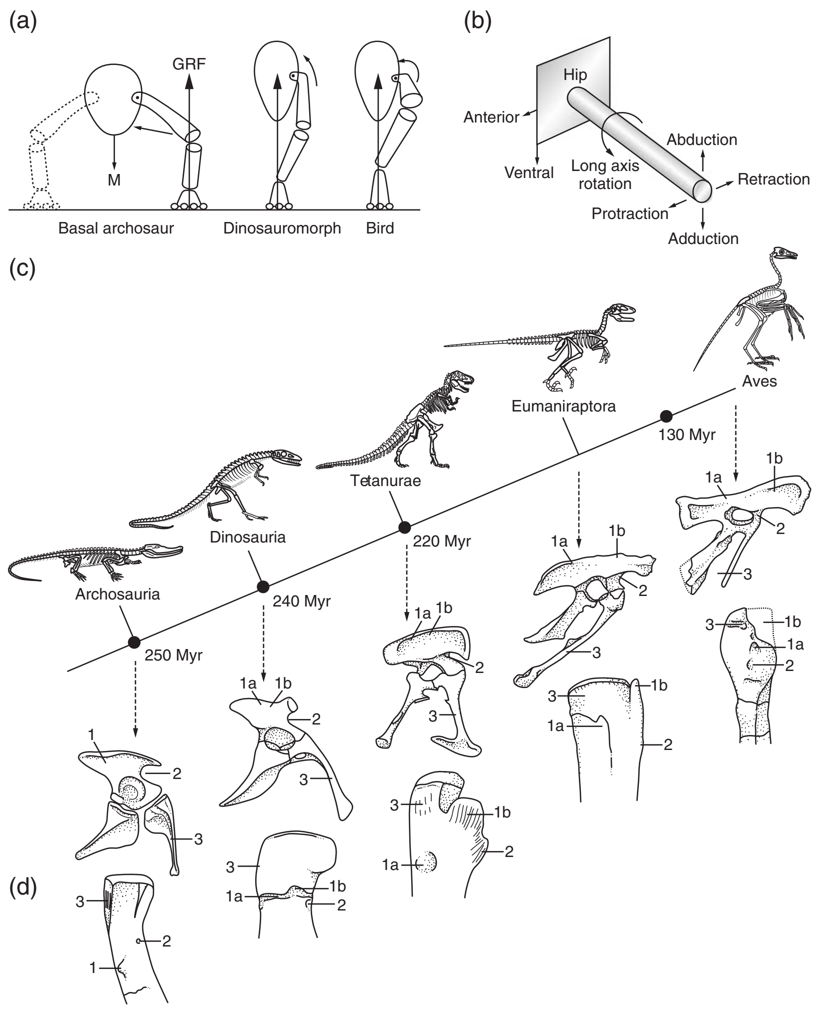


Evolution of archosaur posture: (a) Comparison of a sprawling basal archosaur (left), an erect basal dinosaur (middle) and a bird (right). In the sprawler, the ground reaction force (GRF) and body mass (M) create stresses that result in abduction (heavy arrows), countered by the adductor muscles (thin arrow). In the erect forms, the GRF acts medially to the limb, so the resultant force produces adduction of the femur, which has to be counteracted by abducting muscles. (b) Standard orientations of movements on the femur of a sprawling tetrapod. (c) Five evolutionary stages on the way from basal archosaurs to birds, with silhouettes of typical representatives, the right pelvis and head of the right femur. Muscle origins and insertions are indicated for the iliofemoralis (IF, 1), the iliofemoralis externus (IFE, 1a), the iliotrochantericus (ITC, 1b), the puboischiofemoralis internus (PIFI, 2) and pubofemoralis externus (PIFE, 3). Source: Adapted from Hutchinson and Gatesy (2000).

(Crush, 1984) from South Wales, a lightly built, delicate animal 0.5 m long (Figure 6.9(a–c)). It has a long skull with slender pointed teeth and long hindlimbs that suggest it was occasionally a biped. It probably fed on small reptiles, insects and other invertebrates.

How can this fully terrestrial, insectivorous, slender-limbed, greyhound-like quadruped be a close relative of the crocodilians? *Terrestrisuchus* has a number of diagnostic crocodylomorph characters. The main bones of the wrist (radiale and ulnare) are elongated into rod-shaped elements, instead of being button-shaped (Figure 6.9(c)), the lower element of the shoulder girdle (the coracoid) has a long backward-pointing spine and the pelvis has an open acetabulum (hip socket), a feature lost in later crocodilians. In addition there are a number of crocodylomorph specializations in the skull (Figure 6.9(b)): the quadrate and quadratojugal are displaced inwards towards the braincase and the cheek region is overhung by the squamosal.

Another early crocodylomorph is *Sphenosuchus* from the Early Jurassic of South Africa (Walker, 1990), a slightly heavier animal than *Terrestrisuchus*, 1.4 m long, a fast runner and probably usually quadrupedal. Its skull (Figure 6.9(d,e)) is crocodilian in many regards: the forwards sloping quadrate and quadratojugal, as in *Terrestrisuchus*, and the square skull table at the back, made from the squamosals and postorbitals, which overhangs the temporal region. The position of the upper end of the quadrate is characteristic of crocodylomorphs: in *Sphenosuchus*, the quadrate head contacts the prootic and the

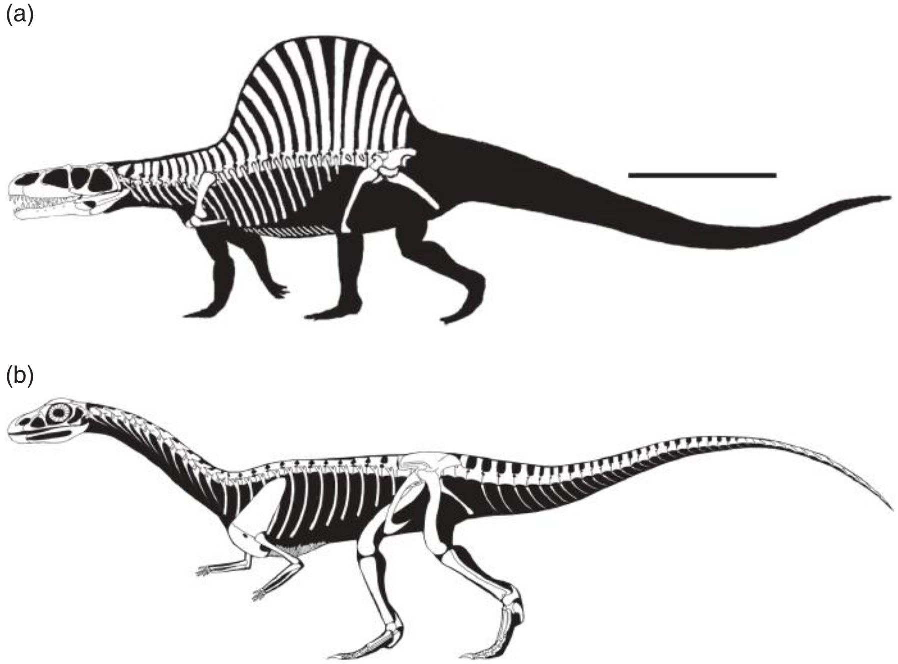


Figure 6.8 Derived crurotarsans: (a) the ctenosauriscid *Arizonasaurus* from the Middle Triassic of North America; (b) the shuvosaurid *Effigia* from the Late Triassic of the United States (b). Source: S. Nesbitt, Field Museum of Natural History, Chicago, IL, USA. Reproduced with permission.

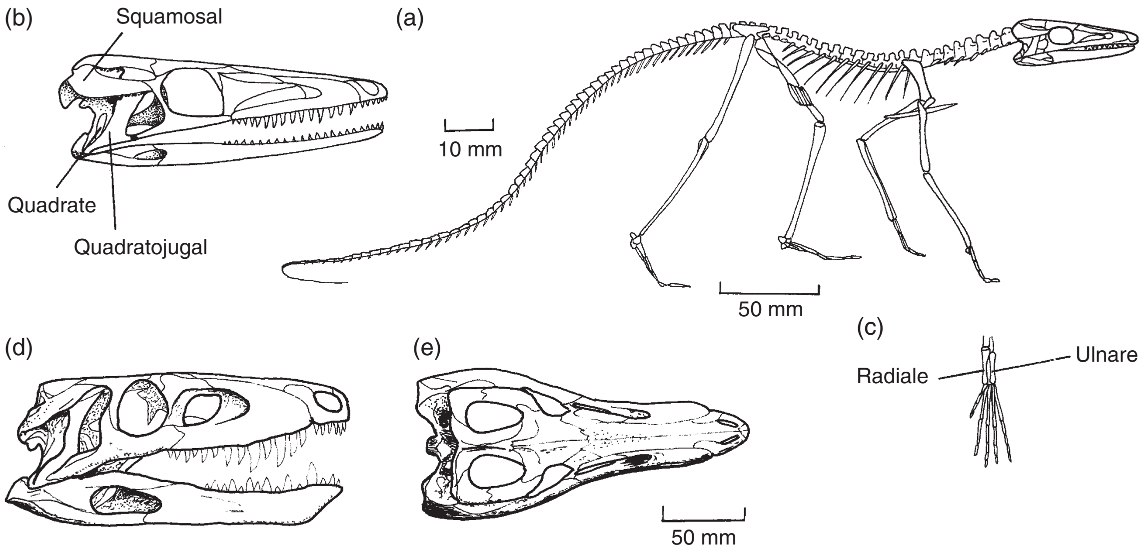


Figure 6.9 Basal crocodylomorphs: (a–c) the basal *Terrestrisuchus*, skeleton and skull in lateral view, hand in anterior view; (d,e) the sphenosuchid *Sphenosuchus*, skull in lateral and dorsal views. Source: (a–c) Adapted from Crush (1984). (d,e) Adapted from Walker (1990).

squamosal, whereas in later crocodilians it slopes further forward and also meets the laterosphenoid, a midline element, typical of archosauriforms, that lies in front of the basipterygoid and prootic. *Terrestrisuchus* and *Sphenosuchus* were grouped as a clade Sphenosuchia in some recent cladistic analyses, but Clark and Sues (2002) and Nesbitt (2011) find that sphenosuchians are paraphyletic with respect to later crocodylomorphs.

6.4 ORIGIN OF THE DINOSAURS

The major radiation of archosaurs in the Middle to Late Triassic, marked by the split of the Crurotarsi and the Avemetatarsalia, the later sometimes termed Ornithodira (see Box 6.1), provided a starting point for the radiation of the dinosaurs. The oldest definitive dinosaurs date from the early Late Triassic (late Carnian), although the oldest member of their sister group, the Silesauridae, is early Middle Triassic, which implies an origin of dinosauromorphs, and possibly also dinosaurs, at least 15 Myr earlier. The dinosaurs radiated dramatically during the last 25 Myr of the Triassic, the Norian and Rhaetian stages, and there has been a heated debate about how this happened, whether by successful competition with the synapsids, the basal archosaurs and the rhynchosaurs, or by opportunistic radiation after one or more extinction events. An understanding of the origin of the dinosaurs must start with a study of the earliest avemetatarsalians.

6.4.1 Avemetatarsalia: dinosaurs and relatives

The closest major outgroup of the dinosaurs is most likely the pterosaurs (see Box 6.1). This may seem an unusual pairing, but Gauthier (1986) noted similarities between the two groups, particularly in the hindlimb. For example, the ankle joint is simplified to a hinge-like arrangement in which the astragalus and calcaneum act together as a kind of 'roller', and the middle three toes are elongated and held in an upright position so that the animal stands up on its toes, the digitigrade posture. Pterosaurs are discussed in more detail later (see Section 8.6).

A small reptile from the Late Triassic of Elgin, Scotland, *Scleromochlus* (Figure 6.10(a,b)), may be either the basal member of Avemetatarsalia or sister group to Pterosauria (Sereno, 1991; Benton, 1999; see Box 6.1). *Scleromochlus* has the bird-like features of a tibia that is longer than the femur, an adaptation seen in some running animals, and a closely bunched group of four elongate metatarsals. It lacks the elongate neck, reduced fibula and the simplified ankle joint (astragalus and calcaneum closely attached to each other and to the tibia) seen in avemetatarsalians. This slender little reptile was only 170 mm long, the size of a blackbird, and it was certainly bipedal – its forelimbs are very much shorter than its hindlimbs. It had been interpreted as a climber or even a glider and hence in some way ancestral to pterosaurs. *Scleromochlus* might even have been able to hop: it has the proportions of the desert-living jerboa, a small mammal that leaps around the sand dunes of North Africa at night.

Two small reptiles from the Middle Triassic of Argentina fall closer to the dinosaurs than to the pterosaurs, *Lagerpeton* and *Marasuchus*. *Lagerpeton* is incompletely known, but is a basal dinosauromorph, whereas *Marasuchus* (Sereno and Arcucci, 1994) is a basal dinosauriform (see Box 6.1), diagnosed by a number of shared characters (Sereno, 1991), such as: a 'swan-neck' in which the cervical vertebrae follow a strongly S-shaped curve, a forelimb less than half the length of the hindlimb, a much reduced calcaneum that is one-third or less of the size of the astragalus and further specialized features of the foot.

Marasuchus (Figure 6.10(c,d)) was a lightly built flesh-eater, some 0.4 m long, which presumably preyed on small fast-moving animals such as cynodonts and procolophonids, as well as perhaps worms, grubs and insects. The skull is incompletely known, but the postcranial remains show many dinosaur-like characters, such as parallelogram-shaped cervical vertebrae

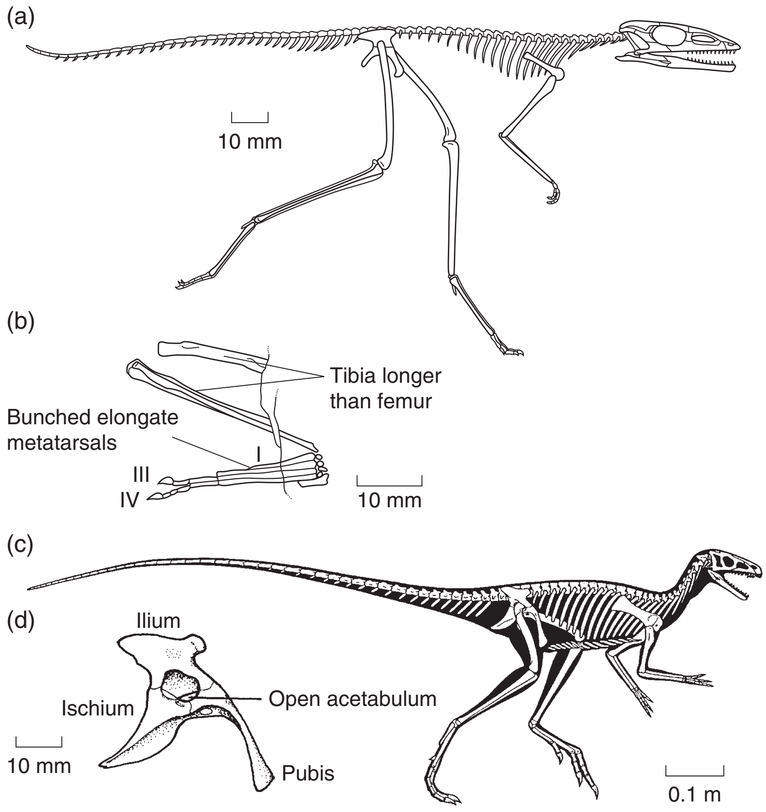


Figure 6.10 Basal avemetatarsalians: (a,b) *Scleromochlus*: (a) skeleton in lateral view; (b) anterior view of the foot; (c,d) the basal dinosauromorph *Marasuchus*: (c) skeleton in lateral view; (d) pelvis in lateral view. Source: (a,b) Adapted from Benton (1999). (c,d) P. Sereno, University of Chicago, Chicago, IL, USA. Reproduced with permission.

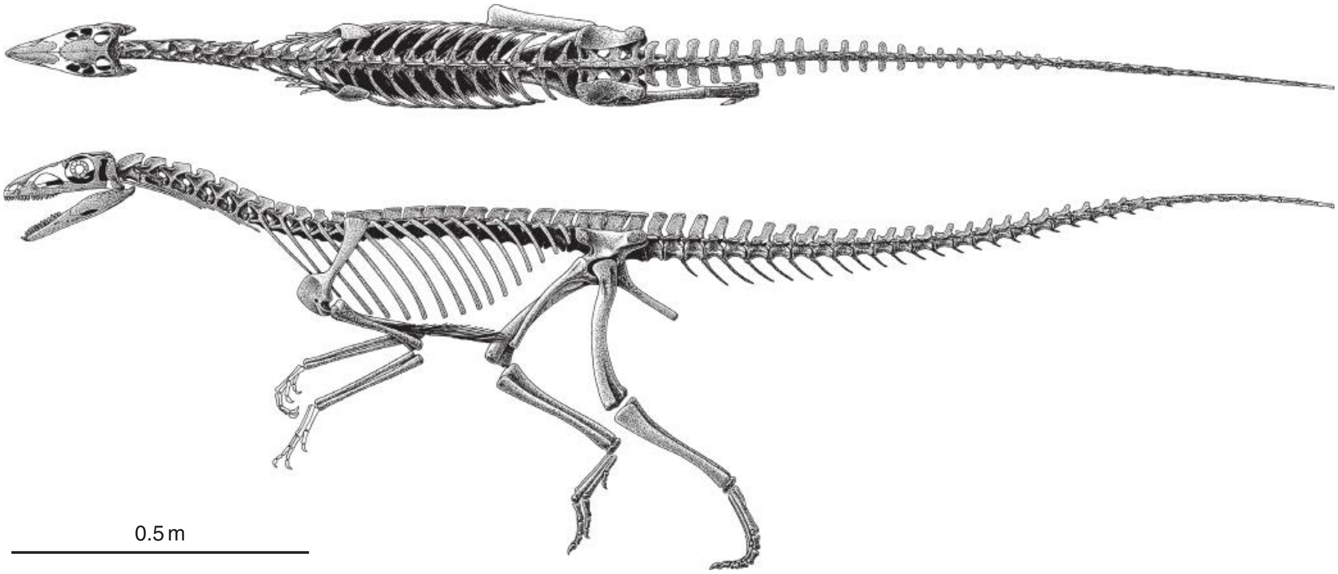


Figure 6.11 The silesaurid *Silesaurus* from the Late Triassic of Poland, one of the closest outgroups of Dinosauria, and with unusual adaptations to herbivory in the teeth. Views are dorsal and lateral. Source: J. Dzik, Institute of Paleobiology, Warsaw, Poland. Reproduced with permission.

(necessary for the S-curved neck), an arm that is less than half the length of the leg, the beginnings of an open acetabulum (Figure 6.8(d)) and other features of the pelvis and limb bones associated with fully erect posture. *Marasuchus* was clearly a biped, running on its hindlimbs, and the long tail was presumably used as a balancing organ. It may have used its hands for grappling with prey and for passing food to its mouth.

An important new discovery has been that the sister group of Dinosauria is Silesauridae (Dzik, 2003; Nesbitt, 2007; Langer *et al.*, 2010, 2013; Nesbitt *et al.*, 2010), a clade comprising some ten taxa from the Middle and Late Triassic of Africa, North America, South America, and Europe. These slender bipeds were formerly variously identified as dinosaurs or generalized dinosauromorphs, but in fact they form a clade diagnosed by a rugose ridge on the anterior edges of the supraoccipital, an ilium with a straight ventral margin of the acetabulum, and a femoral head with a ventral notch and straight transverse groove on the proximal surface. The oldest silesaurid is *Asilisaurus* from the early Middle Triassic of Tanzania (Nesbitt *et al.*, 2010), important evidence for the early origin of dinosaurs, some 15 Myr earlier than had been assumed before. Younger forms include *Eucoelophysis* from the early Norian of North America, and *Silesaurus* probably from the late Carnian of Poland. *Silesaurus* (Figure 6.11) is about 2 m long and has a long, slender body, with a relatively small head, long neck and limbs adapted presumably mainly for quadrupedal walking. The skull is long, but the snout and tooth rows are relatively short, and unexpectedly the teeth look like those of a herbivore – they are short and somewhat leaf-shaped, and not at all recurved in the usual archosaurian manner. Whether silesaurids were herbivores or omnivores is debated, but they had certainly modified their diet from the carnivory of most other non-dinosaurian dinosauromorphs.

6.4.2 The first dinosaurs

Although it is known that dinosaurian lineage must have arisen by 247 Myr ago, early in the Middle Triassic, the oldest true dinosaurs are known from the early part of the Late Triassic (the Carnian Stage, 235–228 Myr ago) from various parts of the world. Evidence for such an early origin comes from the finding of *Asilisaurus*, a silesaurid, and *Nyasasaurus*, a possible basal dinosaur, in the early Middle Triassic, as well as from putative dinosauromorph footprints of similar age, and older. The best early dinosaur specimens come from the Ischigualasto Formation of Argentina (Brusatte *et al.*, 2010b, 2011; Langer *et al.*, 2010), source also of the rauisuchid *Saurosuchus* (see Section 6.3.3). There are seven Ischigualasto dinosaurs, of which *Eoraptor* and *Herrerasaurus* are relatively well known from nearly complete specimens and they give an insight into the days before the dinosaurs rose to prominence.

Eoraptor (Sereno *et al.*, 1993, 2013) is a lightweight animal 1 m long (Figure 6.12(a,b)), with a number of dinosaurian characters: the postfrontal is absent, there are three vertebrae in the sacrum, the deltopectoral crest runs a long way down the shaft of the humerus, the femur is modified for fully erect posture and there are various dinosaurian characters in the ankle, including an ascending process on the astragalus.

Herrerasaurus (Sereno and Novas, 1992) is a larger, more heavily built animal 3 m long (Figure 6.12(c–e)). It shows a number synapomorphies of the Dinosauria, features that are not seen in *Marasuchus* or the pterosaurs: the acetabulum is fully open (Figure 6.12(d)) and the head of the femur is bent inwards (Figure 6.12(e)). *Herrerasaurus* has a short arm and a strong hand (Figure 6.12(f)) with three functional fingers (digits 4 and 5 are reduced to small bone splints), which it probably used for grasping and raking food. Both *Eoraptor* and *Herrerasaurus* were initially classed (Sereno and Novas, 1992; Sereno *et al.*,

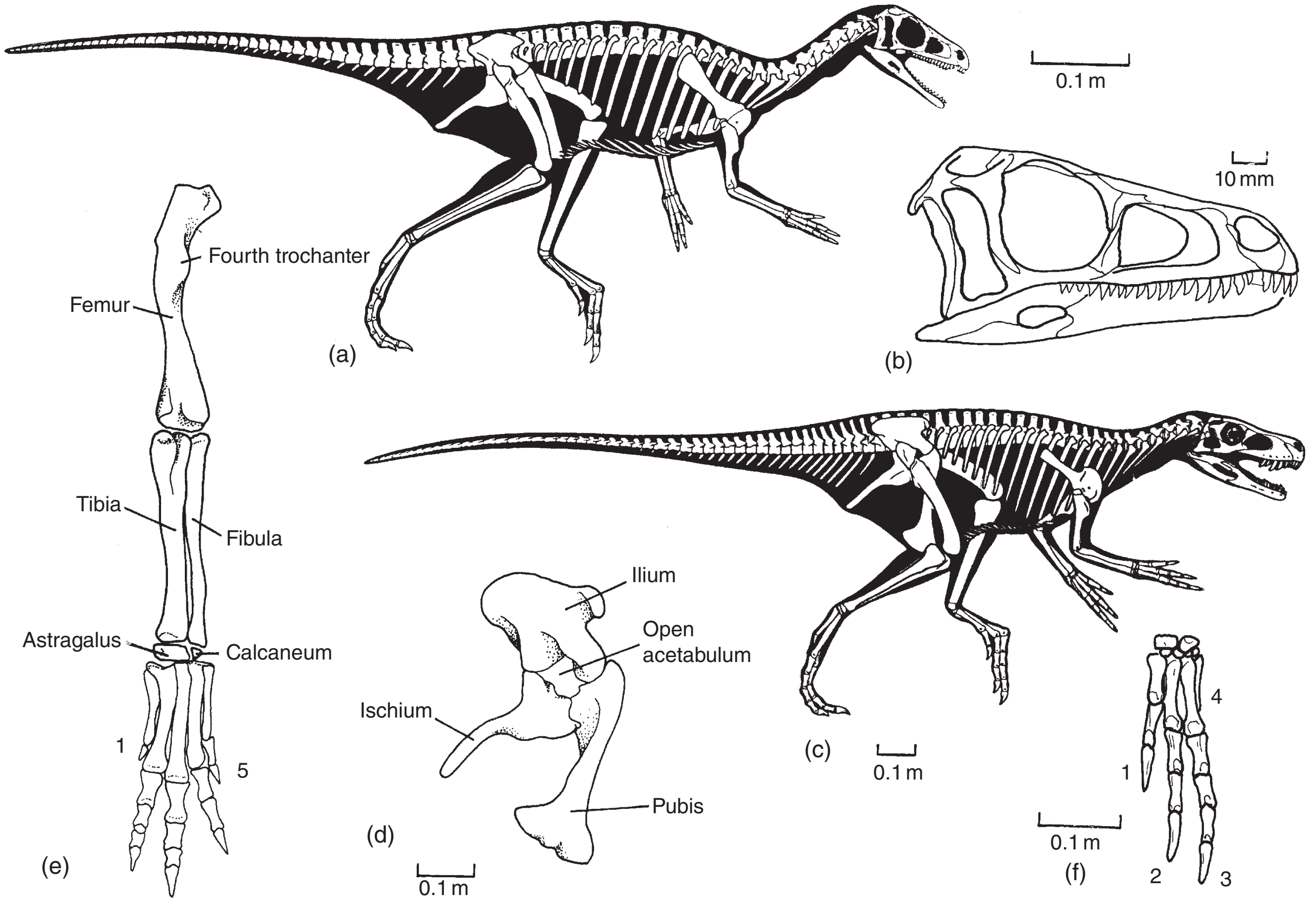


Figure 6.12 The first dinosaurs: (a,b) *Eoraptor*, skeleton and skull in lateral view; (c–e) *Herrerasaurus*, skeleton in lateral view (c), pelvic girdle showing dinosaurian lay-out of the bones and open acetabulum (d), hindlimb, showing large fourth trochanter on femur and long digitigrade foot (e), hand, showing reduced digits 4 and 5 (f). Source: (a,b) Adapted from Sereno *et al.* (1993). (c,f) Adapted from Sereno and Novas (1992). (d,e) Adapted from Galton (1977).

1993) as basal theropods, although they may turn out either to be basal saurischians or even an outgroup to Dinosauria (Langer and Benton, 2006; see Box 8.5).

Other Carnian dinosaurs include basal ornithischians and basal sauropodomorphs (Langer *et al.*, 2010), but they, *Eoraptor* and *Herrerasaurus*, were only rare elements in their faunas (11% of all skeletons). Before the end of the Triassic, however, the dinosaurs had radiated widely to become the most abundant vertebrates on land. How did this happen?

6.5 REPTILE EVOLUTION IN THE TRIASSIC

The origin of dinosaurs in the Triassic marks a fundamental change in global terrestrial ecosystems, and yet understanding of this major clade replacement has remained limited. At one time, such issues were presented as narratives, where the new group (dinosaurs) was seen as having outcompeted precursor groups (synapsids, rhynchosaurs, crurotarsans). New work has cast doubt on such an assumption, but has also extended the question of the origin of dinosaurs back in time so that their origins now become part of the recovery of life from the Permo-Triassic mass extinction (see Section 5.7). These threads in the debate will be explored as an example of changing approaches in macroevolutionary analysis.

Key questions in **macroevolution** (see Section 2.7) include the relative impacts of physical, environmental and biological factors on the fates of clades, the role of mass extinctions, and the nature of diversifications and replacements in the history of life. New methods for exploring the evolution of diversity, disparity, and function, and for mapping and assessing trait evolution across phylogenies have shed new light on major changes in reptilian diversity on land during the Triassic.

6.5.1 Early and Middle Triassic recovery

Very few species or genera of tetrapods survived the Permo-Triassic mass extinction, and of those that did survive, many did not last long. In the reasonably continuous faunal successions of European Russia and the Karoo in South Africa, snapshots of the extinction and recovery can be documented. The Russian data show massive damping of origination and extinction after the mass extinction, and that faunal dynamics had not recovered to normal even by the time of the Bukobay Svita, in the late Middle Triassic (Benton *et al.*, 2004). This is confirmed in a study of faunal **evenness**, the relative proportions of different species within an assemblage: the values decline across the Permian-Triassic boundary, especially in earliest Triassic faunas which were often hugely dominated by *Lystrosaurus*, and evenness recovered to normal only in the Middle Triassic (Irmis and Whiteside, 2012).

Lystrosaurus and some other tetrapod taxa that proliferated in the first 1–2 Myr of the Triassic can be identified as **disaster taxa**, species that profited from the disturbed conditions and spread rapidly, but which did not necessarily form part of the subsequent, more stable ecosystems (Sahney and Benton, 2008). In some locations, for example Russia, earliest Triassic faunas were dominated by fish-eating amphibians, with very few browsers and predators, and these ecological groups re-emerged only in the Middle Triassic. Detailed ecosystem analysis shows how imbalanced those *Lystrosaurus*-age, earliest Triassic ecosystems were in comparison with more stable systems before and after (Roopnarine *et al*., 2007).

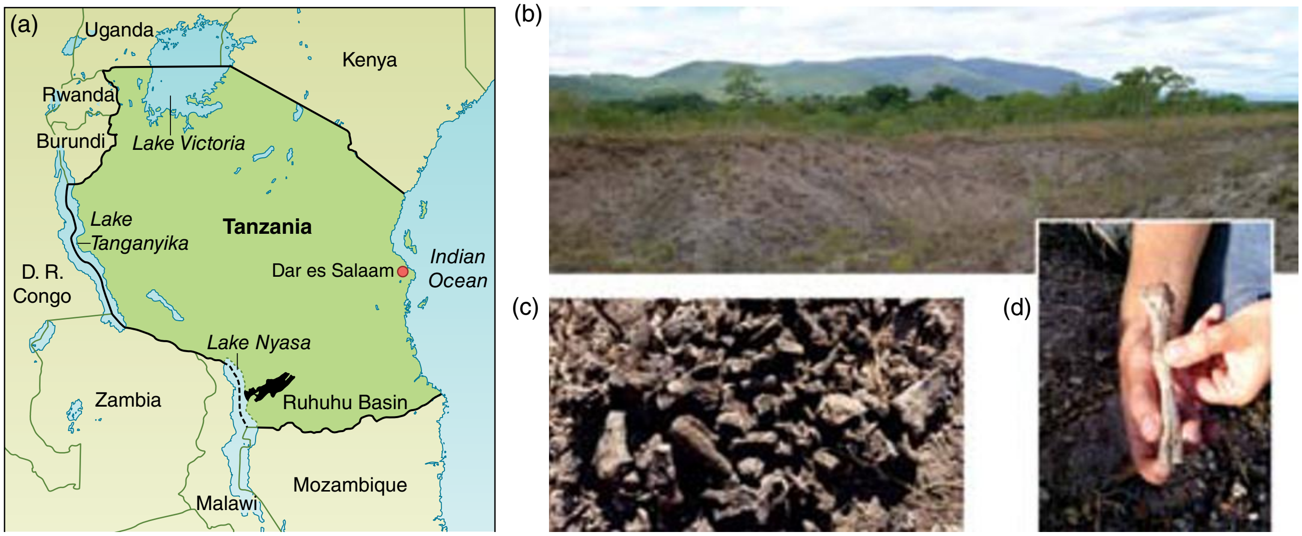
The recovery can be documented in geographic terms as well. In the immediate aftermath of the Permo-Triassic mass extinction, tetrapod faunas appear to have become **cosmopolitan**, with a small number of species, notably the anomodont *Lystrosaurus*, occurring worldwide. After this episode of disaster taxa, faunas became more **endemic**, at least in Gondwana (Sahney and Benton, 2008), with distinct differences between the early Middle Triassic tetrapod faunas of South Africa and Tanzania/ Zambia for example. The Manda beds of Tanzania contain diverse, but rare, archosaurs, including the earliest dinosauromorphs (see Box 6.4), but the middle parts of the *Cynognathus* Zone of South Africa do not. Establishment of geographically endemic faunas was associated with ecological stabilization during the recovery (Sidor *et al*., 2013).

BOX 6.4 THE MARVELLOUS MANDA FORMATION

The Triassic tetrapod-bearing rocks of the Ruhuhu Valley of southwestern Tanzania (illustration (a)) were first explored during the 1930s by European naturalists such as Gordon M. Stockley, Francis R. Parrington, and Ernst Nowack. Since then, other expeditions (illustrations (b–d)) surveyed the Lifua Member (Manda beds), and the age is established as Anisian (Middle Triassic), c. 243 Myr ago. Some recent discoveries in the Manda beds have changed our perceptions of the origin of the dinosaurs.

The commonest elements of the fauna include the medium-sized herbivorous rhynchosaur *Stenaulorhynchus*, the large-bodied herbivorous dicynodonts *Kannemeyeria* and *Sangusaurus*, as well as the aquatic, carnivorous mastodontosaurid *Eryosuchus*, and a variety of small- and medium-sized cynodonts, both carnivores (*Aleodon*, *Angonisaurus*, *Tetragonias*) and herbivores (*Cricodon*, *Diademodon*, *Scalenodon*). The terrestrial archosaur carnivores include the large rauisuchian *Stagonosuchus*, the sail-backed ctenosauriscid *Hypselorhachis*, and the smaller *Parringtonia*, as well as the still poorly understood, possibly non-archosaur archosauromorphs '*Mandasuchus*' and '*Teleocrater*'.

Most exciting has been the discovery of two new dinosauromorphs, *Asilisaurus kongwe* and *Nyasasaurus parringtoni*. *Asilisaurus* is relatively uncontroversially assigned to Silesauridae (Nesbitt *et al*., 2010; Langer *et al*., 2013), and so extends the date of origin of the immediate sister group of Dinosauria back to the Anisian. *Nyasasaurus* was described (Nesbitt *et al*., 2012) as possibly the oldest dinosaur, based on a humerus and some vertebrae. This could be a dinosaur: it has a long deltopectoral crest on the humerus, with a deflected tip, elongate neck vertebrae with hollowed-out sides, and possibly three sacral vertebrae. The last two characters remain uncertain, however, because the vertebrae assigned to *Nyasasaurus* may not belong with the holotype humerus. Even if *Nyasasaurus* is not a dinosaur, it and *Asilisaurus* are close outgroups of Dinosauria, and so the dinosaur lineage arose in the Anisian, during the recovery of life on land from the devastating Permo-Triassic mass extinction.



The Manda dinosauromorphs. (a) Map showing the location of the Manda beds in the Ruhuhu Basin in Tanzania. (b) Field photograph of the Manda beds. (c,d) Field photographs of surface-collected bones, (c) and a long bone of the dinosauromorph *Asilisaurus* (d). See Colour plate 6.3. Source: M. Langer, University of São Paulo, São Paulo, Brazil (map and composition) and R. Smith, Iziko Museum of Natural History, Cape Town, South Africa (photographs). Reproduced with permission.

Macroevolutionary studies shed light on how different clades evolved through this stressful time (Benton *et al*., 2014). For example, among the anomodonts, very diverse in the Late Permian, only three or four lineages survived into the Triassic, and only one of these then gave rise to a re-expansion of the clade in the Middle Triassic (see Section 5.6.5). Comparison of morphological characters shows that disparity of anomodonts was in decline throughout the history of the clade, even though diversity rebounded to almost pre-extinction totals. This then appears to be an example of a **macroevolutionary bottleneck**, an event in which diversity has been massively reduced, with the result that the clade emerges lacking its original potential for generating morphological variety (Ruta *et al*., 2013a).

Other successful clades in the Triassic, such as the procolophonids (see Section 5.4.4), cynodonts (see Section 10.1), and archosauriforms had started from lower diversities in the Late Permian, and so could not be said to have passed through a bottleneck; they simply expanded in diversity and disparity during the Triassic. As is generally the case during such diversifications, disparity expanded first, and then diversity second, in both anomodonts (Ruta *et al*., 2013a) and cynodonts (Ruta *et al*., 2013b). In their studies of archosauromorph diversification during the Triassic, Sookias *et al*. (2012) and Turner and Nesbitt (2013) documented the increase in size among archosauriforms in the Triassic (see Section 2.7), the first authors finding that the size increase followed a passive process, whereas the second study found weak evidence for an active trend, in other words selectivity driving size ever larger.

In detail, Turner and Nesbitt (2013) found that crurotarsans increased in maximum body size through the Early and Middle Triassic, remained constant through the Late Triassic, and decreased substantially in maximum body size towards the end of the Triassic. The earliest avemetatarsalians were much smaller than contemporary crurotarsans, but their mean sizes matched by the mid-Carnian. Avemetatarsalians retained smaller mean body sizes than crurotarsans through the Late Triassic, but their maximum sizes, represented by sauropodomorphs, were always higher.

6.5.2 Models for dinosaurian origins

The older ‘narrative’ explanation for the rise and subsequent great success of dinosaurs was that dinosaurs outcompeted synapsids thanks to their being endothermic (Bakker, 1972) or having adopted an erect, bipedal stance (Charig, 1984). However, such explanations are problematic because they often lack precision and testability, and they are *post hoc*, meaning that they are given after the successful clade is recognized. It is assumed, in a broad view of progress in evolution, that the successor clade must be competitively ‘better’, so any features in which it differs from the precursor clades must be key to their success. However, there is little evidence that evolution is progressive in this simple way – environmental conditions vary continuously, and what is selectively advantageous now may cease to be so in the future (Benton, 1987).

In the case of the origin of the dinosaurs the supposed advantageous characters, erect posture and endothermy (Bakker, 1972; Charig, 1984), can be refuted as explanations of what set dinosaurs apart. First, many archosaurs in the Triassic adopted erect posture, including several crurotarsan clades such as ornithosuchids, poposauroid rauisuchians, and some early crocodylomorphs. Further, erect posture had arisen among avemetatarsalians long before the origin of Dinosauria. In addition, all these examples also show the independent origins of bipedalism numerous times among Triassic archosaurs. Dinosaurian endothermy has long been a contentious issue (see Section 8.5), and it is most unlikely that the condition was ‘switched on’ uniquely at the time of the origin of Dinosauria. Indeed, comparisons of modern birds and crocodilians suggest that endothermy might have originated at the base of Archosauria (Seymour *et al*., 2004), and many lineages of Triassic archosaurs, especially the avemetatarsalians, show fibrolamellar bone and hence high metabolic rates and high growth rates (Ricqlès *et al*., 2008).

Benton (1983a) suggested that the progressive or competitive models were wrong, and he explained dinosaurian origins as opportunistic, a response to the chance extinction of the ecologically significant herbivores, the rhynchosaurs and dicynodonts, in the early Norian, some 225 Myr ago. Since 1983, new finds and new stratigraphies have changed the picture. Dinosauromorphs are known to have originated at least by the early Middle Triassic, some 15 Myr earlier than their oldest fossils. This does not necessarily alter the models for dinosaurian diversification: up to the late Carnian, dinosaurs were apparently rare ecologically speaking in comparison to other Triassic reptile groups. Even in the late Carnian, dinosaurs reached diversities of 1–7 species in certain faunas, but they were still not numerically abundant, some being represented by only one or two specimens. Barring selectivity against the preservation and collection of such early dinosaurs, the stem lineage to Dinosauria seems to have existed for some 20 Myr without diversifying substantially.

Dinosauria expanded in diversity and especially in relative importance within ecosystems during the Norian and Rhaetian. Benton (1983a) linked the extinction of rhynchosaurs and dicynodonts in the early Norian to a major climatic change and floral change. The *Dicroidium* flora of the southern hemisphere gave way to a worldwide conifer flora about this time (see Section 6.1). There were turnovers in marine communities, particularly in reefs, and there was a shift from pluvial (heavy rainfall) climates to arid climates throughout much of the world (Simms and Ruffell, 1990). The climatic and floral changes may have caused the extinctions of the dominant herbivorous tetrapods, and so provided an opportunity for another group to occupy major herbivore niches.

Current understanding on dinosaurian origins (Brusatte *et al*., 2010b, 2011; Langer *et al*., 2010; Irmis, 2011; Benton *et al*., 2014) emphasizes the complexity of the process. Three recent studies though have used innovative macroevolutionary approaches to cast doubt on the idea of a simple competitive explanation, as had been posited (see Section 2.7). Brusatte *et al*. (2008) used a study of discrete character disparity to show that crurotarsans and dinosaurs showed increasing morphospace

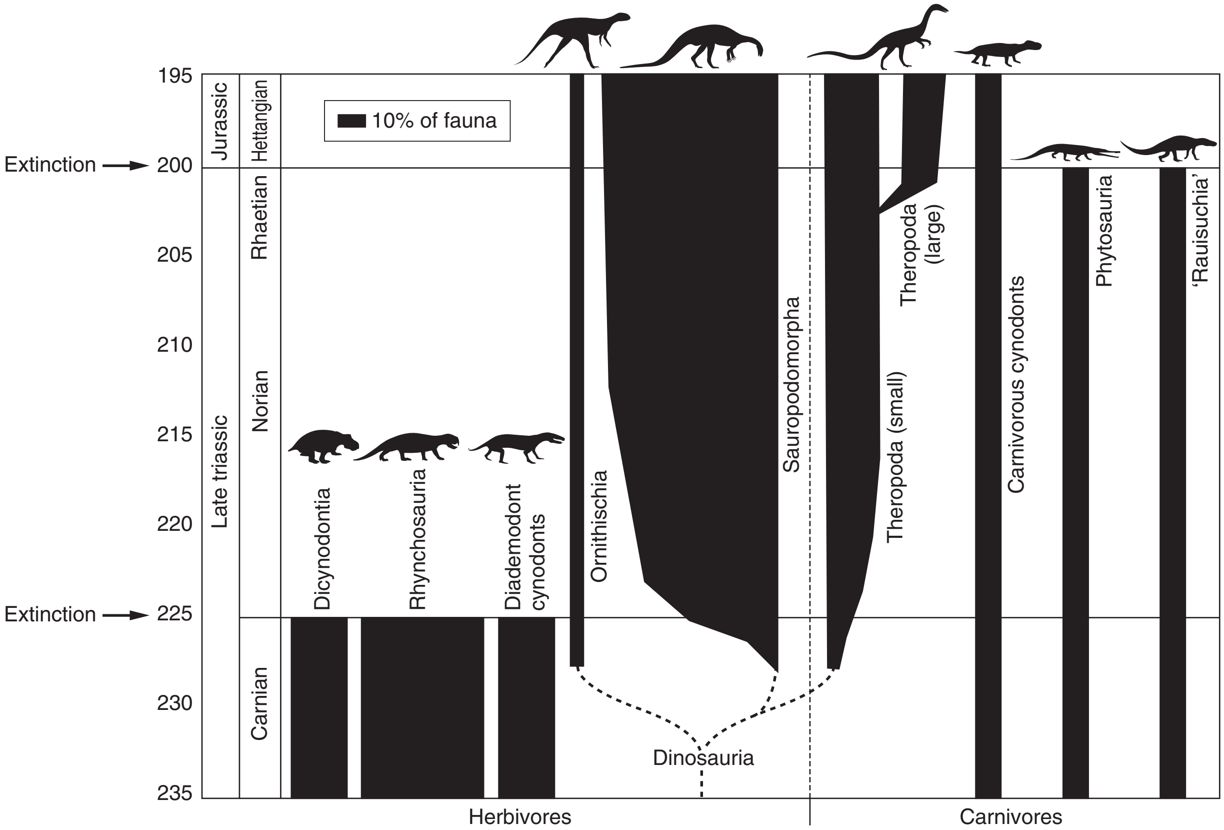


Figure 6.13 The expansion of the dinosaurs in two phases: (1) sauropodomorphs expanded in abundance and diversity in the early Norian, after the extinction of dominant herbivore groups (rhynchosaurs, dicynodonts, chiniquodontid cynodonts); (2) theropods diversified, with the appearance of large species, after the extinction of phytosaurs and 'rauisuchians' at the end of the Triassic.

occupation and statistically indistinguishable rates of trait evolution for cruotarsans and dinosaurs through the Late Triassic, with little evidence that the rise of dinosaurs was impeding other archosaurian clades. Further, Sookias *et al.* (2012) found no evidence for a driven trend in archosauromorph and synapsid body size during the Triassic, although Turner and Nesbitt (2013) found weak evidence for a driven trend among archosauriforms. Either way, these authors did not see evidence that dinosauromorphs in general, or dinosaurs in particular, were evolving at an unusual pace, as might be expected were they profiting against other clades by some special adaptive advantage.

The diversification of dinosaurs seems to have occurred in two steps, one in the early Norian, and the second at the Triassic-Jurassic boundary (Benton, 1993; Langer *et al.*, 2010; Figure 6.13). The first was the expansion of sauropodomorphs into herbivore niches during the Norian-Rhaetian, animals such as *Plateosaurus* in Europe and similar large herbivores in South Africa, South America, and India. In some faunas, basal sauropodomorphs comprised 50–90% of individuals. This sauropodomorph radiation appears to have been delayed in North America until the Early Jurassic. Irmis (2011) is right that the loss of rhynchosaurs and dicynodonts was not a mass extinction, and there were some rare survivors of each clade beyond the early Norian. However, there was a massive ecological change from faunas dominated by *Hyperodapedon* in the late Carnian and early Norian to those that followed (Langer *et al.*, 2010).

6.5.3 The end-Triassic mass extinction

The second phase of dinosaurian diversification happened in the Early Jurassic, after the extinction of crurotarsans such as phytosaurs, ornithosuchids, and rauisuchians during the end-Triassic mass extinction. This was one of the 'big-five' mass extinctions, not as huge as the Permo-Triassic event, but on a par with the Cretaceous-Paleogene (KPg) event. The mass extinction has been recognized for some time on the basis of the extinction of conodonts, and for major turnovers among ammonites, brachiopods, and bivalves. Among tetrapods, the last placodonts, eosauropterygians, and thalattosaurs disappeared, as well as several ichthyosaurian clades.

Current dating of the Triassic-Jurassic transition (Blackburn *et al.*, 2013) makes a strong case to link the mass extinction with a dramatic increase in the rate of eruption of the Central Atlantic Magmatic Province (CAMP), major basalt lava eruptions, that set in chain a series of consequences similar to those at the Permian-Triassic boundary (see Section 5.7): acid rain and killing of plants on land, and marine anoxia. The Triassic-Jurassic boundary is dated at 201.564 Myr, and eruptions occurred four times during a 600,000-year interval. One immediate effect of the eruptions seems to have been extensive wildfires, as indicated by a substantial increase in charcoal (Belcher *et al*., 2010). These wildfires were associated with a change in proportions of land plants from broad-leaved to narrow-leaved forms. Global warming associated with increased atmospheric carbon dioxide levels produced by the CAMP eruptions may have favoured the rise of narrow-leaved plants, which in turn led to an increase in fire activity at the Triassic-Jurassic boundary. Such conditions were probably not attractive for terrestrial tetrapods.

Early in the Jurassic, dinosaurs diversified, especially various armoured and unarmoured dinosaurian clades (see Chapter 8). Further, new clades of theropods emerged, some of them increasingly large, sauropodomorphs invaded North America, and most important of all, the ornithischians rose from extreme rarity in the Late Triassic to high diversity and abundance in the Jurassic. This marks the second step in the initial diversification of Dinosauria, the two steps separated by some 25 Myr.

6.6 FURTHER READING

Research on Triassic vertebrates, including aspects of faunal change and the origin of the dinosaurs, is presented by Fraser and Sues (2010). An array of all aspects archosaurian is offered by authors in Nesbitt *et al*. (2013a), and Brusatte (2012) gives more detail on the origin of dinosaurs. Tetrapods of the Russian Permo-Triassic are summarized in Benton *et al*. (2000), and the broad picture of the origin of dinosaurs is considered by Brusatte *et al*. (2010b), Langer *et al*. (2010), and Benton *et al*. (2014).

QUESTIONS FOR FUTURE RESEARCH

1 More taxonomic work on the Triassic marine reptiles, to make full comparisons between the new Chinese forms and those from other parts of the world.
2 Phylogenetic work to further explore the relationships of those diverse marine reptile groups with other reptilian clades.
3 Search for additional specimens of early turtles in the hope that they might shed some light on the origins of the group.
4 Exploration in detail of how climates and floras evolved through the Triassic, and how these might have affected tetrapod evolution.
5 More macroevolutionary study of the diversification of major tetrapod groups in the Early and Middle Triassic to explore how different clades responded to the post-extinction world, and constructed new ecosystems.
6 More search for very early dinosauromorphs to explore further how dinosaurs originated.

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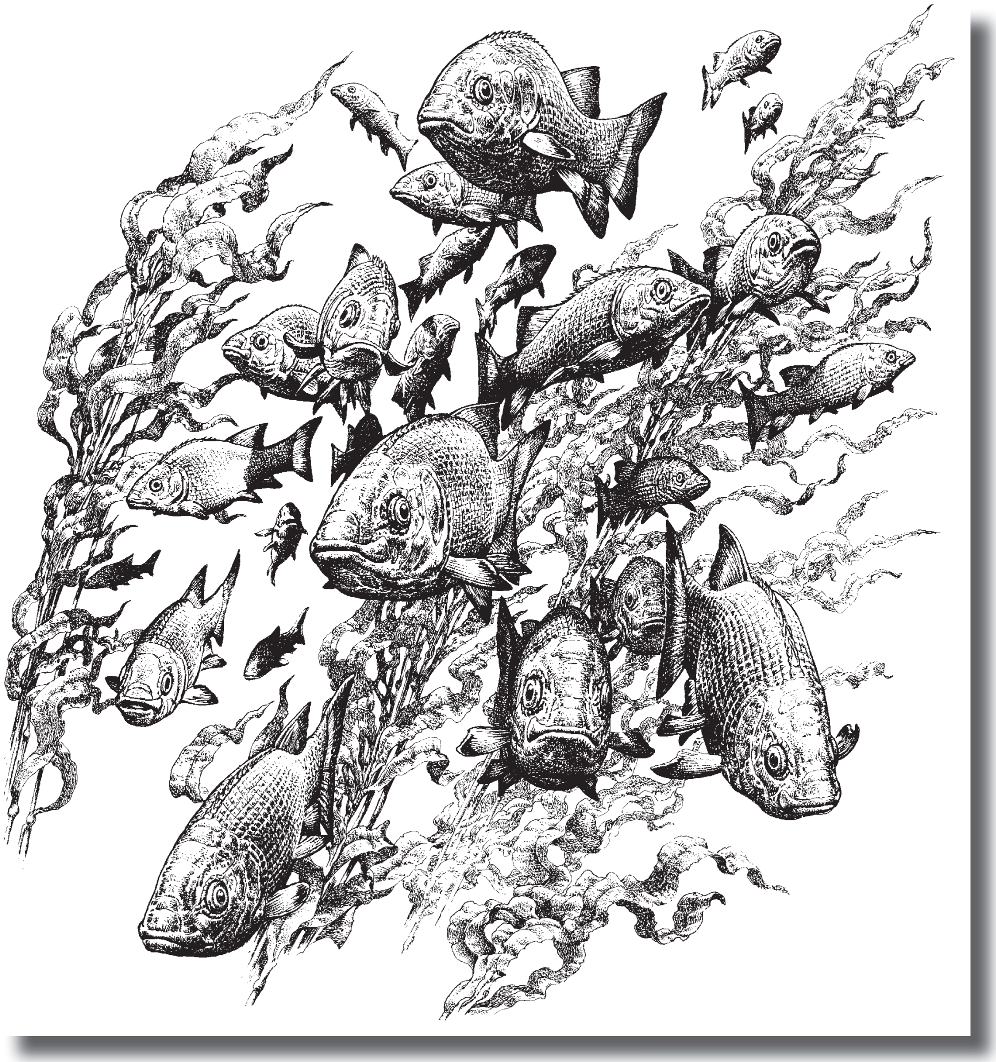
CHAPTER 7

Evolution of Fishes After the Devonian



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KEY QUESTIONS IN THIS CHAPTER

1 How did modern fish groups evolve after the Devonian?
2 What were the early sharks and their relatives like before the modern groups (neoselachians) appeared?
3 Why is it so hard to identify the oldest neoselachians?
4 Did sharks eat dinosaurs?
5 What were the early bony fishes like?
6 What was the effect of the Permo-Triassic mass extinction in triggering diversification of bony fishes?
7 Where do the modern 'living fossil' fishes, such as bichirs, sturgeons, paddlefishes, gars and bowfins, fit into the phylogeny of fossil forms?
8 What are the closest relatives of teleosts?
9 Why are teleosts so successful? Is it their lightness, speed, or their jaws?

INTRODUCTION

After the Devonian and the extinction of many groups of jawless fishes, as well as the placoderms and many acanthodians (see Chapter 3), two main groups filled the seas. The Chondrichthyes (sharks and rays) diversified several times, exploring a variety of life modes. The non-tetrapod Osteichthyes (bony fishes) also radiated several times and they have become a major element of marine and freshwater life today. Most recent fishes, the salmon, cod, herring, goldfish, sea horse, tuna and eel, are bony fishes, and they form part of a vast radiation that began over 150 Myr ago. Several early fish lineages that were important in the Silurian and Devonian – the agnathans and lungfishes, as well as the coelacanths (see Chapter 3) – have lived through the last 360 Myr since the beginning of the Carboniferous, but at low diversity. The purpose of this chapter is to explore the variety of sharks, rays and bony fishes and to account for their great success.

7.1 THE EARLY SHARKS AND CHIMAERAS

About 60 families of sharks and their relatives lived during the late Palaeozoic and Mesozoic, but many of these are known only from teeth and spines. The basal sharks include the Cladoselachidae, such as *Cladoselache* from the Late Devonian (see Figure 3.15), which was surprisingly modern looking. Recent finds, however, have revealed some quite bizarre chondrichthyans in the Carboniferous (see Box 7.1) and the better-known groups of these are reviewed here, as well as their Mesozoic derivatives. The classifications of Coates and Sequeira (2001a), Maisey *et al.* (2004), Coates and Gess (2007), Ginter *et al.*, (2010), Pradel *et al.* (2011), and Grogan *et al.*, (2012) are followed.

7.1.1 Symmoriiformes

The symmoriiforms, or symmoriids, probably a clade (Maisey, 2009; Pradel *et al.*, 2011) include some unusual early sharks. An example is *Denaea* (Figure 7.1(a)), which has a body outline basically like *Cladoselache*. *Denaea* has no fin spines and it has a whip-like extension to the pectoral fin called a **metapterygial axis**. The function of this is uncertain, i.e. whether it was used hydrodynamically, in defence, or in reproductive display. Symmoriiforms were thought to have died out at the Permo-Triassic mass extinction, until the report (Guinot *et al.*, 2013) of a single, highly characteristic multi-spined tooth from the Early Cretaceous of France.

The most striking symmoriiforms are the falcatids and stethacanthids, two families of Carboniferous spined sharks (see Box 7.1). *Falcatus* (Lund, 1985), a small shark up to 145 mm long (Figure 7.1(b)), looks like a dogfish except that a long shelf-like spine-brush complex extends from roots deep in the muscles of the 'shoulder' region to run over the head, superficially like a sunshade. The spine is present only in sexually mature males, identified by the presence of pelvic claspers, specialized elements that are inserted into the female during fertilization. Male *Falcatus* sharks may have aggregated prior to the breeding season in order to carry out display-courtship rituals.

Stethacanthus (Figure 7.1(c)) and *Akmonistion* (see Box 7.1) also have a structure over the shoulder area, this time shaped rather like a shaving brush and with tooth-like denticles covering its upper surface. There is a matching patch of denticles on the forehead. The structure of this spine-brush complex is unusual (Coates and Sequeira, 2001b; Maisey, 2009). It appears to be a modified first dorsal fin, and consists of three portions, a baseplate that sits on the shoulder region, a spine in front and behind it a brush-like structure. The baseplate and brush are composed of globular calcified cartilage, a material known also in placoderms and jawless vertebrates, and thus probably a primitive tissue in stethacanthids. The brush consists of hollow rods of globular calcified cartilage that extend up from the baseplate. The spine is made from dentine, the main constituent of teeth, surrounded by acellular bone.

7.1.2 Eugeneodontiformes and Petalodontiformes

The eugeneodontids, or 'edestids', are known almost exclusively from their teeth, which grew in spiral shapes (Figure 7.1(d)), and are common fossils in the Carboniferous and Permian, especially the genus *Helicoprion* (Zangerl, 1981; Lebedev, 2009; Tapanila *et al.*, 2013). As in chondrichthyans generally, each spiral consists of a series of teeth that are joined together in such a way that the largest teeth at the top are in use and new teeth can rotate into place when the older ones are worn away. This system means that there is a constant supply of teeth available, even when older ones break off. Over the years, some weird and wonderful reconstructions of *Helicoprion* have been produced, with the tooth whorl located on either the upper or lower jaw, and sometimes largely outside the jaws. This would create the bizarre situation of tiny teeth, at the centre of the whorl, being generated somehow in open water. Current reconstructions (Lebedev, 2009; Tapanila *et al.*, 2013) place the whorl entirely within the lower jaw, either at the tip (e.g. Figure 7.1(e)) or occupying the

BOX 7.1 THE AGE OF SHARKS

Two locations provide a detailed insight into the fishes of the mid Carboniferous (Friedman and Sallan, 2012). These sites are in central Scotland (Coates and Sequeira, 1998, 2001b; Ginter, 2009; Finarelli and Coates, 2012; Stewart and Coates, 2011) and Montana, USA (Lund, 1985, 1989; Grogan and Lund, 2009; Lund *et al*., 2012). The Montana fauna, from the Bear Gulch Limestone (Serpukhovian, c. 320 Myr ago), is particularly striking, comprising 85 species of chondrichthyans and 55 of osteichthyans – a world of sharks (see Figure 3.25)! *Stethacanthus* and *Falcatus*, with their extraordinary shoulder spines, are the largest. The unusual petalodontiform sharks, such as *Belantsea* (see Figure 7.1(f)), with their differentiated durophagous dentitions, are also best known here. *Harpagofutator*, a relative of the subterbranchialian *Chondrenchelys*, has forked appendages on the forehead, but only in the male. *Delphyodontos*, a possible early chimaera, seems to have no fins at all and a spherical body covered with small denticles. Another chimaera, *Echinochimaera*, has denticles in different parts of its body. The male also has pelvic claspers and forehead 'claspers', short spines over the eyes, as in some modern forms. The other Bear Gulch fishes include a 'telescoped' coelacanth, *Allenypterus*; a narrow eel-like actinopterygian bony fish, *Paratarassius* amongst others (Mickle *et al*., 2009); and the oldest known true lamprey, *Hardistiella*.

The fossils from Montana and Scotland are preserved exquisitely. The Scottish deposit, at Bearsden near Glasgow, contains marine and non-marine beds, and shark fossils were found in both. The deposit was discovered by Stan Wood (1939–2012), and it has yielded superb specimens of *Akmonistion* (see illustration) and other sharks like those from the Bear Gulch Limestone, as well as numerous palaeoniscoid bony fishes, acanthodians and a coelacanth.

A specimen of *Akmonistion*, a close relative of *Stethacanthus*, from the late Early Carboniferous of Bearsden, Glasgow, Scotland, showing the remarkable shoulder spine. The specimen is 0.5 m long. Source: S. Wood, deceased; formerly of Mr Wood's Fossils, Edinburgh, UK. Reproduced with permission.

length of the lower jaw. In either case, the new teeth are generated within the dental lamina, inside the jaws of the shark.

The rest of the eugeneodontiform skeleton is poorly known, except in *Fadenia* from the Early Carboniferous of Scotland (Figure 7.2(a)). This shark has a long dorsal fin and xenacanth dentition. It was a hunting fish that moved through plant-choked swampy ponds in search of prey.

The petalodontiforms, from the Carboniferous and Permian, include *Janassa* from Germany and England, and *Belantsea* from the Bear Gulch Limestone of Montana, USA (see Box 7.1). *Belantsea* (Figure 7.1(f)) has an extraordinary bulbous body and a short head (Lund, 1989). There were four powerful, ridged teeth set in each jaw segment and the tooth form varies along the jaw. These teeth were arranged as a pavement probably for crushing hard food such as molluscs or corals, and this is indicated also by the armour plates around the mouth, possible guards against abrasion while feeding.

7.1.3 Xenacanthiformes, Ctenacanthiformes and Hybodontiformes

The xenacanths (Hampe, 2003; Ginter, 2004), freshwater forms known from the Devonian to the Triassic, resemble modern sharks in their fin structure. *Xenacanthus* from the Early Permian (Figure 7.2(b)) has a long skull with a long spine just

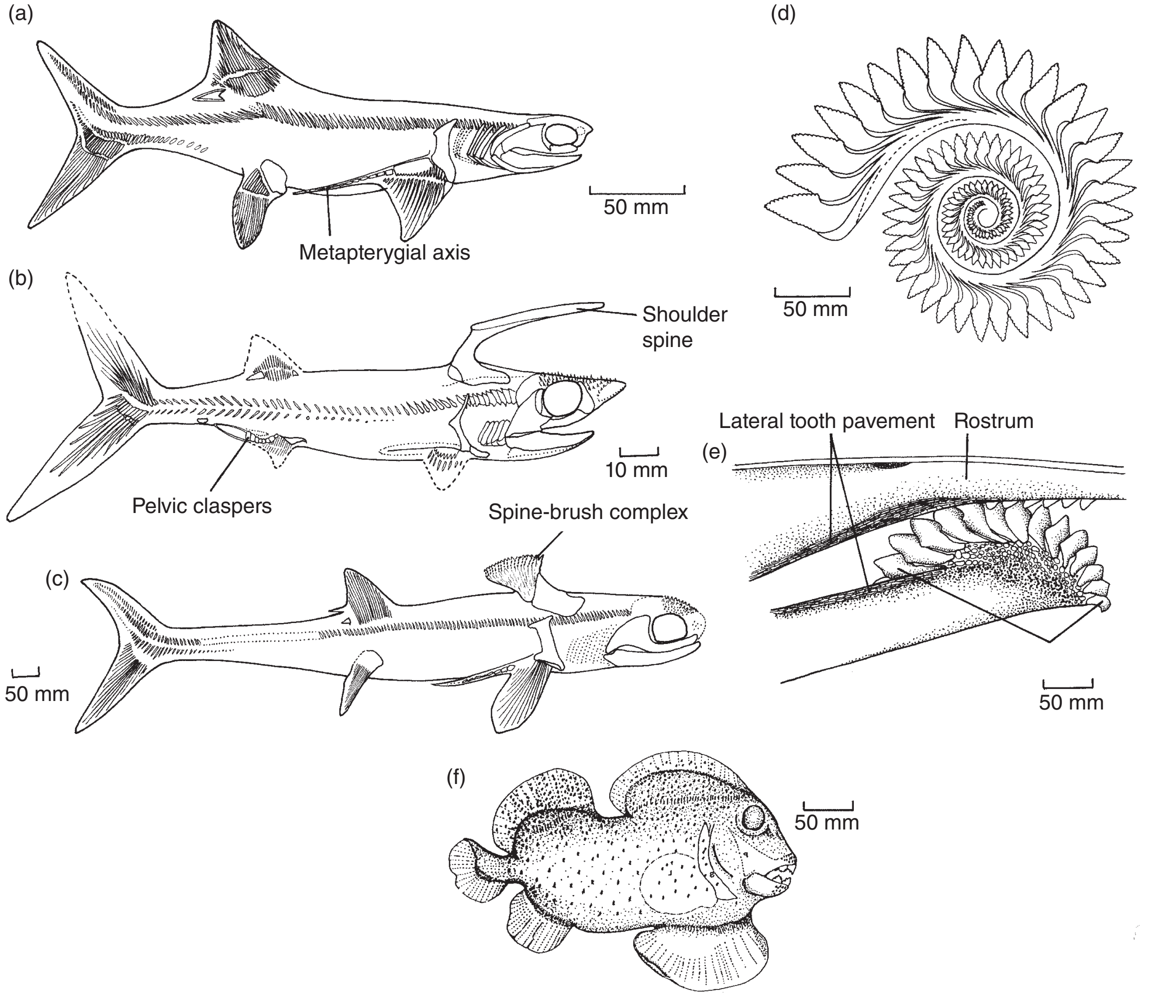


Figure 7.1 Early sharks: (a–c) symmoriiforms, (d, e) eugeneodontiforms and (f) petalodontiform: (a) *Denaea*; (b) male *Falcatus* with spine and claspers; (c) *Stethacanthus*; (d) tooth whorl of *Helicoprion*; (e) tooth whorl of *Sarcoprion* in place at the tip of the lower jaw and acting against a tooth pavement in the snout (rostrum); (f) *Belantsea*. Source: (a) Adapted from Schaeffer and Williams (1977). (b) Adapted from Lund (1985). (c) Adapted from Zangerl (1981). (d,e) Adapted from Moy-Thomas and Miles (1971). (f) Adapted from Lund (1989).

behind, large paired fins, an elongate dorsal fin extending along most of the back and a tapering symmetrical narrow **diphycercal tail**. The strange narrow long form of *Xenacanthus* may have allowed it to swim in and out of closely growing lake vegetation. An Early Permian xenacanth specimen from Germany (Kriwet *et al*., 2008) preserves two temnospondyl amphibians inside its stomach, and inside the stomach of one of those temnospondyls is an acanthodian fish, a remarkable example of three steps in a food chain preserved in a single specimen. Specimens of *Xenacanthus* occasionally show **claspers** (Figure 7.2(b)), paired flexible limb-like elements located just behind the pelvic fins, which are used during mating to hold the female secure while sperm are transferred. The claspers contain a number of small hard parts, so they are frequently preserved in fossil sharks.

The ctenacanths, an ill-defined group, include many forms dating from the Devonian to the Triassic, but they are known mainly from isolated teeth (Ginter, 2009). Their fin spines are similar to those of modern sharks: there are two dorsal fin spines, which have a pectinate ornament, and they are deeply inserted into the muscle mass of the body. *Ctenacanthus* from the Devonian (Figure 7.2(c)) is poorly known, probably because the typical shark skeleton, comprising cartilage, is rarely preserved.

The hybodonts (Coates and Gess, 2007; Rees, 2008) may have arisen as early as the Devonian and certainly by the Carboniferous, but their main diversification occurred in the Triassic and these were the dominant sharks in the Jurassic of Europe and North America. The hybodonts survived into the Late Cretaceous side-by-side with the modern sharks, the neoselachians (see Section 7.2.1). Typical hybodonts, such as *Hybodus* (Figure 7.2(d)), were probably sluggish swimmers, but capable of short fast bursts on occasion. The paired fins were used for steering and stabilization. The tail is fully heterocercal, with the backbone bending upwards. Hybodonts have a number of tooth shapes, some high and pointed and others low, which

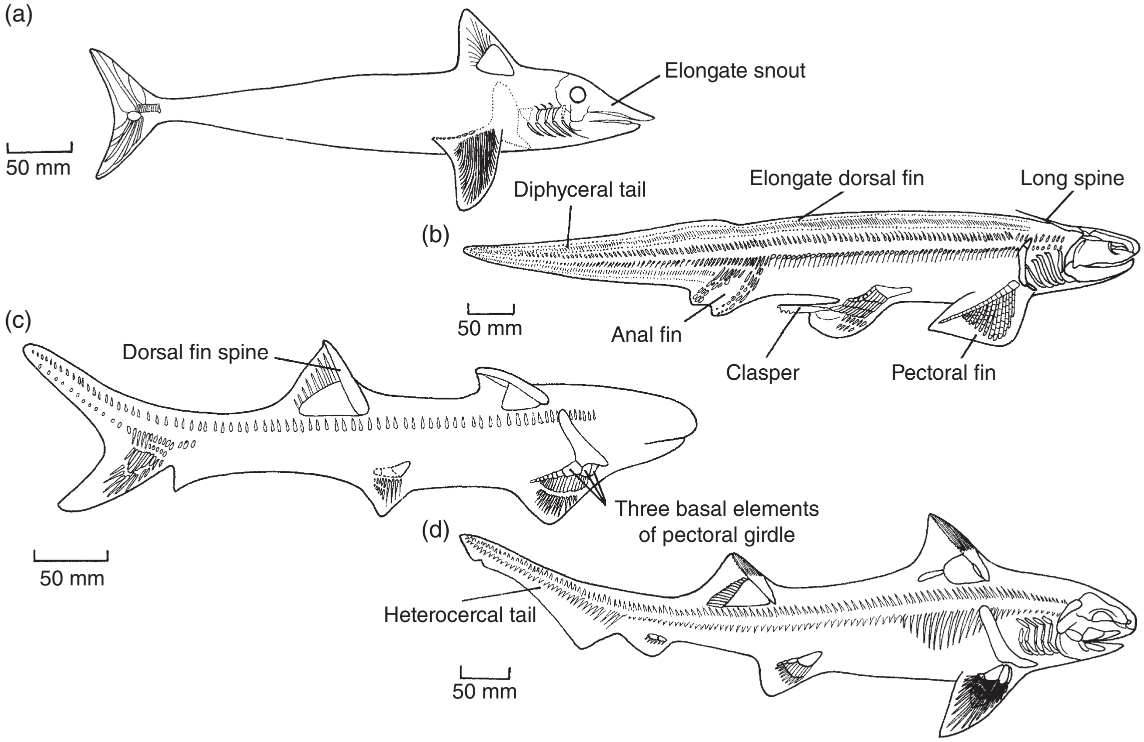


Figure 7.2 Derived Palaeozoic and Mesozoic sharks: (a) eugeneodontiform, (b) xenacanth, (c) ctenacanth and (d) hybodont: (a) *Fadenia*; (b) *Xenacanthus*; (c) *Ctenacanthus*; (d) *Hybodus*. Source: (a) Adapted from Dick (1981). (b–d) Adapted from Schaeffer and Williams (1977).

suggests that they fed on a variety of prey types, ranging from fishes to bottom-living crustaceans. They were essentially a marine group, like all sharks, but many species became adapted to life in fresh waters.

Xenacanths, ctenacanths, hybodontiforms and neoselachians share a number of characters that suggest they form a clade (see Box 7.2). There is usually an anal fin and they share a tribasal pectoral fin (Figure 7.2(c)). The fin is supported by three elements, the metapterygium at the back, as seen in other Palaeozoic sharks, and a mesopterygium and propterygium in front.

7.1.4 Holocephali and extinct stem groups

The chondrichthyans so far described are known largely from the Carboniferous and Permian periods, and they comprise a mix of stem chondrichthyans and members of the clade Elasmobranchii, leading to modern sharks and rays. The other modern chondrichthyan clade, the Holocephali (chimaeras or ratfishes) can also be traced back to the late Palaeozoic, comprising a number of extinct lineages that comprise clades Holocephalimorpha and Subterbranchialia (see Box 7.2). Extinct subterbranchialians include the Iniopterygiformes and Chondrenchelyiformes.

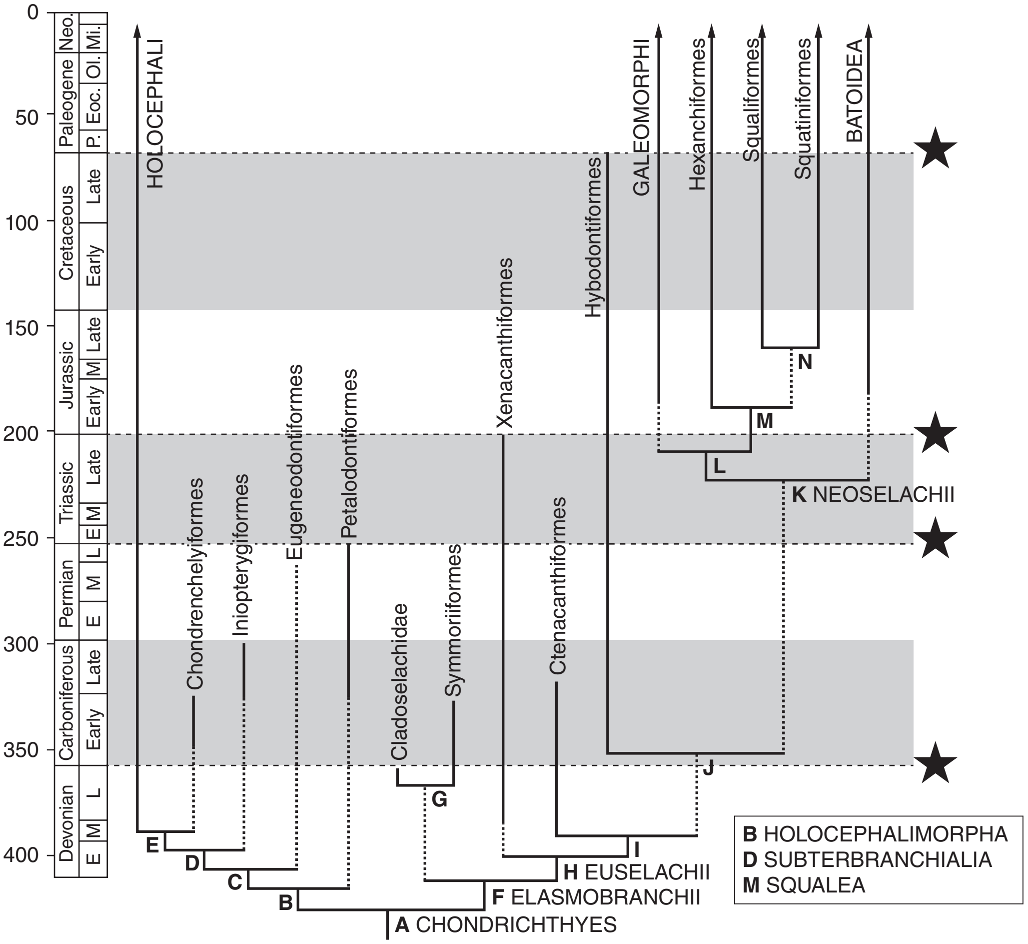
The iniopterygiforms *Sibyrhynchus* and *Iniopteryx* from the Late Carboniferous of midwestern USA (Figure 7.3(a,b)) have large heads, very long pectoral fins and rounded tail fins (Zangerl and Case, 1973; Grogan and Lund, 2009; Pradel *et al.*, 2009). The pectoral fins are attached to the pectoral girdle in a very high position and they probably flapped up and down like the wings of a bird, much as in a modern chimaera. The front of the fin bears a series of hook-like denticles. The chondrenchelyiform *Chondrenchelys* from the Early Carboniferous of Scotland (Figure 7.3(c); Finarelli and Coates, 2012) has a long, eel-like body with no tail fin and a small skull in which the palatoquadrate is firmly fused to the braincase (see Section 3.4.2). The pelvic fin is small and males have claspers.

There are about 40 species of holocephalans today, called variously chimaeras, rat-fishes, and rabbit-fishes, because of their unusual snub-nosed appearance. The head is short, but often with a long anterior projection, the body slender, there are large pectoral fins, and a long, whip-like tail. Holocephalans mostly live close to the seabed, feeding on molluscs and other invertebrates. Holocephalans have broad, slow-growing tooth plates with which they crush their shelly prey.

Typical chimaeras of modern form appeared in the Jurassic, but earlier families appeared in the Carboniferous and Permian, and isolated tooth plates are known from the Devonian and Carboniferous, with the oldest reported from the Middle Devonian (Darras *et al.*, 2008). An example is *Helodus* (Figure 7.3(d)), known from freshwater Carboniferous and Permian of Europe, which has the fins and jaws of a chimaeroid, but has a number of small teeth and a heterocercal tail. Later

BOX 7.2 CHONDRICHTHYAN RELATIONSHIPS

Living chondrichthyans are readily classified as either sharks and rays (elasmobranchs) or chimaeras (holocephalans). Within Elasmobranchii, the three major subclades Galeomorphi, Squalea, and Batoidea are generally recognized in molecular and morphological phylogenetic analyses (Inoue *et al*., 2010; Vélez-Zuazo and Agnarsson, 2011; Li *et al*., 2012; Naylor *et al*., 2012) and, while batoids (rays) were traditionally nested among sharks, based on morphological data, molecular analyses consistently place them outside a monophyletic shark clade, as shown here.



Cladogram showing postulated relationships of cartilaginous fishes, with synapomorphies from Coates and Sequeira (2001a), and Grogan *et al*. (2012). Synapomorphies: **A CHONDRICHTHYES**, prismatically calcified cartilage, second or single dorsal fin situated at pelvic level, a metapterygium articulating with 5+ radials and with an anteriorly directed proximal facet and a posteriorly directed axial radial series, myxopterygial claspers, elongate hyoid rays and various braincase characters (Coates and Sequeira, 2001a, p. 253); **B HOLOCEPHALIMORPHA**, rostrum greater than 180°, median symphysis in palatoquadrate, fewer than nine tooth families, teeth heterodont, tooth root extended below crown; **C**, uncertain; **D SUBTERBRANCHIALIA**, pelvic metapterygium that spans the entire fin base; **E**, quadrate-mandible articulation orbital, about 12 tooth families per jaw, tooth cusps low and rounded, orthodentine absent; **F ELASMOBRANCHII**, hypochordal (lower) lobe of caudal fin large; **G**, hyomandibula crescentic; **H EUSELACHII**, braincase with elongated otic region, anal fin, tribasal pectoral fin (metapterygium, mesopterygium, propterygium); **I**, two dorsal fin spines, fin spines with pectinate ornament, deeply inserted fin spines; **J**, palatoquadrates fused at the symphysis, calcified ribs, pelvic metapterygium articulates with all or all but first radials; **K NEOSELACHII**, extrabranchial cartilages on hyomandibula (epihyal) only, right and left coracoids fused; **L**, molecular results; **M SQUALEA**, ectethmoid process present, orbital articulation present, suborbital shelf absent, basitrabecular process present, notochordal constriction reduced, complete haemal arches in precaudal tail region; **L**, ectethmoid process absent, notochord constricted along entire vertebral column, enlarged supraneurals preceding second dorsal fin, precaudal haemal processes as elongate as lower caudal skeleton, spiracle valve present, longitudinal precaudal keel present; **N**, precaudal haemal process as elongate as lower caudal skeleton, spiracle valve, longitudinal precaudal keel. Abbreviations: **E**, Early; Eoc, Eocene; L, Late; Mi, Miocene; Mid, Middle; Neo, Neogene; Ol, Oligocene; P, Paleocene. Dashed lines and star symbols indicate extinction events.

Continued

Assignment of the fossil clades is more contentious. Most authors assign fossil taxa variously to the holocephalan and the elasmobranch branches, as stem taxa, and we show the more-or-less 'traditional' view here (Coates and Sequeira, 2001a). Chondrenchelyiforms and iniopterygiforms are stem holocephalans, forming the clade Subterbranchialia, and eugeneodontiforms and petalodontiforms also fall on the holocephalan stem, but with considerably less certainty. In some analyses (e.g. Grogan and Lund, 2009; Grogan *et al.*, 2012), the inioppterygians emerge as basal chondrichthyans, not as stem holocephalans. The remainder of Devonian and Carboniferous chondrichthyans are elasmobranchs, the cladoselachiids and symmoriiforms forming a clade, and the xenacanthiforms, ctenacanthiforms, and hybodontiforms successive outgroups to Neoselachii. An alternative view (Pradel *et al.*, 2011) is the group Holocephali and Elasmobranchii as a clade, with most of the Palaeozoic forms comprising a distinct clade, based on braincase characters.

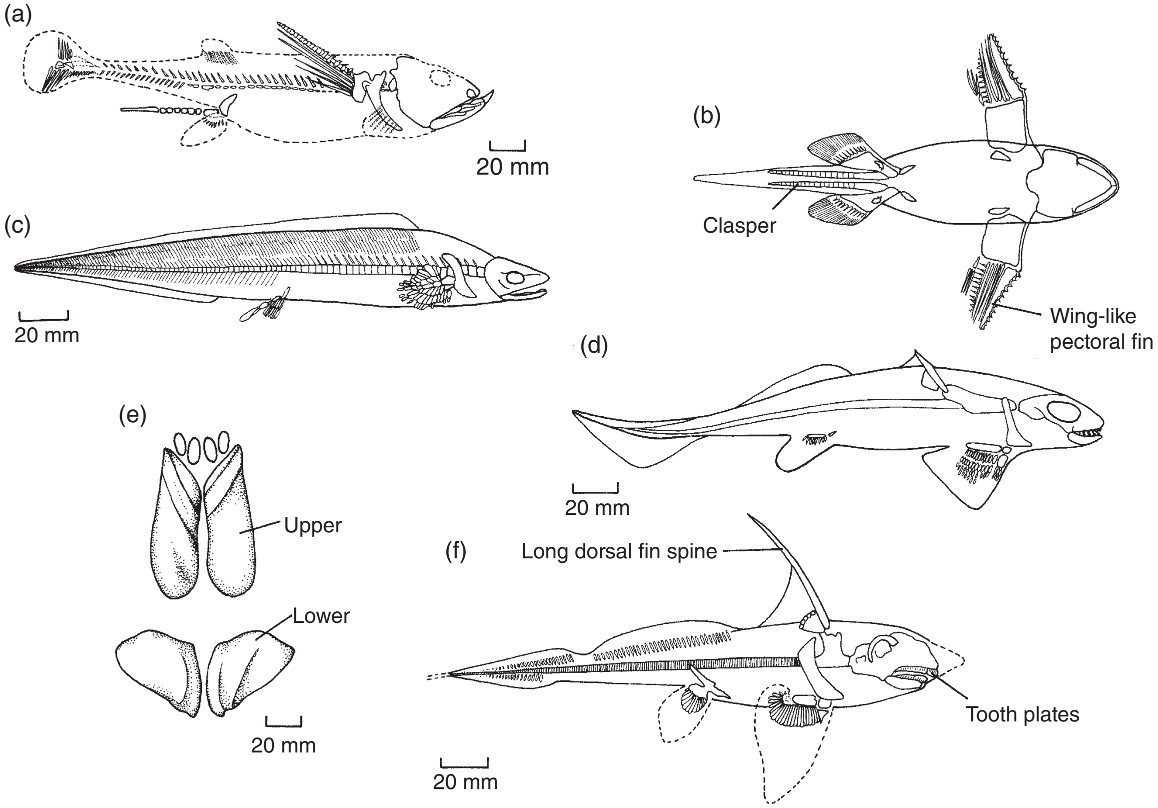


Figure 7.3 Early subterbranchialians (chimaeras and relatives) from (a–e) the Carboniferous and (f) the Jurassic: (a) the iniopterygian *Sibyrhynchus*; (b) the iniopterygian *Iniopteryx* in ventral view; (c) the chondrenchelyiform *Chondrenchelys*; (d) the holocephalan *Helodus*; (e) upper and lower dentition of the holocephalan *Deltoptychius*; (f) the holocephalan *Ischyodus*. Source: (a,b) Adapted from Zangerl and Case (1973). (c,d) Adapted from Moy-Thomas and Miles (1971). (e) Adapted from Patterson (1965). (f) Adapted from Schaeffer and Williams (1977).

chimaeras simplified their dentition to a small number of broad tooth plates, typically two pairs in the upper jaw and one pair in the lower jaw, used for crushing hard food such as molluscs and crustaceans. This pattern is approached in *Deltoptychius*, also from the Carboniferous (Figure 7.3(e)).

Later chimaeras had pointed tails, sometimes called 'rat tails', unlike the more generalized shark-like *Helodus*. An example is *Ischyodus* from the Middle Jurassic of Europe (Figure 7.3(f)), which is essentially the same in appearance as modern chimaeras. The skull is small and its elements are heavily fused, the gills lie beneath the braincase and there are two pairs of tooth plates in the upper jaw and one pair in the lower. The tail is long and whip-like, the pectoral fins are large and the tall spine in front of the dorsal fin may have borne a poison gland as in some modern forms.

7.2 POST-PALAEOZOIC CHONDRICHTHYAN RADIATION

Sharks and chimaeras diversified hugely in the Carboniferous, and their diversity declined during the Permian and Triassic. Some of the Carboniferous groups survived into the Mesozoic, notably the hybodont sharks, some ctenacanths and the holocephalans. Modern sharks, the neoselachians, diversified in Mesozoic and Cenozoic seas.

7.2.1 Neoselachii: the modern sharks

The neoselachians, including all modern sharks and rays, arose in the late Palaeozoic and radiated particularly during the Jurassic and Cretaceous to the modern diversity of some 1100 species distributed among 42 families (Compagno *et al*., 2005). Their early history is hard to track because the sole remains are often teeth (cartilaginous skeletons do not preserve well) and teeth are hard to classify (Maisey *et al*., 2004; Underwood, 2006; Kriwet *et al*., 2009). Neoselachians are diagnosed by numerous derived characters, including the possession of calcified centra. Others relate to a more adaptable feeding system and capabilities of faster swimming than in precursor shark groups.

The jaws of neoselachians open more widely than in earlier forms because of greater mobility about the jaw joint and a highly kinetic palatoquadrate and hyomandibular (see Figure 3.11(c)). This allows most neoselachian sharks to have a wide gape, as the palatoquadrate moves forwards relative to the braincase and the hyomandibular rotates as the lower jaw opens (Wilga *et al*., 2007). The snout is usually longer than the lower jaw and this means that the mouth opens beneath the head rather than at the front. In larger sharks, this jaw apparatus, combined with large numbers of serrated teeth, is extremely effective at gouging flesh from large prey. The serrated teeth of neoselachians contrast with the **cladodont** teeth of earlier groups such as the hybodonts, which had three, five or more major points, and were good for capturing prey and holding it, but not for gouging and butchering. The neoselachian jaw system works well for those sharks that feed on smaller prey: the jaws open rapidly and wide and they produce powerful suction to draw in swimming crustaceans and small fishes.

Neoselachian senses are also enhanced. Neoselachians have larger brains than most other fishes, larger even than amphibians and reptiles of the same body weight, and the sense of smell is improved over earlier sharks (at least to judge by the size of the nasal capsules).

The swimming abilities of neoselachians are evidently better than those of earlier sharks. The notochord is enclosed in, and constricted by, calcified cartilage vertebrae, whereas earlier chondrichthyans had a simple notochordal sheath. This strengthening of the backbone helps neoselachians resist compressional forces during fast swimming. The limb girdles are strengthened by fusion or firm connection in the midline, which allows more powerful muscle activity. The basal elements (the radials) in the paired fins are reduced, and most of the fin is supported by flexible collagenous rods called ceratotrichia or actinotrichia (Figure 7.4(c)).

Modern neoselachians fall into five main clades (Compagno *et al*., 2005; Vélez-Zuazo and Agnarsson, 2011; see Box 7.2).

1 Galeomorphs, or galeans, the largest group of some 340 species, is divided into the orders Heterodontiformes (bullhead sharks, 9 species), Orectolobiformes (carpet sharks, including the whale shark, 43 species), Lamniformes (mackerel sharks, including the great white shark, 16 species) and Carchariniformes (ground sharks, 270 species). Galeomorphs mainly inhabit shallow tropical and warm temperate seas and they feed on crustaceans and molluscs, fishes and, on occasion, humans (see Box 7.3). The basking and whale sharks, up to 17 m long, are the largest living sharks, but they bulk feed on tiny animals that they strain from the water. An even larger fossil shark has been reported. *Carcharodon* (= *Carcharocles*) *megalodon,* a relative of the living great white shark, *Carcharodon carcharias*, is known only from triangular teeth up to 168 mm long, as well as vertebral centra, which are found in sediments dating from the Palaeocene to Pleistocene, but especially in the Miocene and Pliocene. Early reconstructions of its jaws, based on these large teeth (Figure 7.4(a)) gave it a 3-m gape and a total body length of 18–30 m. A comparative study of its teeth (Gottfried and Fordyce, 2001), however, has suggested that *Carcharocles* was a mere 10–20 m long, with females significantly larger than males. The teeth are very like those of the living (but much smaller) species of *Carcharodon*. Nonetheless, this was a terrifying giant marine predator (Figure 7.4(b)).

2 Hexanchiforms, the frilled and cow sharks, comprise six species of mostly benthic, deep-water sharks that are found worldwide. They eat crustaceans, bony fishes and other sharks, and bear live young. Hexanchiforms have a single dorsal fin and six or seven long gill slits, whereas other sharks have two dorsal fins and five gill slits.

3 Squaliforms, some 30 species, include forms such as *Squalus* (Figure 7.4(c)), the spiny dogfish. Squaliforms generally live in deep cold waters and they retain spines in front of the dorsal fins.

4 Squatiniforms are a small group containing one family, known from the Late Jurassic to the present day. These sharks, represented today by 23 species of *Squatina*, the angel shark and monkfish, have changed little since the Mesozoic. They have flattened bodies, broad pectoral fins projecting at the side and a long slender tail. At times, the squatinomorphs have been classified as rays (batoids), sharing with them features of the skull, vertebrae, fins and musculature, but these are all convergences (Vélez-Zuazo and Agnarsson, 2011).

5 Batoids include more than 570 species of skates and rays. They are specialized mainly for life on the seafloor, and have flattened bodies with broad flap-like pectoral fins at the sides and many have long whip-like tails. The eyes have shifted to the top of the head and the mouth and gill slits are underneath. The batoids swim (Figure 7.4(d)) by undulating the pectoral fins. The teeth are usually flattened, arrayed in pavements and are adapted for crushing hard-shelled molluscs.

7.2.2 Changes in hunting style and the neoselachian radiation

The neoselachian sharks underwent a dramatic radiation in the Jurassic and Cretaceous, when they lived side-by-side with the hybodonts, which disappeared at the end of the Cretaceous (Maisey *et al*., 2004; Underwood, 2006; Kriwet *et al*., 2009). Most of the earlier shark groups had died out in the Carboniferous and Permian, but the xenacanths and ctenacanths survived well into the Triassic. Neoselachians existed through the Triassic, but

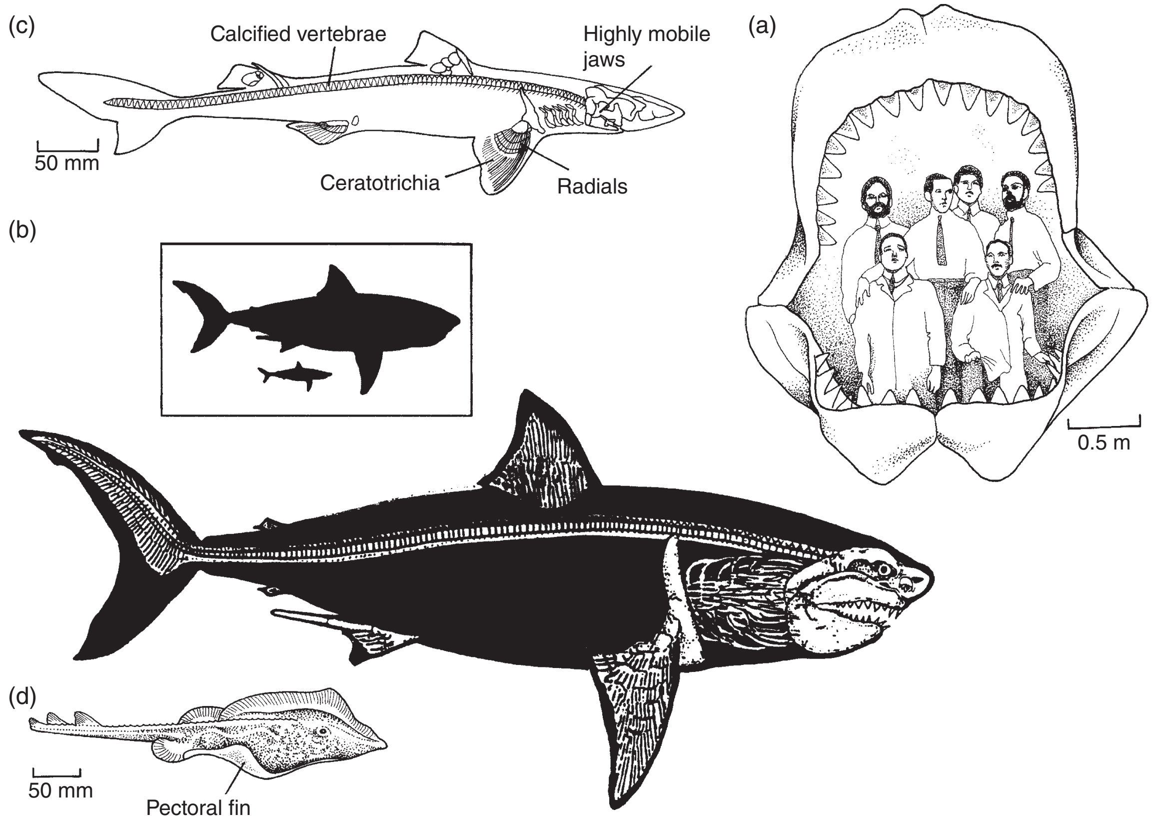


Figure 7.4 Modern sharks and rays: (a) the jaws of the giant Tertiary galeomorph shark *Carcharocles*, reconstructed from isolated teeth and probably too large; (b) restoration of the giant fossil *Carcharocles* and comparison of its size with the living great white shark *Carcharodon* (in box); (c) the modern squalomorph shark *Squalus*; (d) the modern ray *Raja*. Source: (a) Adapted from various sources. (b) M. Gottfried, Michigan State University, East Lansing, MI, USA. Reproduced with permission. (c) Adapted from Schaeffer and Williams (1977). (d) Adapted from Young (1981).

BOX 7.3 CRETACEOUS JAWS!

Stories of shark attacks on humans and other large animals are common. In Cretaceous times, sharks attacked dinosaurs and other large reptiles of land and sea, as shown in studies of lamniform sharks. Shimada *et al*. (2010) document predatory behaviour by *Cretalamna* from the Upper Cretaceous Tamayama Formation of Fukushima, Japan. A specimen of the elasmosaurid plesiosaur *Futabasaurus* is associated with 87 teeth of the shark, five of which are embedded in four bones of the plesiosaur, two of them nearly meeting through a vertebra. The elasmosaurid skeleton is more or less complete, representing an animal that was 7 m long in life, and the *Cretalamna* teeth come from 1.5–4.2-m long sharks. Shimada *et al*. (2010) cannot demonstrate whether the sharks killed the plesiosaur, or whether they were scavenging, but they present evidence for shark bites along the length of the body, and that six or seven different sharks, small, medium, and large, were involved. They see this as an example of a palaeo-feeding frenzy, a case perhaps of a group of sharks descending on the carcass, attracted perhaps by blood in the water, and feeding rapidly and in a group.

While *Cretalamna* was probably an active predator, Schwimmer *et al.* (1997) argue that the Late Cretaceous lamniform *Squalicorax* was a scavenger, feeding on carcasses of mosasaurs, plesiosaurs, marine turtles and even dinosaurs (hadrosaurs and an ankylosaur). *Squalicorax* teeth have been found embedded deeply in mosasaur, turtle and dinosaur bones, and there is no sign of healing. This implies that the shark was scavenging the carcass of a dead animal that was either floating at the surface, or lying on the seabed. Further evidence of scavenging is that other tetrapod bones from marine Upper Cretaceous rocks show scratch marks that match precisely the pattern of serrations on *Squalicorax* teeth, and some large vertebrate carcasses are surrounded by shed *Squalicorax* teeth.

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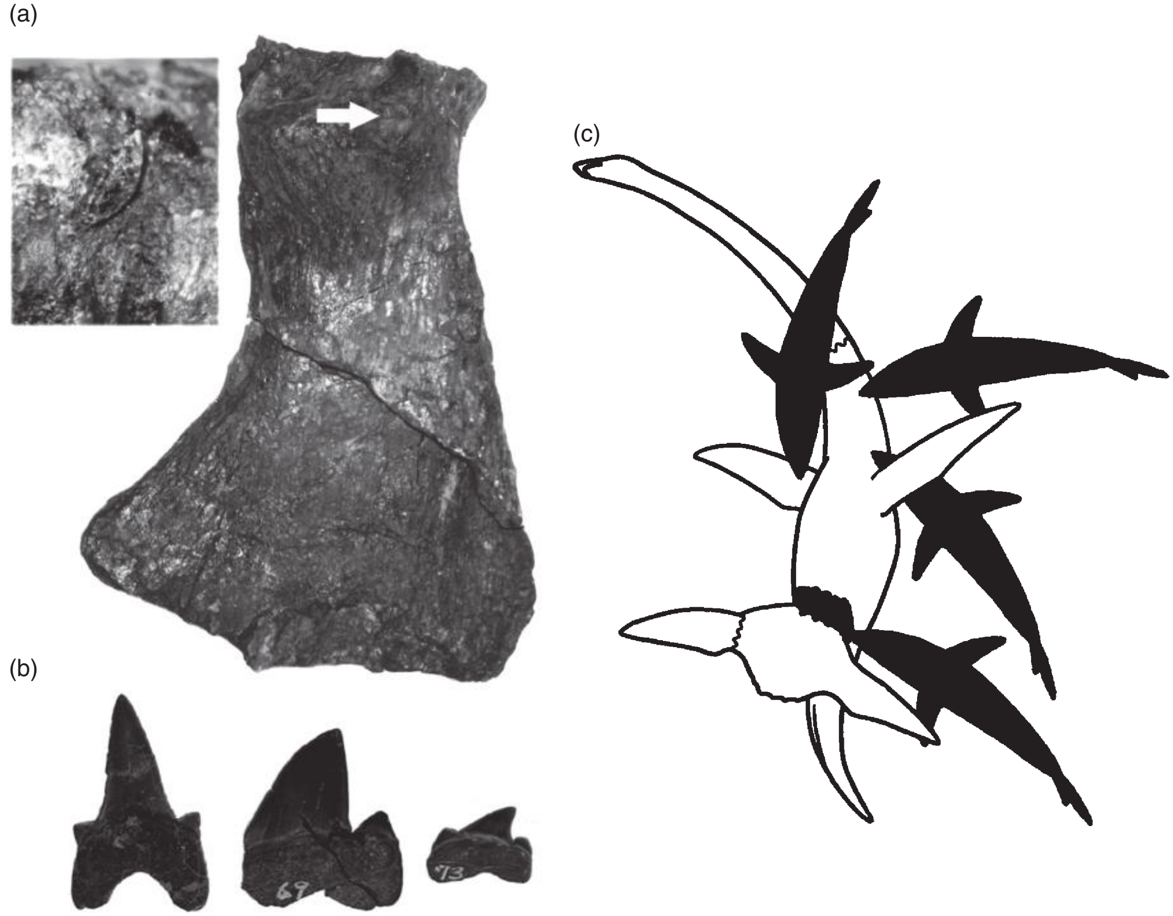


Shark attack in the Late Cretaceous: (a) right humerus of the plesiosaur *Futabasaurus suzukii*, with a shark tooth embedded (arrow); (b) teeth of the shark *Cretolamna appendiculata*; (c) carcass of the plesiosaur, showing positions at which the sharks had bitten the skeleton, reconstructing a possible scene of scavenging. Source: K. Shimada, DePaul University, Chicago, IL, USA. Reproduced with permission.

apparently at low diversity, as represented by sparse tooth records. The clade then diversified in the Early Jurassic, possibly opportunistically, following extinctions of other predatory vertebrates during the end-Triassic mass extinction (see Section 6.5.3), and they adopted a wide variety of predatory modes (Kriwet *et al*., 2009).

Thies and Reif (1985) suggested that the neoselachian radiation was an opportunistic response to the sudden appearance of abundant new sources of food in the radiation of the actinopterygian bony fishes, particularly the semionotids and other basal neopterygians in the Late Triassic and the teleosts from the Early Jurassic onwards. Here were new fish groups, present in vast shoals throughout the world, fast-moving, thin-scaled fishes. The early neoselachians had capabilities of speed, manoeuvrability, a flexible jaw system, and enhanced sensory systems, all essential for hunting the fast-moving bony fishes.

The early neoselachians were all apparently near-shore hunters that probably radiated in response to the evolution of teleost fishes and squid. Many modern sharks still specialize in this activity. A new feeding mode, fast offshore hunting, arose in the mid-Cretaceous, probably in response to increases in size and speed of teleost fishes and squid, and a move by them offshore. Marine reptiles, such as ichthyosaurs and long-necked plesiosaurs, may have been fast enough to compete with the new sharks, and indeed to eat smaller species. The Late Cretaceous mosasaurs (see Section 8.9.2) however, may have been too slow to compete with the sharks and may themselves have been eaten by larger shark species.

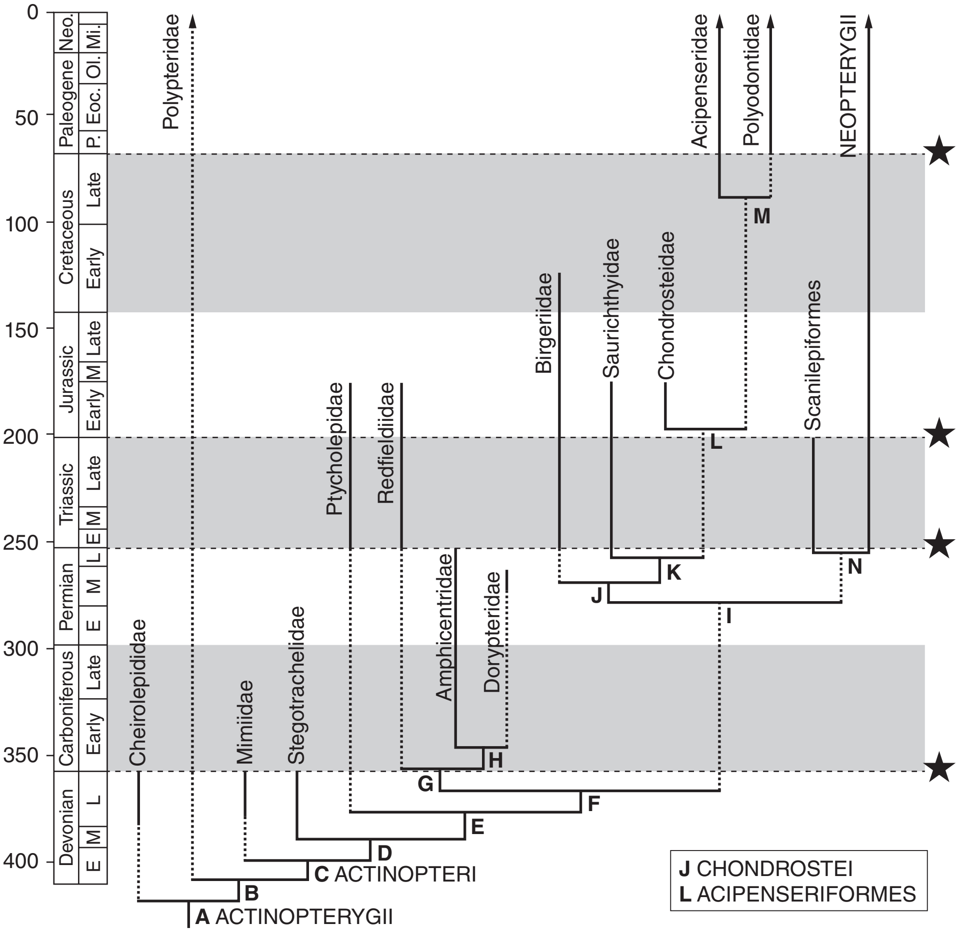
7.3 THE EARLY BONY FISHES

The ray-finned bony fishes, Actinopterygii, arose at least as early as the Silurian, and forms such as *Cheirolepis* radiated in the Devonian (see Section 3.9.1). The clade was traditionally subdivided into three, the chondrosteans, holosteans and teleosts, but the first two refer to paraphyletic groups, and are no longer used in that general sense. The history of actinopterygians consists of several bursts of radiation (see Box 7.4).

1 Basal actinopterygian radiation, Devonian–Triassic.
2 Basal neopterygian radiation, Triassic–Jurassic.
3 Teleost radiation, Jurassic–present.

BOX 7.4 BASAL ACTINOPTERYGIAN RELATIONSHIPS

The phylogeny of the Devonian to Triassic actinopterygians has proved hard to establish, not least because many of these early bony fishes, especially those from the Carboniferous and Permian used to be classified in the ill-defined category of 'palaeonisciforms'. The basic framework can be formed around the three living forms, the polypterids (bichir), acipenserids (sturgeons), and polyodontids (paddlefish), the first of which is sister to the other two, based on morphological and molecular evidence (Inoue *et al*., 2003). Numerous cladistic analyses, updated thanks to extensive new finds from the Triassic of China (Xu and Gao, 2011) confirm the sequence of fossil taxa shown. The Devonian taxa are basal, with the bichir *Polypterus* branching early, but lacking a fossil record. More work is required on Carboniferous and Permian 'palaeonisciforms' to establish their relationships, but several major lineages are shown, followed by a substantial radiation of birgeriids, saurichthyids and others in the Triassic. At the same time, the major clade Neopterygii emerged.



Cladogram showing relationships of the basal ray-finned bony fishes (Actinopterygii), with synapomorphies taken from the work of numerous authors, updated by Hurley *et al*. (2007) and Xu and Gao (2011). Extant families are indicated in bold. See Box 3.7 for context of Actinopterygii and Box 7.6 for neopterygian relationships. Synapomorphies are: **A ACTINOPTERYGII**, dermosphenotic T-shaped and contacts nasal, postorbital absent, squamosal absent, dentary with enclosed mandibular canal, one or two pairs of extrascapulars, single dorsal fin, scales and dermal bones with ganoin, rhomboidal scales with peg-and-socket articulation; **B**, distinct acrodin crown on all teeth, postcleithrum differentiated from anterior body scales; **C ACTINOPTERI**, accessory vomerine tooth plate, branching rays in all fins; **D**, intertemporal bone meets nasal bone, supra-angular element in mandible; **E**, prismatic ganoin in teeth and scales, suborbital bone, antopercular bone; **F**, reduction in number of branchiostegal rays; **G**, snout blunt and rounded, preopercular reduced, suborbitals absent, marginal teeth reduced or absent, crushing tooth plates, body deep and laterally compressed; **H**, marginal teeth peg-like or absent, crushing tooth plates present, two sets of radials in median fins, body deep and laterally compressed; **I**, keystone-shaped dermosphenotic of supraorbital bones; **J CHONDROSTEI**, operculum reduced, elongate posterior extension of the parasphenoid, body scalation reduced to tiny elements or absent; **K**, craniospinal process; **L ACIPENSERIFORMES**, palatoquadrates with anterior symphysis, triradiate quadratojugal, gill-arch dentition confined to first two hypobranchials and upper part of first arch, suboperculum has anterior process, preopercular canal in a series of ossicles and mandibular canal short or absent, infraorbital canal in a series of ossicles, premaxilla and maxilla absent; **M**, operculum absent, fewer than four branchiostegal rays, endocranium with extensive rostrum, dorsal and ventral rostral bones, ventral process of posttemporal bone; **N**, most characters of Neopterygii (see Box 7.6). Abbreviations: E, Early; Eoc, Eocene; L, Late; M, Middle; Mi, Miocene; Neo, Neogene; Ol, Oligocene; P, Paleocene. Dashed lines and star symbols indicate extinction events.

7.3.1 Anatomy of the first actinopterygians

Basal actinopterygians are diagnosed by specialized ganoid scales, which are thick bony elements composed of dermal bone, covered with dentine, and then ganoin on the outside, a layered shiny enameloid material (Figure 7.5(a)). The fundamental condition of the scales in osteichthyans is a rhomboid shape and a system of peg-and-socket articulations that lock them together (see Figure 3.19(b)), as found in the Late Silurian of China and Europe and the Early Devonian of Canada and Australia.

The first complete specimens of actinopterygians are known from the Devonian, taxa such as the cheirolepidid *Cheirolepis* (see Figure 3.19), the mimiid *Mimipiscis* from the Late Devonian of Australia (Figure 7.5(b,c)), and the stegotrachelid *Moythomasia* from the Late Devonian of Europe and Australia (Swartz, 2009). In *Mimipiscis* (Choo, 2011), the teeth are capped with **acrodin**, a dense variety of dentine, and it has a distinctive **postcleithrum**, a dermal element in the shoulder girdle region. The skull of *Mimipiscis* (Figure 7.5(c)) shows a number of actinopterygian characters. The lower jaw has a large dentary bone that bears teeth and encloses a sensory canal. Teeth in the upper jaw are present on the maxilla and premaxilla, as well as on a large median element in the palate, the **parasphenoid** and on many other small bones of the palatoquadrate. The maxilla is locked into the cheek and it is a strong hatchet-shaped element.

The bones of the skull roof are highly variable in actinopterygians. The nasal bone lies at the front and it contacts the **dermosphenotic** above the orbit, which in turn meets the supratemporal behind (Figure 7.5(c,d)). In later actinopterygians, a **dermopterotic** element appears behind the dermosphenotic, produced by fusion of the supratemporal and intertemporal, and **supraorbitals** appear between the nasal and the dermosphenotic. There is no postorbital and no squamosal, bones primitively present in sarcopterygians (see Section 3.9.4). Note also the large eye socket – actinopterygians are visual predators that rely on good eyesight.

Further back in the skull, an array of thin dermal bones, the **opercular** series, covers the gill region. The **preopercular** lies above, and is firmly attached to, the maxilla, and behind it are the opercular and **subopercular**. Below the subopercular, and sweeping round beneath the dentary, is a series of overlapping bony plates, the **branchiostegal** rays, numbering typically 12–13 in basal actinopterygians.

7.3.2 The basal actinopterygian radiation

The cheirolepidids, mimiids, and stegotrachelids, were short-lived clades, and they became extinct at the end of the Devonian (see Section 3.10.2). Further actinopterygian diversifications took place in the Carboniferous, Permian, and Triassic, but some of these imply substantial missing fossil record (see Box 7.4). For example, the ptycholepids, such as *Ptycholepis* (Figure 7.6(a)) are known from the Triassic and Early Jurassic of North America and Europe, and yet must have arisen in the Late Devonian or Early Carboniferous. Ptycholepids have a reduced dermosphenotic element that no longer contacts the nasal and numerous suborbital bones behind the eye socket.

Next in the phylogeny (see Box 7.4), is an unnamed clade that originated early in the Carboniferous, and whose members show reduced numbers of branchiostegal rays in the gill region: some forms have only one, instead of the more typical 12–13 branchiostegal rays. The redfieldiids, such as *Redfieldius* from the Late Triassic and Early Jurassic of North America (Figure 7.6(b)), show modifications to the snout and orbit region. These fishes are known worldwide in the Triassic and

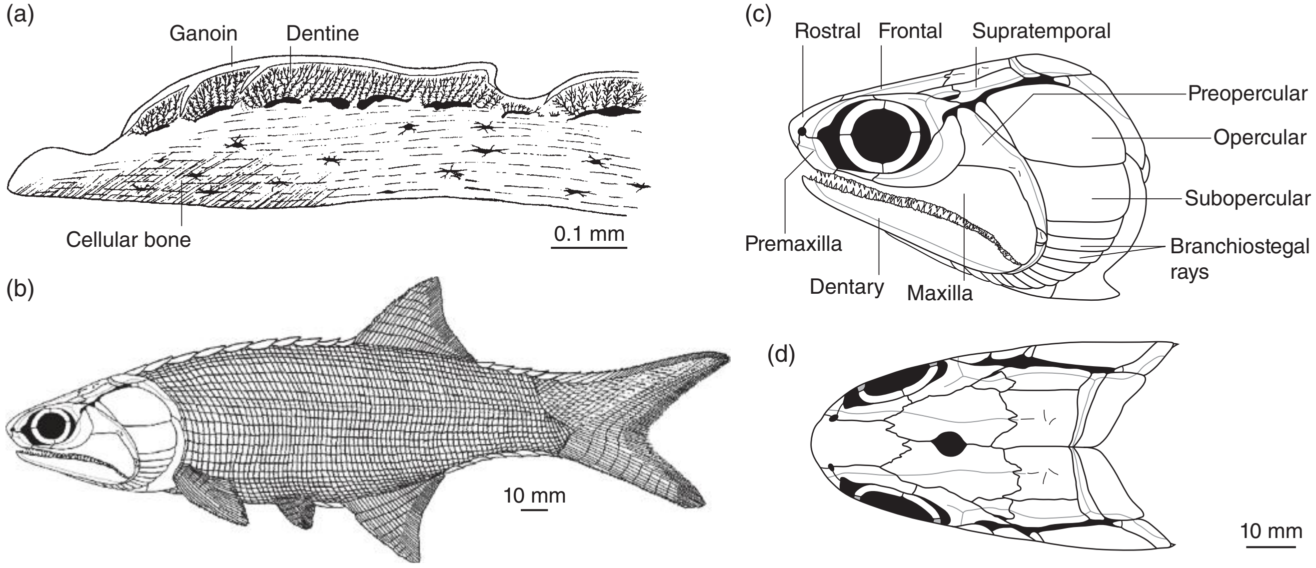


Figure 7.5 Anatomy of *Mimipiscis toombsi*, a basal actinopterygian from the Late Devonian: (a) cross-section of a scale, showing ganoin, a tissue that characterizes actinopterygians; (b–d) body (b) and skull, in lateral (c) and dorsal (d) views. Source: B. Choo, Institute for Vertebrate Paleontology and Paleoanthropology, Beijing, China. Reproduced with permission.

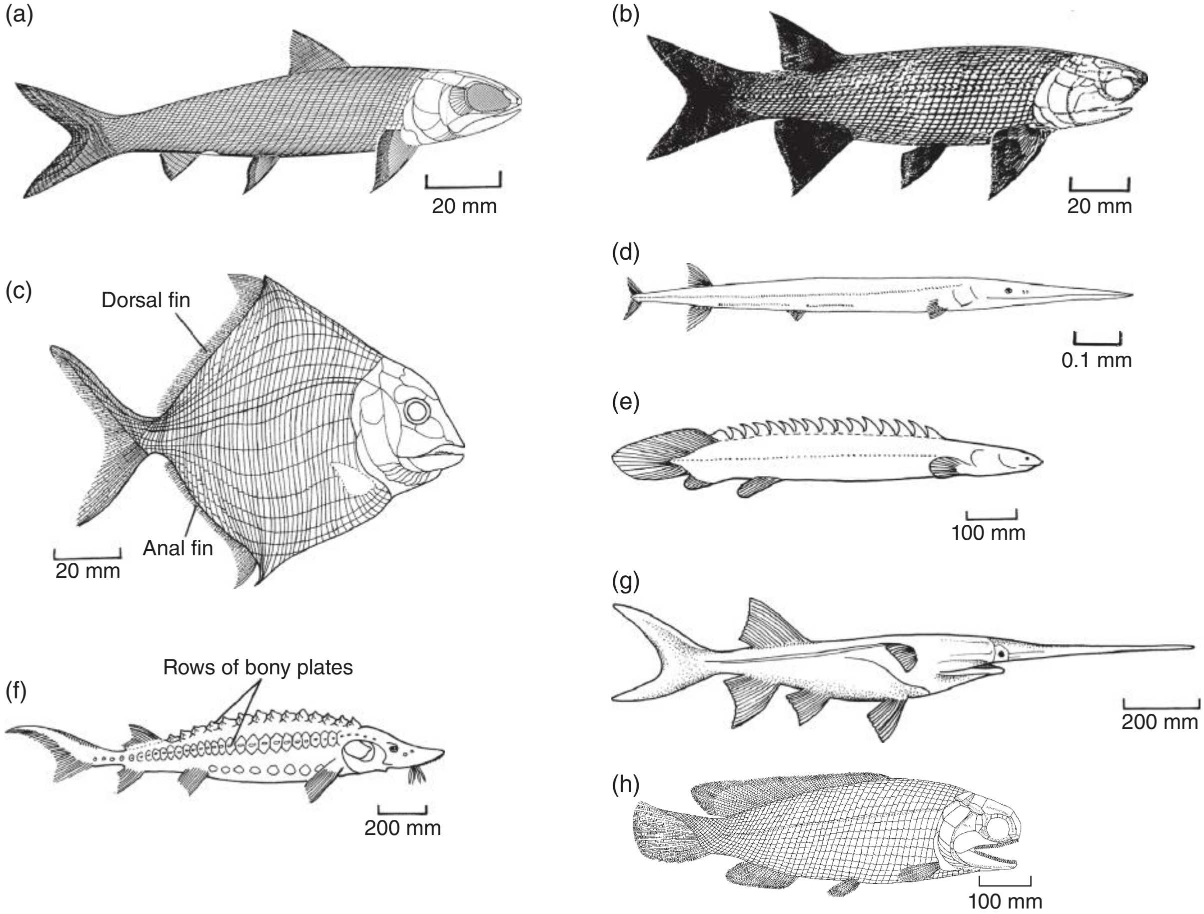


Figure 7.6 Basal actinopterygians from the Carboniferous (c), Triassic (a, b, d) and extant (h): (a) the ptycholepid *Ptycholepis*; (b) the redfieldiid *Redfieldius*; (c) the amphicentrid *Amphicentrum*; (d) the saurichthyid *Saurichthys*; (e) the bichir *Polypterus*; (f) the sturgeon *Acipenser*; (g) the paddlefish *Polyodon*; (h) the scanilepiform *Beishanichthys*. Source: (a) Adapted from Schaeffer *et al.* (1975). (b) Adapted from Schaeffer and McDonald (1978). (c,e,f) Adapted from Nicholson and Lydekker (1889). (d) Adapted from Rieppel (1985). (g) Adapted from Stahl (1974). (h) Xu and Gao (2011). Reproduced with permission from John Wiley & Sons.

especially in the freshwater lakes of the Newark Supergroup (Late Triassic to Early Jurassic) of eastern North America (Schaeffer and McDonald, 1978). *Amphicentrum*, an amphicentrid from the Carboniferous (Figure 7.6(c)) is deep-bodied and compressed from side to side. The dorsal and anal fins are very long and the paired fins tiny. *Amphicentrum* has flattened teeth consolidated into a beak and tooth plates that presumably were used for crushing hard-shelled prey. Other members of this clade, such as the Permian dorypterids, were also deep-bodied, and had elongate dorsal fins.

The Permo-Triassic mass extinction marked the end of certain of these early actinopterygian clades, including many that were traditionally called ‘palaeonisciforms’, and there was a remarkable diversification of ray-finned fishes in the Early and Middle Triassic. New materials from South China show the remarkable extent of this Triassic explosion of ray fins (Benton *et al.*, 2013; see Box 7.5). These form an unnamed clade (‘I’ in Box 7.4) whose members share additional supraorbitals and a keystone-shaped dermosphenotic, characters shared with the neopterygians. This clade in turn divides into two major subclades, the Chondrostei and the Neopterygii. Of some twenty lineages that radiated in the Triassic, five key groups are selected here.

Among Chondrostei, the birgeriids (Romano and Brinkmann, 2009) are known from the Triassic and Early Jurassic; they were large, up to 2 m long and equipped with massive jaws and teeth. The saurichthyiforms such as *Saurichthys* (Figure 7.6(d)) were elongate fishes, up to 1 m long, with the dorsal and anal fins set well back and close to the tail (Rieppel, 1985; Wilson *et al.*, 2013). These were highly successful fishes, known from the latest Permian, and radiating as 30 or more species that were exceptionally abundant in the Early and Middle Triassic of central Europe and southern China. The jaws are narrow and long, and many species of *Saurichthys* were probably ambush predators adapted for rapid bursts of swimming when it leapt at its prey, whereas others adopted different feeding strategies, some even feeding on shellfish (Wu *et al.*, 2011). The third extinct chondrostean family is the Chondrosteidae (Hilton and Forey, 2009), comprising two genera, *Chondrosteus*, ranging from 0.5–1 m in length, and the enigmatic *Gyrosteus*, known only from isolated bones, and supposedly 6–7 m long. These two taxa occur in the marine Early Jurassic of Europe, and they are members of the chondrostean subclade Acipenseriformes.

Living representatives of two phases of these basal actinopterygian radiations are the polypterids and the acipenseriforms (see Box 7.4). The bichirs, Polypteridae, are heavily armoured fishes (Figure 7.6(e)) that live in the streams and lakes of tropical Africa, and famous as so-called 'living fossils' that evolved slowly and at low diversity (Near *et al*., 2014). Their dorsal fin runs the whole length of the body and is divided into finlets, each with a spine at the front. The acipenseriforms (Hilton *et al*., 2011) comprise several extinct subclades, including the Chondrosteidae, as well as the extant acipenserids and polyodontids. The 25 living species of sturgeons, Acipenseridae, are large fishes, 1–6 m long, that live in northern waters and are the source of commercial caviar, their eggs. Sturgeons have very poorly ossified endoskeletons and the scales are reduced to five rows of large bony plates (Figure 7.6(f)). The two species of paddlefishes, Polyodontidae, have long flat snouts that are about one-third of the total length of up to 3 m and they feed by straining plankton out of the water (Figure 7.6(g)).

The final actinopterygian clade to notice here are the scanilepiforms, until recently a rather obscure Triassic clade, known from freshwater environments of Eurasia and North America, with some marine forms from the Late Triassic of Europe. Scanilepiforms possess a long-based dorsal fin, and study of *Beishanichthys* from the Early Triassic of China (Fig. 7.6(h)) shows that these short-snouted, rather large (0.5–0.7 m long) fishes are sister group to the Neopterygii, or indeed basalmost Neopterygii (Xu and Gao, 2011).

7.3.3 The basal neopterygian radiation

A major new actinopterygian clade, Neopterygii, arose in the Late Carboniferous and radiated through the Mesozoic and Cenozoic. The earliest neopterygians, including *Discoserra* from the Early Carboniferous of Bear Gulch, Montana, USA (see Box 7.1) and *Brachydegma* from the Late Carboniferous of Texas and Early Permian of Oklahoma, USA were somewhat isolated forms, and there is no evidence for a major diversification in the Palaeozoic (Hurley *et al*., 2007; Sallan, 2014). The substantial radiation of neopterygians in the Triassic was probably part of the burst of diversification following the Permo-Triassic mass extinction. Neopterygians are diagnosed by major modifications to the feeding apparatus (see Section 7.3.4, below) and tail. In the tail, the terminal portion of the backbone is reduced and the tail-fin rays are symmetrical above and below. The scales covering the body became thinner and flexible in many lineages and changed from a rhomboid to a circular, or cycloid, shape. There are five main groups of neopterygians, a number of Triassic lineages (see Box 7.6), the clade comprising gars and semionotids, the bowfins, further Mesozoic lineages, and the teleosts.

BOX 7.5 LUOPING AND THE EXPLOSION OF TRIASSIC FISHES

There has always been a problem in documenting the diversification of fishes following the Permo-Triassic mass extinction because of a poor record in the latest Permian and earliest Triassic. It seems that many groups went extinct at the end of the Permian, and many new groups emerged in the Triassic, but the timing is hard to determine (Friedman and Sallan, 2012). Spectacular new fossil finds in South China are helping to resolve this question, even though remains of cartilaginous and bony fishes across the Permian-Triassic boundary are still scrappy.

One of the most spectacular finds has been the Luoping biota, a remarkably diverse and well preserved fauna, found around the city of Luoping in Yunnan Province, in Member II of the Guanling Formation. This is dated as mid-Anisian, some 8 Myr after the Permo-Triassic mass extinction. The biota includes arthropods as the commonest fossils (90% of finds), followed by fishes (4%), marine reptiles, bivalves, gastropods, echinoderms, brachiopods, conodonts, foraminifers, and plants (Hu *et al*., 2011; Benton *et al*., 2013). So far, nearly 20,000 individual macrofossils have been identified from the Luoping biota in its main location through detailed bed-by-bed excavation.

The fishes reported so far include two new species of coelacanths, one, *Luopingcoelacanthus eurylacrimalis*, containing two embryos within the mother fish (see Section 3.9.3). The dominant fish taxa are actinopterygians, with 14 new species named so far, including mostly representatives of Perleidiformes and Saurichthyidae. Indeed there were eight species within three genera of saurichthyids lurking and hunting in the shallow Luoping seas. There are also five neopterygians, *Gymnoichthys*, *Kyphosichthys*, *Luoxiongichthys*, *Marcopoloichthys*, and *Sangiorgioichthys*. This was the real surprise of Luoping, that such an early fish fauna included so many neopterygians, an expansion that had been thought to begin mainly in the Late Triassic.

Although this fish assemblage dates from long after the beginning of the Triassic, it represents more-or-less the full recovery of life in the sea, with a full diversity of feeding modes and a complex trophic system, from burrowing seabed organisms through to large predatory reptiles (ichthyosaurs, thalattosaurs, sauropterygians; see Box 6.2). Earlier, less rich fish faunas from the Early Triassic help fill the gaps and point to the shape of the diversification of actinopterygians. In addition, because some twenty major actinopterygian lineages are represented at Luoping or in rocks of similar age from South China, these can be tracked back in the cladogram to show that nearly all of these emerged after the mass extinction in a phase of explosive radiation.

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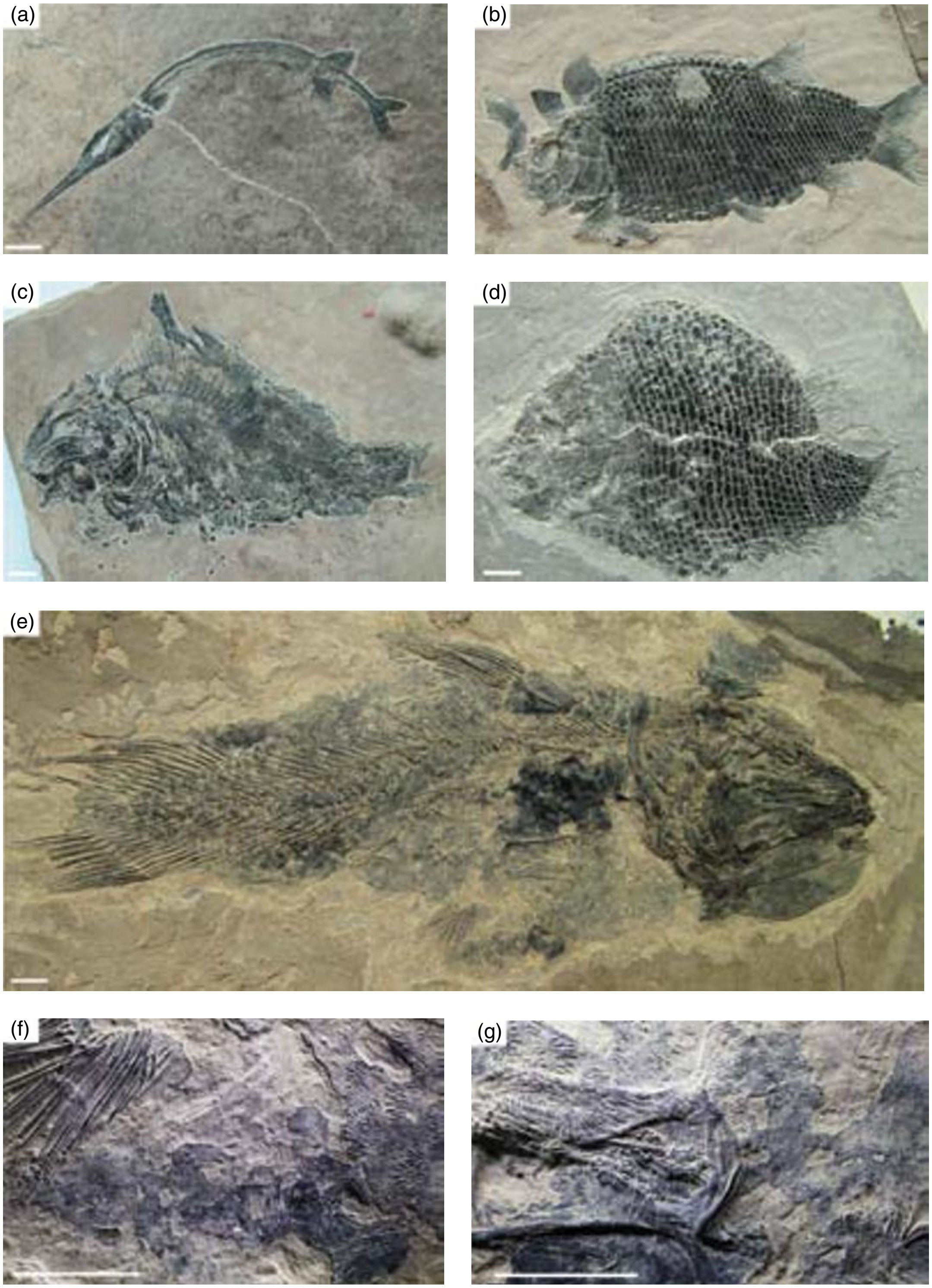
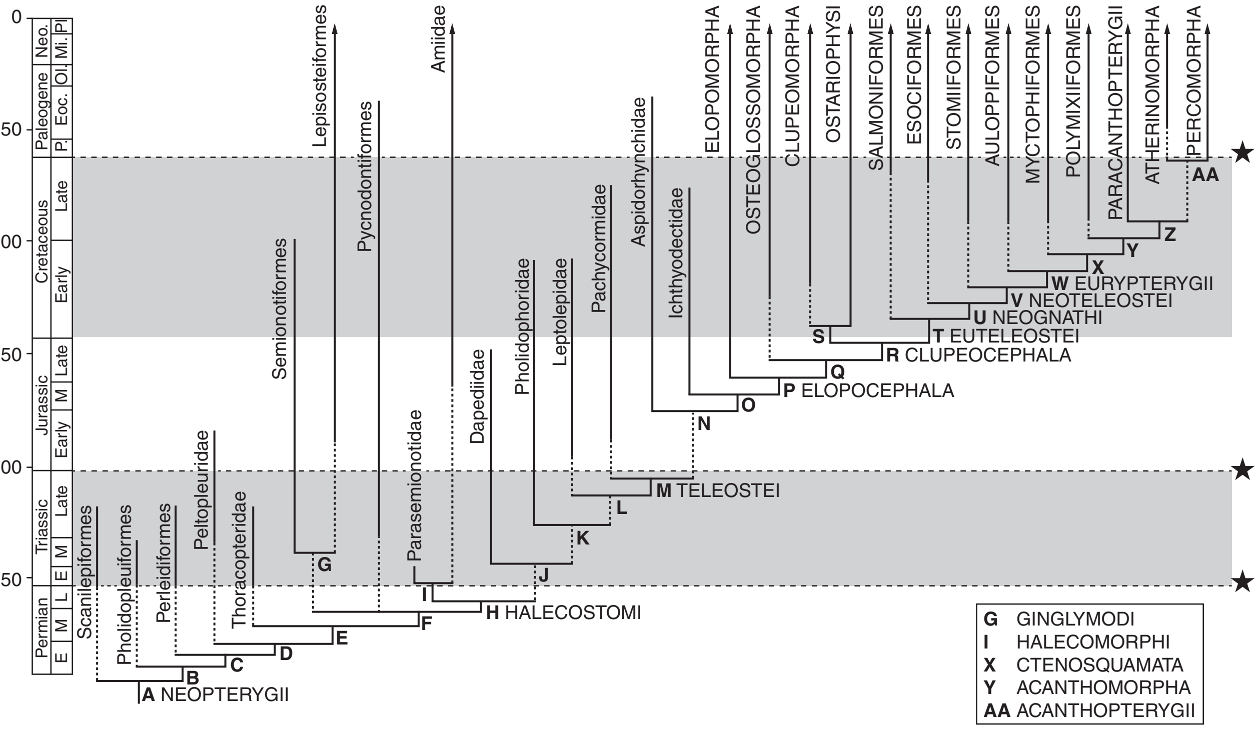


Some actinopterygians from Luoping: (a) the saurichthyid *Sinosaurichthys minuta;* (b) the perleidiform *Luopingichthys bergi;* (c) the neopterygian (basal halecomorph) *Luoxiongichthys hyperdorsalis;* (d) the neopterygian (basal ginglymodian) *Kyphosichthys grandei*; (e–g) the coelacanth *Luopingcoelacanthus eurylacrimalis*, mother (e), and her embryo 1 (f) and embryo 2 (g). Scale bar is 10 mm. See Colour plate 7.1. Source: W. Wen and S. Hu, China Geology Center, Chengdu, China. Reproduced with permission.

BOX 7.6 RELATIONSHIPS OF NEOPTERYGII

The Neopterygii are a vast and diverse group and their phylogeny has been much debated; indeed, the clade became a key testing ground in the early development of cladistic methods. In outline, the basal neopterygians, formerly termed ‘holosteans’, are generally regarded as forming a series of outgroups to the Teleostei. New phylogenetic analyses, incorporating spectacular new fossils form the Triassic of China (e.g. Xu and Gao, 2011; López-Arbarello, 2012; Xu *et al*., 2013) show considerable agreement over the ordering of major clades on non-teleost neopterygians

The succession of taxa within Teleostei has been explored through substantial phylogenomic work since 2000, and it turns out that the broad outlines are the same as had been established from earlier morphological cladistic analyses (e.g. Patterson and Rosen, 1977; Lauder and Liem, 1983; Johnson and Patterson, 1996). Morphological (Johnson and Patterson, 1996; Wiley and Johnson, 2010) and molecular (Nakatani *et al*., 2011; Near *et al*., 2012; Betancur-R. *et al*., 2013; Chen *et al*., 2013; Sallan, 2014) analyses show that, among living clades, Elopomorpha and Osteoglossomorpha are basal clades, followed by Clupeomorpha and Ostariophysi, which pair as the clade Otocephala. The remainder of teleosts are well characterized as the clade Euteleostei (= Euteleostomorpha). The sequence of euteleost taxa, as shown here, represents a broad consensus, but there are differences in recent molecular phylogenies. For example, Near *et al.* (2012) and Betancur-R. *et al.* (2013) find that Salmoniformes and Esociformes form a clade rather than occurring as distinct clades along the stem to Neoteleostei, and they resolve relationships within the crown clade, Percomorpha, to a much greater degree than had been possible before.



Cladogram showing relationships of the derived ray-finned bony fishes (Neopterygii), based on synapomorphies from Patterson and Rosen (1977), Lauder and Liem (1983), Johnson and Patterson (1996), Nakatani *et al*. (2011), Xu and Gao (2011), Betancur-R. *et al*. (2013), Chen *et al*. (2013), and Xu *et al*. (2013). See Box 7.4 for context of Neopterygii. Synapomorphies: **A NEOPTERYGII**, maxilla and preopercular not in contact with palatoquadrate, maxilla mobile, maxilla with peg-like anterior head, interopercular present, four or more infraorbitals, quadratojugal forms brace for quadrate, symplectic present, upper pharyngeal dentition consolidated, presence of coronoid process, fin rays equal in number to their supports in the dorsal and anal fins, posterior margin of caudal fin unforked, clavicle lost or reduced to a small plate lateral to cleithrum; **B**, median neural spines, quadratojugal lost or fused with quadrate; **C**, vomer median; **D**, large median vomer, coronoid process on mandible, axial lobe of tail reduced; **E**, symmetrical tail fin; **F HALECOSTOMI**, a supramaxilla, quadratojugal absent as independent element; **G HALECOMORPHI (= HOLOSTEI)**, symplectic and quadrate bones both contribute to jaw articulation; **H TELEOSTEI**, mobile premaxilla, unpaired basibranchial toothplates, uroneurals (elongate ural neural arches) present; **I**, median tooth plate covers basibranchials 1–3; **J**, enamel layer lost from most skull bones, cycloid scales; **K**, vertically keeled rostrum, prearticular element in lower jaw absent, no enamel layer on skull bones, nine or fewer hypurals; **L**, spiracular canal greatly reduced, loss of separate surangular bone and appearance of retroarticular, three epurals; **M**, four pharyngobranchials, three hypobranchials; **N ELOPOCEPHALA**, two uroneurals extend anteriorly over the second ural centrum; **O CLUPEOCEPHALA**, endopterygoid teeth absent, uroneural 1 extends forward to preural 2; **P OTOCEPHALA**, epicentrals ossified, hypural 2 and ural centrum 1 fused, extrascapulars and parietals fused; **Q EUTELEOSTEI**, supraneurals develop in pattern 2, membranous anterodorsal outgrowth of uroneural 1 present, caudal median cartilages present; **R NEOGNATHI**, tooth attachment type 4 (hinged), third uroneural absent, cheek and operculum scaled; **S NEOTELEOSTEI**, rostral cartilage, ’type-4’ tooth attachment; **T EURYPTERYGII**, reduction of second preural neural spine to a half-spine, fusion of a toothplate to third epibranchial; **U CTENOSQUAMATA**, reduction or loss of pharyngobranchial four; **V ACANTHOMORPHA**, true dorsal and anal fin spines, rostral cartilage, median caudal cartilages absent, medial pelvic process ossified distally; **W**, well-developed ctenoid scales, expansion of ascending and articular premaxillary processes; **X ACANTHOPTERYGII**, enlargement of epibranchials two and three. Abbreviations: E, Early; Eoc, Eocene; L, Late; M, Middle; Mi, Miocene; Neo, Neogene; Ol, Oligocene; P, Paleocene; Pl, Pliocene/ Pleistocene. Dashed lines and star symbols indicate extinction events.

The pholidopleuriforms, such as *Pholidopleurus* from the Middle Triassic of Switzerland (Figure 7.7(a), were slender fishes with large rectangular flank scales (Bürgin, 1992). The perleidiforms, also best known from the Triassic, include mainly small fishes, some such as *Perleidus* (Figure 7.7(b)) with slender bodies, and others such as *Cleithrolepis* (Figure 7.7(c)) with deep bodies. These fishes, as well as contemporary peltopleurids and pholidopleuriforms, had nearly symmetrical tail fins, although the internal skeleton, the backbone, still bent upwards in the primitive heterocercal style. The perleidiforms and some of the other Triassic relatives, such as the peltopleurids, are stem groups of more derived actinopterygians, as suggested by some modifications to the jaws and the increasing symmetry of the tail (see Box 7.6). A final basal neopterygian clade are the Thoracopteridae, remarkable for being the first flying fish (see Box 7.7).

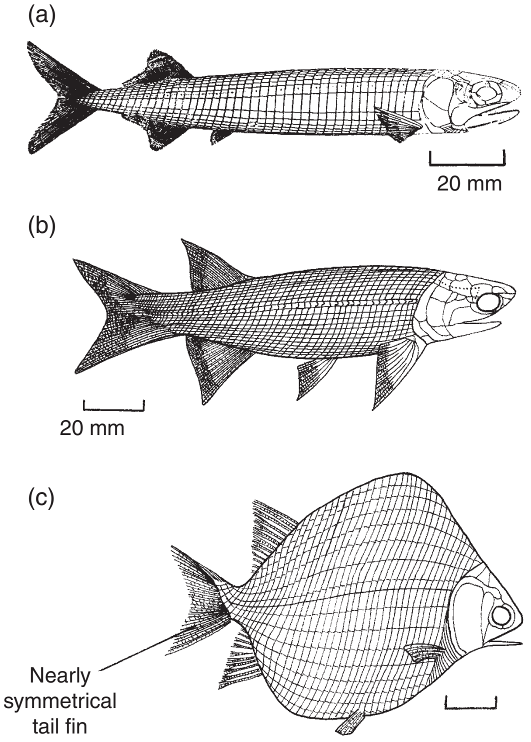


Figure 7.7 Basal neopterygians, from the Triassic (a–c): (a) the pholidopleuriform *Pholidopleurus*; (b) the perleidiform *Perleidus*; (c) the perleidiform *Cleithrolepis*. Source: (a) Adapted from Bürgin (1992). (b,c) Adapted from Lehman (1966).

The gars and semionotiforms, the clade Halecomorphi (=Holostei), also emerged in the Early Triassic, but were most diverse in the Jurassic and Cretaceous (Cavin, 2010; López-Arbarello, 2012; Xu and Wu, 2012). The gars, Lepisosteidae, consist of two genera that live today in North and Central America and Cuba. *Lepisosteus* (Figure 7.8(a)), a 1–2 m predatory fish, lives in warm-temperate fresh and brackish waters of North America. It has long jaws and captures its prey by lunging and grasping with its long needle-like teeth. The genus *Lepisosteus* has been traced back to the Cretaceous, and is a good example of a **living fossil**, an apparently slowly evolving lineage that has generally remained at low diversity. Gars were formerly more widely distributed, occurring in the Cretaceous and Early Tertiary of North and South America, Europe, Africa and India, but their distribution has since shrunk.

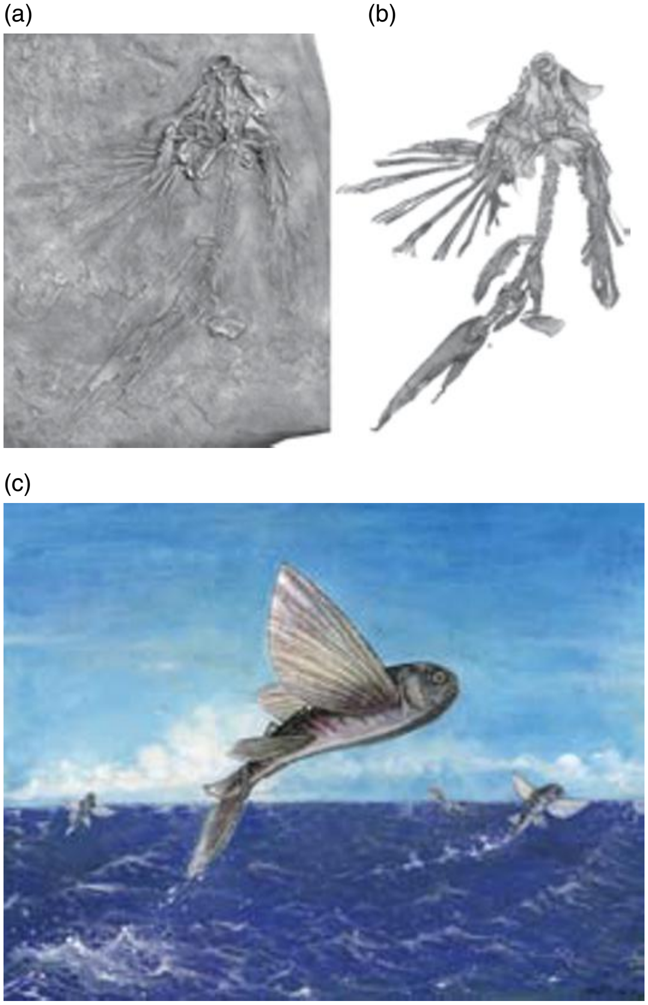
The Semionotiformes includes about 25 genera of small, actively swimming fishes, such as *Semionotus* (Figure 7.8(b)), that have nearly symmetrical tails and large dorsal and ventral fins. The tooth-bearing elements, the maxilla and dentary, project well forwards and they are lined with small sharp teeth. Semionotiforms occur in great diversity in some areas, such as the Newark Group (Late Triassic and Early Jurassic) lakes of the eastern seaboard of North America, where they appear to have

BOX 7.7 THE FIRST FLYING FISH

For many years, palaeontologists had been aware of a rather small basal neopterygian clade, the thoracopterids, known exclusively from the Late Triassic of Austria and Italy. Since their first discovery in 1906, they had been identified as flying fish. A new find from the Middle Triassic of China extends the known geographic and stratigraphic range of the family, and this animal had remarkable adaptations for gliding flight seen in the group.

The new thoracopterid, *Potanichthys*, comes from the Xingyi biota in Guizhou Province, South China, one of the four or five exceptional faunas of marine vertebrates in the region (see Box 6.2). *Potanichthys* is a rather short fish, about 15 cm long, with an enlarged head, a long slender tail, but importantly, much expanded fins (see Illustration). Both the pectoral and pelvic fins are enlarged when compared to those of close relatives (e.g. Figure 7.7(a–c)), and this feature had been noted in other thoracopterids by the great Austrian palaeontologist, Othenio Abel in 1906. The pectoral fins are more than 40%, and the pelvic fins are 20% of total body length. These, in conjunction, provided an aerodynamic design for the gliding thoracopterid rather like a World War I biplane, in which both sets of fins were probably held out horizontally as the animal leapt from the water, and each pair acted as an aerofoil system to keep it aloft for some considerable distance. Other adaptations for flight are the powerful tail, used to propel the fish out of the water, and the substantial loss of scales, which reduced weight and allowed greater flexibility of the body in powering itself up and out of the water.

Why would a fish fly? Almost certainly, just like the flying teleost fishes today, the Exocoetidae, the Triassic Thoracopteridae used the adaptation as a means of escaping predators. The Xingyi biota included the voracious saurichthyid fishes and giant 2-m long birgeriids, as well as predatory reptiles, including tiny pachypleurosaurs, and larger ichthyosaurs, nothosaurs, and thalattosaurs. This early experiment with fishy flying did not last long, and other relatives presumably escaped predation by fast manoeuvering underwater.



The Triassic flying fish, *Potanichthys xingyiensis*. (a,b) The holotype specimen in ventral view, showing the hugely expanded right pectoral fin stretched out to the side, photograph and drawing. (c) Restoration of the possible life appearance of *Potanichthys*. Source: (a,b) Xu *et al*. (2013). Reproduced with permission of the Royal Society. (c) F. Wu and K. Gao, Institute for Vertebrate Paleontology and Paleoanthropology, Beijing, China. Reproduced with permission.

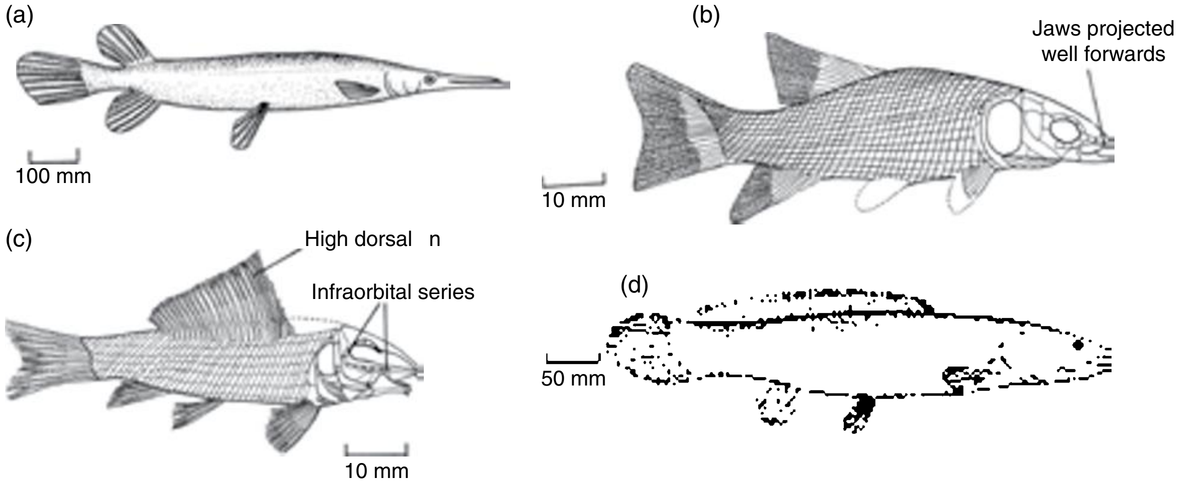


Figure 7.8 The diversity of basal neopterygians, dating from the Triassic (b), Jurassic (c) and recent (a,d): (a) the gar *Lepisosteus*; (b) the semionotid *Semionotus*; (c) the macrosemiid *Macrosemius*; (d) the bowfin *Amia*. Source: (a,d) Adapted from Goode and Bean (1895). (b) Adapted from Schaeffer and Dunkle (1950). (c) Adapted from Bartram (1977).

formed species flocks, in which numerous species lived together, each distinguished by body shape and the midline dorsal scales. Similar species flocks are seen today among cichlid teleost fishes, where every lake in the African rift valley contains its own set of species. Among the semionotiforms, the macrosemiids of the Triassic to Cretaceous were small fishes (Figure 7.8(c)) often with a long high dorsal fin. They have some unusual bones in the skull, a series of seven rolled little bones beneath the orbit (the infraorbitals) and two tubular infraorbitals behind it.

The remaining actinopterygians belong to the clade Halecomorphi, which is divided into two clades, the Halecostomi and the Teleostei and their stem members (see Box 7.6). Halecomorphs are diagnosed by a specialized jaw joint involving an additional ventral element, the **symplectic**, as well as the quadrate (see Section 7.3.4). Basal halecostomes include the parasemionotids of the Triassic, which were small fishes with large eyes and neopterygian jaw patterns. Their closest relatives include the modern bowfin, *Amia* (Figure 7.8(d)), which lives in freshwaters of North America, where it is an active predator on a wide variety of organisms ranging in size up to its own body length of 0.5–1.0 m. Amiids were formerly diverse and have shown slow evolution (Grande and Bemis, 1998).

7.3.4 Jaws and feeding in bony fishes

Amia illustrates an intermediate kind of jaw apparatus between that of the early actinopterygians and the teleosts. In the skull of *Amia* (Figure 7.9(a)) the jaws are relatively shorter than in basal actinopterygians (cf. Figure 3.19(d,e)). The maxilla is highly

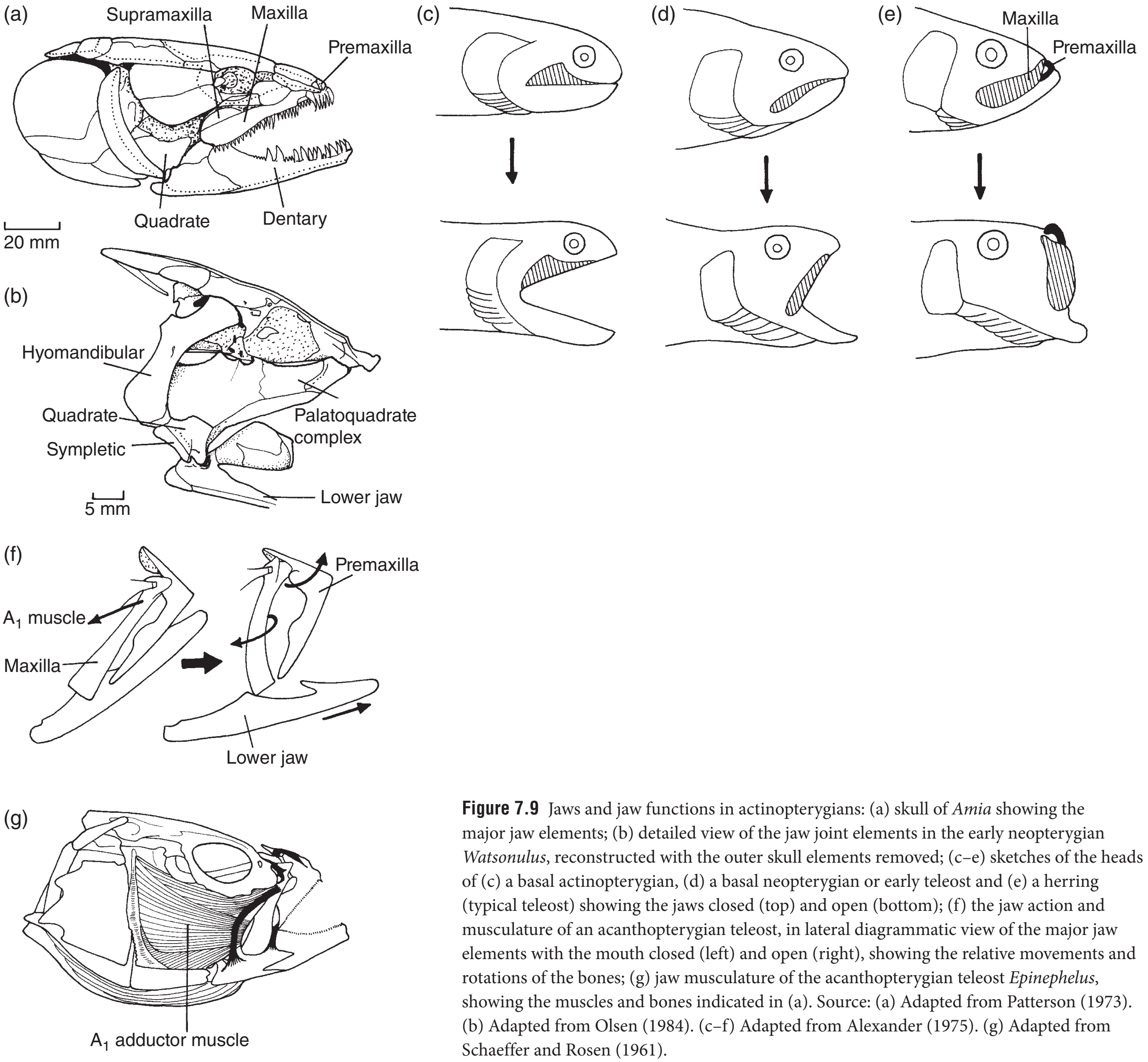


Figure 7.9 Jaws and jaw functions in actinopterygians: (a) skull of *Amia* showing the major jaw elements; (b) detailed view of the jaw joint elements in the early neopterygian *Watsonulus*, reconstructed with the outer skull elements removed; (c–e) sketches of the heads of (c) a basal actinopterygian, (d) a basal neopterygian or early teleost and (e) a herring (typical teleost) showing the jaws closed (top) and open (bottom); (f) the jaw action and musculature of an acanthopterygian teleost, in lateral diagrammatic view of the major jaw elements with the mouth closed (left) and open (right), showing the relative movements and rotations of the bones; (g) jaw musculature of the acanthopterygian teleost *Epinephelus*, showing the muscles and bones indicated in (a). Source: (a) Adapted from Patterson (1973). (b) Adapted from Olsen (1984). (c–f) Adapted from Alexander (1975). (g) Adapted from Schaeffer and Rosen (1961).

mobile and a new element, the supramaxilla, is attached to it. This mobile maxilla hinges at the front and can swing out some way to the side. This is associated with changes to the main jaw joint between the lower jaw and an internal unit composed of the hyomandibular, symplectic (another new element) and palatoquadrate, termed the jaw suspensorium (Figure 7.9(b)). When the jaws of a neopterygian open, the cheek region of the skull expands sideways, which gives a sucking effect, efficient at drawing in small particles of food or prey animals.

The heads of basal actinopterygians, basal neopterygians, and teleosts show three rather different sets of jaw opening adaptations (Figure 7.9(c–e)). Basal actinopterygians opened their jaws in a wide 'grin', suitable for grabbing large prey, whereas most neopterygians protrude their jaws forwards and the open mouth is roughly circular (Schaeffer and Rosen, 1961; Westneat, 2004). This protrusion is most marked in derived teleosts, where the sudden opening of the mouth produces a suction effect. The jaw-closing action is equally important. When the tube-like teleost mouth is closed by pulling the lower jaw and maxilla back, the food is retained, whereas simple closure by raising the lower jaw could blow some of the food out again.

Derived teleosts, the Neoteleostei (see Section 7.4.5), show a further modification of the jaw apparatus. The maxilla loses its role as the main tooth-bearing element in the upper jaw and the enlarged premaxilla takes over, whereas the maxilla acts as a lever, pushing the premaxilla forwards as the jaws open (Figure 7.9(f)). The maxilla is attached to the lower jaw and to the suspensorium. As the mouth opens, an anterior adductor muscle (Figure 7.9(g)) pulls the top of the maxilla back and the lower jaw is pushed forward. The maxilla also rotates slightly about its long axis and a process on the top of the maxilla, which interlocks with one on the premaxilla, causes the premaxilla to be protruded. This complexity and adaptability in the jaw apparatus may have had a substantial role in the dramatic diversification of derived teleosts in the Late Cretaceous and Cenozoic.

7.4 RADIATION OF THE TELEOSTS

The teleosts are an extremely diverse group of fishes, with some 30,000 living species that are classified in 40 orders (Nelson, 2006; Nelson *et al*., 2010; Sallan, 2014). This enormous diversity is clearly impossible to survey in detail and only the main groups are mentioned. The teleosts are diagnosed by modifications to the tail, which has a symmetrical (**homocercal**) appearance, but with the vertebral column not running into the upper lobe. Specialized elements, the **uroneurals**, run alongside the last caudal (ural) vertebrae and help support the upper lobe of the tail. In addition, teleosts have a mobile premaxilla, not seen in basal neopterygians, and some modifications to the jaw musculature. Living teleosts fall into four main clades, Osteoglossomorpha, Elopomorpha, Otocephala and Euteleostei. In addition, a series of extinct forms fall between the basal neopterygians and the stem lineage to the living teleost groups (see Box 7.6).

7.4.1 Teleost outgroups and basal teleosts

After the split of derived neopterygians into halecomorphs and the teleost total group, at about the beginning of the Triassic, a number of key lineages form a series of outgroups to Teleostei, and there is some semantic debate about whether any or all of these should be called teleosts or not. Further, their phylogenetic sequence is debated (Arratia, 1997, 2001, 2004; Hurley *et al*., 2007). Here, a broad outline is given for several of the more striking teleost stem groups, most of which died out in the Late Cretaceous (see Section 7.5), the dapediids, pycnodontiforms, pholidophorids, and leptolepids (see Box 7.6).

The dapediids, formerly regarded as relatives of the semionotids, were deep-bodied fishes of the Triassic and Jurassic. The pycnodontiforms, also of the Triassic to Eocene, are mostly deep-bodied forms with long dorsal and anal fins and a symmetrical (homocercal) tail fin. *Proscinetes* (Figure 7.10(a)) has an elongated snout and a pavement of crushing teeth on the upper and lower jaws that were used to crush molluscs or echinoderms, as indicated by their gut contents (Kriwet, 2001; Poyato-Ariza and Wenz, 2002). The pholidophorids of the Late Triassic and Early Jurassic (Arratia, 2013), such as *Oreochima* (Figure 7.10(b)), were small hunting fishes that show advances in the jaws: there are two supramaxillae, there is an additional tooth-bearing element, the **dermethmoid**, beside the tooth-bearing premaxilla and the quadratojugal is fused to the quadrate. The leptolepids of the Jurassic and Cretaceous (Arratia, 1997), such as *Varasichthys* (Figure 7.10(c)) were also small, often as little as 50 mm long, and they may have fed on plankton. These fishes have fully ossified vertebrae and the scales are **cycloid** (circular, thin and flexible).

The basal teleosts, the pachycormids and aspidorhynchids of the Jurassic and Cretaceous, have long bodies. One of the most astonishing pachycormids, *Leedsichthys* from the Middle Jurassic of England and France (Figure 7.11(a)), was a monstrous scaleless filter feeder up to 10 m in length (Martill, 1988; Liston *et al*., 2013). *Leedsichthys* had a huge branchial basket in the throat region, consisting of the ossified gill arches covered with gill rakers each bearing hundreds of teeth (Figure 7.11(b)). As the fish swam with its mouth gaping, water passed into the mouth and out through the gills, and plankton and small fishes were filtered out. New finds of pachycormids show that these large to very large bony fishes were ecological equivalents of modern filter-feeding whales for some 100 myr of the Middle Jurassic to Late Cretaceous (Friedman *et al*., 2010).

The aspidorhynchids, such as *Aspidorhynchus* (Figure 7.11(c)), were smaller and had long pointed snouts.

Another important extinct group, the ichthyodectids of the Jurassic and Cretaceous (Figure 7.11(d,e)), such as *Xiphactinus*, were mostly large predaceous fishes (Patterson and Rosen, 1977). They swallowed their prey head first, as is normal among predatory fishes. A specimen of *Xiphactinus* from the Late Cretaceous of Kansas, 4.2 m long, was found with a 1.6 m ichthyodectid in its stomach area, and smaller relatives have been found with as many as ten recognizable fish skeletons preserved inside.

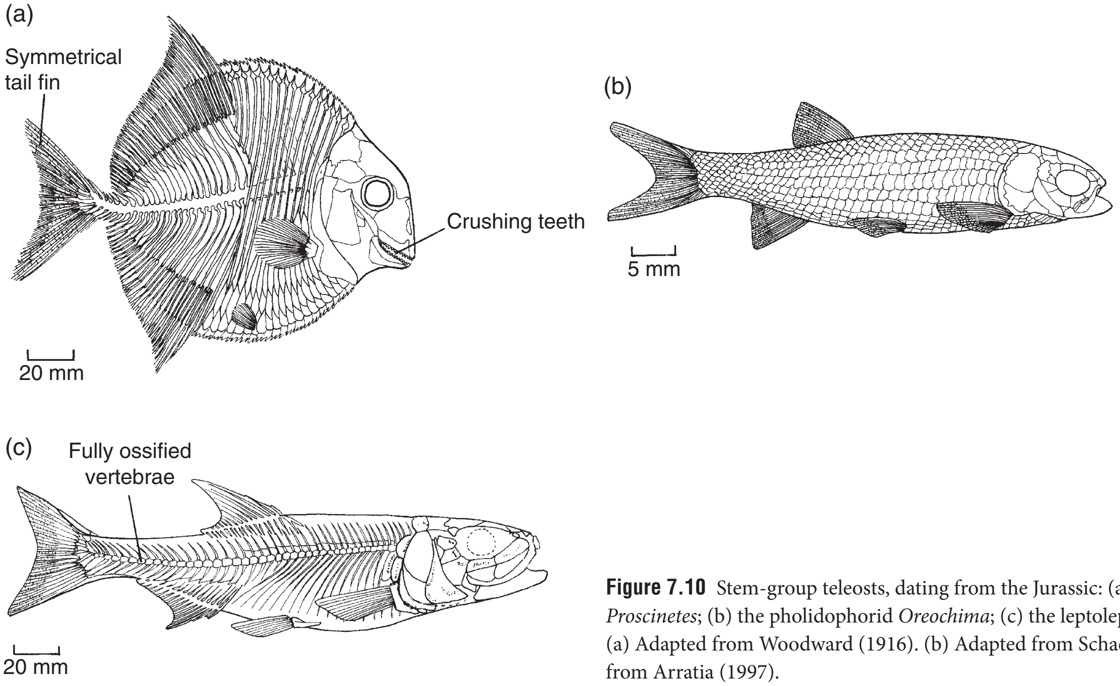


Figure 7.10 Stem-group teleosts, dating from the Jurassic: (a) the pycnodont *Proscinetes*; (b) the pholidophorid *Oreochima*; (c) the leptolepid *Varasichthys*. Source: (a) Adapted from Woodward (1916). (b) Adapted from Schaeffer (1972). (c) Adapted from Arratia (1997).

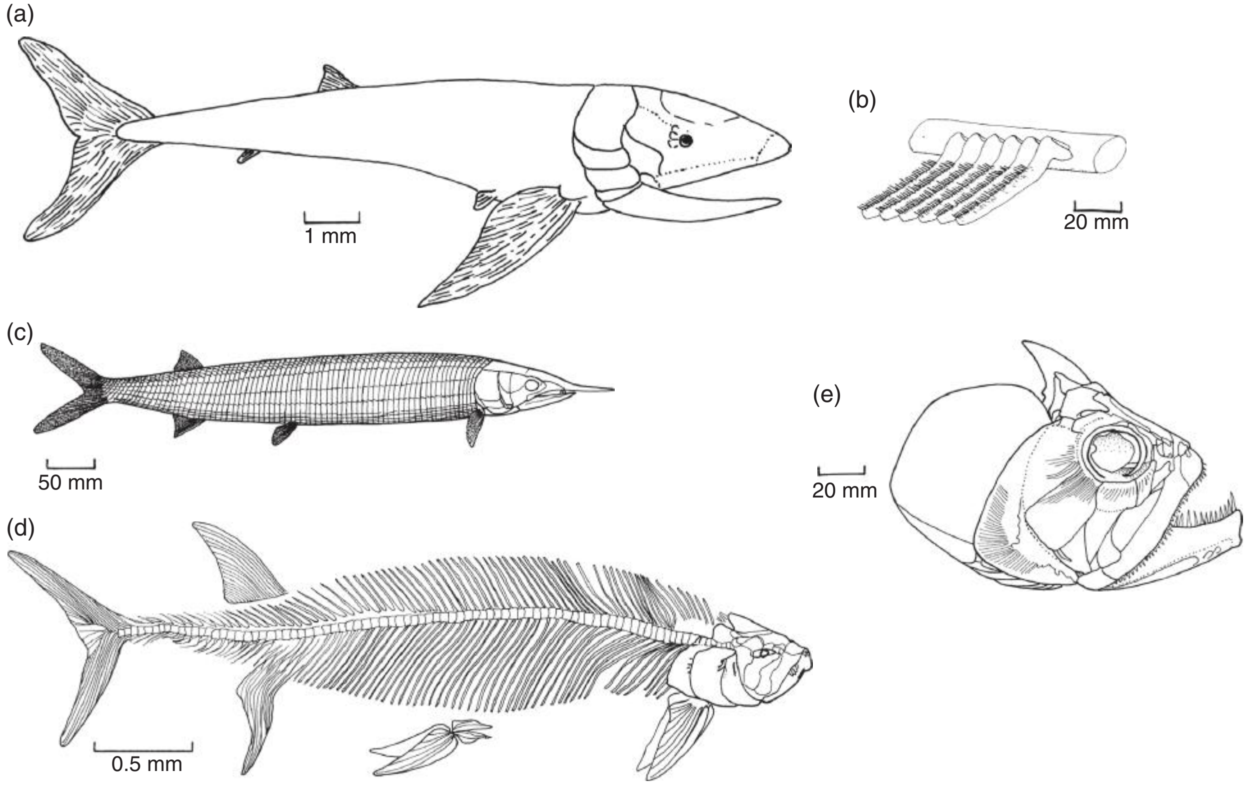


Figure 7.11 Basal teleosts from the Jurassic (a,b) and Cretaceous (c–e): (a) the giant pachycormid *Leedsichthys*; (b) gill rakers on the gill arches of *Leedsichthys*, probably used for filter-feeding; (c) the aspidorhynchid *Aspidorhynchus*; (d) the ichthyodectid *Xiphactinus*; (e) skull of the ichthyodectid *Cladocyclus*. Source: (a,b) Adapted from Martill (1988). (c) Adapted from Nicholson and Lydekker (1889). (d) Adapted From Osborn (1904). (e) Adapted from Patterson and Rosen (1977).

7.4.2 Elopomorpha: eels and relatives

The elopomorphs (literally 'eel forms') include about 800 species of eels, tarpons and bonefishes, and the group is known from the Early Cretaceous (Forey *et al*., 1996; Chen *et al*., 2014). The tarpon, *Megalops* (Figure 7.12(d)), is typically 'fish-shaped' and it seems hard to see how it can be regarded as a close relative of the eel, *Anguilla* (Figure 7.12(e)). All elopomorphs are diagnosed by a specialized marine larval stage, the leptocephalus (Figure 7.12(f)) that is thin and leaf-shaped. The leptocephalus larvae can passively migrate long distances before they metamorphose.

Eels have many skeletal modifications including overall elongation of the body, loss of the caudal fin, loss of the pelvic girdle, loss of ribs, fusion of elements in the upper jaw and loss of scales. The deep-sea eels called saccopharyngoids are even more modified, having lost many skull bones. Indeed the skull (Figure 7.12(g)) is really just a huge pair of jaws with a tiny cranium set in front. These fishes float quietly on the deep dark ocean floors and lever their huge mouths open to seize prey animals many times their own size.

7.4.3 Osteoglossomorpha: bony-tongued teleosts

The osteoglossomorphs, a relatively small group of about 200 species that live in freshwaters mainly of the southern hemisphere, arose possibly in the Late Jurassic (Hilton, 2003; Wilson and Murray, 2008). Living forms include *Osteoglossum* from South America (Figure 7.12(a)), which has posteriorly placed elongate dorsal and anal fins, and the elephant-snout fish *Mormyrus* from Africa (Figure 7.12(b)), which has electric organs in the tail region. Osteoglossiforms are diagnosed by features of the feeding system (Figure 7.12(c)), which have shifted the primary bite away from the maxilla and the lower jaw (Lauder and Liem, 1983). A bony element in the tongue and the basibranchial behind, bear large teeth that bite against teeth on the parasphenoid in the roof of the mouth (hence the name osteoglossomorph, which means 'bony-tongue-form').

7.4.4 Otocephala: herrings and carp

The Otocephala includes the Clupeomorpha and Ostariophysi, previously seen as distinct and successive outgroups to Euteleostei, but paired on the basis of morphological and molecular evidence (Johnson and Patterson, 1996; Peng *et al*., 2006; Chen *et al*., 2013; see Box 7.6).

The clupeomorphs comprise over 350 species of extant herring-like fishes and over 150 fossil species that date back to the Early Cretaceous (Lecointre and Nelson, 1996). They are generally small silvery marine fishes, some of which, like the herring (Figure 7.13(a)) and anchovy, occur in huge shoals and feed on plankton. Clupeomorph characters include a peculiar type of abdominal scute, an unusual arrangement of the bones at the base of the tail in which the first hypural has a free proximal end and the second hypural is fused to ural vertebra 1 (Figure 7.13(b)), and a specialized air sac system in most.

The clupeomorph air sac extends into the exoccipital and prootic bones in the braincase. Most bony fishes have a sausage-shaped air sac called the **swimbladder** in the body cavity that is used to achieve neutral buoyancy. Gas is pumped into the bladder, or removed via the bloodstream in order to match the

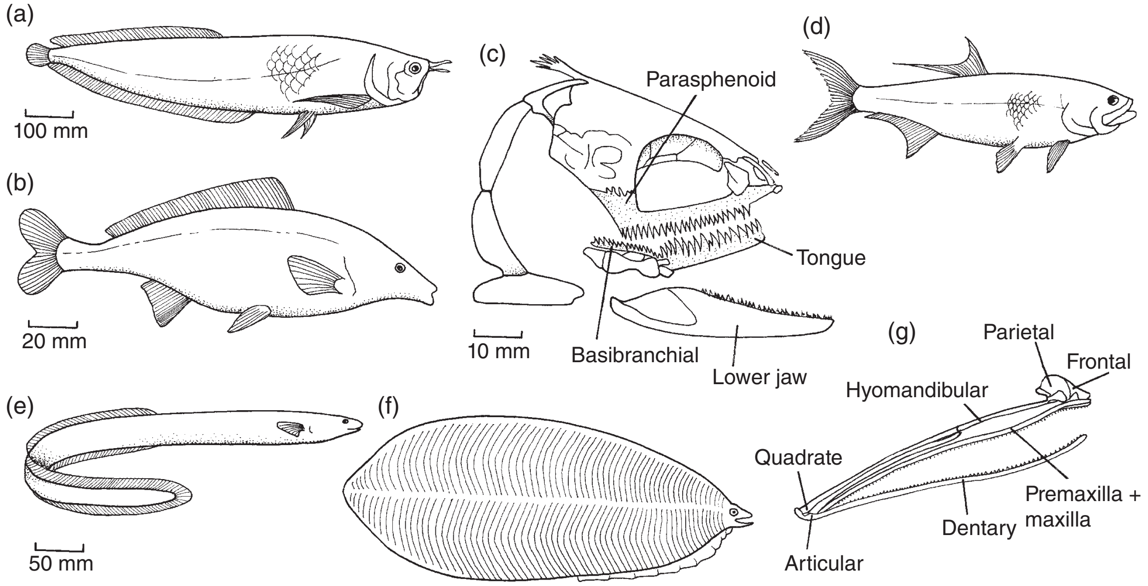


Figure 7.12 The osteoglossomorph (a–c) and elopomorph (d–g) teleosts; all extant: (a) *Osteoglossum*; (b) the elephant fish *Mormyrus*; (c) internal jaw system of *Hiodon*, showing toothed tongue and palate elements (lateral jaw bones removed); (d) the tarpon *Megalops*; (e) the eel *Anguilla*; (f) the leptocephalus larva of an elopomorph; (g) the skull of the saccopharyngoid eel *Eurypharynx*. Source: (a,b,d–f) Adapted from Greenwood *et al.* (1966). (c) Adapted from Lauder and Liem (1983). (g) Adapted from Gregory (1933).

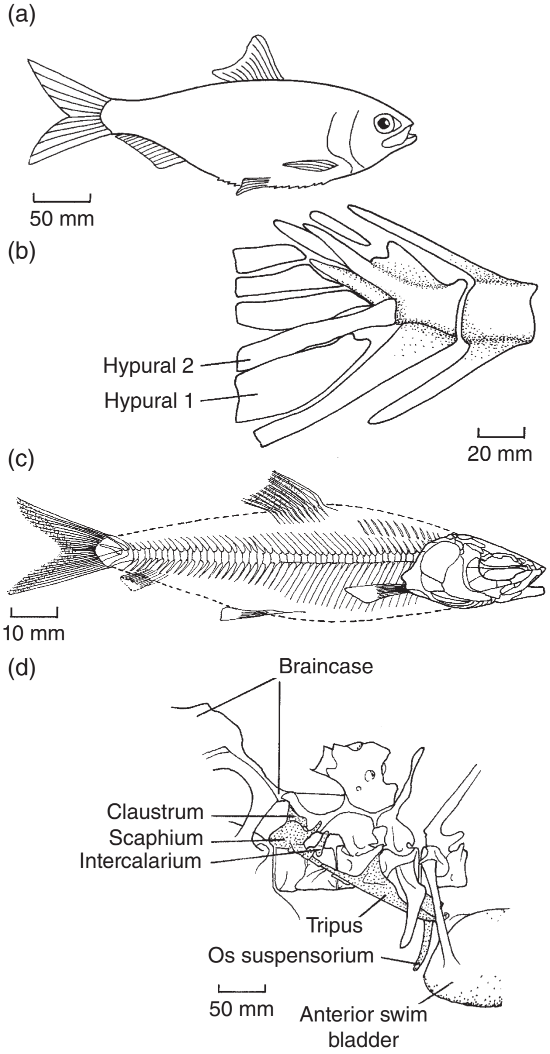


Figure 7.13 The otocephalan teleosts, clupeomorphs (a–c) and ostariophysan (d): (a) the herring *Clupea*; (b) the tail of a clupeomorph, showing the hypural elements; (c) the Cretaceous clupeomorph *Ornategulum*; (d) the Weberian ossicles, which transmit vibrations from the swimbladder to the inner ear in ostariophysan fishes (ossicles are shaded and named). Source: (a) Adapted from Greenwood *et al.* (1966). (b) Adapted from Lauder and Liem (1983). (c) Adapted from Forey (1973). (d) Adapted from Fink and Fink (1981).

'weight' of the fish to the pressure that acts at whatever depth it finds itself. In clupeomorphs, the swimbladder has a unique extension into the braincase and enhances their hearing function by amplifying sounds.

Clupeomorphs assigned to the Ellimmichthyiformes arose in the Early Cretaceous and are not known past the early Oligocene. *Ornategulum* from the Late Cretaceous (Figure 7.13(c)), a possible early clupeomorph, was a small fish. Abundant herring-like fishes, *Knightia*, have also been found in the Eocene Green River Formation, often preserved in huge masses, suggesting that they lived in vast shoals, like modern herring-like fishes.

The Ostariophysi is a huge teleost clade, comprising almost 8000 species, over 25% of known fish species in the world, and they are present on all major continents except Antarctica. Typical forms include carp, goldfish, minnows, catfish and indeed most freshwater fishes (Fink and Fink, 1981, 1996; Mayden *et al.*, 2009; Chen *et al.*, 2013). They are diagnosed by several features, including a specialized hearing system composed of modified cervical vertebrae, ribs and neural arches, called the Weberian ossicles (Figure 7.13(d)). There are five key bony elements that are connected by ligaments and provide a link between the anterior swimbladder and the ear. The os suspensorium and the tripus rest on the taut surface of the swimbladder. When sound waves reach the fish, the swimbladder vibrates and the Weberian apparatus effectively amplifies the sound. The two bones in contact pivot and the vibrations pass via the intercalarium, scaphium and claustrum to the inner ear.

7.4.5 Euteleostei: salmon, pike and derived teleosts

The largest teleost group, the euteleosts, consists of over 22,000 species in 390 families. These may be divided into three main subgroupings, the salmoniforms, the esociforms and the neoteleosts (Lauder and Liem, 1983; Johnson and Patterson, 1996; Near *et al.*, 2012; Betancur-R. *et al.*, 2013). Some of these euteleost clades became enormously species-rich, especially in certain settings such as tropical reefs (see Box 7.8).

The Salmoniformes, some 220 species of smelts, salmon and trout, possibly includes the early form, the tiny *Gaudryella* from the mid-Cretaceous (Figure 7.14(a)). True salmon appeared only later. The Esociformes (López *et al.*, 2004) is a small group containing ten species of pike and mudminnows that date from the Late Cretaceous to the present. Pike appear primitive because their dorsal fin is set far back and appears symmetrical with the anal fin, as in saurichthyids and gars.

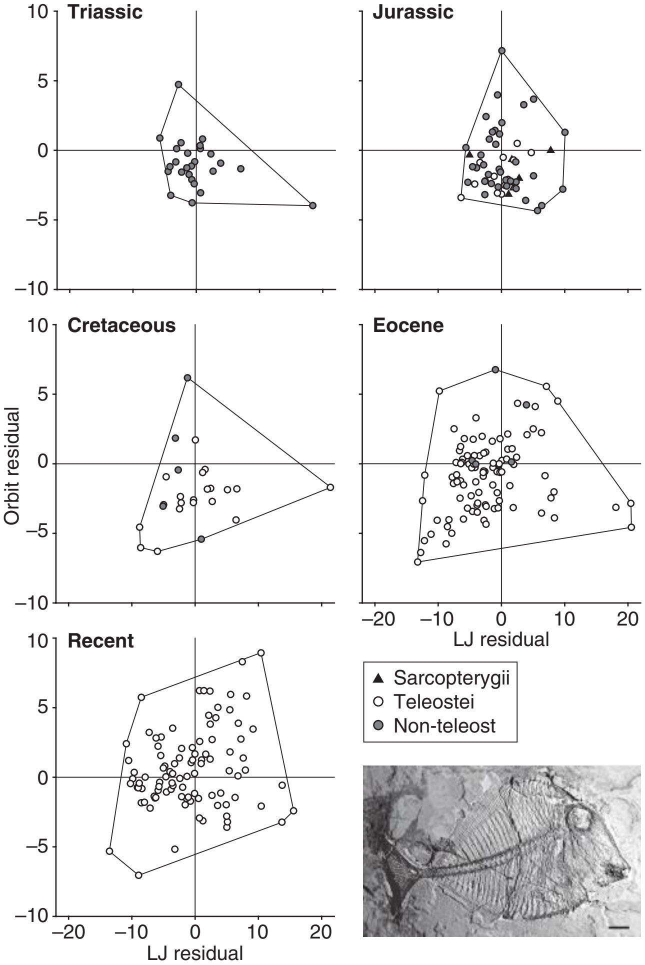
The vast majority of euteleosts, some 21,000 species of advanced teleosts, form the clade Neoteleostei. The Neoteleostei are diagnosed by a specialized muscle in the upper throat region that controls the pharyngeal toothplates in the roof of the pharynx, an important adaptation for manipulating prey.

The basal living neoteleosts include three orders with varying degrees of adaptation to life in the deep sea. The first two are the stomiiforms, about 400 species of dragonfishes and their allies, and the aulopiforms, some 240 species of lizardfishes (Figure 7.14(b)), and the origins of both date back to the Cretaceous. Deep-sea members of these clades show adaptations to the darkness and low food levels, including bioluminescence and massive jaws lined with long, dagger-like teeth. Similar adaptations are seen in another basal neoteleostean group, the myctophiforms, some 250 species of lantern fishes, which possess photophores, light-producing structures that show up when they descend into deep waters. All these groups show modifications to the eyes, some of them becoming tubular, to enable them to capture minute amounts of light; below 1000 m, there is no residual light from the surface, and the only light comes from such bioluminescent structures. Another unusual strategy seen in many aulopiforms is

BOX 7.8 CORAL REEFS PROMOTE TELEOST DIVERSITY

Today, one of the most evocative scenes of teleost abundance and adaptation comes from coral reefs. The image of numerous, small, and highly colourful fishes flickering in and out of the reef confirms one of the main sites of diversification of the clade. Today, reefs are seen as biodiversity hotspots, with up to 1000 species of fishes coexisting in a single location. Recent palaeontological studies (Kiessling *et al*., 2010) show that reefs have always been centres of species origin and that reefs export species to other habitats. Further, comparative phylogenetic studies show that reef-dwellers speciate faster than their non reef-dwelling relatives.

In one such study, Price *et al*. (2011) showed that coral reef species of labrids (wrasses and parrotfishes) have evolved functional morphological diversity twice as fast as non-reef species. Further, coral reef species show 70% more diversity in their dietary modes. The analysis was done by measuring eight traits concerning jaw mechanics for each species, as well as coding each species for its main dietary mode. These traits were mapped onto a detailed phylogeny of wrasses, and rates of trait evolution and phylogenetically corrected morphospace plots were calculated. This study, and others like it, suggest that coral reef habitats not only promote species richness, but also both trophic novelty and morphological diversity within fishes. This is a strong reason for the conservation of tropical reefs today, as well as an illustration of the exploration of ecological and morphological features on a phylogeny.



Plots of relative orbit diameter residuals against relative lower jaw length residuals for 745 fish specimens, according to particular geological time slices. Each point represents the mean residual values of an individual species, indicating divergence from the mean represented by the best-fitting regression line in each case. The photograph shows the Middle Triassic *Pycnodus platessus*, a typical deep-bodied, durophagous and large-eyed reef-dweller. Source: Goatley *et al*. (2010). Reproduced with permission from the Palaeontological Society.

Continued

Looking back in geological time, teleosts seemingly did not initially exploit coral reefs for food in the Triassic or Jurassic, but in the Cretaceous, new feeding modes emerged. Some teleosts began feeding on algae among the corals, while others, such as parrotfishes, crunched and snipped their way through the coral skeleton to extract the fleshy inhabitants. In response, reef types seem to have changed, with a dramatic expansion of reefs formed from grazing-resistant Corallinaceae in the Late Cretaceous and Cenozoic (Bellwood, 2003).

In exploring the theme further, Goatley *et al*. (2010) found major shifts in the morphology of the jaws and eyes of actinopterygians (principally teleosts) in response to coral reef evolution since the Triassic. Morphospace plots (see illustration) show changing dominance in the shape of the lower jaw and the relative eye size. These plots are based simply on residuals (deviations from the best-fitting regression line) of relative lower jaw length and orbit diameter, and so show how the 745 measured specimens differ from the mean values. In comparing the five plots, there is no evident trend in relative lower jaw length through geological time, with roughly equal numbers of short-jawed (left-hand side) and long-jawed (right-hand side) specimens, except in the Eocene, when short-jawed forms were slightly dominant. The main, and unexpected, discovery was that there is a trend of increasing orbit diameter over time, especially among teleosts. Before the Eocene, only two teleosts showed large eyes, whereas this rose to 35% of specimens in the Eocene, and 53% today.

The Eocene appears to mark a dramatic increase in two previously rare feeding modes in fishes: nocturnal feeding and high-precision benthic feeding. Teleosts with large eyes and large gapes became significant on coral reefs from the Eocene onwards, and this enabled hunting at night or in low-light conditions, and feeding on a wide range of prey sizes. This morphometric and functional shift marks an expansion of teleost feeding modes, and it is not clear whether it was triggered by an external environmental trigger, such as the emergence of new prey items, or whether through continuing diversification of teleost feeding modes.

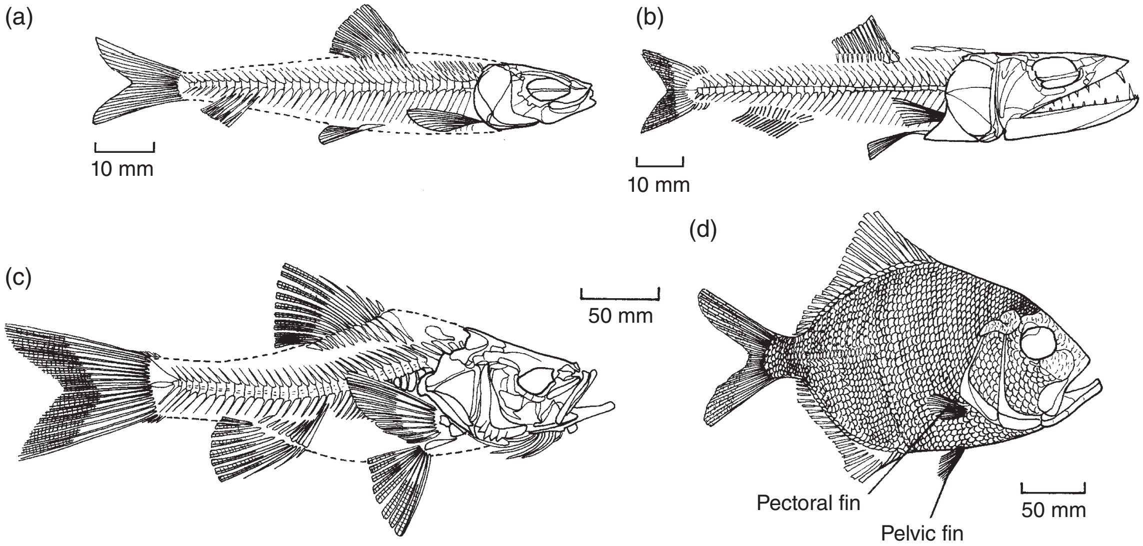


Figure 7.14 Basal euteleosts (a,b) and acanthomorphs (c,d) from the Cretaceous (a,c) and recent (b,d): (a) the salmoniform *Gaudryella*; (b) the aulopiform *Eurypholis*; (c) the paracanthopterygian *Mcconichthys*; (d) the acanthomorph *Berycopsis*. Source: (a) Adapted from Patterson (1970). (b) Adapted from Goody (1969). (c) Adapted from Grande (1988).

simultaneous hermaphroditism, meaning individuals can produce functional eggs and sperm at the same time. This could be a good way to reproduce if individual males and females would rarely meet in the cold, dark abyssal depths; however, there is no evidence that these hermaphroditic fishes self-fertilize. Studies of aulopiform phylogeny (Davis and Fielitz, 2010) show that hermaphroditism arose once only, at the origin of the clade in the Cretaceous, but tubular eyes evolved later, perhaps three times independently.

7.4.6 Acanthomorpha

The remaining neoteleosts, a huge group of more than 18,000 species, are termed the spiny teleosts, or acanthomorphs, because they bear stiff fin spines. The spines can be moved by muscles at the base, allowing them to be erected if the fish is threatened, effectively stopping it from being swallowed – a highly effective defensive strategy! The acanthomorphs show other derived features. The scales are spiny, the so-called ctenoid (i.e. 'comb') type. The body is short and relatively rigid, and thrust in swimming is produced by rapid movements of the tail fin instead of by bending the whole body. This allows great speeds to be achieved – as much as 70 km per hour in the tuna, compared with 10 km per hour in the trout. In addition the acanthomorphs have the toothed premaxilla type of jaw (see Section 7.3.4).

The Acanthomorpha were traditionally divided into four clades (see Box 7.6), Polymixiiformes, Paracanthopterygii, Atherinomorpha, and Percomorpha. The huge order Percomorpha is retained in all phylogenetic studies, but the other three turn out to be polyphyletic in molecular studies (Betancur-R *et al.*, 2013; Near *et al.*, 2013). The 'Paracanthopterygii' had a chequered history. When first proposed, members of the group were distinguished on some complex characters of the tail architecture and the musculature of the mouth, among others, and its validity was defended (Patterson and Rosen, 1989) against criticism. These authors included five orders, the Percopsiformes, Batrachoidiformes, Lophiiformes, Gadiformes, and Ophidiiformes. However, phylogenomic studies did not confirm this result. First, mitochondrial genomic sequences (Miya *et al.*, 2003, 2005) showed that the Batrachoidiiformes, Lophiiformes, and Ophidiiformes were not paracanthopterygians, but rather belonged to the crown group of teleosts, the Acanthopterygii. Miya *et al.* (2003, 2005) redefined the Paracanthopterygii to include Polymixiiformes, Percopsiformes, Gadiformes, Zeiiformes, and Stylephoriformes. This is broadly confirmed in more extensive phylogenomic studies (Near *et al.*, 2012, 2013; Betancur-R. *et al.*, 2013).

The first clade comprises Polymixiiformes and Percopsiformes (Near *et al.*, 2013). The polymixiiforms are a small clade of 10 species of one genus, *Polymixia*, the beardfishes (Figure 7.14(d)). These have deep bodies and the pelvic fin located below the pectoral fin. The fossil record of Polymixiiformes is reasonably rich, with seven genera in the Late Cretaceous, some similar in body outline to modern beardfishes, others much more deep-bodied (Patterson, 1964). Then there was a gap in time before the first appearance of fossil representative of the modern genus *Polymixia* in the late Eocene. The Percopsiformes are nine species of small freshwater fishes, the trout-perch of North American lakes. Four of these species show independent acquisition of adaptations to extreme cave dwelling including the loss of the eyes and of pigmentation (Dillman *et al.*, 2010).

The second clade unites Zeiformes (dories), *Stylephorus* (tube-eye), and Gadiformes (cods). The Zeiformes are some 40 species of dories, deep-bodied fishes that often live in deep waters. The Stylephoriiformes comprise a single species, the tube-eye, a strange, elongate fish with a pair of whip-like caudal rays that extend its length to three times the body length. Long thought to be a derived percomorph, molecular study places it in this basal acanthomorph clade. The Gadiformes, the cod, hake, and relatives, comprise some 200 species of open marine fishes (Roa-Varón and Ortí, 2009). They do not have spines in their fins, and the pelvic fins, if present, may be located in front of the pectoral fins. Various representatives of these groups date back to the Late Cretaceous, with forms such as *Mcconithchthys* (Figure 7.14(c)).

Next come the Lampridiformes, 20 species of opahs and ribbonfishes, which live at middle depths in tropical seas. They generally have laterally compressed bodies, but their shape ranges from the circular opahs to the elongate ribbonfishes; the largest is the oarfish, which has been recorded to reach a length of 17 m. These may be sister lineage to the Acanthopterygii, comprising by far the majority of acanthomorphs. Traditionally, the Acanthopterygii were divided into two clades, the Atherinomorpha and the Percomorpha. Phylogenomic analysis (e.g. Near *et al.*, 2012, 2013; Betancur-R. *et al.*, 2013) confirms the validity of Percomorpha as a clade, but divides atherinomorphs into successive outgroups, primarily the Beryciformes and Holocentriformes. The Beryciformes are 220 species of squirrelfishes and relatives that often live in deep water. They have a rich fossil record back to the Late Cretaceous. The Holocentriformes, 85 species of soldierfishes, are tropical predators, some with poisonous spines.

The percomorphs (Johnson and Patterson, 1996) include a tremendous range of forms, from seahorses to flatfishes and from tunas to porcupine fishes, a total of more than 17,000 species. The group as a whole is known from the Late Cretaceous, with well-preserved representatives in some Eocene fish beds, but most families have a very limited fossil record, often confined to the past 20 Myr or so. The major divisions within Percomorpha are currently fluid, as different approaches and sample taxa are analysed phylogenetically. Betancur-R. *et al.* (2013) provisionally recognize nine clades, whereas Near *et al.* (2013) identify 14 clades.

The Ophidiiformes, are 100 species of cusk-eels and relatives, all with elongate bodies, elongate dorsal fins, and the anal fin generally fused with the caudal fin. The Batrachoidiformes are 80 species of toadfish, marine fishes with broad mouths and short, supposedly frog-like heads. They are camouflaged by numerous short spines and excrescences, as well as irregular colour blotches, and they hide on the sea floor ready to ambush their prey. The Gobiomorpharia, a clade comprising the 2200 species of gobies plus close relatives, are generally small to very small (some are less than 10 mm long as adults). The Syngnathiformes (250 species of pipefishes and seahorses) and Scombriformes (50 species of tunas, mackerels, and bonitos) might seem odd bedfellows, but they form a clade Scombrimorpharia.

The final four clades are grouped in Carangimorpharia (Betancur-R. *et al.*, 2013). First are the Anabantomorphariae, the swamp eels, armoured stickleback, and gouramis. This is a novel grouping, and the fishes assembled here all had a freshwater origin, and they are geographically largely restricted to Africa and South East Asia. Most are able to occupy stagnant waters, and they can obtain oxygen directly from the air using either a suprabranchial organ or suprabranchial pouches with a respiratory function. Second is Carangimorphariae, a motley assemblage of barracudas, swordfishes, jacks, flatfishes, and third is Liparidae, 360 species of snailfish. The fourth clade is Percomorpharia, still a vast, and partly phylogenetically unresolved crown clade, including 11 orders and 15 families, with Perciformes by far the largest included order.

Near *et al.* (2013) confirm the early divergence of cusk-eels (Ophidiiformes) and toadfishes (Batrachoidiformes), a clade uniting angler-fishes and pufferfishes, as well as Ovalentaria, a new clade containing cichlids, engineer gobies (Pholidichthys), silversides, livebearers, and ricefish (Atherinomorpha), surfperches (Embiotocidae), damselfishes (Pomacentridae), mullets (Mugilidae), clingfishes (Gobiesocidae), and blennies. Further, they identify a clade uniting swamp eels (Synbranchiformes), armoured sticklebacks (*Indostomus*), Asian leaffishes (Nandidae), gouramies and snakeheads (Anabantomorpha), flatfishes (Pleuronectiformes), jacks (Carangidae), sharksuckers (Echeneidae), billfishes (Xiphioidei), and barracudas (*Sphyraena*), as well as a clade containing temperate basses (Moronidae) and a large collection of marine percomorphs that include butterflyfishes (Chaetodontidae), grunts (Haemulidae), angelfishes (Pomacanthidae), anglerfishes (Lophiiformes), and pufferfishes (Tetraodontiformes).

7.5 POST-DEVONIAN EVOLUTION OF FISHES

After major evolutionary changes through the Early Palaeozoic, many basal vertebrate groups died out in the Late Devonian extinction events (see Section 3.10). There were then at least three diversification phases among fishes, first a radiation of various basal shark and actinopterygian groups in the Carboniferous and Permian. Following the Permo-Triassic mass extinction (see Section 5.7), both chondrichthyans and osteichthyans underwent substantial diversifications, hybodontiforms among the former, and chondrosteans and neopterygians among the latter. This diversification of all fish groups in the Triassic was part of the establishment of a 'modern-style' marine ecosystem, in which mobile organisms, such as fishes, decapods (crabs, lobsters), and ammonoids, rose from 40% to 60% of the faunas worldwide. In this time of dramatic diversification of many clades in the oceans, the major clades Neoselachii and Teleostei emerged in the Triassic, and expanded in phases through the Jurassic to the present day.

Which of these fish groups are most important for modern biodiversity? In a numerical study of modern vertebrate biodiversity, Alfaro *et al.* (2009) found six substantial diversification shifts (see Section 2.7) that indicate which modern clades contribute most to biodiversity. Among fishes, these are Ostariophysi (catfishes and minnows), Euteleostei (the bulk of teleosts), and Percomorpha (subclade within Euteleostei, including most of the coral reef associated fishes as well as cichlids and perches). Euteleosts and ostariophysans diversified initially in the Jurassic, and percomorphs in the late Cretaceous and Cenozoic.

It has often been assumed that fishes swam and wriggled through the mass extinctions unscathed. This appears to be wrong: new studies find levels of extinction that are entirely comparable with other groups. At the end of the Permian, several groups of chondrichthyans and actinopterygians disappeared, but no family of fishes seems to have disappeared during the end-Triassic mass extinction (Friedman and Sallan, 2012).

The Cretaceous-Paleogene (KPg) event, on the other hand, was marked by the end of hybodont sharks and numerous basal neopterygian groups. Detailed calculations of extinction rates for sharks (Kriwet and Benton, 2004) show that seven out of 39 families (18%) became extinct, corresponding to 34% loss of genera and 45% loss of species. These extinction rates

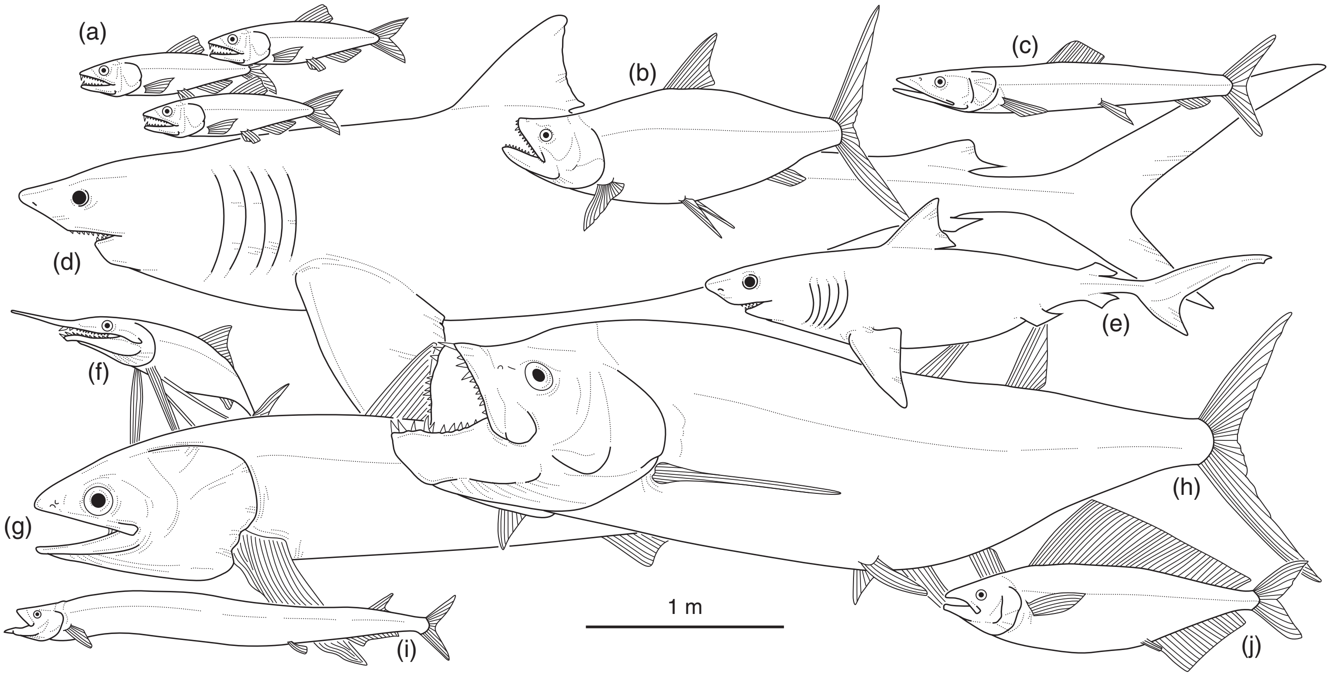


Figure 7.15 Reconstructions of select large-bodied marine chondrichthyans and actinopterygian representing possible victims of the KPg extinction. (a) the aulopiform teleost *Enchodus*. (b) the pachyrhizodontid teleost *Pachyrhizodus*. (c) the aulopiform teleost *Cimolichthys*. (d) the cretoxyrhinid neoselachian *Cretoxyrhina*. (e) the anacoracid neoselachian *Squalicorax*. (f) the pachycormiform teleost *Protosphyraena*. (g) the pachycormiform teleost *Bonnerichthys*. (h) the ichthyodectiform teleost *Xiphactinus*. (i) the ichthyodectiform teleost *Saurocephalus*. (j) the tselfatiiform teleost *Bananogmius*. Source: Friedman and Sallan (2012). Reproduced with permission from John Wiley & Sons.

are entirely comparable with other groups that were also affected by the KPg event. The extinctions were heavy among both sharks and batoids, but most severe among batoids, which lost almost all species (97% loss). Open marine top predators and shell-crushers from the continental shelf and shallow seas were hard hit, whereas deep-sea forms were apparently little affected.

Among actinopterygians, the KPg mass extinction seemingly had mixed effects. The impact on freshwater groups appears to have been modest (Friedman and Sallan, 2012). In the sea, there were more substantial extinctions: among the teleost stem groups that existed in the Late Cretaceous (pycnodontiforms, pachycormiforms, aspidorhynchiforms, ichthyodectiforms and crossognathiforms), only the first survived into the Paleogene. In a review of possible selectivity among marine actinopterygians, Friedman (2009) concluded that fishy victims of the KPg mass extinction (Figure 7.15) included all taxa characterized by large body size and low-to-moderate jaw-closing mechanical advantage, which is typical of fish-eaters.

In the wake of the KPg extinction of large predatory fishes, many of today's ecological equivalents emerged in the Paleogene: carcharinids (requiem sharks), lamnids (makos), and scombroids (tunas and their kin) in the early Palaeocene; carangids (jacks) and xiphioids (billfishes) in the late Palaeocene; and sphyraenids (barracudas) in the early Eocene (Friedman and Sallan, 2012). At the same time, smaller fishes proliferated, notably the acanthomorph teleosts (and especially the Percomorpha) in the oceans, and the ostariophysans primarily in freshwaters. Today, these two clades, Acanthomorpha and Ostariophysi collectively make up nearly half of all living vertebrate species.

7.6 FURTHER READING

Standard introductions to ichthyology include Moyle and Cech (2003), Bone and Moore (2007), and Helfman *et al.* (2009). The diversity of living sharks is covered by Compagno *et al.* (2005) and bony fishes by Nelson *et al.* (2010), and Carrier *et al.* (2012) provides an overview of many sharky themes. Long (2010) is a more popular account of fish evolution. Some masterful overviews of the phylogeny of many chondrichthyan and osteichthyan groups are given in Stiassny *et al.* (1996), and occasional volumes in a series on Mesozoic fishes include Arratia and Schultze (1999), Arratia and Tintori (2004), Arratia *et al.* (2008, 2013). Cavin *et* al. (2008) presents papers about mid-Palaeozoic fishes. Elliott *et al.* (2010) provides a diverse array of essays on fossil fishes, while Nelson *et al.* (2010) contains chapters about the phylogeny of teleosts.

Learn more about the three-dimensional anatomy of modern cartilaginous and bony fishes at: http://digimorph.org/listbygroup.phtml?grp=fish&sort=SpeciesName. For the fish fanatic, 'welcome to the world of fishes' at: http://www.fishbase.org/home.htm.

QUESTIONS FOR FUTURE RESEARCH

1 What was the range of adaptation of the remarkable array of chondrichthyans in the Carboniferous?
2 How did hybodonts and neoselachians divide up ecospace between them through the Mesozoic?
3 We need more complete fossils of sharks and their kin – too many are known only from teeth.
4 What were the places in the food chain of the various neoselachian subclasses during the Cretaceous, and how did these change following the extinction of marine reptiles at the end of the Cretaceous?
5 What are the relationships of the Carboniferous and Permian bony fishes formerly called palaeonisciforms?
6 What happened to bony fishes through the Permo-Triassic mass extinction? Is the general lack of good fossils around this time a preservational bias or the consequences of extinction and low abundance?
7 How did marine and freshwater ecosystems rebuild during the Triassic? What were the key phylogenetic, ecological, and morphometric/adaptive changes in actinopterygians during this diversification episode?
8 What were the key drivers in the origin and later phases of diversification of teleosts?
9 How was actinopterygian evolution in the Mesozoic affected by the contemporary evolution of shark and marine reptile groups?
10 Why are some teleost groups so species-rich in comparison to others?

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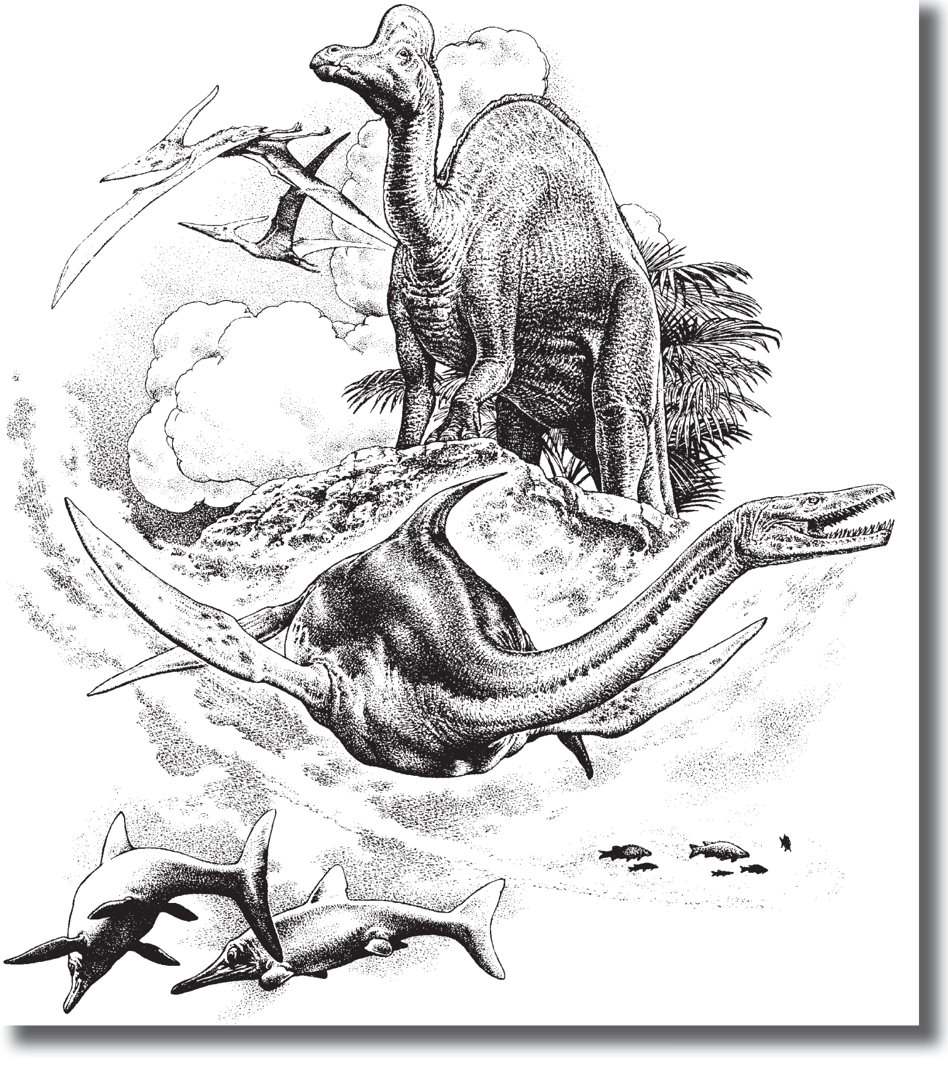
CHAPTER 8

The Age of Dinosaurs



Vertebrate Palaeontology, Fourth Edition. Michael J. Benton.

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KEY QUESTIONS IN THIS CHAPTER

1 How did the dinosaurs live?
2 Why did the dinosaurs become so diverse?
3 What are the relationships of theropod dinosaurs to each other and to birds?
4 Did dinosaurs have feathers, and if so, which ones?
5 What was the largest dinosaur?
6 Why were the ornithopod dinosaurs so successful?
7 Were the dinosaurs warm-blooded or not?
8 How did dinosaurs grow up?
9 How did the pterosaurs fly and walk?
10 What do we know about the ancestry of modern turtles, crocodilians and lizards?
11 Did snakes evolve from swimming or burrowing ancestors?
12 How were plesiosaurs and ichthyosaurs adapted to underwater life?
13 Why did the dinosaurs, pterosaurs, plesiosaurs and mosasaurs die out 66 Myr ago?

INTRODUCTION

The most famous fossil vertebrates, the dinosaurs (literally 'fearfully great lizards') arose in the Triassic, about 245 Myr ago (see Section 6.4), and dominated terrestrial faunas for the next 180 Myr until their extinction at the end of the Cretaceous (66 Myr ago). The earliest dinosaurs were moderate-sized bipedal carnivores, but large quadrupedal herbivores had evolved by the end of the Triassic. During the Jurassic and Cretaceous, the dinosaurs diversified into a great array of carnivores large and small, massive herbivores, small fast-moving specialized plant-eaters, and others armoured with great bone plates, horns, carapaces and clubs.

The pterosaurs, relatives of the dinosaurs, filled the skies, and the birds, descendants of the carnivorous dinosaurs, arose in the Middle to Late Jurassic. Other land vertebrates of the Mesozoic included groups that exist today, the turtles, crocodilians, lizards, snakes and mammals. The seas were populated by ichthyosaurs and plesiosaurs and, in the Late Cretaceous, by mosasaurs, great marine reptiles that preyed on fishes, on squid and on each other. The diversity of these reptiles and their biology will be explored in this chapter.

We begin with a detailed look at one of the oldest, well-documented dinosaurs, *Plateosaurus*, as an introduction to dinosaurian anatomy and research. We then look at the world of the Mesozoic, before beginning a systematic overview of the key groups.

8.1 BIOLOGY OF *PLATEOSAURUS*

The oldest confidently known dinosaurs are dated as Carnian in age (Late Triassic, 237–228 Myr ago) and they include forms such as *Eoraptor* and *Herrerasaurus* from Argentina (see Section 6.4) and *Saturnalia* from Brazil. One of the most abundant Late Triassic dinosaurs was *Plateosaurus*. The first specimens were found in south-western Germany in 1837, and since then dozens of skeletons have been collected from over 50 localities in Germany, Switzerland and France, mostly dated as mid-Norian (c. 220–215 Myr ago). The best locality is Trossingen, south of Stuttgart, where 35 skeletons and fragments of 70 more were excavated from the Löwenstein Formation (Yates, 2003a). The skeletons are of young and old animals, and many have been broken up by scavengers and by water movement.

How did the mass grave of *Plateosaurus* skeletons at Trossingen arise? There have been three suggestions.

1 A herd of *Plateosaurus* perished while migrating across an arid desert in search of plant food. Against this romantic image is that there is no evidence for desert conditions; the enclosing sediments represent water-laid mudstones.

2 The animals died at different times and in different places, and they were washed into a mass concentration in a major river system. This is commonly the case with dinosaur accumulations, but seemingly not here.

3 The animals died where they are now preserved, perhaps by miring in unconsolidated mud (Sander, 1992; Hungerbühler, 1998). Evidence is that the skeletons are generally complete and unbroken, and many of them sit in a belly-down position with their feet trapped beneath.

Plateosaurus (Figure 8.1) is about 7 m long and it has generally been assumed that it could have adopted either a bipedal or a quadrupedal posture. However, a biomechanical study, based on scanned bones in a 3D computer model suggest (Mallison, 2010) that *Plateosaurus* could not have used its forelimbs in locomotion and that they were useful only for grasping objects directly below the torso. It walked on its hindlimbs only, with the foot held in digitigrade posture, and the knee slightly flexed. According to these calculations, many previous reconstructions of the posture and movements of limbs in *Plateosaurus* are impossible.

The body proportions are typical of early dinosaurs: a long tail, long hindlimbs about twice as long as the arms and a long neck, but the skull is small and the limbs are heavily built because of its large size. *Plateosaurus* shows derived dinosaurian characters of the limbs and vertebrae: upright posture, slender pelvic bones and distinctive vertebrae in the neck, trunk and the lower back.

What did the plateosaurs eat? They have generally been regarded as herbivores because of their size, their great abundance and their weak leaf-shaped teeth (Figure 8.1(b,d)). This was disputed at one time because some skeletons were found in association with dagger-like teeth that suggested a diet of meat. These carnivore teeth have been identified (Hungerbühler, 1998) as those of rauisuchians, phytosaurs and theropod dinosaurs that were scavenging on plateosaur carcasses and had shed their teeth when biting on bones. The teeth of *Plateosaurus* have serrated edges, yet are more like the teeth of herbivorous lizards that cut up tough plants than the steak-knife teeth of true carnivores. The jaw joint in *Plateosaurus* is set low (Figure 8.1(b)),

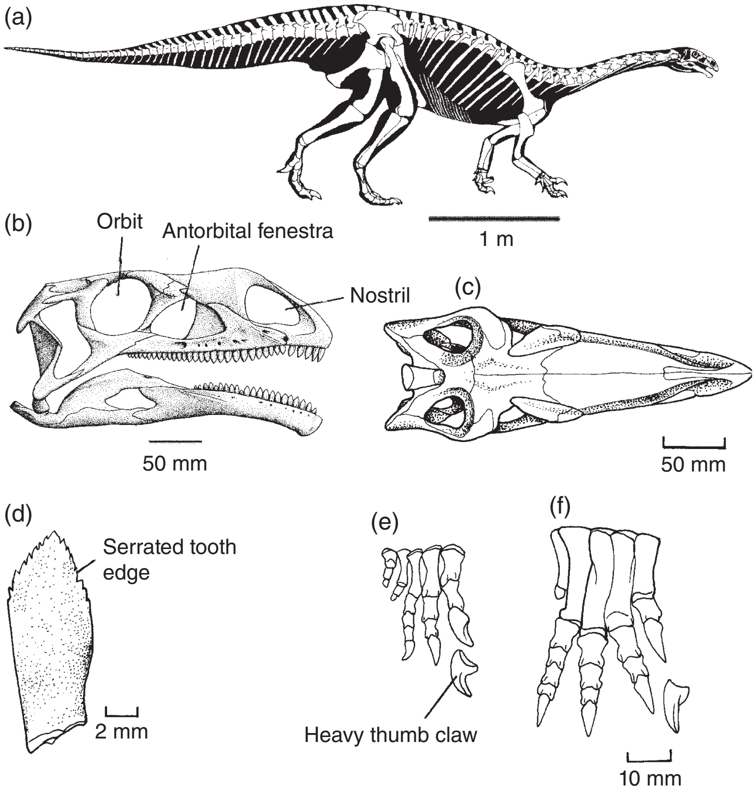


Figure 8.1 The plant-eating dinosaur *Plateosaurus* from the Late Triassic of Germany: (a) skeleton in lateral view; (b,c) skull in lateral and dorsal views; (d) tooth; (e) hand in anterior view, with lateral view of heavy thumb claw; (f) foot in anterior view, with lateral view of heavy claw on digit 1. Source: (a–c) A. Yates, Museum and Art Gallery of the Northern Territory, Darwin, Australia. Reproduced with permission. (d–f) Adapted from Galton (1985).

an adaptation seen in herbivorous synapsids (see Box 5.4) and other dinosaurs (see Section 8.4.3) which gives a sustained and evenly spread bite along the tooth row, useful in dealing with tough plant stems.

Plateosaurus swallowed its plant food whole and could not chew it as modern mammals do because sideways jaw movements were not possible. It may have avoided indigestion by the use of a gastric mill. Just as chickens today swallow grit that lodges in the gizzard, a muscular expansion of the gut above the stomach, and grinds the food up, the plateosaurs may have swallowed pebbles. A herd of feeding plateosaurs must have rattled, grunted and burped furiously as their rough plant diet was reduced to a digestible state!

8.2 THE JURASSIC AND CRETACEOUS WORLD

During the Triassic and Early Jurassic, the supercontinent Pangaea was at its most extensive, with continuous land stretching from North America to Europe and South America to Africa, Antarctica, Australia and India (Figure 8.2). The continents began to break apart in stages through the Jurassic and Cretaceous, with the North Atlantic opening first between Europe/Africa to the east and North America to the west. The South Atlantic opened between Africa and South America through the Cretaceous, but dinosaurs and other land animals were able to move back and forwards over narrow connections. Through much of the Cretaceous, there was a circumequatorial Tethys Ocean that largely separated northern and southern continents. In the mid Cretaceous, there was a phase of extensive mid-ocean ridge volcanic activity; the ocean floor rose, and the seas flooded massively over the land, raising sea levels 100 m higher than they are today (Miller *et al*., 2005) and depositing great amounts of chalk and other forms of limestone over much of the world. These higher sea levels flooded continents, dividing North America with a major north–south ocean, the Western Interior Seaway, flooding much of the northern parts of South America and Africa, and dividing Europe into numerous small islands.

Jurassic climates were moister than in the Triassic (see Section 6.1) and warm conditions prevailed right to the polar regions (Price *et al*., 2013). Ferns and conifers of subtropical varieties have been found as far north as 60° palaeolatitude, and rich floras are known from Greenland and Antarctica. The change to moister conditions is indicated by the fact that evaporite deposits are less common in the Jurassic than Triassic.

There have been intense debates about Cretaceous climates, with some researchers supporting the traditional model of warm conditions and ice-free poles, whereas others have argued for cooler climates throughout. Part of the debate revolves around apparent discrepancies between geological and palaeontological evidence for a much broader equatorial belt than today, and modelling results that predict ice at the poles. A revised compilation of carbon dioxide data recorded from brachiopod and foraminifer shells (Price *et al*., 2013) confirms cooling through the Early Jurassic, relatively steady, warm temperatures through the Late Jurassic and most of the Cretaceous, and then the beginning of a major cooling trend in the latest Cretaceous that continued through the Cenozoic.

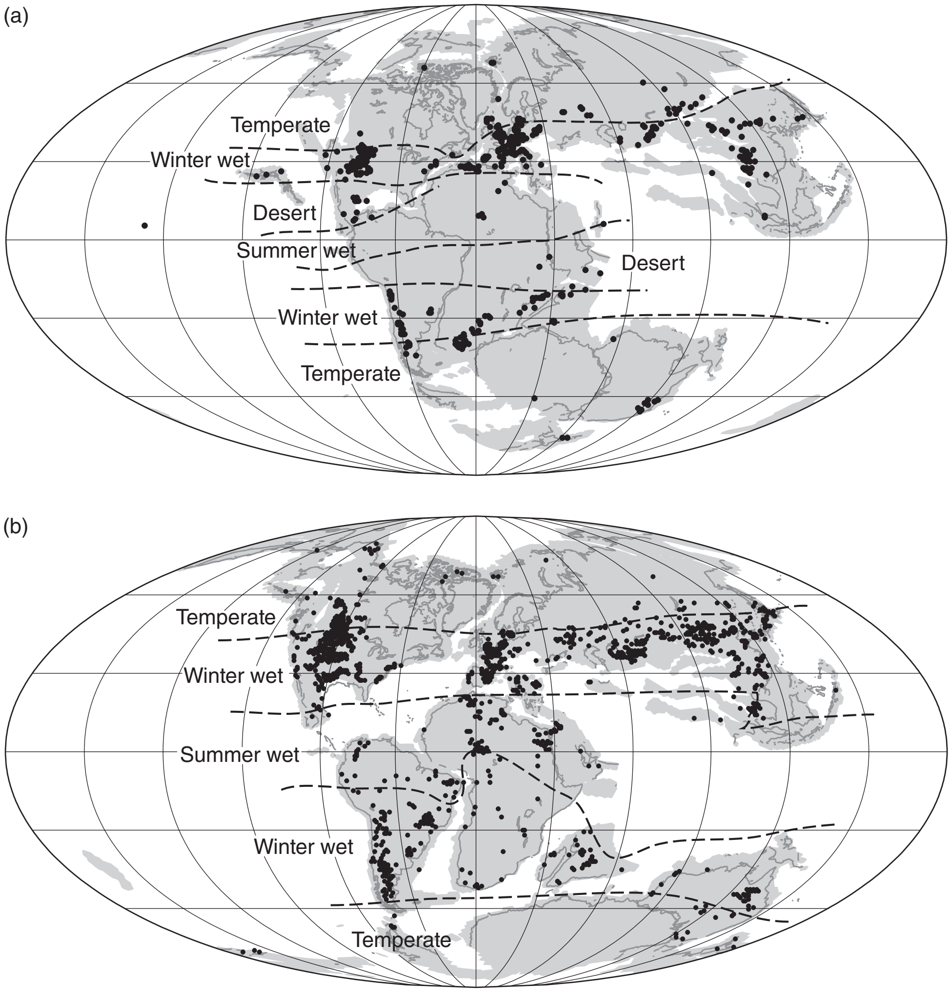


Figure 8.2 Palaeogeographic maps of the world in the Middle Jurassic (a) and Mid Cretaceous (b), showing major climatic belts and the locations of dinosaurian faunas (black dots). Source: Adapted from Hay and Floegel (2012) and Alroy (2013).

Detailed mapping of climate indicators such as coals and bauxites (hot, humid conditions), the evaporite minerals gypsum and anhydrite (hot, arid indicators), and locations of temperature-sensitive organisms such as turtles, crocodiles, and certain plants, indicates Cretaceous climate zones (Hay and Floegel, 2012). The equatorial arid zone extended over most of Africa and South America, as well as southern parts of North America, Europe and Asia. The mid-latitude warm humid belt extended into Canada and northern Eurasia in the north, and Antarctica and Australia in the south. This model has been criticized based on geological and palaeontological evidence: for example, measurements of oxygen isotopes in dinosaur bones from East Asia indicate unusually low temperatures of about 10 °C in the temperate belt (Amiot *et al.*, 2011). There were also numerous cold snaps in the Early and mid Cretaceous. Although much debated, there is limited evidence for permanent ice at the poles in the Cretaceous. Seasonal winter ice is likely, however, but polar dinosaurs and other vertebrates might simply have migrated towards warmer conditions to avoid the cold.

A major change took place in the world's floras during the Cretaceous. Triassic and Jurassic landscapes contained low ferns, horsetails and cycads, and tree-sized club mosses, seed ferns and conifers. In the Early Cretaceous, the first flowering plants (angiosperms) appeared, and they radiated rapidly during the Late Cretaceous until they reached modern levels of ecological significance (Magallón and Castillo, 2009). The Early-Late Cretaceous boundary marks a time when rain forests rapidly appeared in equatorial regions (Couvreur *et al.*, 2011). The earliest angiosperms include magnolia, beech, fig, willow, palm and other familiar flowering shrubs and trees. There were even rare grasses, although these did not become important until later in the Tertiary (see Section 10.4).

8.3 THE DIVERSITY OF SAURISCHIAN DINOSAURS

Dinosaurs have long been understood to comprise two major subclades, the Saurischia and the Ornithischia. These two subclades are diagnosed on the basis of their radically different pelvic regions, as well as other characters of the skull and skeleton. The saurischian dinosaurs, the primarily carnivorous theropods and the herbivorous sauropodomorphs such as *Plateosaurus* and its descendants, will be reviewed here. The ornithischians are considered later (see Section 8.4).

8.3.1 Dinosaur hips and hindlimbs

Saurischian and ornithischian dinosaurs are traditionally identified by the so-called 'lizard hip' and 'bird hip' respectively. The more primitive structure is seen in the saurischians in which the pubis points forwards and the ischium back (Figure 8.3(a)), as in all basal archosaurs of the Triassic (e.g. Figures 6.5–6.12). In ornithischians, on the other hand, the pubis runs back in parallel with the ischium and there is an additional **prepubic process** in front (Figure 8.3(b)).

Many dinosaurian characters of the hindlimbs are related to the acquisition of upright posture (see Box 6.3). The acetabulum is fully open and the pubis and ischium are long slender elements. The legs are brought in close to the vertical midline of the body (Figure 8.3(c)) by a shift of the articulating surface from the top of the femur to a distinct ball on its inside. The reorientation of the limbs from a partial sideways sprawl also changed the angle of the knee and ankle joints to simple hinges. The fibula is reduced, often to a thin splint, and the tibia has a 90° twist so that its proximal head is broadest from back to front and its distal end is broadest from side to side.

The ankle and foot of dinosaurs are also distinctive. The ankle is dominated by a wide astragalus with a distinctive vertical process that wraps round the front of the tibia (Figure 8.3(c)), and the calcaneum is a small block-like element. In the foot, the dinosaur stands up on its toes (the **digitigrade** stance) rather than on the flat of its whole foot (the **plantigrade** stance), as most basal archosaurs (and humans) do. The outer toes, 1 and 5, are much reduced and the dinosaur really uses only the middle three toes, 2, 3 and 4.

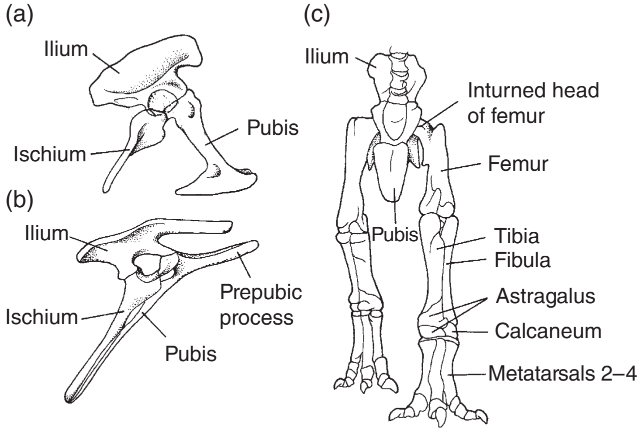


Figure 8.3 Dinosaurian pelvic girdles: (a) the typical saurischian pelvic girdle, in lateral view, in *Tyrannosaurus*; (b) the typical ornithischian pelvic girdle, in lateral view, in *Thescelosaurus*; (c) anterior view of the hindlimbs of *Tyrannosaurus* to show the fully upright posture. Source: (a,c) Adapted from Osborn (1916). (b) Adapted from Romer (1956).

8.3.2 The basal theropods

The theropods include all the flesh-eating dinosaurs and they ranged in size from small jackdaw-like forms to the 10-tonne giants of the Cretaceous. The herrerasaurids from the Carnian of South America (see Section 6.4.2) are often regarded as the first theropods, although others regard them as generalized basal saurischians or basal dinosaurs (Langer and Benton, 2006). There have been numerous studies of theropod phylogeny (e.g. Rauhut, 2003; Carrano and Sampson, 2008; Xu *et al.*, 2009; Choiniere *et al.*, 2010; Carrano *et al.* 2012; Turner *et al.*, 2012), which agree on the broad outlines, that there were some basal branches, including coelophysoids, then a split into Ceratosauria and Tetanurae, and that successive major clades within Tetanurae include Avetheropoda, Coelurosauria, Maniraptora, Paraves, and Aves (see Box 8.1).

The first unequivocal theropods, the coelophysoids, consist of some five or six Late Triassic and Early Jurassic genera. *Coelophysis* from the Late Triassic of North America (Figure 8.4(a)) was a lightweight dinosaur with a long slender tail and a long narrow-snouted skull. It has five sacral vertebrae, a major change from *Herrerasaurus*, which has only two, the standard number in amniotes. It shows coelophysoid characters in the tibia and ankle.

A collection of more than 100 individuals of *Coelophysis* found together at Ghost Ranch, New Mexico includes animals ranging in body length from 0.8 to 3.1 m (Colbert, 1989). Males and females could be identified tentatively on the basis of variations in body proportions, and two adult specimens were thought to give evidence for cannibalism: they both had smaller specimens inside their rib cages, but close inspection (Nesbitt *et al.*, 2006) showed that these supposed juveniles are in fact the remains of small crocodylomorphs, a perfectly expected component of the diet of a theropod. The Ghost Ranch site could represent the mass burial of a whole herd of *Coelophysis* that had been overwhelmed by some catastrophe, such as a flash flood. The skeletons are mainly complete and well preserved, but some are disarticulated, so the bodies were at least moved some distance by water currents before they were buried.

Dilophosaurus (Welles, 1984) from the Early Jurassic of North America is related to coelophysoids, some 5–7 m long, and equipped with two flat-sided crests over the skull roof (Figure 8.4(b)), presumed display structures.

The next major theropod subclade is Ceratosauria, known from the Early or Middle Jurassic to Late Cretaceous (Carrano and Sampson, 2008). Many ceratosaurs have crests and horns, perhaps developed most in the males, and these could have had a function in sexual display. For example, the ceratosaurid *Ceratosaurus* from the Late Jurassic of North America has two pairs of 'horns' on the nasal and lacrimal bones above a short, high snout (Figure 8.4(c)). A second ceratosaur subclade, the abelisaurs, are known from sporadic remains from several continents in the Middle Jurassic and Early Cretaceous, but primarily from South America and other Gondwanan lands in the Late Cretaceous. Many abelisaurs had extremely short skulls, such as *Carnotaurus* (Figure 8.4(d)), in which the frontal and parietal bones were hugely expanded into two triangular 'horns' over the eyes.

BOX 8.1 RELATIONSHIPS OF THE DINOSAURS

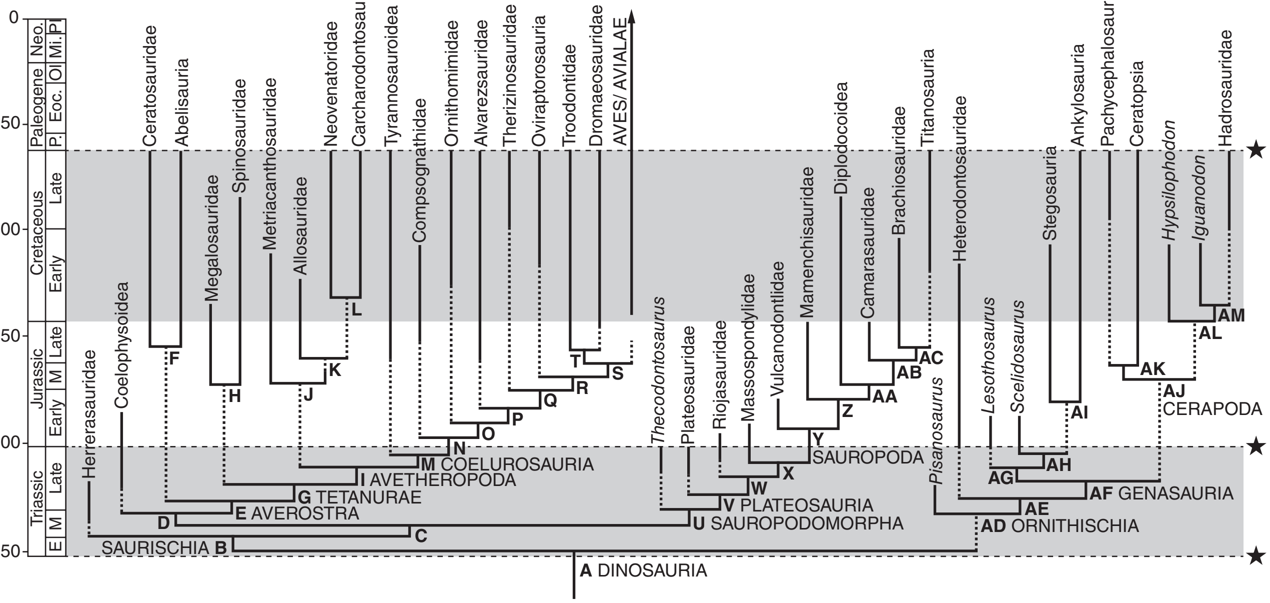
The Dinosauria (see cladogram) consists of two main clades, the Saurischia and Ornithischia. The Saurischia divides into two main subclades, the Theropoda and Sauropodomorpha. The main outlines of the dinosaurian cladogram were established in early, classic, works in the phylogeny of Saurischia (Gauthier, 1986) and Ornithischia (Sereno, 1986), and confirmed many times since (e.g. Weishampel *et al*., 2004; Brett-Surman *et al*., 2012).

Several Triassic dinosaurs appear to fall outside the major clades, being either basal Dinosauria or basal Saurischia, but these inferred relationships are controversial (Langer and Benton, 2006). Comprehensive treatments of theropod phylogeny (e.g. Rauhut, 2003; Carrano and Sampson, 2008; Carrano *et al*. 2012; Turner *et al*., 2012), agree on the broad outlines, that there were some basal branches, including coelophysoids, then a split into Ceratosauria and Tetanurae, and that successive major clades within Tetanurae include Avetheropoda, Coelurosauria, Maniraptora, Paraves, and Aves. Most recent controversy has focused on relationships within Maniraptora, and especially within Paraves, as new fossils and new cladistic analyses move *Archaeopteryx* and close relatives in and out of the avian clade (see Section 9.1.5).

The Sauropodomorpha includes the Triassic and Jurassic prosauropods, probably a sequence of outgroups to Sauropoda (Yates *et al*., 2011). Within Sauropoda (reviewed by Wilson, 2005), the Early and Middle Jurassic vulcanodontids and shunosaurids are outgroups to the Neosauropoda, comprising various families of giant sauropods, mainly Late Jurassic to Cretaceous in age, that divide into the clades Diplodocoidea and Macronaria.

The Ornithischia (Butler *et al*., 2008) have a possible primitive member, *Pisanosaurus*, and two main clades, the armoured Thyreophora and the Cerapoda, jointly the Genasauria. The Thyreophora consists essentially of the Stegosauria and the Ankylosauria with *Lesothosaurus*, once seen as a basal ornithischian, as well as *Scelidosaurus* and *Scutellosaurus*, Early Jurassic forms, as basal representatives.

The Cerapoda include a series of unarmoured bipedal ornithopods of the Jurassic and Cretaceous, leading to the hadrosaurs, as well as the horned ceratopsians and bone-headed pachycephalosaurs, which together make up the Marginocephalia.



D	THEROPODA	**K**	ALLOSAURIA	**S**	PARAVES	**AG**	THYREOPHORA
F	CERATOSAURIA	**L**	CARCHARODONTOSAURIA	**T**	DEINONYCHOSAURIA	**AK**	MARGINOCEPHALIA
H	MEGALOSAUROIDEA	**O**	MANIRAPTORIFORMES	**AA**	NEOSAUROPODA	**AL**	ORNITHOPODA
J	ALLOSAUROIDEA	**P**	MANIRAPTORA	**AB**	MACRONARIA	**AM**	IGUANODONTIA

Cladogram showing the postulated phylogenetic relationships of the main groups of dinosaurs. Synapomorphies from Rauhut (2003), Carrano and Sampson (2008), Carrano *et al*. (2012), Turner *et al*. (2012) on theropods, Langer and Benton (2006), Langer *et al*. (2010), and Yates *et al*. (2011) on basal saurischians and basal sauropodomorphs, Wilson (2005) on sauropods, and Butler *et al*. (2008) on ornithischians. Synapomorphies: **A DINOSAURIA**, foramen-sized post-temporal fenestra, epipophyses on anterior cervical vertebrae, elongate deltopectoral crest on the humerus, extensively perforated acetabulum, arched dorsal margin of ilium, femoral head inturned and distinctly offset from the shaft, asymmetrical fourth trochanter; **B SAURISCHIA**, narial fossa expanded, lacrimal folds over posterior part of antorbital fenestra, atlantal articulation facet in axial intercentrum concave, cervicals 3–6 longer than the axis, accessory articulations between trunk vertebrae (hyposphene–hypantrum), hand more than 40% of humerus + radius, distal carpal V absent, first phalanx of thumb longer than metacarpal I, twisted first phalanx in the thumb, manual

Continued

digit V lacks phalanges, ventral margin of iliac acetabulumn is straight; **C**, premaxilla-nasal suture below naris absent, large subnarial foramen, erect L-shaped lacrimal, cervicals 7–9 longer than the axis, radius less than 80% of the humerus, thumb claw at least as long as claw of digit 2, digit 2 in hand longer than digit 3, posterior margin of iliac blade is square in outline, large expansion of distal end of ischium; **D THEROPODA**, anterior tympanic recess in braincase, 4-branched palatine bone, additional articulation in middle of lower jaw, pleurocoels in cervicals, elongate and curved anterior wing on iliac blade, tibia bears a ridge at the proximal end for contact with fibula, metatarsal I reduced and attached to metatarsal II and does not reach the ankle joint proximally; **E AVEROSTRA**, tooth row ends at anterior rim of the orbit, pleurocoels in cervicals developed as foramina that invade the vertebral body, lesser trochanter in femur broadened and wing-like, distal end of femur well rounded, distal articular facet of tibia broadly triangular in outline, facet for tibia on the calcaneum; **F CERATOSAURIA**, external nares face anterolaterally, upper temporal fenestrae almost meet in front, quadrate foramen absent, neural spines of mid-caudals rod-like and vertical; **G TETANURAE**, maxillary fenestra in antorbital fossa, lesser trochanter proximally placed but lower than greater trochanter, sharp ridge on tibia for close attachment to fibula offset from proximal end; **H MEGALOSAUROIDEA**, ascending process of maxilla offset from anterior rim of maxilla, cervical centra strongly opisthocoelous, metacarpal I very stout and about as broad as long; **I AVETHEROPODA**, chevrons strongly curved, pubis obturator foramen large and oval, metatarsal III has deep notch at proximal end; **J ALLOSAUROIDEA**, scapulocoracoid anterior margin smoothly curved and uninterrupted across scapula–coracoid contact, pubic peduncle elongate, tibia fibular crest extends to proximal end of tibia as low ridge; **K ALLOSAURIA**, dentary posterior end straight or concave; sacral centra have pleuroceoel, coracoid posteroventral process tapers, pubis shows anterior expansion of distal end, ischium symphysis expanded as apron; **L CARCHARODONTOSAURIA**, pneumatic quadrate, pneumatic centra camellate; **M COELUROSAURIA**, maxillary antorbital fenestra more than 40% the length of the external antorbital fenestra, no serrations on premaxillary teeth, feathers; **N**, lacrimal lacks supraorbital crest, supratemporal fossa has only limited extension onto dorsal surfaces of frontal and postorbital, ilium antitrochanter is prominent; **O MANIRAPTORIFORMES**, absence of jugal recess in posteroventral corner of the antorbital fossa, absence of a coronoid ossification, absence of distinct interdental plates, cervical epipophyses proximal to postzygapophyseal facets, broad and short cervical ribs; **P MANIRAPTORA**, maxillary process of premaxilla reduced so that maxilla participates broadly in external naris, fused parietals, maxillary and dentary teeth without serrations anteriorly, premaxillary tooth crowns suboval to subcircular in cross section; **Q**, absence of a basisphenoid recess, downturned symphyseal end of dentary, subquadrangular coracoid, ischail shaft plate-like; **R**, quadratojugal L-shaped, prefrontal absent, parietals form low sagittal crest, coronoid reduced to a thin splint or absent, semilunate carpal; **S PARAVES**, large dentary and maxillary teeth, triangular subglenoid fossa in coracoid, humerus longer than scapula, calcaneum and astragalus fused to each other but not to tibia; **T DEINONYCHOSAURIA**, pterygoid flange well developed, nutirient foramina in deep groove on dentary, large surangular foramen, digit IV of the foot much longer than II and only slightly shorter than III; **U SAUROPODOMORPHA**, skull less than 50% length of the femur, anterior end of premaxilla deflected, lanceolate teeth with coarse serrations, at least ten cervical vertebrae forming elongate neck, dorsal and caudal vertebrae added to sacrum, forelimb at least 50% length of hindlimb, enormous thumb equipped with an enlarged claw; **V PLATEOSAURIA**, five premaxillary teeth, hand claw II is less than 75% the size of claw I in all dimensions; **W**, short hand, femur straight in anterior view, femoral head not offset; **X**, short lacrimal and triangular antorbital fenestra, jugal excluded from margin of antorbital fenstra, four premaxillary teeth, digit I is longest in the hand, phalanges in digits II and III shortened; **Y SAUROPODA**, four or more sacral vertebrae, forelimb is two-thirds the length of the hindlimb or more, metacarpal V enlarged and robust, femur is straight and lesser trochanter is reduced or absent, distal tarsals not ossified, foot claws deep and narrow, digit V of foot weight-bearing; **Z**, fourth trochanter reduced to a low rounded ridge; **AA NEOSAUROPODA**, upper temporal fenestrae separated by broad bone bar, external mandibular fenestra closed, marginal tooth denticles absent, two or fewer carpal bones; **AB MACRONARIA**, external naris broader than orbit, coronoid process on lower jaw, 17 or fewer dentary teeth, posterior dorsal centra opisthocoelous, metacarpal I longer than metacarpal IV; **AC TITANOSAURIFORMES**, mid-cervical centra elongate, dorsal ribs with pneumatic cavities, metacarpal I distal condyle undivided and perpendicular to shaft, iliac preacetabular process semicircular; **AD ORNITHISCHIA**, maxilla buccal emargination, anterodorsal margin of coronoid process formed by posterodorsal process of dentary, maxillary and dentary teeth are tall and blade-like, not recurved, adjacent tooth crowns overlap, crown expanded above root, and greatest crown height in middle of maxillary and dentary tooth rows; **AE**, distal tibia has elongate posterolateral process and backs fibula; **AF GENASAURIA**, dentary symphysis spout-shaped, premaxillary teeth show moderately expanded crown, hand shorter than 40% humerus + radius, loss of strongly curved hand claws; **AG THYREOPHORA**, ridge on lateral surface of surangular is a strong anteroposteriorly extended ridge; **AH**, three palpebrals and supraorbitals incorporated into orbital margin, basipshenoid shorter than basioccipital, pedal unguals wide and hoof-like; **AI EURYPODA**, quadratojugal transversely expanded and triangular, intercentrum of atlas and neural arches fused, epipophyses on anterior cervicals, scapula near parallel-sided, preacetabular process of ilium elongate and deflected more than 30° from midline, femur straight, metatarsals contact at proximal ends and spread distally, metatarsal I reduced and proximally splint-like, fourth toe has four or fewer phalanges; **AJ CERAPODA**, postacetabular process more than 35% of total ilium length, metatarsal 1 is robust; **AK MARGINOCEPHALIA**, parietosquamosal shelf, premaxilla-vomer contact excluded by maxillae meeting in midline, premaxillary teeth show moderate crown expansion above root, scapula blade elongate and strap-like, pubis shaft less than half length of ischium, postpubic shaft very short; **AL ORNITHOPODA**, fossa-like depression on premaxilla-maxilla boundary, paired frontals narrow and elongate, small fenestra located dorsally on surangular-dentary joint; **AM IGUANODONTIA**, dorsal and ventral margins of dentary subparallel, anterior (extensor) intercondylar groove on distal end of femur, lateral condyle of distal femur strongly inset medially and reduced. Abbreviations: E, Early; Eoc, Eocene; L, Late; Mi, Miocene; Mid, Middle; Neo, Neogene; Ol, Oligocene; P, Paleocene; Pl, Pliocene/Pleistocene. Dashed lines and star symbols indicate extinction events.

All other theropods, the tetanurans, are diagnosed by a number of features. They have a large opening in the maxilla, termed the **maxillary fenestra** (Figure 8.5), and the tooth row does not extend behind the antorbital fenestra. The dorsal vertebrae are **pleurocoelous**, in other words, they have cavities on the sides, and there are modifications of the femur and tibia.

The basal tetanurans were all large carnivores and they form a series of subclades, Megalosauroidea, Metriacanthosauridae, and Allosauroidea (Rauhut, 2003; Carrano *et al*., 2012), all sharing the blunt shape of the maxilla, **opisthocoelous** cervical centra (the posterior face of the vertebral centrum is concave) and a very stout first metacarpal. Megalosauroids comprise megalosaurids and spinosaurids. The megalosaurids (Benson, 2010a,b) include *Megalosaurus* from the Middle Jurassic of Europe, its relative, *Dubreuillosaurus* from the Middle Jurassic of Europe (Figure 8.5(a)), as well as other Middle and Late Jurassic forms from Europe, Africa, and China. *Megalosaurus* famously has the distinction of being the first dinosaur ever named, in 1824.

The spinosaurids, first reported from Egypt in 1915, are represented all over North Africa by their characteristic teeth. More complete specimens, of *Baryonyx* from England (Charig and Milner, 1997) and *Suchomimus* from Niger (Sereno *et al*., 1998), show the spinosaurid characters of long spines on their dorsal vertebrae, a huge claw on the hand, and an elongate, crocodile-like skull (Figure 8.5(c)). Were these regular predators on other dinosaurs, or did they perhaps snap up fish out of ponds and rivers? Putative stomach contents include fish, dinosaurs, and pterosaurs. Biomechanical analysis (Cuff and Rayfield, 2013) shows that the

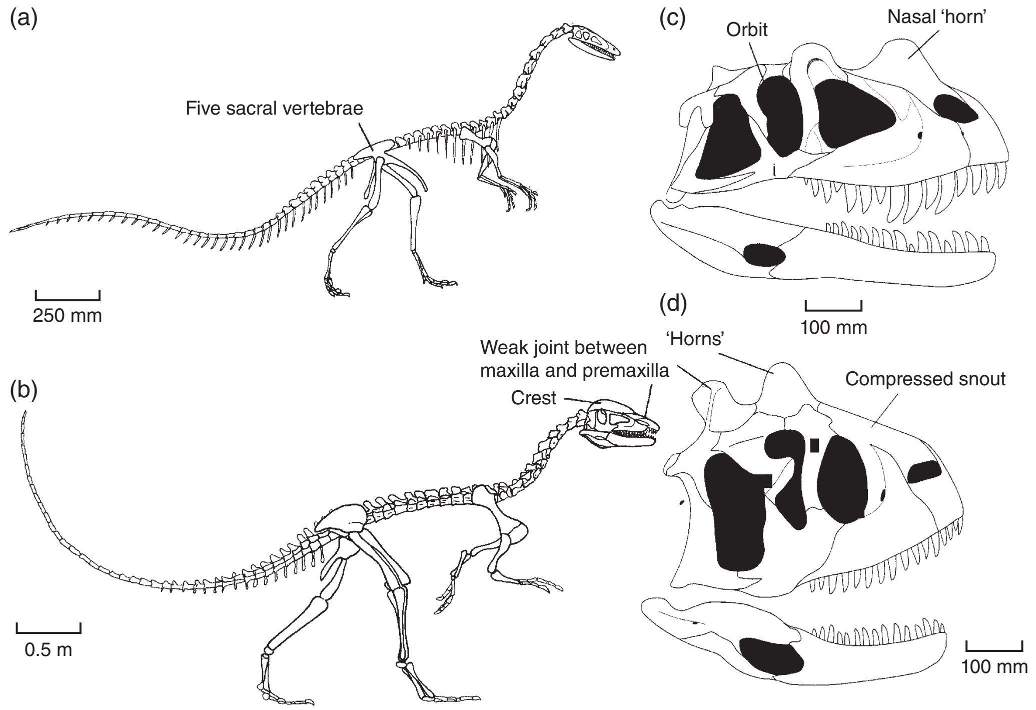


Figure 8.4 Coelophysoids and ceratosaurs: (a) a coelophysoid and (b–d) ceratosaurs, of Triassic (a), Jurassic (b,c) and Cretaceous (d) age: (a) *Coelophysis*; (b) *Dilophosaurus*; (c) *Ceratosaurus* skull; (d) *Carnotaurus* skull. Source: (a) Adapted from Cokbert (1989). (b) Adapted from Welles (1984). (c,d) O. Rauhut, Ludwig-Maximiliens Universität, München, Germany. Reproduced with permission.

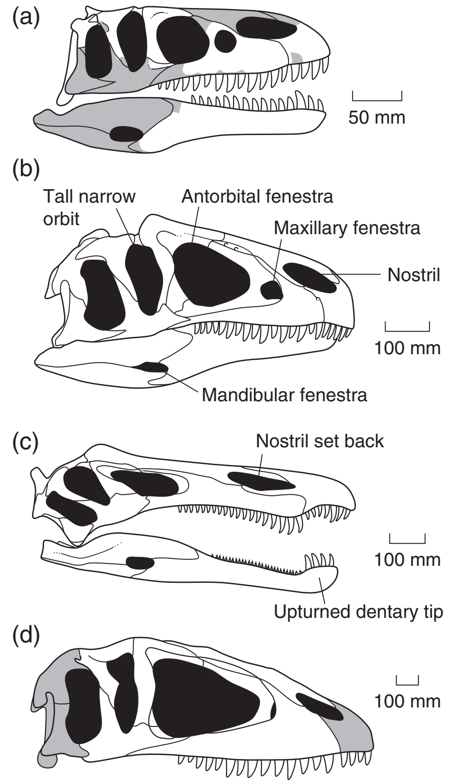


Figure 8.5 Megalosauroid and allosauroid skulls from the Jurassic (a,b) and Cretaceous (c,d): (a) *Dubreuillosaurus*; (b) *Allosaurus*; (c) *Suchomimus*; (d) *Carcharodontosaurus*. Unknown areas are shaded. Source: O. Rauhut, Ludwig-Maximiliens Universität, München, Germany. Reproduced with permission.

unusual rostral morphology of spinosaurs conferred some advantage in dorsoventral bending resistance, yet *Spinosaurus* and *Baryonyx* were poorly equipped to resist mediolateral bending and torsion. When size is accounted for, *Baryonyx* performs mechanically differently from the gharial, whereas *Spinosaurus* does not. This finite element analysis study (see Box 2.3) suggests that the spinosaurs were not obligate piscivores, and their diet was determined by the body size of different individuals.

Tetanurans other than the Megalosauroidea are termed Avetheropoda (Carrano *et al*., 2012; see Box 8.1), and the first avetheropods are the Allosauroidea. This clade includes four families (Brusatte and Sereno, 2008; Benson *et al*., 2010; Carrano *et al*., 2012), the Metriacanthosauridae, Allosauridae, Neovenatoridae, and Carcharodontosauridae. The Metriacanthosauridae are a small clade of Middle Jurassic to Early Cretaceous theropods from Europe and China. The focal taxon is *Metriacanthosaurus* from the Late Jurassic of England, a genus that used to be confused with *Megalosaurus*. Metriacanthosaurids all share a straight posterior margin of the iliac postacetabular process, and an angle of less than 60° between the long axes of the pubic shaft and its terminal 'boot'. Possible metriacanthosaurids include *Siamotyrannus* from the Early Cretaceous of Thailand and *Sinraptor* from the Late Jurassic of China.

The Allosauridae are represented primarily by *Allosaurus* from the Late Jurassic of North America (Figure 8.5(b)), which is 11–12 m long (Madsen, 1976). The skull is short and narrow from side to side. The orbit is high and smaller than the antorbital fenestra, there are heavy crests over the orbits, and the mandibular fenestra is much reduced. The Neovenatoridae are a new family (Benson *et al*., 2010), focused around *Neovenator* from the Early Cretaceous of England, and including large theropods from the mid-Cretaceous of most other continents (Zanno and Makovicky, 2013b). These are diagnosed by certain features of the vertebrae, as well as a short and broad scapula, a pneumatic ilium, and modifications of the femur and tibia. Most neovenatorids were as large as *Allosaurus*, but some such as *Fukuiraptor* from Japan were smaller and had some characters (slender toes, pneumatic skeleton) reminiscent of maniraptorans (see Section 8.3.4). The fourth allosauroid subclade, the Carcharodontosauridae, are best known from Africa. The giant *Carcharodontosaurus* from Morocco had a skull 1.6 m long (Figure 8.5(d)) and was one of the largest carnivorous dinosaurs (Sereno *et al*., 1996).

The intriguing new discoveries of tetanuran theropods and other dinosaurs in Africa and in Madagascar have been the source of active debates about their palaeobiogeographical significance, and especially whether Cretaceous dinosaurs began to show signs of endemism as the continents separated (see Box 8.2).

8.3.3 Coelurosauria

The remaining theropods form the major clade Coelurosauria (Rauhut, 2003; Turner *et al*., 2012), and these share a large number of derived characters with each other and with the birds (see Box 8.1), most notably an enlarged maxillary fenestra and no

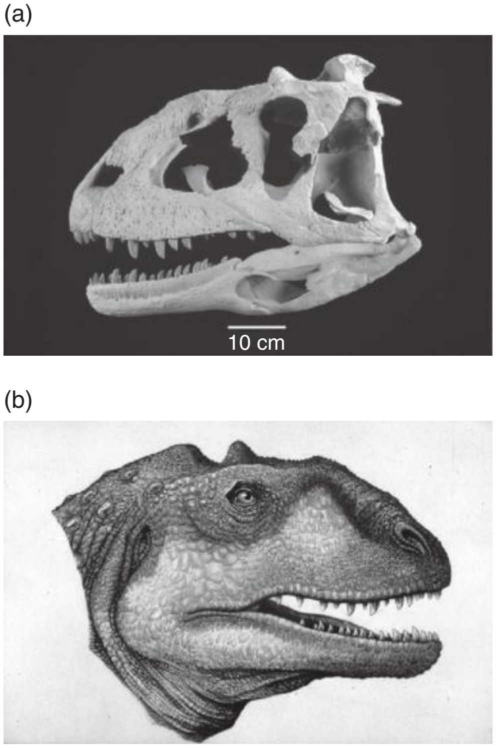
BOX 8.2 OUT OF AFRICA; AFRICA ISOLATED?

The dinosaurs of Africa and Madagascar have attracted intense attention in recent years (e.g. Carrano *et al*., 2002; Sereno *et al*., 2004), and arguments have been made that these faunas were special. For example, some of the dinosaurs from the Late Cretaceous of Madagascar seem to share closer similarities with those from India and South America than those from Africa. The abelisauroid theropods *Majungasaurus* and *Masiakasaurus* from Madagascar (see illustration) both had close relatives in South America (see Figure 8.4(d)). These, together with members of other groups (e.g. sauropods, mammals and crocodiles), suggest close faunal links between South America and India–Madagascar, perhaps indicating a dispersal route via Antarctica that supposedly avoided Africa (Sampson *et al*., 2001).

This might seem a beguiling idea, and it might well be true, but the weakness is that there is no record of comparable dinosaurs in the Late Cretaceous of Africa. A classic statement of scientific method is that ‘absence of evidence does not indicate evidence of absence’. When, and if, rich faunas of Late Cretaceous dinosaurs are found in various locations in Africa, these would provide a test of the African-isolation hypothesis. Until then, palaeontologists should beware of constructing overly elaborate palaeobiogeographic hypotheses (Benson *et al*., 2010; Carrano *et al*., 2012).

It is certainly known that Africa remained linked to South America and other southern hemisphere land masses through most of the Early Cretaceous (see Figure 8.2). Madagascar broke away from the main African land mass by 120 Myr ago and South America followed by 100 Myr ago. However, most dinosaurian clades that have figured in the debates about African–Madagascan disjunction, subclades of Tetanurae and Sauropoda, had originated in the Middle or Late Jurassic, and were often essentially worldwide in distribution.

This is confirmed by consideration of Jurassic and Early Cretaceous dinsoaurs from Africa. For example, the Late Jurassic Tendaguru fauna of Tanzania is very like that of the Morrison Formation in the mid-central USA, sharing closely related genera such as the theropod *Ceratosaurus*/ ‘ceratosaur’, the sauropods *Barosaurus*/ *Tornieria* and *Brachiosaurus*/ *Giraffatitan* and the ornithopod *Dryosaurus*/ *Dysalotosaurus*. The spinosaurid theropod *Suchomimus* from Niger (see Figure 8.5(c)) is virtually indistinguishable from *Baryonyx* from England. Likewise, the carcharodontosaurid *Carcharodontosaurus* from Morocco (see Figure 8.5(d)) is similar to *Giganotosaurus* from Argentina and *Acrocanthosaurus* from North America. The sparse record of dinosaurs from subsaharan Africa in the Cretaceous is currently inadequate to test the fascinating idea that faunas might have become more geographically differentiated as the continents split apart.



The Madagascan abelisaurid theropod *Majungasaurus*, reconstructed skull (a) and restored head (b) in lateral view. Source: S. Sampson, Denver Museum of Nature and Science, Denver, CO, USA and W. Parsons (artist), Stony Brook University, Stony Brook, NY, USA. Reproduced with permission.

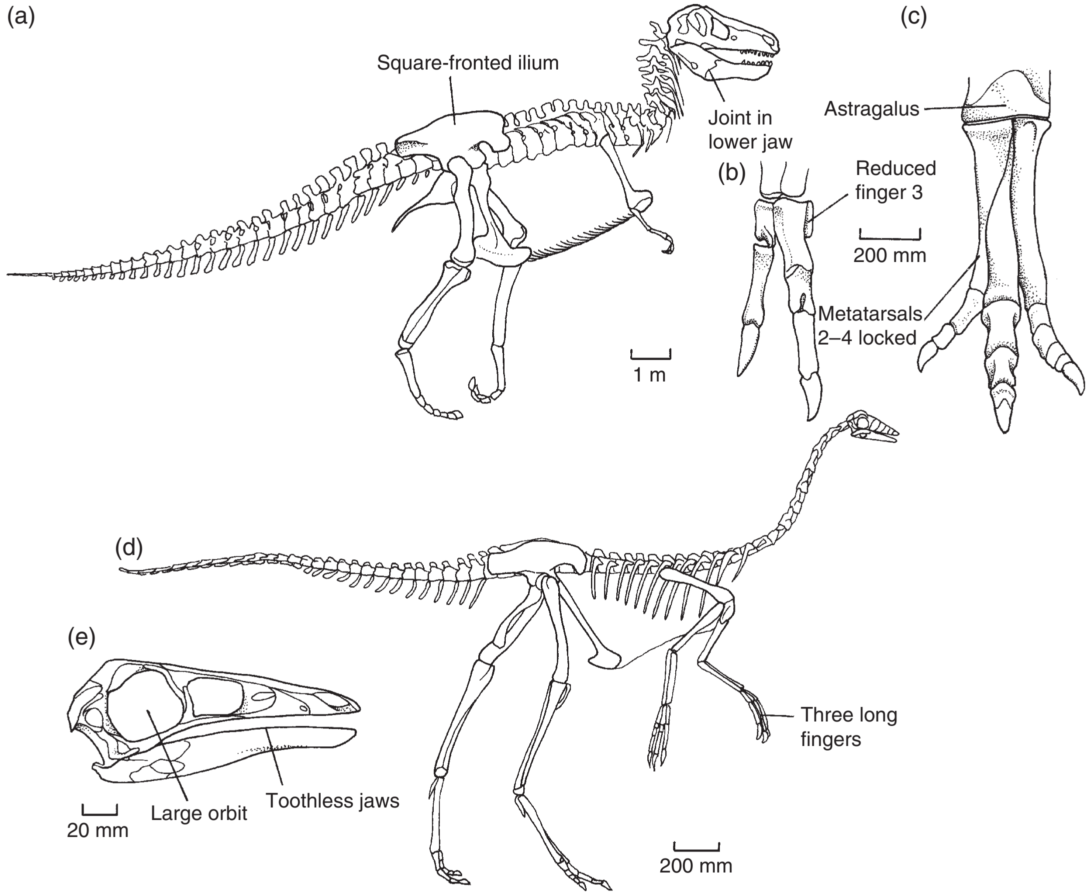


Figure 8.6 Coelurosaurian theropods: (a–c) tyrannosauroids and (d,e) ornithomimids, all from the Cretaceous: (a) skeleton of *Tyrannosaurus*; (b) hand of *Tarbosaurus*; (c) foot of *Albertosaurus*; (d) skeleton of *Struthiomimus*; (e) skull of *Dromiceiomimus*. Source: (a) Adapted from Newman (1970). (b,c) Adapted from Norman (1986). (d,e) Adapted from Russell (1972).

serrations on the premaxillary teeth. Many coelurosaurs also have feathers of various kinds (see Section 8.3.4). Relationships within Coelurosauria are debated, especially the sequence of clades along the lineage to birds, but Tyrannosauroidea appears to be the sister group to the other clades (Turner *et al*., 2012).

The tyrannosauroids are arguably the most notorious dinosaurs of all, the subject of every young person's enthusiasm or nightmares. Tyrannosauroids have nonetheless been studied intensively (Brochu, 2003a; Larson and Carpenter, 2008; Brusatte *et al*., 2010; Hutchinson *et al*., 2011; Brusatte *et al*., 2012a; Parrish *et al*., 2013). Members of the clade are best known from the Late Cretaceous of North America and central Asia, and most were large or very large. *Tyrannosaurus rex*, at some 14 m long and weighing perhaps 10 tonnes, has been claimed as the largest carnivorous dinosaur of all time. Members of other clades, such as the ceratosaur *Ceratosaurus* and the carcharodontosaurids *Carcharodontosaurus* and *Giganotosaurus* may have been equally huge. Estimates from scaling rules (Therrien and Henderson, 2007) suggest the last two reached 13 m in length and 14 tonnes. A large *Spinosaurus* may have measured 12.6 m long and weighed 12 tonnes.

Tyrannosaurus has a large head (Figure 8.6(a)) and jaws lined with massive teeth that were almost circular in cross section. These attest to powerful bite forces. Tyrannosauroids were probably both active hunters and scavengers, and they could certainly bite! Bones from the pelvis of a *Triceratops* (see Section 8.4.6) show puncture marks up to 37 mm deep made by *Tyrannosaurus* teeth, and these indicate a bite force of up to 13,400 newtons, as powerful as the strongest bite of any living carnivore (Erickson *et al*., 1996). Multi-body dynamic modelling indicates even more dramatic bite forces, of 35,000–57,000 newtons (Bates and Falkingham, 2012). This has provided opportunities for exploration of the biomechanical properties of the *T. rex* skull using finite element analysis (see Box 2.3). Tyrannosaur stomach contents show that they digested bones with acid, as modern crocodiles do, although not to such an extent, and a 1-m-long tyrannosaur coprolite full of *Edmontosaurus* bones (Chin *et al*., 1998) and another with bones and putative muscle tissue offer further intimate evidence of their feeding activities.

Tyrannosauroids had tiny forelimbs equipped with either two or three fingers (Figure 8.6(b)), but these would seem to have been quite useless as they could not even reach the mouth. *Tyrannosaurus* may have used them to push its head and torso up from a lying position, by providing a push while the head was thrown back and the legs straightened. Tyrannosauroids have a specialized ankle structure, the **arctometatarsus** (Figure 8.6(c)), in which the three central metatarsals (numbers 2–4) are firmly pressed against each other. Instead of being round in cross-section, the metatarsals are triangular, and metatarsal 3 is 'squeezed' at its upper end in such a way that it barely reaches the astragalus above, or is excluded entirely from contact with it. The arctometatarsus may have had a dynamic function during running, where the three metatarsals bunched tightly at maximum loading and then sprang slightly apart as the foot was raised. This gave tyrannosauroids a stronger metatarsus than in some other theropods which lack the arctometatarsus, but not as rigid as in birds, in which the three elements have fused into one (Snively and Russell, 2003).

But could *T. rex* run fast or not? It may have been able to sprint in the Hollywood films, but in life it probably could not have achieved more than a fast walk. Hutchinson and Garcia (2002) show that running speed depends on the mass of the extensor muscles in the hindleg. Scaling up a chicken to the 6-tonne mass of *T. rex* means it would have to devote 99% of its body mass to leg muscles, which is clearly impossible. With more reasonable leg muscle estimates, *T. rex* could have achieved a fast walk at 11 m s^{-1} (40 km h^{-1} or 25 m.p.h.), but not the wilder speed of 72 km h^{-1} that had been suggested.

Two further subclades of coelurosaurs precede the major clade Maniraptora (see Box 8.1). The compsognathids include *Compsognathus* from the Late Jurassic of Germany, a very small dinosaur, at 0.7–1.4 m long. Other European compsognathids probably include *Scipionyx* from Italy, a small juvenile that, unusually, is preserved together with its intestine and other internal organs intact (Dal Sasso and Maganuco, 2011). Its close relative from China, *Sinosauropteryx*, has feathers (Figure 8.7(a)), and it has been claimed that these feathers were ginger in colour. How on Earth can palaeontologists determine the colour of ancient feathers with any confidence (see Box 9.1)?

The ornithomimids of the Early to Late Cretaceous (Russell, 1972; Makovicky *et al.*, 2004) were highly specialized theropods with a slender ostrich-like body and long arms and legs (see Figure 8.6(d)). The hands in many ornithomimids have three powerful fingers that may have been used for grasping food items. The lightly built body indicates that *Struthiomimus* could have run fast and speeds of 35–60 km h^{-1} have been estimated. The skull is completely toothless in later forms (see Figure 8.6(e)) and

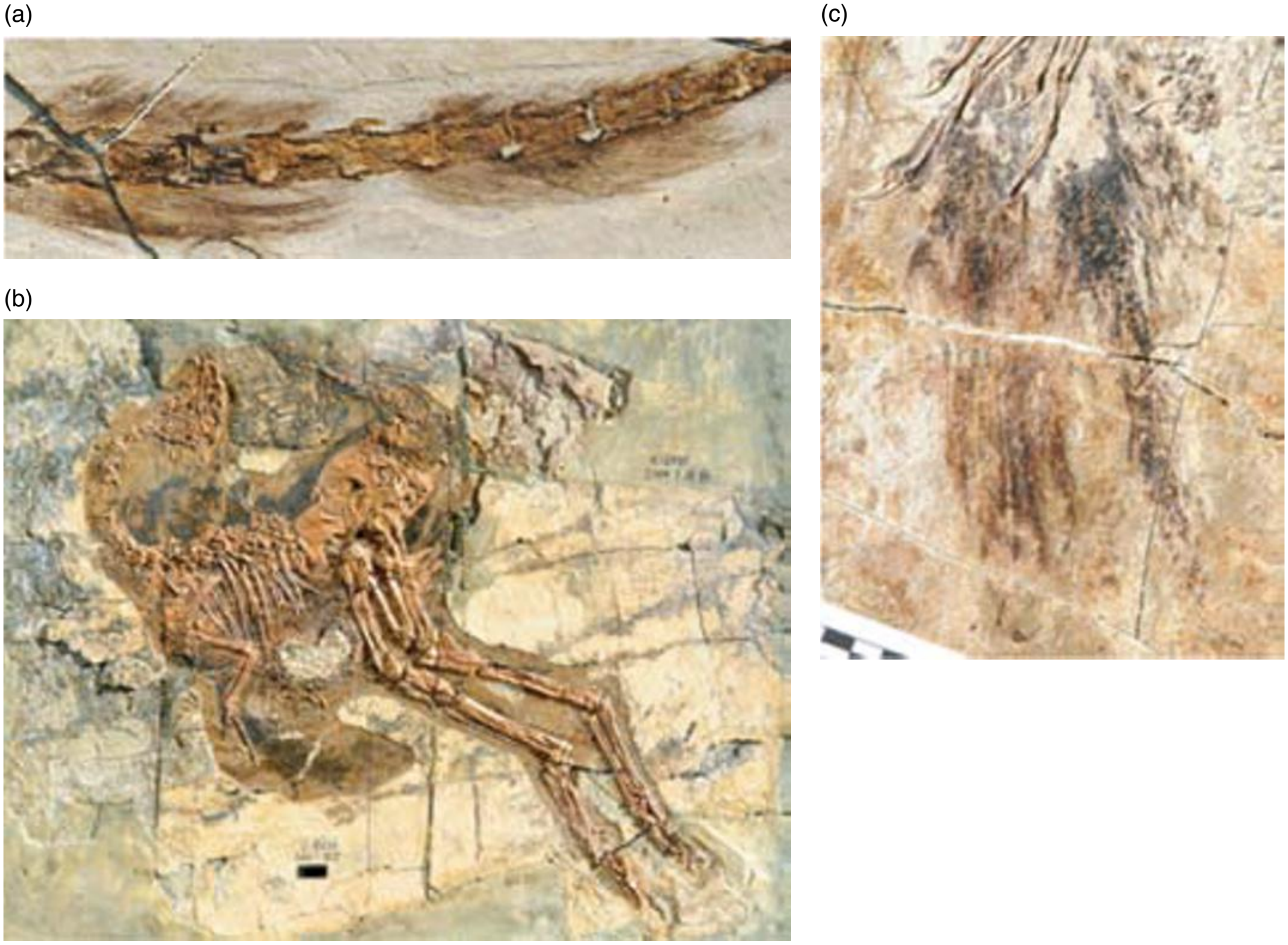


Figure 8.7 Theropods from the Yixian Formation of Liaoning Province, NE China: (a) filamentous feathers around the tail of *Sinosauropteryx*; (b) complete specimen of *Caudipteryx*, showing the presence of filamentous feathers, as well as contour feathers on the arm and tail; (c) contour feathers from the tail of *Caudipteryx*. Source: Z. Zhonghe, Institute for Vertebrate Paleontology and Paleoanthropology, Beijing, China. Reproduced with permission.

this has led to considerable discussion of their possible diets – could they have fed on small prey animals such as lizards or mammals, or even plants? Their toothless jaws were covered in life with a keratinous beak that bore vertical ridges inside, just as in a duck: did they dabble in ponds for small prey and floating plants? Barrett (2005) has reviewed the evidence, and finds those diets extremely unlikely; ornithomimids were probably regular herbivores, and it seems increasingly likely that a number of Cretaceous theropods adopted such a diet (Zanno and Makovicky, 2011).

8.3.4 Maniraptora

The most derived theropods, the Maniraptora (see Box 8.1), include the alvarezsauroids, therizinosauroids, oviraptorosaurs, troodontids, dromaeosaurids and birds. In the first serious cladistic analysis of Theropoda, Gauthier (1986) identified the dromaeosaurids and troodontids as close relatives of birds, forming the clade Maniraptora, and this has been widely confirmed. The other three maniraptoran subclades have had a chequered history: the alvarezsauroids and oviraptorosaurs have sometimes been identified as birds, and the therizinosauroids have enjoyed the wildest array of phylogenetic assignments of any dinosaurs (see below). The dromaeosaurids, troodontids, and birds form the clade Paraves, and they are considered in the Birds chapter (see Section 9.1).

The alvarezsauroids are a small group of some 20 genera, known largely from the Cretaceous of Mongolia, China, Argentina and the USA (Chiappe *et al*., 2002; Choiniere *et al*., 2010; Nesbitt *et al*., 2011). The best-known alvarezsauroid is *Mononykus* from Mongolia (Perle *et al*., 1993), which has a small bird-like head, a short body and long tail, a small pelvis with pubis and ischium that are not fused, a splint-like fibula and a reduced forearm (Figure 8.8(a)). The long slender hindlimb, with a femur shorter than the tibia, shows that *Mononykus* was a fast runner. The most extraordinary feature about *Mononykus* is the tiny arm (Figure 8.8(b)) with a short humerus, ulna and radius, a massive fused wrist consisting mainly of the metacarpal 1 and a short powerful digit 1, as well as reduced digits 2 and 3. The function of this extraordinary little arm is a mystery. Perhaps it was used for scraping and tearing plant food, or for opening termite mounds.

Early therizinosauroids looked like any typical 2 m-long theropod, but later forms such as *Alxasaurus* (Figure 8.8(c)) from Mongolia and China, were the most bizarre theropods of all (Zanno, 2010). Their affinities were for a long time problematic; amazingly, they had been identified at times as turtles, theropods, or something between saurischians and ornithischians. They were large animals, 4–5 m long, weighing 1–7 tonnes (Zanno and Makovicky, 2013a), and with a massive pelvis and short tail. The forelimbs are long and the hands and claws extremely elongated. The neck is powerful, but the skull is small

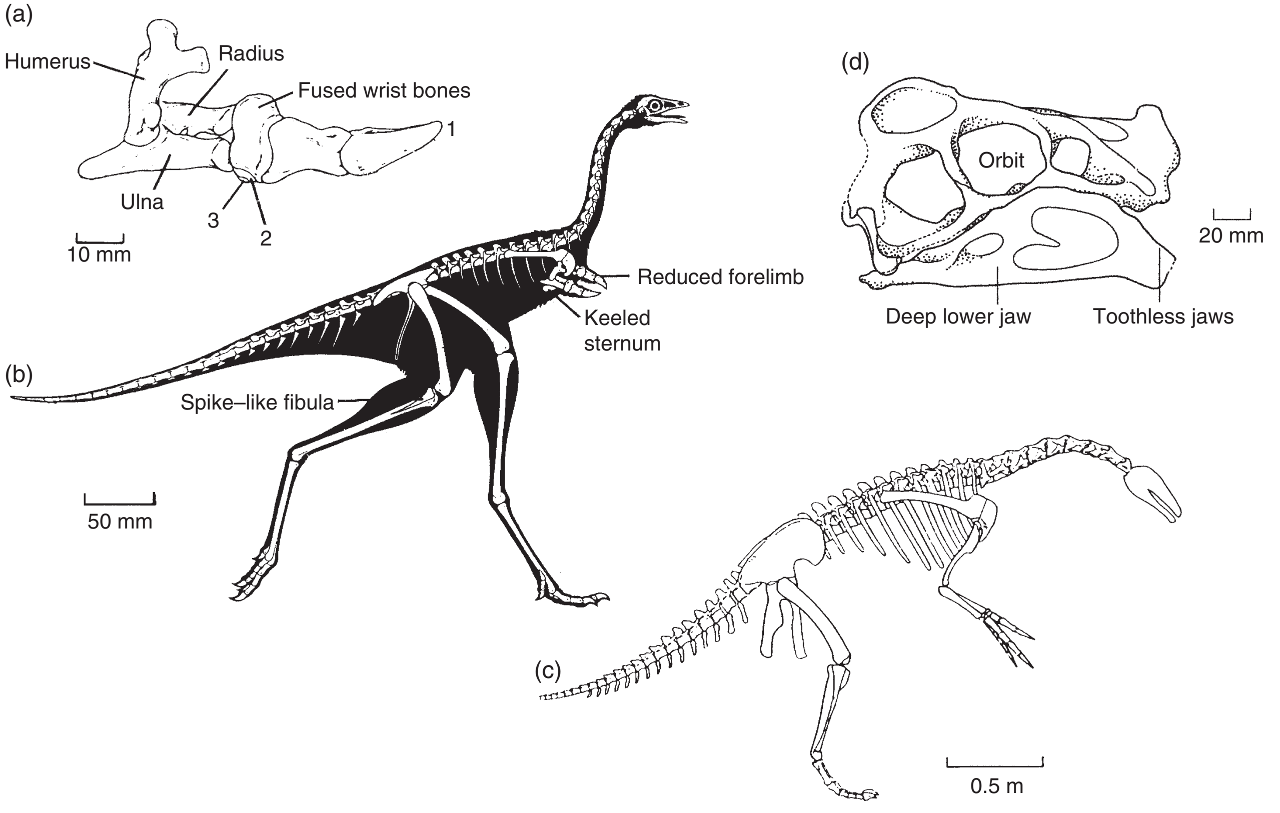


Figure 8.8 Basal maniraptorans, all from the Cretaceous: (a,b) the alvarezsauroid *Mononykus*, reconstructed skeleton and arm in lateral view; (c) the therizinosauroid *Alxasaurus*; (d) skull of the oviraptorosaur *Oviraptor* from the Late Cretaceous of Mongolia. Source: (a,b) Adapted from Perle *et al.* (1993). (c) Adapted from Russell and Dong (1993). (d) Adapted from Zittel (1932).

and equipped with apparently rather feeble peg-like teeth and a toothless beak at the front. Russell and Dong (1993) suggested that the therizinosauroids were foliage-eaters, rather like certain mammals, the giant ground sloths and chalicotheres (see Sections 10.5.3, 10.10.3). *Therizinosaurus* sat balanced tripodally by its massive pelvis and short tail and raked in tree branches with its long slender claws, which it passed to its toothless beak. The snout was covered with a keratinous bneak, like a bird, and this functioned as much to stabilize the jaws as to cut tough plant stems (Lautenschlager *et al.*, 2013).

Oviraptorosaurs include a broad range of Early Cretaceous forms, including the small, feathered *Caudipteryx* (Ji *et al.*, 1998) and the buck-toothed *Incisivosaurus* from China, and the giant, 8-m-long *Gigantoraptor* from Mongolia (Xu *et al.*, 2007). Earlier finds include the oviraptorids and ingeniids from the Late Cretaceous of Mongolia and China and the caenagnathids from the Late Cretaceous of North America (Osmólska *et al.*, 2004). *Oviraptor* from the Late Cretaceous of Mongolia has an odd-looking skull (Figure 8.8(d)), high and full of openings. The snout is very much shortened and it lacks teeth. This dinosaur has famously been given an undeserved bad name: it was called *Oviraptor*, meaning ‘egg thief’ because the type skeleton was found in 1923 lying on top of a nest containing eggs. A further skeleton of *Oviraptor* was found in 1993 (Norell *et al.*, 1995), also located on top of a nest, but this time an embryo was found inside one of the eggs and it turned out to be an unhatched *Oviraptor*. Far from being an egg thief, these *Oviraptor* individuals were apparently brooding their eggs. The most remarkable oviraptorosaur find was one of the first feathered dinosaurs reported from China (Ji *et al.*, 1998) showing a range of feather types (see Figure 8.7(b,c)).

Paraves are considered in Section 9.1.1.

8.3.5 Basal Sauropodomorpha

The Sauropodomorpha, the second major saurischian clade, includes the sauropods, the largest animals ever to live on land (Curry Rogers and Wilson, 2005; Klein *et al.*, 2011). The Sauropodomorpha arose in the Late Triassic and the early forms of the Late Triassic and Early Jurassic were formerly termed prosauropods. This would be a paraphyletic group, as most early sauropodomorphs are outgroups to the Sauropoda (see Box 8.1).

Thecodontosaurus, a basal sauropodomorph from the Late Triassic of England (Figure 8.9), a lightly built herbivore 2.5 m long (Benton *et al.*, 2000a; Yates, 2003b), shows all the basic hallmarks of the clade: a small skull (c. 5% of body length), a downwards curve to the tip of the dentary (Figure 8.9(b)), lanceolate teeth with serrated crowns (see Figure 8.1(d)), a long neck with ten or more cervical vertebrae, a huge thumb claw and no claws on fingers 4 and 5 (Figure 8.9(a)) and a short blade on the ilium. More derived ‘prosauropods’ include *Plateosaurus* (see Section 8.1) as well as animals such as *Riojasaurus* from Argentina and *Melanorosaurus* from South Africa, which were obligatory quadrupeds up to 10 m long.

Other basal sauropodomorphs include forms such as *Saturnalia* from the Santa Maria Formation of Brazil that sit near the base of the clade (Langer and Benton, 2006; Langer *et al.*, 2010), *Plateosaurus* and relatives from Europe (see Section 8.1), the giant riojasaurids such as *Riojasaurus* from the latest Triassic of Argentina, the Early Jurassic massospondylids, and others (Yates, 2003a,b; Yates *et al.*, 2011).

The sauropods appeared first in the Late Triassic of South Africa (Yates and Kitching, 2003) and radiated in the Late Triassic and Early Jurassic with forms such as *Antetonitrus* from South Africa, *Vulcanodon* from Zimbabwe, *Shunosaurus* from China, and *Barapasaurus* from India. *Shunosaurus* from the Middle Jurassic of China is known from several skeletons, and the skull (Figure 8.10(a)) shows a sophisticated dental apparatus, with differing tooth shape along the jaw and evidence of tooth-to-tooth occlusion. Occlusion, in which upper and lower teeth have interlocking surfaces, is well known in mammals (see Section 10.1.2), but rare in reptiles, and is

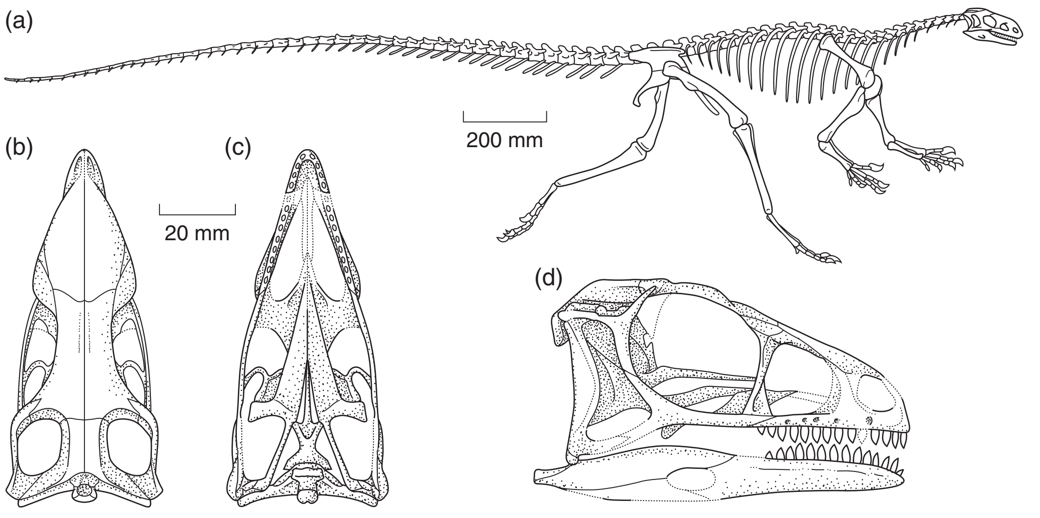


Figure 8.9 The basal sauropodomorph *Thecodontosaurus*, from the Late Triassic: skeleton in lateral view; (b–d) skull in ventral, dorsal and lateral views. Source: (a) Adapted from Benton *et al.* (2000). (b-d) A. Yates, Museum and Art Gallery of the Northern Territory, Darwin, Australia. Reproduced with permission.

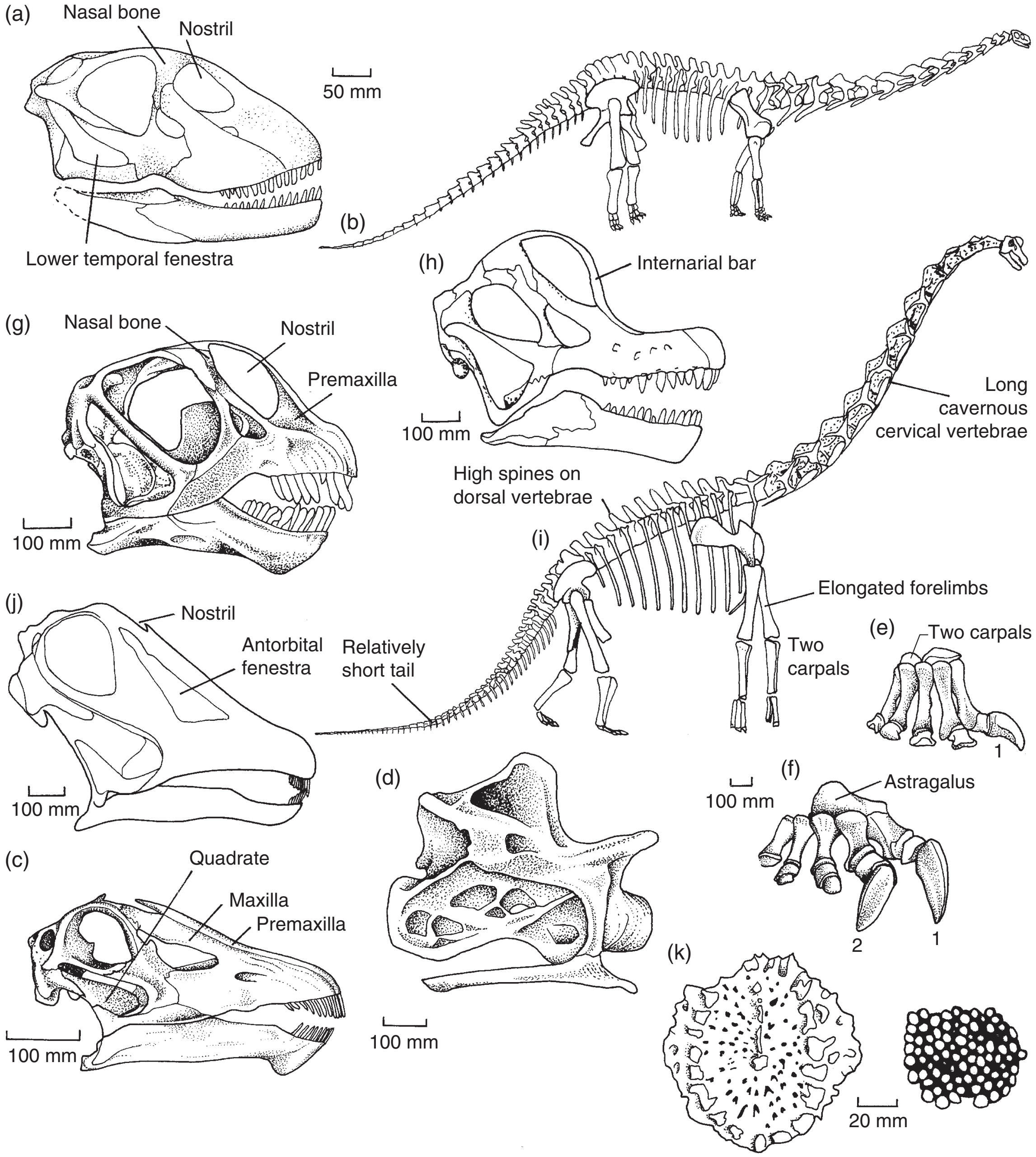


Figure 8.10 Sauropods, all Jurassic in age, except (j,k), Cretaceous: (a) skull of the euhelopodid *Shunosaurus*; (b) the cetiosaurid *Cetiosaurus*; (c) skull of the diplodocid *Diplodocus*; (d) cervical vertebra of *Diplodocus*; (e) hand and (f) foot of *Diplodocus*; (g) skull of the camarasaurid *Camarasaurus*; (h,i) skull and skeleton of the brachiosaurid *Giraffatitan*; (j) skull of the titanosaurid *Antarctosaurus*; (k) armour plate and armour pattern, of the titanosaurid *Saltasaurus*. Source: (a) Adapted from Dong and Tang (1984). (b) Adapted from Crowther and Martin (1976). (c,d) Adapted from Hatcher (1901). (e,f) Adapted from Coombs (1975). (g–i) Adapted from Lapparent and Lavocat (1955). (j,k) Adapted from Bonaparte (1978).

important in improving the efficiency of food processing. These basal sauropods had four fused sacral vertebrae, a straight femur and seemingly no distal tarsals. These features mark the beginning of modifications to the sauropod postcranial skeleton caused by their massive weight. Next in the phylogeny are the Mamenchisauridae, typified by *Mamenchisaurus* from the Late Jurassic of China, which has an immensely long neck, relatively the longest of all the sauropods.

8.3.6 Neosauropoda

Sauropod phylogeny has been much debated, but most authors agree on the separation of these basal forms from the major clade Neosauropoda, which splits into subclades Diplodocoidea and Macronaria (see Box 8.1; Wilson, 2005; Upchurch *et al.*, 2007). Despite intense endeavour, one of the most famous early sauropods, *Cetiosaurus* from the Middle Jurassic of England, has defied phylogenetic placement. This was the first sauropod ever named, by Sir Richard Owen, in 1841. The skeleton (Figure 8.10(b)) shows an elongate neck comprising more than 12 cervical vertebrae. There are five or six sacral vertebrae, the limbs are rather pillar-like, as in elephants, an adaptation for weight-supporting. The fingers and toes are much shortened and phalanges lost (Upchurch and Martin, 2003). In *Cetiosaurus*, the external mandibular fenestra in the lower jaw has been lost and the lower temporal fenestra lies completely beneath the orbit.

The Diplodocoidea (Wilson, 2005; Whitlock, 2011) includes the diplodocids from the Late Jurassic of North America, the dicraeosaurids from the Late Jurassic of Africa and Early Cretaceous of South America, and the rebbachisaurids from the Cretaceous of Africa, South America, and Europe. The diplodocids, such as *Diplodocus* (Figure 8.10(c)), have a steeply sloping quadrate and a long broad snout with a small number of cylindrical pencil-like teeth at the front. The jutting teeth may have been used in a pincer-like fashion to strip vegetation. Additional neosauropod characters in the skull are: the nostrils and nasal bones have moved well back and the skull roof is shortened, and the lower temporal fenestra lies largely beneath the orbit. *Diplodocus* has a massively long neck, comprising 6 m of its 27 m total body length, and consisting of at least 15 elongate cervical vertebrae with complex struts and lamellae indicating internal pneumatization (Figure 8.10(d)). The limbs of *Diplodocus* seem relatively slender, but the hands and feet (Figure 8.10(e,f)) are shortened weight-supporting structures. The wrist contains only two carpals, and the ankle generally only the astragalus, all the other elements having been lost or present only as cartilage. The first finger and the first two toes bear long claws that may have been used in digging, but the other digits bear only small hoof-like nubbins of bone.

The Macronaria (D'Emic, 2012; Carballido and Sander, 2013; Mannion *et al*., 2013) includes the camarasaurids, brachiosaurids, euhelopids and titanosaurians. The camarasaurids and brachiosaurids share a skull pattern (Figure 8.10(g,h)) in which there is an arched internarial bar formed by very narrow premaxillae between the enlarged nostrils and a clearly defined snout. *Giraffatitan* from the Late Jurassic of Tanzania is one of the largest dinosaurs known from a reasonably complete skeleton (Figure 8.10(i)). It is 23 m long, its head reaches 12 m above the ground, and its weight has been estimated as 50 tonnes. *Giraffatitan*, and its relative *Brachiosaurus* from North America, are dinosaurian giraffes, designed to reach high into trees, and the body shape differs from other sauropods in that the forelimbs are as long as the hindlimbs. The neck is greatly elongated and the cervical vertebrae are cavernous in order to save weight. There are massively elongated neural spines on the dorsal vertebrae, which indicate that *Giraffatitan* had powerful muscles and ligaments to lift its crane-like neck up and down.

The titanosaurians (Wilson and Upchurch, 2003; Curry Rogers, 2005; D'Emic, 2012) are best represented in the Late Cretaceous of South America, but they are known from all continents, and comprise 70 or more genera. These ranged in size from relatively small (*Rocasaurus*, 8 m) to truly gigantic (*Argentinosaurus*, 30 m). The smallest of all was *Magyarosaurus*, a petite 6 m long, and hypothesized to have been an 'island dwarf' (see Box 8.3). The titanosaur skull (Figure 8.10(j)) was superficially like that of *Diplodocus* and the body in some such as *Saltasaurus* was covered with an armour of roughly hexagonal bony plates (Figure 8.10(k)). Titanosaurians also showed a characteristic 'wide-gauge' limb posture, in which the forelimbs and hindlimbs were angled out from the side of the body and the hands and feet planted on the ground far apart (Wilson, 2005). This differs from all other sauropods, in which the limbs were vertical and the tracks show the footprints close to the midline. A remarkable nesting site in the late Cretaceous at Auca Mahuevo, Argentina shows hundreds of nests, eggs, embryos, and juveniles laid by herds of titanosaurians 80 Myr ago (Chiappe *et al*., 2005).

8.3.7 On being a giant

Sauropods are notable for their huge size, and there has been much speculation over the years about how they might have achieved their vast dimensions and yet remained successful. At first sight, it might seem impossible that such huge animals, some weighing 50 tonnes or more (ten times the weight of the largest elephant), could survive with such relatively small heads, and eating such apparently poorly nutritious plants. Some speculations have included outlandish ideas such as that they supported their vast body weights by standing around in deep lakes, or that gravity was lower in the Mesozoic than today. There is no evidence for such *ad hoc* suggestions, and it is wiser to work with the data we have.

In a comprehensive assault on this knotty problem, a large, interdisciplinary team (Klein *et al*., 2011; Sander *et al*., 2011; Sander, 2013) has explored every angle, from confirming that our estimates of sauropod body mass are reasonable, to exploring sauropod coprolites (what were they eating?), calculating the nutritional value of various Mesozoic plants, and calculating daily energy budgets. These authors conclude that sauropod gigantism was enabled by a combination of key features – the long neck, the small head, avian-style respiration, high basal metabolic rate, and egg laying (Figure 8.11).

First, the long neck is a typical feature of nearly all sauropods. Its purpose was to enlarge the **feeding envelope**, the range over which the animal could secure food without moving its body. Sauropods then stood still for much of the time, swinging their necks slowly from side to side and up and down, munching plant material off every edible bush and tree within reach. This is a much more energy-efficient feeding mode for a very large animal than constantly moving the whole body when a small food patch has been exhausted.

Second, the small head, which is essential in a long-necked animal, was possible because sauropods probably swallowed their food whole and without chewing. They gathered plant matter by shearing bites, nipping, and branch stripping, and then gulped it down whole. At one time, it was argued that sauropods must have then ground and reduced the particle size of their plant food by means of a gastric mill, as found in birds, a structure between mouth and stomach that contains grit and acts to reduce the food. However, records of so-called 'stomach stones' (**gastroliths**) in sauropods are questioned (Wings and Sander, 2007), and it seems likely that sauropods simply retained their food for a long time in the stomach where it fermented and gave up its nutritious chemicals. Such long retention times are a consequence of their very large body sizes.

Third, avian-style respiration has long been posited in dinosaurs, including sauropods. In birds, unlike in mammals, air enters the lungs and then passes into auxiliary air sacs distributed along the vertebral column and around the thorax. Bird respiration is unidirectional, meaning that oxygen-rich air moves in the same direction through the gas-exchange tissues of the lungs during both inhalation and exhalation. The air sacs allow this by storing some oxygen-rich air, so that it can pass forwards during exhalation. Mammals, including humans, have a tidal respiratory system, in which air passes into the lungs and then passes out again, with the disadvantage that incoming oxygenated air is mixed with spent, deoxygenated air. In birds, the air sacs are partly contained within the bones of the skeleton, creating pneumatic spaces within vertebrae and the humeri for example. In birds, this has the additional advantage of lightening the skeleton for flight (see Section 9.3.1). Sauropods too benefited from lightening of the skeleton, especially the neck, often by complex invaginations from the side shown by cavities and narrow bone struts (see Figure 8.10(d); Wedel, 2009), so

BOX 8.3 DWARF DINOSAURS ON ANCIENT ISLANDS

A well known biogeographic rule among modern birds and mammals is the 'island rule', which says that small animals may become larger, and most notably, large animals become smaller, when they find themselves on islands. The dwarf elephants of the Mediterranean islands are particularly well known. During the late Pleistocene and Holocene, as the level of the Mediterranean Sea rose and fell in connection with melting and expanding ice caps at the north pole, elephants entered islands such as Sicily, Sardinia, Malta, and Crete both from north Africa and southern Europe. At times, for example, Crete was populated by pigmy elephants, pigmy hippos, and pigmy deer, as well as two genera of giant rodents and giant insectivores. The Pleistocene faunas of Sardinia were most diverse of all, with pigmy elephants, pigmy hippos, and pigmy deer, as well as large rodents and shrews.

Why do body sizes change on islands? There have been many debates on the topic (Benton *et al*., 2010), but there are two rather obvious reasons: large animals need large feeding areas, and ecological release. So, a population of normal-sized elephants from the mainland that find themselves on an island that becomes isolated would risk extinction if they did not modify their food requirements. Rapid evolution might very well select for ever-smaller animals that need less and less food while maintaining a viable breeding population. Ecological release explains why large animals might become smaller and small animals larger. This principle relies on the fact that most species are constrained by others, and in the absence of those close competitors, the species may come to occupy a much wider niche at a differing body size range.

Dinosaurs, typically icons of gigantism, could become dwarfed on islands. Most famous are the Late Cretaceous dinosaurs of Haţeg in southern Romania (Benton *et al*., 2010; Stein *et al*., 2010). The Late Cretaceous was a time of unusually high sea levels (see Section 8.2), and much of Europe was beneath the waves, with numerous islands matching current mountain ranges. In eastern Europe, dinosaurs and other terrestrial vertebrates hopped from island to island, and the Haţeg island was particularly diverse, with lizards, crocodiles, pterosaurs, dinosaurs, birds, and mammals. A variety of evidence suggests that the dinosaurs were dwarfs. For example, the ornithopod *Telmatosaurus* was half or one-third the length of its nearest relatives, corresponding to one quarter to one ninth of the body mass. Further, it seems to be a **relict** species, meaning it is somehow primitive and isolated; its nearest relatives are Late Jurassic and Early Cretaceous forms, implying they had survived somewhat unchanged for 20–80 Myr.

The same is true of the titanosaur *Magyarosaurus* (Stein *et al*., 2010). Study of its bone histology confirms that it is a small adult, not a juvenile: the limb bones show considerable secondary remodelling, indicative of reasonably advanced age. None of the specimens shows an external fundamental system (EFS), close rings of low-porosity bone, a sure indication that growth has ceased, but this might have been lost to secondary remodelling.

Magyarosaurus and the dwarf ornithopod *Telmatosaurus* are island dwarfs. Further, their dwarf size represents a form of paedomorphosis (see Section 1.4.3), the retention of juvenile characters in the adult. Of the three processes that can produce paedomorphosis, neoteny (slow development) and post-displacement (development starts late) can lead to adults of the same size as the unaffected relatives, whereas progenesis (development stops early) usually leads to adults of reduced size (Alberch *et al*., 1979). Additional evidence for progenesis is the retention of anatomically juvenile characters in adult *Telmatosaurus*: this suggests that development of the dentition finished early by comparison with larger close relatives, and so this points to progenesis (early offset) as the heterochronic process.

Read more about the dwarf dinosaurs of Haţeg at:
http://palaeo.gly.bris.ac.uk/macro/islandrule/Hateg/Index.html

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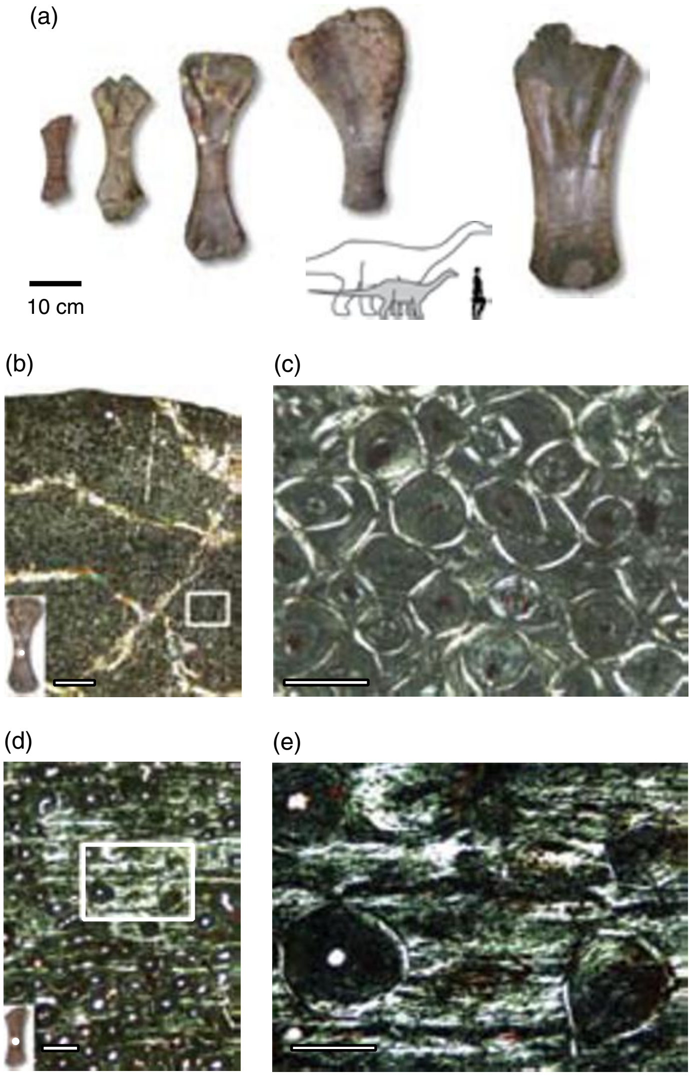


Relative growth and bone histology of the dwarf dinosaur *Magyarosaurus dacus* from the Late Cretaceous of Haţeg in southern Romania. (a) Photographs of sampled humeri, ranging from a juvenile (left; 45% maximum size) to the largest known specimen (second right), and an indeterminate, large titanosaur. Cartoon shows relative size of *Magyarosaurus* (grey), a close relative, and a human. (b,c) Overview of cross section (b) and close-up (c) from a subadult individual, showing the cortex dominated by secondary remodelling (the rounded structures with concentric laminae). (d,e) General view (d) and close-up (e) of largely interstitial laminar primary bone in outermost cortex of the smallest available specimen (45% maximum size), showing the vascular canals oriented circumferentially as in laminar fibrolamellar bone, but the bone matrix between the vascular canals consisting largely of parallel-fibred and lamellar bone, with only a minute fraction of fibrous (or woven) bone tissue. See Colour plate 8.1. Source: Benton *et al*. (2010). Reproduced with permission from Elsevier.

that it took less muscular effort to maintain off the ground and to move it around.

Fourth, and perhaps controversially (see Section 8.5), dinosaurs generally had a high basal metabolic rate (BMR). This was essential in sauropods to enable them to grow to adult size fast. If sauropods had been the slow-moving, lumbering behemoths of earlier days, taking perhaps 100 years to reach breeding age, there would have been a high risk of death before they could breed. Estimates from studies of bone histology suggest that sauropods could increase their body mass by 0.5–2 tonnes per year, and would have reached sexual maturity at ages between 15 and 30 (Lehman and Woodward, 2008; Sander *et al*., 2011; Griebeler *et al*., 2013).

Fifth, and finally, sauropods laid eggs and, despite their large size, retained the r-selected strategy of producing relatively large numbers of small young each breeding season. Eggs are small, and hatchlings were about 0.5 m long (compared to parents 15–80 m long), and there was probably limited parental care. Egg laying then was a low investment for the sauropod parents, and yet it offered the potential for faster population recovery than in large herbivorous mammals which typically produce one or two large young and invest effort in parental care. This permitted lower population densities in sauropods than in large herbivorous mammals, but larger individuals.

Sander *et al.* (2011) argue that these five characteristics of sauropods – long neck, small head, avian-style respiration, high BMR, and egg laying – contrasted with mammals today (short neck, large head, tidal respiration, high BMR, live birth). The only shared character is the high BMR in sauropods and mammals, and this places substantial demands on mammals. Sauropods had apparently evolved some smart strategies to allow them to enjoy the benefits of a mammalian-style high BMR, but without the costs faced by mammals in terms of finding and processing massive amounts of food and investing substantially in reproduction.

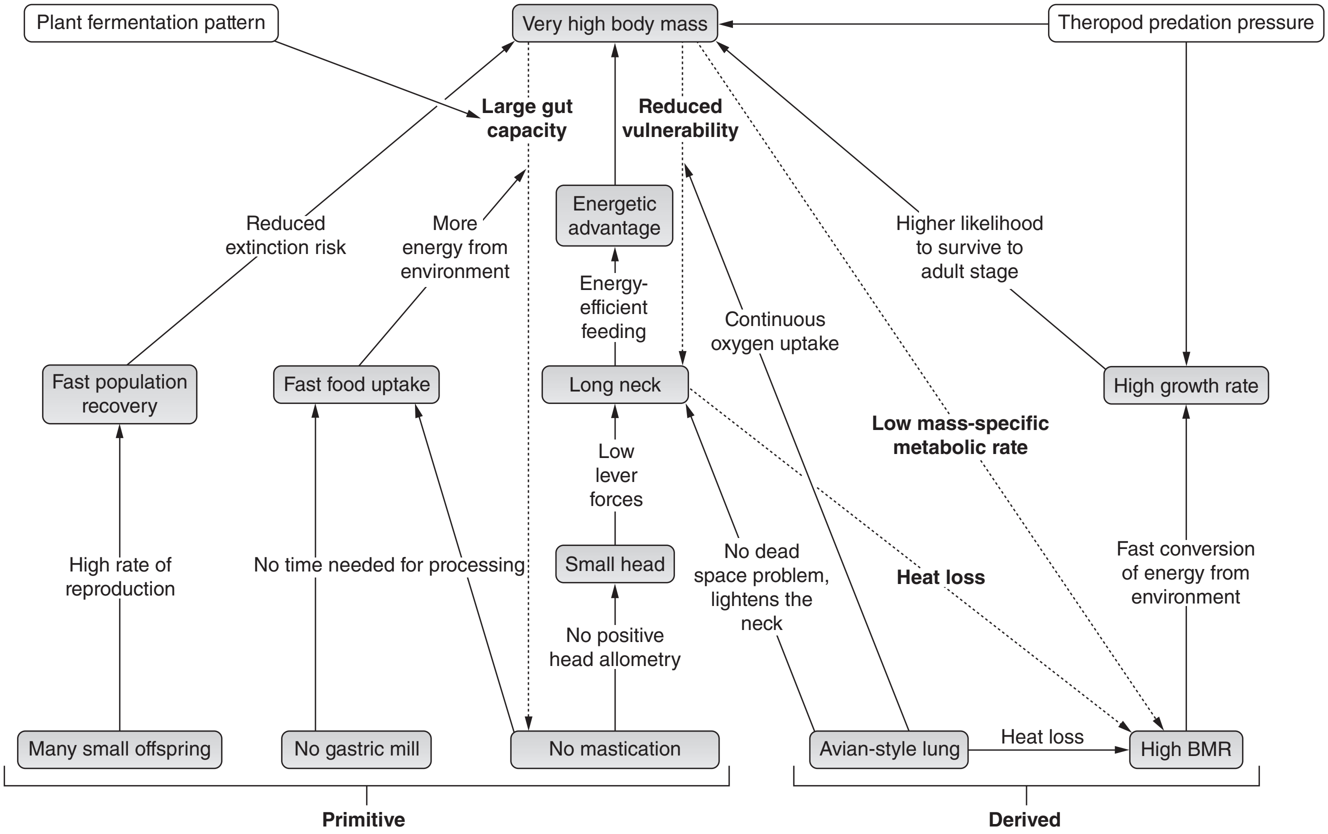


Figure 8.11 Flow chart summarizing the key factors that may have enabled sauropod gigantism. The shaded boxes contain the biological properties of sauropods, and the solid arrows indicate primary evolutionary causation. Theropod predation pressure is indicated as a general selection factor for body size increase. In addition to primary evolutionary causation, sauropod gigantism was also driven by evolutionary feedback loops (dotted arrows). The unboxed terms indicate the selective advantage in the feedback loop. The comments on the solid arrows show the selective advantages conferred on sauropods by the biological properties. BMR, basal metabolic rate. Source: M. Sander, University of Bonn, Bonn, Germany. Reproduced with permission.

8.4 THE DIVERSITY OF ORNITHISCHIAN DINOSAURS

The Ornithischia are the second major dinosaurian clade and they are relatively easy to diagnose. They have a pubis that points backwards (see Figure 8.3(b)) as well as over 30 other derived characters of the skull and skeleton (Sereno, 1986; Butler *et al.*, 2008).

The ornithischians arose during the Carnian (Late Triassic, 237–228 Myr ago), or earlier, but fossils are extremely rare until the Jurassic. The ornithischians were all herbivorous and they divide into two main groups, the Cerapoda (the bipedal ornithopods, bone-headed pachycephalosaurs and horned ceratopsians) and the Thyreophora (the armoured ankylosaurs and stegosaurs) (see Box 8.1). However, several Late Triassic and Early Jurassic taxa have proved hard to determine phylogenetically: *Pisanosaurus*, *Eocursor*, Heterodontosauridae, and Fabrosauridae.

8.4.1 The first ornithischians

Pisanosaurus from the early Norian of Argentina is known from only its jaws, neck and a few limb elements (Bonaparte, 1976; Norman *et al.*, 2004; Langer *et al.* 2010; Sereno, 2012). The cheek teeth (Figure 8.12(a)) have low triangular crowns with a well-developed narrow neck beneath and they are set over to the inside of the jaws, leaving a broad shelf on the outside. This suggests that *Pisanosaurus* had cheeks, pouches of skin that lay on either side of the tooth rows, that could retain unchewed plant material while other food was being processed. Cheeks are typical of ornithischians and other reptiles in which the skin of the face is firmly attached to the jaw margins just below the tooth rows.

Further Late Triassic ornithischians had been identified from isolated teeth from North America and elsewhere, but these are now known to have come from basal archosaurs or to be indeterminate. Others include an uncertain heterodontosaurid from Argentina (Sereno, 2012) and *Eocursor* from the Lower Elliot Formation (late Norian) of South Africa (Butler, 2010). *Eocursor* is the most completely known Triassic ornithischian, consisting of a partial skull and a relatively complete postcranial skeleton (Figure 8.12(b)). It was about 1 m long, and key anatomical features include leaf-shaped teeth adapted for plant-eating, a proportionally large hand with similarities to heterodontosaurids, a pelvis showing a mix of plesiomorphic and derived character states, and elongate distal hindlimbs suggesting well-developed running ability. It shows diagnostic ornithischian characters such as the ilium with a narrow anterior

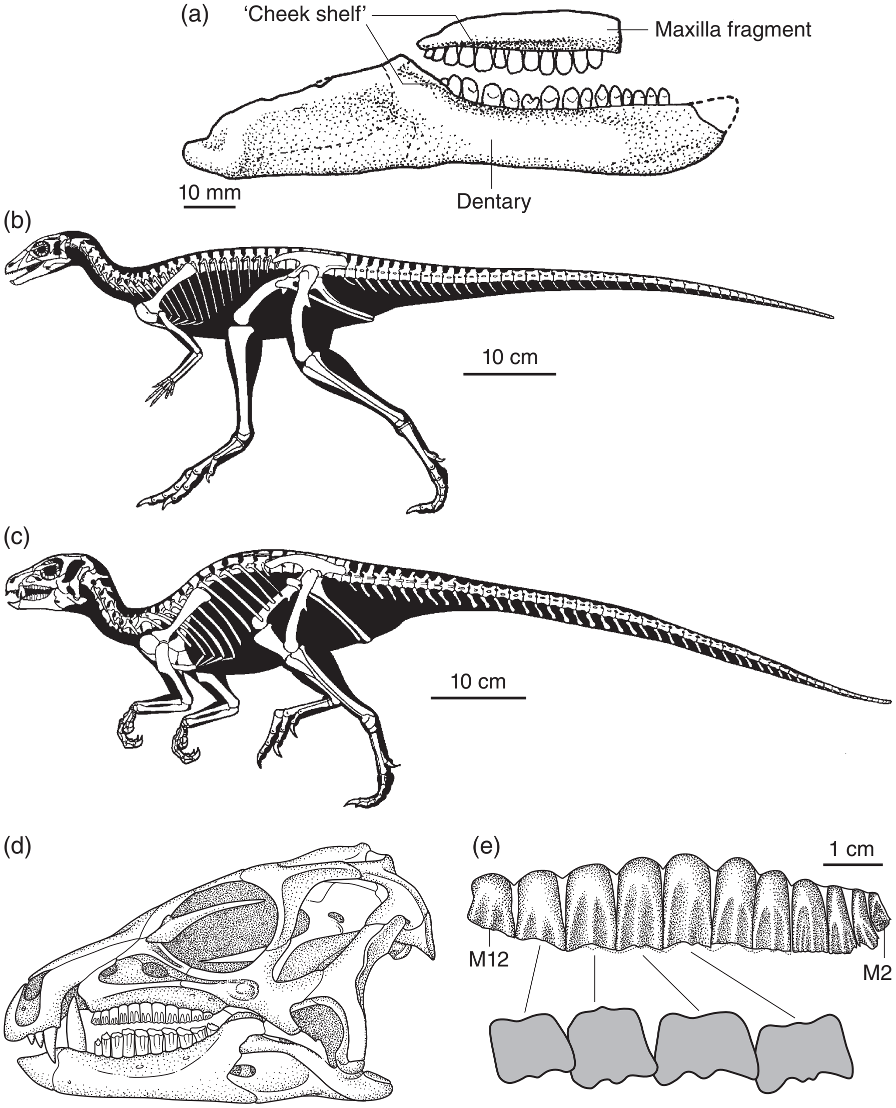


Figure 8.12 Early ornithischians: (a) *Pisanosaurus*, maxilla fragment and partial lower jaw in lateral view; (b) *Eocursor,* skeletal restoration; elements missing from the holotype specimen are restored after *Lesothosaurus*; (c–e) the heterodontosaurid *Heterodontosaurus*, skeleton, skull in lateral view, and maxillary tooth row, in lateral view (above) and outline of occlusal surfaces (below). Source: (a) Adapted from Bonaparte (1976). (b) © S. Hartman (artist), Wisconsin, USA. Reproduced with permission. (c-e) D. Norman *et al.* (2011). Reproduced with permission from John Wiley & Sons.

process, and the back-turned pubis, but other ornithischian characters of the skull cannot be determined because of incompleteness of the fossils.

The third ornithischian clade to originate in the Late Triassic is Heterodontosauridae. The best-known taxon, *Heterodontosaurus*, from the Early Jurassic of South Africa (Norman *et al.*, 2011; Sereno, 2012) was just over 1 m long. Compared to *Eocursor*, the bodily proportions (Figure 8.12(c)) differ only in the slightly longer arms and the shorter body. The skull (Figure 8.12(d)) shows the most unusual features. *Heterodontosaurus* (literally 'different tooth reptile') has differentiated teeth, two incisors, a canine and about 12 cheek teeth. The canines are long and the lower one fits into a deep notch in the upper jaw. One specimen has no tusks and it has been suggested that their presence may be a secondary sexual character of males. If so, the canine tusks may have been used for defence and for sexual display, as in modern herbivorous mammals with tusks, such as certain pigs and the musk deer.

Heterodontosaurus shows several derived features in the skull: the tooth-bearing edge of the premaxilla is a step down from the maxilla, the premaxilla extends back to contact the prefrontal and lacrimal, the jaw joint is set well below the level of the tooth rows to increase the duration and force of the bite (convergent with other herbivorous dinosaurs and synapsids (see Sections 5.6.1, 8.1); the cheek teeth wear against the opposite teeth of the lower jaw forming a straight line at the crest of the teeth (Figure 8.12(e)), and the outer surfaces of the lower teeth fit inside the upper teeth and wear them from the inside. Remarkably, *Heterodontosaurus* was capable of a small amount of sideways chewing by rotation of the lower jaw about its long axis.

Heterodontosaurids are known sporadically throughout the Jurassic, but an unexpected finding was *Tianyulong* from the Late Jurassic or Early Cretaceous of China (Zheng *et al.*, 2009). This heterodontosaurid is a late survivor of the clade, but the fossils also showed evidence of long, singular and unbranched, filamentous external skin structures. If these thin filaments turn out to be homologous to feathers, then this discovery might suggest that *all* dinosaurs, not just derived theropods, originally possessed feathers of some kind (see Section 9.1).

Most cladistic analyses have placed *Pisanosaurus* as the basal-most ornithischian, although that might reflect in part the absence of data from the incomplete specimen. Further, the majority of Ornithischia belong to Genasauria, the clade comprising the two major subclades Thyreophora and Cerapoda. However, *Eocursor* and Heterodontosauridae have been hard to place phylogenetically (Butler *et al.*, 2008; Butler, 2010; Norman *et al.*, 2011), and they are retained as basal to the Thyreophora-Cerapoda split (see Box 8.1).

8.4.2 Thyreophora

The Thyreophora includes the armoured dinosaurs, the Stegosauria and Ankylosauria, two clades that radiated in the Middle Jurassic (see Box 8.1; Carpenter, 2001). At the base of Thyreophora are a number of Early Jurassic dinosaurs, some of which were formerly placed outside the clade. Most notably, the 'fabrosaurids' used to be classed as basal ornithischians, even more basal than Heterodontosauridae in some cases. However, the 'fabrosaurid' *Lesothosaurus* shares one character with other Thyreophora, an anteroposterior ridge on the lateral surface of the surangular, and it is placed at the base of the clade in recent cladistic analyses (e.g. Butler *et al.*, 2008; Norman *et al.*, 2011). The 'fabrosaurid's are likely not a clade.

There are two difficulties in determining the phylogenetic position of 'fabrosaurids' – the limited number of characters shared with other taxa, and the fact that the group consists only of *Lesothosaurus* and a variety of incomplete and scrappy remains from the Early Jurassic that have been given a variety of names (Norman *et al.*, 2004).

Lesothosaurus from the Early Jurassic of southern Africa is reasonably complete. It is a lightly built animal 0.9 m long, with long hindlimbs and short arms (Figure 8.13(a)). It has the typical ornithischian pelvis, and the skull (Figure 8.13(b)) shows even more ornithischian characters, seen also in *Heterodontosaurus*. The tip of the premaxilla is toothless and roughened, and it is matched by an entirely new bone in the lower jaw, the unpaired **predentary**. The orbit also contains a new bone, the **palpebral**. The teeth (Figure 8.13(c)) are more typically ornithischian than those of *Pisanosaurus* because they have a bulbous base to the crown and rounded denticles on the edges. The wear facets lie symmetrically on either side of the pointed tip of the crown, which suggests an up and down jaw action with no possibility of back and forwards or side-to-side chewing.

Lesothosaurus lacks further obvious thyreophoran characters. Two Early Jurassic taxa, *Scelidosaurus* from England and *Scutellosaurus* from Arizona, USA (Colbert, 1981), share a transversely broad postorbital process of the jugal and parallel rows of keeled scutes on the back surface of the body with later Thyreophora. *Scutellosaurus* (Figure 8.13(d)) is a modest-sized biped, with a skeleton similar to that of *Lesothosaurus*, but it has numerous rows of keeled scutes (Figure 8.13(e)) over the back and in regular rows on the flanks.

8.4.3 Stegosauria: the plated dinosaurs

The Stegosauria is a small clade of 10–15 genera of Middle Jurassic to Late Cretaceous armoured dinosaurs (Maidment *et al.*, 2008). Best known is *Stegosaurus* from the Late Jurassic of North America (Figure 8.13(f)), which has a low, almost tubular skull containing what has been identified as the smallest brain (relative to body size) of any dinosaur. The hindlimbs are much longer than the forelimbs, evidence of a bipedal ancestry, and the massive arched backbone supports large triangular bone plates that sit in a double row. The arrangement of the plates has been debated: was there a single row or two? This is hard to determine because the bony plates developed independently within the skin and did not meet the bones of the skeleton at all, but were presumably held firm by massive ligaments. A well-preserved specimen, with the plates in position, confirms the double, alternating row (Carpenter, 1998).

What were these plates used for? The plate surface is covered by branching grooves that probably housed blood vessels in life, meaning that the plates were covered by skin. Postulated functions for the plates include: (1) armour, (2) sexual display and species recognition, (3) deterrent display, and (4) thermoregulatory devices, or some combination of these functions. Doubtless the plates had some protective role (functions 1, 3), but they do not cover the vital organs, so cannot be regarded as armour in the usual sense. Display and species recognition (function 2) cannot be tested readily and could combine with a thermoregulatory (function 4) or some other function. Further, species recognition would presumably only be important if there were several different species of stegosaurs living together, and yet that is not the case (Hone and Naish, 2013). The postulated thermoregulatory function is analogous to that proposed for the sails of pelycosaurs (see Section 5.6.2). Main *et al.* (2005) suggested that the internal arrangement of canals in the plates was not appropriate for a heat-exchange function, whereas Farlow *et al.* (2010) argued that it was. They used CT scans to identify an internal system of five major pipes that branched upwards, and were connected by a broad basal pipe, as well as narrower branching canal impressions on the outside of the osteoderms. By varying blood flow, perhaps *Stegosaurus* could indeed have radiated heat or limited radiation depending on its internal body temperature.

Other stegosaurs had smaller plates, or none at all, but all had spines of some kind, whether restricted to the end of the tail, as in *Stegosaurus*, or more widely distributed, down the back and over the shoulders and hips. One unusual stegosaur, *Miragaia* from the Late Jurassic of Portugal, had an elongate

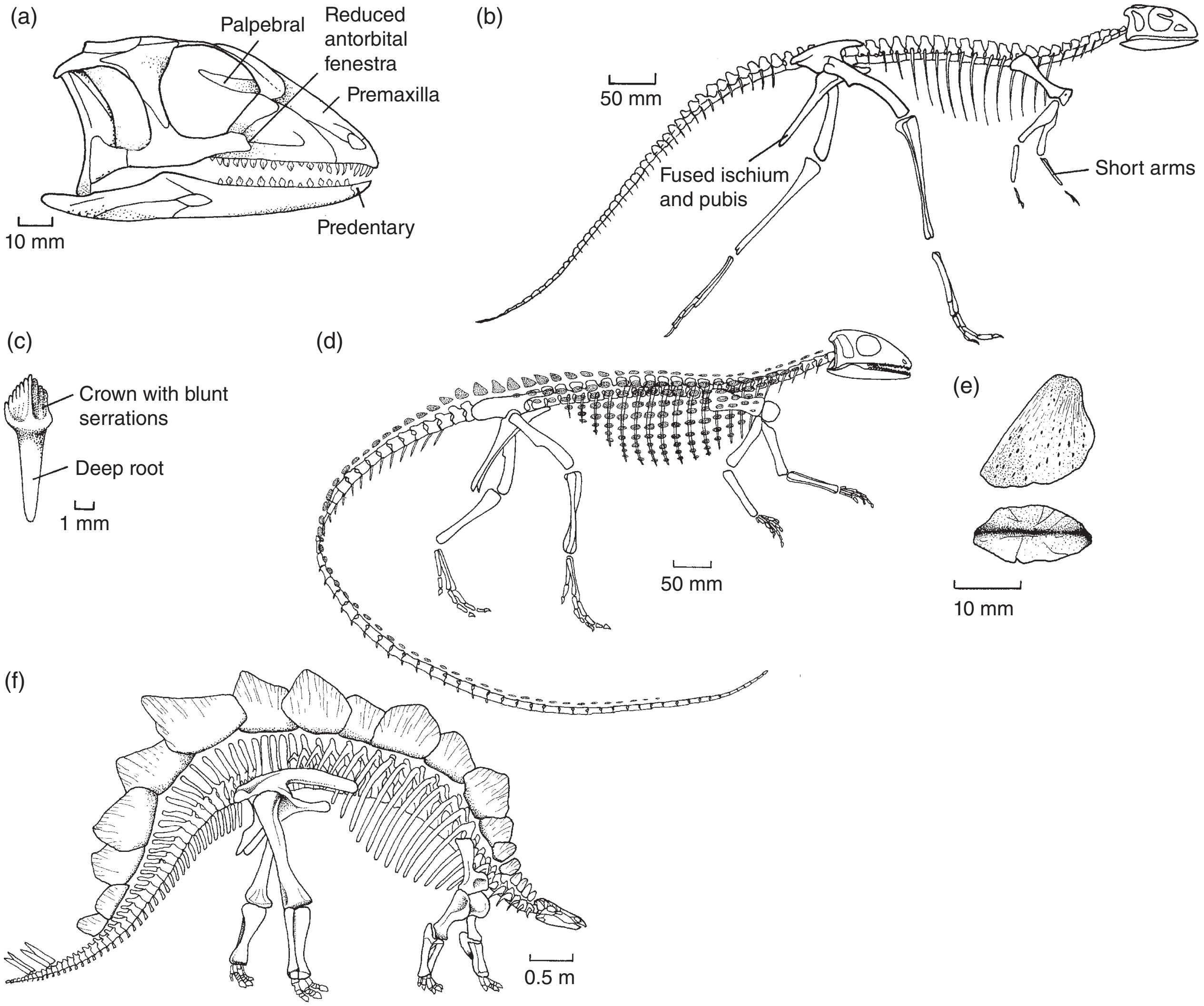


Figure 8.13 Basal thyreophorans (a–e) and a stegosaur (f): (a–c) the fabrosaurid *Lesothosaurus*, skeleton, skull and tooth; (d,e) skeleton of *Scutellosaurus* and an armour plate in lateral and dorsal views; (f) *Stegosaurus*. Source: (a–c) Adapted from Galton (1978). (d,e) Adapted from Colbert (1981). (f) Adapted from Zittel (1932).

neck comprising 17 cervical vertebrae (Mateus *et al.*, 2009), but the reasons for such an adaptation are uncertain.

8.4.4 Ankylosauria: armour-covered dinosaurs

Like the stegosaurs, the ankylosaurs (Thompson *et al.*, 2012) arose in the Middle Jurassic, but they are not well known until the Early Cretaceous. There are more than 50 species. *Polacanthus*, a nodosaurid from southern England (Blows, 1987), is a typical early form with a mixture of spiny plates along the flanks and a fused mass of smaller plates over the hips (Figure 8.14(a)). The ankylosaurids such as *Euoplocephalus* and *Ankylosaurus* (Figure 8.14(b–e)) have broad armoured skulls and a body armour of plates rather than spines covering the neck, trunk and tail. Ankylosaurids also have massive bony bosses at the ends of their tails, formed by the fusion of the last caudal vertebrae and the incorporation of bony plates from the skin (Figure 8.14(c)). A blow from this club could break bones (Arbour, 2009; Farke, 2014), and would readily disable *Tyrannosaurus* or any other contemporary predator.

The ankylosaur skull (Figure 8.14(d,e)) is a heavy box-like structure with massive overgrowths of the normal bones of the skull roof by a mosaic of new bone plates generated within the skin over the head. These cover the upper temporal fenestra in all genera and the lower one in most. Only a small orbit and nostril remain and even these openings are heavily overgrown.

8.4.5 Basal ornithopods

The remaining ornithischians are the Cerapoda, comprising Ornithopoda, Pachycephalosauria, and Ceratopsia. Of these, the ornithopods were the largest and most successful ornithischian

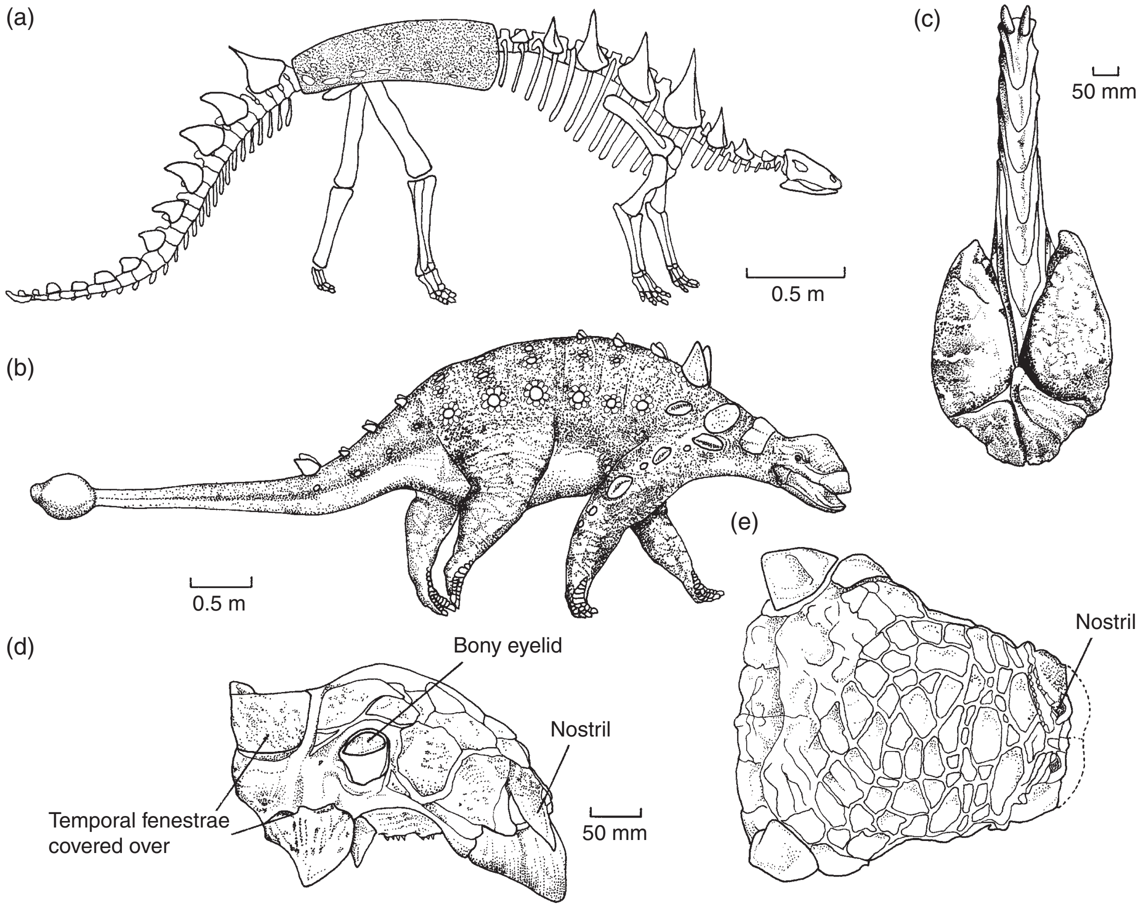


Figure 8.14 The ankylosaurs: (a) *Polacanthus*; (b) *Euoplocephalus* body restoration; (c) *Ankylosaurus* tail club; (d,e) *Euoplocephalus* skull in lateral and dorsal views. Source: (a) Adapted from Blows (1987). (b) Adapted from Carpenter (1982). (c–e) Adapted from Coombs (1978).

group, containing some 150 species and achieving great abundance in Cretaceous faunas. Ornithopods were traditionally divided into 'hypsilophodontids', 'iguanodontids' and hadrosaurids, but the first two terms refer to paraphyletic series.

Among basal ornithopods, *Hypsilophodon* from the Early Cretaceous of England (Galton, 1974) was a biped that ranged in length from 3 to 5 m. The bodily proportions (Figure 8.15(a)) and the skull (Figure 8.15(b,c)) are similar to those of *Heterodontosaurus*, except that the skull lacks tusks and is narrower in the midline. The ventral view (Figure 8.15(c)) shows the extent of the cheeks, represented by the broad area of the maxilla lying outside the tooth rows.

An early view of *Hypsilophodon* was that it lived in trees, grasping the branches with its feet, but the foot (Figure 8.15(d)) was incapable of grasping, being a typical elongate running foot with hoof-like 'claws'. Further, the end of the tail is sheathed in ossified tendons that stiffened it and caused it to act as a stabilizer during running. The limb proportions of *Hypsilophodon* are similar to those of a fast-moving gazelle, especially the very long shin and foot.

Galton (1974) made a detailed restoration of the muscles of the hindlimbs of *Hypsilophodon* (Figure 8.15(e)), based on muscle scars and processes on the bones and comparison with dissections of modern birds and alligators (see Box 6.3). The muscle names record the bones to which they attach at each end. They fall into four groups that define their functions in walking.

1 Protractors, muscles that pull the femur forwards and up: iliofemoris, puboischiofemoralis internus (upper part).

2 Retractors, muscles that pull the femur back: puboischiofemoralis internus (lower part), caudifemoralis longus and brevis, adductor femoralis.

3 Extensors, muscles that extend the lower leg: iliotibialis, femorotibialis.

4 Flexors, muscles that pull the lower leg back: iliofibularis, flexor tibialis internus.

During a single step, all of these muscles came into play. As the leg swung forwards, the protractors pulled the femur forwards and upwards and the extensors extended the lower leg. The foot touched the ground, and the power stroke, in which the body moves forward, was achieved by the retractors and flexors, which pulled the femur and lower leg back respectively.

More derived ornithopods include the second dinosaur ever named, in 1825, *Iguanodon* from the Early Cretaceous of Europe (Norman, 1980, 1986). *Iguanodon* has a horse-like skull, with its long jaws lined with batteries of teeth (Figure 8.16(a)). In the skeleton (Figure 8.16(b)), the prepubic process is expanded, the postpubic process is very short and there is a complex lattice of

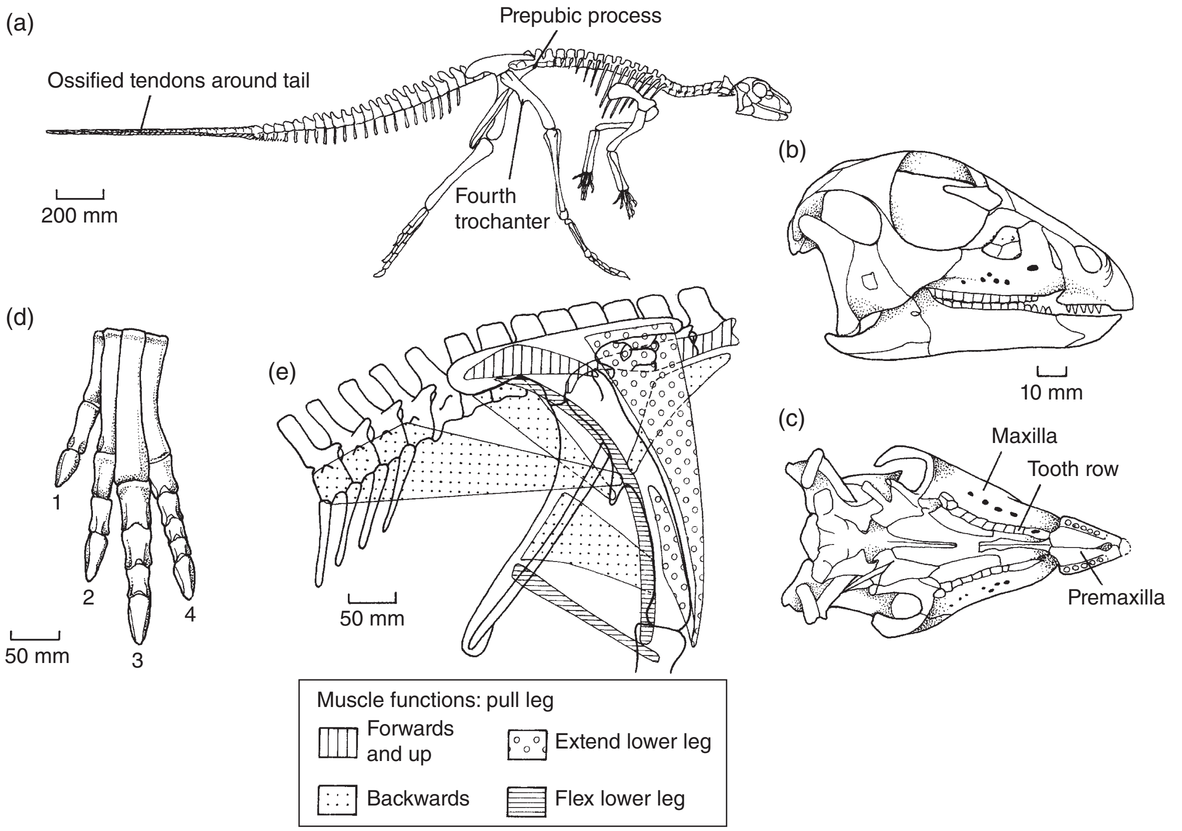


Figure 8.15 The ornithopod *Hypsilophodon*: (a) skeleton in running pose; (b,c) skull in lateral and ventral views; (d) foot in anterior view; (e) restoration of the muscles of the pelvis and hindlimb, coded according to their functions. Source: Adapted from Galton (1974).

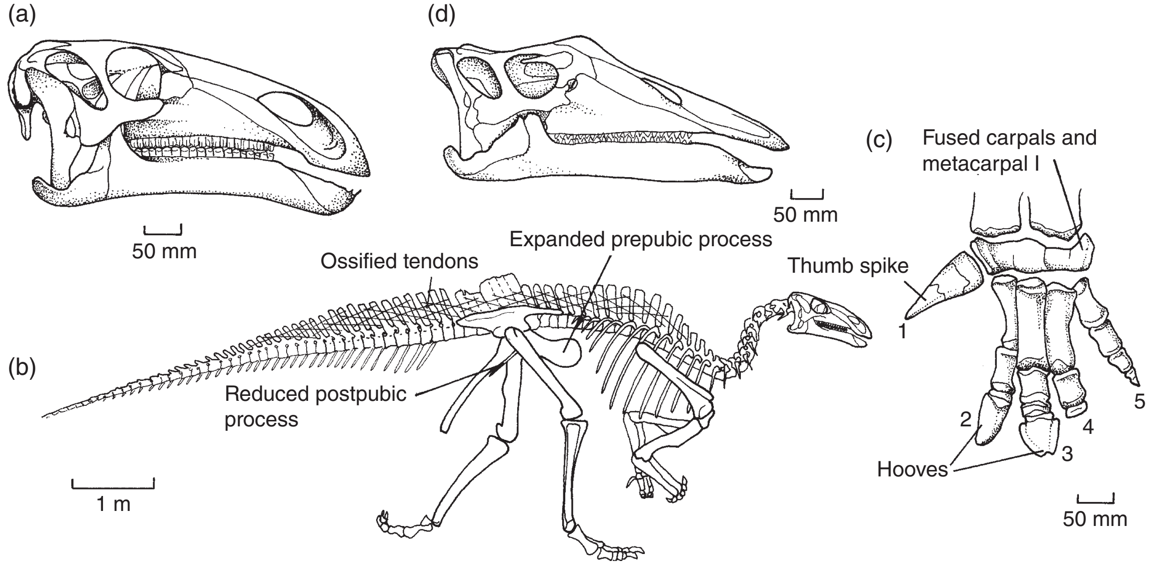


Figure 8.16 Ornithopod anatomy: (a) skull of *Iguanodon*; (b) skeleton of *Iguanodon* in running pose; (c) hand of *Iguanodon* in anterior view; (d) skull of *Ouranosaurus*. Source: (a,b) Adapted from Norman (1986). (c) Adapted from Norman (1980). (d) Adapted from Norman (1984).

ossified tendons over the neural spines of all vertebrae of the trunk and tail. The most remarkable modifications are seen in the hand (Figure 8.16(c)), in which the carpals and metacarpal 1 are fused to form a single block in the wrist, digit 1 is reduced to a thumb spike, digits 2–4 form a bunch and digits 2 and 3 have small hooves. This hand was clearly used in walking (hooves), in defence or display (thumb spike), and in gripping. *Iguanodon* could walk on all fours, or equally well on its hindlegs alone with the tail and the backbone extended horizontally. Whereas the first *Iguanodon* was named on the basis of isolated remains from southern England, numerous complete skeletons were famously recovered in 1877 from a coal mine in Belgium (Godefroit, 2012).

Another ornithopod, *Ouranosaurus* from the Early Cretaceous of North Africa, has spines on its back, perhaps supporting a sail for thermoregulation. The snout (Figure 8.16(d)) is elongate and rather flattened. The rhabdodontids include Late Cretaceous forms from Europe such as *Rhabdodon* and *Zalmoxes*, some seemingly restricted to islands (see Box 8.3)

8.4.6 Hadrosauridae: the duckbills

The most diverse, and most successful, ornithopod clade were the hadrosaurs or 'duck-billed' dinosaurs of the Late Cretaceous (Prieto-Márquez, 2012). They are especially well known from North America, Central Asia and China, where hundreds of specimens have been found. Frequently, three or four distinct hadrosaurian species are found side by side in the same geological formation and it seems evident that large mixed groups roamed over the lush lowlands rather as closely related antelope do today in Africa.

The hadrosaurs are famous for their expanded duck-like bills (Figure 8.17(a,b)) in which both the premaxillae and maxillae are flattened and spread out to the sides. The nostrils are long and low and the orbit and lower temporal fenestra are located well back. The teeth of hadrosaurs consist of long rows of grinding cheek teeth set well back from the front of the mouth and arranged in closely packed batteries within the jaws (Figure 8.17(c)). There may be as many as five or six rows, each containing 45 or 60 teeth that are formed in the gum tissue at the bottom and move up progressively to the jaw margin where they come into wear.

Hadrosaur jaws were used in powerful chewing actions. Wear surfaces on the teeth can be seen in a cross section through a hadrosaur skull (Figure 8.17(d)) as sloping downwards and outwards. Hadrosaurs had complex, grinding teeth (see Box 8.4) and could clearly consume unusually tough vegetation. The jaws could move sideways and back and forwards a little to power the grinding action. Only the top rows of teeth are in use at any time, but they must have worn down quite rapidly because there are so many back-up teeth below ready for use.

This advanced and evidently powerful plant-grinding jaw system (Williams *et al.*, 2009; Fiorillo, 2011; Erickson *et al.*, 2012) may be one reason for the success of the hadrosaurs. But what did they eat? Some hadrosaur specimens have been 'mummified', preserved with their skin and some internal parts intact. These include stomach contents such as conifer needles and twigs, as well as remains of other land plants. The conifer diet is confirmed by hadrosaur coprolites as well as by microwear analysis, the interpretation of microscopic pits and scratches on fossil teeth (Fiorillo, 2011). Hadrosaurs were terrestrial browsers that presumably stripped trees of their foliage by stretching up on their hind legs.

Hadrosaurs were once said to have spent most of their time swimming in lakes, a view perhaps derived from their duck bills. They could doubtless have swum, but the skeleton (Figure 8.17(e)) is particularly adapted for efficient running, although the posture has been debated. Did hadrosaurs habitually walk and run

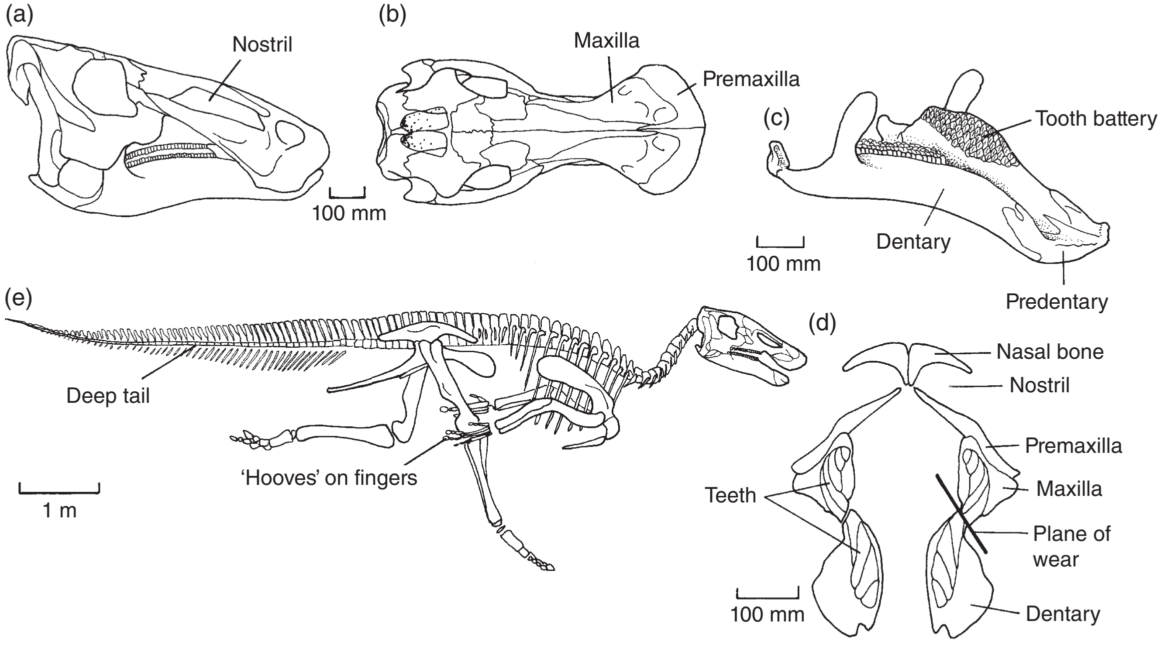


Figure 8.17 Hadrosaur anatomy: (a,b) skull of *Edmontosaurus* in lateral and dorsal views; (c) lower jaw of *Kritosaurus* seen at an angle to show the dental batteries; (d) cross-section through the snout of a hadrosaur to show patterns of tooth replacement; (e) skeleton of *Edmontosaurus* in running pose. Source: (a,b) Adapted from Norman (1984). (c,d) Adapted from Ostrom (1961). (e) Adapted from Galton (1970a).

as bipeds, with the body held horizontally (Galton, 1970a) or as quadrupeds? The consensus, based on postcranial anatomy, soft tissue preservation, and trackways is that hadrosaurs were predominantly quadrupedal (Maidment *et al*., 2012). Their hands bear small hooves on the fingers, and the forelimb bones are more adapted for weight-bearing than grasping.

Hadrosaurs all have essentially the same skeletons and skulls (Figures 8.17, 8.18), but some have an impressive array of headgear. The premaxillae and nasal bones extend up and backwards to form in some a high flat-sided 'helmet', either low or high, square or semicircular, in others a long 'tube', spike, or forwards-directed rod (Figure 8.18(a)). The nasal cavities extend from the nostrils into the crests and it was once assumed that they acted as 'snorkels', especially in *Parasaurolophus*. This is impossible, however, as there is no opening at the top of the crest. There are four separate air passages within the crest (Figure 8.18(b)), two running up from the nostrils, and two running back down to the throat region. Air breathed in or out through the nose had to travel round this complex passage system.

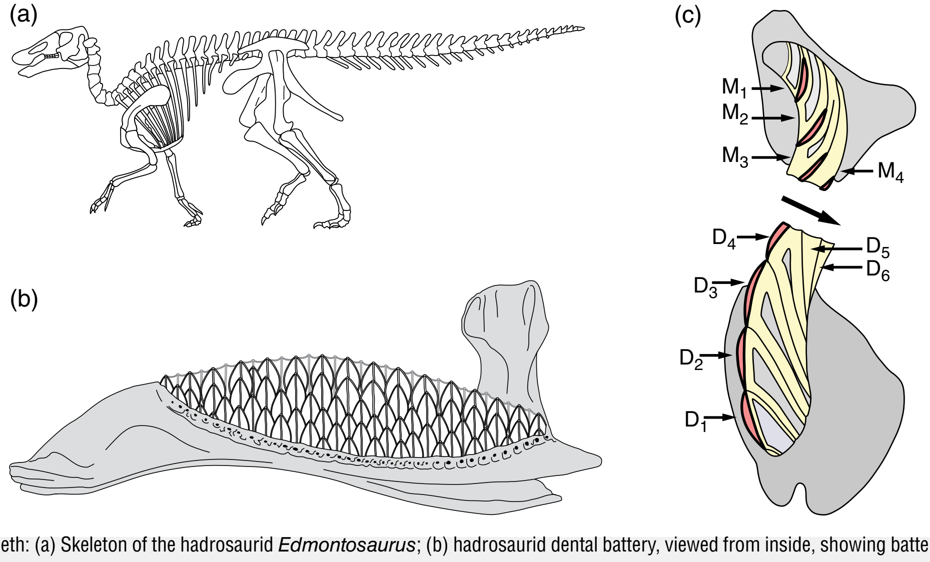
BOX 8.4 HADROSAUR TOOTH WEAR BIOMECHANICS

Ornithopod dinosaurs were unique among reptiles in that they could chew their food. Hadrosaurs in particular had complex teeth comprising six tissues that generated an efficient and complex grinding structure. Further, hadrosaurs, and other ornithopods, might have had specialized joints in their jaw bones that permitted some lateral movement of the teeth across each other, although this has been debated.

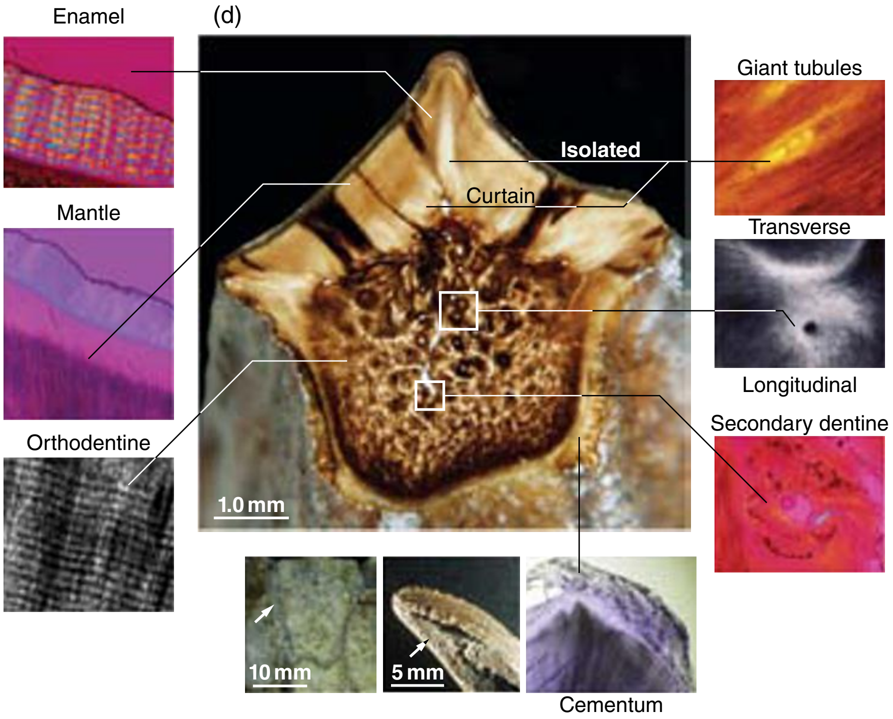
Chewing is normally seen as a mammalian speciality: we chew by being able to move our jaws back and forwards and especially from side to side, so the premolars and molars move across each other, tearing and reducing their food into small pieces. It was argued that ornithopods could all chew in one of two ways. In the early ornithopod *Heterodontosaurus*, a special ball and socket joint at the front of the jaws between the dentary and predentary allowed rotation as the jaws opened and closed. It was proposed also (Norman and Weishampel, 1985) that later ornithopods had an additional joint running along the side of the cheek that allowed the upper jaw to move outwards as the lower jaw closed upwards. This pleurokinetic hinge was said to run between the jaw-cheek unit (maxilla, lacrimal, jugal, quadratojugal and quadrate) and the skull roof bones above. However, more recent study (e.g. Holliday and Witmer, 2008) has cast doubt on the idea of pleurokinesis because such a 'flapping cheek' model requires too many other elements of the skull to be freed for motion, and detailed studies of sutures does not confirm that there was a mobile joint.

Despite the possible rejection of pleurokinesis, hadrosaurs clearly could move their jaws some distance from side to side, as well as back and forwards; tooth wear analysis (Williams *et al*., 2009) shows multiple sets of parallel grooves in these directions. With their massive tooth batteries (Figure 8.17(a–c)) comprising five or six rows of teeth, for a total of as many as 500 teeth in each jaw, hadrosaurs had taken heavy-duty chewing and frequent tooth replacement to an extreme.

In detailed studies of the tissue characteristics and wear rates of hadrosaur teeth, Erickson *et al*. (2012) identified six distinct tissues. These include the four components of mammalian grinding teeth: enamel and orthodentine, as well as independently derived secondary dentine and coronal cementum. In addition, the team identified two further dental tissues, giant tubules (infilled pulp cavity branches) and a thick mantle dentine. These observations suggest that hadrosaur teeth were among the most histologically complex of any animal. Mechanical experiments showed that these tissues wear down at different rates, and can leave a ridge surface, after wear, a feature previously observed only in mammals and that can provide a long-lasting grinding tooth surface.



Hadrosaur grinding teeth: (a) Skeleton of the hadrosaurid *Edmontosaurus*; (b) hadrosaurid dental battery, viewed from inside, showing batteries of developing teeth; (c) the classic 'two-tissue model; in cross section, showing enamel (dark) and dentine (light), with dentary (D) and maxillary (M) teeth numbered in order from youngest to oldest, and the direction of tooth movement indicated by an arrow.



(d) Sections through Edmontosaurus teeth showing tissues such as enamel, orthodentine, and tubules. See Colour plate 8.2. Source: Erickson *et al*. (2012). Reproduced with permission from the American Association for the Advancement of Science.

What was the function of hadrosaur crests? Probably they were used as visual species recognition and sexual signalling devices (Hopson, 1975; Weishampel, 1997), just as modern birds may have colourful and often elaborate patterns of feathers to identify potential mates and to signal their position in dominance hierarchies. Males and females of the same species had rather different crests (Figure 8.18(c)) and the crest was undeveloped in juveniles (Farke *et al*., 2013). There has been a vigorous debate (e.g. Padian and Horner, 2011; Hone and Naish, 2013) about whether hadrosaur crests, and such exaggerated structures in other dinosaurs, were used primarily for species recognition or in pre-mating contests. An exceptionally preserved, 'mummified' spewcimen of the hadrosaur *Edmontosaurus* even had a soft-tissue crest like a cock's comb (Bell *et al*., 2014). Whatever the function of these crests, Weishampel (1997) has shown that the hadrosaurs augmented their visual display with an auditory one too. The shapes of the air passages within the crests are like musical wind instruments. A powerful snort would create a low resonating note and the shape of the air passages in males and females, and in juveniles, would give a different note. Species differences would have been even more marked. We can imagine the Late Cretaceous plains of Canada and Mongolia reverberating to deep growls and blaring squawks as the hadrosaurs went about their business.

8.4.7 Pachycephalosauria: the bone-heads

The pachycephalosaurs ('thick-head reptiles'), a small clade of some 15 mainly Late Cretaceous herbivores from North America and central Asia (Maryańska *et al*., 2004), are diagnosed by their unusually thick skull roofs (Figure 8.19(a)). The parietal and frontal bones are fused into a great dome in some forms with the bone up to 0.22 m thick in a skull that is 0.62 m long. This great, thickened mass of bone is ringed by the normal skull roof elements as well as two supplementary supraorbital elements. Several of the skull bones are also ornamented by lines of bony knobs.

The pachycephalosaurs may have used their thickened heads in butting contests when seeking mates (Galton, 1970b; Snively and Theodor, 2011; Farke, 2014), as seen today among wild sheep and goats. The pachycephalosaur, a biped, adopted a horizontal-backbone posture during the charge (Figure 8.19(b)) so that the force of the impact ran straight round the skull margins and down the neck to the shoulders and hindlimbs. This system of force dissipation was paralleled in the dinocephalian synapsids (see Section 5.6.4). Confirming evidence for this theory is that the presumed males have thicker skulls than the females.

Pachycephalosaurs are also diagnosed by an unusually broad pelvis (Figure 8.19(c)), with gently curved iliac blades that contact the ribs of up to eight sacral vertebrae. This firm attachment

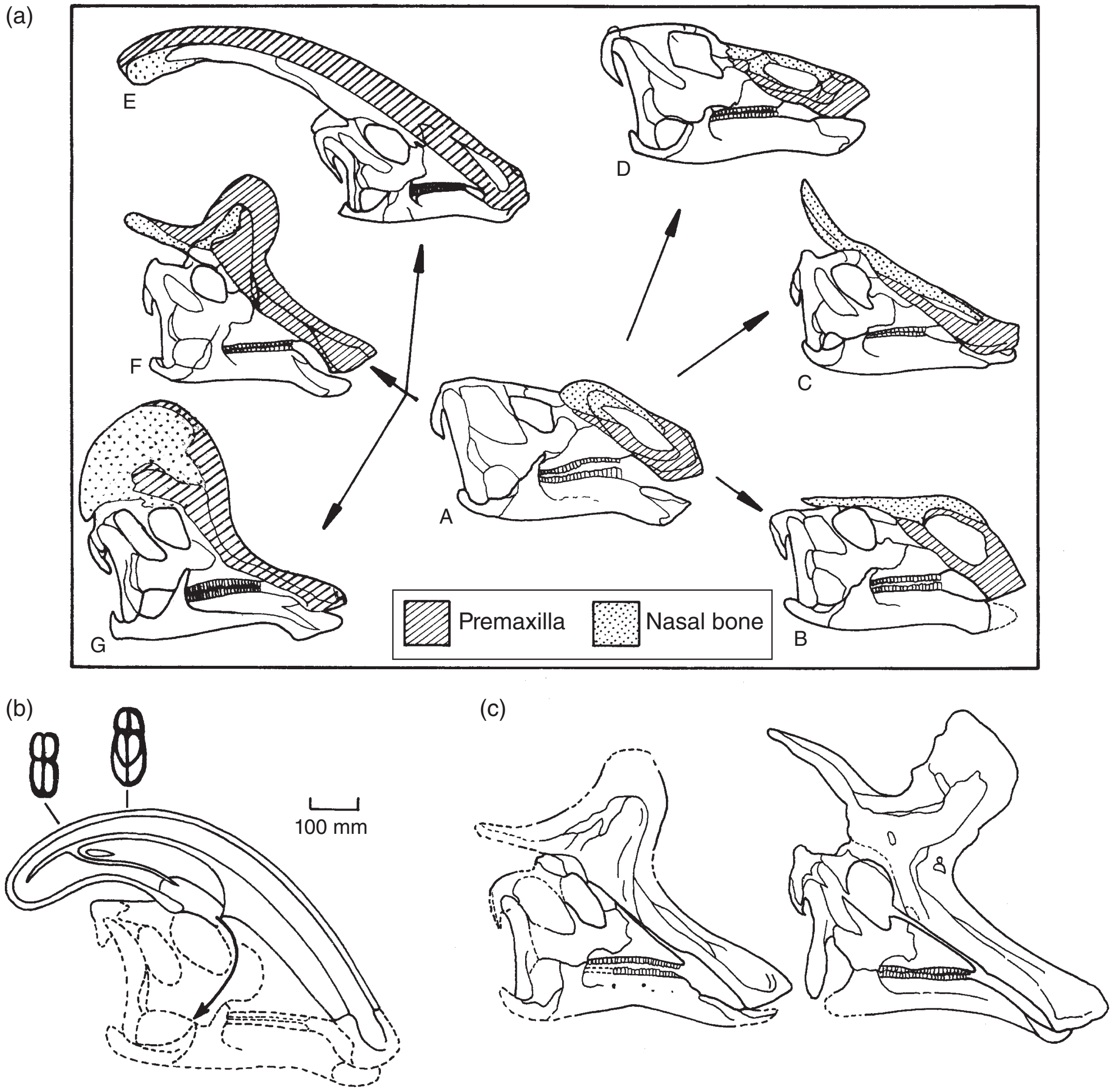


Figure 8.18 Hadrosaur skulls and crests: (a) several lines of hadrosaurian evolution from a crestless form (A, *Kritosaurus*) to crested genera (B, *Brachylophosaurus*; C, *Saurolophus*; D, *Edmontosaurus*; E, *Parasaurolophus*; F, *Lambeosaurus*; G, *Corythosaurus*); (b) internal structure of the crest of a possible female *Parasaurolophus*, showing the complex passages within the premaxillae and nasals, the passage of air (arrow) and two cross-sections through the crest; (c) sexual dimorphism in *Lambeosaurus*, with a probable female (left) and male (right). Source: Adapted from Hopson (1975).

of the pelvis may arise from the need to dissipate the forces of head butting. Pachycephalosaurs are allied to the horned ceratopsians, forming with them a clade Marginocephalia (see Box 8.1) on the basis of several synapomorphies, including the combination of the squamosal and parietal bones in the skull roof to form a narrow shelf that extends over the back of the skull (Sereno, 1986; Butler *et al.*, 2008).

8.4.8 Ceratopsia: the horn-faced dinosaurs

The Ceratopsia (literally 'horned faces') comprise a relatively large group of about 70 genera known mainly from the Early Cretaceous of Asia and the Late Cretaceous of North America (Hailu and Dodson, 2004; Dodson *et al.*, 2004; Ryan *et al.*, 2010). All are diagnosed by a triangular skull when viewed from above (Figure 8.20(c)), an additional beak-like **rostral bone** in the midline at the tip of the snout, a high snout and broad parietals at the back.

Some early ceratopsians, such as *Psittacosaurus* from the Early Cretaceous of eastern Asia (Figure 8.20(a)), were bipeds that had body forms very similar to ornithopods, but the skull is clearly ceratopsian, showing the characteristic parrot-like 'beak'. New studies show some remarkable aspects of juvenile behaviour and postural change during growth in this dinosaur (see Box 8.5). *Protoceratops* from the mid-Cretaceous of Mongolia and China was a quadruped with the beginnings of a nose horn, a thickened bump in front of the orbit (Figure 8.20(b)). It also shows the second major ceratopsian characteristic, a bony

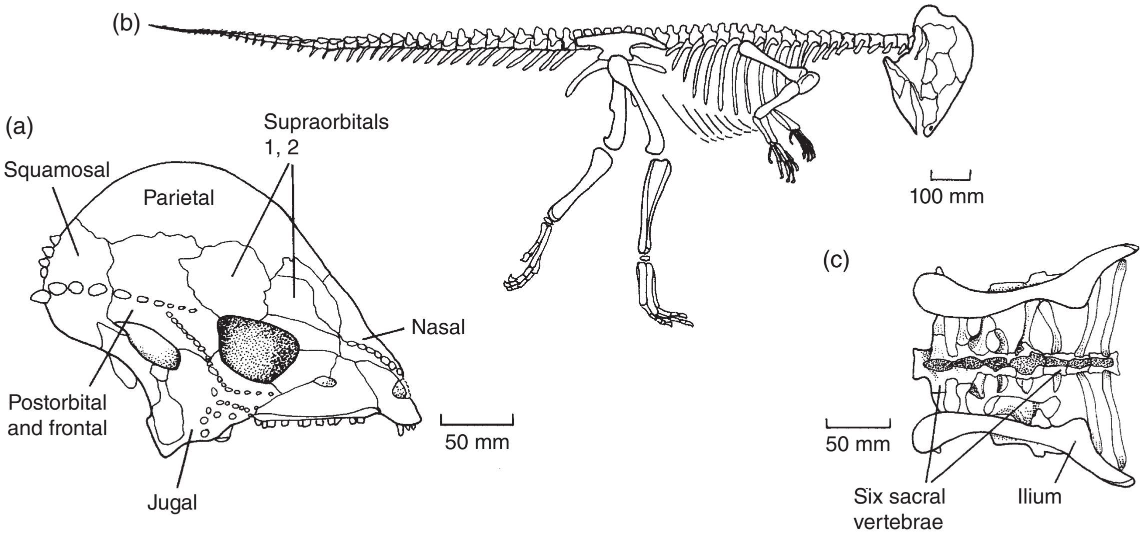


Figure 8.19 The pachycephalosaurs: (a) skull of *Prenocephale*: (b) skeleton of *Stegoceras* in butting position; (c) pelvis of *Homalocephale* in dorsal view. Source: (a,c) Adapted from Maryańska and Osmólska (1974). (b) Adapted from Galton (1970b).

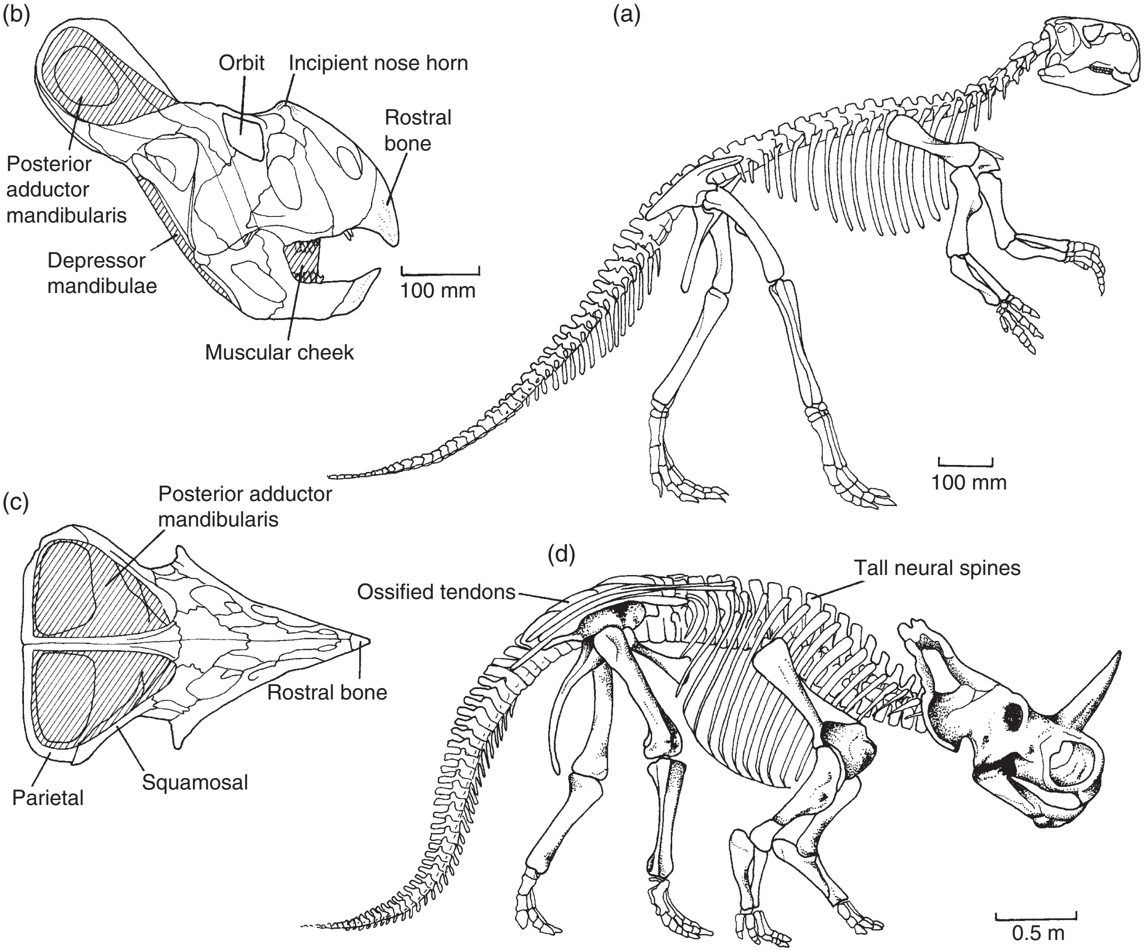


Figure 8.20 The ceratopsians: (a) skeleton of *Psittacosaurus*; (b,c) skull of *Protoceratops* in lateral and dorsal views, with the cheek and major muscles restored; (d) skeleton of *Centrosaurus*. Source: (a) Adapted from Zittel (1932). (b,c) Adapted from Ostrom (1966). (d) Adapted from Brown (1917).

frill formed from the parietals and squamosals (Figure 8.20(c)). The frill probably served as the origin of portions of the jaw adductor muscles, the posterior adductor mandibularis muscle, which would have produced a strong biting force.

The later neoceratopsians have a skeleton with adaptations for galloping (long limbs, digitigrade posture) (Figure 8.20(d)). Vertebrae of the neck and trunk have high neural spines for the attachment of powerful muscles to hold the head up and there are bundles of ossified tendons over the hips. The real variation is seen in the skulls: some forms such as *Centrosaurus* (Figure 8.20(d)) have a simple horn formed by fused nasal bones, whereas others have this and a pair of 'horns' on the jugals. The frill may be short or long, and indeed *Triceratops* (*Torosaurus*) had a 2.6 m long skull, in which the frill is the longest portion, altogether the largest skull known from any land animal. The frills and horns may have been used in defence and as visual species-signalling structures as well as in threat displays. Male ceratopsians may have engaged in head wrestling with the horns interlocked, just as deer do today (Farke, 2014).

8.5 WERE THE DINOSAURS WARM-BLOODED OR NOT?

A heated debate has raged since 1970 concerning dinosaurian physiology. Ever since dinosaur palaeobiologists realized that many dinosaurs were active animals (e.g. Galton, 1970a,1970b), the question has continued to resurface. Bakker (1972, 1986) in particular argued that all dinosaurs were fully warm-blooded, just like living birds and mammals, and that this explains their success. His claim was that the dinosaurs were **endotherms**, animals that control their body temperature internally, rather than **ectotherms**, which rely only on external sources of heat. This is part of an important and wide-ranging discussion among biologists who seek to understand why birds and mammals have such different physiologies from fishes and reptiles (e.g. Clarke and Pörtner, 2010; Nespolo *et al*., 2011). Additional lines of evidence have been brought to bear, but the debate appears to be coming to a resolution. The key evidence comes from feathers, isotopes, bone histology, and locomotory mechanics.

BOX 8.5 DINOSAURIAN CRECHES AND POSTURAL CHANGE

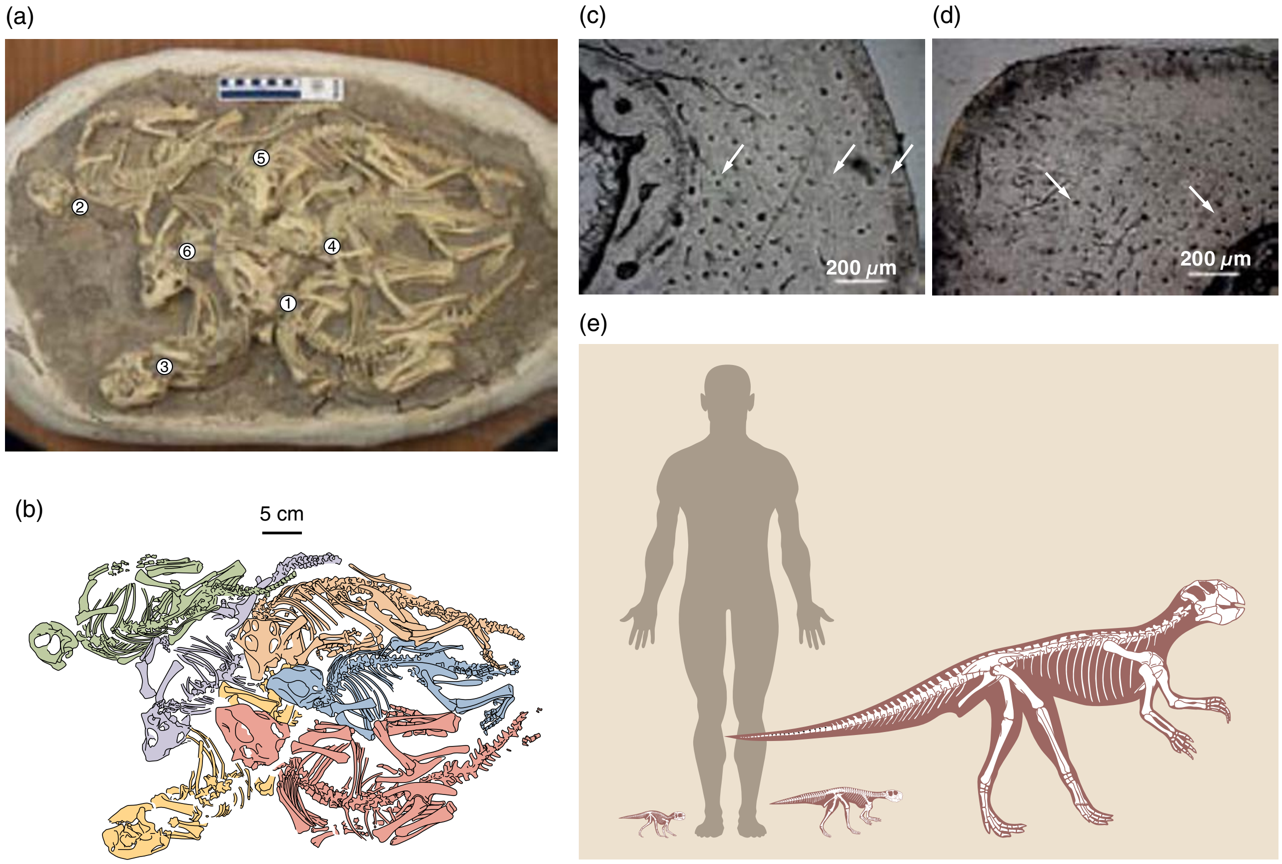
Psittacosaurus juveniles travelled in groups, as shown by spectacular clutches preserved instantly beneath volcanic ashfall deposits in north-east China (Zhao *et al*., 2013a,b). These specimens come from the famous Jehol Group, better known for the remarkable fossils of feathered birds and dinosaurs (see Sections 8.3.3, 9.1). The majority of those fossils are preserved in thin-bedded muddy limestones laid down in lakes. However, around the village of Lujiatun, known as the Chinese 'Pompeii', dinosaur fossils have been preserved under volcanic ash. The sediment is grey in colour and contains fine-scale ash as well as larger pieces of partly molten rock, and the dinosaurs were evidently preserved just like the human victims at Pompeii, instantly and more-or-less in life position. Dinosaurs under the ash are often in a crouching posture. Smaller dinosaurs may occur in groups, all pointing in the same direction, as if running away from the looming ash, and sometimes even with their heads apparently raised, as if gasping for air in the poisonous fumes.

The most common dinosaur at Lujiatun is *Psittacosaurus*, and hundreds of specimens have been found, many of them juveniles, in groups. There is also a flourishing black market in such specimens, and some 'clutches' turn out to be composites of isolated individuals artfully assembled with plaster and filler. It is usually easy for museum experts to identify the fakes (Zhao *et al*., 2013b). Typical clutches from Lujiatun comprise five or six juveniles, but examples of up to 34 individuals have been reported. These probably represent true, original examples of behaviour because the ash fell fast and preserved them instantly. Other kinds of aggregations of dinosaurs are entirely sedimentary, in cases where carcasses were washed together by rivers, for example.

There could be many reasons for such aggregations, and these seem common enough among dinosaurs. Juvenile-only aggregation is not common in modern archosaurs such as crocodilians and birds. In some examples, such as ostriches and ravens, while adults are preoccupied with breeding, nesting, and the care of eggs and hatchlings, nonbreeding juveniles and adults may congregate elsewhere in social groups of mixed age (Varricchio *et al*. 2008). Further, in species of birds and mammals where there are complex breeding rituals, and especially where single dominant males may build harems, the unmated juveniles or subadult males live safely in non-breeding herds, separate from the mated adults. Most of the Lujiatun juveniles appear to be 2–5 years old, so they were probably protective aggregates rather than clusters of frustrated males cruising in search of unattended females. In one example (Zhao *et al*., 2013b), the six juveniles comprise five 2-year-olds and one 3-year-old, as determined from bone histology and LAGs (see Section 8.5).

Psittacosaurus juveniles were quadrupedal and the adults were bipedal; bone histological study shows they switched postures at about the age of four (Zhao *et al*., 2013a). By measuring relative limb lengths and studying bone histological sections of a succession of individuals from one-year-old juveniles to ten-year-old adults, these authors could show how relative changes in the rates of bone growth drove the posture switch. In the babies, fore and hindlimbs were both long. Then, the forelimb showed limited growth, whereas the hindlimb grew much faster during the middle part of ontogeny.

The primitive posture for dinosaurs was bipedal (see Section 6.4), and yet several groups became secondarily quadrupedal, generally associated with large size (sauropodomorphs, thyreophorans, iguanodontian ornithopods, and ceratopsians). It is perhaps surprising then that some basal ceratopsians, such as *Psittacosaurus*, which were still bipedal as adults, retained a quadrupedal hatchling and juvenile posture.



Juveniles of *Psittacosaurus lujiatunensis* from the Early Cretaceous of NE China. (a,b) Cluster of six individuals, photograph and drawing. (c,d) Histological thin sections from the fibula of a three-year old, showing three LAGs (white arrows; c), and a two-year-old, showing two LAGs (white arrows; d). (e) Growth in *Psittacosaurus*, from a one-year old hatchling (left), a three-year old juvenile, and a ten-year-old adult (right). See Colour plate 8.3. Source: Zhao *et al*. (2013a). Reproduced with permission from Nature Publishing Group.

8.5.1 The evidence

Feathers

Until the 1990s, it would have been rash to suggest that dinosaurs had feathers. Even though it was widely accepted that birds evolved from among theropod dinosaurs, *Archaeopteryx* was the oldest feathered animal, and feathers could not be assumed to have existed deeper in the phylogeny, following the principle of the extant phylogenetic bracket (see Section 2.4.1) – dinosaurs are bracketed by birds and crocodiles. However, the abundant finds of feathered theropods from China (see Sections 8.3.3, 9.1) have shown that a broad array of theropods had feathers – and feathers of some kind might also be present among ornithopod dinosaurs such as *Tianyulong* and *Psittacosaurus*, and so perhaps among all dinosaurs. Now, feathers exist for insulation, flight, signalling, and camouflage, and it is well understood that flight came some time after the other two functions. So, insulating feathers in small theropods, and perhaps in juveniles of larger forms, would imply some form of endothermy.

Isotopes

Palaeontologists have had a long love affair with **isotopes** (variants of chemical elements). Measurements of the different isotopic states of carbon and oxygen can be used to reconstruct aspects of the external environment (palaeotemperature, composition of pond water, diet) as well as physiology of ancient animals. Clumped isotope thermometry is a new way of considering oxygen and carbon isotopes at the same time; it is based on the thermodynamic preference of rare heavy isotopes of carbon (^{13}C) and oxygen (^{18}O) to bond with each other (^{13}C-^{18}O), or 'clump,' in carbonate-containing minerals, including the apatite (calcium phosphate) of fossil bone. In a clumped isotope study of six sauropod bone samples from different locations, Eagle *et al.* (2011) reconstructed body temperatures of 36° to 38 °C, similar to those of most modern (endothermic) mammals. This temperature range is 4° to 7 °C lower than predicted by a model that showed scaling of dinosaur body temperature with mass, which could indicate that sauropods had mechanisms to prevent excessively high body temperatures being reached because of their gigantic size. The data support the model of sauropod gigantism that indicates high body temperatures and rapid growth to reach their large adult body size fast (see Section 8.3.7).

Bone histology

Bone histology has long been used as a potential indicator of the thermal state of extinct vertebrates. Early work on the bone histology of dinosaurs showed that they had highly vascular bone, apparently very like that of mammals, but quite unlike the bone of lizards and other living reptiles. Many specimens of dinosaur bone show a vascular primary structure and extensive secondary remodelling with the development of true Haversian systems (Figure 8.21(a)). This was interpreted by Bakker (1972) as evidence for mammal-like endothermy in dinosaurs. True Haversian bone, however, can occur in modern ectothermic reptiles, as well as in endotherms (Reid, 1997), and many small mammals and birds have no Haversian systems, despite having the highest metabolic rates found in endotherms.

A second histological argument for dinosaurian endothermy is based on the presence of fibrolamellar bone in many dinosaurs (Figure 8.21(b)). This is a type of primary compact bone that grows quickly, without formation of growth rings, and it is found today generally in large fast-growing mammals (e.g. cattle) and some birds (e.g. ostriches). Fibrolamellar bone implies only fast growth rates and not necessarily endothermy, so the dinosaurs that have it grew fast to reach sexual maturity (see Section 8.3.7).

Modern reptiles have lamellar-zonal bone, which grows slowly and often intermittently, producing growth rings, or lines of arrested growth (LAGs), when food supplies are limited or climates are unfavourable. Lines of arrested growth are known to be annual in, for example, crocodilians. Lamellar-zonal bone (Figure 8.21(c)) has been reported in many dinosaur groups (Reid, 1997), and indeed LAGs are commonly counted in dinosaurs to indicate their growth rates – it is assumed that these indicate annual seasons of cold climate or low food supplies. Such cyclical growth patterns occur also today in large ruminants in all climate zones (Köhler *et al*., 2012), so confirming that LAGs in dinosaurs need not indicate ectothermy, but that they were perhaps primarily endothermic but suffered slow-downs in growth each year.

Locomotory mechanics

It is commonly understood that modern (ectothermic) reptiles such as lizards and crocodiles may be capable of rapid movement for short periods, but that they soon tire. Indeed, the common image of modern reptiles, especially lizards and turtles, is that they spend much of their time lying around and not moving at all. Mammals and birds on the other hand are in constant motion, and can run or fly for long distances. Their endurance is associated with endothermy and with efficient mechanisms to convert large amounts of food into energy.

In a study of numerous bipedal dinosaurs, Pontzer *et al.* (2009) concluded that all were endothermic. Their approach used two biomechanical methods, one that estimated the locomotor cost from limb length, and the other from active muscle volume (Figure 8.22(a)). Using the first method, it had been shown that hip height explained 98% of the cost of transport in modern mammals, birds, and reptiles, and this is simple to measure in dinosaur skeletons. The second method is more complex and is based on estimates of the volume of the major

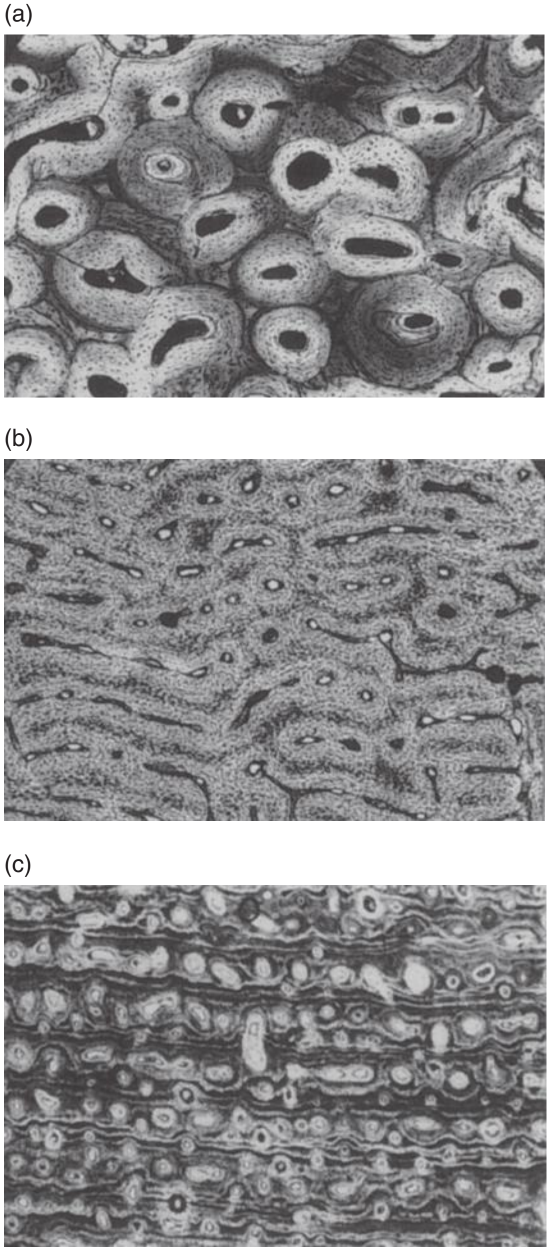


Figure 8.21 Dinosaur bone at high magnification: (a) Haversian bone tissue, showing secondary remodelling; (b) fibrolamellar bone; (c) lamellar-zonal bone, showing growth rings running vertically. Source: R. Reid, deceased; Queen's University, Belfast, UK. Reproduced with permission.

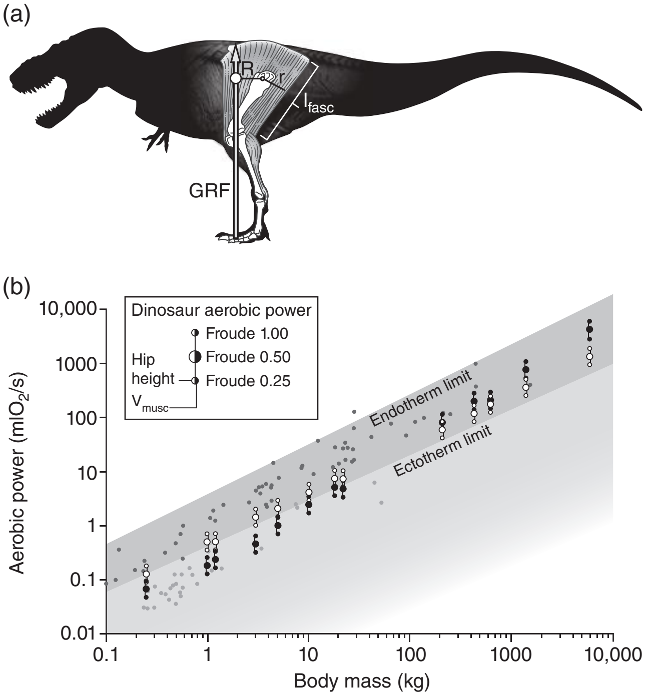


Figure 8.22 Assessing dinosaurian physiology from locomotory criteria. (a) Diagram showing extensor muscle fascicle length (l_{fasc}), the ground reaction force (GRF) vector moment arm (R), and the extensor (antigravity) muscle moment arm (r) for the hip joint. (b) Locomotor power requirements for dinosaurs (aerobic power, mlO_2/s) plotted on a graph of maximum aerobic power (VO_{2max}, mlO_2/s), for extant endotherms (dark grey circles and dark grey-shaded region) and ectotherms (light grey circles and light grey-shaded region) versus body mass. Estimated rates of oxygen consumption for dinosaurs are calculated for walking (Froude 0.25), slow running (Froude 0.50), and moderate running (Froude 1.00) speeds. White symbols are estimates from hip height, black symbols are estimates from active muscle volume, V_{musc}. The upper limit of maximum aerobic power for modern ectotherms (i.e. the upper 95% confidence limit) is indicated by the upper boundary of the light grey region; the upper limit for modern endotherms is indicated by the upper boundary of the dark grey region. Source: (a) S. Hartman (artist), Wisconsin, USA. Reproduced with permission. (b) Hutchinson *et al.* (2011). Reproduced with permission.

leg muscles relative to overall body mass: faster speeds require relatively higher muscle mass and require higher metabolic rates. The calculations required estimates of the ground reaction force for each dinosaur (proportional to body mass and speed of movement as expressed through each limb) and the mean fascicle length of the major leg muscles (a fascicle is a bundle of muscle fibres that share a function), and these depend on the pose of the limbs. When the cost of transport was calculated for dinosaurs large and small, while walking, and running at slow and fast speeds, dinosaurs nearly always plotted in the region of energy requirement seen in modern endotherms (Figure 8.22(b)).

These results indicate that larger bipedal dinosaurs at least were endothermic because there is no other means by which an ectotherm could sustain locomotion and the necessary metabolic rate. Results for the smaller dinosaurs, weighing less than 20 kg, indicated intermediate physiological positions – ectothermic at low speeds and endothermic at high speeds. However, the calculations were conservative and the plots are not exclusive for endotherms; at low energy an endotherm can plot as an ectotherm, but an ectotherm can never plot as an endotherm. Further, additional evidence (e.g. feathers, bone histology) points to endothermy in small bipedal dinosaurs.

8.5.2 Endothermy and gigantothermy

Among living vertebrates, it is commonly understood that birds and mammals gain the advantages of endothermy (e.g. constant activity, ability to operate at night, ability to live in cold climates) at a cost (Clarke and Pörtner, 2010). Typically, an endotherm has to eat ten times as much as an ectotherm of the same body mass. For example, a lion is constantly alert and must bring down prey every few days to feed the internal furnaces that generate her high metabolic rate. Meanwhile, at the nearby waterhole, a crocodile of identical body mass sleeps most of the time, and has to kill an antelope only every couple of weeks or so.

This differential is more marked among smaller animals; small endotherms such as shrews and hummingbirds have to feed nearly continuously in order to sustain their relatively very high metabolic rates. In considerations of feathers in dinosaurs, it is assumed that only smaller species, and the juveniles of large species, had full coverings of insulating feathers. In the warm Mesozoic climates (see Section 8.2), a huge tyrannosauroid or sauropod would have suffered more with problems of heat dissipation. Elephants today waste a great deal of energy by sustaining a high metabolic rate, but at the same time wallowing and flapping their ears to lose heat.

As noted earlier (see Section 8.3.7), sauropods achieved larger size than any mammal today perhaps by taking advantage of a less efficient physiology. This controlled the risk of overheating, while reducing their food requirement substantially. Thermal physiologists have identified this strategy as gigantothermy, the ability to maintain a constant body temperature by virtue of being huge (Reid, 1997; Seebacher, 2009; Seymour, 2013). Experiments on large living reptiles have shown that rates of internal temperature change are very slow during normal subtropical daily air temperature fluctuations. In living reptiles over 30 kg in body weight, the rate of heat loss (thermal conductance) becomes equivalent to that of mammals (Figure 8.23). By extrapolation, the body temperatures of medium- to large-sized dinosaurs living in similar climatic conditions would have remained constant to within 1 or 2 °C inertially without substantial internal heat production. In calculations of likely body temperatures of all dinosaurs in different palaeoclimatic zones, Seebacher (2009) concluded that ectothermy (gigantothermy) was likely in all dinosaur groups, except for coelurosaurian theropods and smaller ornithopods ('hypsilophodontids'), which were presumably endothermic.

8.6 PTEROSAURIA

The pterosaurs (literally 'winged reptiles'), known from about 140 species, existed for nearly the same span of time as the dinosaurs. They were important small fish-eaters in the Jurassic, and adopted a variety of ecological roles in the Cretaceous when some truly gigantic forms arose.

8.6.1 Pterosaur anatomy and ecology

The first pterosaurs from the Late Triassic, such as *Eudimorphodon* from northern Italy (Dalla Vecchia, 2013), show all the unique characters of the group (Figure 8.24(a)): the short body, the reduced and fused hip bones, the five long toes (including a divergent toe 5), the long neck, the large head with pointed jaws and the arm. The hand (Figure 8.24(b)) has three short grasping fingers with deep claws and an elongate fourth finger that supports the wing membrane. In front of the wrist is a new element, the **pteroid**, a small pointed bone that was attached to the wrist and that supported a small anterior flight membrane (Figure 8.24(a)). The pelvis (Figure 8.24(c)) is a solid small structure with short blunt pubes and ischia. An additional element, the **prepubis**, is attached in front and it may have had a function in supporting the guts or in assisting respiration. The tail is stiffened with elongate zygapophyses and chevrons, and it may have been used as a rudder during flight.

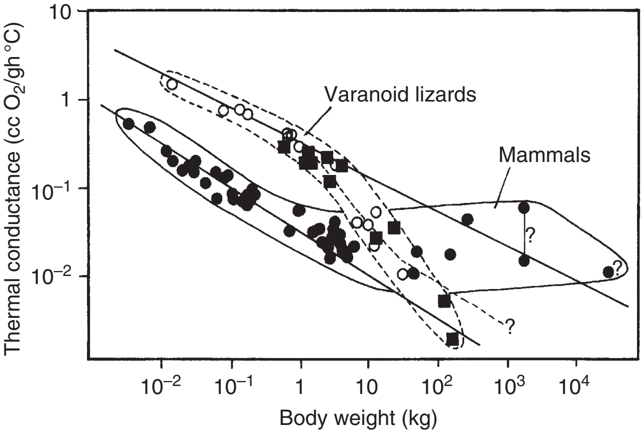


Figure 8.23 The effect of body size on thermal biology of varanid lizards (O), other reptiles (*v*) and mammals (•); as body size increases, thermal conductance values converge. Source: Adapted from McNab and Auffenberg (1976).

Pterosaurs diversified in the Jurassic and Cretaceous (Wellnhofer, 1978; Buffetaut and Mazin, 2003; Witton, 2013; Martill *et al.*, 2014). Basal lines are often grouped in the paraphyletic 'Rhamphorhynchoidea', but most diverse was the clade Pterodactyloidea, which arose in the Middle or Late Jurassic and radiated during the Cretaceous. The greatest diversification in terms of species numbers and morphological disparity (see Section 2.7) was in the Early Cretaceous when pterodactyloids showed the broadest range of sizes, head shapes, and feeding modes (Prentice *et al.*, 2011). The broad outlines of pterosaur phylogeny are well agreed, but the relationships of *Eudimorphodon*, anurognathids, and some of the Cretaceous pterodactyloids are still debated (e.g. Andres *et al.*, 2010; Lü *et al.*, 2012; Dalla Vecchia, 2013).

Much of the diversity of pterosaurs may be appreciated by an examination of a selection of skulls (Figure 8.25). First, skull lengths vary considerably from 90 mm in *Eudimorphodon*, little larger than a seagull, to 1.79 m in *Pteranodon*. These skulls also show some broad evolutionary changes: forward shift of the jaw joint to lie below the orbit, elongation of the skull and fusion of the nostril and antorbital fenestra with reduction of the nasal bone.

Pterosaur skulls suggest a range of feeding styles. The long spaced teeth of *Rhamphorhynchus*, *Pterodactylus* and *Ornithocheirus* (Figure 8.25(b,c,f)) were probably used for piercing and holding fish, whereas the shorter teeth of *Dimorphodon* (Figure 8.25(a)) may have been used for insect eating. *Ctenochasma* and

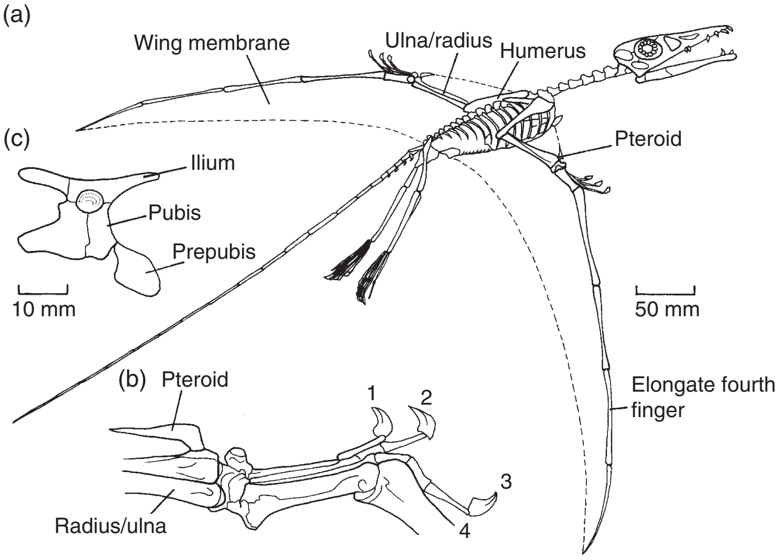


Figure 8.24 One of the first pterosaurs, the Late Triassic *Eudimorphodon*: (a) skeleton in flying pose; (b) hand region of the right wing; (c) pelvis in lateral view. Source: Adapted from Wild (1978).

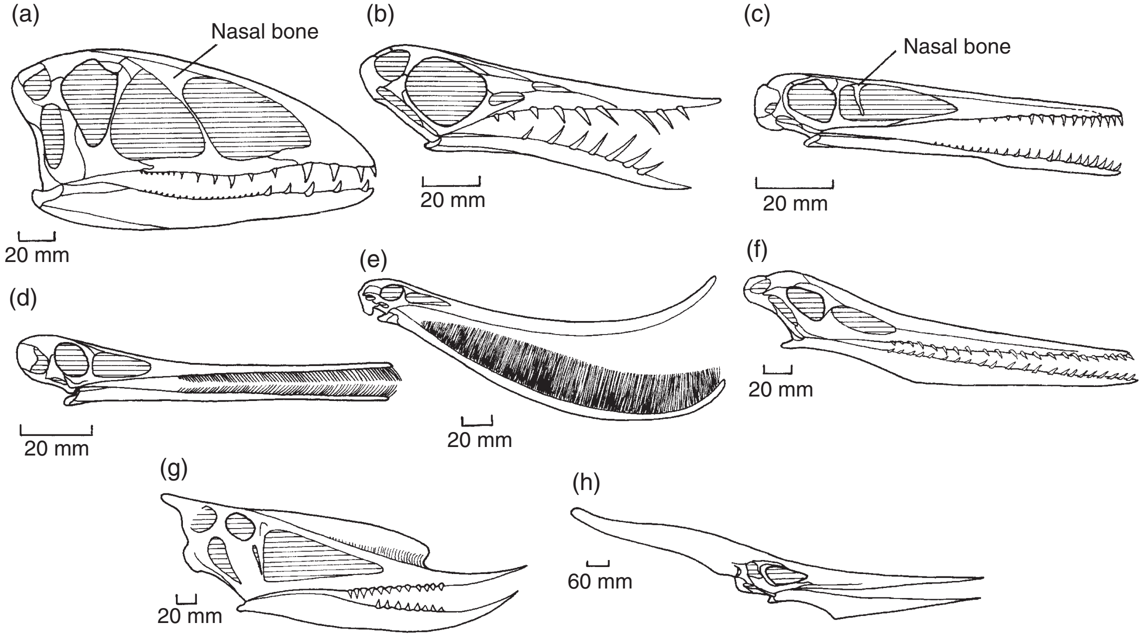


Figure 8.25 Diversity of pterosaurs, shown by their skulls: (a) *Dimorphodon*; (b) *Rhamphorhynchus*; (c) *Pterodactylus*; (d) *Ctenochasma*; (e) *Pterodaustro*; (f) *Ornithocheirus*; (g) *Dsungaripterus*; (h) *Pteranodon*. Source: Adapted from Wellnhofer (1978).

Pterodaustro (Figure 8.25(d,e)) have huge numbers of slender teeth in each jaw, i.e. 400–500 flexible teeth in *Pterodaustro*, which were probably used to filter microscopic plankton from the water. The teeth would have acted as a fine filter mesh for trapping thousands of small organisms that could be licked off and swallowed. The jaws of *Dsungaripterus* and *Pteranodon* (Figure 8.25(g,h)) are deep and hatchet-shaped and bear very few, or no, teeth. *Pteranodon* also probably fished by beak trawling and swallowed its catch so rapidly that no teeth were needed, whereas *Dsungaripterus* had reinforced teeth that suggest a diet of hard-shelled organisms.

Pteranodon, one of the best-known and largest pterosaurs from the Late Cretaceous of North America (Bennett, 2001), has a wingspan of 5–8 m. The skull is longer than the trunk (Figure 8.26(a)) and its length is doubled by the pointed crest at the back in males. The function of the crest has long been debated, but wind tunnel experiments show it had negligible effect as a weathercock to keep the head facing forwards during flight, and was almost certainly solely a sexual display structure (Elgin *et al.*, 2008), as were all the weird and wonderful head crests of other pterosaurs (see Figure 8.25).

Each massive cervical vertebra in *Pteranodon* (Figure 8.26(b)) has a pneumatic foramen in the side that led into open spaces inside, a weight-reducing feature. The dorsal vertebrae are nearly all involved in one or two heavily fused girder-like structures, the **notarium** and the **synsacrum** (Figure 8.26(c,d)), which stabilize and support the shoulder girdle and pelvis. The shoulder girdle is attached to the side of the notarium above and to a large bony **sternum** (Figure 8.26(e)) below, which holds the ribcage firm. The sternum bears a slight keel for the attachment of flight muscles. This massive stabilization of the shoulder girdle and pelvis is typical of pterodactyloids and it was probably related to flight stresses.

Pteranodon was not the largest pterosaur. That honour probably goes to *Quetzalcoatlus* from the upper Cretaceous of Texas (where else?), which is represented by parts of a single wing, giving an estimated wingspan of 10 m (Figure 8.26(f)), although *Hatzegopteryx* from Romania might have been even larger, with a wingspan of 10–11 m. *Quetzalcoatlus* and *Hatzegopteryx* were the largest known flying animals, three times the size of the largest bird, and more like a small aeroplane in size than any familiar living animal. These pterosaurs, the azhdarchids, are known from fragmentary remains from the uppermost Cretaceous of many parts of the world. The mode of life of these amazing animals has, however, been hard to discern (see Box 8.6).

8.6.2 Pterosaur flight

Pterosaurs were sometimes portrayed in the past as rather inefficient gliding animals that were incapable of flight. On the ground, their locomotion was supposed to have been an awkward bat-like form of progression, consisting of staggering and tumbling on all fours like a broken umbrella blowing along the street. Current work (e.g. Wellnhofer, 1978; Padian, 1984; Witton and Habib, 2010; Palmer, 2011; Palmer and Dyke, 2012) counters these views and presents a picture of the pterosaurs as reasonably efficient flapping flyers like modern birds, but adopting different principles. The first line of evidence is the possession of wings and other aerodynamic and flight adaptations (hollow bones, streamlined head). The second key aspect is that the pterosaurs were almost certainly endothermic, as they had

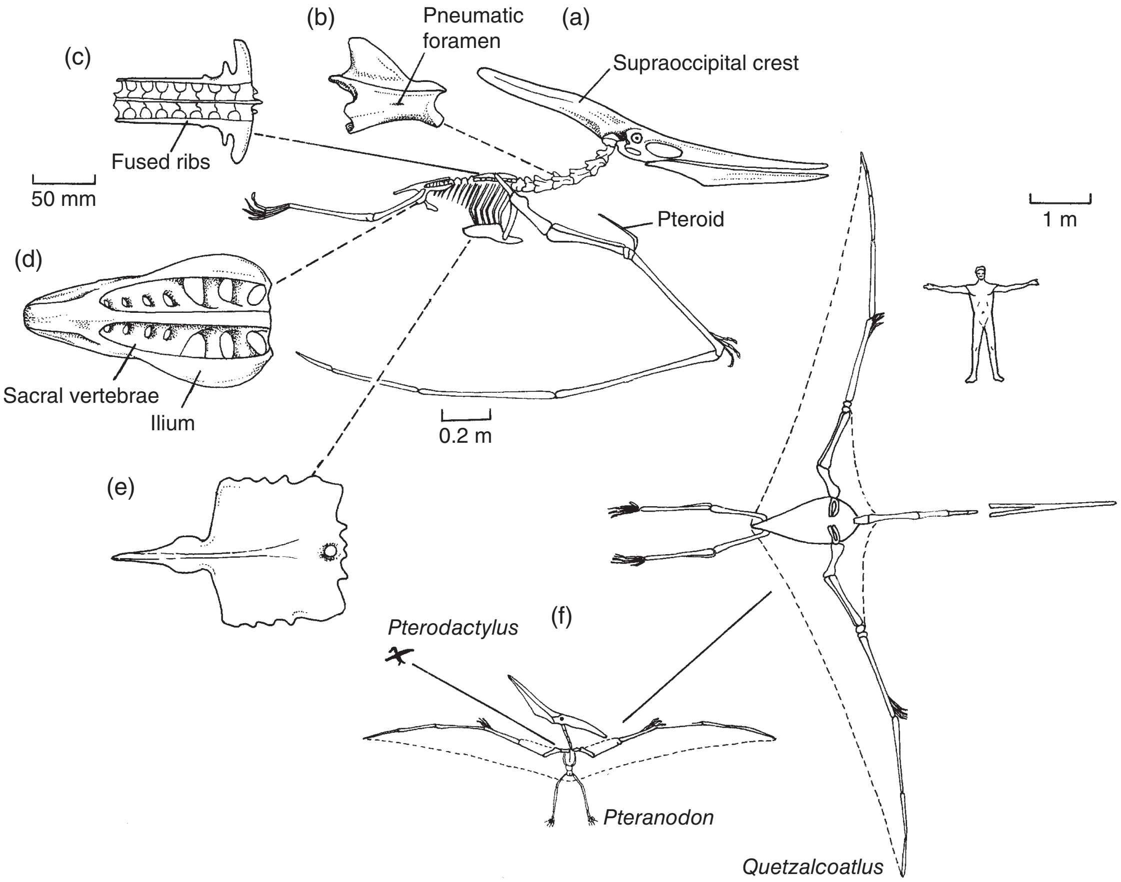


Figure 8.26 Anatomy of the giant Late Cretaceous pterosaurs: (a–e) *Pteranodon*: (a) flying skeleton in lateral view; (b) cervical vertebra in lateral view; (c) notarium in dorsal view; (d) synsacrum in dorsal view; (e) sternum in ventral view; (f) *Quetzalcoatlus* shown in proportion to *Pterodactylus* and *Pteranodon*. Source: (a–e) Adapted from Eaton (1910). (f) Adapted from Langston (1981).

BOX 8.6 FUNCTION OF THE LARGEST FLYING ANIMALS

Azhdarchids are surely the most spectacular of Mesozoic animals, possible fliers that were ten times the size of any flying animal today. When first reported, *Quetzalcoatlus*, with its 10 m wing span, was seen as unbelievable, and palaeontologists have struggled ever since to understand how an animal that stood as tall as a giraffe could be light enough to fly (see illustration). And if it did not fly, why did it have wings?

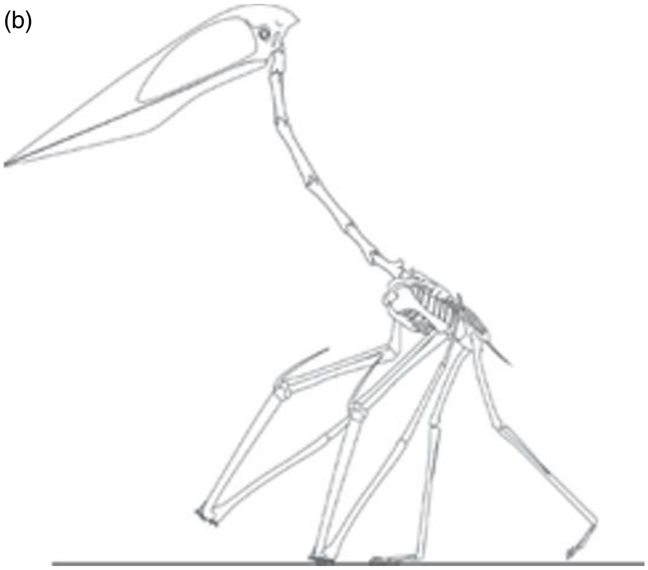
The diversity and success of azhdarchids has only become evident in the past decades. Remains are known throughout the final 50 Myr of the Cretaceous, and these range in estimated size from *Montanazhdarcho* from North America (2.5 m wing span) to *Hatzegopteryx* from Romania (12 m wing span). Morphological features common to all azhdarchids include a long, shallow beak; elongate, cylindrical cervical vertebrae that formed a long and unusually inflexible neck; and proportionally short wings with an abbreviated fourth phalanx.

The mode of life of azhdarchids has been intensively debated (Witton and Naish, 2008). Possible interpretations have included suggestions that they lived as vulture-like scavengers, sediment probers, swimmers, waders, aerial predators, or stork-like generalists. Most authors have seen them as massive fliers, skimming for fish across the surface of the ocean, trawling their lower jaws through the water during flight and seizing aquatic prey from the water's surface. Although this view had been widely accepted, the skim-feeding model lacks support from anatomy and functional morphology. Witton and Naish (2008) note that azhdarchids lack the many cranial specializations exhibited by living skim-feeding birds, most notably the laterally compressed lower jaw and shock absorbing apparatus in the jaw joint required for this feeding style. Well-preserved azhdarchid skulls are rare, but their beaks and lower jaws appear to have been sub-triangular in cross-section, and thus different from the blade-like cross sections seen in living skim-feeders and sediment probers.

Key in all these discussions is whether azhdarchids could fly or not. *Quetzalcoatlus* has been most studied in this respect, and numerous estimates of its body mass have been given, ranging from 62 to 136 kg for a wing span of 10–15 m. However, these masses are based more on back-calculation from the weight a particular wing area could support rather than primary evidence of mass. Such estimates would imply that pterosaur soft tissues had mean densities less than 0.25 g/cm^3, the lowest estimated for any animal (the normal density of flesh is closer to 1 g/cm^3).

Independently, Henderson (2010) and Witton and Habib (2010) used different methods to estimate the body mass of *Quetzalcoatlus*, allowing for reasonable estimates of the mass of flesh and for maximum amounts of air spaces within bones and body tissues. Their estimates of 544 kg and 200–250 kg respectively are still widely different, and led Henderson (2010) to conclude that this giant azhdarchid could not have heaved its half-tonne body off the ground, whereas Witton and Habib (2010) found evidence that this behemoth could actually have flown.

Azhdarchids were adept walkers, and the wings may then have existed largely for terrestrial locomotion. Geological evidence shows that azhdarchids predominantly inhabited inland settings, rather than seas or coasts. Further, their anatomy indicates that they were poorly suited for all proposed lifestyles other than wading and terrestrial foraging. However, azhdarchid footprints show that their feet were relatively small, padded and slender, and thus not well suited for wading. Witton and Naish (2008) argue that azhdarchids were stork- or ground hornbill-like generalists, foraging in diverse environments for small animals and carrion. Proficient terrestrial abilities and a relatively inflexible neck are in agreement with this interpretation.



Extremes in pterosaur morphology. (a) The giant azhdarchid *Arambourgiana* from the Late Cretaceous of Jordan had a 10 m wingspan, and was as tall as a giraffe (here, a 5.6-m tall bull). The small insectivorous *Anurognathus* from the Late Jurassic of Germany is seen flying in the centre. (b) Reconstructed walking azhdarchid, *Zhejiangopterus* from the Early Cretaceous of China, a small form with a 3.5 m wingspan. Source: M. Witton, University of Portsmouth, Portsmouth, UK. Reproduced with permission.

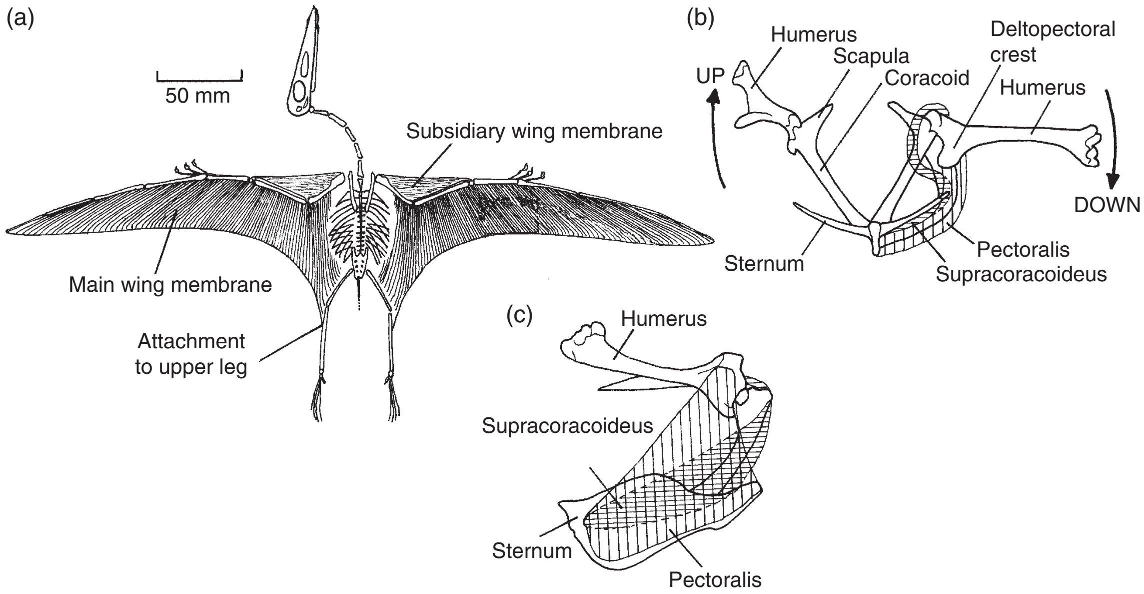


Figure 8.27 Pterosaur wings and flight: (a) skeleton of *Pterodactylus* with the wing membranes preserved and showing partial attachment to the legs; (b,c) anterior and lateral views of the shoulder girdle and humerus of a pterosaur showing the humerus in the upstroke and downstroke positions and the main flight muscles (pectoralis, downstroke; supracoracoideus, upstroke). Source: (a) Adapted from Wellnhofer (1987). (b,c) Adapted from Padian (1984).

short hairs over the thorax, neck and upper arms (Unwin and Bakhurina, 1994). Only endotherms have external insulation and endothermy gave the pterosaurs the high, sustained metabolic rates necessary for flight.

The pterosaur wing is composed of skin that attached to the side of the body and along the entire length of the arm and of the elongated flight finger 4 (Figures 8.26(a) and 8.27(a)). It was once argued that the pterosaur wing was a slender structure rather like that of a gull, but it was in fact broader as the flight membrane also attaches to the femur (Figure 8.27(a)) in well-preserved specimens (Wellnhofer, 1987; Unwin and Bakhurina, 1994). Understanding the exact shape of the pterosaur wing is difficult because so much of it is composed of soft tissue, but study of specimens and calculations of maximum aerodynamic efficiency point to a wing whose anterior margin swept well forward, and whose wing tip was curved backward during the downwards power stroke (Palmer and Dyke, 2012).

The wing membrane was composed of several skin layers, up to 1 mm thick in all, reinforced with parallel stiff fibres, termed actinofibrils, particularly in the distal region (Unwin and Bakhurina, 1994). The actinofibrils were located primarily in the outer sector of the wing, radiating backwards from the wing finger. They acted to spread the wing and keep it spread by transferring forces in the wing membrane back to the fourth digit along the leading edge (Bennett, 2000).

The pterosaur power stroke was directed down and forward and the recovery stroke up and backward, so that the wing tip, viewed from the side, described a figure-of-eight shape. At slow flight speeds, the downstroke was powered by the massive **pectoralis muscle**, and the upstroke may have been powered by the **supracoracoideus muscle** (Figure 8.27(b,c)), which ran from the sternum, over a pulley arrangement at the shoulder joint, to the dorsal face of the humerus, or largely by the shoulder muscles (Bennett, 2003).

Pterosaurs flew relatively slowly because of their large wings, but efficiently, and they were highly manoeuvrable (Witton and Habib, 2010; Palmer, 2011). Wind tunnel tests (Palmer, 2011) show that pterosaur wing sections had rather higher profile drag and maximum lift coefficients than assumed before. This indicates that large pterosaurs were aerodynamically less efficient and could fly more slowly than previously estimated. Unlike most modern birds, pterosaurs had wings that were adapted to low-speed flight, unsuited to marine style dynamic soaring, as in albatrosses and gulls, but adapted for thermal/slope soaring and controlled, low-speed landing. Pterosaurs could not cope with strong or turbulent winds in the way that smaller, short-winged birds can, and their extensively hollow bones also created risks of damage.

Pterosaurs may have taken off from trees or cliffs, or jumped into the air after a short run to pick up speed. A novel alternative has been the suggestion by Witton and Habib (2010) that pterosaurs launched themselves from a quadrupedal pose, as vampire bats do today, vaulting their hindquarters upwards and pushing on the ground with their muscular forearms. Landing was awkward for the larger pterosaurs, just as it is for large birds, and the reinforced pelvis and sacrum would have had to withstand large impacts. Pterosaur senses and brains seem to have been adapted for flying – pterosaurs have the large eyes and bulbous heads of birds. Indeed, reconstructed pterosaur brains suggest (Witmer *et al.*, 2003) that these animals had good vision and balance areas in the brain, although overall their brains were relatively smaller than those of birds.

8.6.3 Pterosaur walking

Just as pterosaurian flying capabilities have been debated, so too has their terrestrial ability. Padian (1984) argued that pterosaurs walked on fully erect hindlimbs. He reconstructed the pelvic girdle of various pterosaurs as firmly fused beneath, and the limb motions just like those of a small bipedal dinosaur. The wings were held tucked horizontally beside the body during running. This view has been fairly conclusively disproved on the basis of three independent lines of evidence (Unwin, 1999; Witton and Naish, 2008; Costa *et al*., 2014).

1 Three-dimensionally-preserved pterosaur specimens show that the pelvis is wide open at the bottom and that the hindlimbs point sideways in an awkward sprawling posture. The legs could not be pulled into an upright posture, and hence bipedality would be impossible.

2 Calculations of balance show that bipedality would have been hard for the smaller pterosaurs and impossible for the larger Cretaceous forms.

3 Most fossil tracks show that pterosaurs walked quadrupedally, with the feet wide apart (hindlimbs in the John Wayne posture) and the hands far out on either side.

During walking, the pterosaur used all four limbs, its legs in the middle and its hands a short distance in front and to the side, with the wing tips sticking up on either side of the head. The rolling, awkward locomotion of the Early Cretaceous pterosaur *Anhanguera* may be viewed at: http://palaeo.gly.bris.ac.uk/dinosaur/animation.html.

8.7 TESTUDINATA: THE TURTLES

The turtles and tortoises, Testudinata or Chelonia, arose in the Late Triassic and later achieved a diversity of 25 families, of which 14 families and 325 species exist today. It seems that early on they achieved a successful design, the 'shell', and stuck with it. Turtle diets are broad ranging, including herbivores and insectivores on land, and herbivores and carnivores in the water, with diets from jellyfish to fishes.

8.7.1 Turtle anatomy

The shell of turtles is composed of two portions, a domed **carapace** on top and a flat **plastron** below, which are attached to each other at the sides, leaving broad openings at the front for the head and arms, and at the back for the legs and tail. The carapace is composed of bony plates that form within the skin and these are covered by broad horny scutes in regular patterns (Figure 8.28(a,f)). The plastron is a smaller unit (Figure 8.28(g)) that protects the belly area. The main plates of the carapace are attached to the vertebrae and ribs, whereas the plastron is formed from expanded elements of the shoulder girdle and equivalents of the gastralia of other reptiles (see Section 5.1.2).

The neck of turtles is long and flexible (Figure 8.28(a)), and the head is relatively small, but strongly constructed. The shoulder girdle of modern turtles (Figure 8.28(a,b)) is triradiate with two scapular heads, one facing upwards and one inwards, and a long narrow coracoid running back. The pelvis is smaller, but also three-pointed (Figure 8.28(a,c)), with a narrow iliac blade running up and back, and a narrow pubis and ischium running forwards and backwards respectively. The limbs are short and held in a sprawling posture, and the hands and feet are large in swimming forms.

The turtle shell has always been interpreted as a specialized structure that evolved from the ribs in some way, but the fact the turtle shoulder girdle lies inside the rib cage has been a conundrum. A combination of new fossil finds and developmental work has resolved these questions (see Box 8.7).

8.7.2 The first turtles

The origin of turtles is an enduring mystery, with several possibilities at present. Much palaeontological evidence suggests turtles are parareptiles, sharing their anapsid skulls and numerous other characters with pareiasaurs and procolophonids. Molecular evidence is unequivocal, that turtles are diapsids, and specifically archosauromorphs (see Section 5.2.2; Box 5.1).

The oldest turtle is *Odontochelys* from the early Late Triassic of China (see Box 8.7). This taxon confirms evidence from development that the plastron evolved first, and that the carapace evolved from expanded ribs. The next most ancient turtles, *Proganochelys* and *Proterochersis*, both from the later Late Triassic of Germany, show the key features that are common to all modern forms (Gaffney and Meeker, 1983). The skull (Figure 8.28(d,e)) is anapsid (no temporal fenestrae) and massively built, being firm and immovable. *Proganochelys* could no doubt have survived a head-crushing stomp from *Plateosaurus*. In side view (Figure 8.28(d)), the skull shows three further turtle characters: toothless jaws, evidence of a horny beak and a deep curved embayment on the quadrate that supports a large ear drum. The palate (Figure 8.28(e)) is primitive for turtles because it retains teeth on the vomer and pterygoid, and is linked only loosely to the braincase. In later forms, the teeth are lost and the palate fuses firmly to the base of the braincase.

The carapace of *Proganochelys* (Figure 8.28(f)) is broad, and it consists of several large midline plates, a number of lateral plates and smaller marginal plates that form sharp projections round the margins. The plastron of *Proterochersis* (Figure 8.28(g)) is similar to that of modern turtles in being much smaller than the carapace and in leaving spaces for the neck and legs to emerge.

The fourth Late Triassic turtle, *Palaeochersis* from the Los Colorados Formation of Argentina (Sterli *et al*., 2007), appears to be sister to *Australochelys* from the Early Jurassic of South America (Figure 8.28(h)). Both show fusion of the braincase and palate, and partial enclosure of the middle ear region, but they still retain some palatal teeth and the tail in the South American form at least is still long. There are two further Early

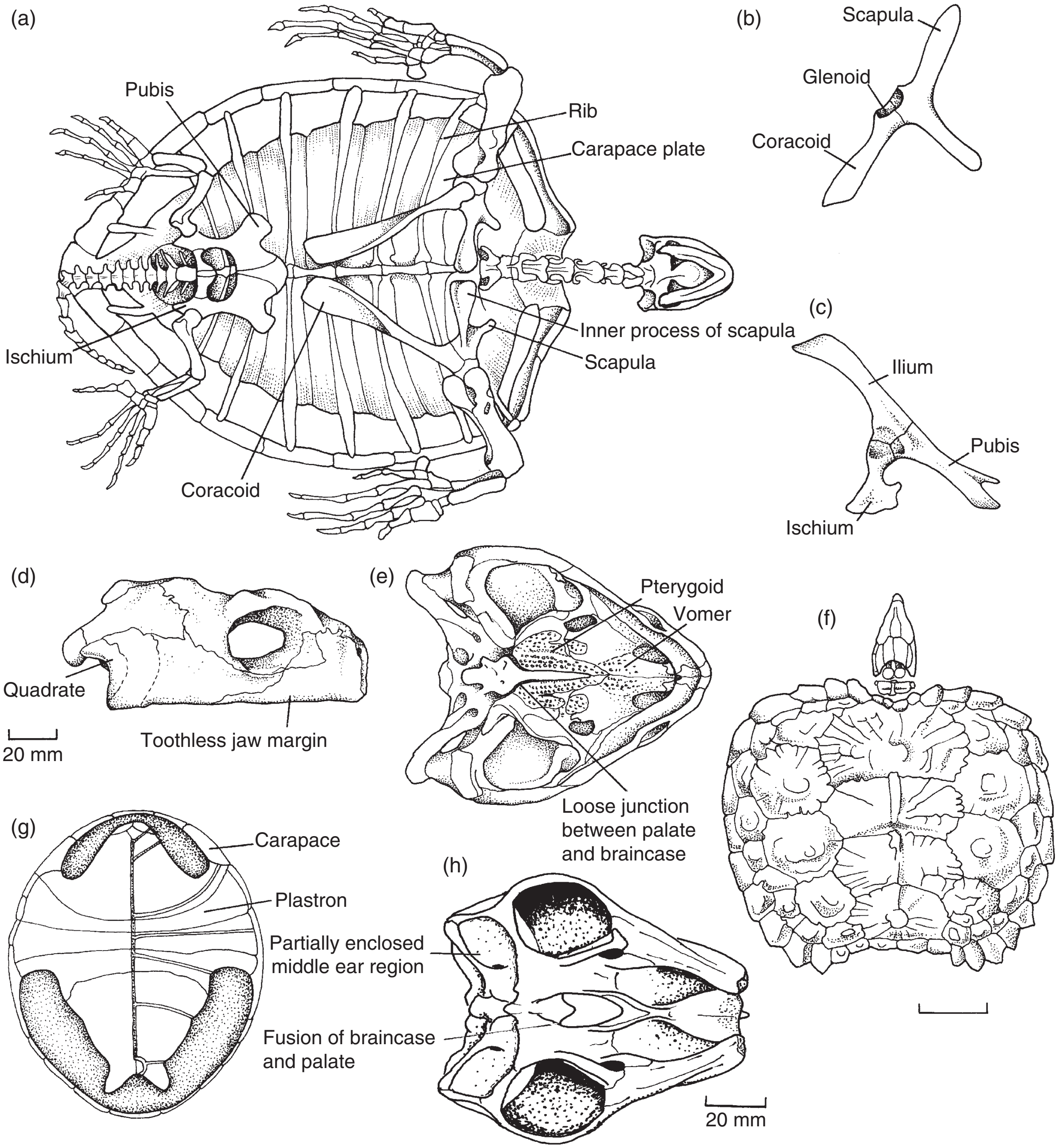


Figure 8.28 Turtle anatomy: (a–c) *Chelone*, a modern turtle, skeleton in ventral view, pectoral and pelvic girdles; (d–f) *Proganochelys* from the Late Triassic of Germany, skull in lateral and ventral views and carapace and skull in dorsal view; (g) *Proterochersis* from the Late Triassic of Germany, reconstructed plastron showing the divisions between the bones (left) and between the horny covering scutes (right); (h) *Australochelys* from the Early Jurassic of South Africa, skull in ventral view. Source: (a) Adapted from Young (1981). (b,c) Adapted from Carroll (1987). (d,e) Adapted from Gaffney and Meeker (1983). (f,g) Adapted from Zittel (1932). (h) Adapted from Gaffney (1994).

Jurassic turtles, *Indochelys* from India, and *Kayentachelys* from Arizona, USA. *Kayentachelys* retains pterygoid teeth in the palate, definitely not a feature of modern turtles, and it has been said to show a cryptodire-like otic capsule trochlea (Gaffney and Jenkins, 2010; see Section 8.7.3), but this is not accepted by Sterli and Joyce (2007). There are limited numbers of turtles in the Middle Jurassic, and the record expands dramatically in the Late Jurassic.

In some cladistic works (e.g. Gaffney, 1994; Gaffney and Jenkins, 2010), many of the Late Triassic and Early Jurassic turtles were assigned to the derived clades Pleurodira and Cryptodira, but revised analyses (Joyce, 2007; Sterli, 2010; Anquetin, 2012; Joyce and Sterli, 2012) show they are outgroups to crown Testudines, which originated in the Middle Jurassic. Among the testudine outgroups are a few unexpected, later taxa, including the meiolanids (Figure 8.29(f)), known mainly from

BOX 8.7 MAKING AN INSIDE-OUT REPTILE

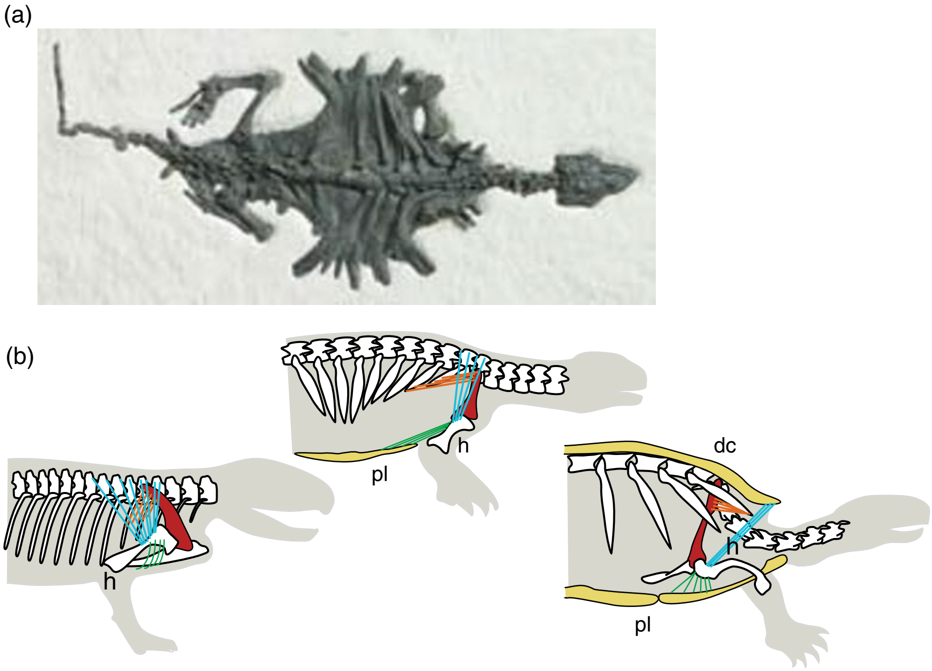
The turtle shoulder girdle has become something of a *cause célèbre* in evolution and development. In most vertebrates, the shoulder girdle lies *outside* the rib cage, whereas in turtles it lies *inside*. How could such a complex, functioning structure, with bones, muscles and nerves, somehow hop from outside to inside? Lyson and Joyce (2012) argue that in fact the turtle scapula lies *in front of* the rib cage in embryos, and that this is the ancestral location for amniotes in general. In most groups, the scapula shifts outside the ribcage during development; in turtles on the other hand it shifts inside.

The developmental origin of the turtle carapace also sheds some light on the conundrum (Nagashima *et al*., 2012; Hisasawi *et al*., 2013). The carapace indeed forms from the ribs. In most amniotes, the ribs sprout from the vertebrae in the axial midline of the embryo and grow downwards between the anterior limbs, whereas in turtles, the proto-ribs grow sideways and form the carapace above the limbs. Early in development, the body wall folds down and towards the centre of the turtle's body, and the fold defines the edge of the future carapace. Because the trunk ribs are short, and the fold occurs, the scapula ends up beneath the ribs, rather than outside them, as in most tetrapods. Developmentally then the true novelty in turtles is in the axial arrest of the rib growth as well as in the folding at the hinge between the axis and body wall (Nagashima *et al*., 2009).

A new fossil find, the oldest fossil turtle yet, *Odontochelys* from the Late Triassic (Carnian) Xiaowa Formation of Guanling, South China (220 Myr), seems to provide a perfect intermediate (Li *et al*., 2008). This marine turtle has a fully developed plastron, but the carapace is less complete, consisting of the midline neural plates only. This matches what is seen in embryos of modern turtles, in which the carapace forms from expansion of the ribs rather than the fusion of dermal osteoderms, as had sometimes been suggested.

There was still a problem in determining what came before *Odontochelys*, since it and other turtles emerge in the Late Triassic without a hint of their ancestry. Lyson *et al*. (2013) resurrect an older idea, that the unusual reptile *Eunotosaurus* from the Middle Permian of South Africa is a turtle precursor. This is suggested by the fact that *Eunotosaurus* has a reduced number of elongate trunk vertebrae (nine), nine pairs of T-shaped ribs, presumed loss of intercostal muscles, reorganization of respiratory muscles to the ventral side of the ribs, (sub)dermal outgrowth of bone from the developing perichondral collar of the ribs, and paired gastralia that lack both lateral and median elements. This fossil taxon then matches the presumed turtle precursor and show that the turtle carapace is a set of fused bony plates that became modified from primary ribs.

The new views about turtle development and the new fossils *Eunotosaurus* and *Odontochelys* all provide evidence for a plausible sequence of events in turtle origins, and explain the peculiarities of turtle anatomy. However, in making *Eunotosaurus* the unequivocal sister group of Testudines, Lyson *et al*. (2013) comment that the 'initial transformations of the model thus occurred by the Middle Permian, which is congruent with molecular-based divergence estimates… for the lineage, and remain viable whether turtles originated inside or outside crown Diapsida.'



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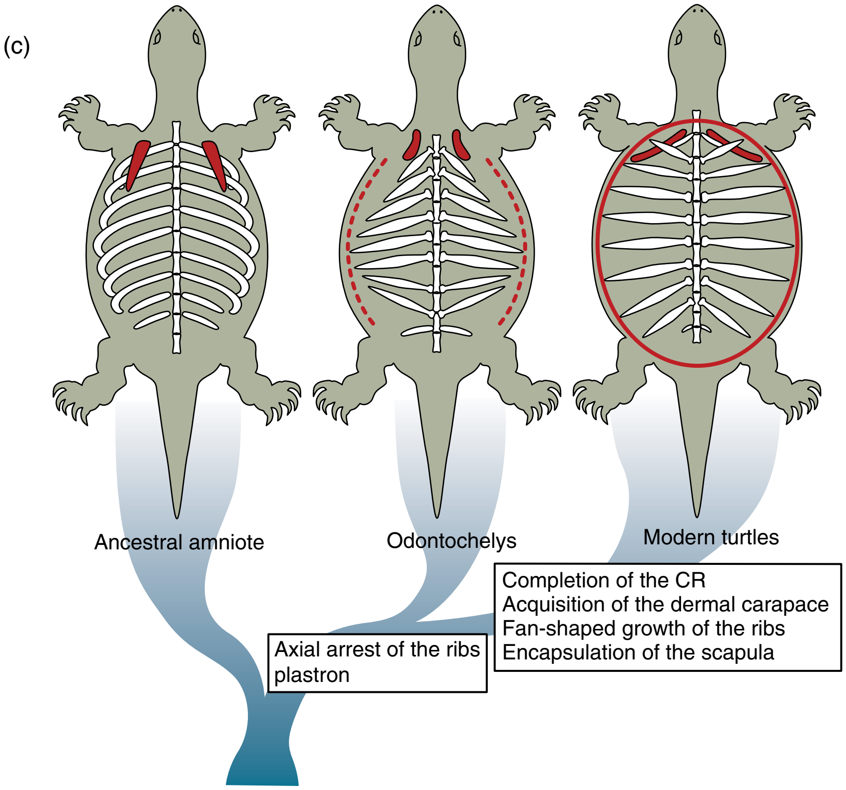


The oldest turtle, and evolution of the turtle body plan. (a) Skeleton of the type specimen of *Odontochelys semitestacea*, showing the rib-like plastron. (b) Evolution of the ribs, scapula, and carapace in an ancestral amniote (left), in *Odontochelys* (centre), and in a modern turtle (right), seen in lateral cross section (b) and in dorsal view (c). The scapula is black, and key shoulder muscles are indicated. In *Odontochelys*, the serratus anterior anlage would have connected the scapula and distal tips of anterior ribs antero-posteriorly. In *Odontochelys*, the carapacial ridge (CR; broken line) may have developed only temporarily and incompletely in the embryo. In the modern turtle, the CR (solid line) forms a complete circle, inducing the fan-shaped growth of the ribs. See Colour plate 8.4. Abbreviations: dc, dermal carapace; h, humerus; pl, plastron. Source: (a) C. Li, Institute for Vertebrate Paleontology and Paleoanthropology, Beijing, China. (b) H. Nagashima, Meiji University, Meiji, Japan. Reproduced with permission.

the Pleistocene of Australia, which have broad skulls up to 500 mm wide and armoured with horns.

8.7.3 Pleurodires and cryptodires

The remaining turtles from the Middle Jurassic to the present day form a clade, the Testudines or Casichelydia (see Box 8.8), composed of two major groups, Pleurodira and the Cryptodira. Pleurodires and cryptodires show modifications to the skull, such as the loss of the lacrimal bone and the tear duct that normally runs through it. There is a single vomer in the palate. The middle ear region is completely enclosed by ventral extensions of the pterygoid and opisthotic to form a bony tube.

Most testudine turtles, unlike the proganochelyids and australochelyids, can retract their heads under the carapace when they are threatened by danger, and the way in which they achieve this distinguishes the two subclades today. The pleurodires pull the head in by making a sideways bend in the neck (Figure 8.29(a)), whereas the cryptodires make a vertical bend (Figure 8.29(b)). This distinction works for living turtles, but basal members of both groups cannot retract their necks. Gaffney (1994) identified a specialization in the palate to reorient the direction of pull of the main jaw muscle mass, the adductors, so that the height for retraction is reduced. In pleurodires, the adductor muscle mass passes over a rounded boss, or **trochlea**, formed by the pterygoid (Figure 8.29(c)), a synapomorphy of the clade (Joyce, 2007). Gaffney (1994) argued further that cryptodires had a different system, in which the trochlear process is formed further back by the otic capsule, the part of the braincase involved with hearing and balance (Figure 8.29(d)). However, Joyce (2007) and Sterli (2010) found that the cryptodire muscle pulley system actually occurs deeper in the cladogram, before the origin of Testudines.

Living pleurodires, the snake necks and matamatas, are fresh water in habitat and are limited to the southern continents. Fossil forms are known from all continents and include terrestrial and possibly marine forms. The largest non-marine turtle, a 2.2-m-long pleurodire from the Pliocene of Venezuela has been named, not surprisingly, *Stupendemys*.

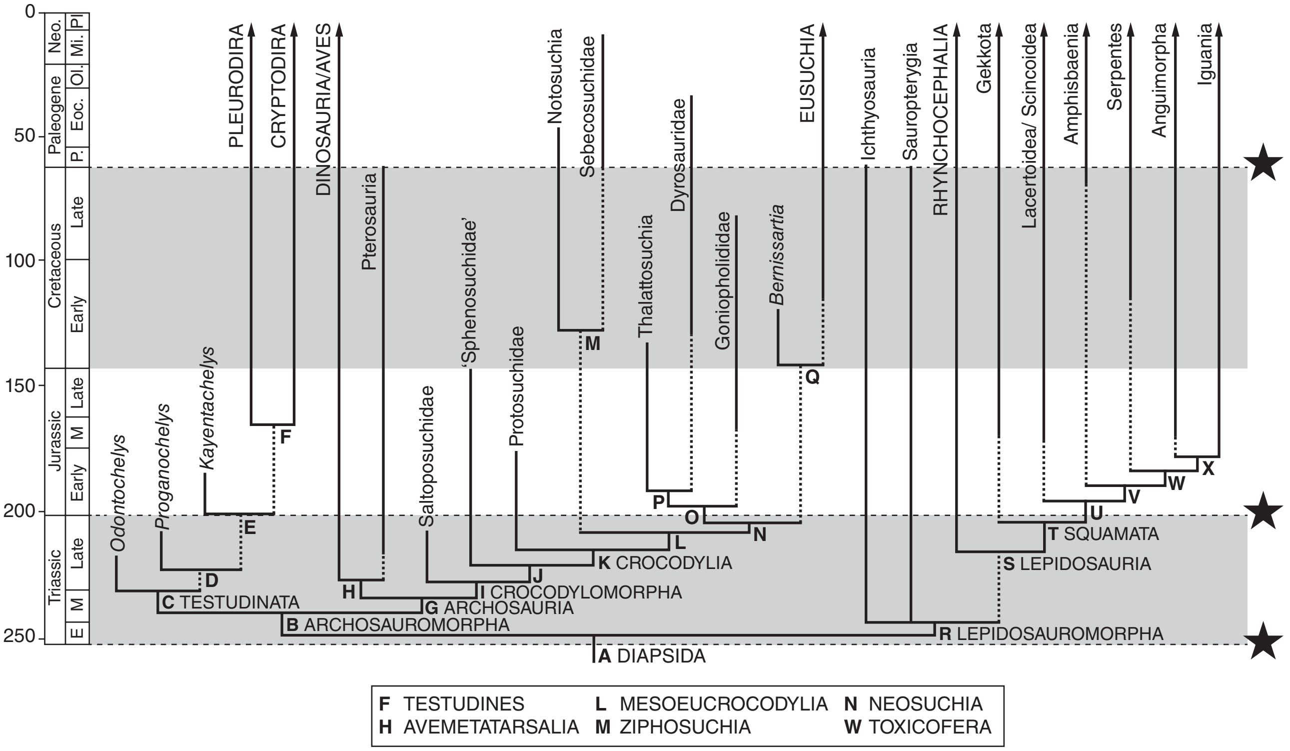
BOX 8.8 RELATIONSHIPS OF MESOZOIC REPTILES

The terrestrial reptiles of the Triassic, Jurassic and Cretaceous periods (Chapters 6 and 8) were mainly diapsids, with a few anapsids, essentially the turtles, and their cladistic relationships (see cladogram) are clear in broad outline.

The turtles and tortoises, Testudinata, form a well-characterized clade that is probably part of the larger clade Diapsida, possibly within Archosauromorpha (see Boxes 5.1, 6.1). Within Testudinata, the Late Triassic and Early Jurassic forms, *Odontochelys*, *Proganochelys*, and *Kayentachelys*, among others, are outgroups to the Testudines, consisting of Pleurodira and Cryptodira, all subsequent turtles (Joyce, 2007; Sterli, 2010; Anquetin, 2012).

The other archosauromorph clade of the Mesozoic and Cenozoic, the archosaurs, split in the Triassic into a line that led to crocodiles, and another, the Avemetatarsalia, that led to pterosaurs, dinosaurs and birds (see Box 6.1). The Crocodylomorpha includes some basal forms, *Terrestrisuchus* and 'Sphenosuchidae' (probably paraphyletic), from the Late Triassic and Early Jurassic, and the Crocodylia, which arose in the Early Jurassic. The Crocodylia (Pol *et al*., 2009; Sereno and Larsson, 2009; Young and Andrade, 2009; Andrade *et al*., 2011; Bronzati *et al*., 2012) are divided into a number of Jurassic and Cretaceous families that are outgroups to the Eusuchia, the clade containing modern crocodiles, alligators and gavials, and which arose in the Early Cretaceous.

The Lepidosauromorpha, the other major diapsid clade (see Box 6.1) may include ichthyosaurs and sauropterygians as subclades, but their exact basal relationships are uncertain. The extant lepidosauromorphs are lepidosaurs. Lepidosauria includes the rhynchocephalians and the squamates, six 'lizard' clades plus the snakes (Hedges and Vidal, 2009; Gauthier *et al*., 2012; Wiens *et al*., 2012; Jones *et* al., 2013; Pyron *et al*., 2013). The relationships of snakes (Serpentes) are unclear, i.e. whether a sister group of Amphisbaenia or Anguimorpha (see Box 8.10).



Cladogram showing the postulated phylogenetic relationships of the main groups of Mesozoic and Cenozoic reptiles. Synapomorphies taken from Joyce (2007), Pol *et al*. (2009), Sereno and Larsson (2009), Sterli (2010), Andrade *et al*. (2011), Gauthier *et al*. (2012), and Jones *et al*. (2013): **A DIAPSIDA**, upper and lower temporal fenestrae, suborbital fenestra, ossified sternum, complex tibio-astragalar joint, first metatarsal less than half the length of the fourth metatarsal; **B ARCHOSAUROMORPHA**, posterodorsal process on premaxilla, sagittal crest, slender and tapering cervical ribs, notch on anterior margin of interclavicle, small anterior process and larger posterior process on iliac blade, medial centrale in carpus absent; **C TESTUDINATA**, postfrontal absent, quadrate concave posteriorly and exposed laterally on cheek, postparietals absent, stapes solid and rod-like, maxilla, premaxilla and dentary lack teeth, bony shell consisting of a plastron; **D**, development of bony carapace; E, lacrimals absent, supratemporals absent, fused external nares, medial fusion of vomer, central constriction of the middle ear region, fully developed cavum tympani, reduction of the peripherals to 11 pairs, complete loss of supramarginals, elongate scapular process, coracoid foramen absent; **F TESTUDINES**, exclusion of frontal from the orbit, reduction of the posterior entoplastral process, loss of large cervical ribs, reduction of tenth thoracic rib, loss of extensive acromial ridge, glenoid neck, addition of phalanges to most digits of hands and feet, reorganization of fifth pedal digit; **G ARCHOSAURIA**,

Continued

antorbital fenestra in snout wall between nostril and orbit, laterally flattened teeth with serrations, ossified laterosphenoid in braincase, lateral mandibular foramen in posterior lower jaw bones; **H AVEMETATARSALIA**, forelimb/hindlimb ratio less than 0.55, pubis longer than ischium, tibia/ femur ratio more than 1.0, distal tarsal 4 subequal in transverse width to distal tarsal 3, compact metatarsus with metatarsals I–IV tightly appressed, metatarsals II–IV more than 50% tibial length, absence of dorsal body osteoderms; **I CROCODYLOMORPHA**, maxillae enter secondary palate, squamosal broadly overhangs quadrate laterally, postfrontal absent, primary contact of quadrate head with prootic, quadratojugal contacts postorbital, pneumatic basisphenoid and prootic, proximal carpals elongate; **J**, antorbital fenestra small, parietals fused; **K CROCODYLIA**, basisphenoid rostrum dorsoventrally expanded, basipterygoid processes reduced, lower portion of coracoid expanded and anterior margin concave, scapula very broad dorsally; **L MESOEUCROCODYLIA**, secondary palate formed from maxillae and palatines, 'skull table' with nearly flat dorsal surface, two large palpebrals, dorsal head of quadrate contacts laterosphenoid, quadrate hollow and equipped with fenestrae in dorsal surface; **M ZIPHOSUCHIA**, teeth serrated and recurved (convergence with basal archosaurs and theropods), reduced number of teeth, anterior dorsal convexity ('wave') in dentary dorsal margin, skull ornamentation dominated by grooves, external mandibular fenestra small; **N NEOSUCHIA**, maxilla subvertical, antorbital fenestra absent, retroarticular process narrow, maxilla and dentary with two sinusoidal waves of teeth; **O**, tooth row and occipital condyle in the same plane, longirostrine skull, antorbital cavity strongly elliptical, frontal is wide, postorbital makes up most of upper temporal bar, symphysis constricted at fifth-sixth alveoli, mid to posterior maxillary teeth lack lateral compression, enamel bears ridges that are close and sometimes anastomose; **P**, supratemporal fenestra larger than orbit, postorbital bar elliptical in cross section, symphysis extremely long making mandible 'Y-shaped', splenials extensively involved in symphysis; **Q**, inset postorbital bar, biconvex first caudal vertebra, osteoderms in more than two longitudinal rows; **R LEPIDOSAUROMORPHA**, external nares close to the midline, sphenethmoid absent, presacral intercentra absent, entepicondylar foramen in humerus absent, radius as long as ulna, fifth distal tarsal absent; **S LEPIDOSAURIA**, lacrimal reduced or absent, postparietal and tabular absent, thyroid fenestra (between pubis and ischium), fused astragalus and calcaneum, loss of centrale, loss of distal tarsals 1 and 5, metatarsal 5 hooked in two planes; **T SQUAMATA**, high degree of skull kinesis, premaxillae fused, nasals reduced, squamosal reduced or absent, parietals fused, quadratojugal absent, posterior conch-like notch on quadrate, proatlas absent, ribs single-headed, gastralia absent; **U**, one egg tooth, vomeronasal prey discrimination; **V**, forked tongue, Jacobson's organ epithelium well developed; **W TOXICOFERA**, venom-secreting oral glands; **X**, tongue prey prehension, ambush foraging mode. Abbreviations: E, Early; Eoc, Eocene; Mi, Miocene; Mid, Middle; Neo, Neogene; Ol, Oligocene; P, Paleocene; Pl, Pliocene/ Pleistocene. Dashed lines and star symbols indicate extinction events.

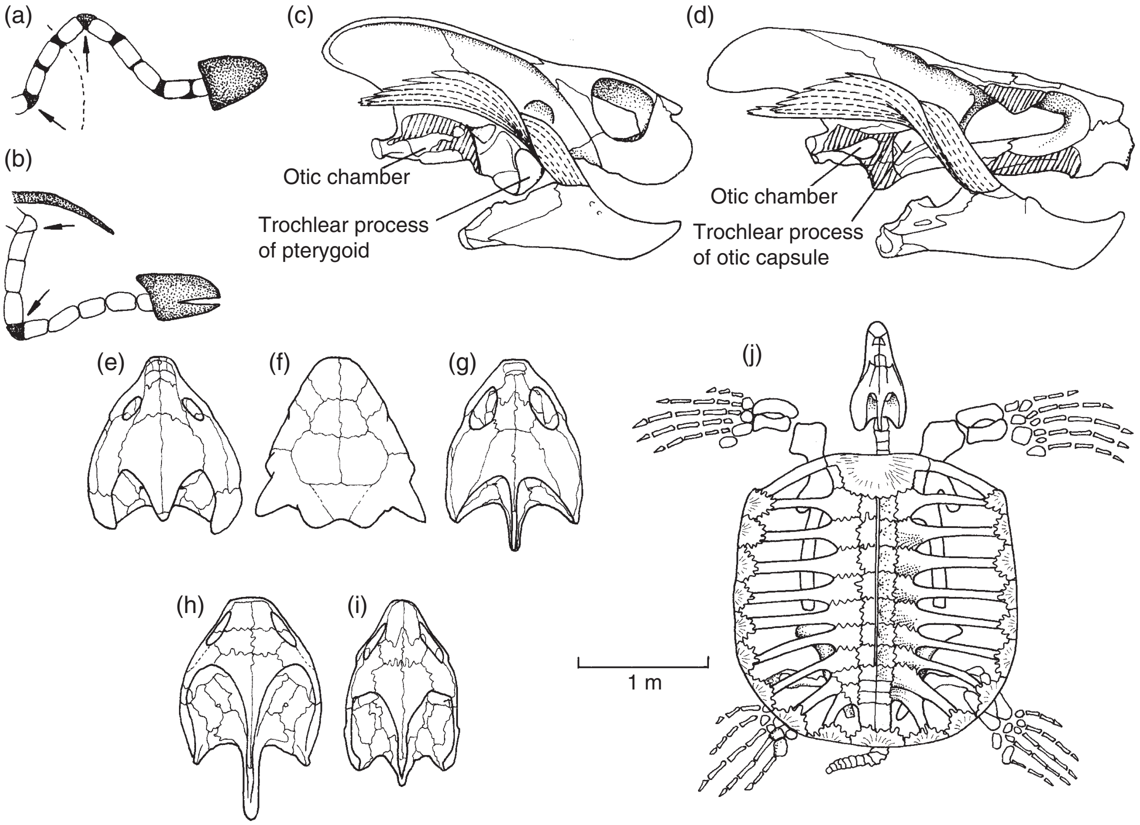


Figure 8.29 Turtle classification and diversity: mode of neck folding in (a) a typical pleurodire in dorsal view and (b) a cryptodire in lateral view; course of main jaw adductor muscle mass in *Emydura*, a pleurodire (c) and *Chelydra*, a cryptodire (d); (e–i) the diversity of turtle skulls, all in dorsal view: (e) *Eubaena*, a baenid; (f) *Meiolania*, a meiolanid; (g) *Toxochelys*, a chelonioid; (h) *Adocus*, a trionychoid; (i) *Mauremys*, a testudinoid; (j) the giant Cretaceous marine turtle *Archelon* in dorsal view. Source: (a,b) Adapted from Mlynarski (1976). (c–i) Adapted from Gaffney and Meylan (1988). (j) Adapted from Zittel (1932).

The cryptodires date back to the Middle Jurassic, and they fall into several clades, each diagnosed by features of the skull and shell (Gaffney and Meylan, 1988; Joyce, 2007). Among basal families, the pleurosternids are known from the Late Jurassic and Early Cretaceous of North America and Europe. The baenids (Figure 8.29(e)) are known from the Cretaceous to Eocene of North America, and have a narrow snout region.

The living cryptodires, the chelonioids (marine turtles), trionychoids (soft-shells) and testudinoids (tortoises), are distinguished from their extinct relatives by characters of the vertebrae and ribs. They also share a general skull outline (Figure 8.29(g–i)) in which the parietals and supraoccipitals extend backwards as a vertical plate with a deep curved conch cut into the skull table on each side. The chelonioids have their forelimbs modified as long paddles that they beat like wings to 'fly' through the water. Some, such as the leatherback, reach shell lengths of 2 m and weights of 500 kg, and *Archelon* from the Late Cretaceous of North America (Figure 8.29(j)) is 4 m long.

8.8 CROCODYLOMORPHA

Today, crocodilians comprise a small group of 23 species of crocodiles, alligators and gavials, that live in fresh and salt waters of the tropics (Ross and Garnett, 1989). This limited modern diversity conceals the breadth of their former radiations and their range of adaptations. Crocodilians arose within a larger clade Crocodylomorpha in the Late Triassic, and their first representatives were small bipedal animals that may even have eaten insects (see Section 6.3.4). Since the Triassic, most crocodilians have been semi-aquatic and some Jurassic forms were highly adapted to marine life. In the Cenozoic, other groups became fully terrestrial and, in South America, disputed the top carnivore niches with birds and mammals. This extraordinary history is quite unexpected if one considers only modern crocodilians.

8.8.1 Crocodilian characteristics

Crocodilians have long snouts with the nostrils at the tip (Figure 8.30(a,b)) so that they can breathe with only the nostril bump showing above water. There is a secondary palate formed from ingrowths of the premaxillae, maxillae and palatines and, in derived forms, the pterygoids also (Figure 8.30(c)), which separates the air stream from the mouth cavity and allows the crocodilian to breathe with its mouth open underwater while feeding (Iordansky, 1973). Crocodilians will sometimes seize antelope and other mammals by a leg and drag them underwater until they drown, and then tear off chunks of flesh by sinking their sharp teeth well into the flanks and twisting with the whole body. In this way they are able to achieve much greater force for tearing at the meat than by simply twisting their heads from side to side, and this feeding mode is matched biomechanically by the adaptation of a broad snout (McHenry *et al.*, 2006).

On land, crocodilians appear to be capable of four modes of locomotion.

1 Belly run, in which the body is pushed along like a toboggan by the hindlimbs only, for escape down river banks.

2 Sprawling, in slow locomotion, with the knees and elbows sticking out sideways.

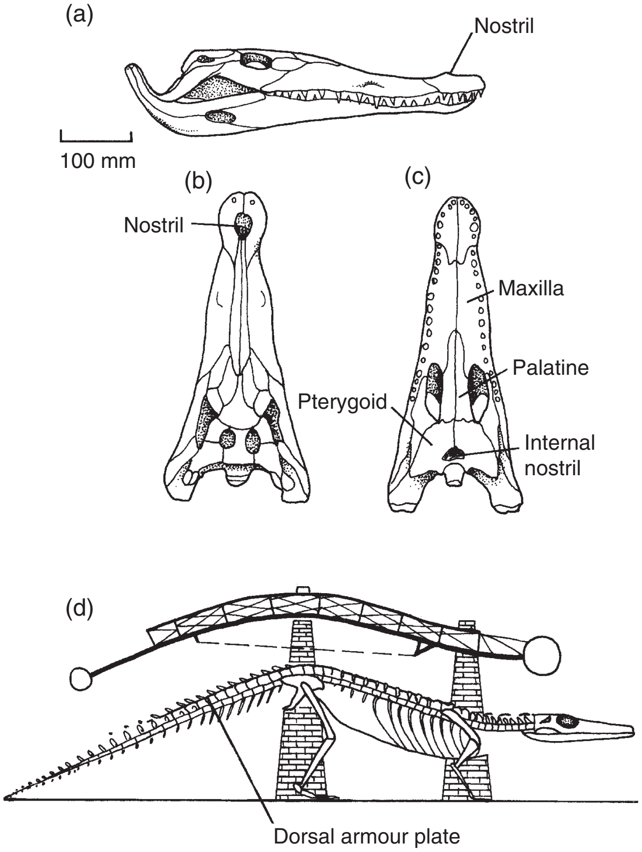


Figure 8.30 Crocodilian anatomy: (a–c) skull of the modern African crocodile *Crocodylus* in (a) lateral, (b) dorsal and (c) ventral views; (d) mechanical analogy between the box-like girder structure of the crocodilian backbone and dorsal scutes and a box-girder bridge. Source: (a–c) Adapted from Iordansky (1973). (d) Adapted from Frey (1984).

3 High walk, in which the limbs are tucked well under the body, for faster movement.

4 Galloping, the most unexpected mode, in which the forelimbs and hindlimbs act in pairs.

The skeleton of crocodilians does not seem to be well adapted for this last mode, galloping. Nevertheless, crocodilian backbones are braced in a manner analogous to a box-girder bridge (Schwarz-Wings *et al.*, 2009). There is a double row of dorsal bony scutes in the skin that adhere closely to the backbone, and the vertebral column is braced by longitudinal muscle systems that attach to the dorsal armour over the back and tail (Figure 8.30(d)).

8.8.2 The first crocodilians

The first crocodylomorphs such as *Saltoposuchus* from the Late Triassic (see Section 6.3.4) were lightly built and probably bipedal. The sphenosuchid *Sphenosuchus* from the Early Jurassic was more crocodilian in appearance. The first true crocodilians, protosuchids such as *Protosuchus* (Colbert and Mook, 1951) and *Orthosuchus*, appeared in the Early Jurassic. These small 1-m long animals were quadrupedal (Figure 8.31(a)), but the

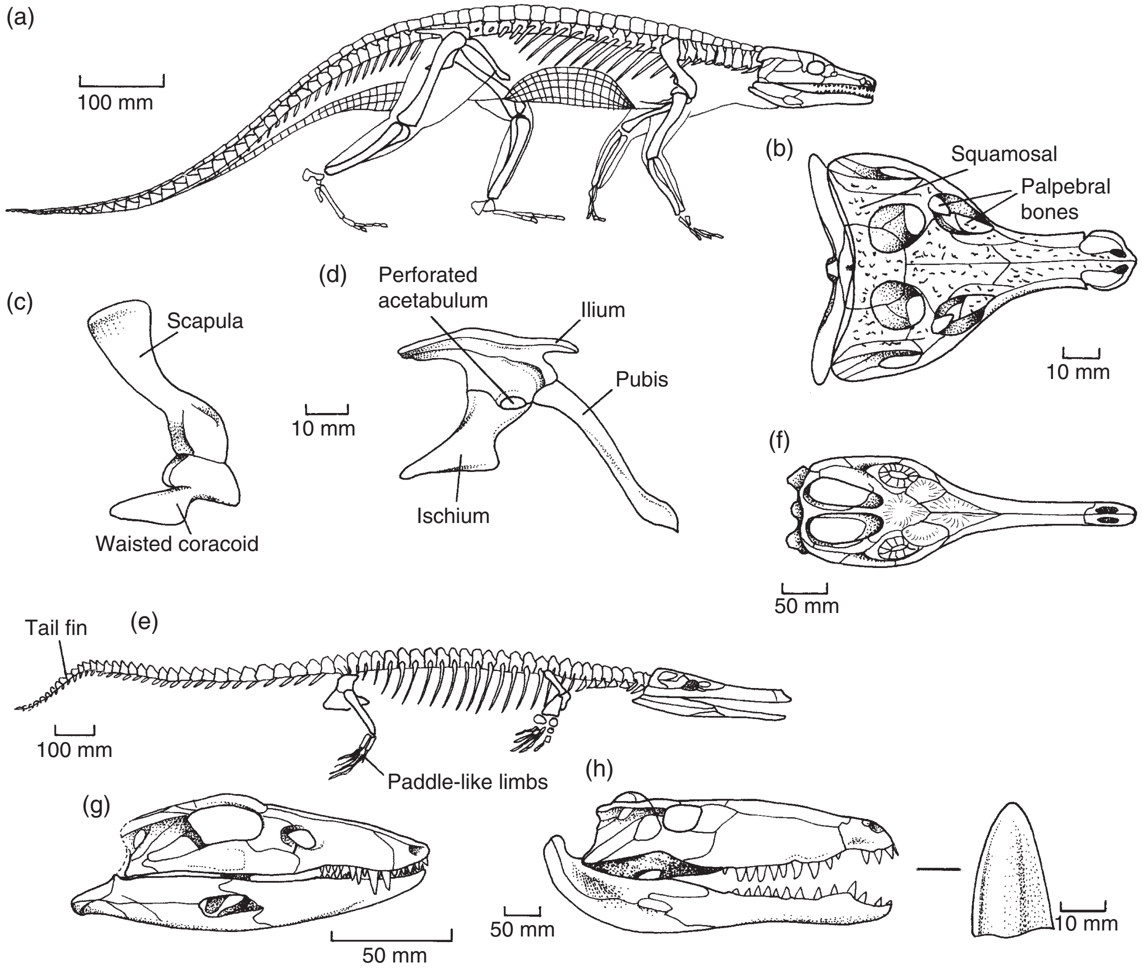


Figure 8.31 Mesozoic crocodilians: (a–d) the Early Jurassic protosuchids *Protosuchus* (a,c,d) and *Orthosuchus* (b), (a) skeleton and armour plates; (b) skull in dorsal view; (c) shoulder girdle; (d) pelvic girdle; (e,f) the Late Jurassic metriorhynchid *Geosaurus*, skeleton and skull in dorsal view; (g) the Late Cretaceous notosuchid *Argentinosuchus*; (h) the Cenozoic sebecid *Sebecus*, skull in lateral view and a characteristic flattened (ziphodont) tooth. Source: (a,c,d) adapted from Colbert and Mook (1951). (b) Adapted from Nash (1975). (e–h) Adapted from Steel (1973).

hindlimbs are longer than the forelimbs, betraying their bipedal ancestry. Traditionally, all crocodilians from *Protosuchus* to the present day are termed Crocodylia, and this term is used here, although crown-clade usage terms this node Crocodyliformes, and Crocodylia is a subdivision of Eusuchia (see Section 8.8.4).

Protosuchids display a variety of crocodilian synapomorphies. The skull is ornamented with irregular pits in the bone surface (Figure 8.31(b)), as in modern crocodilians, and the posterior part of the skull roof is square in outline because of the great overhang of the squamosals on either side. The squamosal bears a specialized ridge to which a fleshy ‘ear lid’ attached in life, a device to keep out the water during diving. There are additional palpebral bones in the eye socket, an independent evolution of bones also seen in some ornithischian dinosaurs (see Section 8.4.2). The whole posterior region of the skull is **pneumatic**, with complex air passages whose function is not clear. *Protosuchus* shows crocodilian characters in the skeleton as well: an elongate ‘waisted’ coracoid (Figure 8.31(c)), a perforated acetabulum and reduced pubis (Figure 8.31(d)), elongate wrist elements and extensive armour covering. *Protosuchus* probably fed mainly on small terrestrial animals.

8.8.3 Jurassic–Cretaceous crocodilians

Recent studies have revealed a huge diversity of some 200 species of Mesozoic crocodilians. After the primarily Early Jurassic Protosuchidae, marine clades were important through the Jurassic. Terrestrial clades diversified in the Cretaceous, including survivors of earlier radiations and neosuchians in the northern hemisphere, and especially diverse forms in the southern hemisphere, including notosuchians, peirosaurids, sebecids, and mahajungasuchids. The majority of these reside in the clade Mesoeucrocodylia, within which Metasuchia, Neosuchia, and Eusuchia represent ever smaller clades leading to Cenozoic and modern crocodilians (see Box 8.8). After a burst of activity as marine piscivores through the Jurassic, crocodilians diversified into a broad range of terrestrial habits and diets (Stubbs *et al*., 2013)

The marine Thalattosuchia of the Jurassic and Early Cretaceous are highly derived mesoeucrocodilians (Pol *et al.*, 2009; Sereno and Larsson, 2009; Young and Andrade, 2009; Andrade *et al.*, 2011; Bronzati *et al.*, 2012). Thalattosuchia includes two families, the teleosaurids (=steneosaurids) of the Early and Middle Jurassic had long narrow snouts, and they hunted fishes in shallow seas and estuaries around Europe in particular. The metriorhynchids, such as *Geosaurus* from the Late Jurassic of Europe (Young and Andrade, 2009; Figure 8.31(e,f)), were heavily modified for a wholly aquatic existence and for swimming by powerful undulations of the body. The caudal vertebrae bend down to support a tail fin, the limbs are paddle-like and the body armour is lost, which would improve the hydrodynamic efficiency of the body. It is likely that the metriorhynchids had difficulty in walking on land. These crocodilians may have hunted cephalopods and fishes by sudden accelerations through the water. Functional studies (e.g. Pierce *et al.*, 2009; Young *et al.*, 2010) show that diet is associated with snout length in teleosaurids and with snout width in metriorhynchids. This suggests that teleosaurid skulls were adapted for speed of attack and metriorhynchid skulls for force production. Teleosaurids and long-snouted metriorhynchids attacked by sideways movements of the head and neck, but short-snouted metriorhynchids may have been able to employ grasp and shake and/or 'death roll' feeding and foraging behaviours.

Among Cretaceous crocodilians, the Notosuchia are most notable, comprising some 25 genera known best from South America and Africa, but extending to Asia and Europe. They are remarkable for their range of adaptations, ranging from terrestrial carnivory (*Baurusuchus*) to omnivory (*Simosuchus*) and herbivory (*Chimaerasuchus*). As an example, the notosuchid *Argentinosuchus* (Figure 8.31(g)), less than 1 m long, has differentiated teeth. The pointed teeth at the front may have been used in seizing prey and the flatter 'cheek teeth' for cutting up the flesh. Other notosuchians such as *Armadillosuchus* sported complex arrays of armour plates arranged in flexible bands as in a modern armadillo, and others had horns on their heads. *Simosuchus*, especially well known from finds in Madagascar is one of the strangest (see Box 8.9).

BOX 8.9 MINIATURE HERBIVOROUS CROCODILIAN FROM MADAGASCAR

We have such a clear mental image of crocodilians today that it is hard to imagine the remarkable range of adaptations they showed in the Mesozoic. Most notable were the notosuchians, a clade that included many southern continents forms with remarkable convergences towards mammal-like sructures and habits. One of the oddest is *Simosuchus* from the Late Cretaceous of Madagascar.

The first fossils of *Simosuchus* were reported in 2000, and since then further individuals have been found. All are from the Late Cretaceous Maevarano Formation of Madagascar, home also to remarkable theropod and sauropod dinosaurs, mammals, and others, all of which lived in a semi-arid climate. Perhaps in the face of such diverse carnivorous animals, this crocodilian had become remarkably uncrocodilian. *Simosuchus* was small, about 75 cm long, but relatively long-limbed, so it had the proportions of a lap dog. Added to its small size was a short, pug nose, and a broad flat-fronted snout, giving a nearly square palate (Kley *et al.*, 2010). In addition, the teeth were strange and small, often described as 'clove-shaped'. Indeed, each of the dozens of tiny teeth was only 5 mm long, with a peg-like root, and a crown that seemed to expand substantially and terminated in seven or eight little lobes.

The skeletons of *Simosuchus* were associated with numerous osteoderms, or bony plates, and these have been reconstructed in some detail (Hill, 2010). They were organized into discrete 'shields' covering the back and the belly, as well as the tail. *Simosuchus* has armour shields over the limbs, unusual among crocodilians. The individual shields had some hinging along the length of the body, which allowed the animal to move relatively freely, but it probably could not have swum very freely. The armour plates over the limbs also probably limited manoeuvrability to some extent, but overall, the armour probably was necessary to protect this modestly sized herbivore from attacks by theropod dinosaurs.

See a brief presentation about the armour of *Simosuchus* at: http://www.youtube.com/watch?v=z7XAxV--dNU, and the *Simosuchus* restoration at: http://www.youtube.com/watch?v=XDnyVLSj5oY .

Skeleton of *Simosuchus,* as reconstructed with armour shields in place. Source: © D. Gordon E. Robertson/CC-BY-SA-3.0.

Close relatives of Notosuchia, all members of the clade Ziphosuchia, include the Peirosauridae, a small group of Cretaceous terrestrial crocodilians with superficially dog-shaped skulls. The Mahajungasuchidae (Sereno and Larsson, 2009) include two genera from the Late Cretaceous of Africa, and they are noted for massive jaws and hornlike projections at the back of the skull. Finally, the Sebecidae, known from the Palaeocene to Miocene (60–10 Myr ago) of South America have large skulls (Figure 8.31(h)) with a high snout, no antorbital fenestra and unusual flattened teeth. The sebecids were successful carnivores that probably preyed on mammals, but they were replaced ecologically by mammalian carnivores in the Neogene.

More derived crocodilians, the neosuchians, include some long-snouted aquatic forms, the dyrosaurids from the Early Cretaceous to late Eocene, including some giant forms (Schwarz-Wings *et al*., 2009), probably sister clade to the much older Thalattosuchia. A further major aquatic group were the goniopholidids, abundant in freshwater and marine deposits from the Middle Jurassic to the end of the Cretaceous (Andrade *et al*., 2011). The sister clade of these aquatic forms (see Box 8.8) includes unusual crocodilians such as *Bernissartia* and *Hylaeochampsa* from the Early Cretaceous of Europe (Martin and Delfino, 2010), which are outgroups to Eusuchia, sharing with them an inset postorbital bar, a biconvex first caudal vertebra (that is, both articular faces are ball-like) and osteoderms (bony scutes) arranged in more than two longitudinal rows along the body.

8.8.4 Eusuchia: modern crocodilians

The Eusuchia (literally 'true crocodilians') appeared in the Late Cretaceous and most of the early representatives are very like modern forms. The group is distinguished from basal crocodilians by a full secondary palate formed from the maxillae, palatines *and* pterygoids (Figure 8.30(c)), and some other skull features.

Modern crocodilians are divided into three families, consisting of the crocodiles, alligators and gavials (Brochu, 2003b; Oaks, 2011). The first two families are known from the Late Cretaceous and all through the Cenozoic, when they were much more widespread than they are now, with dozens of species reported from Europe and North America as far north as Sweden and Canada, as well as all tropical regions and southern continents. Gavials, more fully aquatic forms with long narrow fish-eating snouts, date back to the Eocene. Several other euschian families are known only from fossils, some with massive broad ducks' bill-shaped skulls and others with serrated dinosaur-like teeth.

The present array of crocodilians is a much reduced representation of their former glory. Some may have died out following regional-scale events, such as the uplift of the Andes and consequent changes in river patterns about 5 Myr ago, when formerly diverse crocodilians dwindled to none (Scheyer *et al*., 2013). Others likely suffered from continuing cooling conditions through the Cenozoic (see Section 10.4) and the advances and retreats of ice sheets in the past 5 Myr. Crocodilians on the whole like the warmth.

8.9 LEPIDOSAURIA: LIZARDS AND SNAKES

Lepidosaurs today include 5650 species of lizards and 3380 species of snakes, as well as the tuatara, *Sphenodon* from New Zealand, an isolated member of the clade, comprising over 96% of all living reptiles (Pincheira-Donoso *et al*., 2013). The pairing of *Sphenodon* plus Squamata as Lepidosauria is confirmed by molecular evidence (Rest *et al*., 2003; Townsend *et al*., 2004; Kumazawa, 2007; Hedges and Vidal, 2009; Wiens *et al*., 2012; Jones *et al*., 2013; Pyron *et al*., 2013). The first known lepidosaurs are Triassic rhynchocephalians, distant ancestors of the living tuatara, and the Lepidosauria radiated in the Middle Jurassic, coincident with the oldest known lizards, and again in the mid Cretaceous, with the origin of snakes. The Cretaceous radiation of various lepidosaur groups may have been stimulated by massive diversification of flowering plants and associated pollinating and leaf-eating insects, a new dietary resource for insect-eating vertebrates (see Section 9.7). Lepidosaurs form part of a larger clade Lepidosauromorpha, which traces its origin back to the Permian (see Box 5.1).

8.9.1 Rhynchocephalia: reptilian 'living fossils'

Sphenodon, the living tuatara (Figure 8.32(a–c)), is an unusual lizard-like animal known today only from some offshore islands in New Zealand. It reaches a length of 600 mm and it has nocturnal habits, feeding mainly on invertebrates. *Sphenodon* was originally classified as a lizard, but all the evidence places it as the sister group of lizards and snakes (Hedges and Vidal, 2009; Evans and Jones, 2010). *Sphenodon* was often called a 'living fossil' because it lacks the special features of lizards and snakes (for example, the skull is immobile) and because it is the single surviving member of a group known only much earlier in time.

Rhynchocephalians arose in the Triassic, with the oldest representative a jaw from the Middle Triassic of Germany (Jones *et al*., 2013), and the clade then expanded to as many as eight or nine genera. These animals vary in body length from 150 to 350 mm and the skulls and teeth of different forms vary, suggesting diets ranging from insectivory to herbivory. *Planocephalosaurus* (Fraser and Walkden, 1984) is about 150 mm long (Figure 8.32(d)), smaller than *Sphenodon* and it has a blunt-snouted skull. The long slender limbs and body outline are very lizard-like, and indeed the Triassic rhynchocephalians show all the characters of the Lepidosauria, such as the **thyroid fenestra**, a broad opening in the pelvis between the pubis and ischium, a fused astragalus and calcaneum in the ankle and a metatarsal 5 hooked in two planes (Figure 8.32(e)).

Later rhynchocephalians include bizarre forms from the Late Jurassic and Early Cretaceous of North America and the Late Cretaceous of South America, with broad grinding teeth, and some aquatic forms. The pleurosaurs, such as *Pleurosaurus* from the Late Jurassic of Germany (Figure 8.32(f)), were slender snake-like lepidosaurs, from 0.5 to 1.5 m long, with reduced limbs that cannot have been much use on land. The tail was longer than the body and it was probably used as a propulsive

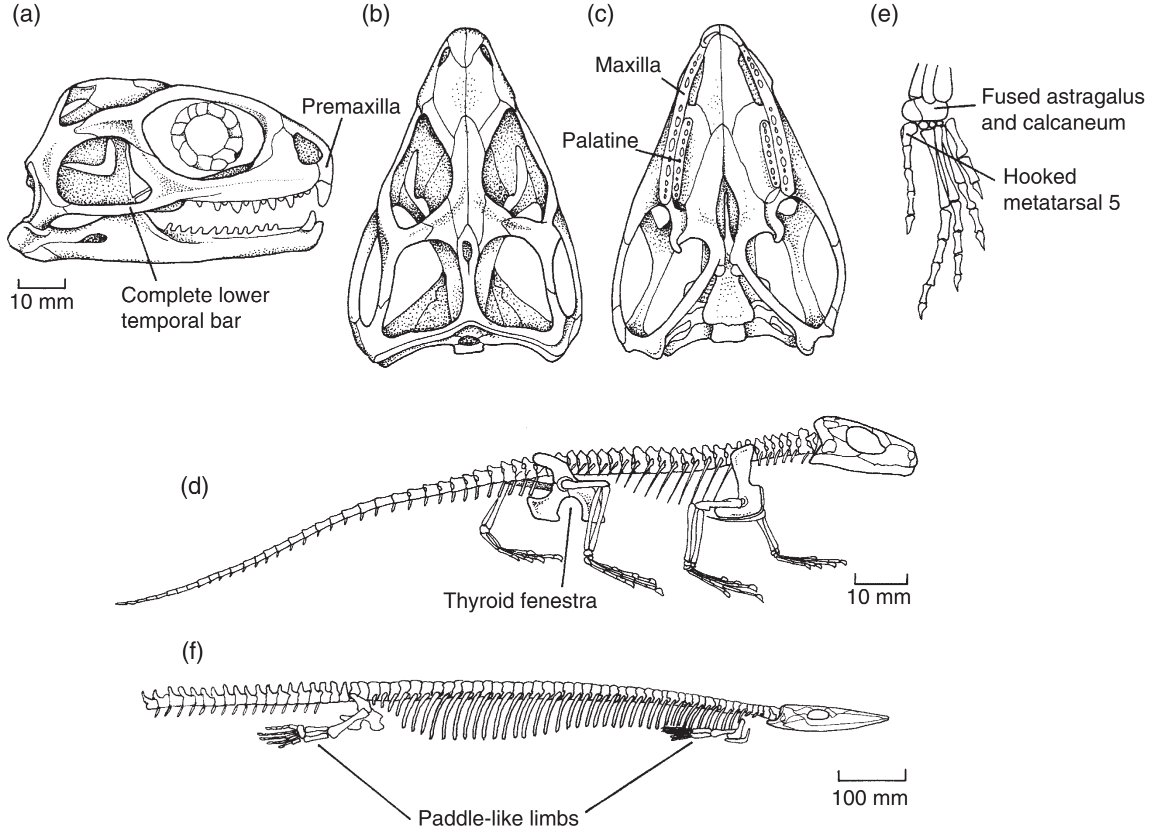


Figure 8.32 The rhynchocephalians: (a–c) skull of the living *Sphenodon* in lateral, dorsal and ventral views; (d) skeleton of the Late Triassic sphenodontian *Planocephalosaurus*; (e) left foot and lower leg of the Jurassic sphenodontian *Homoeosaurus*; (f) skeleton of the Late Jurassic pleurosaur *Pleurosaurus*, with most of the tail omitted. Source: (a–c) Adapted from Zittel (1932). (d) Adapted from Fraser and Walkden (1984). (e) Adapted from Cocude-Michel (1963). (f) Adapted from Carroll (1987).

organ, with the short limbs restricted to steering. Pleurosaurs share with other rhynchocephalians a specialized pattern of tooth implantation in which the teeth are fused to the jawbone, the **acrodont** condition (Figure 8.32(a)). However, skull and jaw shapes vary substantially between living *Sphenodon* and the various extinct forms, implying a wide range of diets (Jones, 2008).

8.9.2 Squamata: the lizards

Early lizard fossils might be expected in rocks of Triassic age, in view of the date of origin of the rhynchocephalians. Indeed, a number of poorly preserved skeletons of small diapsid reptiles were once described as the first lizards, but these have all turned out to lack clearcut characters of Lepidosauria and Squamata (Evans and Jones, 2010). Lizards and snakes form a clade, the Squamata (see Box 8.8), which is diagnosed by a number of synapomorphies, including a high degree of skull **kinesis**, or mobility.

The cranial kinesis of most lizards consists of up to three separate hinging systems (Figure 8.33(a,b)).

1 Between the frontal and parietal in the skull roof and a matching joint in the palate, the **mesokinetic joints**.

2 Between the braincase and the skull (parietal, supratemporal, quadrate and pterygoid), the **metakinetic joints**.

3 Between the quadrate and (supratemporal + squamosal + paroccipital process) at the top, and the quadrate and pterygoid at the bottom, the **streptostylic joints**.

When the jaws open (Figure 8.33(a)), the snout tips up and the quadrate is nearly horizontal. When the jaws close (Figure 8.33(b)), the snout tips down and the quadrate becomes more vertical. This kinetic system has important adaptive advantages (Smith, 1980; Frazzetta, 1986; Metzger, 2002). The pterygoideus muscle, which runs from the pterygoid to the outside of the lower jaw (Figure 8.33(c)), is able to deliver a strong closing force to the kinetic lizard skull because of the rotations. Both of the jaws of a lizard effectively close on a food item at the same time, exerting equal perpendicular forces on it (Figure 8.33(d)). With akinetic (immobile) jaws there is a risk of losing a food item because the forces are not perpendicular and there is a force directed out of the mouth (Figure 8.33(e)).

The Squamata is divided into seven clades, one of which is the snakes (Serpentes) and the other six of which (Gekkota, Scincoidea, Lacertoidea, Amphisbaenia, Anguimorpha, Iguania) are generally called lizards. The lizard group, formerly termed Lacertilia (or Sauria), is paraphyletic as it excludes the snakes. The relationships among the seven squamate clades are not certain (see Box 8.8). In comprehensive analyses of morphological data, Conrad (2008) and Gauthier *et al.* (2012) support earlier

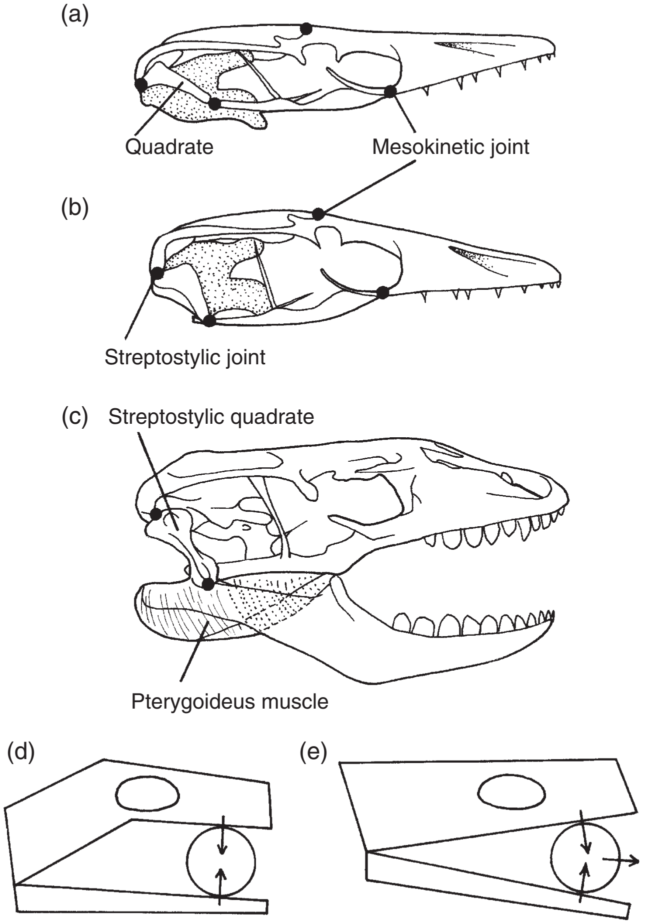


Figure 8.33 Lizard jaw mechanics: (a,b) skull of *Varanus*, showing the skull flexed up (a) and (b) down; (c) lizard skull with the jaws open and the streptostylic quadrate swung back so that the pterygoideus jaw muscles have their maximum effect; (d,e) diagrammatic lizard skulls showing the advantages of kinesis in holding a food particle (left) which would otherwise be forced out by the bite in a non-mobile skull (right). Source: (a,b) Adapted from Alexander (1975). (c) Adapted from Smith (1980). (d,e) Adapted from Frazetta (1986).

cladistic solutions, with Iguania at the base, and the remaining clades forming Scleroglossa, all of which share a keratinized tongue. Within Scleroglossa, they find a sister-group relationship between Gekkota and Autarchoglossa, and divergence between Anguimorpha and Scincomorpha. Molecular analyses, on the other hand (e.g. Kumazawa, 2007; Wiens *et al*., 2012; Pyron *et al*., 2013) all agree with each other in finding that Gekkota is the basal clade, followed by Scincoidea, Lacertoidea, Amphisbaenia, Serpentes (snakes), Anguimorpha, and Iguania. In light of this broader difficulty, there is currently a heated debate about the placement of Serpentes: are the snakes the sister group of Amphisbaenia, Varanidae or Anguimorpha (see Box 8.10)?

The early history of squamates (Evans and Jones, 2010) is patchy. Three of the six clades are recorded tentatively from the Middle Jurassic of England, the Gekkota, Scincoidea and Anguimorpha, and their locations in the cladogram (see Box 8.8) suggest that all groups, including the snakes must also have arisen in the Jurassic, even though their oldest fossils at present are Cretaceous. The Middle Jurassic scincoids (three species) and the anguimorph (one species) are represented by jaws, skull bones and vertebrae, and the gekkotan by some vertebrae (Evans, 1998).

Lizards diversified in the Late Jurassic and Early Cretaceous. Some taxa have been placed in modern orders, but many probably lie on the stem to modern clades. For example, *Ardeosaurus* from the Late Jurassic of Germany (Mateer, 1982) is probably a stem taxon, but it has been classed sometimes as a gekkotan. This lizard reached a total length of only 120–140 mm. The skeleton (Figure 8.34(a)) is like that of most modern lizards, with a slender flexible body, long tail, and short sprawling limbs. The skull (Figure 8.34(b)) shows a number of squamate derived characters: the parietals are fused and they meet the frontals on a broad transverse suture, the lacrimal and quadratojugal bones have been lost and the quadrate is streptostylic.

The Gekkota, comprising more than 1450 living species, includes the tiny geckos that can cling to walls and ceilings, as well as the limbless pygopodids. Gekkotans are recorded first

BOX 8.10 THE ORIGIN OF SNAKES

Biologists and palaeontologists have debated the origin of snakes for more than a century. Morphological data suggests that snakes are either closely related to amphisbaenians, or they are part of the anguimorph clade possibly close to the mosasaurs and aigialosaurs (mosasauroids). If the former, their origin is from land-dwelling burrowers, if the latter, snakes were primitively marine. Molecular data, on the other hand, suggests a close alliance of snakes with iguanians and anguimorphs, forming a clade Toxicofera, the venomous reptiles (Hedges and Vidal, 2009). The debate is far from resolved.

Snakes belong to Squamata and they originated from among lizards at the latest by the Early Cretaceous. It is evident that the ancestors of snakes had legs and that those limbs were lost either in a burrowing lizard that required legs less and less, or in a marine form that lost its limbs as it came to rely more and more on serpentine locomotion, or as a developmental consequence of body elongation. There are indeed several groups of limbless lizards today that are burrowers (and are not snakes), and the marine aigialosaurs and dolichosaurs had reduced limbs and long tails.

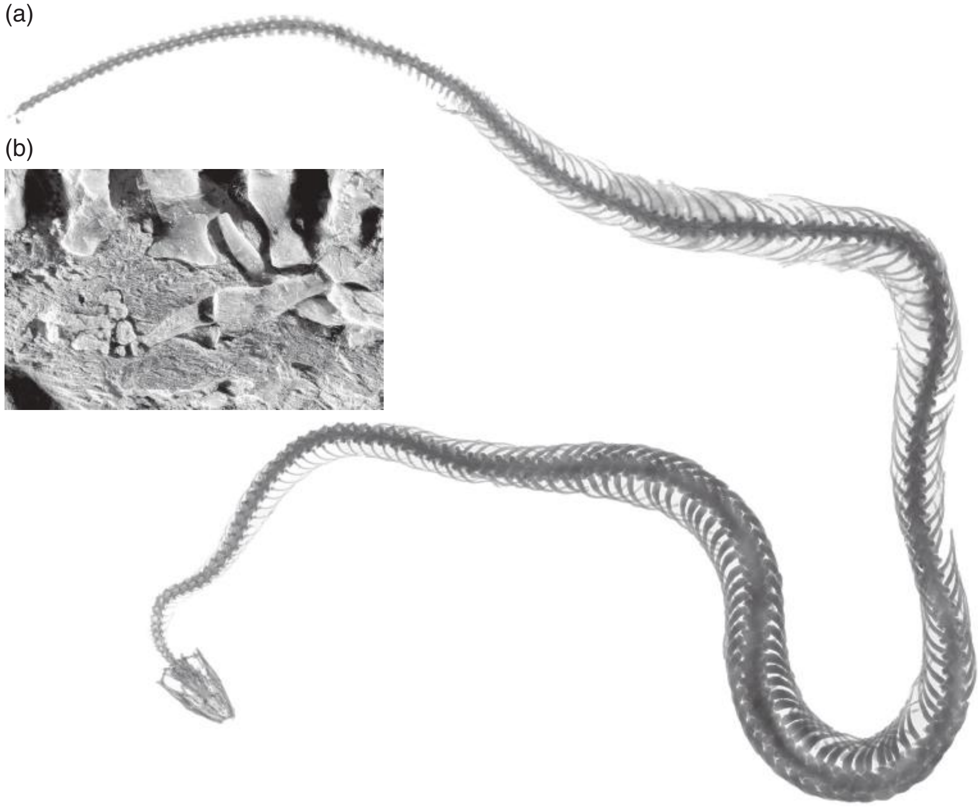
The debate began with a redescription by Caldwell and Lee (1997) of the squamate *Pachyrhachis* from the mid-Cretaceous of Israel. *Pachyrhachis* is about 1.5 m long and has 146 presacral vertebrae. There are no forelimbs, but there is a small pelvis and much reduced hindlimbs. These authors, and Caldwell (1999) argued that *Pachyrhachis* was a snake, basal to the living forms, and that snakes were anguimorphs close to the mosasauroids. Mosasauroids and snakes share reduced ossification of the pelvis and hindlimbs, reduced metakinesis and mesokinesis, enlarged pterygoid teeth and a hinge halfway along the lower jaw that allows some lateral movement. Lee (2005) reaffirmed this view in a series of cladistic analyses of skeletal and soft-tissue morphological data for living squamates and living and fossil squamates.

The opposition began almost immediately, with close questioning of the alleged mosasauroid–snake link. Tchernov *et al*. (2000) described a new Cretaceous snake with limbs, *Haasiophis*, but they found that the limbed snakes fell in the cladogram some way from the base, nested within Macrostomata, the main clade of living snakes. *Haasiophis* (see illustration) is about 1 m long and has 155 presacral vertebrae and broad ribs, superficially like a boa. The forelimb is absent, but there is a small pelvis and much reduced hindlimb, consisting of a femur, tibia, fibula, astragalus, calcaneum and remains of four rudimentary toes. The skull is small and highly kinetic, with double rows of recurved teeth. It shows snake characters of a mobile premaxillary–maxillary contact, marginal teeth fused into sockets, an elongate body composed of more than 140 presacral vertebrae and shoulder girdle and forelimb absent.

Zaher and Rieppel (2002) and Rieppel *et al.* (2003) redescribed *Pachyrhachis* and *Haasiophis* respectively and questioned the reality of many of the supposed homologies between snakes and mosasauroids, most notably in the braincase and in the lower jaw. They highlighted the traditional view that snakes arose from terrestrial burrowers, possibly amphisbaenian lizards, with which they share loss, reduction and consolidation of skull bones, enclosure of the braincase, dorsal displacement of the jaw adductor muscles, loss or reduction of limbs and girdles and uniformity along the vertebral column. This view has been corroborated by the findings of molecular phylogenetics (Vidal and Hedges, 2004; Hedges and Vidal, 2009).

What next? There are two disputed issues. (1) Are the limbed snakes basal to all other known snakes in the phylogeny, or do they nest higher, among the Macrostomata? (2) What are the closest relatives of snakes? Much of the difference in results depends on how characters are defined and used in the cladistic analysis: if intramandibular joint characters are emphasized, a relationship between snakes and mosasauroids is found, and if skull element reduction and loss is highlighted, snakes move closer to amphisbaenians. The cladistic result then drives the biological model for understanding the origin of snakes: did they become long and thin and lose their limbs as an adaptation to constant burrowing in the soil, or to improve their serpentine swimming efficiency in the sea? Findings from developmental biology (Woltering, 2012) could fit either model; *Hox* genes control the overall elongation of snakes, allowing many more vertebrae to be generated by increased frequency of the molecular oscillator that triggers formation of body segments. Most of the additional vertebrae seem to be in posterior parts of the body, rather than the neck, and a short-necked snake ancestor strengthens arguments for a terrestrial origin.

Watch Blair Hedges talking about snake origins at: http://videos.howstuffworks.com/sciencentral/2895-snake-origins-video.htm



The snake with limbs *Haasiophis terrasanctus* from the mid-Cretaceous of Israel, an essentially complete specimen, shown as an X-ray (a), and showing the retention of tiny hindlimbs, seen in a normal, light photograph (b). Source: O. Rieppel, Field Museum of Natural History, Chicago, IL, USA. Reproduced with permission.

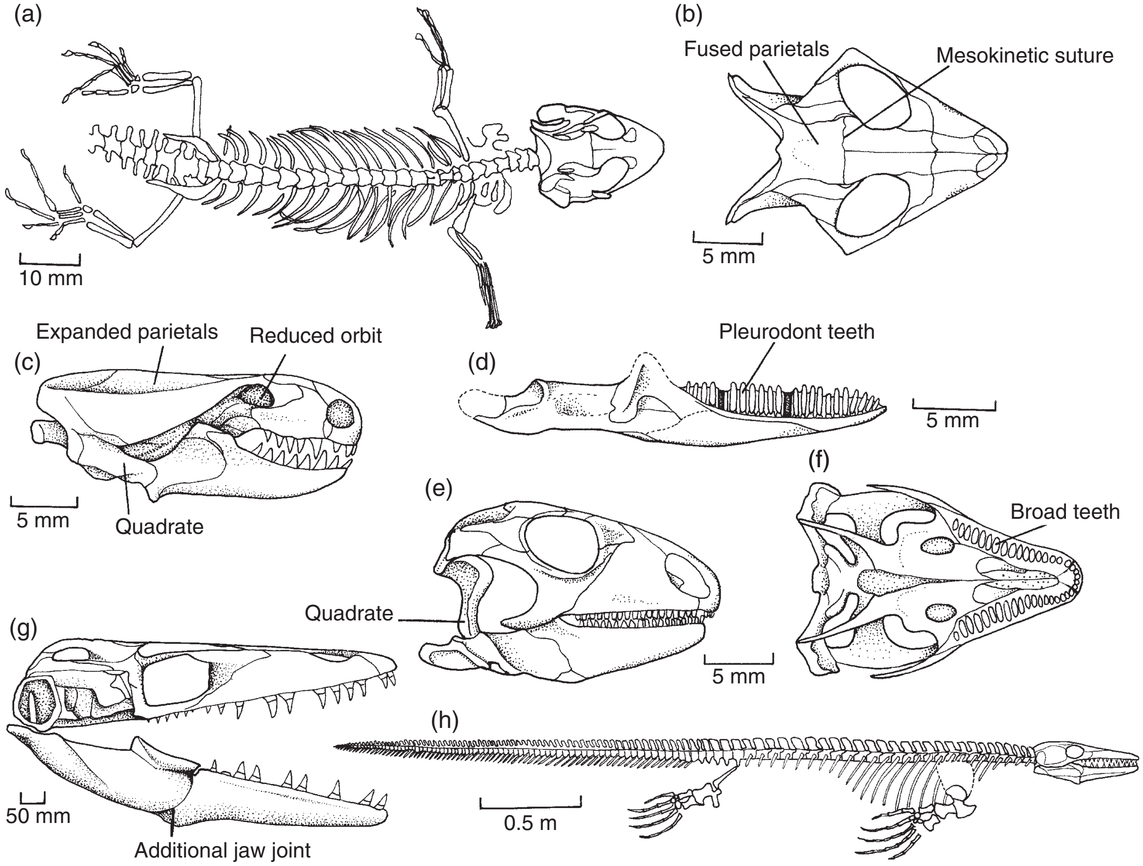


Figure 8.34 Fossil lizards: (a,b) skeleton and skull of the Late Jurassic lizard *Ardeosaurus* in dorsal view; (c) skull of the living amphisbaenid *Amphisbaena* in lateral view; (d) lower jaw of the Early Cretaceous scincoid *Paramacellodus* in internal view; (e,f) skull of the Late Cretaceous polyglyphanodont *Polyglyphanodon* in lateral and ventral views; (g,h) the Late Cretaceous mosasaur *Platecarpus*, skull in lateral view and skeleton in swimming pose. Source: (a,d–f) Adapted from Estes (1983). (b) Adapted from Mateer (1982). (c) Adapted from Romer (1956). (g,h) Adapted from Russell (1967).

with confidence in the Late Cretaceous, although Middle Jurassic and Early Cretaceous forms have been noted. The oldest well-documented fossil gecko is *Gobekko* from the Late Cretaceous of of Mongolia (Daza *et al.*, 2014). The skeletons all come from adult animals, and yet they show unfused nasals, frontals, and parietals. Gekkotans today have tubular frontals and dentaries and these may be structurally related to the loss of the postorbital and supratemporal bars. Gekkotans all lack a parietal foramen, and presumably the light-sensitive parietal eye, and this might be linked to the nocturnal lifestyle of many geckos.

The Scincoidea and Lacertoidea, sometimes grouped together as scincomorphs, include today some 2140 species of skinks, European lacertids and others. An early form, *Paramacellodus*, is known from the Late Jurassic of North America and Early Cretaceous of southern England. It shows **pleurodont** dentition (Figure 8.34(d)), with the teeth set in a 'half groove', as is typical of most lizards. These peg-like teeth in such a tiny animal were probably used in penetrating the tough skins of insects and centipedes. Scincoids and lacertoids became especially diverse from the Late Cretaceous onwards, when the herbivorous teiids, such as *Polyglyphanodon* (Figure 8.34(e,f)), arrived in the Americas from Asia. The skull is strong and deep-sided, and the broad cheek teeth show that this lizard fed on tough vegetation.

The Amphisbaenia, some 170 species today, are heavily modified for a life of burrowing, with elongate, snake-like bodies, often lacking limbs, and heads reduced to miniature battering rams or chisels with which they force a passage through the soil. The front of the skull is tipped downwards and the whole structure is reinforced (Figure 8.34(c)). The orbit is reduced and the temporal bar has disappeared so that the back of the skull is largely the parietal fixed to an enlarged braincase and palate. The fossil record of amphisbaenians is limited: the oldest fossils come from the Palaeocene and Eocene of North America and France, but some modern families are unknown in the fossil record. An older putative amphisbaenian from the Late Cretaceous of Mongolia turns out (Kearney, 2003) to be a polyglyphanodont. *Cryptolacerta*, a lacertid-like lizard from the Eocene Messel locality of Germany provides evidence for lacertid–amphisbaenian monophyly on the basis of its reinforced, akinetic skull roof and braincase (Müller *et al.*, 2011). The fossil suggests also that the reinforcement of the head of amphisbaenians likely arose first as an adaptation to burrowing, and the elongate, snake-like body and limblessness came later.

The anguimorphs comprise today some 200 species, including monitor lizards (varanids), the anguids, mainly limbless forms, the gila monster, a venomous form, and others. Fossil anguimorphs date back to the Late Jurassic (Conrad *et al.*, 2011). The clade includes a wide size range, from the 7-cm long California legless lizard *Anniella pulchra* to 15-m long extinct mosasaurs. Most striking today is the Komodo dragon, *Varanus komodoensis*, up to 3 m long, and capable of attacking livestock and even humans. Even larger was *Varanus* (=*Megalania*) *priscus* from the late Pleistocene (40,000–30,000 years ago) of Australia. The incomplete remains have been interpreted variously to indicate an original body length of 4.5–7.9 m and weights of 100–500 kg (Molnar, 2004). This extinct giant, like the living Komodo dragon, produced venom from specialized glands in its mouth region, and was the largest venomous animal ever (Fry *et al.*, 2009).

Most striking in the history of anguimorphs, and of lizards in general, were the mosasaurs, dolichosaurs, and aigialosaurs, which became highly adapted to marine life in the Late Cretaceous. Aigialosaurs and dolichosaurs were slender, aquatic varanoids known especially from the mid Cretaceous of Europe, North America, and Asia. More imposing were the mosasaurs, 40 genera of Late Cretaceous predators that ranged in length from 3 to 15 m (Russell, 1967; Polcyn *et al.*, 2013). *Platecarpus*, a typical smaller form, has an elongate body, deep tail and paddle-like limbs (Figure 8.34(g,h)). Mosasaurs have large skulls and the strong jaws are lined with sharp conical teeth, clearly for capturing fishes and other marine animals. Some ammonite shells have been reported that bear puncture holes that exactly match the tooth spacing of a mosasaur that has bitten them across, but failed to crush them – although the puncture holes have been interpreted as limpet resting marks. In addition to some of the typical lizard flexibility of the skull, mosasaurs have an extra joint in the lower jaw to increase the gape and so allow them to feed on larger prey.

The Iguania includes some 1550 species of iguanas, agamids and tree-living chameleons today. The chameleons are famed for their ability to change colour, and for their rather odd hands and feet that permit them to grasp branches, two digits on one side and three on the other. They can remain still for long spans, waiting to snatch insects with their elongated, projectile, tongues that adhere to prey largely by suction. One of the world's smallest tetrapods, the miniature chameleon from Madagascar, *Brookesia micra*, is only 29 mm long. The Iguania may have arisen in the Jurassic, but a more convincing fossil is an unusual 30-cm long lizard from the mid Cretaceous of Mexico, *Huehuecuetzpalli* (Reynoso, 1998). The genus *Euposaurus* from the Late Jurassic of France was formerly classified as an iguanian, but it turns out to be a composite of several specimens, including a possible lizard and some rhynchocephalians.

8.9.3 Serpentes: the snakes

The seventh squamate group, the snakes (Serpentes or Ophidia), arose from 'lizard' ancestors, but whether from within Toxicofera, the clade of Anguimorpha + Iguania + Serpentes (see Box 8.8) or from extinct, marine groups of varanoids is still debated (see Box 8.10). Determining the phylogenetic position of Serpentes among Squamata will indicate whether the limblessness and other special features of the clade arose in a terrestrial, burrowing setting or through adaptation to serpentine swimming in Cretaceous seas. The main characters of snakes include of course limblessness (living boas and other non-venomous snakes still have a small remnant of a hindlimb), a greatly increased number of vertebrae (120–500), venom in certain forms, and a great increase in skull kinesis (Lillywhite, 2004).

The snake skull (Figure 8.35(a,b)) is of very light construction, with several points of flexure. On opening, the palate moves forward, the fangs (when present) are erected and the supratemporal–quadrate system enlarges the jaw opening two or three times. The snake then strikes at its prey, seizes it and passes it down its throat by moving the lines of backwardly pointing teeth on its maxillae, palatines and pterygoids. Each side of the palate can be moved independently, creating a ratchet system that allows the snake to literally stuff the prey down its throat and entirely prevent its escape. In advanced venomous snakes, the action of striking at the prey squeezes a poison sac above the palate and venom is squirted down a groove or canal in the main fang.

Snakes are known from the early Late Cretaceous and they radiated greatly during the Cenozoic (Rage, 1984; Pyron and Burbrink, 2012) in line with the radiation of the small mammals, especially rodents, on which they preyed. These first snakes may have fed on insects and other small prey. Reanalysis

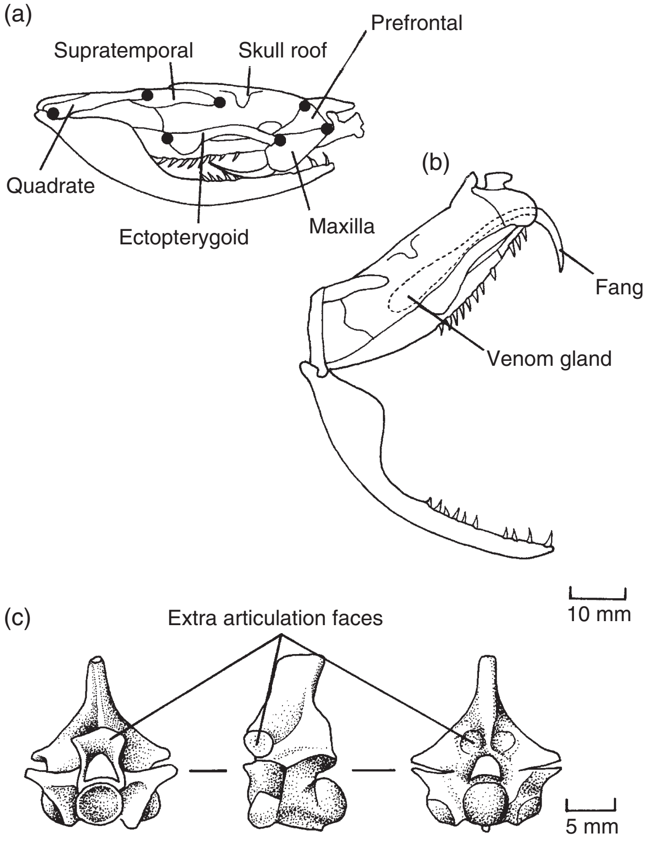


Figure 8.35 Snake anatomy: (a,b) skull of a viperid snake in lateral view, showing the jaws closed and open; (c) mid-trunk vertebra of the living *Python* in posterior, lateral and anterior views. Source: (a,b) Adapted from Alexander (1975). (c) Adapted from Rage (1984).

of *Coniophis* from the Late Cretaceous of North America shows it is phylogenetically the most basal snake, and it retains a lizard-like skull with the maxilla firmly united to the skull. The fossils are found in an entirely terrestrial location and the head and body indicate it was a digger, so enhancing evidence for a burrowing origin for snakes (Longrich *et al.*, 2012a).

Only later did some snakes evolve the ability to kill their prey by suffocation, as boas and pythons do today: they coil tightly around the ribcage of the victim and tighten up when it breathes out. Death is by asphyxiation rather than crushing of the body, as is often assumed. These habits arose in the Late Cretaceous especially among the madstoiids, such as *Sanajeh* from the Late Cretaceous of India. One specimen of this 3.5-m-long snake was found within a sauropod dinosaur nest, coiled around an egg and beside the remains of a ca. 0.5-m-long sauropod hatchling (Wilson *et al.*, 2010). Other examples show that *Sanajeh* perhaps regularly frequented nesting grounds and preyed on hatchling sauropods. Poisonous snakes are known first in the Late Eocene, and venomous colubroids are by far the most successful snakes today.

Snakes range in length up to 6–7 m in a large python, but some huge remains of *Titanoboa* from the Palaeocene of Colombia indicates a 12–15 m monster (Head *et al.*, 2009). Snake vertebrae have a complex shape (Figure 8.35(c)) with extra processes on the sides of the neural arches that control the sideways and vertical bending of the body and give the snake considerable flexibility.

8.10 THE GREAT SEA DRAGONS

Jurassic and Cretaceous seas were filled with basal neopterygian and teleost fishes and the neoselachian sharks that preyed on them (see Chapter 7). A broad range of predatory reptiles also hunted fishes, ammonites, belemnites and other marine life. Pterosaurs and crocodilians seized fishes near the surface (see Sections 8.6, 8.8), and mosasaurs (see Section 8.9.2) were important carnivores in the Late Cretaceous. Certain groups of birds also fed on marine fishes (see Chapter 9), but the main reptilian predators were the ichthyosaurs and plesiosaurs, both of which had appeared in the Triassic (see Section 6.2). After early finds in the 1820s and 1830s, most notably by Mary Anning in southern England, ichthyosaurs and plesiosaurs came to be known collectively as 'sea dragons'.

Plesiosaurs and ichthyosaurs are members of Diapsida, possibly close to the deep branching of Lepidosauromorpha ((see Boxes 6.1, 8.8). Both groups lack the lower temporal fenestra. After great success in the Triassic, many important marine reptile lineages died out in the Late Triassic, some at the end-Triassic mass extinction event, and the clades re-radiated in the Early Jurassic (Thorne *et al.*, 2011).

8.10.1 Plesiosauria

The first true plesiosaurs are known from the Late Triassic and they are closely related to the Triassic pistosauroids (see Section 6.2.2). Plesiosaurs were generally larger, ranging typically from 2 to 14 m in total body length. Plesiosaurs are generally divided into two clades, the plesiosauroids and the pliosauroids (Ketchum and Benson, 2010).

The plesiosauroids include five families. The plesiosaurids are the Early Jurassic forms such as *Plesiosaurus*, known especially from Europe. The elasmosaurids have very long necks and some Late Cretaceous forms boast as many as 76 cervical vertebrae. The cryptoclidids from the Middle to Late Jurassic (Figure 8.36(a–c))

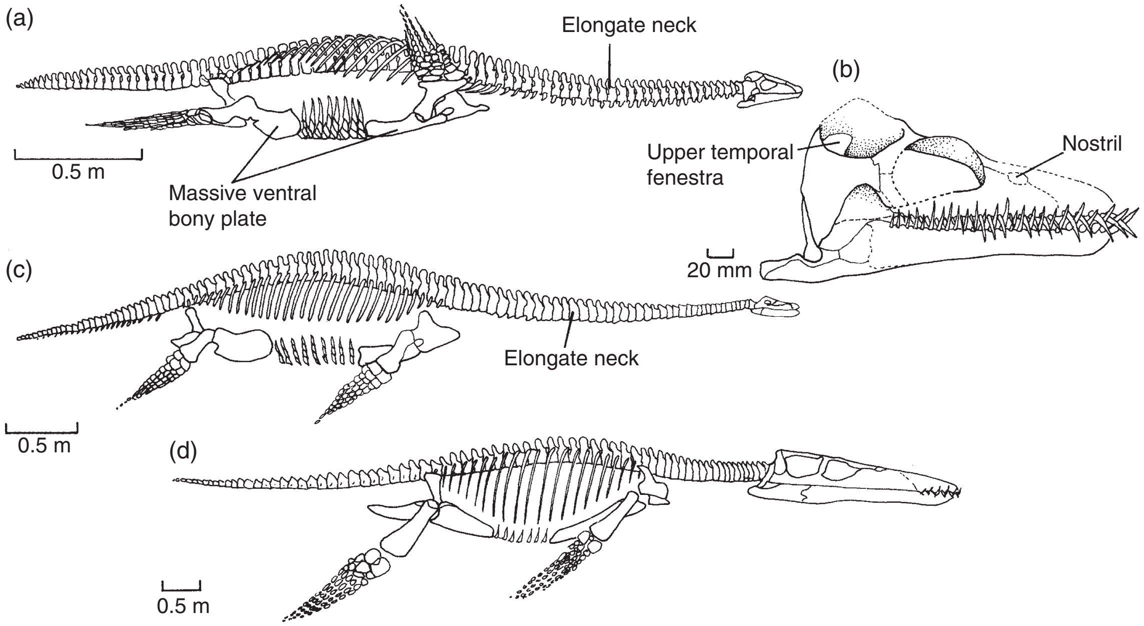


Figure 8.36 The plesiosaurs: (a,b) the Middle Jurassic cryptoclidid *Cryptoclidus*, skeleton in swimming pose and skull in lateral view; (c) the Late Jurassic cryptoclidid *Muraenosaurus*; (d) the Late Jurassic pliosaur *Liopleurodon*. Source: (a,b) Adapted from Brown (1981). (c,d) Adapted from Robinson (1975).

have long necks with 30 cervical vertebrae and a skull with a long snout, single (upper) temporal fenestrae, and nostrils set back from the tip of the snout. The jaw joint is set below the level of the tooth row, and this shifts the strongest biting point forwards. The long pointed conical teeth interlock when the jaws are shut, an adaptation to retain slippery fishes and molluscs in the mouth as the jaws close. The leptocleidids are a family that spanned the Cretaceous, and their placement phylogenetically has been controversial (Benson *et al.*, 2013a). They show a range of body plans, some with long necks, others with short necks, and some occupied freshwater or marginal habitats. The polycotylids are short-necked Late Cretaceous forms, long classified with the pliosauroids.

The pliosauroids include the Jurassic rhomaleosaurids (see Figure 2.8) and the pliosaurids, such as the Late Jurassic *Liopleurodon* and *Pliosaurus* (Figure 8.36(d)), up to 12 m long, and with a long heavy skull and a relatively short neck (Benson *et al.*, 2013b). Pliosauroids may have fed on smaller plesiosaurs and on ichthyosaurs. Pliosauroids had vast low-snouted heads, armed with powerful jaws and broad-based sharp teeth. The skull was designed like a lattice reinforced with girders to resist the great bending moments produced during biting (see Section 2.4.1) and the mandible was like a box girder for the same reasons, but at the same time it retained a streamlined shape to assist in fast swimming. The neck was shorter than in other plesiosaur groups, but pliosauroids nonetheless retained large numbers of cervical vertebrae.

The revised phylogeny of plesiosaurs allows exploration of how the clade responded to major events. After the Jurassic radiation, it seems that plesiosaur diversity was hit hard by events across the Jurassic-Cretaceous boundary, with only three lineages surviving (Benson and Druckenmiller, 2014). These then radiated primarily as Leptocleididae, Polycotylidae, and Elasmosauridae. The extinctions may have been related to climate change from the largely monsoonal Late Jurassic to a more arid Early Cretaceous, and consequent effects on ocean oxygenation and plankton supplies. However, the fact that marine crocodylomorphs and ichthyosaurs show different patterns of diversification and extinction at the time suggests the cause of end-Jurassic extinctions among plesiosaurs might be more specific to the taxa.

Plesiosaurs were highly adapted for submarine locomotion, with powerful paddle-like limbs and heavily reinforced limb girdles. Three swimming modes have been proposed (Figure 8.37(a–c)): rowing, in which the paddles beat backwards and forwards; underwater flying as in sea turtles and penguins, in which the paddle describes a figure-of-eight pattern; or a modified version of the flying model as in sealions, in which the paddle describes a crescent-shaped path. All proposed swimming modes must take account of the fact that the plesiosaur pectoral and pelvic girdles are both flattened heavy units of bone that form an immovable ventral bony plate with the gastralia between the limb girdles (Figure 8.37(d)), and that the limb girdles are too weak for strong vertical movements. The rowing mode has been widely rejected because it is inefficient – one sweep back and one forward would cancel each other. In comparing the penguin and sealion modes, Carpenter *et al.* (2010) experimented with swimmers in pools and computer models, and rejected the rowing and sealion models. The shoulder joint in plesiosaurs allows the necessary 'flying' movements, and movements were probably semi-synchronous for maximum efficiency, meaning the fore flipper described a figure-of-eight slightly out of synchrony with the hind flipper.

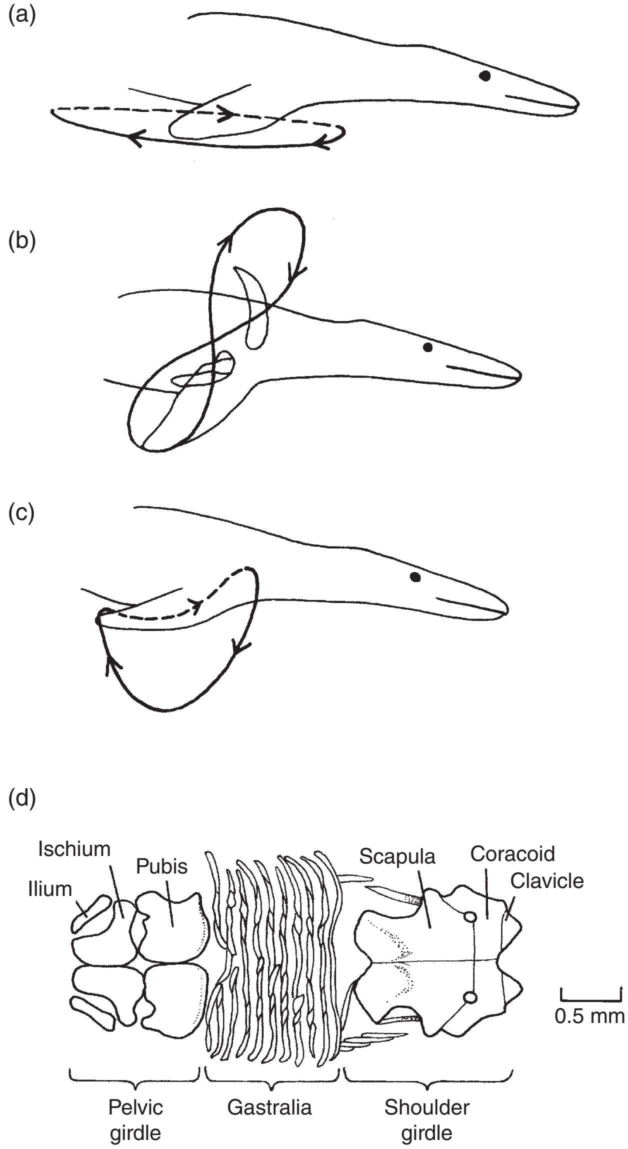


Figure 8.37 Plesiosaur locomotion: (a–c) three hypotheses: (a) rowing underwater like a duck, (b) flying underwater like a penguin and (c) an intermediate style like a sealion; (d) ventral view of the heavy bony covering of the plesiosaur belly. Source: (a–c) Adapted from Taylor (1986). (d) Adapted from Robinson (1975).

The mode of reproduction of plesiosaurs was uncertain until the report of a Late Cretaceous polycotylid, *Polycotylus*, with an embryo enclosed within the rib cage (O'Keefe and Chiappe, 2011). These authors argue that plesiosaurs apparently gave birth to large, probably single progeny. They interpret the plesiosaur breeding model as a K-selected strategy, more in line with modern mammals than with ichthyosaurs, for example, which had large numbers of live young (see Section 8.10.2). Whether plesiosaurs extended this to parental care after birth may never be known.

8.10.2 Ichthyopterygia

Ichthyosaurs first occurred in the Triassic (see Section 6.2.3), diversified in the Early Jurassic and became much reduced in diversity in the Late Jurassic and Cretaceous, being represented then only by the Ophthalmosauridae (McGowan and Motani, 2003; Motani, 2005; Maisch, 2010). Whereas the Jurassic-Cretaceous boundary interval marked severe reduction in plesiosaurian diversity (see Section 8.10.1), this was not the case for ichthyosaurs: several lineages survived through the boundary, although the clade never reached Triassic or Early Jurassic disparities in the Cretaceous (Fischer *et al.*, 2012). There is considerable variation in the size of ichthyosaurs, with lengths of 1–16 m, but the dolphin-like body shape, long snout and large eyes remain common features throughout (Figure 8.38(a)).

The body outline of ichthyosaurs (Figure 8.38(b)) is well known because of the exquisite preservation of specimens especially in the Early Jurassic of southern Germany where they may show in some cases a black 'ghost' of the skin outline. This shows that the paddles were extended by skin and connective tissue, that the tail fin was roughly symmetrical, even though the vertebral column bends down, and that there was a high dorsal fin made entirely from soft tissues. Stomach contents include tiny hooklets from the arms of cephalopods and fish scales, but seemingly no belemnites or ammonites possibly because their hard shells were spat out or shaken off. One Early Cretaceous ichthyosaur from Australia contains bones of a hatchling protostegid turtle and an enantiornithine bird (Kear *et al.*, 2003), an eclectic dietary selection.

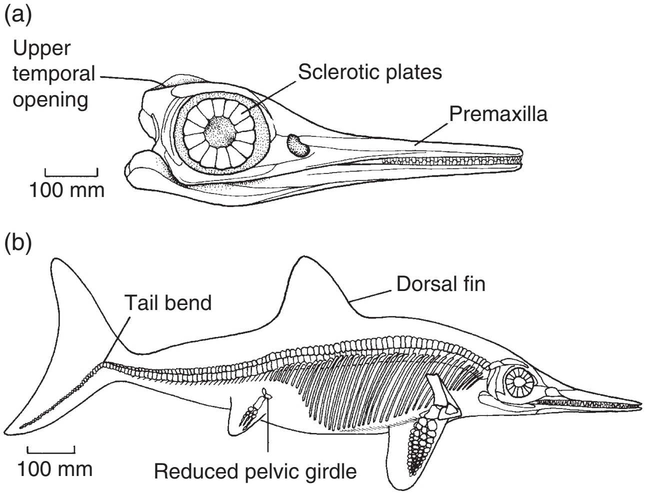


Figure 8.38 The ichthyosaurs: (a) skull and (b) skeleton of the Early Jurassic *Ichthyosaurus*; the body outline is based on skin impressions preserved with some European material. Source: Adapted from Andrews (1910).

Ichthyosaurs were substantially modified for life at sea. They swam by beating their tails from side to side, and used their paddles to change direction and to control roll and pitch, as in large cruising fishes such as tunas and sharks (Motani, 2002). Based on comparisons with living forms, *Stenopterygius* probably cruised at about 1.5 m s^{-1} (or 5.4 km h^{-1}) and it probably had an 'elevated ectothermic' physiology, like a tuna, in which control of body temperature is by external means, by high levels of exercise maintaining a blood temperature higher than the surrounding seawater. Ichthyosaurs had the largest eyeballs of any known animal: the 9-m-long *Temnodontosaurus* had an eyeball some 300 mm in diameter (Motani *et al.,* 1999). Such huge eyes must have been for detecting prey in conditions of very low light, at water depths of up to 600 m. The identification of melanin (see Box 9.1) within the body outlines of ichthyosaur fossils suggests (Lindgren *et al.*, 2014) that some at least were black all over, showing no sign of the counter-shading seen in many marine vertebrates; this may reflect their deep-diving habit, like the black-all-over sperm whales today.

The weakness of the limb girdles of ichthyosaurs and their overall 'fishy' body shape suggest that they could not venture onto land. Marine turtles, penguins and seals, which spend most of their time at sea, do creep out onto a beach to lay their eggs. Ichthyosaurs, however, bore live young underwater as dolphins and whales do, and they were born tail-first in order to avoid drowning: the head would emerge last and the juvenile could swim to the surface rapidly to take its first breath.

Remarkable specimens from the Early Jurassic of Germany and England show embryos within the ribcages of some specimens, usually one or two, but sometimes as many as 10 or 11 (Motani, 2005). Several specimens show the young apparently in the process of being born (Figure 8.39). The usual, romantic, interpretation of these specimens is that the mother sacrificed her life while giving birth. Much more likely in many cases is that the juveniles were expelled after death of the mother by gases of putrefaction.

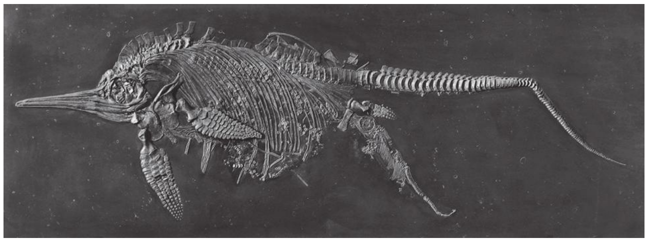


Figure 8.39 Adult specimen of the ichthyosaur *Stenopterygius*, from the Early Jurassic of Holzmaden, Baden-Württemberg, southwest Germany, pictured with juvenile specimens of the same species. This is one of more than 50 specimens with associated young, and these are interpreted as embryos and juveniles that have just been born. Source: R. Wild, deceased; Staatliches Museum für Naturkunde, Stuttgart, Germany. Reproduced with permission.

8.11 THE CRETACEOUS-PALEOGENE MASS EXTINCTION

The most commonly asked question about dinosaurs is why they died out. Paraphrasing the words of Malcolm in *Macbeth*, 'nothing in [their] life became [them] like the leaving it'. Over the years, hundreds of theories for this disappearance 66 Myr ago at the Cretaceous–Paleogene (KPg) boundary have been proposed (this event was formerly called the KT event, from Cretaceous–Tertiary). It might seem odd that there is still so much debate: after all, the KPg boundary is the most studied point in geological time. Yet, despite all this effort, there are still many questions about the timing of the event, the patterns of what died out and what survived, and the precise nature of the physical environmental crisis. The key question that is often missed is not whether an impact happened (it did), nor whether there was massive volcanism (there was), but how one or other, or a combination, of these physical crises, as well as sea level and temperature changes, actually caused the selective killing.

8.11.1 What died out?

Among terrestrial tetrapods, the non-avian dinosaurs and pterosaurs disappeared, as well as numerous lizards, crocodiles, birds, and mammals. Lizards and birds were thought to have escaped relatively unscathed, but new studies suggest they too were hit hard (Longrich *et al*., 2011, 2012b). In the sea, plesiosaurs, mosasaurs and some families of sharks and teleost fishes disappeared (Kriwet and Benton, 2004; Friedman and Sallan, 2012). The ichthyosaurs had dwindled and died out 30 Myr earlier. Among non-vertebrates, many important Mesozoic groups disappeared: the ammonites, belemnites, rudist bivalves and various plankton groups. However, other animals, such as diatoms, radiolaria, benthic foraminifera, brachiopods, gastropods, some fishes, amphibians, turtles, crocodiles, and terrestrial plants, were apparently little affected (MacLeod *et al*., 1997).

It is hard to separate the survivors and non-survivors into simple ecological categories. Most of the land and freshwater animals that survived were small, except for certain crocodilians. Most of the marine forms that died out were free-swimmers or floaters (plankton, ammonites, belemnites), but of course many open-water fishes survived. Among forms that lived on the seabed, it was mainly the filter-feeders like corals, bryozoans and crinoids that suffered extinction (possibly by loss of plankton food?), whereas forms that fed on detritus were little affected.

Are there any convincing ecological correlates of extinction risk and survival? Jablonski (2005) notes that for many groups, geographic range is the key determinant of survival: widespread organisms survive and geographically restricted relatives do not. Other correlates of survival include wide environmental tolerance, modest body size, and broad diet: this is why cockroaches and humans might survive physical environmental challenges well, but elephants (too big) and pandas (diet too restricted) might not. Such generalizations can explain to some extent why dinosaurs and plesiosaurs died out, but the story is not so simple. For many groups, the KPg event seems to have been non-selective, and the particular families, genera and species of birds and mammals that died out cannot be explained only in terms of natural selection – many of them were simply unlucky.

8.11.2 How long did it take?

Some geologists assume that all major extinctions occurred instantaneously, in as little as a day or a month. Others posit a 'sudden' event, but allow several thousands or tens of thousands of years. At the level of discrimination in dating, there is no way to distinguish such time spans because both appear to be the same in the geological record. Nonetheless, the quality of dating of this event has improved substantially in the past twenty years.

The KPg boundary is dated and correlated using magnetostratigraphy and radiometric dating. Magnetostratigraphy depends on the polarity of magnetization of rocks. Every few Myr, the Earth's north and south magnetic poles flip over, and all iron-bearing minerals in rocks that are just being formed acquire the relevant magnetization. In the latest Cretaceous, Earth's polarity changed eleven times, the KPg boundary lying in polarity band 29R (i.e. reversed), which lasted as little as 0.5 Myr. Further, radiometric dating of KPg boundary ashes using the ^{40}Ar/^{39}Ar technique (Renne *et al*., 2013) establishes the date of the KPg boundary as 66.032 ± 0.058 Myr.

A key debate has concerned the relative dating of the KPg boundary, asteroid impact, and extinction. The new stratigraphic studies confirm that the KPg boundary is synchronous with the mass extinction and the impact to within 32,000 years (Renne *et al*., 2013). Further, while many would debate the simple link between impact and extinction, the fact that an asteroid struck the Earth at a site called Chicxulub in Mexico is not debated.

8.11.3 Evidence for impact

The revolution in understanding of the KPg mass extinction began with a classic paper published in 1980 (Alvarez *et al*., 1980). In this, the authors made the startling proposal that the dinosaurs had been killed by an asteroid impact, and their key evidence was an iridium anomaly that they observed in two KPg boundary sections, in Italy and Denmark. At the time, this proposal caused an uproar: how could such a startling claim be made on the basis of so little evidence? However, since 1980, the iridium anomaly has been observed worldwide in hundreds of KPg boundary sections, and other predictions made by Alvarez *et al.* (1980) have been confirmed.

There are four key pieces of evidence that an impact occurred at the KPg boundary.

1 An iridium anomaly worldwide. Iridium is a platinum-group element that is rare on Earth's crust and reaches Earth from space in meteorites at a low average rate of accretion. At the KPg boundary, that rate increased dramatically, giving an iridium spike (Figure 8.40).

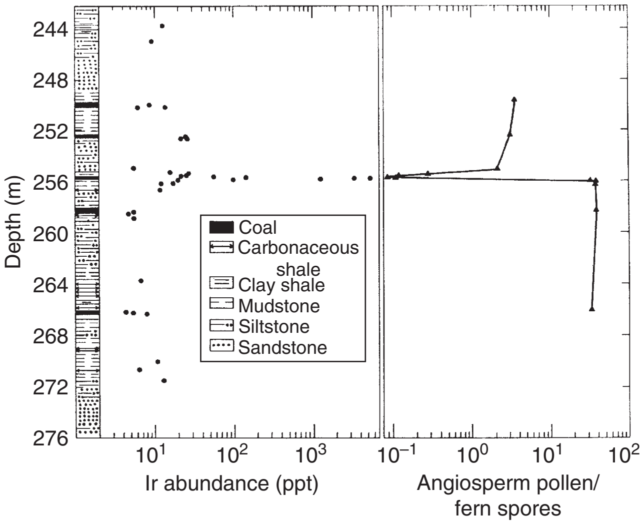


Figure 8.40 A typical iridium spike (left) and fern spike (right) from a core taken through the KPg boundary in freshwater coal swamp deposits in York Canyon, New Mexico, USA. Note that both the iridium abundances, measured in parts per trillion (ppt), and the ratios of angiosperm-pollen:fern-spores are plotted on logarithmic scales. Source: C. Orth, formerly, Los Alamos National Laboratory, Los Alamos, NM, USA. Reproduced with permission.

2 Shocked quartz has been found in many sections, especially close to the impact site (Smit, 1999). These are grains of quartz bearing criss-crossing lines produced by the pressure of an impact.

3 Glassy spherules also occur abundantly at the base of the boundary clays from locations close to the impact site. These were produced by melting of the rock beneath the crater and were then thrown through the air in the aftershock.

4 A fern spike (Figure 8.40) is found in many terrestrial KPg boundary sections, indicating an abrupt shift in pollen ratios from angiosperm-dominated to fern-dominated. This indicates the aftermath of a catastrophic ash fall, whether from impact or massive volcanic eruption: ferns recover first and colonize the new surface, followed eventually by the angiosperms after soils begin to develop. This interpretation has been made by analogy with observed floral changes after major volcanic eruptions.

The reality of impact was debated through the 1980s, but the discovery of the crater in 1990 convinced most doubters. The Chicxulub Crater, on the Yucatán Peninsula, Mexico (Figure 8.41(a)) is 195 km in diameter, with inner rings at 130 km and 80 km, and is filled with Cenozoic sediments (Morgan and Warner, 1999). Coastline deposits some 500 km away show evidence for tsunami (massive tidal wave) activity, presumably set off by a vast impact into the proto-Caribbean (Smit, 1999; Schulte *et al.*, 2010). Further, the KPg boundary clays ringing the site also yield abundant shocked quartz and glassy spherules that match geochemically the bedrock under

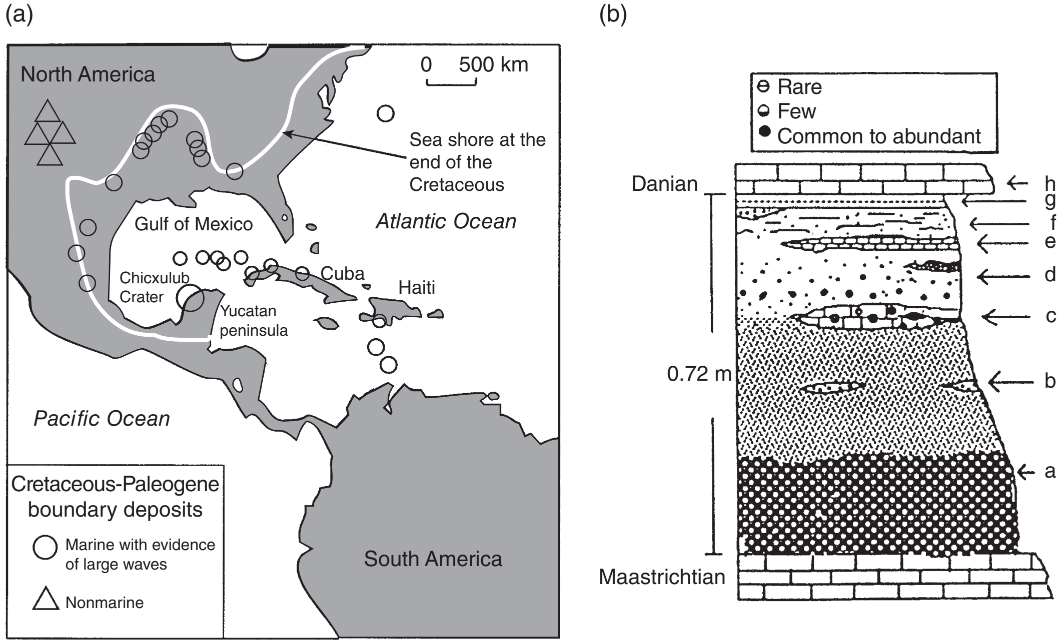


Figure 8.41 Evidence for the impact site: (a) location of Chicxulub Crater, on the Yucatán Peninsula, Mexico, as well as the end-Cretaceous coastline of the Proto-Caribbean Sea and sites indicating activity of tsunamis (tidal waves); (b) the KPg boundary section at Beloc, showing the sequence of arrivals of airfall debris and tsunamis (a, spherule layer; b, layer with smaller spherules; c, spherule-bearing marl lens; d, sandy marl and micrite; e, chalk lens; f, sandy marl with lenses of coarse spherules; g, fine clay with iridium spike; h, limestone); airborne melt spherules arrived first (a,b), then the tsunamis (b–f) and finally the dust-borne iridium (g), before a return to normal marine deposition (h). Source: (a) Adapted from various sources. (b) Adapted from Maurrasse and Sen (1991).

the crater. Further afield, the boundary layer is thinner, there are no tsunami deposits, spherules are smaller or absent and shocked quartz is less abundant.

Detailed studies of KPg boundary sections around the proto-Caribbean have allowed geologists to reconstruct what happened. The famous section at Beloc on Haiti (Figure 8.41(b)), with a boundary layer that is 0.7 m thick (Maurrasse and Sen, 1991), documents a three-phase process.

1 The spherule layers, the lower 0.5 m of the section, are two bands of glassy spherules that have two geochemical compositions, some indicating a source from melting of basement rocks and the others indicate a source from evaporites and limestones (the rock underlying Chicxulub). The glassy spherules were melted and thrown up by the impact and came hurtling through the air, and were scattered throughout the proto-Caribbean.

2 The tsunami beds, 0.2 m thick, consisting of marls and clays with large limestone clasts and capped by a thin clay layer. The tsunami followed, moving rapidly over hundreds of kilometres of sea, but more slowly than the airborne spherules, and churning up the limestones and other sediments in the area.

3 The iridium spike and the shocked quartz occur in a fine clay band about 0.1 m from the top of the section. Several hours or days later, the iridium and fine dusty material fell from the upper atmosphere, long after the heavier spherules had been deposited.

This boundary succession represents some very extraordinary circumstances, and then deposition reverted to normal limestone, as it had been before the impact. This three-phase pattern is seen in all other KPg boundary layers throughout the world (Smit, 1999), although the tsunami layers are not seen outside the proto-Caribbean. For example, Wolfe (1991) noted the arrival of coarser debris first, combined with freezing, and then the airborne dust and iridium some time later 3000 km away in Wyoming.

The KPg impact has been anatomized, and it has been dated in a broad way – and it apparently happened in early June! Wolfe (1991) examined KPg boundary sediments in Wyoming that had been deposited in a lily pond less than 2 m deep. He tracked a series of catastrophic events in the pond, including freezing of the fossil lily leaves, which is shown by irregular folds on the surface. The fossil lilies have modern representatives, and their flowering state corresponds to June: this is a classic application of uniformitarian principles, 'the present is the key to the past'. In all, the sequence of catastrophic events, Wolfe (1991) argues, lasted from 3 to 4 months.

8.11.4 The pattern of extinction

Did all the plant and animal groups that died out near the end of the Cretaceous do so essentially at the same time (catastrophic event) or over a span of several million years (gradual event)? The evidence suggests that some groups disappeared catastrophically right at the KPg boundary, whereas others were in long decline before the end of the Cretaceous.

The ichthyosaurs, for example, disappeared 30 Myr earlier than the KPg boundary, and the ostracods, bryozoa, ammonites, bivalves, plesiosaurs and pterosaurs had apparently dwindled to low diversities (MacLeod *et al*., 1997). Such claims require careful checking because of the patchy quality of the fossil record. A seemingly gradual pattern of extinction may arise if all the last fossils have not been collected, and additional collecting may fill those gaps, turning a gradual pattern catastrophic. Likewise, an apparently catastrophic pattern can arise if there is a gap in sedimentation: many species apparently disappear at one level, but that is simply because a long interval of time is missing above.

Table 8.1 Data on the rates of extinction of vertebrates at the KPg boundary. Figures are based on the numbers of families extant during the Maastrichtian stage and the numbers that died out some time during that time interval.

Group	Families extant	Families extinct	Extinction rate
Chondrichthyes	44	8	18%
Bony fishes	50	6	12%
Amphibians	11	0	0%
Reptiles	71	36	51%
Turtles	15	4	27%
Lizards and snakes	16	1	6%
Crocodilians	14	5	36%
Pterosaurs	2	2	100%
Dinosaurs	21	21	100%
Plesiosaurs	3	3	100%
Birds	12	9	75%
Mammals	22	5	23%
Basal groups	11	1	9%
Marsupials	4	3	75%
Placentals	7	1	14%
All vertebrates	210	64	30%
Fishes	94	14	15%
Tetrapods	116	50	43%
Amniotes	105	50	48%

Adapted from Benton (1993).

What of the dinosaurs and other vertebrates? The stratigraphic ranges of vertebrates across the KPg interval certainly indicate a mass extinction. Results calculated (Table 8.1) from chapters in Benton (1993), indicate an overall loss of 64 out of 210 families of vertebrates, an extinction rate of 30%. This is made up (Figure 8.42) from the extinction of 14 out of 94 families of fishes (15% loss) and 50 out of 115 families of tetrapods (43% loss). The highest extinction rates, inevitably, are for non-avian dinosaurs, pterosaurs and plesiosaurs (all 100%), with high rates also for birds and metatherian mammals (both 75%). Among other groups, crocodilians (36%) and turtles (27%) lost more than a quarter of families, but extinction rates for fishes, amphibians, lizards and snakes, basal mammals and eutherian mammals are all lower than 15%, and hence not different from normal, or 'background', extinction rates.

There are two problems with these calculations, that the time scale and the taxonomic scale are crude. The time bins are stratigraphic stages, and the last stage of the Cretaceous, the Maastrichtian, was 6 Myr long. It is hard to correlate precisely the ages of rocks from Asia to Europe to North America, so it is

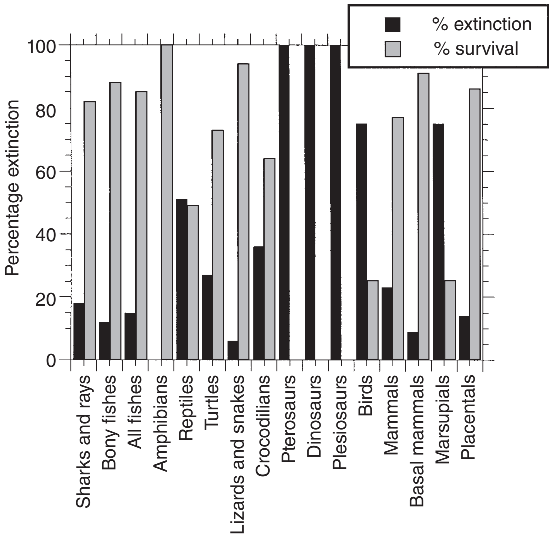


Figure 8.42 The proportions of different vertebrate families that became extinct during the KPg event, based on data from Benton (1993), listed in Table 8.1. Note the 100% extinction of pterosaurs, dinosaurs and plesiosaurs, but 0% extinction of amphibians, and extinction rates of less than 20% for fishes, lizards and snakes, basal mammals and placental mammals. Source: Adapted from Benton (1993).

not clear whether all the dinosaurs, pterosaurs, plesiosaurs, mosasaurs and other groups died out right at the end of the Maastrichtian, or scattered through much of the time span. In terms of taxonomic scale, the calculations are at family level, which may conceal a great deal of upheaval at lower taxonomic levels. For example, although lizards and snakes show relatively low familial extinction rates at the KPg event, they were much more seriously affected at species level (Longrich *et al*., 2012b).

Dinosaur diversity seemed to remain high right to the end of the Cretaceous, but there were reductions among some larger herbivores, which might have de-stablized communities (Brusatte *et al*., 2014). Further, morphological disparity showed varying patterns. Brusatte *et al.* (2012b) found that large-bodied bulk-feeding herbivores (ceratopsids and hadrosauroids) and some North American taxa declined in disparity during the Campanian and Maastrichtian, whereas carnivorous dinosaurs, mid-sized herbivores, and some Asian taxa did not. Whether these apparent declines in morphological variability in certain clades mean anything in terms of a decline towards extinction is unclear: they may be part of a pattern of variability between clades, and studies are needed for the whole Cretaceous.

Local studies are required. The richest terminal Cretaceous dinosaur beds are in western North America, the Hell Creek Formation of Montana and the Lancian (Ferris Formation) of Wyoming, but detailed collecting has thrown up controversial results. Early studies of the Hell Creek Formation suggested that there had been a long-term decline among dinosaurs and other tetrapods through the last 5 Myr of the Cretaceous. In a series of exceptionally thorough studies that included hundreds of thousands of specimens and tens of thousands of hours of collecting, two viewpoints emerged: either the dinosaurs had declined steadily over some 5 Myr, or they died out rapidly at the very end of the Cretaceous.

In Montana and Wyoming, several dinosaur families lasted right to the end of the Cretaceous: the tyrannosauroids, ornithomimids and dromaeosaurids among theropods, the nodosaurid and ankylosaurid ankylosaurs, the hypsilophodontid and hadrosaurid ornithopods, the pachycephalosaurids and the protoceratopsid and ceratopsid ceratopsians. The latest Cretaceous of western North America teemed with familiar, and highly successful, dinosaurs such as *Ankylosaurus*, *Triceratops* and *Tyrannosaurus*, and their disappearance was abrupt (Brusatte *et al*., 2014; Wilson *et al*., 2014).

8.11.5 Theories of extinction

Over the years, more than a hundred hypotheses have been presented for the extinction of the dinosaurs (Benton, 1990). A common view in the latter half of the nineteenth century and in the first three decades of the twentieth was that the dinosaurs died out because their time had come – they were described by many palaeontologists as prime victims of racial senility – their genetic potential was exhausted, they exhibited gigantism (if not acromegaly), excessive spinosity, and even a loss of the ability to adapt. From about 1920, dozens of hypotheses were put forward, ranging from the physiological (slipped discs, excessive hormone production, loss of their sex drive) to the ecological (competition with mammals, change in plant food), from the climatic (too hot, too cold, too wet) to the terrestrial catastrophic (vulcanism, magnetic reversal), from the topographic (marine regression, mountain building) to the extraterrestrial (sunspots, cometary impact). Many of these explanations were little more than whims, and most were hard to couch in terms that would allow them to be tested. Present hypotheses are more 'scientific'.

There are three current models to explain the KPg event.

1 The impact hypothesis explains the extinction as a result of the after-effects of a major extraterrestrial impact on the Earth.

2 The volcanic hypothesis explains the extinction as the result of a major volcanic eruption that caused abrupt extinction.

3 The multiple causes hypothesis finds evidence of numerous killing agencies, including impact, marine regression, volcanic activity, and changes in climate.

These three viewpoints have evolved over the years, and they are neatly summarized in three position papers, Schulte *et al.* (2010) for impact, Courtlillot and Fluteau (2010) for volcanic causes, and Archibald *et al.* (2010) for multiple causes.

The **impact hypothesis** (Alvarez *et al*., 1980) is that the extinctions were caused by the impact of a 10 km diameter asteroid on Earth. The impact caused massive extinctions by throwing up a vast dust cloud that blocked out the sun and prevented photosynthesis, and caused freezing, and hence plants died off, followed by herbivores and then carnivores. Schulte *et al.* (2010) conclude 'The temporal match between the ejecta layer and the onset of the extinctions and the agreement of ecological patterns in the fossil record with modeled environmental perturbations (for example, darkness and cooling) lead us to conclude that the Chicxulub impact triggered the mass extinction.'

The **volcanic hypothesis** explains the KPg event by volcanic activity (Courtillot, 1999; Courtillot and Fluteau, 2010). The Deccan Traps in India represent a vast outpouring of basalt lava that occurred in three pulses, spanning the KPg boundary. In some interpretations, the volcanic model explains instantaneous catastrophic extinction, whereas in others it allows a span of 3 Myr or so, for a more gradual dying off caused by successive eruption episodes. Proponents of this view focus on the fact that most people accept that such large igneous provinces were the key drivers of previous mass extinctions, notably the Permo-Triassic and end-Triassic events (see Sections 5.7, 6.5), and argue, quite rightly, that the Deccan Traps, equally massive, should not be ignored. They note further that current evidence suggests that basalt eruptions can be much more sudden and catastrophic in effects than had been assumed.

The **multiple causes** hypothesis comes from an older view, that the decline of the dinosaurs and other taxa lasted for 5–10 Myr of the Late Cretaceous, and is as much to do with gradually cooling climate and other long-term palaeoecological processes, as the final *coup de grâce* administered by the Deccan Traps eruptions and the Chicxulub impact. Archibald *et al.* (2010) argue that 'Patterns of extinction and survival were varied, pointing to multiple causes at this time—including impact, marine regression, volcanic activity, and changes in global and regional climatic patterns'. Certainly sea levels were falling and climate was cooling in the 5 Myr before the end of the Cretaceous, and Renne *et al.* (2013) note some short, sharp cooling episodes in the last 1 Myr of the Cretaceous, including a particularly sharp drop in temperature of 6–8 °C less than 100,000 yr before the KPg boundary.

Much has been established since 1980: the occurrence, location and immediate physical consequences of the Chicxulub impact; the timing and scale of the Deccan Trap eruptions; the exact synchroncity of KPg boundary, impact, and mass extinction; the climate cooling in the 5–10 Myr before the KPg boundary; and varying extinction patterns among many clades, with some showing long-term declines, and others (e.g. lizards, dinosaurs, birds, mammals) showing dramatic taxic loss exactly at the KPg boundary. There clearly were regional-scale extinctions associated with falling sea levels and cooling temperatures through the Campanian and Maastrichtian, but the main extinctions happened at the KPg boundary. The Deccan Traps must have generated acid rain, ocean anoxia, and other effects, as in previous mass extinctions, but the Chicxulub impact was clearly instrumental as the main driver of the KPg mass extinction.

Just as the Permo-Triassic mass extinction triggered a remarkable series of diversifications among vertebrates in the Triassic (see Chapter 6), the KPg mass extinction had a similarly stimulating effect on Paleogene vertebrates. There were remarkable bursts of radiation among sharks and bony fishes (see Section 7.5), lizards and snakes, but especially among birds, and mammals, and these will be explored in Chapters 9 and 10 respectively.

8.12 FURTHER READING

Brusatte (2012) and Fastovsky and Weishampel (2005) are the best introductions to dinosaurs for students. Brett-Surman *et al.* (2012) has articles on every aspect of dinosaurs, and Weishampel *et al.* (2004) is the 'bible' for dinosaur-lovers, with full documentation of all dinosaur groups, their anatomy, relationships and distributions. Colbert (1984) is the classic history of dinosaur collectors, and Cadbury (2001) investigates the rivalry between Mantell and Owen and the first dinosaur discoveries. There must be hundreds of dinosaur books on the market, and it is invidious to select any particular titles. However, particularly innovative, and comprehensive titles include Barrett *et al.* (2001), Holtz and Rey (2007), Brusatte (2010), and White (2012). Particular dinosaur groups are covered by Currie *et al.* (2004) and Parrish *et al.* (2013) on theropods, Curry Rogers and Wilson (2005) and Klein *et al.* (2011) on sauropods, Carpenter (2001) on the stegosaurs and ankylosaurs, Ryan *et al.* (2010) on ceratopsians, and Carpenter *et al.* (1994) on dinosaur eggs and babies.

Smaller Mesozoic animals are considered in Fraser and Sues (1994), pterosaurs by Buffetaut and Mazin (2003), Witton (2013), and Martill *et al.* (2014), and marine reptiles by Callaway and Nicholls (1996). Mesozoic tetrapods of Mongolia and Russia are described in Benton *et al.* (2000b). Read about the diversity and biology of modern reptiles in Pough *et al.* (2003) and Vitt and Caldwell (2013), about lizards in Pianka (2006), and snake structure and function in Lillywhite (2014). There are many books on the KPg extinction event, but Alvarez (1997), Courtillot (1999), and Archibald (2011) expound the impact, volcanic, and multiple models respectively.

There are more excellent web sites about dinosaurs than stars in the heavens, so these are not listed. Indeed, Wikipedia has a dedicated team of writers who update the dinosaur entries daily. All the latest dinosaur news stories from *New Scientist* are at: http://www.newscientist.com/topic/dinosaurs, *Scientific* American at: http://www.scientificamerican.com/dinosaurs, The Discovery Channel at: http://news.discovery.com/animals/dinosaurs, *The New York Times* at: http://topics.nytimes.com/top/news/science/topics/dinosaurs/index.html, the *Huffington Post* at: http://www.huffingtonpost.com/news/dinosaurs/, *The Guardian* at: http://www.guardian.co.uk/science/dinosaurs, and *The Telegraph* at: http://www.telegraph.co.uk/science/dinosaurs/. News and media materials on dinosaurs are also available from the BBC at: http://www.bbc.co.uk/nature/life/Dinosaur. Watch and hear the sounds made by a model of the hadrosaur *Parasaurolophus* at: http://www.youtube.com/watch?v=lBU6zfI1b0U. Everything about pterosaurs may be found at: http://www.pterosaur.org.uk/PDB2012/ and http://pterosaur.net/, and everything on modern crocodilians at: http://crocodilian.com/cnhc/csl.html. For a mass of information about ichthyosaurs, go to: http://www.ucmp.berkeley.edu/people/motani/ichthyo/. Three-dimensional images of skulls of some dinosaurs are at: http://digimorph.org/resources/dino.phtml.

QUESTIONS FOR FUTURE RESEARCH

1 Was the evolution of dinosaurs and other Mesozoic tetrapods affected by changing continental positions, vegetation, and climate?
2 What was the effect of the end-Triassic mass extinction on the evolution of Mesozoic reptiles?
3 Did the ecological roles of large theropods differ according to time and phylogenetic position?
4 Just how active were the small theropods?
5 Are the bristles of ornithischians and the 'hairs' of pterosaurs homologous with the feathers of theropods and birds?
6 What was the full range of colours and patterns seen in the feathers of Mesozoic archosaurs?
7 Did the different clades of Cretaceous theropods divide up food and feeding modes, and what were the adaptations for each?
8 How often did theropods revert to plant-eating, why did they do this, and what were the associated anatomical changes?
9 How did dinosaurs switch between bipedal and quadrupedal posture?
10 Did dinosaurs, and other Mesozoic vertebrates, suffer an extinction at the Jurassic-Cretaceous boundary?
11 How did marine reptiles divide predatory roles, and why did different clades of ichthyosaurs, plesiosaurs, crocodilians, and mosasaurs rise and decline at different times?
12 How did turtles originate?
13 Could the giant pterosaurs fly?
14 What was the full range of crocodilian adaptation in the Mesozoic, and why have they lost so many ecological roles today?
15 What were the relative roles of the Chicxulub impact and the Deccan Trap eruptions in causing the KPg mass extinction?
16 More fine-scale, regional studies of vertebrates through well dated KPg sections are needed to pinpoint the exact patterns of decline and selectivity.

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CHAPTER 9

The Birds

Vertebrate Palaeontology, Fourth Edition. Michael J. Benton.

Companion Website: www.wiley.com/go/benton/vertebratepalaeontology

KEY QUESTIONS IN THIS CHAPTER

1 How did birds originate?
2 How are birds adapted to flight, and could *Archaeopteryx* fly?
3 Was *Archaeopteryx* really the first bird?
4 What do the new Cretaceous birds from China tell us?
5 How did the KPg mass extinction event affect birds?
6 What is the fossil and molecular evidence about the timing of the origin of modern birds?
7 What are the relationships of the major modern bird groups – and why has it proved so hard to work this out?
8 Did birds eat horses?
9 How did penguins achieve their extreme adaptations?
10 Why are songbirds so hugely diverse?

INTRODUCTION

Birds are a large group of highly successful flying vertebrates, with around 10,500 living species. The oldest bird, *Archaeopteryx* from the Late Jurassic, is known in detail on the basis of several well-preserved specimens, and extensive new finds especially in China have hugely expanded our knowledge of the first half of bird evolution, through the Late Jurassic and Cretaceous. Nonetheless, birds have delicate skeletons and finds are generally patchy. However, most living families have fossil representatives in the Cenozoic.

Birds diversified during the Cretaceous, giving rise to numerous clades that then died out either before, or during the Cretaceous-Paleogene (KPg) mass extinction. Modern bird groups may have emerged in the latest Cretaceous, but they diversified markedly in the Paleogene, and then in several phases in the Neogene, until the clade reached its current high biodiversity. Key problems remain in understanding bird phylogeny: ironically, we seem to understand as little about the relationships among living orders as among Cretaceous birds.

9.1 THE ORIGIN OF BIRDS

The major theropod subclade, Paraves, includes dromaeosaurids, troodontids, and birds, and there is currently some debate about which was actually the oldest bird, and about the relationships of these three subclades (Turner *et al*., 2012; Agnolín and Novas, 2013; Godefroit *et al*., 2013a,b; O'Connor and Zhou, 2013). Here we review the non-avian paravians, and consider the position of *Archaeopteryx* – oldest bird or not? Further, we look at the extended evolution of feathers, once thought to be uniquely avian, but now apparently widespread among theropods – or even all dinosaurs.

9.1.1 Paraves

New discoveries from China have revolutionized our understanding of maniraptoran phylogeny (see Section 8.3.4), and especially the taxa closest to birds. These are known collectively as Paraves, and there has been some dispute over the relationships of some of the Jurassic and Cretaceous finds. The Middle to Late Tiaojishan Formation and equivalents (c. 165–153 Myr) have yielded particularly important specimens (Hu *et al*., 2009; Xu *et al*., 2011; Godefroit *et al*., 2013a,b), which come very close to *Archaeopteryx*, long reckoned to be the world's first bird (see Section 9.1.3), and some of which threatened to knock *Archaeopteryx* off its perch. It has been argued that *Archaeopteryx* is no longer the most basal bird, and some of the Chinese Jurassic paravians may vie for that position (see Section 9.1.5). Alternatively, these enigmatic new taxa might be basal troodontids, returning *Archaeopteryx* to its traditional position (Turner *et al*., 2012).

Troodontids were identified first from the Late Cretaceous of North America and Mongolia (Makovicky and Norell, 2004), but the clade originated much earlier, in the Middle Jurassic. A spectacular early form is *Anchiornis* from the Tiaojishan Formation of NE China (Hu *et al*., 2009). This tiny paravian was the size of a jackdaw, with long tail and long, slender limbs. What was most spectacular was that the fossils showed extensive feathers over the arms, body and tail, which enabled the animal to glide. These feathers were sufficiently well preserved to allow a full reconstruction of their colours and patterns (see Box 9.1). Early Cretaceous troodontids include *Mei long* (Xu and Norell, 2004), preserved in three dimensions under ash beds at Lujiatun in NE China (see Box 8.5). The specimen is curled up, with its legs folded up under its body, and its head tucked under one arm, apparently in a sleeping posture as seen, for example, in ducks today.

The Late Cretaceous troodontids include *Saurornithoides* with its long slender skull (Figure 9.1(a)) and the orbits facing partly forwards, suggesting that it might have had binocular vision (Russell, 1969). The braincase is bulbous and relatively large, which has led to the interpretation of the troodontids as the most intelligent (or least stupid?) dinosaurs. The foot (Figure 9.1(b)) has three toes, of which number 3 is the longest, and these animals ran on toes 3 and 4, holding the second, sickle-clawed toe clear of the ground.

The dromaeosaurids, a family of some 30 genera from the Cretaceous worldwide, have also been identified on the basis of isolated teeth (Norell and Makovicky, 2004). The best known dromaeosaurid is *Deinonychus* from the Early Cretaceous of North America (Ostrom, 1969), a small animal about 3 m long, 1 m tall and weighing 60–75 kg (Figure 9.1(c–j)). The snout is long, and the curved sharp teeth have serrated edges, as in all other theropods, which were presumably as effective in cutting flesh as a steak knife.

Deinonychus held its backbone roughly horizontal when it was moving. At one time, bipedal dinosaurs were reconstructed in kangaroo mode, with the backbone sloping or close to vertical. There are three lines of evidence that *Deinonychus* and others adopted the posture shown here: (1) it allows the body weight to balance correctly with the centre of gravity over the hips; (2) the joints between the cervical vertebrae show that the neck curved up in a swan-like S-shape; and (3) the dorsal vertebrae bear scars on the front and back of the neural spines that are like those which in flightless birds such as the ostrich prevent flexing of the back. The tail acted as a stiff rod, probably in balancing. It is reinforced on all sides by stiff bony rods formed above from the **prezygapophyses**, normally a pair of short processes in front of the neural spine that interlock with the **postzygapophyses** of the vertebra in front, and below by the **chevrons**, separate bony elements that normally run back and down a short distance and provide attachment sites for the tail muscles. In *Deinonychus*, the prezygapophyses and chevrons have unusually long anterior rods, probably formed from ossified tendons that intertwine above and below the vertebrae. These rods did not entirely immobilize the tail because they remain separate and could slide across each other to some extent.

The arms are strong and the hands armed with deep claws on the three long fingers. Indeed, the hand is nearly half the length of the arm, a bird-like feature. The wrist of *Deinonychus* is unusually mobile and the hands could be turned in towards each other. The hand was clearly used for grasping prey and the claws for tearing at flesh.

The hindlimbs have long bird-like proportions: a short femur, long tibia and fibula, long metatarsals, and three functional toes. The astragalus has a high process that wraps around the tibia, and the calcaneum is a small block of bone firmly attached to it. The key feature of the foot is the robust second toe, which is armed with a vast sickle-shaped claw up to 120 mm long. This claw could be bent right back and then swung down, but the whole toe could bend only a short way below horizontal. This foot claw would have got in the way during walking, so it must have been held in the upright position most of the time. Ostrom's (1969) functional interpretation was based on his insight that *Deinonychus* was an active biped like a modern flightless bird that could balance readily on a single foot. The toe claw is ideal for disembowelling prey. *Deinonychus* (literally 'terrible claw') ran up to its victim with the claw held up to keep it from scraping on the ground, raised one foot, balanced and slashed with a backwards kick at its flanks causing a deep gash

BOX 9.1 THE COLOUR OF DINOSAUR FEATHERS

Some fossils may show colours. For example, dinosaur bones may be preserved white, yellow, purple, or even black. It is usually understood that these colours do not reflect the original colours of the bones, but reflect different taphonomic processes that have occurred between burial and discovery (see Section 2.3.1). Likewise, fossil feathers may show a range of colours, from white to purple, but they are mostly dull brown, or match the colour of the rock. Again, artists do not reconstruct fossil birds and theropods with drab brown plumage. There was a sensation in early 2010 when two research teams independently announced that they had unequivocal evidence for the original, living colours of dinosaur feathers.

The teams had been working on different dinosaurs from China, Zhang *et al*. (2010) on the Early Cretaceous compsognathid *Sinosauropteryx*, and Li *et al*. (2010) on the Middle–Late Jurassic paravian *Anchiornis*. These two dinosaurs represent the entire phylogenetic span of feathered dinosaurs, from the root of Coelurosauria to the transition from theropod dinosaur to bird. Both teams used the same insight (Vinther *et al*., 2008), that many, if not most, fossil feathers contain minute capsules called melanosomes. Feathers, like mammalian hairs, are composed of the flexible, plastic-like protein keratin. During early growth, as a feather emerges from its follicle in the bird's skin, colours, in the form of various proteins, such as melanin (black, brown, grey, and ginger colours), porphyrins (purples, greens), and carotenoids (reds, yellows), enter the shaft of the developing feather. Uniquely, the melanins are not distributed throughout the keratin, but are contained in discrete melanosomes, and the melanosomes show two shapes depending on the form of melanin they contain: sausage-shaped for the black/ brown/ grey form and spherical for the ginger form (illustrations (a,b)). Melanosomes are commonly preserved within the tough keratin, even in the fossils and, although they suffer shrinkage and distortion during fossilization, as shown by taphonomic experiments with modern feathers (McNamara *et al.*, 2013), the original shapes and arrangements are more-or-less preserved intact.

In their work on the feathers of *Sinosauropteryx*, Zhang *et al*. (2010) investigated the simple, tufty 'protofeathers' along the midline of the head and back, and arranged in stripes around the tail (illustration (c)). These bristles are 8–13 mm long down the back, and there are about ten per millimetre; towards the end of the tail, the bristles may be up to 40 mm long. When *Sinosauropteryx* was described (see Section 8.3.3), there was uncertainty about whether these bristles were homologous with feathers; Zhang *et al*. (2010) showed they contained melanosomes as in modern bird feathers, so that question was resolved. Further, in the bristles around the base of the tail, there were melanosomes in the dark stripes, but not in the pale stripes, suggesting colour banding. Not only that, the melanosomes were entirely of the spherical type indicating that *Sinosauropteryx* sported a regularly striped ginger and white tail.

In their study of *Anchiornis*, Li *et al*. (2010) sampled feathers from across the head, neck, wings, and body. They discovered both melanosome types, and so could reconstruct a general black base colour, enlivened with bars of white across the wings, and mixed patches of black, grey, white, and ginger over the head and neck.

Both research teams drew the same conclusions. First, feathered dinosaurs showed a wide range of colours and colour patterns, often as elaborate as in modern birds. Second, these were non-flying dinosaurs, and so the feathers must have had a function in insulation and temperature control (see Section 9.1.2), but the colours and patterns also strongly suggested a display function. Whether these dinosaurs hopped about waving their colourful heads, tails and limbs to impress potential mates or to alarm and confuse their predators cannot, of course, be said. New work in this field will expand our knowledge of colours and patterns across all major theropod and early bird groups. Further, new chemical means may be developed to detect characteristic organic or metallic components of melanins, but also of the other key colouring proteins.

Read more about the discoveries and see colour images of the fossils at: http://palaeo.gly.bris.ac.uk/melanosomes/Index.html and http://sse.royalsociety.org/2013/exhibits/prehistoric-colours/, and see video explanations of the discoveries at: http://www.youtube.com/watch?v=D2thNibmfY0 and http://www.youtube.com/watch?v=VgQ6FrEVhPo.

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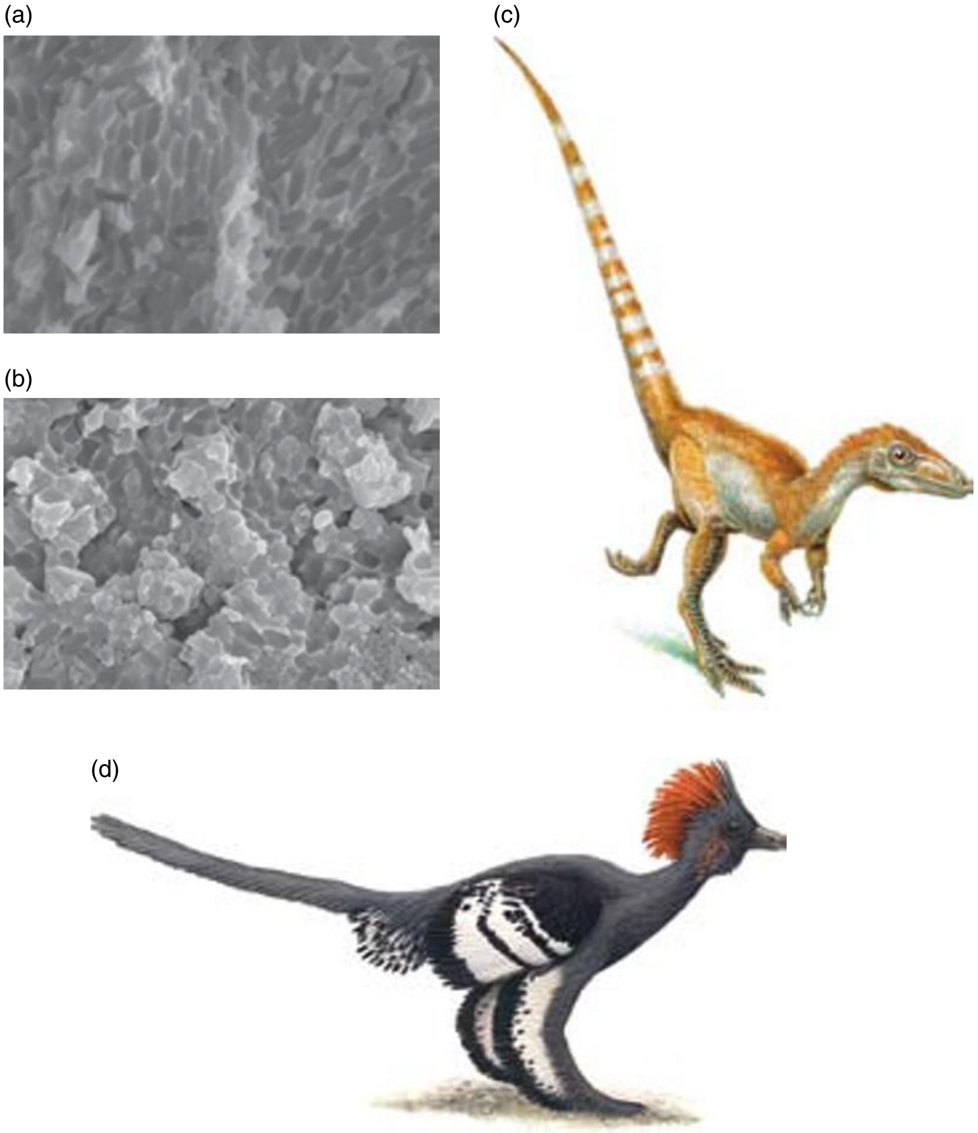

The colours of dinosaur feathers: (a,b) scanning electron microscope photographs of sausage-shaped eumelanosomes, indicating black, grey, or brown original colours (a), and of spherical phaeomelanosomes, indicating ginger colours (b); (c) reconstruction of *Sinosauropteryx*, showing the ginger and white striped tail; (d) reconstruction of *Anchiornis*, showing the black, grey, ginger, and white colour stripes and patches. See Colour plate 9.1. Source: (a,b) Zhang *et al*. (2010). Reproduced with permission from Nature Publishing Group. (c) J. Robins (artist), Bath, UK. Reproduced with permission. (d) M. DiGiorgio, Madison, CT, USA. Reproduced with permission.

up to 1 m long. The most likely prey for *Deinonychus* seems to have been the large ornithopod *Tenontosaurus*, which reached 6–7 m in length. *Deinonychus* may have hunted in packs like certain wild dogs today, which would have enabled it to harry and weaken much larger prey animals before killing them with fatal slashes to the belly region.

The unenlagiine dromaeosaurids are somewhat controversial. These are small, superficially bird-like forms, such as *Rahonavis* from the Late Cretaceous of Madagascar, which was initially described as a basalmost bird (Forster *et al*., 1998). It was later allied to other similar forms and assigned to Dromaeosauridae (Makovicky *et al*., 2005; Turner *et al*., 2012), whereas Agnolín and Novas (2013) find that the Unenlagiinae are close relatives of basal birds. *Rahonavis* has a reversed **hallux** (a backwards-pointing digit 1, the big toe) and the ulna bears small knobs, or **papillae**, for the insertion of wing feathers. *Rahonavis* was the size of a raven, and it had an enlarged claw on its second toe, perhaps used for killing prey by slashing.

The tiny dromaeosaurid *Microraptor* from the Early Cretaceous of China (Xu *et al*., 2003) shows extensive feathers over its body and limbs (Figure 9.2). There are rows of 'flight

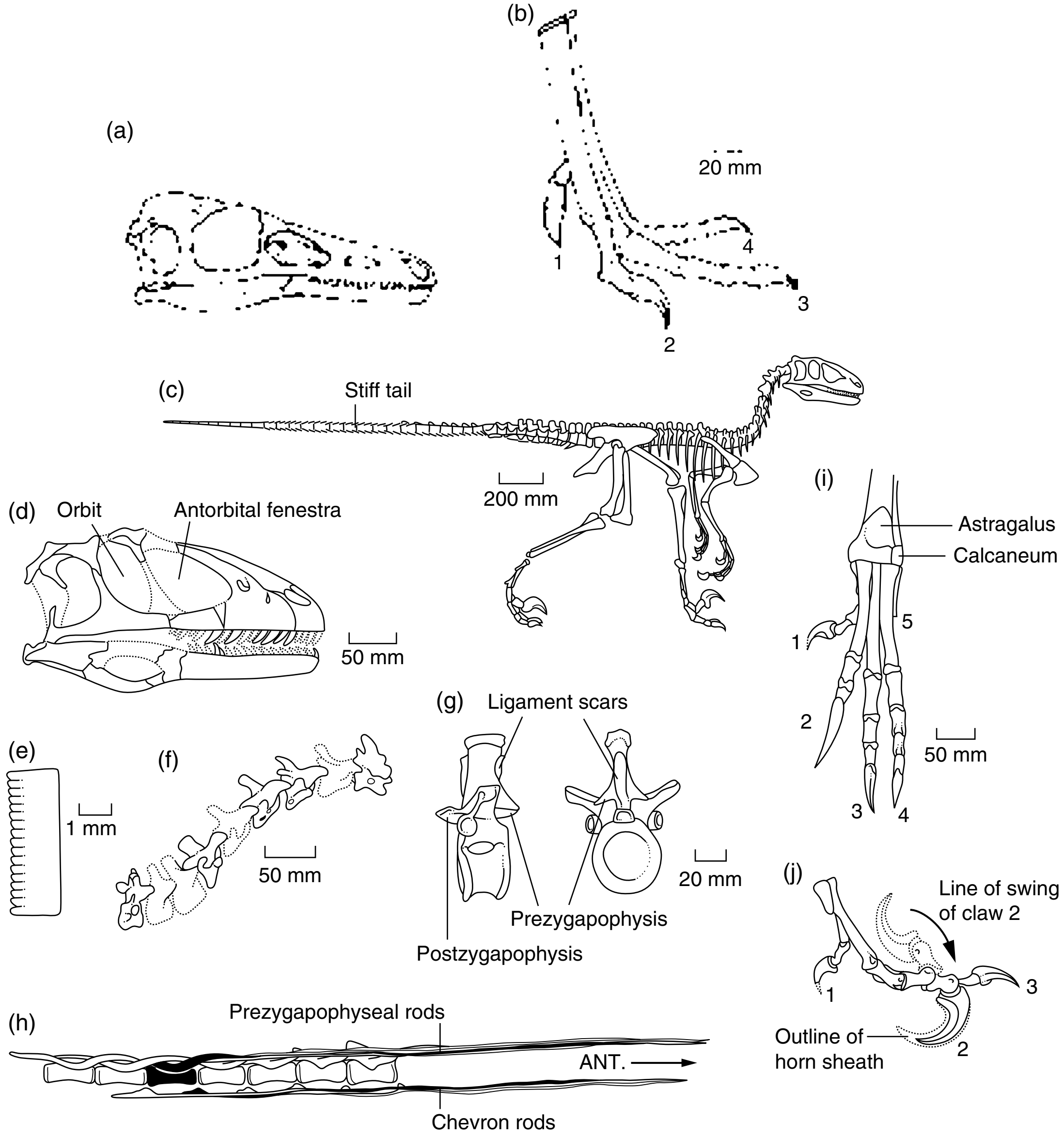

Figure 9.1 Cretaceous troodontids (a,b) and the dromaeosaurid *Deinonychus* (c–j). (a) *Saurornithoides* skull in lateral view; (b) *Troodon* foot; (c) *Deinonychus* skeleton in running pose; (d) lateral view of the skull; (e) posterior edge of a maxillary tooth, showing the serration; (f) reconstructed neck, showing the curvature; (g) a dorsal vertebra in lateral and posterior views; (h) outline of a series of caudal vertebrae, with one vertebra and its elongate prezygapophyseal rods (above) and chevron rods (below), shaded black (ANT, anterior); (i) left foot in anterior view; (j) left foot in lateral view, showing the swing of the scythe claw. Source: (a) Adapted from Russell (1969). (b) Adapted from Sternberg (1932). (c–j) Adapted from Ostrom (1969).

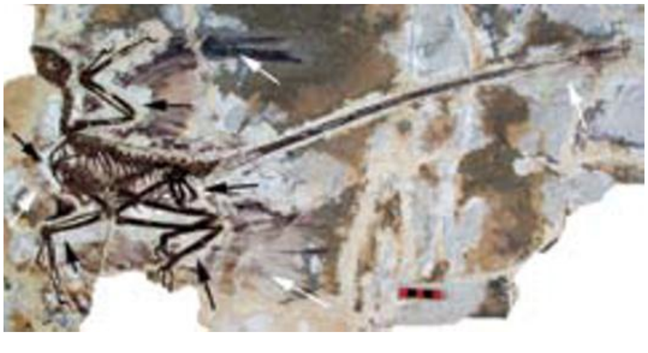

Figure 9.2 The derived dromaeosaurid *Microraptor gui* (IVPP V 13352), photographed under normal light. This shows the preserved feathers (white arrow) and the 'halo' around the specimen where they appear to be absent (black arrows). Scale bar is 50 mm. See Colour plate 9.2. Source: Z. Zhonghe, Institute for Vertebrate Paleontology and Paleoanthropology, Beijing, China. Reproduced with permission.

feathers' behind the arm bones, but also attached along the hindlimb. *Microraptor* could not perform flapping flight – the 'wings' are not large enough to support its body weight, but Xu *et al*. (2003) argue that it might have glided with all four limbs outstretched. It is likely that many of the Middle Jurassic to Early Cretaceous paravians showed flying abilities of various kinds (see Section 9.3).

9.1.2 Feathers

Feathered dinosaurs are now well known (see Figures 8.7, 9.2). When the first feathered dinosaurs from China were announced in 1996, they created a sensation. Not only did these specimens finally resolve the long-rumbling debate about whether birds originated from among theropod dinosaurs, or elsewhere (see Section 9.2.3), they then raised profound questions about the history and function of feathers. As more and more feathered dinosaurs were reported from China, including new species of tyrannosaurids, compsognathids, alvarezsaurids, therizinosaurids, troodontids, and dromaeosaurids, it became clear that simple feathers were a synapomorphy at least of Coelurosauria. Far from being unique to birds, feathers had evidently emerged much deeper in the phylogenetic tree. This raises two questions: how many dinosaurs had feathers, and what were the original functions of feathers?

It is widely accepted that feathers were present from the origin of Coelurosauria, but feather-like epidermal structures have been noted more widely among Dinosauria and even Avemetatarsalia. For example, the ornithopod *Tianyulong* and the ceratopsian *Psittacosaurus* both bore elongate bristle-like structures (Mayr *et al*., 2002; Zheng *et al*., 2009). Are these feathers, or something else? Even more distant from birds, phylogenetically speaking, the pterosaurs were also covered with short hair-like structures (see Section 8.6.2). Does this mean that all dinosaurs, or even all avemetatarsalians had feathers, and that simple whisker-like feather precursors originated in the Triassic? These questions have yet to be resolved.

Feathers come in many shapes and sizes. The most familiar kind of feather is a flight feather from the wing, a quill, with a central shaft, the **rachis**, which is hollow at the base, and a **vane** on either side. In flying birds the vanes are typically asymmetrical. Each vane is composed of lateral barbs that stick out at acute angles to the rachis, and the barbs bear fine thread-like lateral branches, the barbules, which interlock. There are in fact five main kinds of feathers in a modern bird (Figure 9.3(a)):

- bristles, composed just from the rachis
- down feathers, which consist of tufts of thin hair-like structures radiating from a basal attachment
- filoplumes, a long rachis with a tuft of fine barbs at the top
- semiplumes, which have fine barbs like a down feather, but also a rachis
- contour feathers, which are the 'typical' feathers with a rachis and stiff barbs on either side

Developmental studies (Prum and Brush, 2002) suggested a sequence for the evolution of avian feathers from reptilian scales: reptilian scale → bristle → branching feather → simple contour feather or down feather with barbs, but no barbules → contour feather with barbs and barbules → contour feather in which barbules interlock and produce a closed vane → flight feather with asymmetrical vanes.

These are not the only types of feathers: surprisingly, some of the dinosaurs from China show additional feather forms that are not seen in any living bird: elongate filaments (as in the ornithischians), elongate broad filamentous feathers (as in *Sinosauropteryx*), and proximally ribbon-like feathers (as in oviraptorosaurs and some basal birds) (Figure 9.3(b), numbers 1, 2, 7).

The feathered dinosaurs from China confirm that feathers evolved in the earliest coelurosaurs, if not earlier (Figure 9.3(b)). The first feathers, in tyrannosaurs, compsognathids, and therizinosaurids, were short filaments, perhaps located along the middle of the back and tail, or perhaps more widely over the body. They presumably had a function in insulation, and probably also in display if they were brightly patterned and coloured. Some paravians such as *Microraptor* (Figure 9.2), had flight feathers extensively along their arms and legs. Clearly, by this point, these small paravians of the Late Jurassic and Early Cretaceous were using their well-feathered forewings and hindwings in flight – presumably gliding from tree to tree.

Palaeontologists have long cautioned that, while we can perhaps reconstruct aspects of the mechanics of feeding and locomotion of ancient organisms, we shall never know the sounds they made or their colours. One of these caveats has been set aside in spectacular fashion by the recent demonstration of the colour of dinosaur feathers (see Box 9.1).

9.1.3 *Archaeopteryx* specimens and preservation

Archaeopteryx has justly been famous since its first discovery in 1860. At that time, one year after publication of Charles Darwin's 'On the Origin of Species', the new fossil seemed to be a perfect 'missing link' between the reptiles and the birds. Enthusiasts for evolution, such as Thomas Henry Huxley, used it as evidence for the new theory: here was an animal with a long bony tail, a hand with three separate clawed fingers with claws and toothy jaws (all primitive reptilian characters), but also asymmetric feathers, a **furcula** (the fused clavicles, or 'wishbone') and wings (all advanced bird characters). *Archaeopteryx* has continued to attract attention since then as it is seen as a focal animal in evolution: as we have seen, it is no longer a lone species with broad gaps on either side, but now it is one of a tightly-packed phylogenetic tree with numerous exquisitely preserved Jurassic and Cretaceous 'dino-birds' surrounding it.

Ten skeletons of *Archaeopteryx* are now known, as well as a single feather impression (Figure 9.4), all collected from the Late Jurassic limestones of Solnhofen, Bavaria. The first specimen to be found, a single feather (Figure 9.4(a)), was collected in 1860, and the first skeleton with clear feather impressions, the

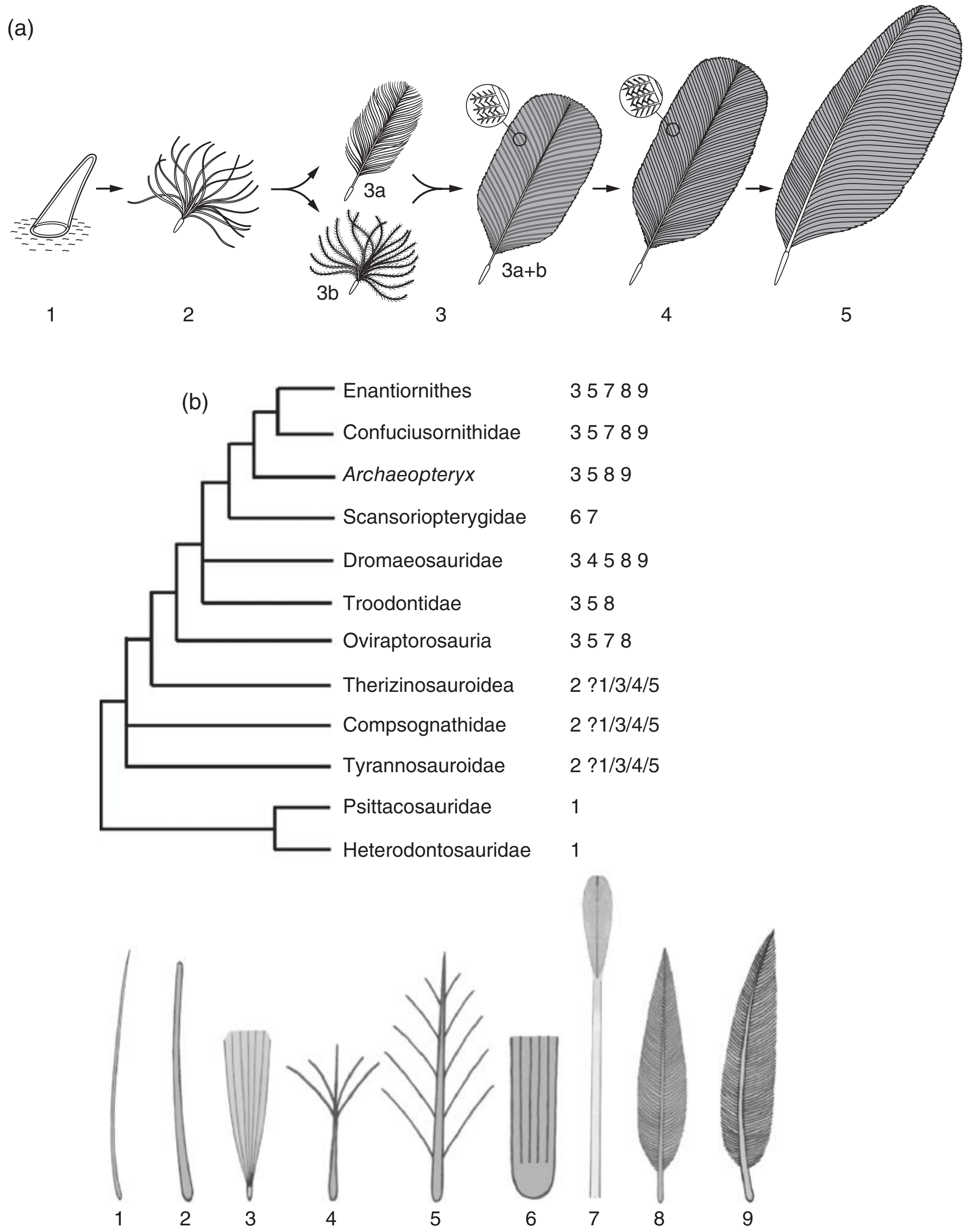

Figure 9.3 Feather evolution in theropod dinosaurs: (a) the five main feather types in modern birds; (b) simplified phylogenetic tree showing the successive appearance of nine feather morphs (1–9), illustrated below. The detail of feather types in compsognathids, tyrannosauroids, and therizinosauroids is unclear, indicated by '?'. Source: (a) Adapted from various sources. (b) X. Xing, Institute for Vertebrate Paleontology and Paleoanthropology, Beijing, China. Reproduced with permission.

London specimen (Figure 9.4(b)), was named *Archaeopteryx lithographica* in 1861. The most famous example, the Berlin specimen (Figure 9.4(d)), was found in 1877. It is a virtually complete skeleton, with the limbs and head in articulation and the feathers of the wing and tail well preserved. Eight more skeletons were described in 1951, 1956, 1970 (found in 1855), 1987, 1992, 1997, 2001, and 2004. The history of these discoveries and their interpretation is summarized by Wellnhofer (2010), and the anatomy of *Archaeopteryx* is explored by Wellnhofer (1974, 1988, 1993), Mayr *et al.* (2007), and Rauhut (2014).

One species or many? The ten skeletons vary greatly in size: the Eichstätt specimen was about 300 mm long, and the sixth (Solnhofen) specimen was 500 mm, or more, in length. Most would assign all specimens to the single original species, *Archaeopteryx lithographica*, except perhaps the sixth (Solnhofen) specimen, which Elzanowski (2001) assigned the

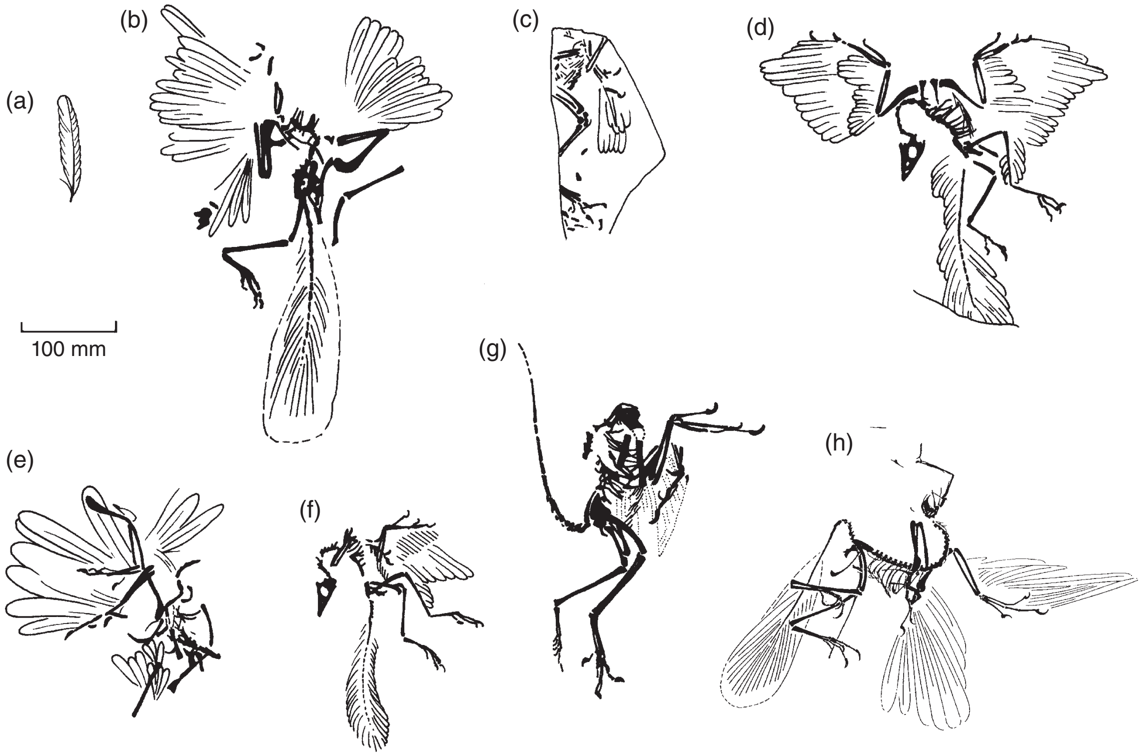

Figure 9.4 Eight of the ten specimens of *Archaeopteryx*, all drawn to the same scale, with the bones shown in black and the feathers in rough outline. The commonly used specimen names and dates of discovery are as follows: (a) Berlin/München 1860; (b) London 1861; (c) Haarlem 1855 (1970); (d) Berlin 1877; (e) Maxberg 1956; (f) Eichstätt 1951; (g) Solnhofen 1987; (h) München 1992. The eighth skeleton, reported in 1997, is in a private collection and has not been described, and the tenth skeleton is in a private museum in the United States. Source: Adapted from Wellnhofer (1988, 1993).

new genus and species, *Wellnhoferia grandis*, on the basis of its large size and differences in the numbers and proportions of bones of the hand and foot, and its short tail. In addition, others had assigned the first four specimens to additional species. However, after several statistical investigations, Bennett (2008) could find no evidence to argue that the simplest explanation for size variations among the nine specimens then available is that they form a growth series of a single species.

The skeletons of *Archaeopteryx* were found at different levels in the upper Solnhofen Lithographic Limestone (Obere Solnhofener Schiefer), a fine sediment consisting of alternating layers of pure limestone and marly limestone containing clay. The pure limestones were quarried for the manufacture of printing blocks, hence their description as lithographic limestones. The limestones were deposited in a subtropical lagoon and the fossils include marine or brackish-water forms (plankton, jellyfish, ammonites, crinoids, starfish, crustaceans, fishes), as well as terrestrial plant remains, insects, pterosaurs, crocodilians, sphenodontians, rare dinosaurs (*Compsognathus*, *Juravenator*, *Sciurimimus*) and *Archaeopteryx*.

The carcasses of *Archaeopteryx* appear to have drifted for some time at the surface, buoyed up by the gases of decomposition. Eventually, the guts burst and the carcasses sank rapidly to the bottom, where they were moved around before reaching their final resting place. Most specimens lie on their sides with all limbs and other elements in articulation. The neck is always bent firmly back as a result of the contraction of strong muscles and ligaments during preservation.

9.1.4 Anatomy of *Archaeopteryx*

Archaeopteryx is a medium-sized bird, 300–500 mm long from the tip of its snout to the end of its tail (Figure 9.5(a)), and it may have stood 250 mm tall, about the size of a common magpie. The skull (Figure 9.5(b,c)) is lightly built, and it may have been kinetic, with a movable quadrate (**streptostyly**), a bird feature paralleling that seen in lizards (see Section 8.9.2). It is not certain whether the skull of *Archaeopteryx* was as kinetic as that of living birds, which can also move their beaks up and down relative to the rest of the skull (**prokinesis** or **rhynchokinesis**). The lower jaw is narrow and robust, and both jaws bear several small widely spaced sharp teeth set in sockets.

The teeth show some derived and some primitive features. As in later birds, the teeth do not have serrated edges and there is a constriction between the root and the crown of the tooth, although these two characters evolved in parallel in some theropod clades. The seventh (Munich) specimen shows that *Archaeopteryx* had interdental plates (Figure 9.5(d)), bony projections on the inside of the jaw that extend up between the teeth, a feature shared with theropods and basal archosaurs, but absent in later birds (Wellnhofer, 1993; Rauhut, 2014). *Archaeopteryx*

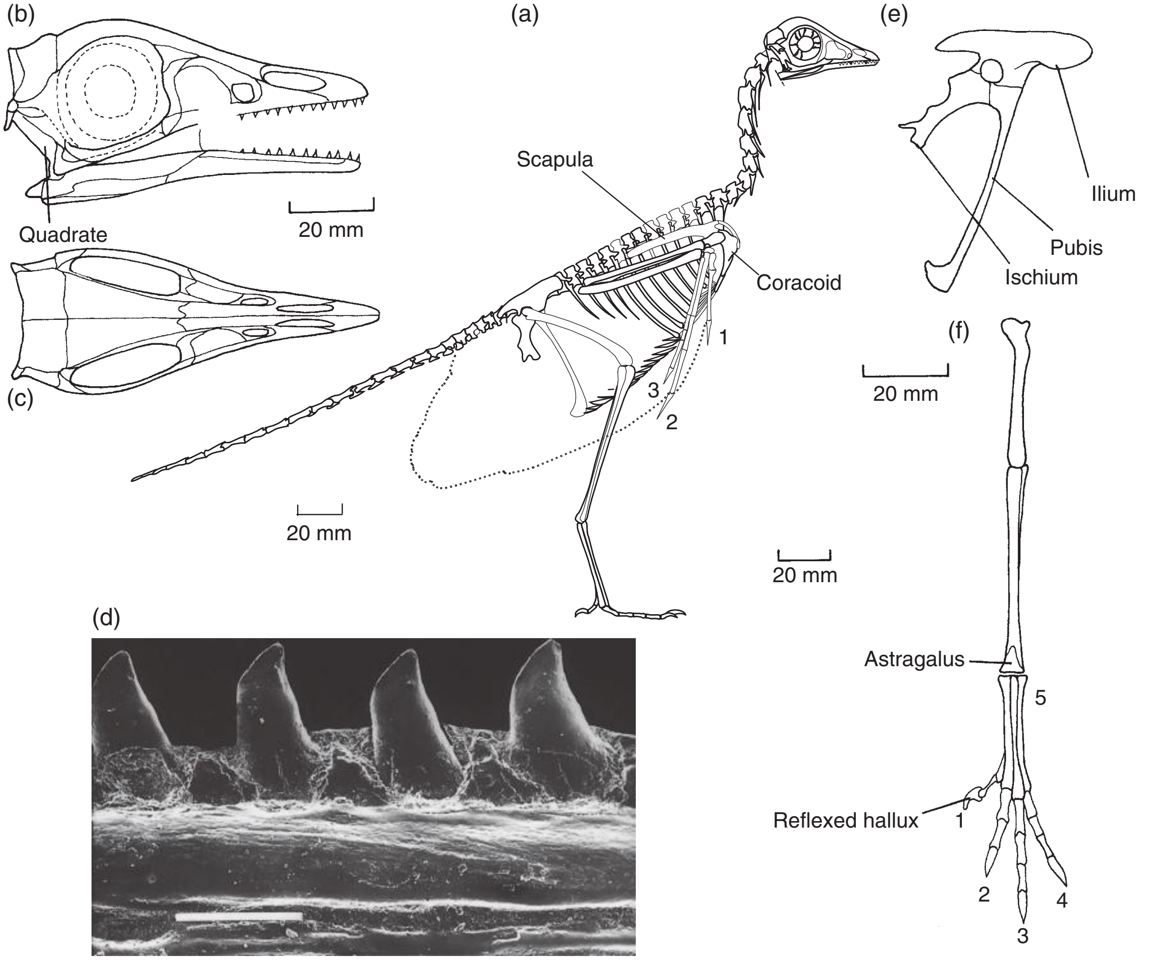

Figure 9.5 The anatomy of *Archaeopteryx*: (a) skeleton in lateral view; (b, c) skull in lateral and dorsal views; (d) right lower jaw of the seventh specimen, showing slightly recurved teeth and interdental plates (scale bar, 1 mm); (e) pelvis in lateral view; (f) hindlimb in anterior view. Source: (a) Adapted from Yalden (1984). (b,c,e) Adapted from Wellnhofer (1974). (d) P.Wellnhofer, formerly, Bayerische Staatsammlung für Paläontologie und Geologie, Munich, Germany. Reproduced with permission. (f) Adapted from Wellnhofer (1988).

had large eyes and a bird-like brain with large optic lobes, which indicates that sight was a key sensory system.

Archaeopteryx has an S-curved neck, as in theropod dinosaurs, a short back and a long straight tail with 21–22 caudal vertebrae. As in other theropods, there were air spaces inside the cervical and thoracic vertebrae, as well as in the pubis, indicating the presence of at least two of the five air sacs found in modern birds (Christiansen and Bonde, 2000). The shoulder girdle is lightly built, with a long narrow scapular blade and a short subrectangular coracoid. It was thought that the seventh (Munich) skeleton showed an ossified sternum, typical of later birds, but this turned out to be a coracoid. There are three fingers on the hand and these are greatly elongated and bear long curved claws.

The pelvis is theropodan, but there has been some controversy over its reconstruction and in particular over the orientation of the pubis, which may have run essentially vertically, as in some theropods, or backwards as in living birds and some theropods. The new specimens confirm the first view (Figure 9.5(e)). The hindlimb (Figure 9.5(f)) is also like that of small theropods: the femur is short and slightly arched, the tibia is straight and the fibula very thin, the astragalus and calcaneum are firmly attached to the ends of the tibia and fibula, there is an ascending process associated with the astragalus, the outer (5) toe is virtually lost and the inner (1) toe is short and inserts on the medial side of the tarsometatarsus, but a reflexed hallux typical of extant birds was absent. The foot could be used for climbing tree trunks, based on comparisons of the toes and claws of *Archaeopteryx* with living birds.

The specimens of *Archaeopteryx* are famous for preservation of soft(ish) tissues. All the claw bones of the hands and feet bear horn (keratin) sheaths that extend the claw length considerably. There is no trace of a horny beak. The feathers (also made from keratin, see Box 9.1) show considerable detail. There are short contour feathers over the lower neck, body, base of the tail and legs. The wings have 11 or 12 primary flight feathers attached to the hand and at least 12 secondaries attached to the ulna. These flight feathers were overlapped by long dorsal and ventral coverts, quite unlike the very short covert feathers in modern birds (Longrich *et al.*, 2012). There are enlarged feathers also along the femur and tibia in each hindlimb, and in life these spread out and provided 12% of lift, compared to 88% from the forelimb wings (Longrich, 2006). The 16–17 pairs of tail feathers attach to the caudal vertebrae, one per vertebra, from the sixth caudal backwards.

9.1.5 Paravian relationships

Until recently, the question of bird origins focused on *Archaeopteryx* and dinosaurian relatives such as *Deinonychus* and *Troodon*, and yet there have been two areas of contention or confusion. The first area of confusion has come from some scientists who did not accept that birds are dinosaurs, and sought older ancestors in the Triassic. The problem with this view has been that it was not supported by an alternative phylogenetic hypothesis, and at the same time the evidence for the paravian model has massively increased in recent years. The second area of confusion has come from creationists who focus massively on this question, and use all kinds of approaches to prove that *Archaeopteryx* is or is not a bird, the classic 'missing link'. In both cases, the massive increase in numbers of paravian taxa is often ignored. In resolving the question of the origin of birds, the phylogeny is now densely populated by dozens of taxa, and *Archaeopteryx* sits in the phylogenetic tree surrounded by a huge cacophony of little feathered paravians.

In his classic review, Ostrom (1976) catalogued dozens of similarities between the skull and postcranial skeleton of *Archaeopteryx* and those of derived theropod dinosaurs such as *Deinonychus*. Subsequent cladistic analyses (see Box 8.1) have fully supported this view and established that birds are derived theropod dinosaurs, part of the clade Paraves.

Indeed, some of the new finds from the Jurassic of China come so close to the line between bird and dinosaur that there has been debate over whether *Archaeopteryx* is a bird or not. For example, Xu *et al.* (2011), in describing the new paravian *Xiaotingia* found that *Archaeopteryx* was a deinonychosaur, closely related to *Xiaotingia* and *Anchiornis*, and not a bird. This certainly ruffled feathers, and there was a to-and-fro of papers detailing alternative analyses that kept *Archaeopteryx* on its avian perch. This view was supported in an independent study (Godefroit *et al.*, 2013a) of a new basal troodontid, *Eosinopteryx*, and *Archaeopteryx* remained as a basal deinonychosaur, neither a dromaeosaurid nor a troodontid.

A further new find, *Aurornis*, seemed to restore order (Godefroit *et al.*, 2013b), with *Archaeopteryx* switching back to Aves, but this time not as the most basal bird: *Anchiornis* and *Aurornis* lie below *Archaeopteryx* in the cladogram, more basal members of Aves. In the end, it is evident that there is little to discriminate between the different phylogenetic solutions, and new fossil finds and new anatomical study may keep this area of the phylogenetic tree fluid for some time. What ever their exact relationships, these new paravians from China have had a major influence on thinking about the origin of flight.

9.2 THE ORIGIN OF BIRD FLIGHT

Birds have wings and feathers, and they can fly. The ability to fly is fundamental and the whole bird skeleton is modified for this mode of locomotion. Flight has also modified the soft anatomy of birds, with flight muscles occupying much of the trunk, and a highly efficient metabolism and respiratory system designed to cope with the demands of fast or long-term flapping of the wings. It is essential to understand these unique attributes of birds before considering the various hypotheses for the origin of flight.

9.2.1 The flight apparatus of modern birds

In the forelimbs of modern birds (Figure 9.6), the hand and wrist elements are fused with each other, leaving essentially a single bony crank system that supports the feathers and forms the leading edge of the wing. Whereas *Archaeopteryx* has digits 1, 2 and 3 (or is it 2, 3 and 4?; see Box 9.2) present and bearing claws, the modern bird has lost the claws and retains only a splint-like remnant of metacarpal 1, metacarpal 3 is reduced to a slender element fixed to metacarpal 2, and digits 1 and 3 retain reduced phalanges. The distal carpals are fused to the metacarpals to form a simple hinge joint. The humerus has a

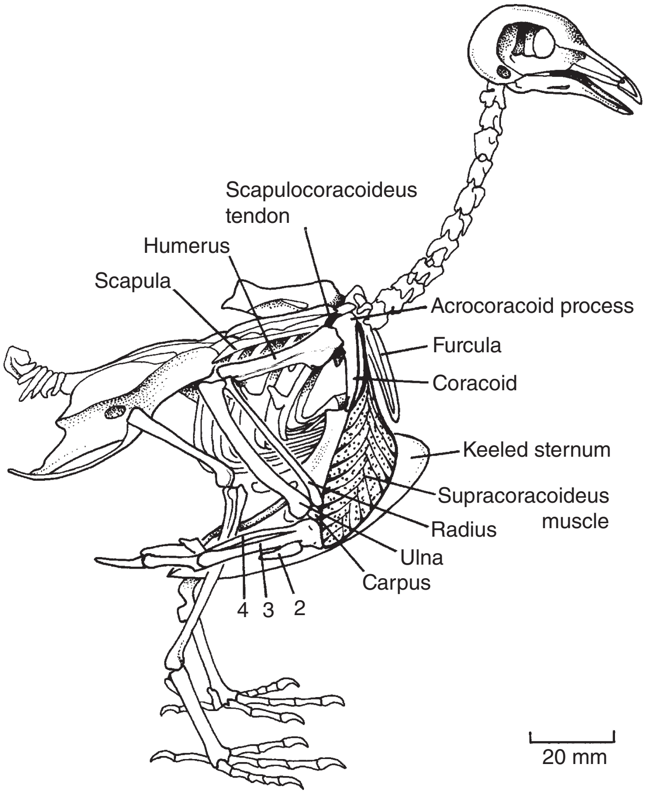

Figure 9.6 The skeleton of a typical modern bird, the pigeon *Columba*, showing the wing and the supracoracoideus muscle that raises the wing by acting over the acrocoracoid process, a pulley-like system. Source: Adapted from Young (1981) and other sources.

BOX 9.2 BIRD FINGERS: 1, 2, 3 OR 2, 3, 4?

How do you number the fingers of a bird? This may seem a bizarre question – surely modern birds don't even have fingers, or if they do, they are reduced to having almost no function? All birds, from *Archaeopteryx* onwards, have three fingers. It is clear in the evolution of theropods, that digits four and five (equivalent to our ring finger and little finger) were reduced and then lost, and that the three digits of *Deinonychus* and of *Archaeopteryx* have to be the numbered 1–3. Studies of the embryos of modern birds, however, show that all five fingers are present as cartilage condensations at an early stage of development, but that digits 1 and 5 are lost. So the three fingers of adult modern birds are 2–4. How can there have been a jump from 1–3 to 2–4 in evolution?

During development, the fourth digit condenses first in the hand and foot in all tetrapods (see Section 4.2.2), forming the primary axis, and then digit 5 develops posterior to this, and digits 1–3 form the digital arch anterior to the primary axis. In birds, digits 1 and 5 appear in cartilaginous form early in development, but are lost before ossification. The three digits that ossify are then unequivocally numbers 2–4. This mismatch between dinosaurian digits 1–3 and avian digits 2–4 has been regarded by some (e.g. Feduccia, 2002) as decisive evidence against any close relationship between the two clades.

However, new fossil and developmental evidence suggests that evolution from basal theropods to birds is not compromised (Xu and Mackem, 2013). The Jurassic ceratosaur *Limusaurus* has a reduced finger 1, hinting that the functional digits are 2,3,4, as in birds (Xu *et al*., 2009). This discovery was a surprise, as early theropods usually show reduction of fingers 5, and then 4. Xu *et al*. (2009) note, further, that the three fingers of basal tetanurans are similar in many metacarpal features to digits 2,3,4, but in phalangeal features to digits 1,2,3, of more basal theropods. So, it could be that theropods in general show the 2,3,4 pattern of birds, and not 1,2,3 as had been assumed.

An alternative, developmental solution is the frameshift hypothesis. This was proposed by Wagner and Gauthier (1999), who confirm that the fingers of *Archaeopteryx* are the theropod digits 1–3, and indeed the numbers of phalanges in each (2, 3, 4 respectively; see illustration) are the numbers seen in the first tetrapods (see Section 4.2.2). They suggest that embryologists were right to identify the initial cartilaginous condensations as numbers 2–4, but that these ossify as digits 1–3. The early loss of condensation 5 means there is no digit 5, and that is not controversial. Wagner and Gauthier (1999) argue then that condensation 1 does not appear because of an embryological constraint: if a tetrapod loses digital condensations from the hand or foot, condensation 5 goes first and then condensation 1 (this is confirmed from embryological studies of modern amphibians, lizards and mammals). But, in the evolution of theropods, ossified digit 5 was lost first (between *Herrerasaurus* and *Coelophysis*) and then digit 4 (between *Coeolophysis* and *Allosaurus*). Functionally, those two fingers were reduced and lost, but embryologically this could only have been achieved by a developmental 'frameshift': the cartilaginous precursors of digits 1–4 shifted so that precursor 1 was lost at the same time as the loss of digit 4 and precursors 1–3 ossified as digits 2–4.

Subsequent studies of gene expression patterns in hand and foot digits confirm that the first digit in birds shares expression profiles with finger 1 in mouse and alligator (which have not lost any fingers). Further, comparisons of gene expression profiles of different avian digit primordia by deep sequencing reveal close similarityacross all genes between the first digit region of the wing and the digit 1 region of the hindlimb, lending more support to the view that the first digit in the avian wing corresponds to digit 1 (Wang *et al*., 2011). Some developmental data even suggest that a 1,2,4 pattern might be possible, by deletion of the middle digit (Xu and Mackem, 2013).

Among a number of possible hypotheses for changes between theropods and birds, Xu and Mackem (2013) identify the frameshift and lateral shift hypotheses as plausible.

1 The frameshift hypothesis is that the theropod digit 1,2,3 arise from digits in positions 2,3,4, via simultaneous, complete homeotic transformations of three neighbouring digits in theropod evolution. This could be achieved by a change in the Sonic hedgehog (Shh) morphogen gradient in the limb bud (see Section 4.2.2), as Shh levels regulate both digit number and digit identity in concert during limb development. The original (Wagner and Gauthier, 1999) and modified versions (Bever *et al*., 2011) of the frameshift hypothesis differ in the timing of the frame shift: the former suggests a shift in a three-fingered hand of early tetanuran theropods and the latter in a four-fingered hand of more basal theropods.

2 The lateral shift hypothesis (Xu *et al*., 2009) accepts that the tetanuran fingers are 2,3,4, and suggests that the three functional fingers took on features that primitively characterized more medial ones in theropod evolution via three partial homeotic changes. It suggests a three-stage scenario of hand evolution in theropods: first, reduction of digits 4 and 5 near the base of Theropoda; second, reduction of digit 1 by the time of divergence between ceratosaurs and tetanurans; third, complete loss of digit 1 and reappearance of a fully functional digit 4 in early tetanuran evolution. The core proposal of the lateral shift hypothesis is that, while a frameshift took place, it was incomplete and piecemeal, so that the transformed digits retained some aspects of their original morphology.

In both models, digit 5 is lost first, then digit 4 is reduced, and then a fully formed, functional digit re-emerges in position 4. The frameshift hypothesis then sees fingers 1–3 shifting one place sideways to become fingers 2–4, whereas the lateral shift hypothesis sees fingers 2 and 3 retaining their original locations, and the re-emergence of a functional digit 4. Xu and Mackem (2013) identify **homeosis** as a key process; this is the transformation of one body part into another, generally caused by mutation of Hox genes. The frameshift hypothesis requires complete homeosis of three adjacent digits, whereas the lateral shift hypothesis requires partial homeosis occurring at different times, a process that is apparently more likely and demonstrable in modern organisms. Further palaeontological and genomic work is needed to fully unravel the fascinating story of the origin of bird fingers.

Explore the interactive media and lectures about regulatory genes at: http://www.hhmi.org/biointeractive/browse?field_bio_biointeractive_topics=23479&kw, http://www.nature.com/scitable/topicpage/hox-genes-in-development-the-hox-code-41402.

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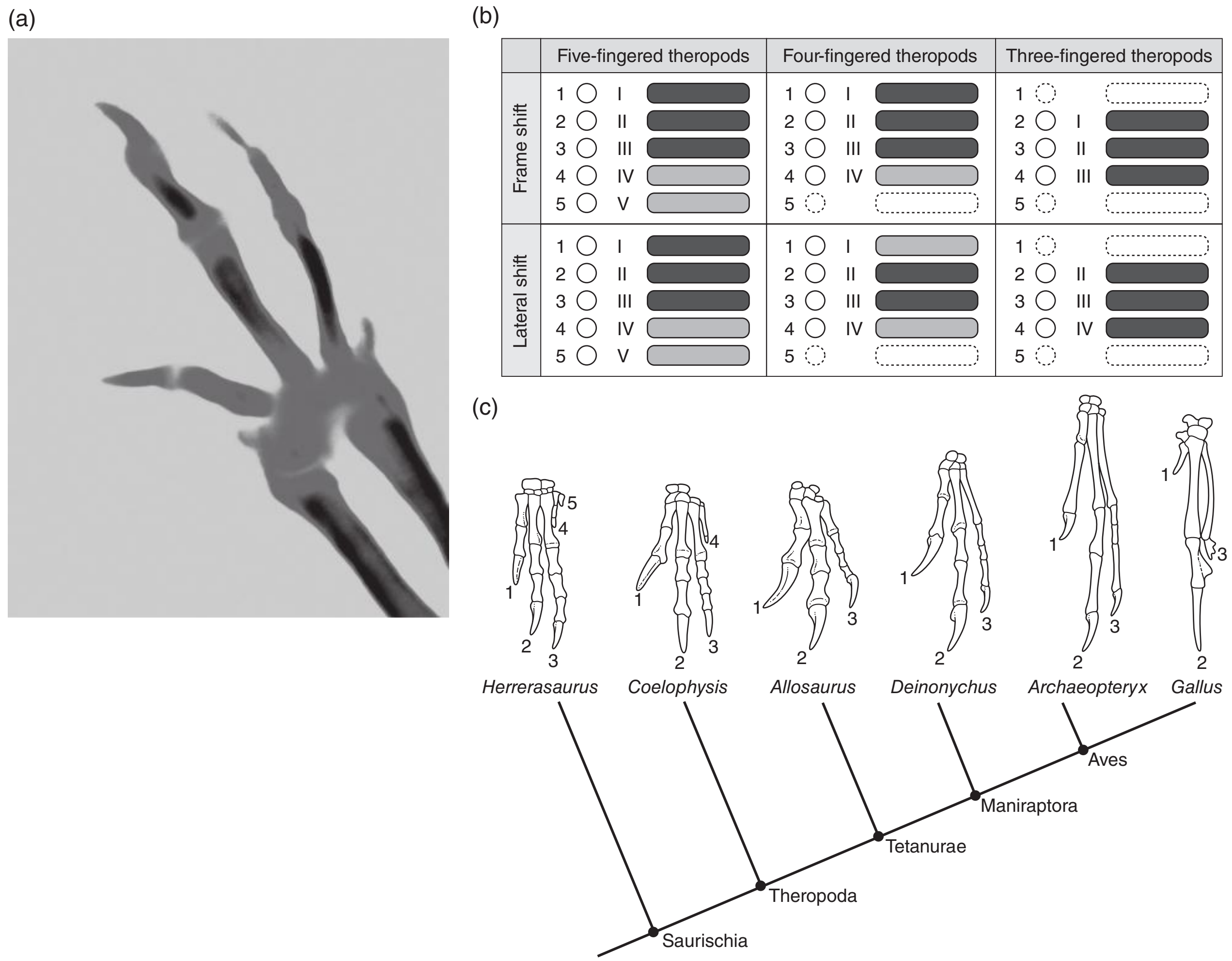


Understanding evolution and development: (a) photograph of the hand of a bird embryo, showing the presence of all five digits; (b) the frame-shift hypothesis (above), in which digits 2–4 are expressed in the adult before the shift and digits 1–3 after, and lateral shift hypothesis (below) in which digits 2–4 are expressed in the adult before the shift and digits 2–4 after, but with the lateral shift occurring at the 4-fingered stage; (c) phylogeny of theropods, showing the reduction of hand digits seen in fossils, and the implied frame shift between *Archaeopteryx* and the modern bird *Gallus*. Source: (a) A. Feduccia, formerly, University of North Carolina, Chapel Hill, NC, USA. Reproduced with permission. (b) Adapted from Xu and Mackem (2013). (c) Adapted from various sources.

well-defined bony crest at its proximal end for the attachment of flight muscles, and often a pneumatic foramen leading to an air space inside the bone.

The most dramatic modifications of the modern bird skeleton are seen in the shoulder girdle and sternum. In flying birds, there is a deep sternal keel that provides extensive areas of origin for the pectoralis muscle (downstroke) and the supracoracoideus muscle (upstroke and flight control), and these insert on the lower and upper faces of the humerus respectively. The supracoracoideus runs over the **acrocoracoid process** on the coracoid and through the **triosseal foramen** between the coracoid, scapula and furcula, a pulley-like arrangement seen also in pterosaurs (see Section 8.6.2). The sternum is a key element in the flight apparatus of modern birds, and it is stabilized by a long strut-like coracoid, very different from the squarish element in *Archaeopteryx* (Figure 9.5(a)).

9.2.2 Flight mechanics and modes in birds

There is a great deal of variation in the flight styles of modern birds. A key insight came from comparisons of wing loadings and aspect ratios (Tobalske, 2007). Wing loading is a measure of the size of the wing, and it is defined as the body weight of the bird divided by the wing area. Generally, of course, larger birds have larger wings and wing area (especially length) increases with body weight. The aspect ratio of a wing is a measure of wing shape, defined as $(\text{wingspan})^2$ divided by wing area. A high aspect ratio indicates narrow wings and a low aspect ratio indicates broad wings.

Low wing loadings (i.e. relatively large wings) are associated with lower flight speeds, improved manoeuvrability, improved soaring performance and reduced agility. High aspect ratios are associated with greater aerodynamic efficiency, whereas low aspect ratios (shorter wingspans) facilitate take-off and flight in cluttered environments, such as forests. Birds fall into four categories depending on their wing loadings and aspect ratios (Rayner, 1988), and these correspond to flying styles, which can then be predicted for extinct flyers (Wang *et al*., 2011).

1 **Marine soarers and aerial predators** (high aspect ratio and low wing loading). These are generally large birds, some of which (albatrosses, tropic birds) remain airborne for long periods, soaring on air currents to save energy, and others, the aerial predators such as swallows, gulls, falcons and kites, require manoeuvrability and endurance.

2 **Diving birds** (high aspect ratio and high wing loading). These include birds of various sizes, such as gannets, auks, some ducks and grebes, that fly, dive and (sometimes) swim underwater, but do not generally fly in cluttered habitats. Some diving birds, such as penguins, have wings lacking flight feathers, so that they cannot fly in the air.

3 **Thermal soarers** (low aspect ratio and low wing loading). These include herons, hawks, eagles, storks, vultures and the condor, a range of small to large birds. The low wing loading allows the larger birds to soar on thermals and the smaller ones to be manoeuvrable in pursuit of aerial prey, especially in forests.

4 **Poor fliers** (low aspect ratio, high wing loading). These include turkeys, peacocks, pheasants, cormorants and tinamous, birds that are generally happier on the ground. Their flight performance is poor as their wings seem to be too small for their fat bodies, although they can move about in forests and take off rapidly from the ground.

9.2.3 Flight capabilities of paravians

Could *Archaeopteryx* and the other paravians fly or not? It is important to define some terms first. By 'flight', most people mean flapping or powered flight, as seen in modern birds, bats, and insects. There are, however, other forms of flight, such as gliding and parachuting, seen much more widely, for example in flying fishes, as well as certain frogs, lizards, snakes, and mammals that have extended flaps of skin between their ribs, limbs, or toes. In all cases, the extra skin flaps allow the animals to extend the distance they can jump from tree to tree, generally to escape predators or to reach scattered food resources quickly. Parachuting forms can simply slow their rate of descent, whereas gliders travel some distance horizontally, as well as vertically.

With these definitions in mind, it is evident that the Late Jurassic and Early Cretaceous woods were full of flying paravians. All the small, feathered deinonychosaurs and avians could fly in one way or another. Some concentrated on forelimb wings, as in modern birds, but others achieved lift both fore and aft, with wings on all four limbs. Even *Archaeopteryx* may have achieved 12% of lift from flight feathers along its hindlimbs (Longrich, 2006), but *Microraptor*, famously, had full-scale wings fore and aft (Figure 9.2). The key transformations that enabled flight of any kind were miniaturization and forelimb elongation. Unlike other theropods, birds, and paravians in general, were much smaller. It is now known that this episode of miniaturization took place at the origin of Paraves, and that forelimb elongation happened at the same time, apparently very fast, as shown by a comparative phylogenetic study (Puttick *et al*., 2014).

It is challenging to understand how a four-winged paravian might have operated. It seems clear that *Microraptor* did not beat its hind wings, like some sort of giant-sized dragonfly, and all calculations indicate that the total available wing area was more suited to gliding than flapping flight (Xu *et al*., 2003). One model (Chatterjee and Templin, 2007) represented *Microraptor* like a World War I biplane, the forewings located above the hindwings in flight. Another model (Alexander *et al*., 2010) simply had the hindwings sloping downwards and backwards at different angles. When the model was launched, it glided for 15–20 m or more, at an angle of 6–8° below horizontal, a very effective boost to an animal that might have moved about in the trees. Steering would have been by raising or lowering the wings, or indeed by moving the head from side to side. An even more thorough study of a new *Microraptor* model (Dyke *et al*., 2013) using wind tunnel experiments and flight simulations, shows that sustaining a high-lift coefficient at the expense of high drag would have been the most efficient strategy for *Microraptor* when gliding from, and between, low elevations. Experiments with different wing configurations and leg positions, show that these would have made little difference to aerodynamic performance.

If the four-winged deinonychosaurs could glide, but not fly, what about *Archaeopteryx*? Most researchers had assumed that it could have engaged in powered, flapping flight, even if perhaps not as efficiently as a modern bird. Ostrom (1976), however, in his classic investigation, argued that *Archaeopteryx* could hardly fly at all because it lacks two bony elements that seem to be essential for flight in modern birds: a keeled sternum for the attachment of the pectoralis and supracoracoideus muscles, and the triosseal foramen between the coracoid, scapula and humerus.

Four lines of evidence have been presented, however, to show that *Archaeopteryx* was probably a good flyer (Rayner, 2001).

1 It has wings formed from a forelimb and feathers that are similar to those of any modern flying bird.

2 The pectoralis muscle could readily have originated from the robust furcula and from the broad coracoid, and the supracoracoideus muscle is not necessary for the recovery stroke of the wing. Bats, which are good powered fliers, have no keel on the sternum and they also lack the triosseal foramen, although they have large deltoid muscles.

3 *Archaeopteryx* has asymmetrical vanes on its feathers as in modern flying birds (flightless birds have more symmetrical feathers) and the feathers are curved. The asymmetry and the curve are necessary to allow the feathers to adjust aerodynamically to all stages of the wing beat.

4 Reconstructions of the flight muscles of *Archaeopteryx* suggest that it would have had adequate power for ground-upward takeoff and for sustained flapping flight (Elzanowski, 2002), even though the estimated mass of the pectoralis muscles was lower than in modern flying birds.

There is some evidence that *Archaeopteryx* and *Confuciusornis*, another early bird, had rather narrow rachises in their primary flight feathers. Indeed, if their flight feathers were slightly bendy, these early birds could not have had stiff enough wings to withstand the reaction against a downwards flight stroke. However, as Longrich *et al.* (2012) pointed out, *Archaeopteryx* had a different arrangement of primary and covert feathers in the wing, with multiple long coverts overlapping the primaries much more extensively than in modern birds, and so perhaps sufficiently reinforcing the wing feathers to keep them together during flight.

Nonetheless, it seems likely that *Archaeopteryx* could not have engaged in slow flight, and it was not agile or manoeuvrable in the air. It would have been capable of fast or cruising flight, because this mode requires smaller forces from the pectoralis muscles, the mechanical energy demands are less and the wing-beat geometry is simpler (Rayner, 2001). Taking off and landing would have been a problem, because slow-flying techniques are required.

In various paravians, the feathered hindlimbs must have been an impediment to running on the ground (Xu *et al*., 2003; Alexander *et al*., 2010). In a comparison of a series of paravians, Zheng *et al*. (2013a) note that the early feathered coelurosaurs such as the compsognathid *Sinocalliopteryx* merely had whiskery legs, whereas paravians such as the deinonychosaur *Anchiornis* and basal birds such as *Sapeornis* have large pennaceous feathers on their legs and feet, forming a crest-like structure. Even the enantiornithine birds (see Section 9.3.3) retained large feathers on the shin. Only later, did ornithurine birds (see Section 9.3.5) finally lose these pennaceous leg feathers. Zheng *et al*. (2013a) note that the reduction and loss of feathers on the legs reflects decoupling of the forelimbs from the hindlimbs in the locomotor system of ornithurine birds, in which the arms became specialized for flight and the legs for terrestrial locomotion.

9.2.4 Trees down or ground up?

A persistent debate has been whether birds evolved powered flight from ancestors that hopped and glided among the trees, or from running ancestors that used their wings for other purposes. These have been termed the arboreal ('trees down') and cursorial ('ground up') hypotheses (Figure 9.7).

The arboreal hypothesis is based on the older idea that *Archaeopteryx* could climb trees using the claws on its hands and feet. Maniraptoran ancestors initially leapt between branches and then, with forms such as *Microraptor*, evolved to parachute and glide between trees, or from the trees to the ground. In the end, gliding flight evolved into powered flapping flight. *Archaeopteryx* has hand claws that are well adapted for trunk climbing, and Rayner (1988, 2001) and others have presented aerodynamic arguments that gliding flight is pre-adapted for the evolution of flapping flight.

The cursorial hypothesis developed from the idea, first proposed by Baron Franz Nopcsa in 1907, and later championed by John Ostrom, that *Archaeopteryx* was essentially a small running theropod dinosaur that used its feathered wings and tail as a kind of insect-catching system. Caple *et al.* (1983) presented an aerodynamic model in which the bird ancestors leapt into the air in pursuit of insect prey. Feathers and wings assisted and extended their leaps until eventually true powered flight evolved. A modification to the cursorial model that has gained traction is termed wing-assisted incline running (WAIR), based on the observation that some living birds ascend steeply inclined, vertical, and even slight overhanging surfaces with the aid of a powerful flight stroke (Dial, 2003; Baier *et al*., 2013).

The arboreal and cursorial models are debated. In favour of the arboreal model, it has been noted (Xu *et al*., 2003; Zheng *et al*., 2013a) that the feathered hindlimbs of *Microraptor*, *Archaeopteryx*, and other paravians suggest poor running ability. Further, the diversity of Jurassic to Cretaceous paravians that were evidently gliding and parachuting and experimenting with flight suggests life in trees by analogy with all modern gliding tetrapods. So far as is known, all the parachuting and gliding frogs, lizards, snakes, and mammals are arboreal and their gliding is to enhance their locomotion from tree to tree and tree to

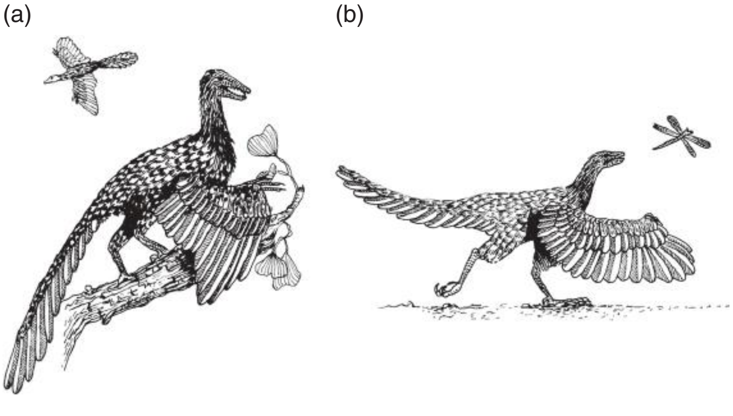


Figure 9.7 Two models for the origins of flight: (a) *Archaeopteryx* as a tree-dweller that flew from branch to branch and (b) as a ground-dweller that leapt up to catch insects. Source: Adapted from Rayner (1988).

ground. If powered flight evolved from gliding, then all modern examples of gliders suggest that flight arose from the trees down.

Contrary evidence came from a comparison of morphological correlates of climbing and running (Dececchi and Larsson, 2011) in which the small, feathered deinonychosaurs and *Archaeopteryx* consistently clustered with fully terrestrial extant mammals and ground-based birds. This was queried by Birn-Jeffrey *et al.* (2012), who found that claw shapes confirmed the traditional view that *Microraptor* was a climber and a percher, that *Anchiornis* might have been a percher, and that *Archaeopteryx* showed a mix of arboreal and ground-dwelling features. A problem in such studies may be that the bony claw, usually all that is found in the fossils, provides some information, but the true massive curvature in tree-climbers is seen only when the horny outer sheath of the claw bone is measured, and such studies indicate that *Microraptor*, *Archaeopteryx*, and other feathered paravians had climbing adaptations (Burnham *et al.*, 2011).

9.3 CRETACEOUS BIRDS, WITH AND WITHOUT TEETH

Until 1990, there was a long gap in the fossil record of birds between *Archaeopteryx*, dated at 150 Myr ago, and *Hesperornis* and *Ichthyornis* from the Late Cretaceous of North America, dated at 90–65 Myr ago. This time span represents the first half of the history of birds, and it was embarrassing that so little was known. New discoveries from the Early Cretaceous of China, Mongolia, Spain and other parts of the world have helped to fill this gap, and they have revealed the existence of several unique Cretaceous bird lineages, and especially, the radiation of a diverse group, the Enantiornithes.

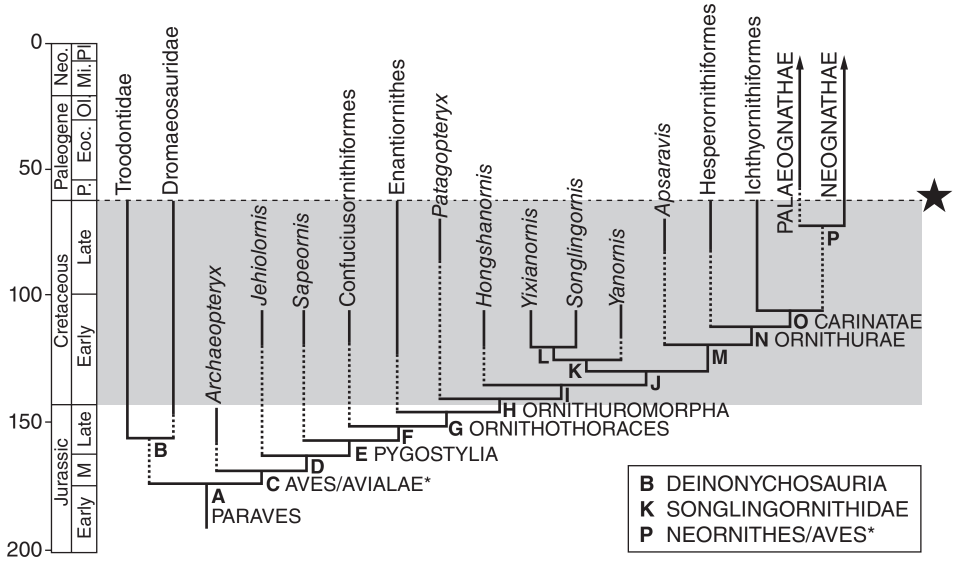
The new discoveries have added many new branches and twigs to the phylogenetic tree of basal birds (see Box 9.3). The relationships of Cretaceous birds have been confirmed in recent cladistic analyses (e.g. Turner *et al.*, 2012; O'Connor and Zhou,

BOX 9.3 RELATIONSHIPS OF THE BASAL BIRDS

Archaeopteryx is the basal bird, the sister group of some long-tailed basal forms such as *Jeholornis* and *Sapeornis*, and the Pygostylia (Turner *et al*., 2012; O'Connor and Zhou, 2013), which includes all other birds (see cladogram). The Pygostylia, consisting of the Confuciusornithiformes and the Ornithothoraces, share the pygostyle (fused caudal vertebrae) and a backwards-pointing pubis. Ornithothoraces comprises Enantiornithes and Euornithes. The major Cretaceous clade Enantiornithes is diagnosed by features of the limb elements, and it shares a number of typical avian characters with more derived forms, the Ornithuromorpha.

The Ornithuromorpha comprises a number of Early and Late Cretaceous lineages, including *Patagopteryx*, *Hongshanornis*, Songlingornithidae, and *Apsaravis*, among others, all showing the acquisition of features of modern birds. The Ornithurae includes hesperornithiforms, ichthyornithiforms and Neornithes, the modern groups (Turner *et al*., 2012; O'Connor and Zhou, 2013). These are all diagnosed by a pointed orbital process of the quadrate (see Figure 9.12(c)), a shortened back and pelvic elements that run back almost in parallel (see Figure 9.12(a)). *Ichthyornis* shares features of the hand with modern birds. Modern birds, termed the Neornithes (illustration I) are distinguished from the extinct groups by further derived characters, including loss of teeth and a pneumatic foramen in the humerus that provides access to an air space inside the bone. The air spaces in some major bones both reduce weight and provide air storage spaces so that the efficiency of respiration is improved.

Modern birds fall into two clades, the Palaeognathae, flightless ratites and tinamous, and the Neognathae, all other flying birds. The palaeognathous palate (illustration II(a)) has a large vomer firmly attached to the pterygoid, no joint between the pterygoid and the palatine, and a movable joint between the pterygoid and the base of the braincase. The 'neognathous palate' (illustration II(b)) is more loosely constructed and more mobile. The vomers are reduced or lost completely, there is a movable joint between the palatine and the pterygoid and the pterygoid/ braincase joint has been lost.



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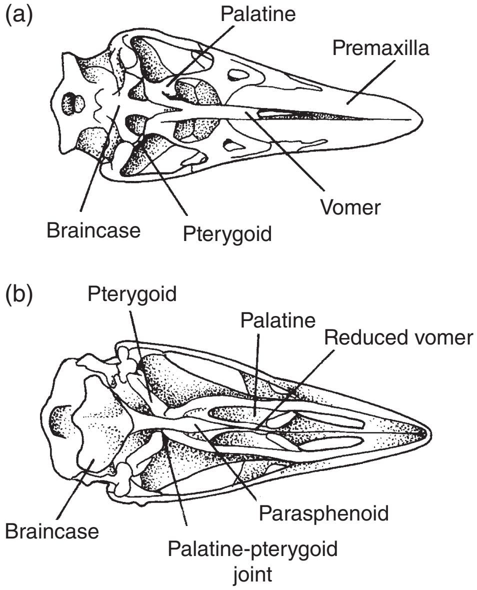
(I) Cladogram showing the postulated relationships of the major groups of birds, based on O'Connor and Zhou (2013), with additional characters from Turner *et al*. (2012). For the location of birds among theropod dinosaurs, see Box 8.1, and for the phylogeny of Neognathae, see Box 9.5. Asterisks (*) indicate alternate usages of the same name. Synapomorphies: **A PARAVES**, large dentary and maxillary teeth, triangular subglenoid fossa in coracoid, humerus longer than scapula, calcaneum and astragalus fused to each other but not to tibia; **B DEINONYCHOSAURIA**, pterygoid flange well developed, nutirient foramina in deep groove on dentary, large surangular foramen, digit IV of the foot much longer than II and only slightly shorter than III; **C AVES/ AVIALAE***, symmetric vaned feathers on forelimb, parietals separate, lateral border of quadrate shaft straight, thoracic vertebral centra approximately equal in length and midpoint width, preacetabular portion of ilium markedly longer (more than 2/3 of total ilium length) than postacetabular part, metatarsal I articulates with the medial surface of metatarsal II at the distal end, ulna/femoral length ratio equal to or greater than one, ratio of femur to humerus less than 1; **D**, six to seven sacral vertebrae, semilunate carpal and metacarpals exhibit incomplete proximal fusion, obturator process of ischium absent, fibula is short and not in contact with proximal tarsals, distal end of astragalus and calcaneum form distinct condyles separated by a prominent tendoneal groove on the anterior surface, distal tarsals fuse to the metatarsals forming a tarsometatarsus; **E PYGOSTYLIA**, dentary subtriangular in lateral view, symphyseal foramina present at the mandibular symphysis, Meckelian groove covered by splenial and not exposed, abbreviated tail with fewer than eight free caudal vertebrae, distal caudal vertebrae are fused into a pygostyle, proximo-posterior surface of deltopectoral crest of humerus is concave, distal condyles are developed on anterior surface of the humerus, pubic boot absent in with no anteroposterior projections; **F**, cervico-thoracic vertebrae have prominent ventral processes, metatarsal II tubercle at about the centre of the proximodorsal surface; **G ORNITHOTHORACES**, pneumatic quadrate, posterior mandibular fenestra absent, 11–12 thoracic vertebrae, thoracic vertebrae laterally excavated, scapula articulating below the shoulder end on coracoid, supracoracoidal nerve foramen displaced medially, interclavicular angle less than 70°, rostral margin of sternum broad and rounded, semilunate ridge on dorsal condyle of ulna, condyles of the tibiotarsus equal in cranial projection, alula present; **H ORNITHUROMORPHA**, curved scapular shaft, shelf-like articular surface on alular metacarpal for alular digit, alular digit short, cnemial crests on tibiotarsus; **I**, procoracoid process present on coracoid, phalanx 1 of hand digit II is strongly dorsoventrally compressed, condyles of tibiotarsus are approximately equal in mediolateral width; **J**, dentary with subparallel dorsal and ventral edges, preacetabular part of ilium roughly as long as the postacetabular part, anterior end of ilium gently rounded or straight; **K SONGLINGORNITHIDAE**, cervical vertebrae not completely heterocoelous; coracoid without groove at medial opening of n. supracoracoideus foramen; medial posterior process of sternum joined to sternal midline to enclose a sternal fenestra; base of furcula with a truncate or squared base; **L**, uncertain; **M**, cervical and anterior trunk vertebrae at least partially heterocoelous, ten or more sacral vertebrae, pubes compressed mediolaterally, pubes not contact each other distally, tarsometatarsus bears a distinct, well-developed, and globose intercotylar eminence, metatarsal I is absent; **N ORNITHURAE**, anterior trunk vertebrae have large hypapophyses, acromion margin of scapula is laterally everted, humerus has a brachial fossa developed as a flat scar or as a scarred fossa, demarcation of muscle origins on dorsal edge of the distal humerus as pit-shaped scars or scar-bearing tubercles or facets, ulnare is V-shaped with well-developed dorsal and ventral rami, tibiotarsal condyles bear an extensor canal present as an emarginated groove, two proximal vascular foramina on the tarsometatarsus, distal plantar surface of metatarsal II possesses a fossa (in the form of a shallow notch) for metatarsal I; **O CARINATAE**, thoracic vertebrae completely heterocoelous, alular metacarpal bears an extensor process equal in size to the width of the articular facet, distal tarsometatarsus shows metatatarsal II slightly displaced with respect to III and IV; **P NEORNITHES/ AVES***, teeth absent, dentaries fused anteriorly, 11 or more sacral vertebrae, pneumatized coracoid, pneumatic fossa and foramen in humerus, projected surface or grooves on proximoposterior surface of tarsometatarsus. [Traditional clade terms are indicated, with *Archaeopteryx* accepted as the oldest bird, basal member of Aves. If crown-clade terminology is used, Aves replaces Neornithes, and earlier birds are all members of clade Avialae.] Abbreviations: Eoc, Eocene; Mi, Miocene; Mid, Middle; Neo, Neogene; Ol, Oligocene; P, Paleocene; Pl, Pliocene/Pleistocene. Dashed lines and star symbols indicate extinction events.



(II) The (a) palaeognathous and (b) neognathous palates, from a cassowary and a bronze turkey respectively. Source: Adapted from various sources.

2013), which confirm a series of basal forms, known mainly from China, then the major clades Confuciusornithiformes and Enantiornithes, followed by a sequence of Chinese and South American forms before the split of the classic North American Hesperornithiformes and Ichthyornithiformes, and the crown-clade modern bird groups. This succession of taxa documents the transition from *Archaeopteryx* to modern birds through the loss of teeth, reduction of the bony tail to a pygostyle, and continuing lightening of the skeleton, improvements in wing mechanics, and enhancement of brain and senses.

9.3.1 Tails and pygostyles of Early Cretaceous birds

Several basal birds from the Early Cretaceous of China document the reduction of the long bony tail to a reduced stump, the pygostyle, a feature of the clade Pygostylia. *Jeholornis* and *Sapeornis* show the transition: Turner *et al.* (2012) find *Sapeornis* is most basal within Pygostylia, whereas O'Connor and Zhou (2013) find it is more derived, and this latter view confirms a one-way switch from the long bony tail of theropods to the snub, shortened bony tail of modern birds.

Jeholornis (Zhou and Zhang, 2002) from the Early Cretaceous Jehol Group of China (see Box 9.4) was about the size of a pheasant, up to 80 cm long (Figure 9.8(a)). It has three teeth in the lower jaw, but few, or no teeth in the upper jaw. Further, it has a long bony tail, longer than in *Archaeopteryx*, and this was embellished with two distinct sets of feathers, one near the base (the usual avian tail fan), and an additional frond of feathers at the tip of the tail (O'Connor *et al.*, 2013). The proximal fan and distal frond may have generated lift in flight, but also probably functioned in display. *Jeholornis* also shows advances in the structure of the hand and shoulder region, perhaps indicating improved flying ability. One specimen preserves over 50 seeds in the crop area, direct evidence of diet. A similar form, *Jixiangornis* has been synonymized with *Jeholornis* by some (e.g. Zhou and Zhang, 2006), but equally emphatically retained as a distinct taxon (e.g. Turner *et al.*, 2012) based on differences in the vertebrae and limb bones.

One remarkable find shows eggs maturing within the ovary of a female *Jeholornis* (Zheng *et al.*, 2013b). The specimen shows about 20 ovarian follicles, 7–9 mm in diameter, in a cluster just below the vertebral column and in front of the pelvis, the location of the ovary in modern birds. These appear to be on the left side of the animal, which is more convincingly seen in two enantiornithine specimens, also with ovarian follicles preserved. Zheng *et al.* (2013b) suggest that these basal birds already showed advanced avian reproductive behaviour, having perhaps lost the right oviduct, to save weight for flight, and perhaps laying eggs daily, as modern birds do, rather than in a single mass, as crocodiles do.

Sapeornis (Zhou and Zhang, 2003) has only a few teeth at the front of its jaws (Figure 9.8(b)). Its hands are much reduced when compared to *Archaeopteryx*, with the outer two fingers with two phalanges, and the middle finger with three, and a well fused carpometacarpus. The tail is reduced to a pygostyle comprising at least four fused caudal vertebrae. One species, *Sapeornis chaoyangensis*, was the largest Jehol bird, 50 cm long, but with the relatively huge wingspan of 1.4 m. *S. chaoyangensis* was as large as a buzzard, and its long, pointed wings suggest it was a soaring bird that hunted on the wing.

BOX 9.4 IMPACT OF THE JEHOL BIRDS

The birds and feathered dinosaurs from north-east China are well known, and they have surely revolutionized our understanding of paravian and bird evolution. The first reports of spectacular bird fossils from Liaoning Province in north-east China emerged in 1984. Farmers and school children had excavated specimens from limestone quarries in their fields and these were sent piecemeal to palaeontologists in Beijing and Nanjing. More concentrated researches began in the 1990s and so far some 25 genera of birds have been described (Zhou and Zhang, 2006; Li *et al.*, 2010).

The fossiliferous horizons are in the Dabeigou, Yixian and Jiufotang formations of the Jehol Group, some 2600 m of sediments, and bird fossils have come from all levels through the succession. Early workers suggested these beds might be Late Jurassic in age, but radiometric dating and biostratigraphy show they are Early Cretaceous (late Hauterivian to early Aptian, 131–120 Myr ago). Most birds come from the Yixian and Jiufotang formations.

The fine limestones, laid down by slow accumulation of sediments in ancient lakes, have produced rich floras and faunas (Zhou *et al.*, 2003). The flora is dominated by conifers, and many other groups, including angiosperms, are represented by leaves, flowers, fruits, stems and roots. Invertebrates include insects (mayflies, dragonflies, cockroaches, bugs, flies), spiders, ostracods, conchostracans, crayfish, bivalves and gastropods. Other than birds, the vertebrates include bony fishes, frogs, salamanders, turtles, choristoderes, lizards, pterosaurs and dinosaurs, including the feathered theropods (see Box 9.1 and Figure 9.2), the ceratopsian *Psittacosaurus* (see Box 8.5), and mammals (see Section 10.3.1).

Some of the vertebrates from the Jehol Group are **relicts**, late-surviving members of groups that had died out much earlier elsewhere, such as *Sinosauropteryx* (close relative of *Composgnathus* from the Late Jurassic of Germany) and an anurognathid pterosaur (otherwise known also only from the Late Jurassic). In addition, some of the plants, fishes, turtles, the psittacosaurid dinosaurs and the confuciusornithiform birds are also unique to eastern Asia.

What has been the impact of these discoveries on our understanding of dinosaurian and bird evolution? Surprisingly, despite finds of dozens of new dinosaurs, most species belong to existing families. The real impact has been among paravians and especially birds, where numerous finds have filled large and small gaps in the phylogeny. The birds include basal, long-tailed forms, confuciusornithiforms (a major unique group), and enantiornithines, and together these have effectively doubled our knowledge of Cretaceous birds worldwide. Paravians such as *Microraptor* and *Anchiornis* have shed substantial new light on the closest relatives of birds and on the origins of flight. The Jehol theropods have been a major new find.

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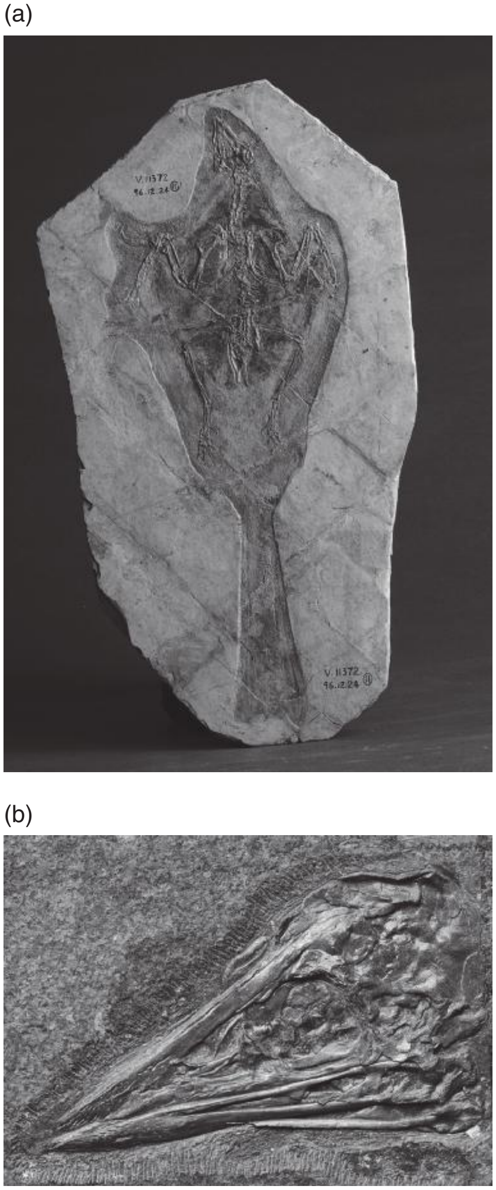


The Early Cretaceous bird *Confuciusornis*: (a) complete (?) male specimen, with long tail; (b) lateral view of the skull. Source: Z. Zhonghe, Institute for Vertebrate Paleontology and Paleoanthropology, Beijing, China. Reproduced with permission.

9.3.2 Confuciusornithiformes: toothless birds from China

The confuciusornithiforms, comprising seven species and four genera, are basal pygostylians (Chiappe *et al*., 1999; Zhou and Zhang, 2006; Zhang *et al*., 2008). Specimens were first reported in 1995 and ever more material is being found in the spectacular Jehol deposits of China (see Box 9.4). *Confuciusornis* was about the size of a rook and it is known from thousands of specimens; *Changchengornis* was starling-sized. *Jinzhouornis* is known from two species that differ little from *Confuciusornis*, and may be the same. *Eoconfuciusornis* is up to 11 Myr older and shows transitional features (Zhang *et al*., 2008). For example, the sternum seems to be fused (in earlier paravians there are two distinct sternal plates), but there is no midline sternal crest, as seen in later birds. The sternal crest is a key feature of modern birds, providing a substantial area for attachment of the flight muscles (see Section 9.2.1).

Confuciusornithiforms (Figure 9.9(a)) have no teeth and they have a horn beak (probably absent in *Archaeopteryx*). The nostril is large and only separated from the antorbital fenestra by a thin bar of bone composed of the nasal and maxilla. The antorbital fenestra in turn is separated from the huge round orbit by only a thin boomerang-shaped lacrimal. The temporal openings appear primitive, with the jugal and postorbital bar in close contact, preventing cranial kinesis. The quadratojugal is much reduced and the quadrate appears to be streptostylic. The lower jaw is slender, with a downturned pointed tip and a large mandibular fenestra.

In the skeleton, the confuciusornithiform sacrum is composed of seven fused vertebrae, and it can be termed a

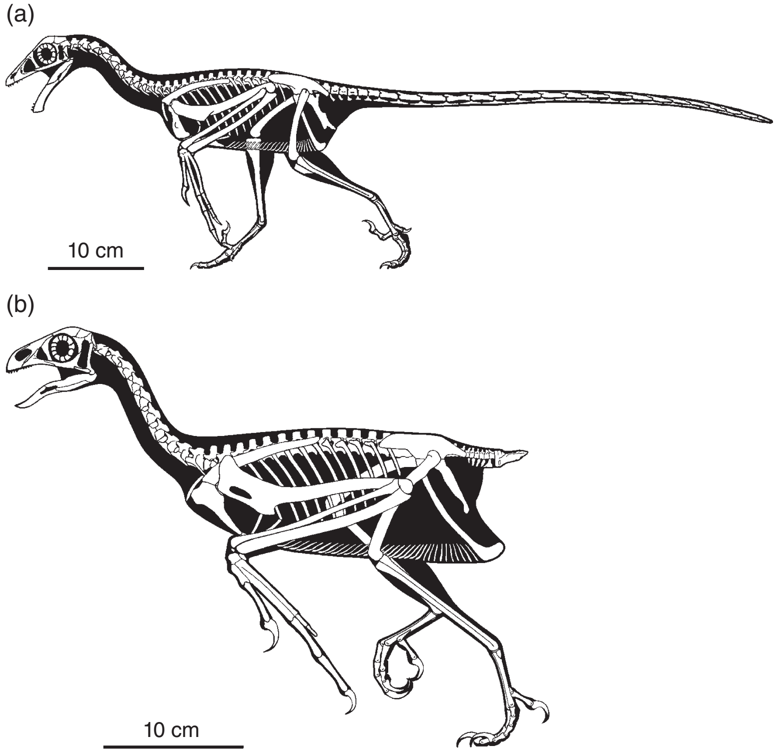


Figure 9.8 Skeletal reconstructions of basal birds from the Early Cretaceous: (a) *Jeholornis*; (b) *Sapeornis*. Source: S. Hartman (artist), Wisconsin, USA. Reproduced with permission.

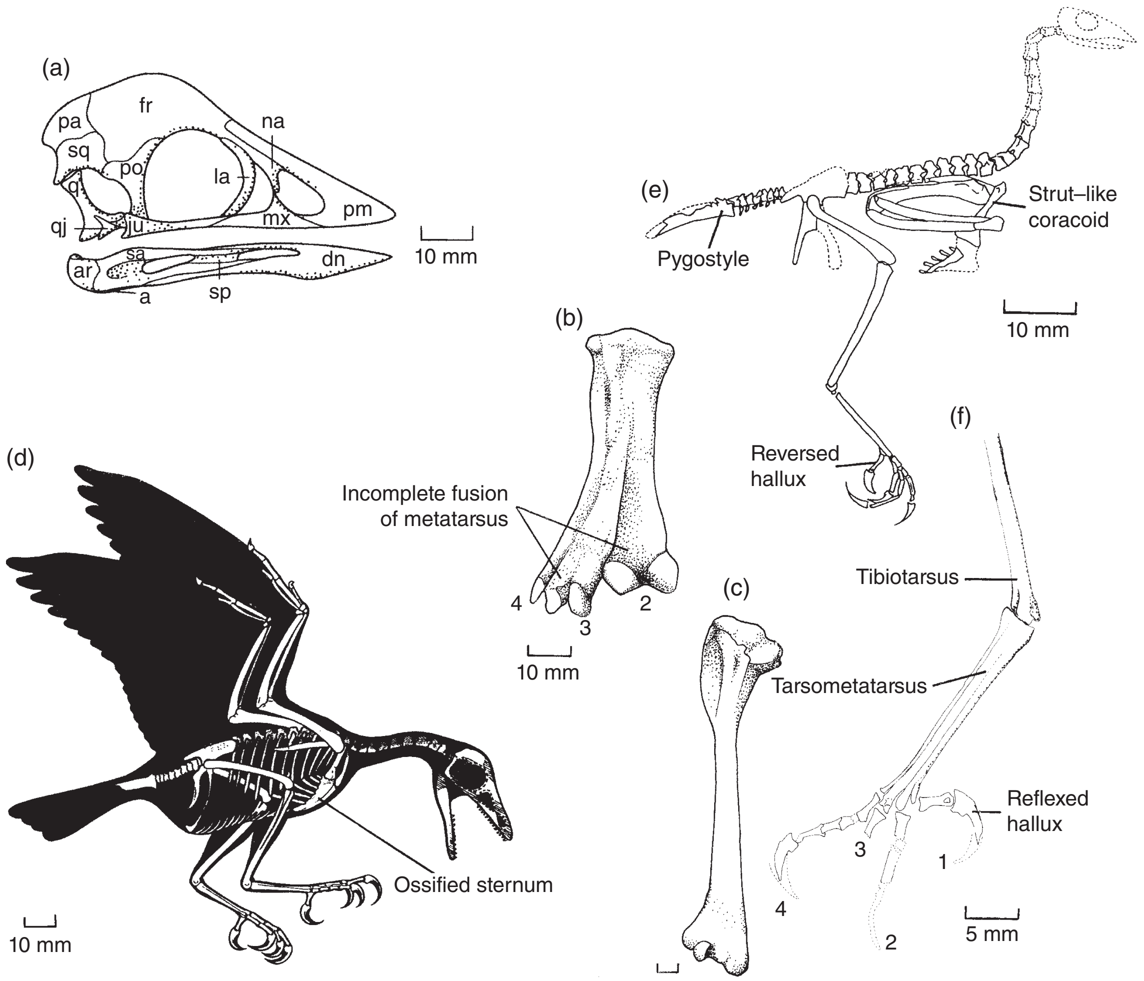


Figure 9.9 Basal birds from the Cretaceous: (a) skull of the confuciusornithiform *Confuciusornis* from the Early Cretaceous of China; (b) tarsometatarsus of *Yungavolucris* from the Late Cretaceous of Argentina; (c) humerus of an unidentified enantiornithine from the Late Cretaceous of Argentina; (d) reconstructed skeleton of *Sinornis* from the Early Cretaceous of China; (e) *Iberomesornis* from the Early Cretaceous of Spain, reconstructed skeleton; (f) hindlimb of *Concornis* from the Early Cretaceous of Spain. Source: (a) Z. Zhonghe, Institute for Vertebrate Paleontology and Paleoanthropology, Beijing. Reproduced with permission. (b,c) Adapted from Chiappe and Walker (2002). (d) P. Sereno, Field Museum of Natural History, Chicago, IL, USA. Reproduced with permission. (e,f) Adapted from Sanz et al. (2002).

synsacrum. The tail is also much modified, forming a **pygostyle**, the bony element formed from fused caudal vertebrae, eight or nine in the case of confuciusornithiforms. *Confuciusornis* may have been a slightly better flyer than *Archaeopteryx*: it has a somewhat larger sternum with a slight keel and the wrist was more flexible, useful in flexing (folding) the wing for the recovery stroke. The wing also retains three long fingers with claws, presumably used in climbing. The pelvis and hindlimb are also like those of *Archaeopteryx*.

Most spectacular of course are the feathers. These are exquisitely preserved in all specimens (see Boxes 9.1, 9.4) and show short feathers over the neck, body, upper legs, the front of the wings and the top of the tail. Long flight feathers extend behind the wings. The tail feathers are most extraordinary, being generally short and radiating like a fan from the pygostyle, but these are primitive contour feathers, not a fan of retricial feathers as in modern birds. But half the specimens, perhaps males, have two extremely elongated tail feathers, each longer than the body and forming dramatic pennants that may have been used as display structures. Statistical study shows two size classes, and it might be assumed that these represent males and females; however, there is not a clear correlation between these size classes and the presence or absence of tail feathers (Marugán-Lobón *et al*., 2011). Proof of gender came from the discovery of medullary bone in a *Confuciusornis* specimen without elongate tail feathers (Chinsamy *et al*., 2013); medullary bone is unique to reproductively active females, and it is deposited as spongy tissue on the walls of the medullary cavity in the centre of the bone for retrieval of calcium to construct eggshells.

9.3.3 Enantiornithes: most diverse Cretaceous bird clade

The Enantiornithes was the most diverse Cretaceous bird group, comprising more than 50 species, known from the Early Cretaceous of China, Australia and Spain and the Late Cretaceous worldwide (Chiappe and Walker, 2002; O'Connor and Chiappe, 2011; O'Connor *et al*., 2011). Enantiornithines have been found rarely in near-shore marine deposits, but occur mainly in freshwater settings, and they ranged in size from *Iberomesornis*, the size of a sparrow, to *Enantiornis*, with a wingspan of 1 m.

Most enantiornithines had teeth, although *Gobipteryx* from the Late Cretaceous of Mongolia was toothless. They may have had varying diets: an *Eoalulavis* specimen preserves remains of aquatic crustaceans within the rib cage, whereas *Enantiophoenix* shows fragments of amber, possible evidence that this bird fed on tree sap. Others may have been adapted for eating a range of aquatic prey, including molluscs and fish, and others may have used their long, thin beaks to probe for prey in waterside mud.

The Enantiornithes have a short back with fewer than 13 thoracic vertebrae. They have a strut-like coracoid, interpreted as a support for the flight apparatus (Figures 9.6, 9.9(e)). They also have an alula, a supplementary winglet (see below).

Enantiornithines ('opposite birds') were recognized first in 1981 from the Late Cretaceous of South America, where isolated limb bones pointed to a new group of birds diagnosed by a distinctive articulation between the scapula (concave) and coracoid (convex), the opposite to the nature of this joint in other birds. Further, enantiornithines have an unusual **tarsometatarsus** (Figure 9.9(b)), the fused distal tarsals and metatarsals, in which metatarsal 4 is very thin. The humerus of derived enantiornithines (Figure 9.9(c)) shows diagnostic characters at the proximal end: a concave portion in the middle of the articular face and a prominent bicipital crest. During the 1990s a whole flock of new enantiornithine species came to light. Some, such as *Gobipteryx* from the Late Cretaceous of Mongolia, had been misidentified long before as related more directly to modern birds, others had been announced as theropod dinosaurs and yet others were entirely new finds, most importantly from Early Cretaceous deposits of China and Spain.

The ancient lake deposits of the Jehol Group of north-east China (see Box 9.4), have yielded skeletons of the enantiornithines *Sinornis*, *Otogornis*, *Boluochia, Longipteryx*, *Rapaxavis*, and many more (Sereno *et al*., 2002; O'Connor and Chiappe, 2011; O'Connor *et al*., 2011). These were sparrow-sized birds that could fly actively and their feet show that they were well adapted for perching on branches. Sereno *et al.* (2002) conclude that *Sinornis* (Figure 9.9(d)) lived mainly in the trees and that it was capable of sustained flight, as it flitted around in search of insects. *Sinornis* shares primitive features with *Archaeopteryx*, such as a flexible hand with claws, but it has the pygostylian features of a larger ossified sternum, a pygostyle and a partially **reflexed hallux**, as well as the ornithothoracine features noted above. *Rapaxavis* (Figure 9.10; O'Connor *et al*., 2011) has an elongate beak with only a few teeth at the tip, characteristic of the enantiornithine family Longipterygidae, and perhaps indicating that they snatched fish from the water, like modern kingfishers (O'Connor and Chiappe, 2011).

Spectacular bird skeletons from the Las Hoyas Formation of central Spain (Barremian, 130 Myr ago) include three enantiornithines, *Iberomesornis*, *Concornis* and *Eoalulavis* (Sanz *et al*., 2002). *Iberomesornis* is a sparrow-sized bird (Figures 9.9(e)) with eight free caudal vertebrae, a strut-like coracoid and a large plate-like pygostyle. The foot is specialized for perching, with a reversed hallux. *Concornis* is known from an incomplete skeleton, lacking the skull. The hindlimb (Figure 9.9(f)) is comparable to modern perching birds, with a reflexed hallux, long curved claws and a largely fused lower limb. This fused portion consists of a tibiotarsus (astragalus and calcaneum fused to tibia) and an enantiornithine tarsometatarsus, although the metatarsals are fused only proximally. The wing shows 'modern' proportions, but the fingers are still equipped with claws. *Eoalulavis* is represented by the wings and thorax, and these show a key feature relating to flight. The first finger is separate from the other two and bears its own tuft of feathers, lying in front of the main portion of the wing. This is the first record of the **alula**, or bastard wing, a structure seen in all modern flying birds that is used to improve their manoeuvrability at slow flying speeds. Normally,

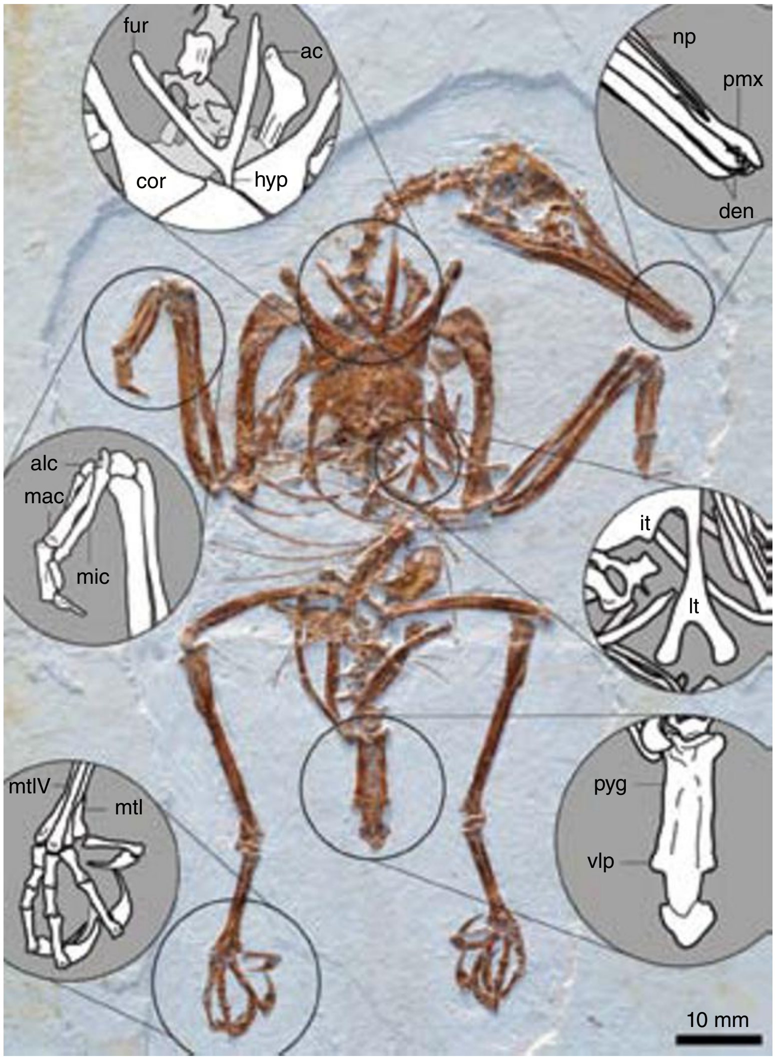


Figure 9.10 Key anatomical features of the enantiornithine *Rapaxavis* from the Jiufotang Formation (Early Cretaceous) of Liaoning, China (Dalian Museum of Natural History D2522; O'Connor *et al.*, 2011). Enlarged areas highlight the unique characteristics of Enantiornithes; note the specialized dentition (rostrally restricted in this case), the Y-shaped furcula with long hypocleidium (broken during preparation in this case), the large unique pygostyle, the small intermediate trabeculae with large distal expansions on the lateral trabeculae, the minor metacarpal extending distally farther than the major metacarpal, the reduced hand (paralleling evolution in Ornithuromorpha), the reduced shaft of the metatarsal IV, and the distally elongate pedal phalanges and large curved claws indicating cursorial habits. Anatomical abbreviations: ac, acromion process of the scapula; alc, alular metacarpal; cor, coracoid; den, dentary; fur, furcula; it, intermediate trabecula (of the sternum); lt, lateral trabecula (of the sternum); mac, major metacarpal; mic, minor metacarpal; mtI, metatarsal I; mtIV, metatarsal IV; np, nasal (frontal) process of the premaxilla; pmx, premaxilla; pyg, pygostyle; vlp, ventrolateral processes. See Colour plate 9.3. Source: J. O'Connor, Institute for Vertebrate Paleontology and Paleoanthropology, Beijing, China. Reproduced with permission.

the alula lies parallel to the leading edge of the wing, but the thumb can move forward, creating a slot between the alula and the wing. This extra winglet allows the bird to avoid stalling at slow speed and at a steep angle of attack, for example when landing or taking off. Similar devices are used in aeroplanes.

9.3.4 Basal ornithuromorphs

More derived than the Confuciusornithiformes and Enantiornithes is the clade Ornithuromorpha (see Box 9.3. Ornithuromorphs include modern birds as well as a series of outgroups from the Early and Late Cretaceous. These show modifications to the flight apparatus that link them closely to modern birds, such as the modified shoulder girdle (coracoid with procoracoid and sternolateral processes, curved and tapered scapula, U-shaped furcula), deeply keeled sternum, larger number of sacral vertebrae, small plough-shaped pygostyle, and fused tarsometatarsus. Some key basal ornithuromorphs are considered in phylogenetic sequence, and then the members of included, successive subclades, the Ornithurae and Carinatae (see Box 9.3),

The most basal ornithuromorph is *Archaeorhynchus*, a Jehol bird without a well-developed keel, a short imperforate sternum, no sternolateral process on the coracoid, but toothless, although the anatomy is uncertain as the specimens are subadult (Zhou *et al.*, 2013). All other ornithuromorphs are younger, including *Patagopteryx* from the Late Cretaceous of Argentina (Chiappe, 2002), a chicken-sized flightless bird, known from three specimens that represent the whole skeleton except the tip of the snout and the end of the tail (Figure 9.11(a)). The hindlimbs are much heavier than in any earlier Cretaceous bird, and the wings are too small to have been able to sustain this bulky bird in flight. *Patagopteryx* was a terrestrial bird, but it does not show adaptations for fast running or large size, as seen in modern ostriches and emus. There were a number of flightless birds in the Late Cretaceous, evidence that flight adaptations are repeatedly lost among many bird groups when circumstances do not require it.

Next is *Hongshanornis* (Zhou and Zhang, 2005; O'Connor *et al.*, 2010), from the Early Cretaceous of China, about the size of a blackbird (Figure 9.11(b)). It is more derived than the enantiornithines, and shares numerous characters with ornithurines, including a very short pygostyle, a strut-like coracoid with a well developed procoracoid process, a U-shaped furcula, an elongate

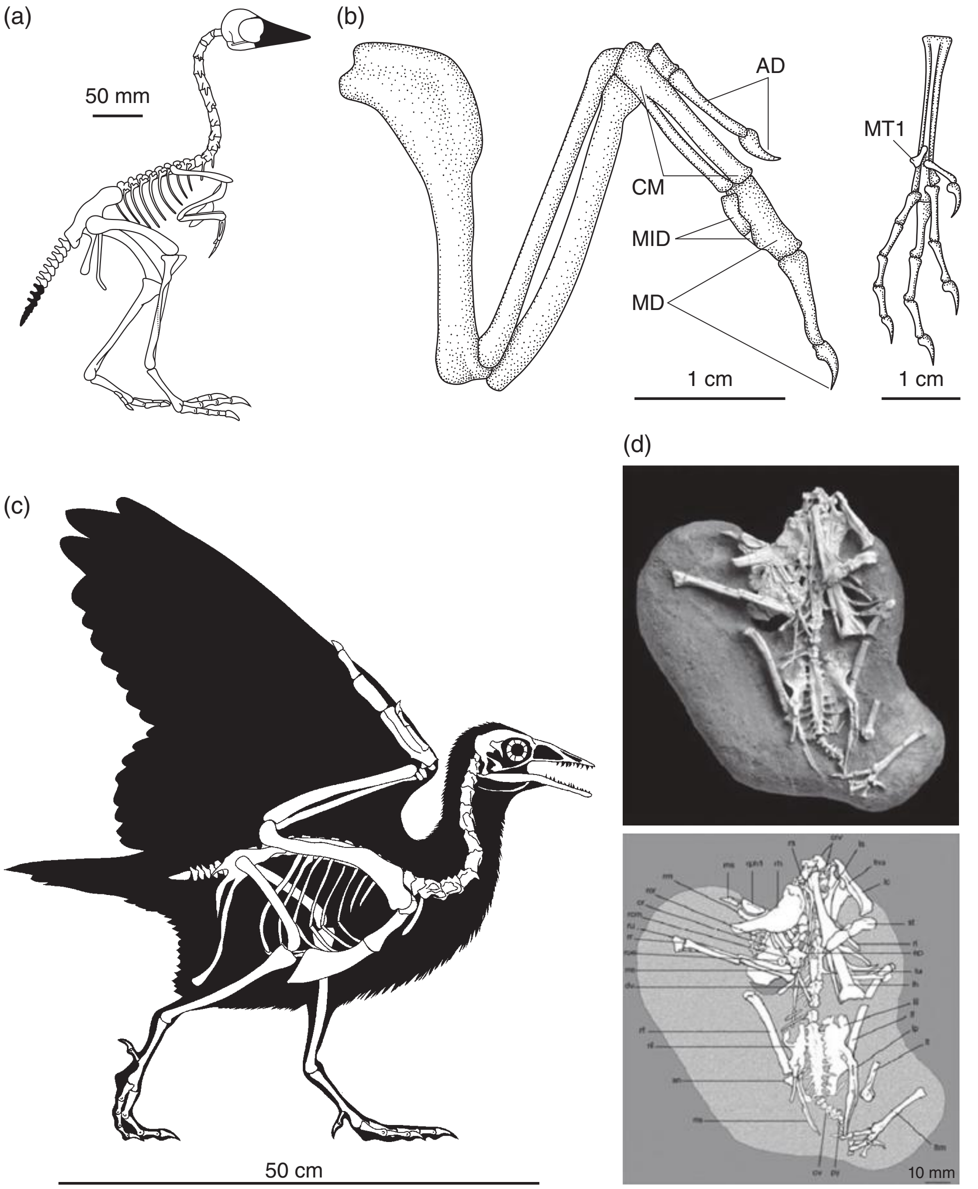


Figure 9.11 Ornithuromorph birds from the Early Cretaceous (b) and Late Cretaceous (a): (a) *Patagopteryx* from Argentina (black areas are unknown); (b) *Hongshanornis* left wing and left foot; (c) *Yanornis* skeletal restoration, in flight mode; (d) *Apsaravis* skeleton. Abbreviations: AD, alular digit; CM, carpometacarpus; MD, major digit; MID, minor digit; MT1, metatarsal I. Source: (a) L. Chiappe, Natural History Museum of Los Angeles, Los Angeles, CA, USA. Reproduced with permission. (b) Z. Zhonghe, Institute for Vertebrate Paleontology and Paleoanthropology, Beijing, China. Reproduced with permission. (c) A. Wroblewski (artist). Reproduced with permission. (d) Adapted from Norell and Clarke (2001).

sternum, a laterally expanded first phalanx of the major finger, with a reduced minor finger very tightly by its side, and a completely fused tarsometatarsus.

Above these in the cladogram (see Box 9.3) are three taxa from the Early Cretaceous Jehol Group of China, *Yixianornis*, *Songlingornis*, and *Yanornis*. *Yixianornis* is known from a single excellent skeleton of a chicken-sized flying bird (Zhou and Zhang, 2001; Clarke *et al*., 2006). The jaws carry tiny teeth. This was a powerful flyer, with a strongly keeled sternum, strut-like coracoids, a humerus as long as the ulna, and largely fused wrist bones. *Songlingornis* shows similar features, but an elongate sternum that expands substantially at the back and a broadly U-shaped furcula (O'Connor and Zhou, 2013). *Yanornis* (Zhou and Zhang, 2001) has along skull with about 10 teeth in the upper jaw, and 20 in the lower, and it was a fish-eater. The shoulder girdle is essentially modern, and *Yanornis* could have swung its wings high over it back to maximize the power of the flight downstroke (Figure 9.11(c)). These three taxa are grouped as a clade by Clarke *et al*. (2006) and O'Connor and Zhou (2013), but not by Turner *et al*. (2012), who find they are successive outgroups to Ornithurae. Songlingornithidae are diagnosed by large openings in the posterior part of the sternum, among other characters.

These birds mark another step in avian evolution, the ability to open and shut the tail fan. *Yixianornis* has eight large tail feathers, each nearly as long as the body. Clarke *et al*. (2006) note that confuciusornithiforms and enantiornithines had acquired a rod-like pygostyle, but it was only with *Yixianornis* and relatives that the modern-style, upwardly-turned pygostyle appeared. This may have been associated with a muscular structure (the chewy 'parson's nose' on a chicken) that enables modern birds to fan their tail feathers out to the sides and raise the tail fan, whether for aerodynamic use in landing or for display purposes (such as the peacock's tail).

The final pre-ornithurine bird is *Apsaravis* from the Late Cretaceous of Mongolia (Norell and Clarke, 2001). Compared to songlingornithids, *Apsaravis* (Figure 9.11(d)) has a modern avian sacrum and pelvis, with ten fused sacral vertebrae and the pubis and ischium sub-parallel and closely appressed, the pubis medio-laterally compressed, a patellar groove on the distal femur, a lateral condyle of the tibiotarsus equal to, or surpassing, the width of the medial, and metatarsal 3 pinched proximally between 2 and 4. A further modification to the forelimb suggests that *Apsaravis* may be the first bird to have had an adaptation that enables the hand to extend automatically as the wing extends; there is a small process on metacarpal 1 for the hand extensor muscle. When the wing reaches its highest point, the hand and attached feathers are automatically extended, so expanding the effective wing area and maximizing the power of the down stroke.

9.3.5 Hesperornithiformes: flightless divers

The hesperornithiforms were about 25 species of mainly Late Cretaceous flightless diving birds, known largely from the northern hemisphere (Rees and Lindgren, 2005). This diverse group all show adaptations for diving and underwater swimming: a streamlined body, powerful hindlimbs behind the body rather than beneath, and a reduced wing. They range in size from the grebe-sized *Enaliornis* to the giant *Hesperornis* which was larger than an Emperor penguin.

The best-known of these birds, *Hesperornis* (Figure 9.12(a)) is more than 1 m tall and has a long neck, reduced tail and long powerful legs. The forelimb is represented by only a pointed humerus that looks like a hatpin. The remains of *Hesperornis* and the related smaller *Baptornis* (Figure 9.12(b)), have been found abundantly in the Late Cretaceous Niobrara Chalk Formation of Kansas, USA, which was deposited in the shallow warm waters of the great sea channel that ran from north to south through North America at the time. *Enaliornis* from the mid Cretaceous of England may be the earliest hesperornithiform.

The hesperornithiforms were clearly flightless, and they are interpreted as foot-propelled divers that swam rapidly by kicking their feet. The toes are long and could spread widely. In life, the toes were probably linked by webs of skin, or at least bore lobes to increase the surface area for swimming (Figure 9.12(b)). The tiny wing stumps may have had a modest function in steering. Parts of the jaws are lined with small pointed teeth, and hesperornithiforms ate sea fishes, as is shown by their coprolites. Hesperornithiforms share a pointed anterior process of the quadrate (Figure 9.12(c)), and other features, with later birds (see Box 9.3).

9.3.6 Ichthyornithiformes: toothed fishers

Ichthyornis, also from the Niobrara Chalk Formation of Kansas, as well as from other sites in North America and in Europe (Clarke, 2004), is smaller than *Hesperornis*, being the size of a small gull (Figure 9.12(d)). The wings are fully developed and there is a deeply keeled ossified sternum, as in modern birds. The tail is more reduced than in *Hesperornis* and the body is deeper. The head is large and the massive jaws are lined with short pointed teeth set into a groove as in *Hesperornis*. *Ichthyornis* presumably caught fishes in the Niobrara Sea by diving into the water from the wing, as terns do.

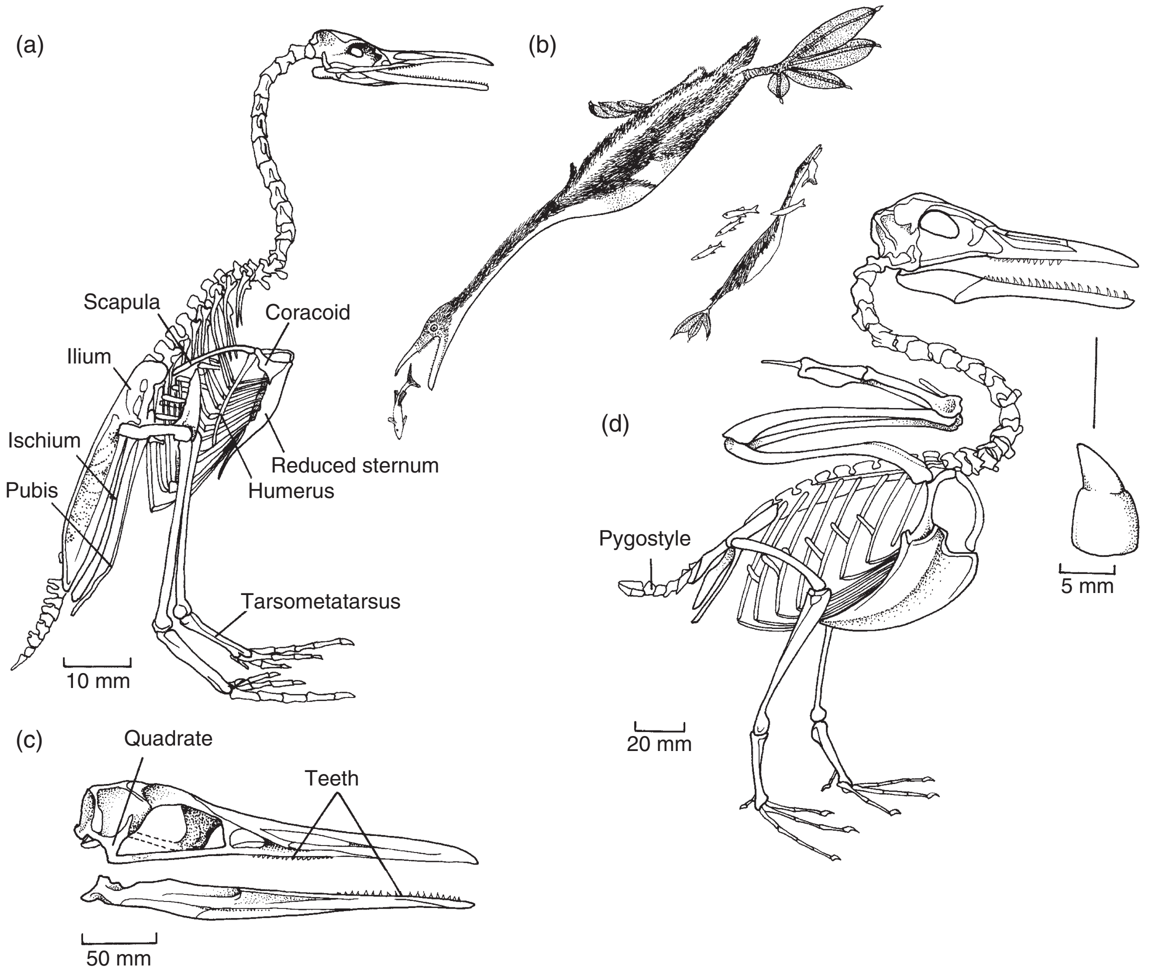


Figure 9.12 The Late Cretaceous toothed birds: (a) skeleton of *Hesperornis* in standing pose; (b) restoration of *Baptornis* swimming; (c) skull of *Hesperornis*; (d) *Ichthyornis* skeleton and tooth. Source: (a,d) Adapted from Zittel (1932). (b) Adapted from Martin and Tate (1976). (c) Adapted from Martin in Carroll (1987).

9.4 THE RADIATION OF MODERN BIRDS: EXPLOSION OR LONG FUSE?

There are two entirely divergent viewpoints on the diversification of modern birds, the Neornithes, either that they radiated explosively after the KPg boundary, or that they had originated much earlier, in the Cretaceous, and had a long span of history at low diversity until their radiation in the Paleogene. The first view has been accepted for some time by ornithologists and palaeontologists (e.g. Feduccia, 2003), namely that modern birds radiated only after the extinction of Cretaceous flying forms such as enantiornithines, hesperornithiforms, and ichthyornithiforms, as well as pterosaurs

The alternative ‘long fuse’, or early origins, model emerged from efforts to date the timing of origin of clades using molecular phylogenies. For example, Hedges *et al.* (1996) and Cooper and Penny (1997) found evidence that the modern bird orders had originated some 100 Myr ago, in the Early Cretaceous. This leaves a long gap between the molecular estimate to the oldest fossils that are confidently assigned to modern orders (65–50 Myr ago), the so-called ‘long fuse’ or time of suppressed evolution.

Both models agree that birds diversified rapidly in the Paleogene, but they differ in identifying the timing of origins. Supporters of the early origins viewpoint argue that there are some Cretaceous birds belonging to modern orders, and also that the Late Cretaceous consisted largely of marine sediments and so such fossils might be expected to be rare. Supporters of the traditional view say that these early records are suspect, and yet there are enough Late Cretaceous bird fossils, but they do not belong to modern orders. Further, they argue that the molecular dates are too old and there are problems with the dating techniques. It is worth exploring these points.

9.4.1 Cretaceous neornithines

First, the Cretaceous record of neornithines. Up to 2000, more than 100 Cretaceous neornithine fossils had been recorded. However, most of these supposed earliest representatives of flightless birds, ducks, flamingos, pelicans, loons, woodpeckers and the like have been rejected mainly because the specimens are too incomplete to show diagnostic characters or, in some cases, were wrongly dated. So far, all Cretaceous records of palaeognaths have proved to be unacceptable (Hope, 2002). Among neognaths, Hope (2002) and Dyke and Van Tuinen (2004) recognized valid specimens of Anseriformes (ducks and geese), Gaviiformes (loons) and Pelecaniformes (pelicans), and were less certain of other records. The supposed gaviiform *Polarornis* from the latest Cretaceous of Antarctica is too incomplete to assign it to either Gaviiformes or Neornithes (Mayr, 2009).

The only Cretaceous neornithines that are currently accepted as valid are possibly *Teviornis* and definitely *Vegavis*. First, *Teviornis* is known from a partial right wing from the Nemegt Formation (Maastrichtian = latest Cretaceous) of Mongolia (Kurochkin *et al*., 2002). Even though the remains are limited (Figure 9.13(a)), the carpometacarpus and digits show one diagnostic character of Anseriformes, the clade of ducks and relatives, and several diagnostic characters of a family within that order, the Presbyornithidae. These extinct ducks (see Section 9.6.2) were generally large, long-legged waders. In a revision, however, Clarke and Norell (2004) argued that the *Teviornis* material does not share any synapomorphies with Presbyornithidae, Anseriformes, or even with Neornithes. Stand off.

The second Cretaceous neornithine is *Vegavis* from the middle or upper Maastrichtian of Vega Island, Antarctica (Clarke *et al*., 2005). The fossil (Figure 9.13(b)) is a disarticulated skeleton preserving most postcranial elements, but lacking the skull. It shows twenty synapomorphies that place it successively within Ornithurae (e.g. at least ten sacral vertebrae, domed humeral head, patellar groove present), Neornithes (e.g. at least 15 sacral vertebrae, anteriorly deflected humeral deltopectoral crest), Neognathae, Anseriformes (diminutive pectineal process on pelvis, hypotarsus with well developed cristae and sulci), and Anatoidea (e.g. lack of sternal pneumatic foramen, apneumatic coracoid). The Anatoidea today include the 150 species of ducks, geese, swans, and screamers. Phylogenetically, Clarke *et al*. (2005) could not determine where *Vegavis* lies within Anatoidea, and it is part of an unresolved trichotomy between Presbyornithidae and Anatidae (modern ducks, geese, and swans).

The character support for phylogenetic placement of *Vegavis* has not been seriously challenged, and its identification as an anatoid, a member of a modern clade, implies at least five divergences of Neornithes before the KPg boundary: the Anatoidea, Anseriformes, Galloanserae, Neognathae, and Neornithes. The find of *Vegavis* in the last 2–3 Myr of the Maastrichtian still does not resolve the early origins vs. Paleogene explosion debate. It could still be that birds as a whole were little affected by the KPg event, or that many modern lineages that had originated much earlier passed through.

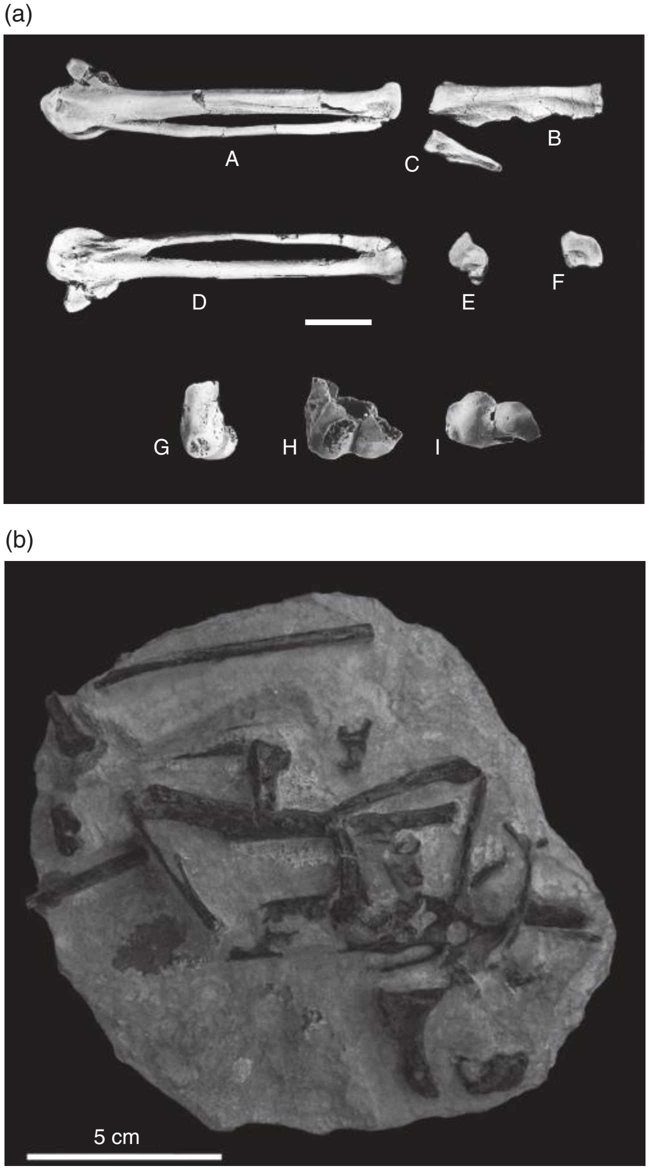


Figure 9.13 Two latest Cretaceous neornithines: (a) *Teviornis* from Mongolia; (b) *Vegavis* from Antarctica, partial skeleton. In (a), elements are: A, right carpometacarpus in dorsal view; B, right phalanx 1 of digiti majoris in dorsal view; C, right phalanx of digiti minoris in dorsocaudal view; D, right carpometacarpus in ventral view; E, distal end of right carpometacarpus in distal view; F, proximal end of right phalanx 1 of digiti majoris in proximal view; G, fragment of right humerus in dorsal view; H, in cranial view; and I, distal view. Scale bar is 10 mm. Additional imagery of *Vegavis* is at http://www.ctlab.geo.utexas.edu/pubs/clarke_et_al/clarke_et_al.htm. Source: (a) Kurochkin *et al*. (2002). Reproduced with permission from the American Museum of Natural History. (b) Clarke *et al*. (2005). Reproduced with permission from Nature Publishing Group.

9.4.2 Birds and the KPg mass extinction

It has been traditional to claim either that the KPg mass extinction 66 Myr ago (see Section 8.11) had little effect on birds, or that it was highly selective, weeding out non-neognathous clades such as enantiornithines, hesperornithiforms, and ichthyornithiforms (Feduccia, 2003). One aspect that can be resolved is whether the ‘archaic’ bird clades died out gradually through the Late Cretaceous or were hit hard by the KPg event. Clearly, in the absence of a rich record of Cretaceous neornithines, it is impossible to judge the effects of the extinction event on that clade.

In a study of a rich avifauna from the latest Maastrichtian of western North America, Longrich *et al.* (2011) show that a range of archaic birds were abundant to within 300,000 y of the KPg boundary. They studied collections of Lancian-age specimens from the Hell Creek Formation of Montana, North Dakota, and South Dakota, the Lance Formation of Wyoming, and the Frenchman Formation of Saskatchewan. These rocks were deposited during the final 1.5 Myr of the Cretaceous, but most of the fossils can be dated to the last 300,000 y, immediately below the KPg boundary. Seventeen species were identified, including seven species of archaic bird, representing Enantiornithes, Ichthyornithiformes, Hesperornithiformes, and an *Apsaravis*-like bird, as well as ten species of ornithurine. All the archaic clades disappeared at the boundary (Figure 9.14(a)), so the study confirms the dramatic effect of the KPg mass extinction on non-neornithine birds (Feduccia, 2003).

The second finding was that derived ornithurines dominated the fauna, not enantiornithines. The fossils include hesperornithiforms and ichthyornithiforms (see Sections 9.3.5, 9.3.6), but none of the Lancian fossils studied by Longrich *et al.* (2011) can be identified unequivocally as neornithine. Many though are demonstrably more derived than *Ichthyornis*, and these authors argue that this is evidence for a substantial diversification of advanced ornithurines, if not neornithines, in the latest Cretaceous.

The Lancian birds ranged in estimated body mass from 0.2 kg to 5 kg, a much narrower range than that estimated for modern birds (10 g–10 kg). Perhaps the size range represented by the fossils (Figure 9.14(b)) has been truncated by inadequate sampling, but Longrich *et al.* (2011) argue that the Lancian fossil sites are so well searched that larger bird bones would have been identified if they had existed, and that palaeontologists have recovered so many tiny bones through screen washing that they might also hope to find some evidence of smaller birds if they were there. The truncated size range then may indicate that Maastrichtian birds were somewhat limited in ecological potential by competitors such as pterosaurs, dinosaurs, and mammals.

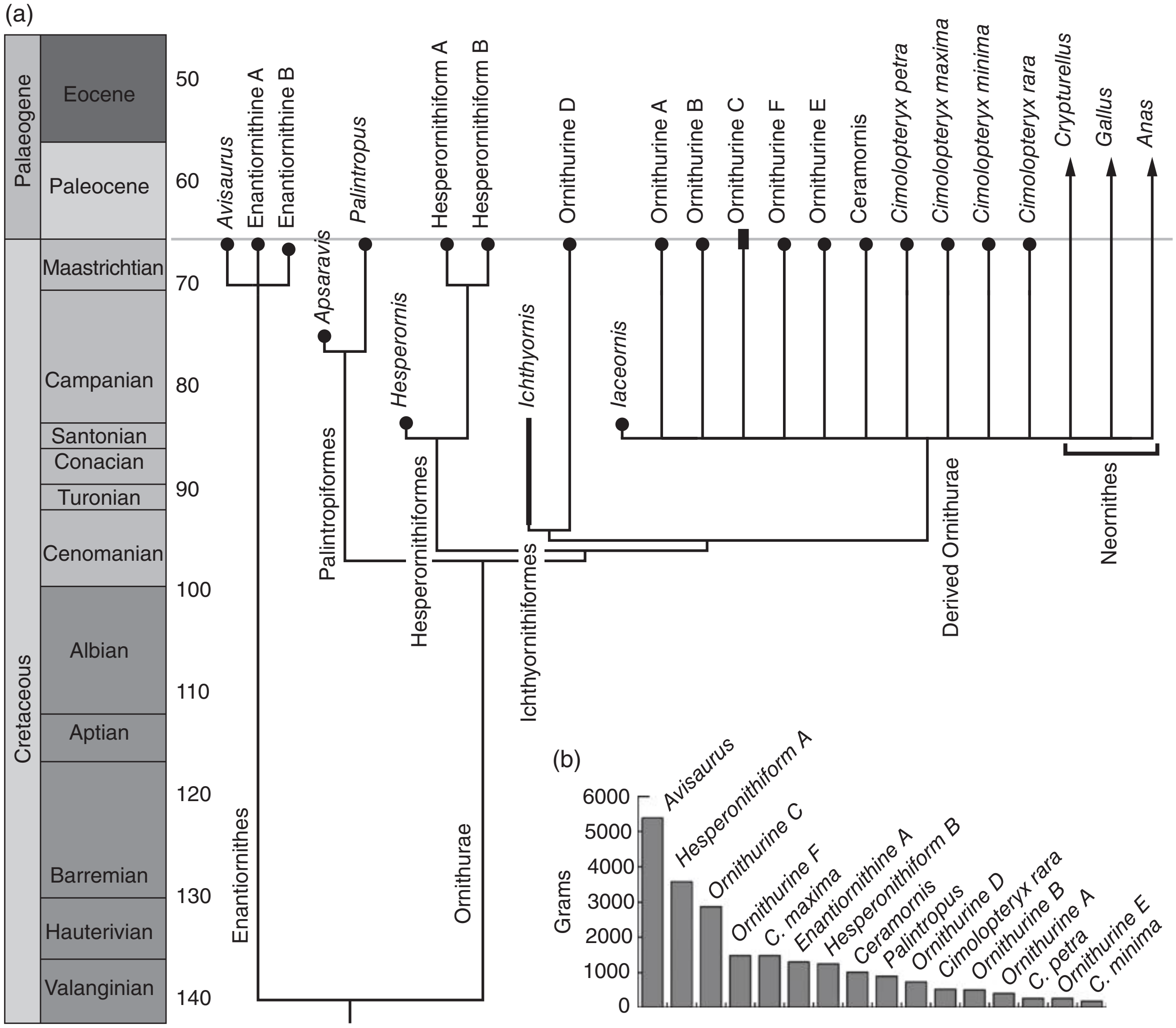


Figure 9.14 Patterns of extinction of birds at the end-Cretaceous mass extinction: (a) phylogeny showing relationships and stratigraphic distribution of late Maastrichtian birds (bold) and other avians (note that the extension of neornithine branches into the mid Late Cretaceous is artificial, and results from an unresolved multitomy); (b) size range in late Maastrichtian birds. Source: N. Longrich, University of Bath, Bath, UK. Reproduced with permission.

9.4.3 Molecular dates

Since Hedges *et al.* (1996) and Cooper and Penny (1997) suggested that the modern bird orders had originated in the Early Cretaceous, there has been much debate and re-analysis. The phylogenomic studies all indicate a very early origin for Neornithes (e.g. Ericson *et al.*, 2006; Pereira and Baker, 2006; Van Tuinen *et al.*, 2006; Brown *et al.*, 2008; Pratt *et al.*, 2009; Pacheco *et al.*, 2011; Haddrath and Baker, 2012), supported also by a combined morphological phylogenetic and dating study (Lee *et al.*, 2014). Since the 1990s, methods have improved in several ways: analysts use more taxa and multiple calibration fossils (not just one), and especially they use 'relaxed clock' methods that permit differing molecular clocks in different lineages.

Phylogenomic analyses all indicate Cretaceous origins for the major avian clades, but there are two categories, one set showing really deep origins, with Neornithes emerging at 140–120 Myr, and the other rather more recent origins, at 90–100 Myr. For example, Pereira and Baker (2006) found a date of 139 Myr for the origin of crown Neornithes by comparison with a wide range of tetrapods. On the other hand, Ericson *et al.* (2006), in comparisons of five nuclear genes, found a Late Cretaceous origin of Neornithes at about 95 Myr. Ten lineages crossed the KPg boundary, and all other divergences took place in the Paleogene. Van Tuinen *et al.* (2006), using DNA sequence and hybridization data, found Late Cretaceous origins for major bird clades, and then two pulses of ordinal-level splitting, the first around the time of the KPg boundary (66 Myr), and the second around the Eocene-Oligocene boundary (34 Myr).

These widely different results were explored by Brown *et al.* (2008) in a comprehensive study of mitochondrial DNA of modern birds, and using a variety of methods of calculation. They dated the origin of Neornithes at 102–133 Myr, of Palaeognathae at 66–110 Myr, of Neognathae at 93–127 Myr, of Galloanserae at 79–110 Myr, and Neoaves at 86–124 Myr. The dating estimates differ according to the methods used: PATHd8 (rate smoothing across sister lineages) finds all dates in the Late Cretaceous and 30 lineages crossing the KPg boundary for example, whereas r8s (smoothing in an ancestor-descendant fashion) finds 39 neornithine lineages emerging in the Early Cretaceous, and about 70 crossing the KPg boundary. The older dates of the r8s method are in line with the other dating methods employed.

Many recent studies of particular bird clades tend to confirm these deeper time estimates. For example, Haddrath and Baker (2012) find a date of origin of crown Palaeognathae of 131 Myr (range 122–138 Myr), and so even earlier than that for crown Neornithes. Pratt *et al.* (2009) found that the root of Neoaves was dated at about 85 Myr, and that 12 neoavian lineages survived the KPg boundary. This was confirmed by Pacheco *et al.* (2011), in a deliberately conservative analysis of mitochondrial DNA, using the most variable molecular rates, minimal ages for calibration fossils, and multiple methods of calculation. They find a date of 88 Myr for the origin of Neoaves, and a range of dates, from 50 to 78 Myr for individual neoavian orders. The most recent of these dates (50 Myr) is for Columbiformes (pigeons) and the oldest (78 Myr) for Coraciiformes (kingfishers, bee-eaters, rollers, hornbills). The results indicate that 22 neoavian lineages crossed the KPg boundary.

The key differences in the implied timing and shape of the neornithine radiation depend on the calibration software used. For example, Ericson *et al.* (2006) found their later origin of Neornithes, and largely Paleogene diversification of crown taxa using PATHd8, as confirmed by Brown *et al.* (2008). However, the latter authors note that the PATHd8 result is out of agreement with the patterns obtained with other dating software (r8s, Multdivtime, Dating5, BEAST), all 'relaxed clock' methods, and they argue that the BEAST results are best because they do not involve so many restrictive assumptions as the other methods.

A phylogenetic analysis of morphological data on Mesozoic and modern birds (Lee *et al.*, 2014) suggests a date of 116 Myr for the origin of Neornithes (crown Aves) and split of Palaeognathae and Neognathae, and 89 Myr for the origin of Galloanserae. This study uses a new method in which the phylogeny and the dates are established at the same time, and offers an intriguing suggestion of a compromise between conflicting viewpoints. Coverage of modern bird orders is modest, and so dates for their origins were not calculated.

In all recent molecular studies, even those that purport to find closest agreement with the fossil evidence (e.g. Ericson *et al.*, 2006; Van Tuinen *et al.*, 2006), there are still major discrepancies, with five or six deep divergences in Neornithes around 100–90 Myr, at least 20–30 Myr before the first neornithine fossils. This continuing mismatch of data for bird phylogeny contrasts with recent findings for mammals (see Section 10.4).

9.5 FLIGHTLESS BIRDS: PALAEOGNATHAE

The palaeognathous palate (see Box 9.3) shows primitive theropod and avian characters, but there are several synapomorphies (the extensive vomer–pterygoid joint, the elongate basipterygoid processes that meet the pterygoid). Palaeognaths also share synapomorphies in other parts of the skull (Johnston, 2011).

Most living palaeognath groups have short fossil records, extending back only to the Miocene or Pliocene. The oldest palaeognaths, the extinct lithornithiforms (Houde, 1986; Mayr, 2009), are known from the Palaeocene and Eocene of Europe and North America (Figure 9.15(a)). Lithornithiforms have the classic palaeognathous palate, showing a caudal process of the palatine, and more derived forms, including modern kiwis and ostriches and the fossil *Lithornis* and *Palaeotis*, have an additional feature, a pterygoid fossa (both features lost in the ostrich). *Lithornis* and relatives from North America were hen-sized birds that retained the power of flight, whereas *Palaeotis* was a crane-sized flightless bird.

Modern palaeognaths fall into two groups, the tinamous, flying, partridge-sized birds from South and Central America, and the other ratites. The other ratites include such well-known

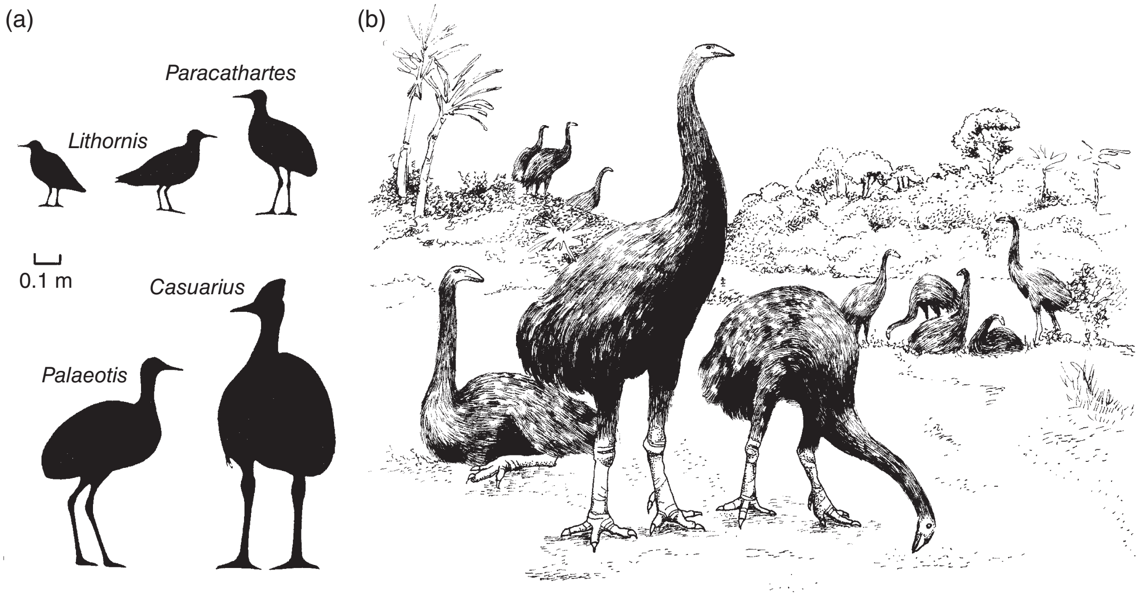


Figure 9.15 Palaeognath birds: (a) comparison of size and form of the flighted Palaeocene and Eocene *Lithornis* and *Paracathartes*, the flightless Eocene *Palaeotis* and modern *Casuarius* (cassowary); (b) restoration of the giant flightless *Dinornis* from the subrecent of New Zealand. Source: (a) Adapted from Houde (1986). (b) Adapted from a painting by Charles R. Knight.

flightless birds as the rheas of South America, the cassowaries and emus of Australia, the kiwis of New Zealand and the ostriches of Africa. These all have reduced wings and they have lost the keel on the sternum, having evolved from ancestors that could fly.

The geographical distribution of modern ratites across the southern hemisphere suggests that the group originated in Gondwana. When Houde (1986) showed that the lithornithiforms were also palaeognaths, he argued that the group had originated in the northern hemisphere and ratites had reached southern continents only 30–40 Myr ago. However, molecular and morphological data from modern ratites (Johnston, 2011) indicates a sequence of splitting in the Cretaceous, with the *Aepyornis* lineage on Madagascar separating first, at 110 Myr, the ostrich in Africa and the rhea in South America about 100 Myr ago, and finally the cassowary in Australia and the moas and kiwi in New Zealand 50–60 Myr ago.

Some of the most spectacular ratites are now extinct, the elephant bird of Madagascar and the moas of New Zealand. Both groups are known from subfossil and fossil bones no older than the Pleistocene, with moa eggshells having been found also in the middle Miocene of New Zealand. There were nine species of moas (Figure 9.15(b)), which ranged from turkey size to heights of over 3 m. In studies of DNA recovered from their subfossil bones, Bunce *et al.* (2009) show that the clade originated only 5–8 Myr ago. All older lineages were wiped out during a major flooding event about 23 Myr ago, when most of New Zealand sank beneath the waves. The moas originated in South Island, and some crossed to North Island during a phase of low sea level 1.5–2 Myr ago. Moas fed on a variety of plants and, together with kiwis, flightless rails, ground parrots, geese and others, formed unique communities in the absence of mammals. After the arrival of polynesian settlers about AD 1250, it seems the moas were hunted to extinction in 100 years or less (Oskam *et al.*, 2012).

9.6 NEOGNATHAE

There are some 10,000 species of neognaths, by far the majority of living birds, assigned to over 140 families. Most of these families have a fossil record and in many cases this runs back to the Eocene, except for the hugely diverse songbirds, the passeriforms, which arose in Australasia in the Eocene and radiated dramatically in the Miocene and Pliocene.

Because of the diversity of the modern bird groups and the incompleteness of many fossils, no attempt will be made here to catalogue them all. The key groups are noted and some unusual fossil taxa are highlighted.

9.6.1 Neognath characters and embryology

Neognaths are diagnosed by features of the palate (see Box 9.3), as well as by a peculiar character of the ankle: the ascending process of the ankle bones that runs up in front of the tibia seems to have switched allegiance from the astragalus to the calcaneum.

The theropod ancestors of birds have a thin plate of bone that is attached to the enlarged astragalus and hugs the lower end of the tibia (Figure 9.16(a)). This process in ratites (Figure 9.16(b)) has been interpreted as a new element called the **pretibial bone**. Hence, it could be argued that birds arose from some other source among the archosaurs and that the ratites are degenerate neognaths. Embryological evidence (McGowan, 1985; Maxwell

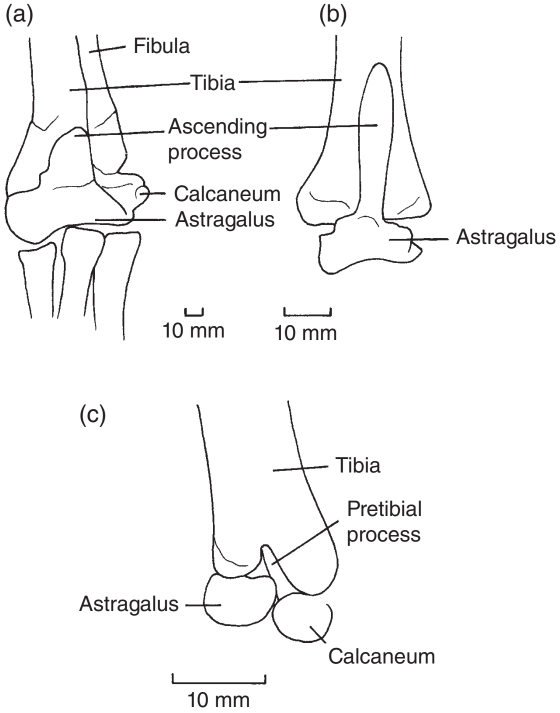


Figure 9.16 Anterior views of the tarsal regions of (a) the theropod dinosaur *Allosaurus*, (b) a juvenile ostrich and (c) an embryonic chicken, to show the different origins of the ascending process. Source: Adapted from McGowan (1985).

et al., 2012), however, shows that the process in ratites is homologous with that of the theropod dinosaurs. The neognath ascending process (Figure 9.16(c)) starts development as a small cartilaginous nubbin associated with the astragalus, but shifts to an attachment on the calcaneum before it ossifies. It is unclear when this shift occurred, but the calcaneal ascending process is a synapomorphy of all neognaths.

9.6.2 Neognath phylogeny

The phylogeny of Neognathae has proved to be very hard to resolve. The tentative tree (see Box 9.5) includes much uncertainty, but one result that has been widely agreed is that the Anseriformes (ducks) and Galliformes (fowl and game birds) form a clade, the Galloanserae (or Galloanseres), and this is the sister group of all other neognaths, termed Neoaves.

Neoaves, the majority of birds have proved remarkably difficult to classify. Most of the orders are clear enough, although some taxa such as flamingos, bustards, shoebills, the hammerkop, and others, jump from order to order. The real problem has been to sort out the relationships of the neoavian subclades, and there are still profound disagreements between morphological and molecular analyses, and even between differing molecular studies. The best cladograms in many cases lack robustness, meaning that the relationships can be overthrown by changes to very few characters.

These resolution problems could indicate poor quality analyses, but more likely there are real issues about the way in which neoavians diversified. It is likely that Galloanserae branched early, in the latest Cretaceous, as shown by *Vegavis* (see Section 9.4.1), and that Neoaves radiated explosively, perhaps just after the KPg mass extinction (Ericson *et al.*, 2006; Van Tuinen *et al.*, 2006). An explosive radiation, in which all modern neoavian orders were established within say 1–2 Myr could produce a ‘star phylogeny’ where it is impossible to find shared characters, either morphological or molecular, between any pair of subclades.

Earlier molecular studies of neoavian relationships, such as Fain and Houde (2004) and Ericson *et al.* (2006), found a split into Metaves (doves, sandgrouse, mesites, flamingos, grebes, kagu, sunbittern, hoatzin, tropicbirds, swifts, treeswifts, hummingbirds, and nightjars) and Coronaves (the rest). However, this division has not been widely accepted since, and McCormack *et al.* (2013) did not recover Metaves reliably. They argue that this ‘clade’ may have emerged because of long-branch attraction, a phenomenon where subclades that emerged deep in the past may have acquired similar characters by convergence; this is especially seen in molecular analyses.

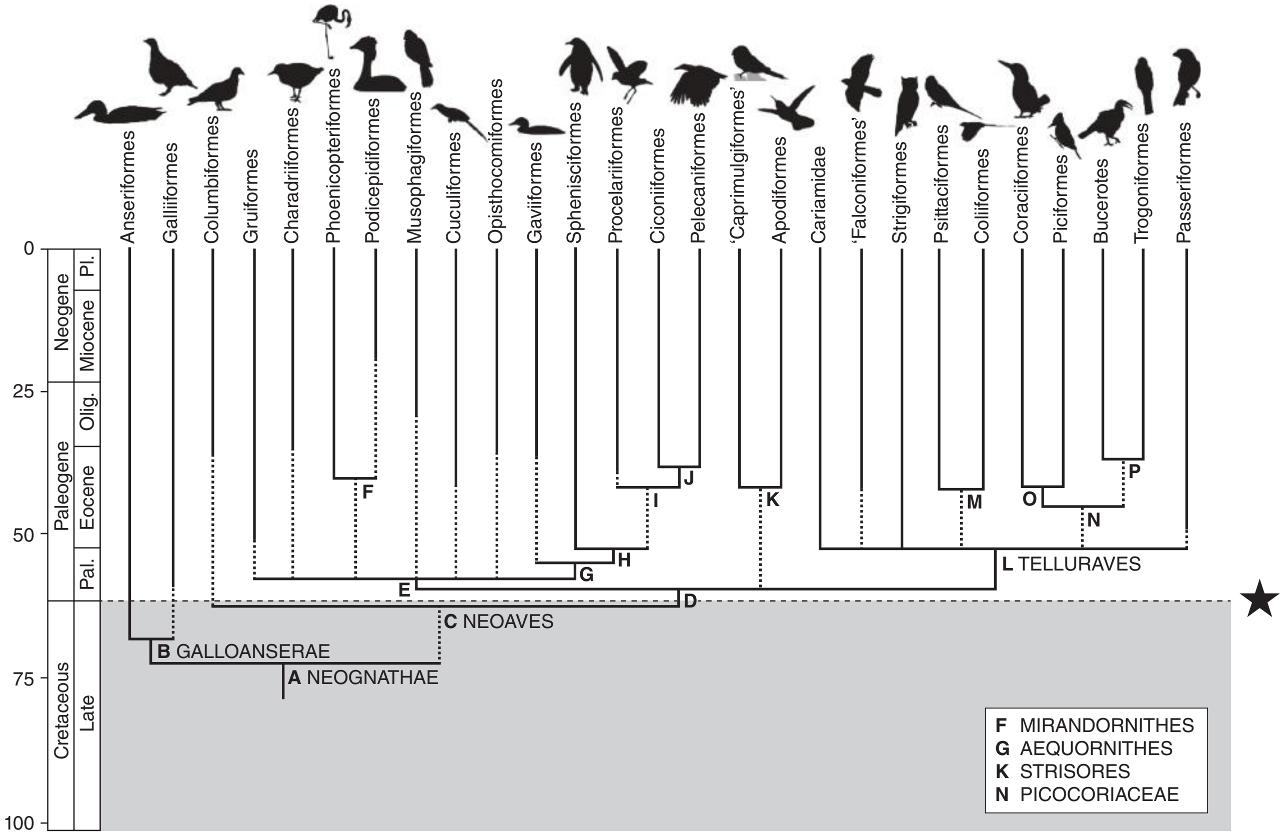
In their comprehensive phylogenomic study of Neoaves, McCormack *et al.*, (2013) used target enrichment (sequence capture) and high-throughput sequencing of ultraconserved elements to explore relationships of 32 members of Neoaves and one outgroup (chicken) using 1541 genomic loci. They found support for the waterbird clade, Aequornithes, and the landbird clade that had been discovered before (Ericson *et al.*, 2006; Brown *et al.*, 2008; Hackett *et al.*, 2008) as well as for the controversial sister relationship between passerines and parrots and the non-monophyly of raptorial birds in the hawk and falcon families. In addition, they found some novel pairings, for example close relationships between tropicbirds (Phaethontidae) and the sunbittern (Eurypygidae) as well as between bustards (Otididae) and turacos (Musophagidae).

The landbird clade, Telluraves, includes all other neoavians, and their relationships have proved very hard to disentangle. McCormack *et al.* (2013) identify several subclades: passerines + parrots + falcons, hawks + vultures, the ‘near passerines’ or CPBT clade (Coraciiformes, Piciformes, Bucerotes, Trogoniformes), and owls. These were found in earlier studies (summarized in Mayr, 2014).

Many bird orders fall outside the waterbird and landbird clades (Mayr, 2011a, 2014; McCormack *et al.*, 2013), including ‘Gruiformes’ (cranes, rails, and allies), Cuculiformes (cuckoos), Opisthocomiformes (hoatzin), Phoenicopteriformes (flamingos), Podicipediformes (grebes), Charadriiformes (shorebirds and allies), Columbiformes (doves and sandgrouse), and Strisores (nightjars and allies, swifts, and hummingbirds). Following Mayr (2011a), the neognath clades will be considered in sequence from Galloanserae, through the noted unassigned clades, Aequornithes, Strisores, and the Telluraves.

BOX 9.5 NEOGNATH RELATIONSHIPS

The relationships of the majority of flying birds, the neognaths, have proved remarkably intractable, even after 20 years of repeated efforts to re-examine the morphological data, and especially new phylogenomic information (see Section 9.6.2). Some neognath subclades are widely accepted, most notably the split into Galloanserae and Neoaves, and within Neoaves, possibly the waterbird clade Aequornithes, and some others (Mayr, 2014). This is the least secure cladogram in the book.



Cladogram showing the postulated relationships of the major groups of neognath birds, based on the cladistic analysis by Mayr and Clarke (2003), the review by Mayr (2011a), and the overview study by McCormack *et al.* (2013). This is still tentative and synapomorphies have yet to be discovered for many nodes. Silhouette images are all open source, from Mike Keesey and the phylopic website. Synapomorphies: **A NEOGNATHAE**, vomers mediolaterally narrow, vomers form a midline narrow and dorsoventrally high lamella, palatine and pterygoid separate, fronto-parietal suture closed, pygostyle not perforated at postero-ventral end, humerus with distinct brachial fossa, humerus with well-developed scapulotricipital groove, pelvis ilioischiadic foramen posteriorly closed, tarsometatarsus is a hypotarsus with well-developed crests and grooves; **B GALLOANSERAE**, lacrimal lacks descending process, vomers fused posteriorly, basipterygoid processes with large facet for articulation with pterygoid, basiparasphenoid plate broad and meets the parasphenoid rostrum at a very acute angle, quadrate has articular eminence on otic process, quadrate with large lateral condyle, articular surface of mandible with single ridge and lacking walls, mandible with retroarticular process, mandible with long narrow, and dorsally oriented medial process, third cervical centra with osseous bridge from transverse process to the caudal articular process; **C NEOAVES**, palatine with well developed crista ventralis, palatine lateral part present and well developed, basipterygoid articulation absent in adulthood, pelvic preacetabular tubercle absent or vestigial; **D**, no morphological synapomorphies identified; **E**, no morphological synapomorphies identified; **F MIRANDORNITHES**, zygomatic process present, fourth to seventh cervical vertebrae strongly elongate and spinal processes form a marked ridge, 23 or more praesacral vertebrae, several thoracic vertebrae fused to a notarium, humerus with marked oval depression for m. scapulohumeralis cranialis, ulna distal end with marked radial depression, femur short and stout, hypotarsus has strong lateral crests delimiting a marked groove for all flexor tendons, wing has 11 primary feathers, eggs covered with a chalky layer of amorphous calcium phosphate; **G AEQUORNITHES**, elongate tubular nostrils in rhamphotheca; **H**, nasolabial grooves along sides of the beak; **I**, no morphological synapomorphies identified; **J**, no morphological synapomorphies identified; **K STRISORES**, elongated crus longum of the ulnar carpalbone; **L TELLURAVES**, no morphological synapomorphies identified; **M**, unique derived morphology of the deep flexor tendons; **N PICOCORIACEAE**, mandible of the hatchling projects distinctly beyond the upper beak; **O**, no morphological synapomorphies identified; **P**, no morphological synapomorphies identified. Abbreviations: Olig, Oligocene; Pal, Paleocene; Pl, Pliocene/Pleistocene. Dashed lines and star symbols indicate extinction events.

9.6.3 Galloanserae: ducks and fowl

The Anseriformes, some 150 species of ducks and swans (Livezey, 1997), date back to the Eocene when some goose-like fossils appeared. Even older are the presbyornithids, for long a mystery, but now firmly allied with ducks (Ericson, 1997; Livezey, 1997). The first presbyornithids are reported from the latest Cretaceous (see Section 9.4.1) and the group was particularly diverse in the Eocene. *Presbyornis* (Figure 9.17(a)) has a duck-like head and neck, but its legs are much longer than in typical anseriforms.

Galliformes, including today some 250 species of chickens and game birds such as pheasants and partridge, are runners and reluctant flyers. Their relationships (Dyke *et al.*, 2003; Ksepka, 2009; Mayr, 2009) are debated in detail, as are the phylogenetic positions of some basal taxa from the Eocene.

Unusual extinct relatives of the ducks and game birds include the giant flightless gastornithiforms from the Palaeocene and Eocene of North America and Europe. *Gastornis* (=*Diatryma*), the best-known form (Figure 9.17(b)), was over 2 m high and it had the massive leg bones and reduced wings seen in other large ground-dwelling birds. This is not a ratite, however, because it shares features of the limb bones and jaw joint with game birds and with ducks in particular.

But what did *Gastornis* eat? Witmer and Rose (1991) noted that the deep jaws and the curved beak are very similar to those of parrots and other seed-eaters, which are capable of delivering powerful bites to nuts and seeds. They argued, however, that *Gastornis* was much too big to be a seed eater and its beak was designed for enormous biting forces. They suggested that it is much more likely that it was a flesh-eater, and that it fed on the diminutive mammals found with it, horses and other ungulates and monkeys. Andors (1992) disagreed and argued for herbivory. He noted that *Gastornis* lacks a hooked beak, as seen in raptorial birds, and that as a galloanserine it belongs to a herbivorous clade. He argued that *Gastornis* crushed and sliced rank vegetation in the forests and savannas of early Eocene Europe and North America, although it might occasionally have scavenged carcasses, or seized small animals for food.

9.6.4 Diverse neoavians

A broad range of important modern bird groups, from doves and rails to gulls, flamingos, and cuckoos, do not apparently fit any of the larger clades of neoavians, and they are considered here in sequence, following Mayr (2011a).

The Columbiformes, more than 300 species of pigeons, doves, and sandgrouse, may occupy a basal phylogenetic position among Neoaves (McCormack *et al.*, 2013), but their relationships have been heavily debated (Mayr, 2011a). Fossil columbiforms date back to the late Eocene/ early Oligocene of the famous Phosphorites de Quercy, a French deposit that has yielded many bird fossils (Mayr, 2009). One of the most famous extinct pigeons is the dodo (Figure 9.18(a)), a hefty flightless pigeon that was formerly abundant on the island of Mauritius (Parish, 2012). Sailors in the sixteenth century first discovered the tameness of these birds and they overcame their initial distaste for the 'hard and greasie' flesh as they clubbed them all to death. Specimens of this

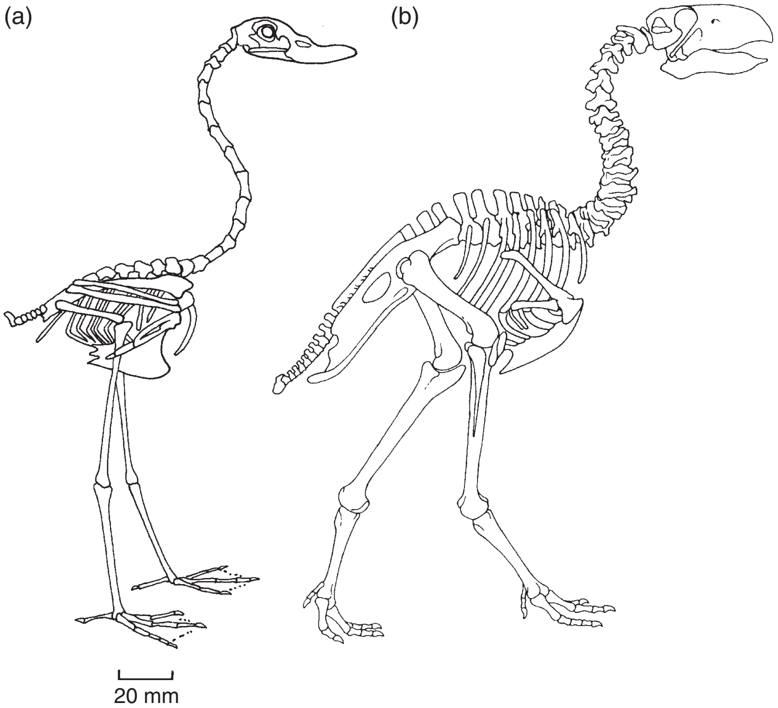


Figure 9.17 Galloanserines, the duck-gamebird clade: (a) *Presbyornis*, an anseriform from the Palaeocene/ Eocene; (b) *Gastornis* (=*Diatryma*), a large ground-dwelling galloanserine that may have fed on plants or on prey. Source: (a) Adapted from Olson and Feduccia (1980). (b) Adapted from Zittel (1932).

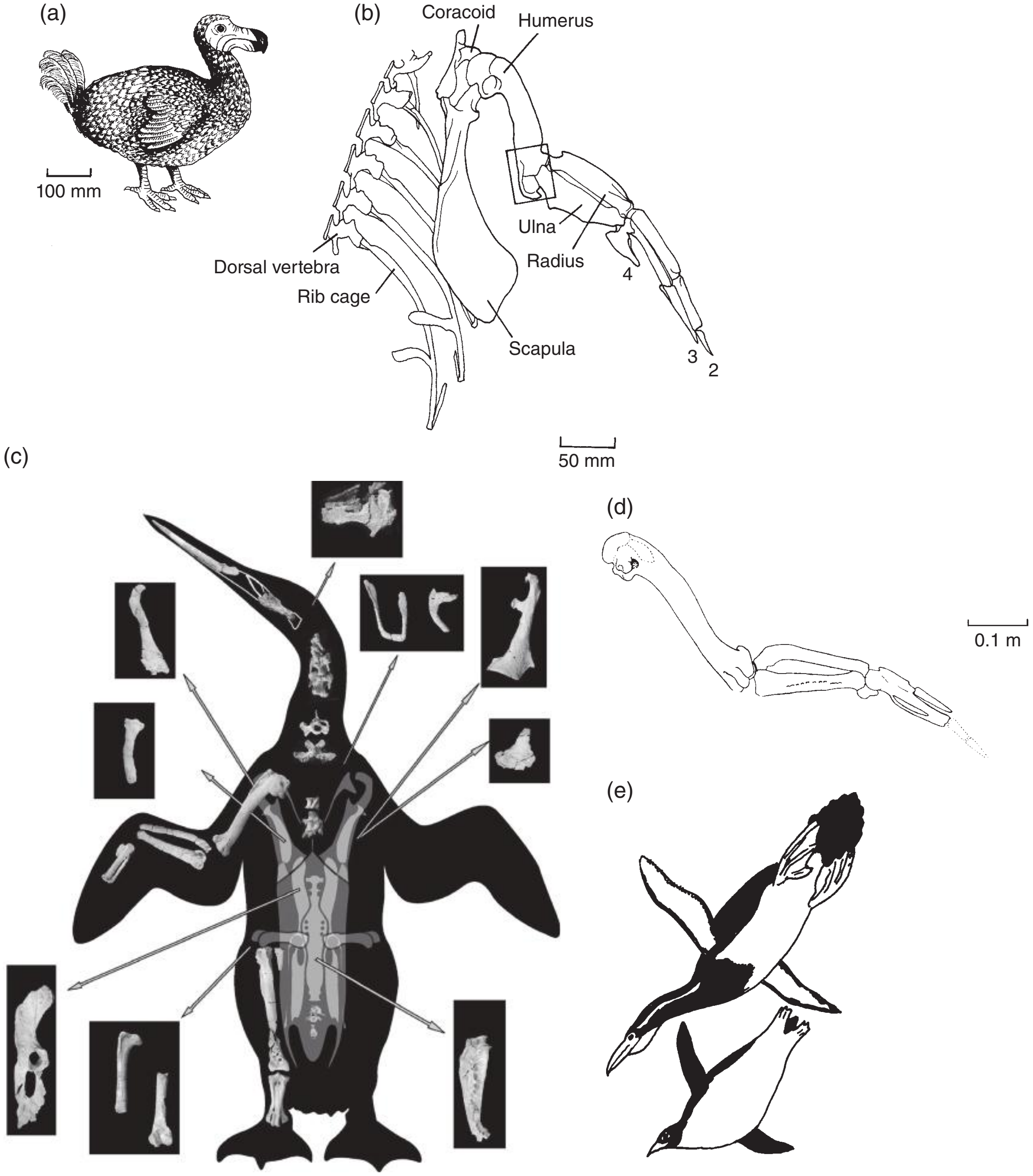


Figure 9.18 Diverse neoavians: (a) *Raphus*, the dodo, a kind of pigeon; (b) the highly modified wing bones of a penguin in dorsal view; (c) reconstruction of *Waimanu*, a Palaeocene penguin, showing preserved bones against a reconstruction silhouette; (d) modified wing of a 2-m-long flightless pelecaniform from the Miocene of Japan; (e) scale drawing of a reconstructed swimming plotopterid and Emperor penguin. Source: (a) Adapted from various sources. (b) Adapted from Van Tyne and Berger (1976). (c) T. Ando, Ashoro Museum of Palaeontology, Hokkaido, Japan. Reproduced with permission. (d,e) Adapted from Olson and Hasegawa (1979).

'strange fowle' were exhibited in London in 1638 and a stuffed one was preserved in the Oxford University Museum. The last living survivor was reported in 1681 and the Oxford specimen became so foul-smelling that it was burned in 1755.

The 'Gruiformes' (cranes, rails, and allies) was a well-established order of birds, but phylogenetic analysis shows that certain families are allied elsewhere. For example, the South American Eurypygidae and the New Caledonian Rhynochetidae, each containing a single species, form a distinct clade, Turnicidae are part of Charadriiformes, and Cariamidae may be associated with falcons in the higher landbird assemblage (Mayr, 2011a). The core gruiforms, some 160 species of cranes and rails, are known worldwide today; most have long legs and they seek food by wading in shallow water. Fossil cranes and rails are not uncommon, and include the relatively abundant messelornithids, long-legged ground birds, from Messel and other Eocene localities in Europe and North America (Mayr, 2004, 2009).

The Charadriiformes, about 350 species of shorebirds, gulls and auks, mostly have long legs and seek food by wading in shallow water. Gulls are highly successful diving hunters, whereas auks are wing-propelled divers, rather like penguins. Their phylogeny has been debated, with differing results from morphological and molecular data (Mayr, 2011b). At one time a diverse array of fragmentary bird fossils from the Maastrichtian (latest Cretaceous) of New Jersey, USA, were assigned to charadriiforms (Hope, 2002). However, these do not show any diagnostic characters of charadriiforms, and indeed the oldest accepted fossils of the clade are from the middle Eocene (Mayr, 2009, 2011b).

The Phoenicopteriformes, six species of flamingos, and Podicepediformes, 22 species of grebes, appear to form a clade (Ericson *et al.*, 2006; Hackett *et al.*, 2008; Mayr, 2011a; McCormack *et al.*, 2013), the Mirandornithes. Flamingos are known first from the early Oligoocene of Europe (Mayr, 2009), and they are familiar water birds in tropical regions, often living and feeding in highly saline lake waters. Grebes are foot-propelled diving birds. The oldest grebe fossils are Miocene in age (Ksepka *et al.*, 2013a).

Three small bird orders, the Musophagiformes (turacos), Cuculiformes (cuckoos), and Opisthocomiformes (hoatzin) may be variously related to each other, but such suggestions are controversial (Mayr, 2011a). The 23 species of turacos are known today from Africa south of the Sahara, but with fossils from the Oligocene of Germany and Egypt (Mayr, 2009). The Cuculiformes (cuckoos) are first reported form the early Eocene of England. The hoatzin is famous for the fact that juveniles retain claws on their wings for climbing around in trees, a possible hint of earlier bird evolution. Hoatzins are specialist leaf-eaters, and their oldest fossils are from the Oligo-Miocene of Brazil and the middle Miocene of southern Africa, showing that the clade has reduced its geographic distribution to the Amazon and Orinoco deltas in South America (Mayr *et al.*, 2011).

9.6.5 Aequornithes: the waterbird clade

The waterbird clade Aequornithes (Mayr, 2011a, 2014), discovered on the basis of several molecular analyses (Ericson *et al.*, 2006; Brown *et al.*, 2008; Hackett *et al.*, 2008; McCormack *et al.*, 2013) includes Gaviiformes (loons), Sphenisciformes (penguins), Procellariiformes (albatrosses), Ciconiiformes (storks), and Pelecaniformes (pelicans) except Phaethontidae (tropicbirds). In their phylogenetic analysis of morphological data, Livezey and Zusi (2006, 2007) recovered a similar clade, which also included Phaethontidae, Phoenicopteriformes, and Podicipediformes. The clade was not robust, and these authors could not identify a synapomorphy, but Hieronymus and Witmer (2010) noted most of the waterbirds share a composite rhamphotheca, and, possibly related with this, many also show marked furrows along the sides of the beak, termed nasolabial grooves (Mayr, 2011a).

The Gaviiformes are foot-propelled diving birds, five species of the loon *Gavia*. These are often compared to the Late Cretaceous hesperornithiformes (see Section 9.3.5), but similarities in their modes of life are convergences: modern loons and divers retain the power of flight. Fossil gaviiforms are known from the Eocene and Oligocene of Europe, as well as from the later Cenozoic of Europe and North America.

The Sphenisciformes (penguins) comprise 20 species today, and they are well known for their flightlessness, their swimming abilities, and their distribution around Antarctica and the coasts of southern continents. Their adaptations to the cold include counter-current heat exchangers that allow them to retain core warmth while standing on frozen ice as well as remarkable incubation strategies to keep their developing eggs warm. Their adaptations to underwater swimming include shortened wings, but powerful flight muscles and deeply keeled sternum (Figure 9.18(b)), dense bones to counteract buoyancy, scale-like waterproofed feathers, and underwater vision. The largest living penguin, the Emperor, can dive to 500 m depths.

Penguin fossils, especially the rather solid limb bones, are relatively common, with over 4000 specimens reported, belonging to more than 30 species (Kspeka and Ando, 2011). Penguin evolution shows three main phases (Ksepka and Clarke, 2010a), the origin of flightlessness near the KPg boundary, dispersal throughout the Southern Hemisphere during the early Paleogene, and a late Cenozoic origin, perhaps 20 Myr ago (Subramanian *et al.*, 2013), for the crown clade Spheniscidae, including all the living penguins. *Waimanu*, the oldest known penguin (Figure 9.18(c)), comes from the Palaeocene of New Zealand (Slack *et al.*, 2006), and by the late Eocene, penguins had reached more or less their full latitudinal spread, from 65° south to the Equator (Ksepka and Clarke, 2010a; Ksepka and Ando, 2011). These early penguins were large, and giant size has been a recurring them in penguin evolution (see Box 9.6).

The Procellariiformes, comprising 125 species today of albatrosses, petrels and shearwaters, storm petrels, and diving petrels, includes some very large birds, with wingspans up to 3.5 m. Fossils are known from the Eocene, and the group is better represented from the Oligocene onwards (Mayr, 2009). The extinct diomedeoids of the Oligocene (Mayr and Smith, 2012) are the main fossil representatives. Albatrosses are known from the early Oligocene.

Two of the aquatic bird orders have long been seen as close relatives, the Ciconiiformes (storks, herons, ibises) and the Pelecaniformes (pelicans, frigate birds, gannets, cormorants). There has been much debate about the placement of individual taxa within a larger ciconiiform-pelecaniform clade (Mayr, 2011b; McCormack *et al.*, 2013), but the two subclades are supported in more or less their traditional format in a phylogenetic study of complete mitochondrial genomes (Gibb *et al.*, 2013). The tropicbirds (Phaethontidae), long seen as pelecaniforms, are possibly related to Eurypygidae (Hackett *et al.*, 2008; Gibb *et al.*, 2013; McCormack *et al.*, 2013), and the shoebill is a pelecaniform, not a ciconiiform. Storks date back perhaps to the Eocene of China, or at least the Oligocene of Egypt. Ibises and spoonbills may date back to the early Eocene of North America and Europe (Smith *et al.*, 2013).

Pelecaniforms are medium-sized to large fish-eating birds, with fossil representatives known from the Eocene and Oligocene of Europe and North America (Smith, 2010). They have extensively webbed feet for swimming and flexible throat pouches that allow them to hold large fishes. An unusual extinct pelecaniform family, the Plotopteridae, from the Eocene to Miocene of the Pacific Ocean (western North America and Japan), were giant flightless birds that converged on penguins (Dyke *et al*., 2011). The wing (Figure 9.18(d)) is reduced to a curved paddle used for rapid flight underwater, and it has converged strikingly on the swimming wing of auks and penguins. Plotopterids ranged from the size of a cormorant to lengths in excess of 2 m (Figure 9.18(e)), and indeed they are close relatives of modern cormorants (Smith, 2010).

9.6.6 Strisores: nightjars, swifts, and hummingbirds

Two terrestrial bird orders, the 'Caprimulgiformes' (nightjars, oilbirds, frogmouths) and Apodiformes (swifts, hummingbirds) have long been allied with each other, and indeed the caprimulgiform families are paraphyletic with respect to the apodiforms (Ericson *et al*., 2006; Hackett *et al*., 2008; Pratt *et al*., 2009; Mayr, 2010, 2011a, 2014). This clade Strisores may be related to the 'landbird clade', but evidence is inconclusive.

Both apodiforms and 'caprimulgiforms' date back to the Eocene of Europe or North America (Mayr, 2009, 2010). The hummingbirds, which feed on insects or nectar and include the smallest living birds (50 mm long), are known as fossils only from the Pleistocene and Holocene. However, *Eocypselus* from the early Eocene Green River Formation of Wyoming, USA is a stem apodiform (Ksepka *et al*., 2013b). It shows neither the elongate, pointed wing of the swift, adapted for continuous and acrobatic flight, nor the short wing of the hummingbird, which enables them to hover in front of flowers by generating lift on the upstroke and the downstroke (Figure 9.19(a–c)). The nightjars and goatsuckers are nocturnal insect-eaters that have large gaping mouths in which they engulf their prey.

9.6.7 Telluraves: the landbird clade

One of the big questions of bird phylogeny has been to establish the nearest relatives of Passeriformes, the songbirds, by far the largest clade of neoavians. Candidates have included woodpeckers, kingfishers, and parrots. These three consistently emerge as close relatives on the basis of morphological (Livezey and Zusi, 2006, 2007) and molecular evidence (Ericson *et al*., 2006; Hackett *et al*., 2008; McCormack *et al*., 2013; Mahmood *et al*., 2014). Indeed, molecular evidence points to a wider 'landbird assemblage' including two predatory orders, the falcons and owls, as well as rollers and trogons (Mayr, 2014).

BOX 9.6 GIANT PENGUINS

The remarkable life cycle of the largest of modern penguins, the Emperor penguin, *Aptenodytes forsteri*, is well known. Males and females can reach a height of 1.2 m and weights of 22–45 kg, depending on season and diet. The Emperor is the only penguin that breeds during the Antarctic winter – it has to do this because of the length of time required for the young to develop, and that depends on their size. The Emperors trek 50–120 km inland to the breeding colony sites where the female lays a single egg and then returns to the sea to feed. The male stays put, balancing the egg, and then the hatched juvenile, on his feet until the female returns to feed the chick and the male can trudge back to the sea to feed.

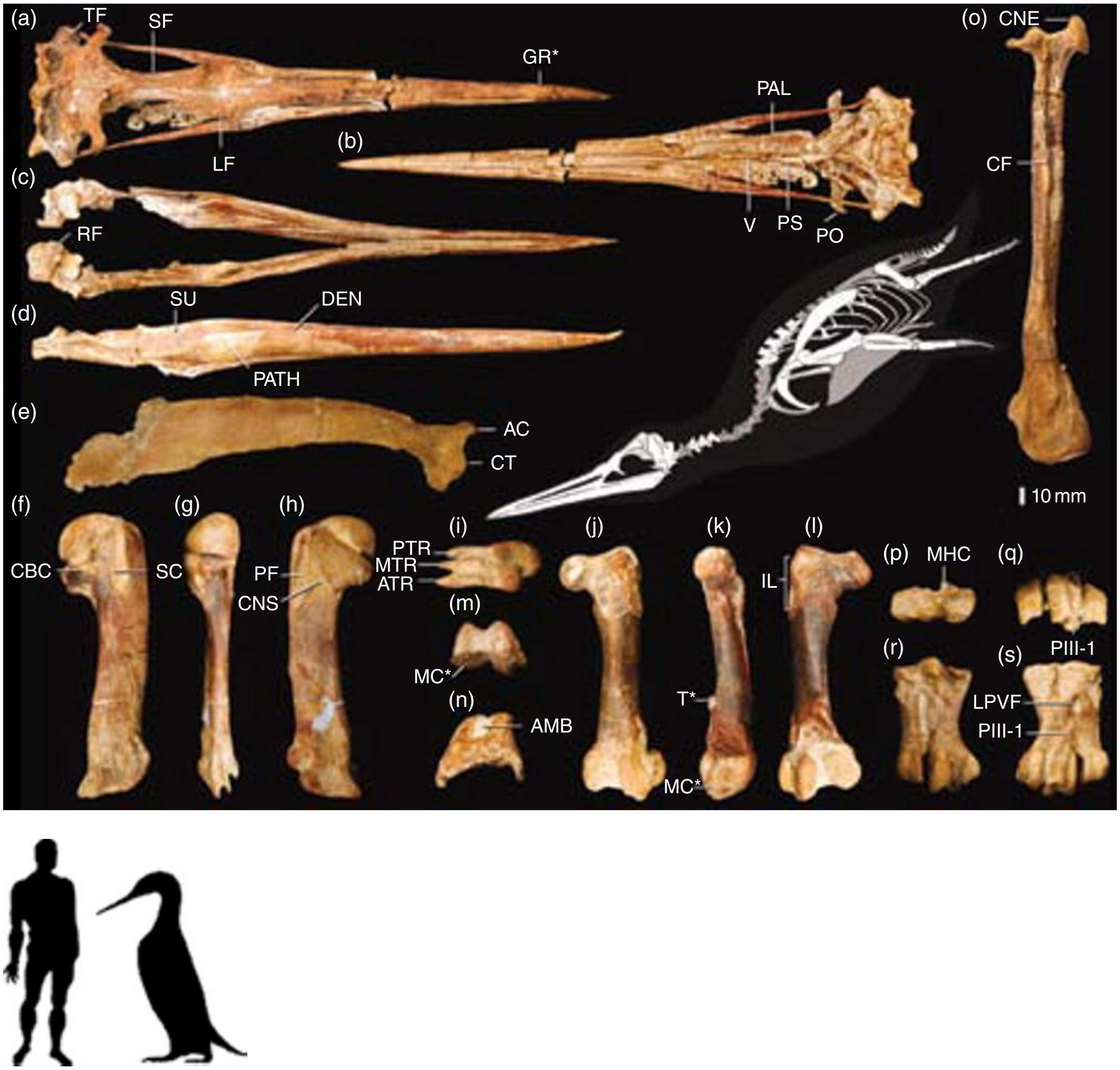
There were even larger penguins in the past, but it is not clear whether their size also entailed such incredible feats of endurance. Some were estimated to have reached heights of 1.7–2.0 m and weights of 81–97 kg, in other words larger than average adult human beings. However, these maximum measures may be slightly exaggerated (Kspeka and Ando, 2011), as there are no complete skeletons; the heights and weights are extrapolated from the measurements of the Emperor penguin and isolated fossil bones.

Large size in penguins evolved early. Even the first penguin, *Waimanu*, was 0.8 m tall and weighed about 20 kg. Penguins larger than the Emperor had appeared in Antarctica by the late Palaeocene, South America by the middle Eocene, and Australia and New Zealand by the late Eocene. An example is *Inkayacu* from the late Eocene of Peru (Clarke *et al*., 2010), which reached a swimming length of 1.5 m. The fossil (see illustration) is remarkably complete, and even the feathers are preserved. Study of the melanosomes (see Box 9.1) shows that *Inkayacu* may have been grey and reddish-brown in colour.

The ecology and behaviour of the giant penguins has been debated. It had been suggested that these early giants were restricted to surface swimming, but there is in fact little evidence that they could not dive deep, as modern penguins do (Ksepka and Ando, 2011). In terms of diet, modern penguins are opportunistic, feeding on fish, squid, and crustaceans when available. Different species today show specializations in the jaws and beak for fish or plankton feeding, but it seems that all the early penguins had a narrow, slender bill, which would have been adapted for spearing large prey such as fish and squid.

The giant penguins died out during the late Oligocene and early Miocene, just before the origin of modern forms, the crown clade Spheniscidae, when the mean size of penguin species declined. There have been many suggestions about why this might have happened, whether because of continuing cooling of climates or because of competition with new marine mammal groups such as seals or whales. In either case, the expansion of modern, generally smaller, penguins in the Miocene was associated with a broadening of their diets to include krill specialists (Kspeka and Clarke, 2010a).

Read Dan Ksepka's fossil penguin blog at: http://fossilpenguins.wordpress.com/, and see the National Geographic video about *Inkayacu* at: http://video.nationalgeographic.co.uk/video/news/history-archaeology-news/giant-penguin-discovery-vin/.



Reconstruction of *Inkayacu paracasensis* in oblique anterior view showing recovered elements in white on the reconstructed skeleton, and photographs of the holotype specimen: skull and mandible in (a and c) dorsal, (b) ventral, and (d) lateral views; scapula in (e) lateral view and humerus in (f) posterior, (g) ventral, (h) anterior, and (i) distal views; femur in (j) dorsal, (k) medial, (l) ventral, and (m) distal views; patella in (n) anterior view; tibiotarsus in (o) lateral view; and tarsometatarsus in (p) proximal, (q) distal, (r) anterior, and (s) plantar views. Anatomical abbreviations: AC, acromion; AMB, pathway of m. ambiens tendon; ATR, anterior trochlear process; CBC, m. coracobrachialis caudalis insertion; CF, fibular crest; CNE, cnemial crests; CNS, coracobrachialis nerve sulcus; CT, coracoid tuberosity; DEN, dentary; GR, groove on premaxilla; IL, m. iliofemoralis and iliotrochantericus insertions; LF, lacrimal facet; LPVF, lateral proximal vascular foramen; MHC, medial hypotarsal crest; MC, medial condyle; MTR, middle trochlear process; PIII-1, manual phalanx III-1; PAL, palatine; PATH, pathology; PF, pectoralis fossa; PO, postorbital process; PS, parasphenoid rostrum; PTR, posterior trochlear process; SC, m. supracoracoideus insertion; SF, salt gland fossa; SU, surangular; T, tab-like process; TF, temporal fossa; V, vomer. Asterisks demarcate autapomorphies referenced in the diagnosis. Below is a restoration of *Anthropornis* (right), a 1.7 m penguin from Seymour Island, Antarctica, compared to a 1.8 m human. See Colour plate 9.4. Source: Clarke *et al*. (2010). Reproduced with permission from the American Association for the Advancement of Science.

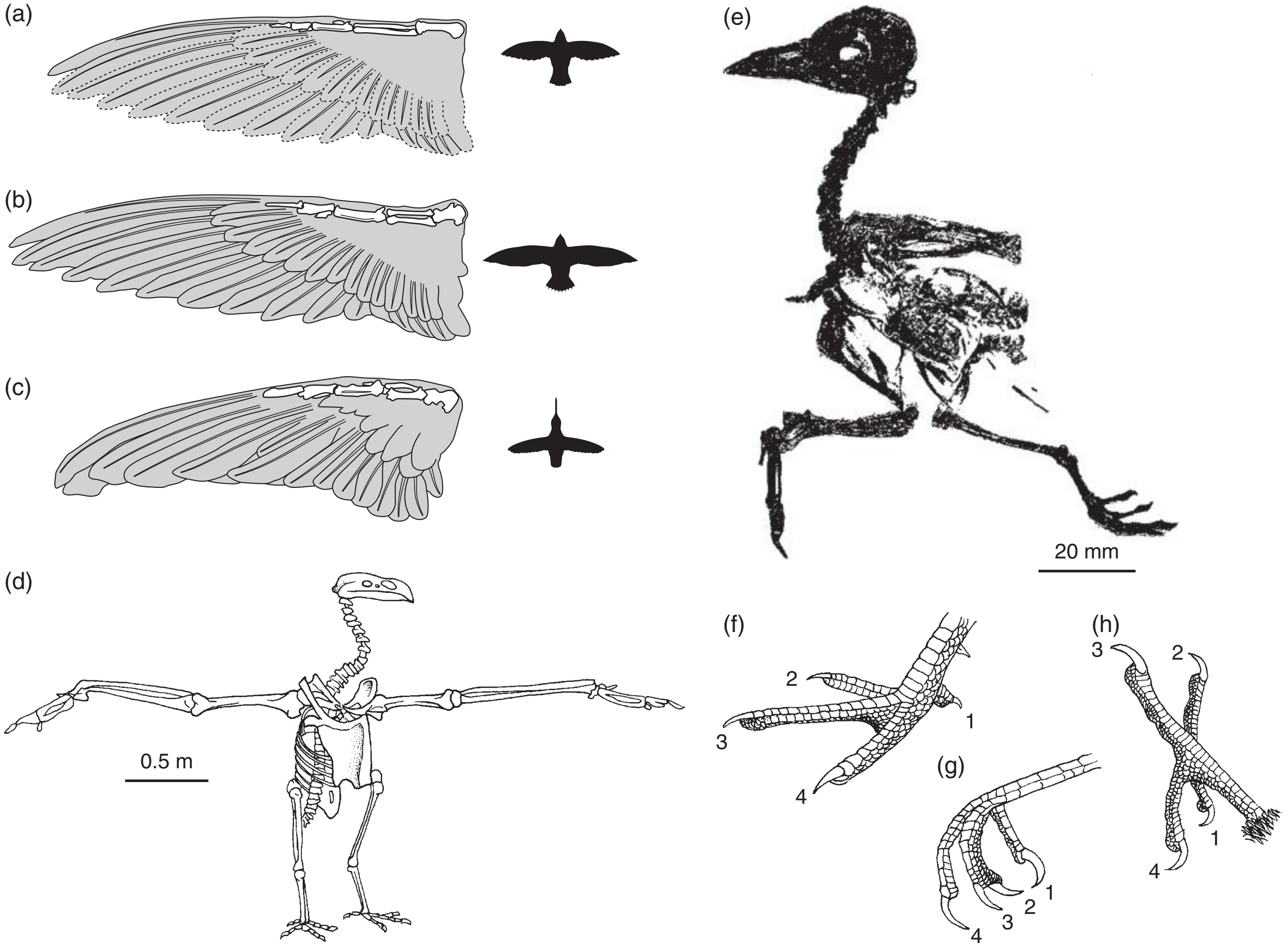


Figure 9.19 Members of the Strisores (a–c) and Telluraves (d–g) clades: (a) the reconstructed wing of the early Eocene apodiform *Eocypselus*; compared to the wings of a modern swift (b) and hummingbird (c); (d) *Teratornis*, an extinct giant New World vulture; (e) 'speedy Gonzales', a famous Eocene specimen of the coraciiform *Primobucco* from the Green River Formation, showing one wing and one leg; (f) the walking and scratch-digging foot of a pheasant; (g) the grasping foot of a sparrow; (h) the zygodactyl climbing foot of a woodpecker. Source: (a–c) D. Ksepka, North Carolina State University, Raleigh, NC, USA. Reproduced with permission. (d) Adapted from Van Tyne and Berger (1976). (e–h) Adapted from various sources.

Most unexpected in the landbird clade are Cariamidae, formerly classified as part of Gruiformes (see Section 9.6.4). The extant seriemas, or cariamids, are two species of 90-cm tall, long-legged predatory ground birds from Brazil and Argentina. They hunt insects, frogs, lizards, snakes, birds, and mammals, which they seize and beat on the ground. From their appearance and behaviour, it is perhaps no surprise that seriemas are related to the extinct phorusrhacids, the 'terror birds' of South America (see Box 9.7).

The 'Falconiformes' traditionally include all the daytime predatory birds, over 300 species, including falcons (Falconidae), eagles, hawks, and Old World vultures (Accipitridae), the osprey (Pandionidae), the secretary bird (Sagittariidae), and New World vultures (Cathartidae). These were commonly split into the falcons on the one hand and the other families in a separate order, and this is confirmed by molecular analyses (Hackett *et al*., 2008; McCormack *et al*., 2013), which link hawks and vultures as one clade (Accipitriformes), and ally the falcons with parrots and songbirds.

The oldest possible falcon fossils are Eocene (Mayr, 2009), but these records are questionable, and the earliest unambiguously identified fossils are from the early Miocene of South America. The New World vultures, the Cathartidae, possibly arose in the Old World, with the oldest forms coming from the latest Eocene of France, and then crossing to the Americas in the Oligocene or Miocene. The New World vultures include the largest living flying bird, the condor, with a wingspan of 3 m, as well as the largest flying birds of all time, the teratorns.

The teratorns arose in the Late Miocene of South America, but they are best known from the Pleistocene of North America. Hundreds of specimens of *Teratornis* (Figure 9.19(d)) have been found in the La Brea tar pits of California. Predatory birds such as *Teratornis* and a dozen species of hawks and eagles were attracted to feed, some becoming trapped as well. Teratorns may have been more capable on the ground than modern vultures, and their beaks and skulls were kinetic and adapted for dealing with struggling prey, rather than for delving among the bloody

BOX 9.7 GIANT HORSE-EATING BIRDS OF THE EOCENE

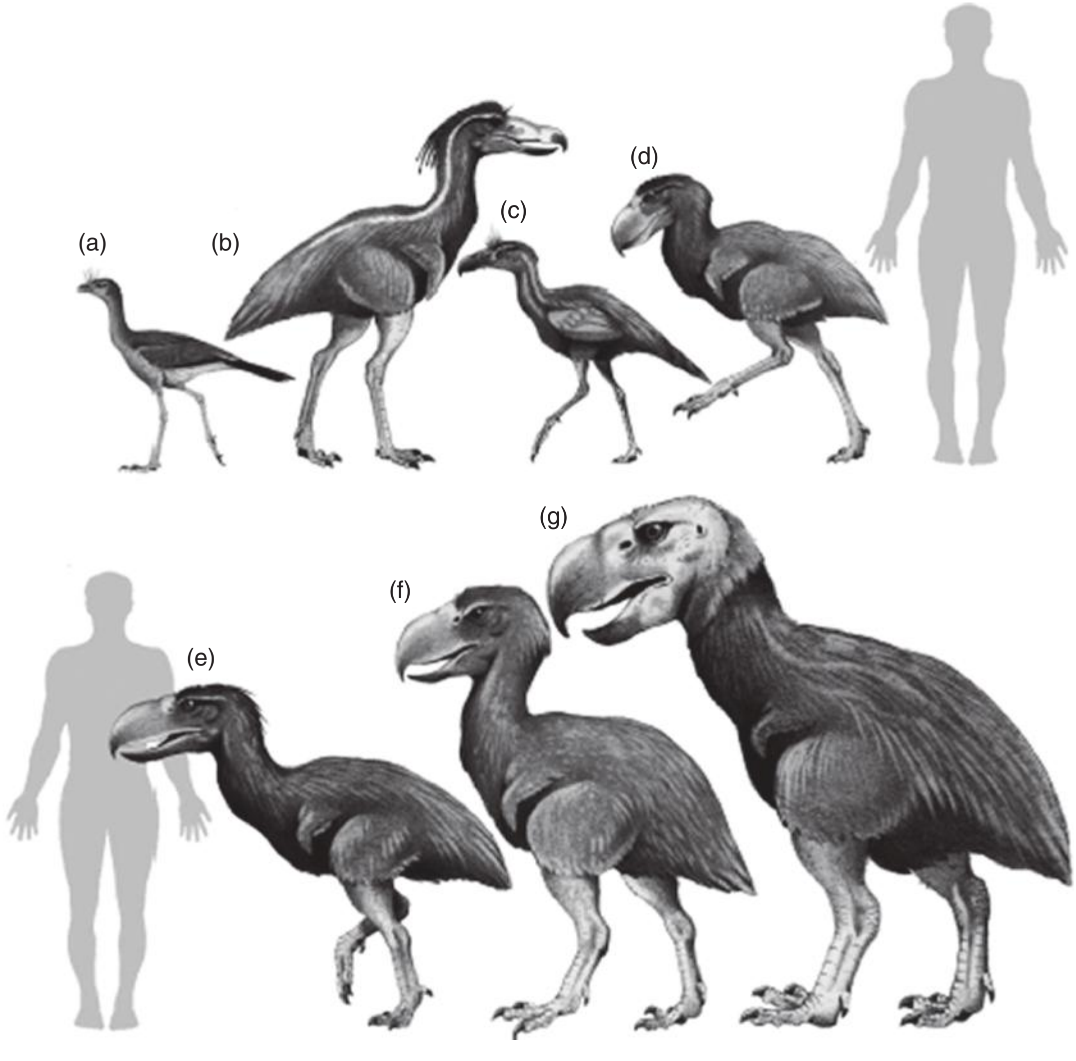
If tetrapod history had proceeded differently, the major carnivores on land today might have been giant birds. The radiation of mammals in the Palaeocene and Eocene after the extinction of the dinosaurs did not include any very large carnivores (see Section 10.8) and birds seem to have become top predators in some parts of the world. The gastornithiforms such as *Gastornis* (see Figure 9.17(b)) may have fulfilled this role in the Palaeocene and Eocene of North America and Europe, although their diet is controversial (see Section 9.6.3).

There are no such doubts about the extinct phorusrhacids (Alvarenga and Höfling, 2003; Alvarenga *et al*., 2011), which are related to the modern seriemas, predatory ground-living birds of South America. Once thought to be related to cranes and rails (Guiformes), seriemas have emerged as possible relatives of the falcons, parrots, and songbirds, based on molecular evidence (Hackett *et al*., 2008).

Phorusrhacids existed from the Paleocene to the end of the Pleistocene, some living side-by-side with nandus, the South American ratites. Many skeletons have been excavated, and these are assigned to 18 species in 14 genera, ranging in height from just under 1 m to the 2 m-tall *Brontornis* (see illustration). The 0.7 m-long skull of *Kelenken* from the Miocene of Argentina indicates an animal originally 3 m tall. The smaller phorusrhacids have slender skeletons and relatively modestly reinforced skulls, whereas the very large *Phorusrhacus, Paraphysornis, and Brontornis* have massive limb bones and huge, deep-sided beaks, as in *Gastornis*.

The deep-sided, slightly curved beak, indicates bone-crushing abilities, as in *Gastornis* (see Section 9.6.3), and these larger phorusrhacids have been pictured attacking a horse-like mammal of the Pliocene by seizing it with a huge clawed foot and tearing the flesh with its powerful beak. The short wings and tail feathers would have helped it to balance.

The phorusrhacids probably arose, with the seriemas, in South America in the Palaeocene, and some early relatives entered Africa and Europe in the Eocene. The terror birds lived on in South America much longer than for example the gastornithids in Europe, possibly feeding on larger prey than did the carnivorous mammals of the day. Some also entered North America in the Pliocene and Pleistocene. They were eventually replaced ecologically by predatory cats and dogs.



Restorations of some phorusrhacids compared to their nearest living relative, the cariama (a). The fossil forms are *Mesembriornis* (b), *Psilopterus* (c), *Andalgalornis* (d), *Phorusrhacus* (e), *Paraphysornis* (f), and *Brontornis* (g). The silhouette human is 1.75 m tall. Source: Alvarenga *et al*. (2011). Reproduced with permission from John Wiley & Sons.

entrails and sinews of long-dead animals. The South American teratorn *Argentavis* was the largest bird ever, with a wingspan of 7 m and an estimated body mass of 70 kg. Biomechanical models (Chatterjee *et al*., 2007) show that it was an excellent glider, with a cruising speed of 67 km per hour, and it could have soared on thermals rising from the slopes of the Andes. Take-off for such a monster was problematic, and it probably had to leap from a perch or run downhill to pick up enough speed.

The Strigiformes were commonly allied with Falconiformes, but they appear to be a distinct subclade of the landbird clade (Mayr, 2011a; McCormack *et al*., 2013; Mahmood *et al*., 2014). The 200 living species of owls are well known nocturnal predators, typically with huge forward-facing eyes to enable them to see their small mammalian prey in the dark. Fossil owls are known worldwide from the first Palaeocene forms (Kurochkin and Dyke, 2011).

The Psittaciformes (parrots) are a very familiar group, consisting of some 370 species today that occupy the tropics. They are diagnosed by a short, deep, hooked beak and a shortened, downward-curved lower jaw, both part of their adaptation for cracking hard nuts and seeds. The oldest confidently identified parrots come from the Eocene of North America, Europe, and Asia (Mayr, 2009; Ksepka and Clarke, 2012) and include some spectacularly well-preserved specimens from the Middle Eocene lake deposits of Messel in Germany (Figure 9.20).

Close relatives are the Coliiformes, six species of mousebirds that scurry through trees in sub-Saharan Africa in search of berries and buds. Most African fossil coliforms are Neogene, but the clade is well represented in the Eocene and Oligocene of Europe (Mayr, 2009). An Oligocene form from Germany, *Oligocolius*, has a parrot-like beak and some large fruit stones in the area of its crop (Mayr, 2013a). Perhaps the early mousebirds fed on hard food and had the ecology of parrots. Mousebirds have been related to parrots, passerines, and owls in various phylogenetic analyses (Mayr, 2011a; McCormack *et al*., 2013).

One subclade of Telluraves emerges in numerous morphological and molecular phylogenetic studies, the Picocoraciae (Mayr, 2011a), or so-called CPBT clade, named after its main members, the Coraciiformes, Piciformes, Bucerotes and Trogoniformes. The Coraciiformes, bee-eaters, rollers and kingfishers, have included other taxa now associated phylogenetically with other picocoracian subclades. Their fossil record extends back to the Eocene in Europe (Mayr, 2009). The Piciformes, over 400 species of woodpeckers and toucans, date back to the Miocene of Europe and Eocene of North America, with early forms such as the coraciid *Primobucco* from the Green River Formation (Figure 9.19(e); Ksepka and Clarke, 2010b). The remaining picocoracian subclades, Bucerotes (hoopoes and hornbills) and Trogoniformes (trogons) both date back to the late Eocene of France (Mayr, 2009).

Many members of the Telluraves share adaptations for grasping branches with the songbirds. In most birds there are three toes in front (numbers 2–4) and a small one (1) behind (Figure 9.19(f)), ideal for running on the ground, but more or less useless for perching. This posterior toe is enlarged in songbirds in order to help them grasp small branches (Figure 9.19(g)). Some perching forms, such as the woodpeckers, also have the outer toe (4) pointing backwards as well to improve their grip, the **zygodactyl** condition (Figure 9.19(h)).

The Passeriformes or passerines consist today of 5800 species of songbirds such as robins, thrushes, sparrows, crows, as well as tyrant flycatchers and antbirds, representing 60% of all living bird species. Large-scale phylogenetic analysis (Barker *et al*., 2004; Ericson *et al*., 2014) highlights a series of divergences among passerines. First, the Acanthisittidae, the New Zealand 'wrens' branch off, then the Old World suboscines (broadbills and relatives) and New World suboscines (tyrant flycatchers, antbirds, and relatives), and the oscines. The oscines comprise some basal families from Australia (lyrebirds, fairy wrens, honeyeaters), and then two large clades, the Corvoidea (crows, orioles, shrikes, and relatives) and Passerida (larks, swallows, warblers, tits, starlings, wrens, sparrows, finches, buntings).

The concentration of Australasian clades low in the phylogenetic tree suggests (Barker *et al*., 2004) multiple waves of oscine dispersal from Australasia into Eurasia, Africa, and the New World. The traditional division of passeriforms into corvids (crows and relatives) originating in the Australo-Papuan region, and passerids (all other songbirds) originating in the Afro-Eurasian region is incorrect. The two major subclades of Passeriformes trace their origins to New Zealand on the one hand, and to New Guinea/Australia on the other.

The fossil record now confirms this palaeobiogeographic model. For a long time, the oldest passeriform finds came from the early Oligocene and early Miocene of Europe (Manegold, 2009; Mayr, 2009), with worldwide finds of most of the modern families from the middle and late Miocene and Pliocene. Limited southern hemisphere fossil sites meant that the early Tertiary history of Passeriformes was unknown until various lineages penetrated the northern hemisphere in the Oligocene and Miocene. However, the first passeriform fossils are now known from the earliest Eocene of Australia, a partial carpometacarpus and tibiotarsus that show passerine features (Boles, 1995 Mayr, 2013b).

The open question, as with the origins of Neornithes (see Section 9.4), is when did it all happen? Molecular results suggest that much of the deep splitting among passerines happened in the Late Cretaceous and was associated with the breakup of Gondwana (Barker *et al*., 2004; Ericson *et al*., 2014). However, such a model consistently predates the oldest fossils by 30 Myr or more; a literal reading of the fossil record implies that the splitting among passerines happened at various times in the Eocene, Oligocene, and Miocene (Mayr, 2013b).

More broadly, systematists are still wrestling with the phylogeny of the landbird clade. One solution (Ericson, 2012) has been to identify a clade with broadly Australasian origins and one with African origins, termed respectively the Australaves ('southern birds') for the clade with falcons, cariamas, passerines and parrots, and Afroaves ('African birds') for the clade that consists of all coraciiform and piciform birds, owls, diurnal

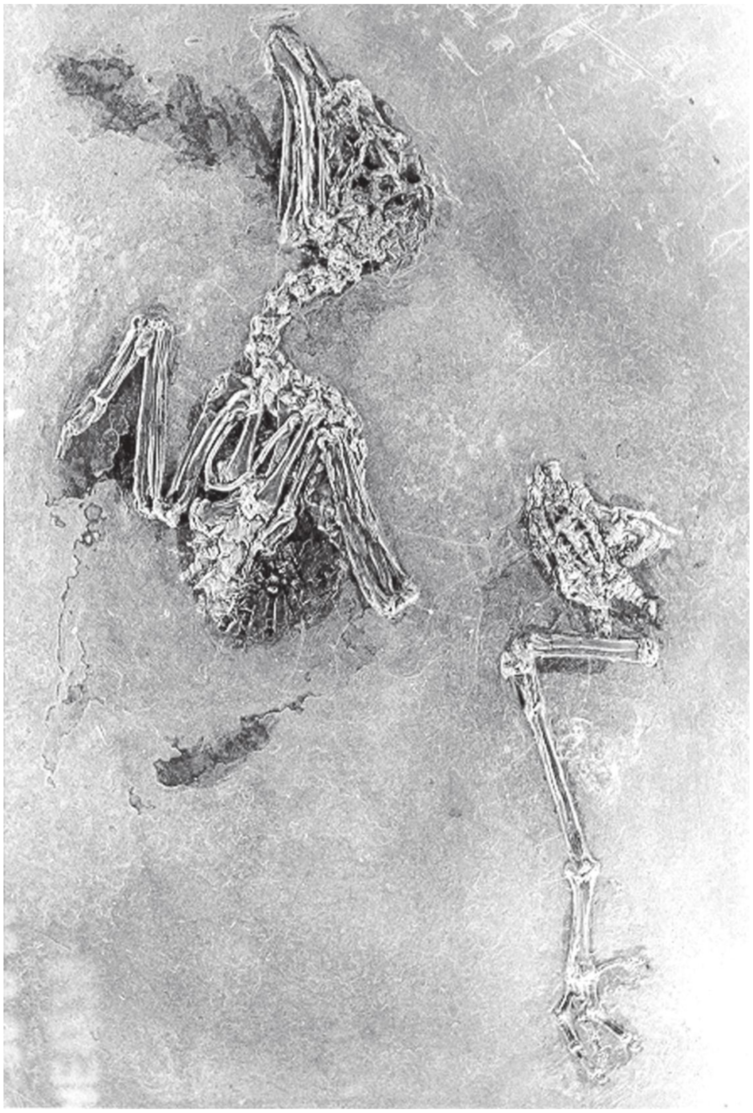


Figure 9.20 The early parrot *Psittacopes*, from the Middle Eocene lake-beds of Messel, Germany. The skull shows the familiar large, bulbous head with shortened, downcurved beak. The backbone curves down and the wings are spread out to the side. The pelvic girdle and hindlimb have broken away to the lower right. The Messel oil shales have produced early representatives of at least 13 of the 24 orders of birds, a richness matched only by the mammals (see Box 10.8). Source: G. Mayr, Senckenberg Institute, Frankfurt, Germany. Reproduced with permission.

raptors (except falcons), New World vultures, trogons, mousebirds and cuckoo-rollers. If this phylogeny is confirmed, then the division mimics to some extent some major mammal clades, and key splitting events can be tied to ancient geographic distributions.

9.7 THE THREE-PHASE DIVERSIFICATION OF BIRDS

Birds have shown an unusual pattern of evolution, and this has become evident only recently thanks to improvements in the fossil record and numerical studies of large phylogenies. Their evolution is commonly interpreted as if it were a single event or process, with the origin of powered flight acting as the trigger for continued and substantial diversification. At the same time, they have commonly been classed as a group with a poor fossil record which cannot show much of that story.

In fact, the data tell a rather different story. There were at least three bursts of substantial diversification among birds, and this is confirmed by both fossils and by phylogenomics.

1 First was the Mesozoic radiation, starting with *Archaeopteryx* and close relatives in the Late Jurassic, and continuing with the Enantiornithes and other clades throughout the Cretaceous. The KPg mass extinction then terminated a number of these successful non-neornithine clades, and a limited number of species passed through into the Paleogene (see Section 9.4.2).

2 The second major burst of avian evolution happened in the Paleogene, with most modern orders originating in the

Palaeocene or Eocene, and diversifying substantially some 60–50 Myr ago (see Box 9.5).

3 Finally, several clades, most notably the Passeriformes, showed apparently explosive diversification in the Miocene, perhaps 20–15 Myr ago.

These three phases can be explored further. The Cretaceous expansion of birds was part of the **Cretaceous Terrestrial Revolution** (KTR), the upheaval in terrestrial ecosystems caused by the diversification of angiosperms, the flowering plants (Lloyd *et al*., 2008). The explosive radiation of angiosperms from 125 to 80 Myr ago completely rebuilt terrestrial ecosystems, and provided opportunities for pollinating insects, leaf-eating flies, as well as butterflies and moths, all of which diversified rapidly. These in turn provided new food resources for insect-eating arthropods and other invertebrates, as well as lizards and snakes, mammals, and birds. It is likely that the great diversification of bird groups such as confuciusornithiforms, enantiornithines, and ornithines in the mid-Cretaceous was linked in part at least to the KTR. The major radiation of birds in the Early Cretaceous is marked by a switch to short tails in Pygostylia (see Section 9.3.1) and a burst in hindlimb evolutionary diversification (Benson and Choiniere, 2013). Whether of course these diversifying clades included modern bird orders is very much open to debate (see Section 9.4). The KTR marked the point at which life on land became more diverse than life in the sea (Benton, 2010; Vermeij and Grosberg, 2010).

The second phase of avian diversification is detected from the exploration of large phylogenetic trees. Numerical methods to identify diversification shifts (see Section 2.7) have highlighted that the bulk of modern vertebrate biodiversity, for example, is accounted for by a relatively small numbers of clades. Alfaro *et al*. (2009) identified that 85% of the modern biodiversity of species of jawed vertebrates is accounted for by six clades, three of fishes (Euteleostei, Ostariophysi, Percomorpha; see Section 7.5), and three of tetrapods: non-gekkonid squamates (i.e. most lizards), Neoaves (most modern birds), and Boreoeutheria (most eutherian mammals). The roots of neoavian radiation occurred in the Late Cretaceous and/ or Paleogene, depending on how the fossils and phylogenies are dated.

The third burst of avian radiation was primarily among Passeriformes, representing today over half the 10,500 species of birds. The fossils indicate that passeriforms originated in the Palaeocene or earliest Eocene, but remained at low diversity until they radiated explosively in the Miocene (see Section 9.6.7). Dating the tree according to assumptions about the breakup of Gondwana as the driver (e.g. Barker *et al*., 2004; Ericson *et al*., 2014) brings the date of passeriform diversification down from the Neogene to the Late Cretaceous and Paleogene, but this was contested by Mayr (2013b). These issues of dating have yet to be resolved.

In a comprehensive study of diversification shifts among birds, Jetz *et al*. (2012) find that birds have undergone a strong increase in diversification rate from 50 Myr ago to the near present. This acceleration is a combination of many significant rate increases, primarily among songbirds, but also a number of other young and mostly temperate radiations including the waterfowl, gulls, and woodpeckers. These authors found that modern bird faunas in Asia, North America, and southern South America contain a disproportionate number of species from recent rapid radiations.

Central to many of these debates about patterns and dating of avian evolution is the question of the quality of the fossil record of birds. The problem is that there is no sure way to determine whether the bird fossil record is reasonably informative or not. On the one hand, the massive increase in knowledge of Mesozoic birds brought about by the discoveries in China (see Box 9.4) suggests that further chance discoveries might similarly change things. Equally, it is true to say that the Chinese discoveries, even though they have multiplied the number of good quality Mesozoic bird specimens from 40 or 50 worldwide to more than 5000, have simply added detail to the phylogeny; they have not overturned it. Nor have the Jehol beds, for example, yet yielded any examples of modern bird clades.

Comparisons of changes in knowledge of bird evolution through time, as well as comparisons of fossil counts with records of fossiliferous rocks confirm that the bird fossil record is not fantastic (e.g. Fountaine *et al*., 2005; Brocklehurst *et al*., 2012). However, the bird fossil record is *adequate* for many kinds of detailed anatomical studies and for reconstructing phylogenetic trees because individual fossil specimens often show considerable detail. The open question at present is whether the record is good enough to provide adequate dates for the origins of particular clades (see Section 9.4), or whether the early representatives were so rare or geographically restricted that we lack information in many cases for the first 20–50 Myr of evolution of those clades.

9.8 FURTHER READING

There are several ornithology texts that focus mainly on living birds: Proctor and Lynch (1998), Gill (2006), and Scott (2010) provide detailed accounts of bird diversity (including fossils forms) and on bird anatomy, and Kaiser (2007) is an imaginative introduction to bird anatomy. Chiappe and Witmer (2002) and Dyke and Kaiser (2011) offer collections of papers on Mesozoic bird evolution, and Mayr (2009) is an introduction to Paleogene fossil birds. Martyniuk (2012) provides a novel 'field guide' to the Mesozoic birds and their relatives. There are many wonderful illustrated guides to the Jehol fossils, but Chang (2008) is probably the best.

Everything about modern birds and their classification can be found at the Encyclopedia of Life bird pages: http://eol.org/pages/695/overview.

http://avibase.bsc-eoc.org/avibase.jsp?lang=EN&pg=home is a searchable index of all 10,000 plus species of living birds. A list of fossil birds is at: http://en.wikipedia.org/wiki/List_of_fossil_birds.

QUESTIONS FOR FUTURE RESEARCH

1 What are the relationships of paravians around the origin of birds? New morphological characters are needed to help resolve the phylogeny.
2 How do claw shape and other characters distinguish between climbers, ground-dwellers, and other life modes? Can such measurements shed light on paravian locomotory modes?
3 What were the different modes of flight in early paravians, and how did these flight modes relate to each other and to the flapping flight of modern birds?
4 What are the relationships of the basal long-tailed birds that came before the evolution of the pygostyle?
5 What was the sequence of changes in the flight apparatus after *Archaeopteryx*, and how did these change the flight capabilities of various Cretaceous birds?
6 How did the Cretaceous birds specialize in different feeding modes, and so divide up ecospace?
7 What were the key adaptations of Enantiornithes, reasons for their success, and then reasons for their demise at the end of the Cretaceous?
8 How did ornithuromorph birds diversify?
9 When did modern birds (neornithines) arise, and when did the modern orders diversify? What was the role of the KPg mass extinction in the transition from pre-neornithine to neornithine birds?
10 How did palaeognath birds evolve? Are they a Gondwana radiation? We need many more Cretaceous and Paleogene fossils.
11 Have galloanserines always been poor flyers?
12 What are the relationships of Neoaves? What are the main subclades?
13 Why are some bird clades such as Passeriformes so diverse, and others are not?

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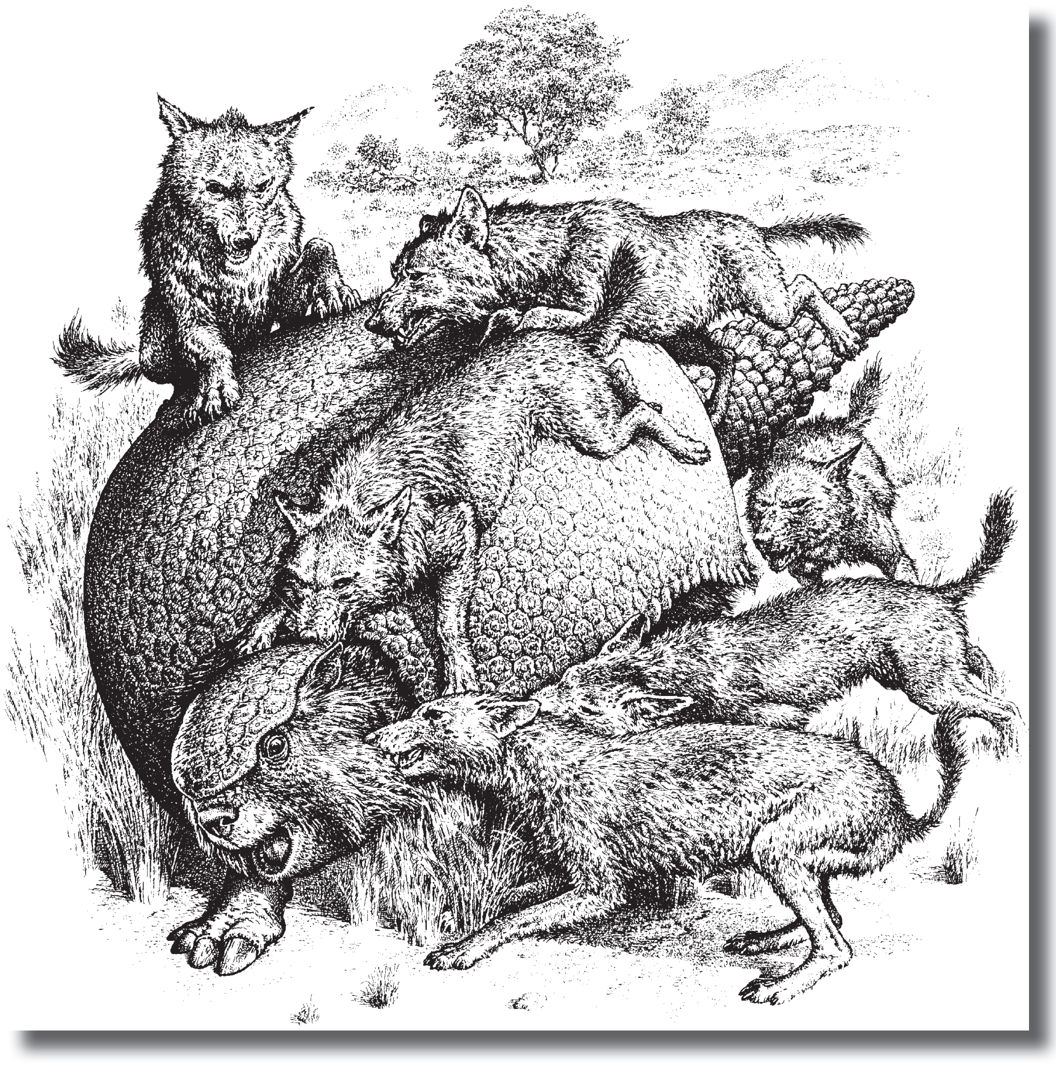
CHAPTER 10

Mammals



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KEY QUESTIONS IN THIS CHAPTER

1 How did mammals originate?
2 How were basic 'mammalian' characters acquired through the evolution of Permian and Triassic cynodonts?
3 Why were mammals so rare in the Mesozoic?
4 How are the modern mammalian groups, the monotremes, marsupials and placentals related to each other, and what are their closest Mesozoic relatives?
5 Why do marsupials today live only in Australasia and the Americas?
6 Why does South America have its own unique faunas of mammals?
7 Was Africa once isolated from other continents?
8 What are the closest living relatives of elephants?
9 Are there major disagreements between molecular and morphological evidence about the phylogeny of placental mammals?
10 Was the history of Cenozoic mammals affected by climate and vegetation change?
11 Was the ancestor of whales like a dog or a pig?
12 Why were perissodactyls so big and diverse in the past, but not now?
13 How big can a rodent be?
14 What are the closest living relatives of primates?
15 Were the large Pleistocene mammals killed by human hunters or by climate change?

INTRODUCTION

Modern mammals are easy to identify. They have hair, they generally have large brains, they feed their young on milk from mammary glands (hence the name 'mammals') and they care for their young over extended periods of time. In the Late Triassic, when mammals arose, the boundary line between mammals and non-mammals was much less clear. Indeed, a succession of Triassic carnivorous synapsids, the cynodonts, successively acquired 'mammalian' characters over 30–40 Myr, and it is an arbitrary choice where we draw the line between non-mammalian synapsids and mammals.

There is a debate about terminology in identifying the extent of the clade Mammalia. The traditional view is to place the base of the clade at a node from which *Morganucodon* and the other morganucodonts branched off the cynodont lineage. This node is associated with the acquisition of a 'key' mammalian character, the single dominant jaw joint between the dentary and squamosal bones. The strength of the traditional view is that it follows 200 years of practice by palaeontologists and allows us to call the small furballs of the Mesozoic mammals, but the weakness is that the *Morganucodon* node, or any other node is arbitrary. The alternative is to use major clade names such as Mammalia for the crown group only; that is, the clade that minimally encompasses all living mammals in this case. Crown-group Mammalia then is considerably smaller than traditional Mammalia, and this concept has the great advantage of having a clear definition: for example, 'the most recent common ancestor of all modern mammals (e.g. from platypus to human) and all of its descendants'. If the name Mammalia moves up the tree, then the *Morganucodon* node is named Mammaliaformes. The weakness of the crown-group concept is that, while clearly defined, it is extremely flexible as to content, moving up and down the tree substantially depending on the particular cladogram of Mesozoic mammals that is accepted, and where among these the monotremes fit. For the present, I use the traditional term, but will include crown-group terms in cladograms (e.g. Boxes 10.1, 10.3).

10.1 CYNODONTS AND THE ACQUISITION OF MAMMALIAN CHARACTERS

Cynodonts first appeared in the Late Permian, when forms such as *Procynosuchus* already showed mammalian characters in the cheek region and palate and in the lower jaw. During the Triassic, several cynodont families appeared, mostly weasel-sized to dog-sized carnivores, but including some major herbivorous clades. As cynodonts diversified through the Late Permian and Triassic, they acquired a large number of the characters commonly identified as 'mammalian' (see Box 10.1).

10.1.1 The first cynodonts

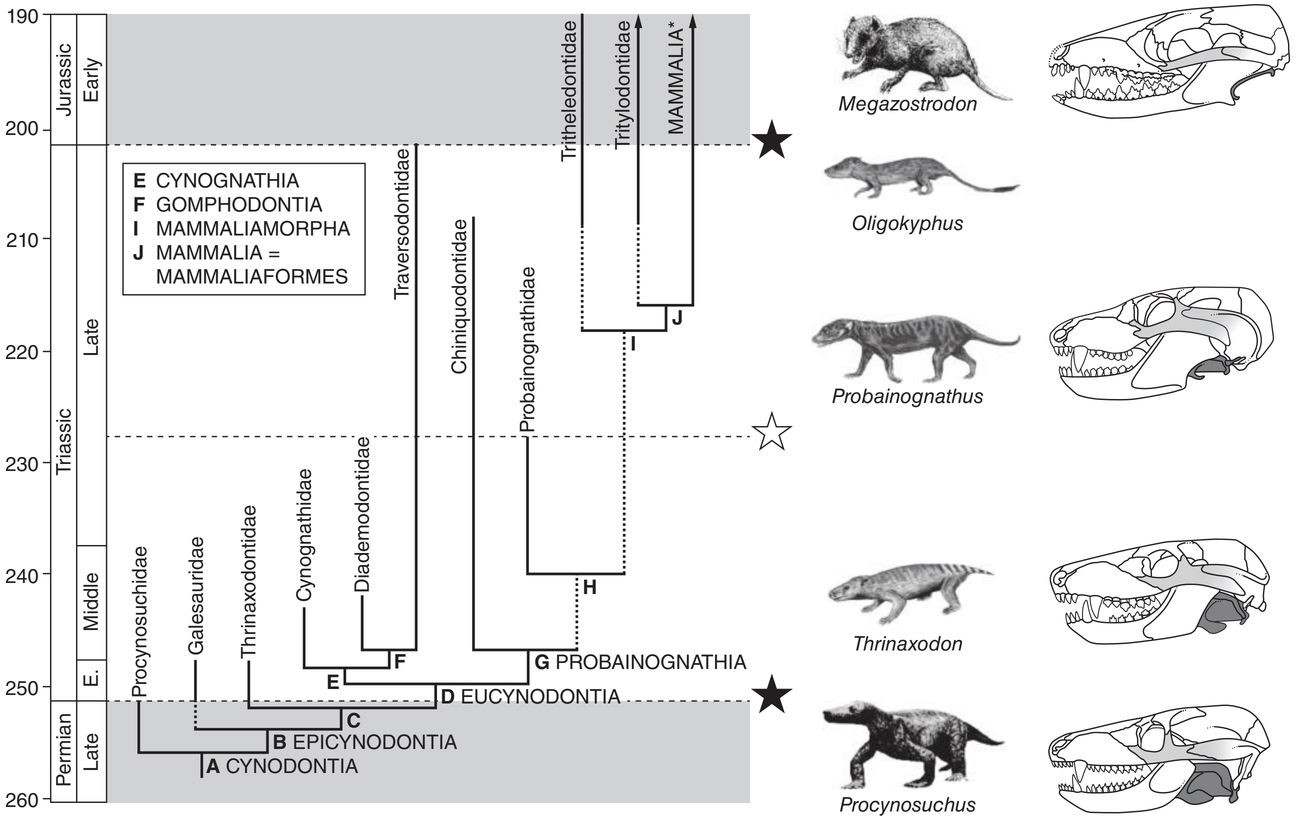
The first cynodonts include three Late Permian genera, *Charassognathus* from South Africa, *Procynosuchus* from South Africa, Tanzania, Zambia, Russia, and Germany, and *Dvinia* from Russia (Botha *et al*., 2007; Ivakhnenko, 2013). These show largely plesiomorphic conditions of other Permian synapsids (see Section 5.6), but with some derived features, especially in the skull. *Procynosuchus* for example (Figure 10.1(a)) was capable of both sprawling and semi-erect posture, but retains the largely lateral flexibility of the vertebral column, and a series of ribs running well back into the lumbar area.

The skulls are more derived, showing the diagnostic cynodont features of a contact between the nasal and lacrimal, and the frontal excluded from the orbital margin (Figure 10.1(b)). There is a double occipital condyle, a classic mammalian character. Other features in the lower jaw also point towards later cynodonts including mammals, such as the dentary angle lying below the postorbital bar and a reflected lamina on the angular, a vertical plate on the postero-ventral margin of the element, seen also in earlier synapsids (see Section 5.6.3). Importantly, the notch at the base of the coronoid process in *Charassognathus* is the first indication of an invasion of occlusal musculature onto the dentary (Botha *et al*., 2007).

Even these earliest of cynodonts are generally restored with hair (Figure 10.1(c)). This is based on the observation of multiple tiny foramina over the snout region, which have generally been interpreted as passages for multiple nerves. The argument

BOX 10.1 CYNODONT PHYLOGENY

The evolution of cynodonts through the Late Permian to Jurassic has been established as a result of some classic cladistic analyses (e.g. Kemp, 1982; Hopson and Kitching, 2001), and confirmed by more recent work (e.g. Abdala, 2007; Botha *et al*., 2007; Liu and Olsen, 2010; Ruta *et al*., 2013). There was a succession of clades through the Late Permian and Early Triassic, the survivors of the Permo-Triassic mass extinction being the Epicynodontia. There was then a substantial diversification of the major clades Cynognathia and Probainognathia in the Middle Triassic. The Cynognathia continued to the end of the Triassic when the clade finally disappeared, whereas Probainognathia gave rise to traditional Mammalia, as well as Tritheledontidae and Tritylodontidae, all of which continued into the Jurassic. Relationships among these three mammaliamorph taxa are unresolved.



Synapomorphies are from Botha *et al*. (2007) for basal taxa, and Hopson and Kitching (2001), Abdala (2007), and Liu and Olsen (2010) for the remainder (convergences marked*): **A CYNODONTIA**, contact between nasal and lacrimal, frontal excluded from the orbital margin, double occipital condyle, angle of dentary at same level or posterior to postorbital bar, reflected lamina of angular a smooth plate with slight depressions, notch at base of coronoid process; **B EPICYNODONTIA**, facial process of septomaxilla short, interpterygoid opening absent, zygomatic arch moderately deep dorsoventrally, lateral crest of dentary incipient, masseteric fossa in dentary extends to the angle; **C**, foramen incisivum present, maxilla covers vomer in palatal view, bony palate complete, foramen on external surface of lower jaw between dentary and angular absent, reflected lamina of the angular hook-like; **D EUCYNODONTIA**, lateral crest of dentary well developed, dentary–surangular dorsal contact closer to cranio-mandibular joint, surangular–squamosal articulation with mandible reduced, upper postcanine series extends below orbit; **E CYNOGNATHIA**, carotid artery foramen in basisphenoid absent, canine serrations, lateral crest of dentary well developed, zygomatic arch very deep, infraorbital process is descendant process of jugal, posterior extension of squamosal dorsal to squamosal sulcus well developed; **F GOMPHODONTIA**, inferior margin of jugal in the zygomatic arch is well developed and high, upper tooth series extends below orbit*, postcanine occlusion by tooth-to-tooth contact because of widened postcanines, upper postcanine teeth widened*, transverse crest in upper postcanines with two cusps; **G PROBAINOGNATHIA**, bony palate extends to posterior margin of tooth row or behind, ectopterygoid absent, upper tooth series extends below orbit*; **H**, incipient maxillary platform lateral to dentition in posterior portion of the teeth row, upper postcanine teeth widened*, posterior postcanine teeth lack a strongly curved main cusp; **I MAMMALIAMORPHA**, prefrontal absent, postorbital bar absent, paroccipital process differentiated into anterior and posterior processes, mediolateral thickening of anterior margin of coronoid process, mandibular symphysis unfused, zygomatic arch slender, upper postcanine teeth have buccal cingulum; **J MAMMALIA**, fusion of prootic and opisthotic at an early ontogenetic stage, lateral flange vascular canal present venous drainage exiting from the back of the cavum epiptericum, completely divided postcanine roots. Source: Cynodont restorations adapted from various sources. Skulls drafted by S. Mitchell in Ruta *et al*. (2013). Abbreviations: E, Early. Dashed lines and star symbols indicate extinction events.

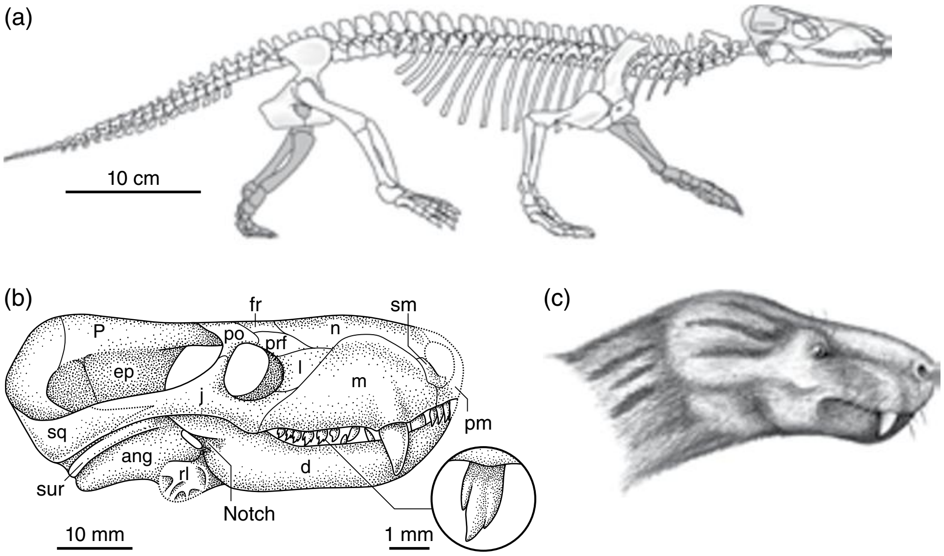


Figure 10.1 Late Permian cynodonts: (a) *Procynosuchus*, (b) *Charassognathus* skull reconstruction, (c) *Charassognathus* life restoration. Abbreviations: ang, angular; d, dentary; ep, epipterygoid; fr, frontal; j, jugal; l, lacrimal; m, maxilla; n, nasal; p, parietal; pm, premaxilla; po, postorbital; prf, prefrontal; rl, reflected lamina; sm, septomaxilla; sq, squamosal; sur, surangular. Source: (a) J. Merck, T. Rowe and the University of Texas Digital Morphology Group, Texas, USA. Reproduced with permission. (b) Botha *et al.* (2007). Reproduced with permission from John Wiley & Sons. (c) © Mojcaj/CC-BY-SA-3.0/GFDL.

is that early cynodonts had sensory whiskers on their snouts, each supplied with a nerve, and that if they had whiskers, they must have had hair more generally.

After the Permo-Triassic mass extinction (see Section 5.7), one or more cynodont lineages survived, and the clade Epicynodontia began its Triassic diversification (see Box 10.1). The galesaurids, five or six species from the Early Triassic of South Africa such as *Galesaurus* (Figure 10.2(a)), had large temporal openings and a substantial secondary palate. Their limbs allowed them to sprawl or to stand and run in an erect posture.

Thrinaxodon from the Early Triassic of South Africa (Figures 10.2(b), 10.3(a)) shows more derived, mammal-like characters than the Late Permian cynodonts. For example, there is a well-marked **sagittal** crest, a ridge running down the midline of the skull roof; the **zygomatic arch**, beneath the orbit and formed from the jugal and the squamosal, follows a wide curve and bends up a little; the dentary makes up most of the lower jaw and it sends a high **coronoid process** up inside the zygomatic arch; the numbers of incisors are reduced to four above and three below (other cynodonts, including early mammals and some living marsupials may retain four or five incisors); the cheek teeth are elaborated; and the secondary palate is nearly complete, formed by the medially directed plates of the maxillae and palatines in the roof of the mouth below the nasal passage. Many of these characters relate to an increased volume of jaw muscles, which allowed more efficient food processing, perhaps necessary to sustain a more mammal-like metabolic rate.

Thrinaxodon shows further major changes towards the mammalian condition (Jenkins, 1971a). It has double occipital condyles (Figure 10.3(a,c)) as in mammals, whereas typical reptiles, including the early synapsids, have a single occipital condyle (Figure 10.3(b)). The vertebrae of *Thrinaxodon* (Figures 10.2(a), 10.3(a)) also show mammal-like features. The

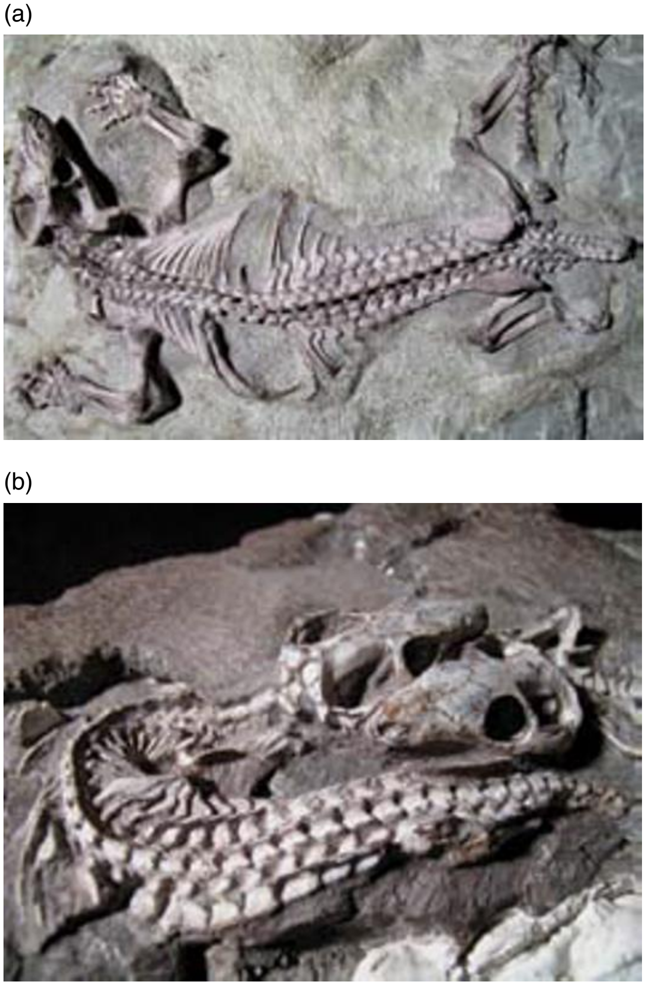


Figure 10.2 Early Triassic cynodonts: (a) *Galesaurus*, (b) two juveniles of *Thrinaxodon*. See Colour plate 10.1. Source: R. Smith, Iziko Museum of Natural History, Cape Town, South Africa. Reproduced with permission.

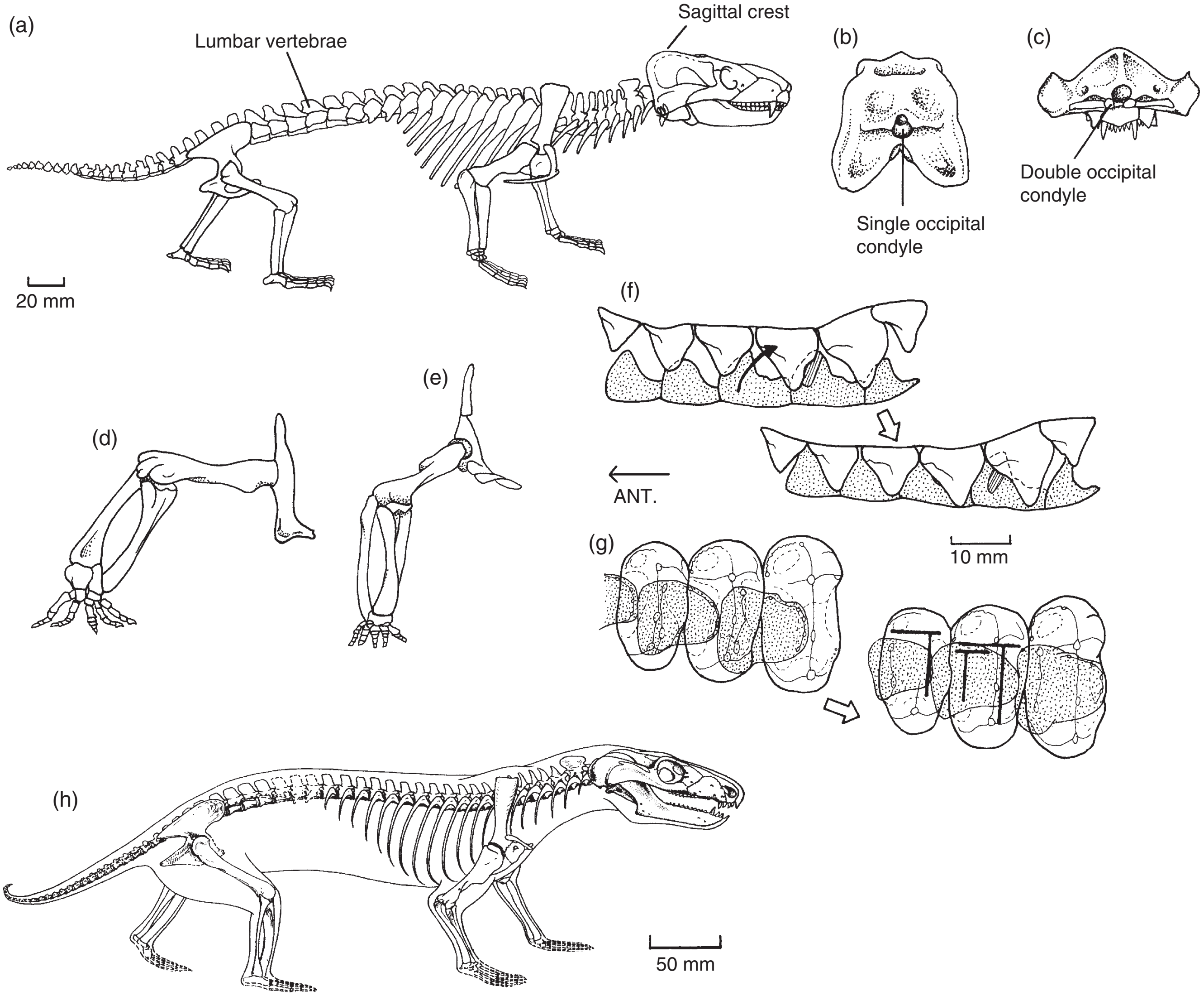


Figure 10.3 Early and Middle Triassic cynodonts: (a) skeleton of the thrinaxodontid *Thrinaxodon*; (b,c) splitting of the single generalized amniote occipital condyle, seen in (b) early synapsids, into (c) two in later cynodonts; (d,e) postural evolution; (d) the sprawling hindlimb of an early synapsid and (e) the semi-erect hindlimb of a cynodont; (f,g) tooth occlusion in the traversodontid gomphodont *Scalenodon*, showing the final stages of jaw closing and firm occlusion, in lateral view (f), and occlusal views of the same two jaw positions to show the backwards and sideways slide of the lower teeth (stippled) across the much broader upper teeth (g); in all cases, the front of the mouth is on the left (ANT, anterior); (h) skeleton of the traversodontid *Massetognathus*. Source: (a–e) Adapted from Jenkins (1971a). (f,g) Adapted from Crompton (1972). (h) Adapted from Jenkins (1970).

dorsal vertebrae and ribs are divided clearly into two sets, the 13 **thoracic** vertebrae in front and seven **lumbar**, or lower back, vertebrae behind, the latter of which have short ribs fused to the vertebrae, unlike the longer, more mobile ribs of earlier forms. The tail is long and slender, much like that of a cat.

Innovations in the hindlimb and pelvic girdle of *Thrinaxodon* and later forms are associated with a major shift in posture in the Early Triassic. This postural shift, from sprawling to erect, was paralleled in synapsids (primarily cynodonts) and archosaurs through the Triassic, and may have been triggered by the Permo-Triassic mass extinction (see Box 6.3). Early synapsids, like most basal tetrapods and most lizards today, had a sprawling posture, with the limbs held out sideways and the belly just above the ground, whereas *Thrinaxodon*, as with earlier therapsids, shows a more erect or upright posture with the hindlimbs pulled in closer to the body. This resolved a conflict between breathing and running at the same time that had to be faced by sprawling therapsids, and allowed the effective stride length to increase. The major joints changed their orientation and the shapes of the ends of the limb bones were much altered (Figure 10.3(d,e)). The hip bones are also very different in shape because of changes in the layout of the leg muscles. The new primary hindlimb retractor was the **gluteal** muscle, the main component of the human buttocks and not a generalized amniote feature. The pubis and ischium of *Thrinaxodon* (Figure 10.3(a,e)) are reduced in size and they extend back a little, and the blade of the ilium is relatively large, especially in front.

After the divergence of *Thrinaxodon*, the major cynodont clade, Eucynodontia (see Box 10.1), expanded rapidly in the later Early Triassic and Middle Triassic. Eucynodonts show modifications to the lower jaw and jaw joint, with increasing emphasis on the dentary and reduction of the articular-quadrate jaw joint. Eucynodontia divided into two clades, Cynognathia and Probainognathia. Cynognathia comprises *Cynognathus* and Gomphodontia, a clade of herbivorous forms (see Section 10.1.2). *Cynognathus* from the early Middle Triassic of South Africa has a dentary that makes up more than 90% of the length of the lower jaw, and the bones behind the dentary form a narrow rod that lies in a groove inside the dentary. The cheek teeth show wear from processing meat.

10.1.2 Gomphodontia: the herbivorous cynodonts

Cynodonts were generally carnivores, but several Triassic lineages became secondarily herbivorous: the diademodontids, traversodontids and tritylodontids. At one time, these were grouped phylogenetically (e.g. Hopson and Kitching, 2001) as they all share expanded cheek teeth and precise occlusion between those teeth. These are adaptations for grinding plant food and they are absent in the other cynodonts, but the bulk of phylogenetic evidence shows that chiniquodontids and tritylodontids are probainognathians, and the shared features of the teeth are convergences (see Box 10.1; Abdala, 2007; Liu and Olsen, 2010; Ruta *et al*., 2013).

Gomphodontia includes the diverse and successful diademodontids and traversodontids (see Box 10.1). The diademodontids from the Early and Middle Triassic of Africa and South America, such as *Diademodon*, were modest-sized animals. In the palate, the ectopterygoid is tiny. The cheek teeth of *Diademodon* occlude extensively, the smaller lower tooth forming a deep facet in the broad upper tooth. **Occlusion** (precise fitting of the upper and lower wear facets, is seen in diademodontids, traversodontids, and tritylodonts, as well as in mammals. This marks a major step towards the mammalian feeding mode. The ability to occlude meant that these animals could chew their food and thus they could modify their tooth types to match a broad range of specialized diets for the first time in tetrapod history.

Occlusion is well developed in *Scalenodon*, a traversodontid from the Middle Triassic of Tanzania (Figure 10.3(f,g)). The jaw cycle ends with a pronounced backwards pull of the lower jaw, and a powerful shearing and crushing movement is initiated in which all seven lower cheek teeth move tightly back into curved facets of the broad upper cheek teeth. Food items are sheared by a double cutting system, between the raised transverse ridges of lower and upper teeth, and between longitudinal ridges on the external side of both sets of teeth. Finally, as the backwards movement ends, the main faces of both teeth nearly meet and any food particle caught between would be crushed effectively.

The traversodontids, known particularly from the Middle and Late Triassic of South America, as well as from southern Africa, Madagascar, India, North America and Europe (Abdala and Ribeiro, 2003), were the most successful herbivorous cynodonts, with more than 20 species. *Massetognathus* and *Scalenodon* from the Middle Triassic of South America were present in vast numbers, foraging for tough vegetation at the feet of the large dicynodonts. In the skeleton (Figure 10.3(h)), *Massetognathus* has an erect mammalian hindlimb and sprawling generalized amniote forelimb. The traversodontids survived to the end of the Triassic, with forms such as *Exaeretodon* and *Scalenodontoides* in South America, South Africa, and India.

10.1.3 Probainognathia

The probainognathians (see Box 10.1) include largely carnivorous forms, and among them the immediate ancestors of mammals. The chiniquodontids (Abdala and Giannini, 2002) were small and medium-sized carnivores that became immensely abundant, especially in the Middle Triassic. They have large heads, a long trunk and a long tail (Figure 10.4(a)). The limbs are short and adapted for rapid movement, and the chiniquodontids could probably have twisted and turned in pursuit of prey as actively as any modern weasel.

The chiniquodontids show additional mammal-like features such as the absence of the parietal foramen, a secondary palate that is longer than in earlier forms, a deep zygomatic arch, and a further increase in the volume of the jaw muscles. In the skeleton (Figure 10.4(a)), the lumbar ribs are reduced (such ribs are

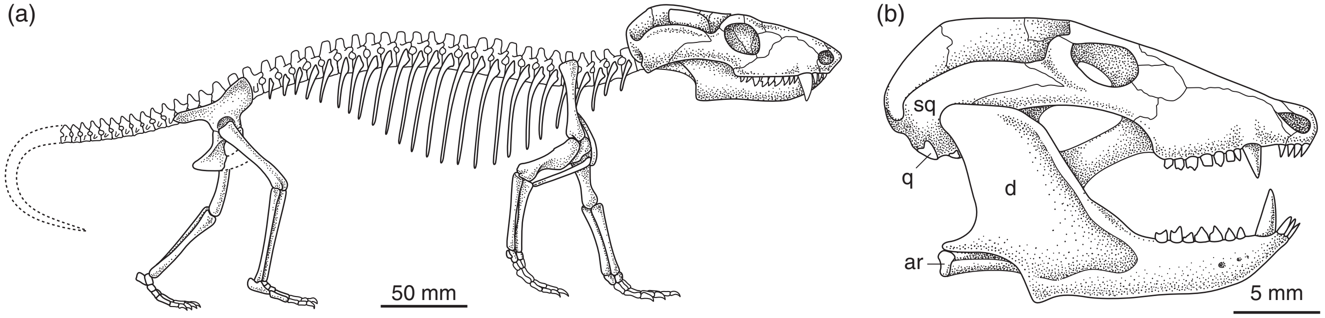


Figure 10.4 Probainognathian evolution: (a) skeleton of the chiniquodontid *Chiniquodon* (formerly *Probelesodon*); (b) skull of *Probainognathus*. Abbreviations: ar, articular; d, dentary; q, quadrate; sq, squamosal. Source: (a) Adapted from Romer and Lewis (1973). (b) Adapted from Romer (1970).

absent in mammals), which might indicate the evolution of a **diaphragm**. In modern mammals, the diaphragm is a tough sheet of muscle that separates the chest region from the abdomen and improves breathing efficiency, essential for the maintenance of a high metabolic rate. The reduced lumbar ribs of Middle and Late Triassic eucynodonts suggest they too had high metabolic rates.

Chiniquodon shows postural advances over *Thrinaxodon*, having its hindlimbs locked into a fully erect mammalian posture. The femur could only swing back and forwards in a **parasagittal** plane, that is, parallel to the midline axis of the body. The main change is that the acetabulum in *Chiniquodon* and later cynodonts is deeper than in *Thrinaxodon*, and the articulating head of the femur is bent more inwards. This mammalian posture seems to have arisen in *Cynognathus* and *Diademodon*, and it is a characteristic of mammals and, independently, of derived archosaurs, dinosaurs and birds (see Box 6.3). Tom Kemp (1982) compared these cynodonts to a wheelbarrow, where the hindlimbs stride along in an erect posture and the more sprawling forelimbs are forced to move rapidly to keep ahead.

Probainognathus from the same beds as *Chiniquodon*, and yet more derived than the chiniquodontids (see Box 10.1), has a low zygomatic arch, additional cusps on the cheek teeth and a second jaw joint (Figure 10.4(b)). Incredible as it may seem, *Probainognathus* and some other advanced cynodonts have a double jaw joint (see Box 10.2). Other characters of *Probainognathus* and subsequent cynodonts relate to modifications in the development of the brain.

Subsequent probainognathians are the tritheledonts, tritylodonts, and mammals (see Section 10.1.5).

10.1.4 Cynodonts: steps to increasing mammal-ness

Triassic cynodonts document the transition from reptile to mammal with exquisite detail. As a series of closely spaced fossils, continuing modifications of all parts of the skull and skeleton can be tracked, with especial changes occurring in the jaws, ear, palate, teeth, jaw muscles, braincase, and limbs.

Most astonishing is the transformation of the reptilian jaw joint into part of the mammalian hearing system (see Box 10.2). In modern reptiles, the jaw joint is between the quadrate at the back of the skull and the articular at the back of the lower jaw. In modern mammals, the jaw hinges on a new joint between the squamosal and the dentary. Fossil intermediates show how the transition happened: two reptilian jaw bones shifted into the middle ear. At the same time, a new bony process arose from the rear of the dentary, formed a contact with the squamosal, and eventually became the sole jaw joint. The migration of these small bones

BOX 10.2 JAW JOINT TO MIDDLE EAR

One of the most spectacular evolutionary transitions is the modification of the ‘reptilian’ jaw joint of basal cynodonts into two of the three ear ossicles of mammals (Allin, 1975; Kemp, 2005; Takechi and Kuratani, 2010; Luo, 2011). The jaw joint in *Thrinaxodon* (illustration I(a,c)) is between the quadrate in the upper jaw and articular in the lower jaw, as in the generalized gnathostome condition, but the quadrate is much reduced. The surangular, just behind the coronoid process of the dentary, comes very close to the squamosal, and the stapes touches the quadrate, as in gnathostomes more widely.

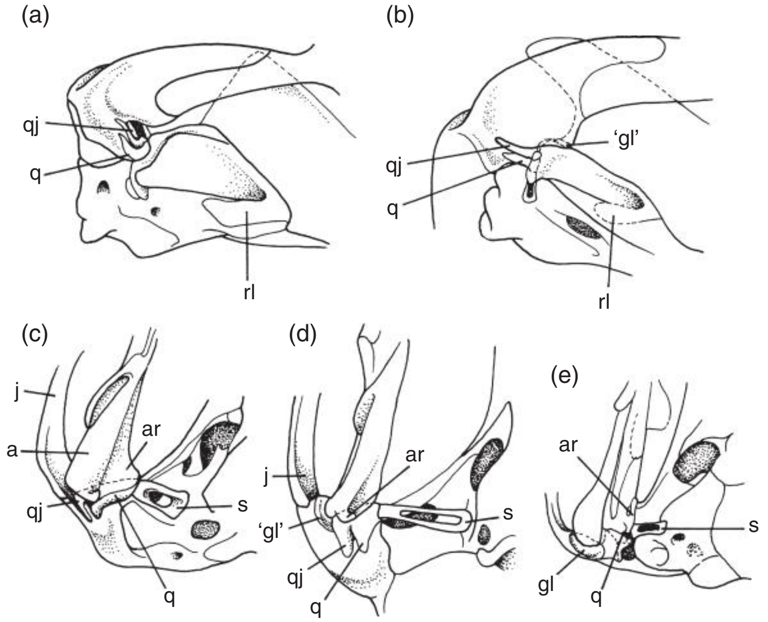
A few subtle changes in *Probainognathus* (illustration I(d)) mark the beginnings of the switch. The surangular now meets the squamosal in a special hollowed facet, the glenoid, which allowed rocking movements. The articular forms part of a narrow rod (including the reduced angular, prearticular and surangular), which is loosely held in a groove on the inside of the dentary. By this stage the ‘reptilian’ jaw joint, and a new joint, are both present, very close together, and apparently functioning in tandem.

The next stage is seen in the mammal *Morganucodon* (illustration I(b,e)), in which the dentary contacts the squamosal. The surangular loses contact with the squamosal and is replaced by a distinctive enlarged process of the dentary, the condylar process, that fits into the glenoid on the squamosal.

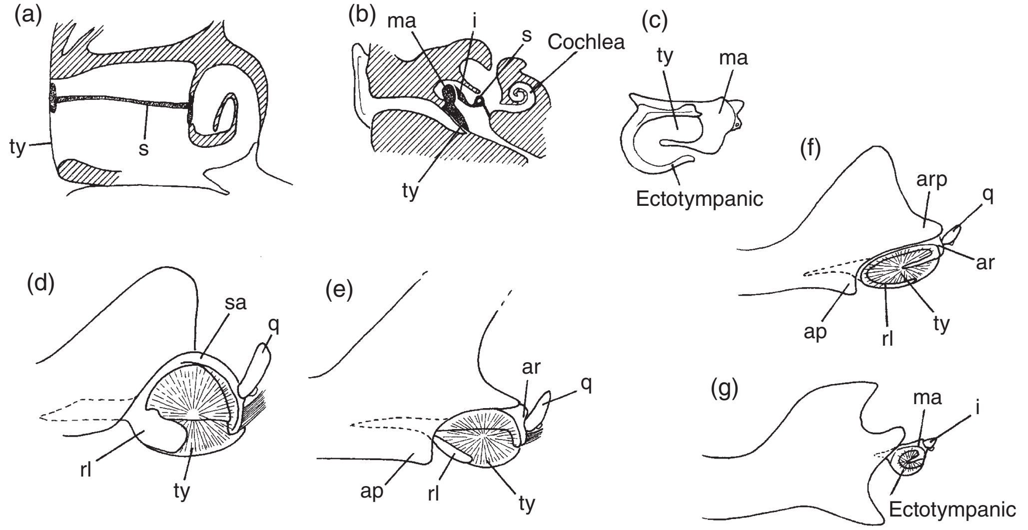
In typical reptiles and birds, the eardrum, or tympanum, is a circular sheet of skin held taut in the curve behind the quadrate. Sound is transmitted to the inner ear within the braincase in the form of vibrations across the middle ear space by the stapes, a rod of bone extending from the tympanum to the inner ear (illustration II(a)). In modern mammals, sound is transmitted via a set of three tiny bones within the middle ear, the **auditory ossicles**: the **malleus**, **incus** and **stapes**, or hammer, anvil and stirrup (illustration II(b)). The tympanum is held taut by the curved **ectotympanic,** which sits just behind the squamosal–dentary jaw joint (illustration II(c)). The mammalian stapes is the same as the generalized amniote stapes, the malleus is the articular and prearticular, the incus the quadrate and the ectotympanic the angular. The generalized amniote jaw joint is present within our middle ear, and the close association explains why we can still hear our jaw movements when we chew.

The evolution of the cynodont and mammalian jaw joint and middle ear was reconstructed as a four-stage process by Allin (1975). He assumed that the angular, articular and quadrate bones were already involved in sound conduction in therapsids (illustration II(d,e)). He restored a large tympanic membrane beneath the dentary, held taut by the reflected lamina of the angular below and the surangular above. Vibrations of the tympanum passed through the articular and quadrate to the stapes. In other words, the lower jaw was a key part of the hearing equipment of early cynodonts. The tympanum became smaller and was pushed behind the new squamosal–dentary jaw joint in early mammals (illustration II(f,g)). At the same time, the articular–quadrate crank became reduced and separated from the rest of the skull and lower jaw, and moved fully into a separate auditory passage.

These transformations had been predicted from early embryological studies, and the development of modern mammals shows four processes that contribute to the separation of the middle ear from the jaw (Takechi and Kuratani, 2010; Luo, 2011). First, the developmental precursors of the three ear ossicles are displaced medially from the lower jaw. Second, the developing middle ear is displaced behind the dentary-squamosal joint. Third, the middle ear shows negative allometry with respect to the mandible (the middle ear elements are relatively large in early embryos, but the mandible grows faster in later stages). Fourth, Meckel's cartilage is reabsorbed to permit the middle ear to be disconnected from the mandible. Meckel's cartilage, originating from the first branchial arch, serves as scaffolding for the development of mandibular and middle ear elements. Normal development of Meckel's cartilage includes its eventual reabsorption, and the production of the ear bones, and these stages in development are controlled by a complex series of signals from many structural and some homeobox genes (Takechi and Kuratani, 2010; Luo, 2011) that direct development first according to the generalized vertebrate model, and then impose modifications to bring about separation of primary mandible and middle ear.



(I) Evolution of the mammalian jaw joint: (a,b) posterolateral and (c–e) ventral views of the posterior right-hand corner of the skull and lower jaw of (a,c) the early cynodont *Thrinaxodon*, (d) the later cynodont *Probainognathus* and (b,e) the early mammal *Morganucodon*, showing the move of the quadrate and articular towards the middle ear region. Abbreviations: a, angular; ar, articular; gl, glenoid; j, jugal; q, quadrate; qj, quadratojugal; rl, reflected lamina; s, stapes; sa, surangular. Source: Adapted from Crompton and Hylander (1986).



(II) Structure of the ear, in vertical section, in (a) a typical reptile and (b) a mammal; (c) the ear ossicles of a modern mammal in lateral view; (d–g) Allin's (1975) theory for the origin of the mammalian jaw joint and middle ear system; lateral views of the posterior portion of the lower jaw of (d) an early cynodont; (e) an advanced cynodont; (f) an early mammal; and (g) a modern therian mammal. Abbreviations as in illustration (I); and: ap, angular process; arp, articular process; i, incus; ma, malleus; s, stapes; ty, tympanum. Source: (a–c) Adapted from various sources. (d–g) Adapted from Allin (1975).

from the jaw to the ear might have been linked to expansion of the brain in mammals, a process that drove the dentary-squamosal joint outward, while leaving the ancestral jaw bones attached in a medial position to the ear region of the skull.

There were also major changes in the feeding system, in the palate, dentition, and especially in the jaw muscles (Crompton, 2005; Kemp, 2005). In early cynodonts such as *Procynosuchus* there was a modest secondary palate that extended back a short way behind the tip of the snout. Through the Triassic, the secondary palate extended further and further back, effectively separating breathing (nasal chamber) from feeding (mouth), an essential feature for an animal with a high metabolic rate, so it could eat and breathe at the same time. The secondary palate has an equally important function in bracing the skull against strain from contraction of the powerful jaw muscles.

There were two major changes in the dentition. First, all cynodonts show differentiation of the uniform generalized amniote teeth into mammal-like incisors, canines, and multicusped cheek teeth, each with different functions in feeding. The second change was to reduce the number of cycles of tooth replacement. In reptiles and other vertebrates, teeth are replaced more or less continuously, as the animal grows older, or as the old ones wear out. In mammals, on the other hand, there is only one replacement, when the milk teeth of the juvenile give way to the adult set. This reduced dental replacement was essential for the development of cheek tooth occlusion, where upper and lower teeth have to match surfaces precisely. Constantly replacing teeth, as in reptiles, would make overall occlusion impossible.

The jaw muscles changed also. An early synapsid (Figure 10.5(a)) had three main jaw closing muscles, as in all amniotes, the external adductor, the posterior adductor and the internal adductor (which included the pterygoideus). In cynodonts and mammals, the internal and posterior adductors are much reduced and the key jaw muscles (Figure 10.5(b)) are the pterygoideus, as well as a deep **temporalis muscle** and a more superficial **masseter muscle**, both derived from the generalized amniote external adductor. We can tell the presence of the masseter in cynodonts as there is a distinctive hollow on the outside of the lower jaw for its insertion, the masseteric fossa. In yet more derived cynodonts (Figure 10.5(c,d)), the volume of the adductor muscles is greater, as shown by the extensive outwards bowing of the zygomatic arch.

The shift in jaw articulation and the rearrangement of jaw muscles that began in the Permian and Triassic cynodonts paved the way for an important advance in their mammalian descendants, namely chewing. Mammals are able to move their jaws through a triangular orbit of motion, with chewing on each side of the mouth in turn, and these actions are essential for the complex grinding activities of the cheek teeth. The new masseter muscle helps to produce the lateral motion of the jaw.

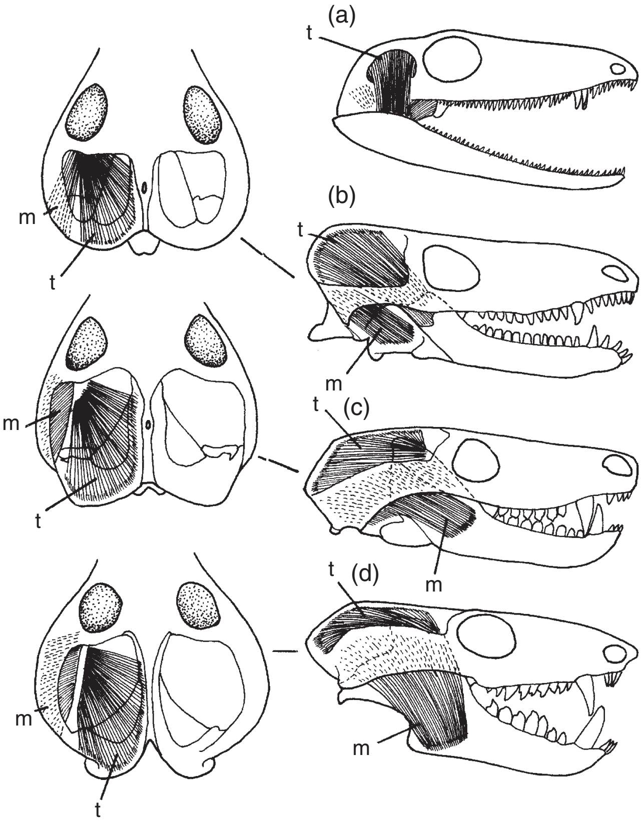


Figure 10.5 The evolution of cynodont jaw muscles: (a) lateral view of the skull of *Ophiacodon*, showing the small external adductor (temporalis) muscle; dorsal and lateral views of the skulls of (b) *Procynosuchus*, (c) *Thrinaxodon* and (d) *Chiniquodon*, showing progressive differentiation and expansion of temporalis and masseter muscles, and their invasion of larger and larger areas of the bones of the skull roof. Abbreviations: m, masseter muscle; t, temporalis muscle. Source: Adapted from Kemp (1982).

The braincase changed also in two major ways. First, the brain of mammals is larger, proportional to body size, than the generalized amniote brain. This expansion of the brain began with the first cynodonts. Instead of being retained largely inside the basisphenoid-basipterygoid-supraoccipital braincase, as in reptiles (see Section 5.1.1), the expanded cerebrum grew to fill the cranium behind the eyes. The whole posterior part of the skull expanded laterally and dorsally to accommodate the burgeoning grey matter. A further consequence was that the jaw muscles moved laterally, and the zygomatic arch emerged as an independent structure for attachment of some of those muscles.

The second change was in the sidewall of the braincase. Here, a typical mammalian bone, the alisphenoid, came to cover much of the side of the mid-portion of the brain, and to encompass the important nerve openings V_2 and V_3, passages for the trigeminal nerve maxillary and mandibular branches. The alisphenoid evolved from part of the generalized amniote epipterygoid.

There were numerous other anatomical and physiological changes associated with the transition from reptile to mammal: modification of the posture from sprawling to erect, with the hindlimb changing first, and the forelimb later; development of a diaphragm to power the breathing, associated with loss of the lumbar ribs; increased metabolic rate, associated probably with the emergence of insulating hair; ever more complex behaviour associated with the expanding brain. One transformation that is less clear is in reproduction. It seems likely that cynodonts and most Mesozoic mammals continued laying eggs, and the placenta and live birth emerged only with Theria in the Late Jurassic (see Boxes 10.1, 10.3). However, parental care was a long-established feature, from the origin of Synapsida, and the egg-laying pre-therians presumably cared for their offspring just as assiduously as do many birds today.

10.1.5 Tritheledonts, tritylodonts, and brasilodonts

Two cynodont clades, the tritylodonts and tritheledonts, are close relatives of mammals, forming together the clade Mammaliamorpha. All possible pairings of these three taxa are supported by different analysts: Kemp (1983) argued that tritylodonts and mammals are sister groups, Hopson and Kitching (2001) that tritheledonts and mammals are sister groups, and Abdala (2007) paired tritheledonts and tritylodonts in the clade Ictidosauria. In older works, tritylodonts had even been paired with traversodontids as part of the Cynognathia. At least, all now agree that tritylodonts are members of Probainognathia, but Liu and Olsen (2010) could not determine whether tritheledonts or tritylodonts are closer to mammals. Ruta *et al.* (2013) found good support for a tritylodont-mammal pairing (see Box 10.1).

The tritheledonts are a rather poorly-known group of small animals that are mammal-like in many respects (Kemp, 1982; Martinelli and Rougier, 2007). Seven species are known from fragmentary skulls from the Late Triassic and Early Jurassic of South Africa and South America, and these show a number of mammalian characters (Figure 10.6(a–c)) such as the loss of the postorbital bar between the orbit and the temporal fenestra, a slender zygomatic arch, enlargement of the nasal cavity, the formation of a bony wall between the eyeballs and an external **cingulum**, or ridge, on the upper cheek teeth.

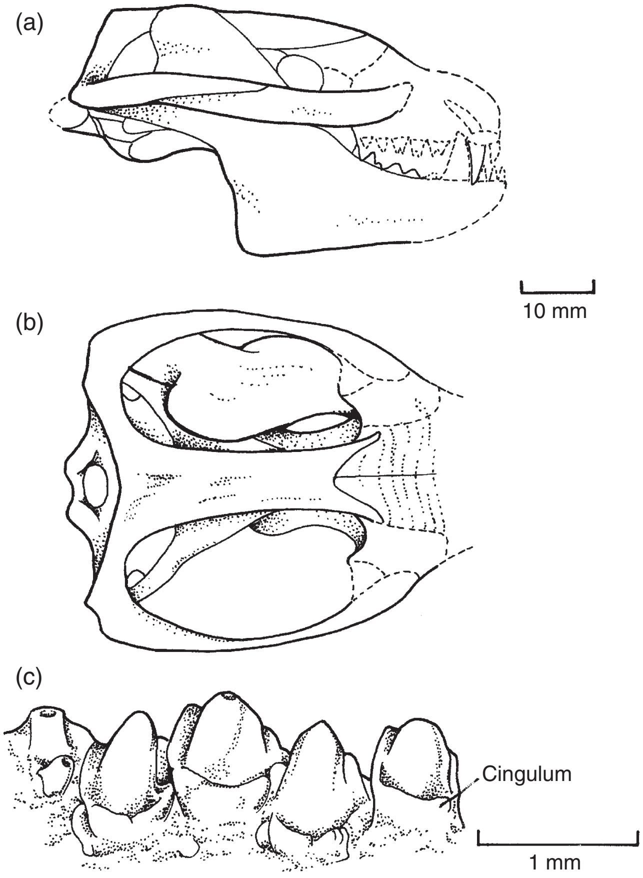


Figure 10.6 The tritheledonts: (a,b) *Diarthrognathus* skull in lateral and dorsal views; (c) teeth of *Pachygenelus*, both from the Early Jurassic of South Africa. Source: (a,b) Adapted from Kemp (1982). (c) Adapted from Gow (1980).

The jaw joint in tritheledontids was almost entirely between the dentary and squamosal. The postdentary bones were reduced to a thin rod and this helped to transmit sound to the inner ear. The jaws were modified for extensive chewing by sideways movements. In reptiles, the lower jaws are firmly fused at the front, at the **symphysis**, but in tritheledonts and mammals the two jaws are unfused and mobile – held together merely by connective tissue. This allowed lateral movements during chewing.

The tritylodonts, represented by 17 species from the Late Triassic to Early Cretaceous of most parts of the world (Kühne, 1956; Sues, 1986; Watabe *et al.*, 2007), were highly successful herbivores that ranged in skull length from 40 to 220 mm. *Kayentatherium* from North America has the typical rodent-like tritylodont skull (Figure 10.7(a–c)) with a deep lower jaw, deep zygomatic arch and high sagittal crest, indicating powerful jaw muscles and a highly specialized dentition. There are elongate incisors and six to eight massive cheek teeth in straight rows. The upper cheek teeth of *Oligokyphus* from the Early Jurassic of Wales all bear three longitudinal rows of crescent-shaped cusps, whereas the lower teeth bear two rows (Figure 10.7(d,e)). When the jaws closed, the lower teeth moved back and the crescent-shaped cusps were drawn across the food, tearing it up along four parallel grating surfaces (Figure 10.7(f)). This is analogous to how rodents chew their food, but in the opposite direction: rodents pull the lower jaw *forwards* rather than backwards. This type of jaw motion allows the left and right sets of teeth to be occluded simultaneously. *Oligokyphus* (Figure 10.7(g)) has a long body and short limbs.

The skeletons of tritheledonts and tritylodonts show many mammal-like features. The vertebrae of the neck are short and mobile, and the thoracic vertebrae are distinct from the lumbar vertebrae. The ilium is reduced to a rod-like blade (Figure 10.7(a)), as in mammals. The shoulder and hip girdles are further modified to allow the limbs to make a wide range of movements. All of these changes suggest that tritheledonts and tritylodonts moved like mammals, flexing the backbone up and down to lengthen the stride. In addition, mammals time their breathing to correspond to strides, so that they breathe in when the backbone is at full stretch, and out when the limbs come together below and the backbone arches. Tritheledonts and tritylodonts may have been the first to achieve this adaptation, essential in animals with high metabolic rates (endotherms) and a need to pump oxygen rapidly.

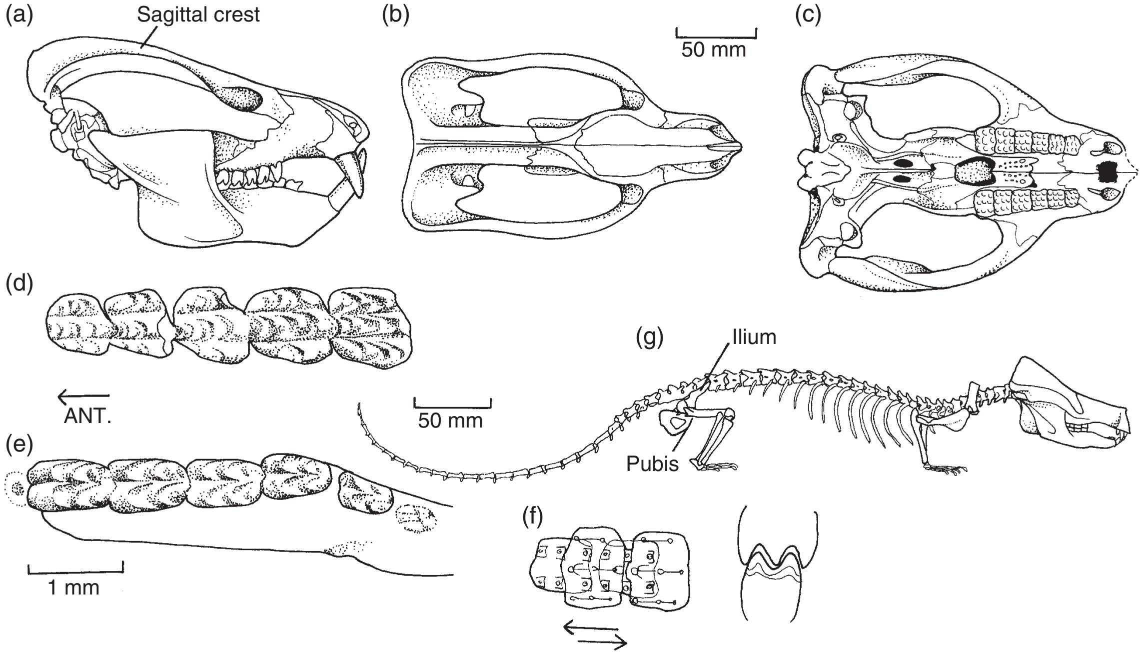


Figure 10.7 The tritylodonts (a–c) *Kayentatherium* and (d–g) *Oligokyphus*: (a–c) skull in lateral, dorsal, and ventral views; (d) cheek teeth of the upper jaw, in occlusal view; (e) cheek teeth of the lower jaw, in occlusal view; (f) occlusion of upper and lower cheek teeth, occlusal view showing the direction of movement (arrow), and vertical section; (g) skeleton (ANT, anterior). Source: (a–c) Adapted from Sues (1986). (d,e,g) Adapted from Kühne (1956). (f) Adapted from Crompton (1972).

Two additional taxa, *Brasilodon* and *Brasilitherium* from the Late Triassic of Brazil (Bonaparte, 2013), appear to be even closer sisters to Mammalia than either tritheledonts or tritylodonts (Liu and Olsen, 2010; Ruta *et al*., 2013). These tiny animals, with skulls barely 40 mm long, were likely insect-eaters. They share with mammals an elongate snout, a promontorium on the skull for the inner ear cochlea (see Section 10.2.1), four upper incisor teeth, small incisors and a reduced lower canine, and delayed postcanine eruption.

10.1.6 Cynodont macroevolution

The Triassic diversification of cynodonts can be understood as part of the recovery of life after the Permo-Triassic mass extinction (see Sections 5.7, 6.1, 6.5.1). In a study of the recovery of cynodonts, Ruta *et al*. (2013) found a disparity-first pattern (see Section 2.7), with a peak in morphological variance among cynodonts in the Early–Middle Triassic, and near-constant levels after that. Meanwhile, diversity rose steadily from the Early Triassic, with a major expansion in the Late Triassic and Early Jurassic. The early burst in cynodont evolution was expressed then in the expansion of morphospace occupied rather than in number of species. Cynognathians were characterized by high evolutionary rates and high diversity early in their history, whereas probainognathian rates were low.

In terms of morphospace occupation, the Early Triassic cynodonts were similar to those of the Late Permian. Then, the Middle Triassic split into Cynognathia and Probainognathia opened up substantial new morphospace, but distinct areas, for the two clades. The first mammals were not remarkably distinctive in morphological terms, occupying similar areas of morphospace to the tritheledonts, whereas the tritylodonts, perhaps surprisingly, diverged substantially.

10.2 THE FIRST MAMMALS

The first mammals appeared in the Late Triassic, but the fossils are incomplete. *Adelobasileus* and *Sinoconodon* appear to be the most basal mammals, but the first reasonably well-represented mammals are the morganucodonts from the Early Jurassic. All these early mammals were tiny, with 20–30-mm skulls and total body lengths of less than 150 mm. They probably looked generally like shrews, but may have lacked external ears (as these are lacking in monotremes today).

10.2.1 The most basal mammals

The oldest known mammal, *Adelobasileus* from the earlier part of the Late Triassic of Texas, USA (Lucas and Luo, 1993), is based on a specimen representing the braincase region (Figure 10.8(a)). This is enough, however, to show that it is very probably a mammal. The braincase shows a number of features diagnostic of early mammals. The generalized amniote epipterygoid, typically a thin column of bone, has become a broad sheet, termed the **alisphenoid** in mammals. In front of

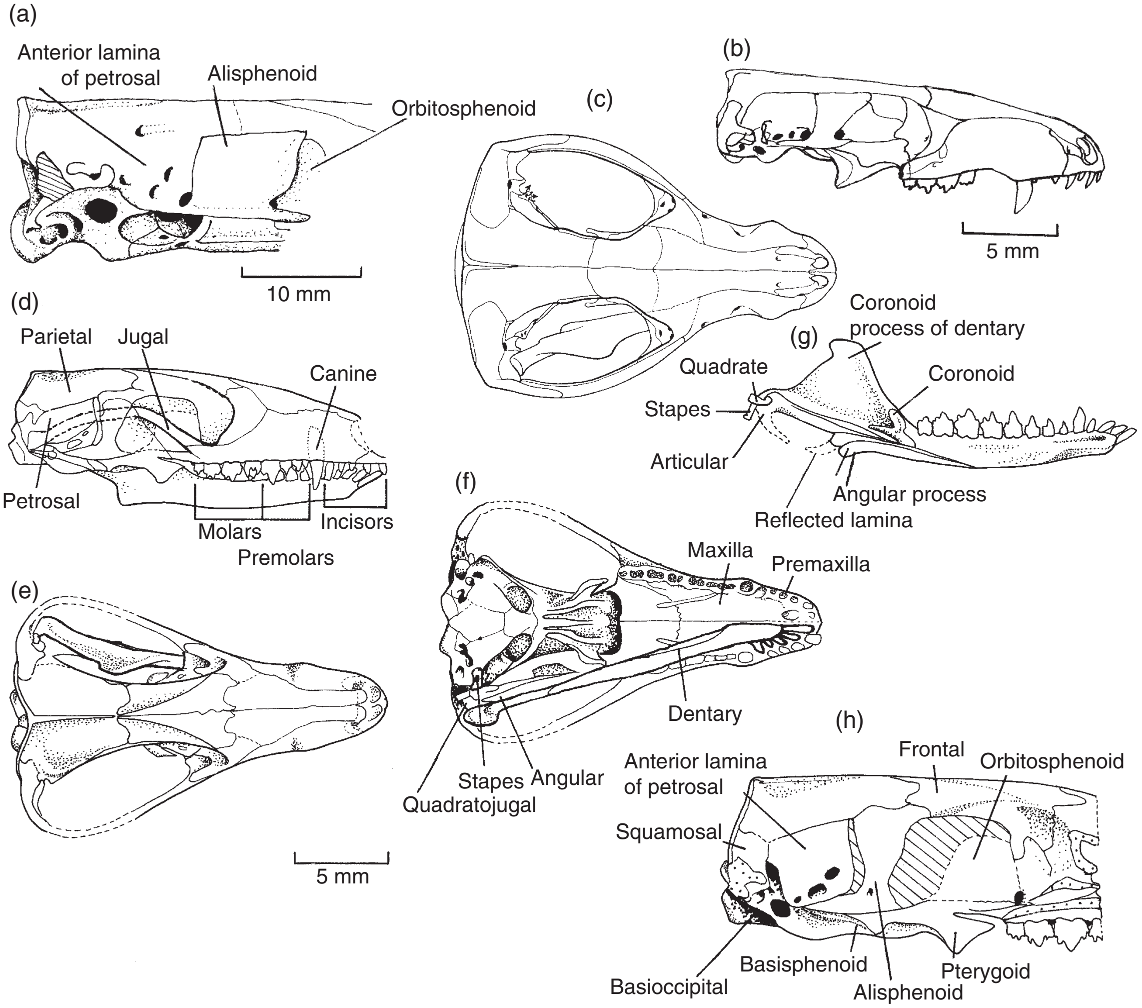


Figure 10.8 Skulls of basal mammals, (a) *Adelobasileus*, (b,c) *Sinoconodon* and (d–h) *Morganucodon* in (a,b,d) lateral, (c,e) dorsal and (f) ventral views; (g) lower jaw in medial view; (h) lateral wall of the braincase (unossified areas shown with regular hatching). Source: (a) Adapted from Lucas and Luo (1993). (b,c) Adapted from Crompton and Luo (1993). (d–h) Adapted from Kermack *et al.* (1981).

this, a new element, the **orbitosphenoid**, contacts the frontal and palatine in front and forms a solid internal wall in the back portion of the eye socket. Towards the rear, the brain is expanded and it is enclosed almost completely in bone. Basal amniotes have the brain enclosed at the side only by the prootic, opisthotic and epipterygoid bones (see Section 5.1.1). In *Adelobasileus*, the prootic sends a large sheet of bone forwards, the anterior lamina of the periotic (or **petrosal**), which meets the parietal above and alisphenoid in front. The trigeminal nerve, cranial nerve number V, sends two major branches to the snout, temporal and lower jaw regions, through the anterior lamina of the petrosal. There are numerous other mammalian characters in this remarkable early specimen (see Box 10.3).

Sinoconodon from the Early Jurassic of China (Figure 10.8(b,c)) also appears to occupy a basal position in mammalian phylogeny (Crompton and Luo, 1993; Zhou *et al.*, 2013). It shows all the braincase features (Figure 10.8(b)) seen in *Adelobasileus*, and the rest of the skull shows a fully developed jaw joint between the dentary and squamosal and a fully developed petrosal promontorium for the inner ear cochlea. These are the classic mammalian characters. The back part of the skull is expanded (Figure 10.8(c)) and the orbit and lower temporal fossa are a single opening, bounded by a slender zygomatic arch. The cheek teeth, however, did not occlude precisely. Some posterior cheek teeth appear to have been replaced in the adult, accompanied by sustained, slow growth of the skull late in the individual's life. These are plesiomorphic features of the indeterminate growth of cynodonts.

10.2.2 Morganucodont anatomy

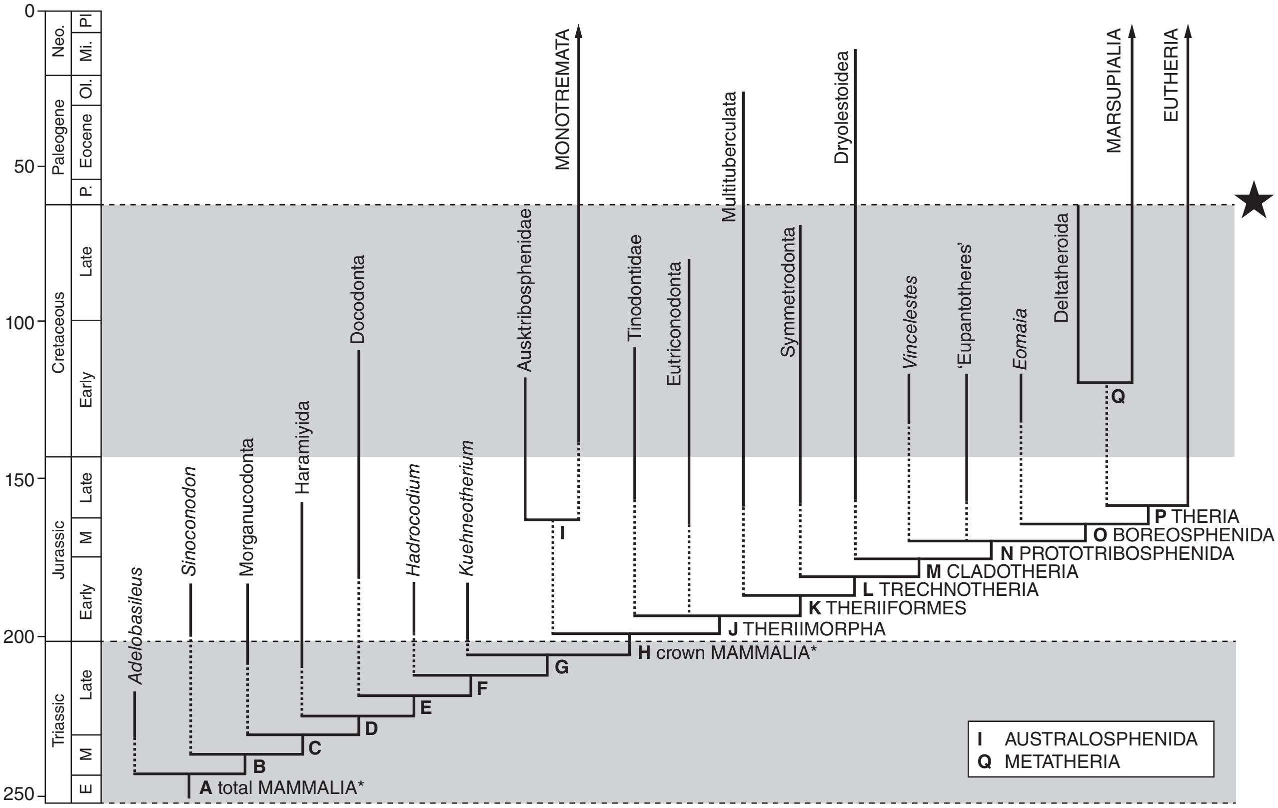
The Morganucodonta was a clade of more than 15 mammal species known mainly from the Early Jurassic of Europe, North America, China and South Africa, but with a late survivor in the Middle Jurassic of England (Kermack *et al.*, 1973, 1981; Clemens, 2011). The skull of *Morganucodon* from the Early Jurassic of the United Kingdom and China (Figure 10.8(d–h)) shows all the

BOX 10.3 RELATIONSHIPS OF THE MESOZOIC MAMMALS

A traditional view of mammalian evolution was that the group was diphyletic, that is, it had two ancestral lines, one leading to the 'therians' and the other to the 'prototherians'. The 'therians', those forms with a triangular array of cusps on the molars, included *Kuehneotherium*, the symmetrodonts, marsupials and placentals. The 'prototherians' had the molar cusps aligned and included the morganucodontans, docodontans, triconodontans, multituberculates and monotremes.

The first cladistic analyses (Kemp, 1983; Rowe, 1988) disproved this view, showing that 'prototherians' are not a clade, and suggesting that monotremes are more closely related to marsupials and placentals than *Morganucodon*. The linear alignments of tooth cusps in *Morganucodon*, multituberculates, docodontans and triconodontans are plesiomorphic characters that do not indicate close relationships to monotremes.

All cladistic analyses agree that the three living mammal groups are arranged as (Monotremata (Marsupialia + Placentalia)), with the Marsupialia plus Placentalia forming the clade Theria. A key question has been the relationships of various extinct clades, notably the Multituberculata. Kemp (1983) found multituberculates, and most Mesozoic taxa, as outgroups to the clade of modern mammals, whereas others (Luo *et al*., 2002, 2011; Zhou *et al*., 2013) find a broad separation between Monotremata and its closest outgroups (Australosphenida) and Theria and its closest outgroups (Boreosphenida). Averianov *et al*. (2013) find an alternative arrangement of taxa within Trechnotheria, with a clade comprising Symmetrodonta and Meridiolestida as sister to Cladotheria, and *Vincelestes* classed as a dryolestid.



Cladogram showing the postulated relationships of the major groups of mammals, and of the Mesozoic groups in particular, based on the work of Luo *et al*. (2002, 2011), Zhou *et al*. (2013), and O'Leary *et al*. (2013). Synapomorphies: **A MAMMALIA**, well-developed jaw articulation between squamosal and dentary, double-rooted cheek teeth, medial wall of orbit enclosed by orbitosphenoid and ascending process of palatine, expansion of brain vault in parietal region, squamosal large, tabular bone absent, occipital condyles large and separated by a notch or groove, trigeminal nerve exits all in anterior lamina of petrosal and well behind alisphenoid, alisphenoid makes broad contact with frontal; **B**, petrosal promontorium; **C**, cheek teeth divided into premolars and molars, precise cusp-to-cusp occlusion developed through wear, mandibular symphysis reduced, diphyodont dentition (juvenile and adult only); **D**, groove for replacement dental lamina absent, five or fewer upper postcanine teeth, petrosal lateral flange and crista parotica connected, occiuput sloping anterodorsally, procoracoid foramen absent, extratarsal spur present, hair preserved; **E**, jugular fossa absent, paroccipital process extending ventral to cochlear housing; **F**, overhanging medial ridge above postdentary trough absent; **G**, no unambiguous synapomorphies; **H crown MAMMALIA**, presence of occlusal surfaces that match precisely between upper and lower molars upon eruption, distinctive masseteric fossa with well – defined ventral margin, cochlear canal elongate, ossified pila antotica separating cavum epiptericum from braincase is absent (except multituberculates), astragalus and calcaneus in partial superposition (except *Ornithorhynchus* and *Jeholodens*), greatly enlarged gyrencephalic cerebral hemispheres; **I AUSTRALOSPHENIDA**, tribosphenic molars with continuous and shelf-like mesial cingulid that extends to the lingual side of the molar rather than cingulid cusps, ultimate lower premolar with fully developed trigonid, transversely wide talonid, talonid placed posterior to the trigonid; **J**, **THERIIMORPHA**, postdendary trough absent, separate scars for surangular/prearticular absent, Meckelian sulcus vestigial or absent, pterygoid fossa on dentary present, medial pterygoid shelf present; **K THERIIFORMES**, acromion process of scapula strongly downturned, proximal head of humerus is spherical and inturned, proximal head of femur ball-like, inturned and set off on a constricted neck, calcaneal tuber is longer than wide; **L TRECHNOTHERIA**, hypertrophied postvallum/ prevallid shearing mechanism, squamosal with postglenoid depression, petrosal, post-tympanic recess present, caudal tympanic process present, atlas rib absent in adults, moderate torsion (30°–15°) of humerus, pelvic acetabulum with complete rim (without cotyloid notch, greater trochanter directed dorsally; **M CLADOTHERIA**, angular process of dentary well-developed and posteriorly positioned, paraconid shorter than metaconid, talonid has at least one cusp, interclavicle absent; **N PROTOTRIBOSPHENIDA**, broad contact between alisphenoid and frontal, cochlea is elongated and coiled up to 360°; **O BOREOSPHENIDA**, absence of postdentary trough and scars for the postdentary bones (except coronoid) in the dentary, tribosphenic molars, talonid placed posterior to the trigonid on lower molars, distinctive cingulid cuspule; **Q THERIA**, tribosphenic molar, anterior lamina of prootic is absent, acetabulum bears an inverted U-shaped articular region for the femoral head, astragalus with distinctive neck, calcaneum with enlarged sustentacular process; **R METATHERIA**, three premolars, postnatal tooth replacement limited to third premolar. angular process that is equal to half but less than the length of the dentary ramus. Abbreviations: E, Early; Mi, Miocene; Mid, Middle; Neo, Neogene; Ol, Oligocene; P, Paleocene; Pl, Pliocene/Pleistocene. Dashed lines and star symbols indicate extinction events.

mammalian characters of *Adelobasileus* and *Sinoconodon*. It retains greatly reduced generalized amniote jaw bones, including the quadrate-articular jaw joint, but these elements now function largely as part of the middle ear system (Figure 10.8(f, h)), with the mammalian squamosal-dentary joint as the principal jaw hinge. The braincase of *Morganucodon* (Figure 10.8(h)) also shows all the features of *Adelobasileus* and *Sinoconodon*.

The lower jaw of *Morganucodon* (Figure 10.8(d,g)) is composed almost solely of the dentary bone, but the posterior bones are still present: a reduced splenial and coronoid, and a rod comprising the surangular, prearticular, angular and articular. *Morganucodon* has rather derived teeth with several changes from those of the advanced cynodonts and *Sinoconodon*. The cheek teeth (Figure 10.8(d)) are divided into **premolars** (single-cusped and replaced) and **molars**, (tricuspid and not replaced), as in later mammals. *Morganucodon* appears to have **diphyodont** ('two-type teeth') tooth replacement, with only a juvenile, or milk, set of teeth, replaced once by the adult set. *Sinoconodon* retained a generalized amniote pattern of several tooth replacements during its life. Milk molars are present in the juvenile dentition and then replaced by permanent premolars, and the true molars are present only in the adult dentition.

The cheek teeth of *Morganucodon* all occlude and wear surfaces can be seen on the incisors as well as on the cheek teeth. The main chewing movement in *Morganucodon* followed a triangular route, one side of the jaw moving outwards initially, pulled by the masseter muscle, with occlusion occurring as the jaw was pulled back to the centre line by other muscles, rather than being simply up and down, as in other amniotes in general. The lower jaws are closer together than the upper jaws, the **anisognathous** condition, typical of most mammals, and an adaptation for chewing the food on one side of the mouth at a time. *Morganucodon* sheared its food by the longitudinally cutting crests on the teeth.

The skeleton of *Morganucodon* is poorly known, but its close relative *Megazostrodon* from South Africa (Jenkins and Parrington, 1976) has a long low body, rather like that of *Oligokyphus*, but the limbs are rather longer (Figure 10.9(a,b)). The ribcage is restricted to the thoracic vertebrae, with no ribs on the lumbars (cf. Figure 10.1(a)). The forelimb and shoulder girdle (Figure 10.9(c)) are rather cynodont-like, still sprawling, whereas the pelvis and hindlimb (Figure 10.9(d)) are typically mammalian. As in the extant monotremes, the coracoid is still present in the shoulder girdle, and the scapula was immobile. The posture is erect, the ilium is a rod-like element pointing forwards and fused to a reduced pubis and ischium, and there is a very large **obturator foramen**, a circular gap in the pelvis between the pubis and ischium, seen also in earlier cynodonts. The femur (Figure 10.9(e)) is also mammalian, with a ball-like head that fits sideways into the acetabulum, a necessary feature in an erect animal and seen also in dinosaurs and birds (see Box 6.3). In addition, there are distinct processes on either side, the minor and major trochanters, which provided sites for insertion of the important muscles that moved the leg back and forwards during walking.

10.2.3 Morganucodont biology

Morganucodon and *Megazostrodon* were seemingly agile insectivores. Their locomotion was mammalian, with the possibility of rapid and variable movements, even if sustained running might have been difficult. The well-developed pointed cutting teeth suggest a carnivorous diet, presumably insects, judging from the small size of the morganucodonts. Unlike their contemporaries such as tritylodontids and *Sinoconodon*, the morganucodonts show a narrow range of body sizes and hence probably had determinate growth, a mammalian character. It is also most likely that the morganucodonts were endothermic (fully warm-blooded) and nocturnal. Other mammalian characters include the large brain and probable possession of mammary glands. What is the evidence for all these features, some of which are not obviously fossilizable?

Endothermy, the generation of heat and control of body temperature by internal means (see Section 8.5) is indicated by several lines of evidence (Crompton *et al*., 1978). *Morganucodon* has a fully developed secondary palate, as in most cynodonts, which allowed these animals to breathe rapidly while feeding as the air stream was separated from the mouth. In addition, its

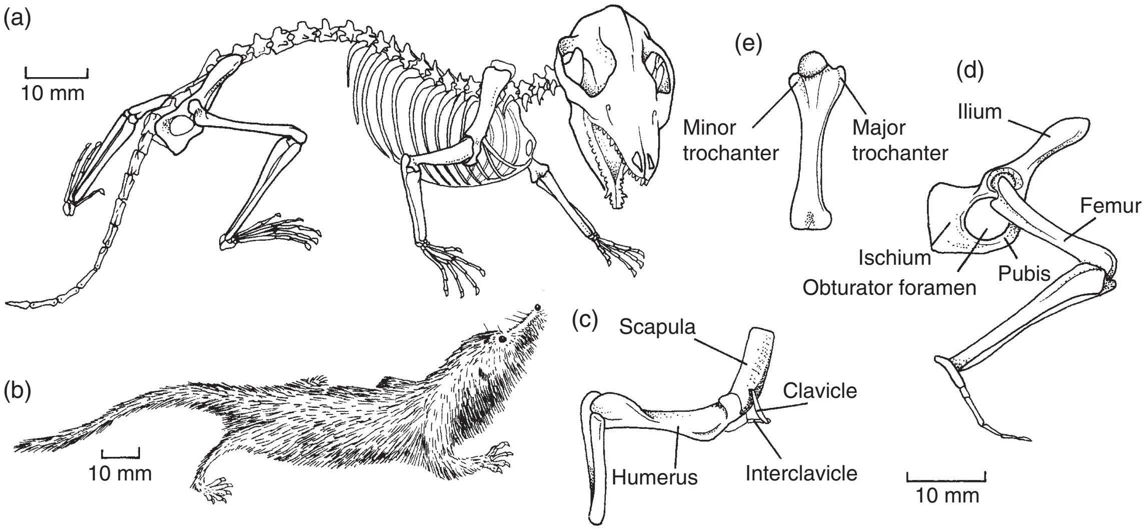


Figure 10.9 The skeleton of morganucodonts: (a) skeleton of *Megazostrodon*; (b) body restoration; (c) forelimb and pectoral girdle; (d) hindlimb and pelvic girdle of *Morganucodon*; (e) femur. Source: Adapted from Jenkins and Parrington (1976).

bone histology shows fibro-lamellar bone formed early in its life, so indicating a high metabolic rate and high growth rate (Chinsamy and Hurum, 2006).

The suggestion that morganucodonts, and indeed all early mammals, were nocturnal comes from their greatly enlarged brain with enlargement in the areas associated with the senses of hearing and smell, both of which are useful for a nocturnal animal. Also mammals have lost one of the receptor proteins (opsins) in the retina and the associated genes that are seen in other amniotes, giving them rather poor (dichromatic) colour vision; colour vision is not much use in the dark, and the rod-dominated retina of mammals, good for detecting low levels of light, is also a derived mammalian feature. Of course, we (and other anthropoid primates) have duplicated the opsin genes to regain a type of trichromatic vision. Further, most small living mammals are nocturnal, and hence avoid competing for food with birds and lizards.

Finally, did *Morganucodon* have mammary glands? If it had hair, it may have had mammary glands, which are developmentally related to hair follicles and the sebaceous glands that provide lubrication to skin and hair. A second line of argument relates to the precise tooth occlusion of mammals and the fact that *Morganucodon* is probably the first mammal with diphyodont tooth replacement. Mesozoic mammals, like modern ones, probably delayed the appearance of their teeth until rather late when the head was near to its adult size, thus indicating that the young fed on milk. Mammals, then, need only two sets of teeth, the milk and the adult, during their lives.

10.3 THE MESOZOIC MAMMALS

Adelobasileus, *Sinoconodon*, *Morganucodon* and *Megazostrodon* were some of the first mammals. Another 30 or so mammalian families have been recorded in the Jurassic and Cretaceous (Kielan-Jaworowska *et al.*, 2004), but many of these are based on incomplete material and their relationships are hard to assess (see Box 10.3). The main groups will be reviewed here in phylogenetic order, and the clades leading to modern mammal groups, Australosphenida and Boreosphenida, will then be considered separately.

When the doyen of mammalian palaeontologists, George Gaylord Simpson, surveyed his classic work on Mesozoic mammals (Simpson, 1928), he declared that he could fit all these tiny fossils, then extremely rare and incomplete, into his hat (Simpson had a large cranium, reflecting his awesome mental powers, and his hat was large). Nonetheless, the situation has changed remarkably, especially since 2000, with the discovery of numerous complete and spectacular skeletons of mammals from the Jurassic and Cretaceous of China.

10.3.1 Diverse Jurassic and Cretaceous mammals

One group of early mammals has become remarkably well known thanks to new finds from China. For a long time, the clade Haramiyida was known only from isolated teeth and jaws from the Late Triassic and Jurassic of Europe, Africa, and Greenland. Then, a series of complete skeletons of haramiyids were reported from the Middle and Late Jurassic of China. Two come from the Tiaojishan Formation (latest Middle Jurassic) of northern China, *Megaconus* (Zhou *et al.*, 2013) and *Arboroharimaya* (Zheng *et al.*, 2013). *Megaconus* was about 27 cm long (Figure 10.10(a,b)), and *Arboroharimaya* perhaps 35 cm long. The first was interpreted as a ground-dweller, the second as a tree-climber because of its grasping feet and hands. Both show evidence that haramiyids were the first herbivorous mammals, having longitudinal cusp rows on the upper molars that occlude alternately with those of the lower molars (Figure 10.10(c-e)). These authors differ in their views on haramyid relationships, Zhou *et al.* (2013) positioning them outside crown Mammalia (see Box 10.3),

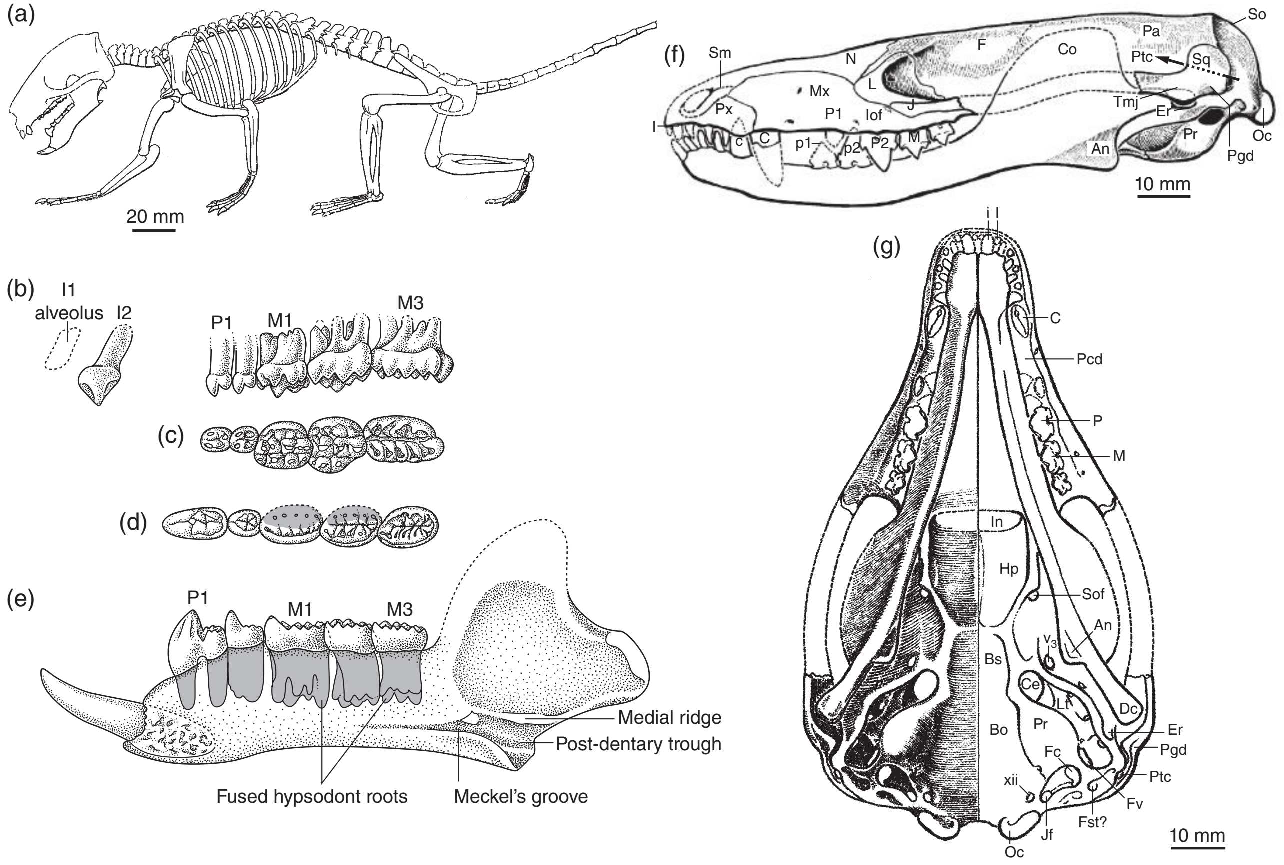


Figure 10.10 Jurassic basal mammals: (a–e) the haramiyid *Megaconus*, (a) reconstruction of skeleton, (b) lingual (medial) view of the upper dentition, (c) occlusal view of the upper cheek teeth, (d) occlusal view of the lower cheek teeth, (e) and the whole mandible in lingual (medial) view; (f,g) skull of *Hadrocodium* in lateral (f) and ventral (g) views. Source: Luo *et al.* (2001). Reproduced with permission from the American Association for the Advancement of Science.

whereas Zheng *et al.* (2013) argued that the broad grinding molars indicate relationships with multituberculates, and so a position within crown Mammalia.

The docodontans, about 12 species from the Middle and Late Jurassic of Europe, Asia and North America were known originally from isolated jaw bones (Figure 10.11(c)). These showed how the teeth converged on a functionally tribosphenic-like structure (Luo and Martin, 2007). Recent finds include more complete specimens from Portugal and China. The Portuguese Late Jurassic *Haldanodon* was a tiny, perhaps 10-cm-long, ground dweller that shows adaptations for digging, including stout and short limb bones and humeri with greatly expanded distal joints and strong deltopectoral crests (Martin, 2005). The braincase is more derived than that of morganucodonts in having an elongate and curved cochlear canal, no anterior paroccipital process, and constriction of the squamosal (Ruf *et al.*, 2013). *Castorocauda* from the Middle Jurassic of China (Ji *et al.*, 2006) was a remarkable docodontan, the first mammal to show substantial adaptations for swimming (see Box 10.4).

Hadrocodium from the Early Jurassic of China (Luo *et al.*, 2001) appears to fall phylogenetically between Docodonta and crown Mammalia (see Box 10.3). This tiny mammal, known only from its tiny skull (Figure 10.10(f,g)) was probably little more than 32 mm long and weighed perhaps 2 g. Its importance rests in its relatively large brain, and in its derived ear structure in which the postdentary trough has entirely disappeared and the middle ear ossicles are entirely separated from the lower jaw for the first time. Note that this separation between jaw and ossicles seems to have happened independently several times in early mammals, and certainly between monotremes ands therians.

Kuehneotherium from the Early Jurassic of South Wales (Kermack *et al.*, 1968) has been difficult to interpret because its remains consist of isolated teeth and jaw fragments. The genus has gained some notoriety, however, because the three principal cusps of its teeth are arranged in a very shallow triangle and this was once said to be a forerunner of the tribosphenic molar, important in later mammalian evolution (see Section 10.3.2). The upper and lower molar teeth (Figure 10.11(a,b)) have a main central pointed cusp and smaller accessory cusps placed low on the shoulders of the main cusp.

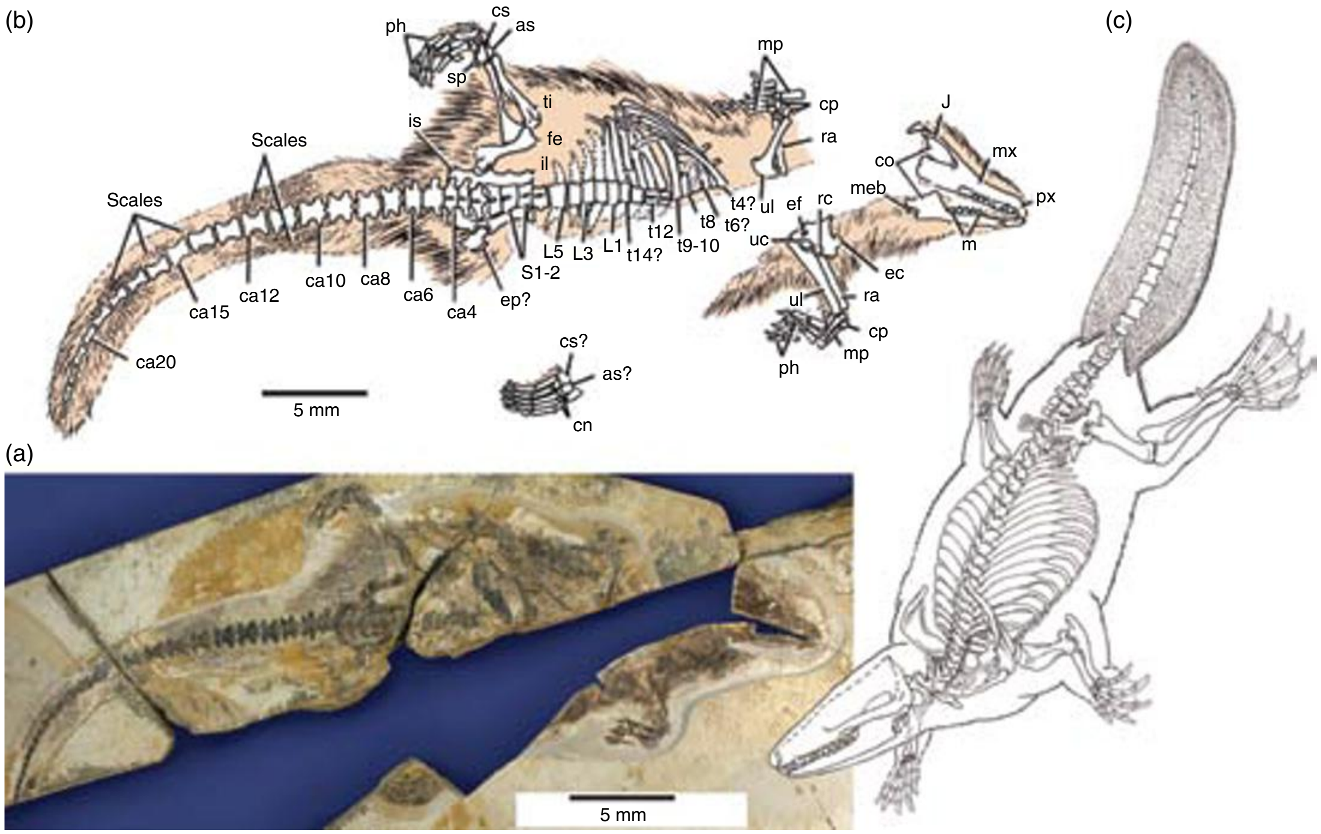
A small group of Jurassic and Cretaceous mammals, Tinodontidae, formerly classed as symmetrodontans, appear to follow next phylogenetically (see Box 10.3). *Tinodon* shares some superficial similarities in its teeth with *Kuehneotherium*.

BOX 10.4 THE FIRST SWIMMING MAMMAL

There are always remarkable new fossils from China, and the Jurassic mammals from that country have revolutionized our understanding of Mesozoic mammal evolution (see Section 10.3.1, Box 10.3). The docodontan *Castorocauda* was no different (Ji *et al*., 2006). The remarkable fossil (see Illustration a, b) shows a 43-cm long somewhat beaver-like animal, with adaptations for swimming (and burrowing) and with a poison spur on its ankle.

The fossil comes from the Middle Jurassic Jiulongshan Formation, and was associated with pterosaurs, a theropod dinosaur, lissamphibians, and insects. It preserves nearly all of the skull and skeleton. The first two molars are narrower than in other docodontans, and have recurved cusps in line, interpreted as a plesiomorphic feature retained in *Castorocauda* to help it grasp fish and other aquatic prey. The body was covered with fur, and the tail outline is broad, and covered with interspersed guard hairs and scales, as in a modern beaver. The limbs are short and powerful, with adaptations for swimming and digging. *Castorocauda* may have been 50 cm long and weighed 500 g, similar in size and shape to a modern otter, and perhaps showing similar adaptations to swimming and hunting in fresh waters.

Castorocauda had a poison spur on its ankle, a feature also seen in the haramiyid *Megaconus* (Zhou *et al*., 2013), in multituberculates, and in many other Mesozoic mammals (Hurum *et al*., 2006). This interpretation is based on the structure of the astragalus, which carries a bony base and a keratin spur. Perhaps such a feature was plesiomoerphic for mammals. The modern platypus (see Section 10.3.2) has such a spur, which develops initially in both males and females, but is retained only in the adult male, and delivers poison. This is perhaps an offensive weapon in male–male fights, as well as being used in defence.



The first swimming mammal *Castorocauda*, showing the original specimen (a), an outline drawing of this specimen showing skeleton and surrounding hair (b), and a reconstruction as a swimmer and burrower (c). Abbreviations: as, astragalus; ca, caudal vertebrae; cn, ento-, meso-, and ecto-cuneiforms; co, coronoid process of dentary; cp, carpals; cs, calcaneus; ec, ectepicondyle and supinator shelf (humerus); ef, entepicondyle foramen; ep?, probable epipubis; is, ischium; J, jugal; L1-6, lumbar ribs 1 to 6; m, molars; meb, manubrium of malleus; mp, metacarpals; mx, maxilla; px, premaxilla; ra, radius; rc, radial condyle; S1-2, sacrals 1 and 2; sp, extratarsal ("poisonous") spur; t4-t14 (preserved ribs through thoracic 17); uc, ulnar condyle; ul, ulna. See Colour plate 10.2. Source: Ji *et al*. (2006). Reproduced with permission from the American Association for the Advancement of Science.

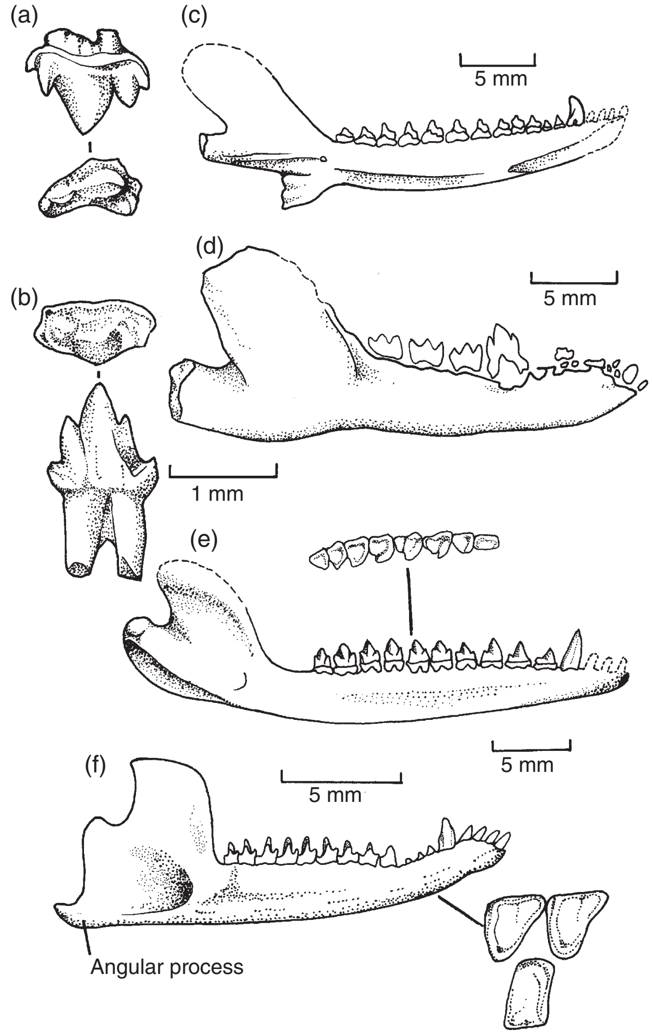


Figure 10.11 Mesozoic mammals: (a) upper molar of *Kuehneotherium* in medial and occlusal views; (b) lower molar of *Kuehneotherium* in medial and occlusal views; (c) lower jaw of the docodontan *Docodon*, in medial view; (d) lower jaw of the triconodontan *Triconodon* in lateral view; (e) lower jaw of the symmetrodont *Spalacotherium* in lateral view and occlusal view of the molars; (f) lower jaw of the dryolestid *Crusafontia* in medial view and occlusal view of two upper and one lower cheek tooth. Source: (a,b) Adapted from Kermack *et al.* (1968). (c) Adapted from Woodward (1898). (d) Adapted from Flower and Lydekker (1891). (e) Adapted from Cassiliano and Clemens (1979). (f) Adapted from Krebs (1994).

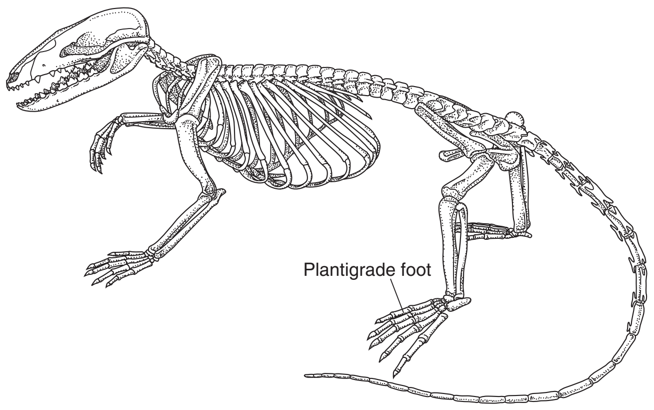


Figure 10.12 Skeleton of the triconodontan *Jeholodens* in left lateral view, restored from a nearly complete specimen from the Early Cretaceous of China. Source: L. Zhe-xi, Field Museum of Natural History, Chicago, IL, USA. Reproduced with permission.

The eutriconodontans comprise some 40 species from the Middle Jurassic to the Late Cretaceous of Europe, North America and Central Asia that are known mainly from isolated teeth and jaw bones (Kielan-Jaworowska *et al.*, 2004; see Chapter 7). *Triconodon* (Figure 10.11(d)) has pointed shearing molars with three main cusps in a line (hence 'tri-cono-dont'). Partial skeletons have, however, been found in the Early Cretaceous of North America, and an even more remarkable complete tiny skeleton of *Jeholodens* (Ji *et al.*, 1999) from the Early Cretaceous sediments of Liaoning, source of spectacular dinosaur and bird fossils (see Box 9.4). The skeleton (Figure 10.12) is slender and the head and teeth indicate a diet of insects. *Jeholodens* is reconstructed as a ground-dwelling animal that had a plantigrade posture (feet flat on the ground), with sprawling hindlimbs and forelimbs. The scapula is surprisingly derived, looking like that of modern therians, but much of this may be convergent. The shoulder girdle was, nonetheless, mobile, which allowed this little eutriconodontan to twist and turn and to lengthen its forelimb stride. One of the Jehol eutriconodontans, *Volaticotherium*, was even a glider, with a broad patagium stretched between fore and hindlimbs, densely covered with hair, and insect-eating teeth (Meng *et al.*, 2006).

Some Late Jurassic and Early Cretaceous mammals show hints of a new kind of tooth pattern in which the three main cusps on the lower and upper molars form a low triangular shape. Symmetrodontans (Kielan-Jaworowska *et al.*, 2004; see Chapter 9) such as *Spalacotherium* (Figure 10.11(e)) have the central cusp set well over from the other two. The Early Cretaceous Yixian Formation in China has produced a diversity of symmetrodontan taxa living side by side, including *Zhangeotherium* (Hu *et al.*, 1997) and *Akidolestes* (Chen and Luo, 2013), tiny long-snouted terrestrial insect-eaters with some adaptations for climbing.

Four or five other families of mammals with similar molars are the dryolestoids from Europe (Krebs, 1994), North America, and South America (Rougier *et al.*, 2011). The lower jaw of the dryolestoid *Crusafontia* (Figure 10.11(f)) has a larger coronoid process than in *Spalacotherium* and there is an angular process on the dentary, the insertion site for the parts of the masseter muscle block that produce lateral movements of the jaw during chewing.

One clade of dryolestoids, the Meridiolestida, diversified in the Late Cretaceous of South America, and one genus, *Peligrotherium*, survived the KPg mass extinction into the earliest Palaeocene (Rougier *et al.*, 2011). Even more unexpectedly, the Miocene *Necrolestes* also appears to be a meridiolestid (Rougier *et al.*, 2012), a most unusual late survivor of a Mesozoic non-therian clade. The tiny, insect-eating meridiolestidans may have survived very late in South America because it was isolated from other continents for much of the Cenozoic (see Section 10.6). The affinities of Meridiolestida have been debated, and some evidence (Averianov *et al*., 2013) suggests affiliation with Symmetrodonta.

10.3.2 The tribosphenic molar

A key evolutionary acquisition of mammals was the tribosphenic molar (Figure 10.13), in which a newly evolved cusp of the upper molar, the **protocone** macerates food in a facing basin of the lower molar, the **talonid**. The name tribosphenic (literally, 'rubbing-wedge') refers to the derived mortar-and-pestle type of occlusal action of these teeth. The occlusal surface is a triangle of three cusps with the point facing outwards in a lower molar, followed by the talonid basin in which the inward-facing point of the triangle of an upper molar, the protocone, occludes.

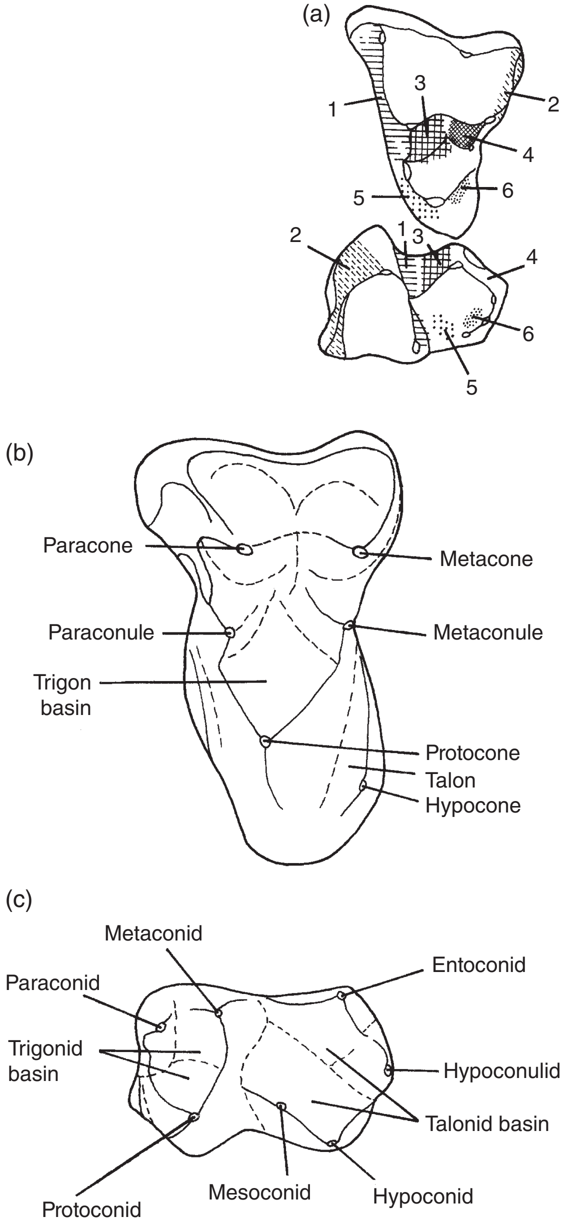


Figure 10.13 The tribosphenic molar: (a) the tribosphenic Cenozoic placental mammal *Didelphodus*, showing the postulated sequence of assembly of shearing surfaces on both upper (top) and lower (bottom) molars; (b,c) nomenclature of the main cusps, ridges and basins, of the Late Cretaceous placental mammal *Gypsonictops* (b) upper and (c) lower molars. Source: Adapted from Bown and Krause (1979).

The tribosphenic molar (Figure 10.13(a)) has six shearing surfaces. The nomenclature of the cusps, ridges and facets of typical mammalian molar teeth such as these is complex (Figure 10.13(b,c)). The main terms to note are for the triangles of three cusps: the **paracone** (anterolateral), **metacone** (posterolateral) and **protocone** (medial) in the uppers, and the **paraconid** (anterointernal), **metaconid** (posterointernal) and **protoconid** (external) in the trigonids of the lowers. The talonid, occupying the posterior half of lower molars, is bounded by the **entoconid** (medial), **hypoconid** (lateral) and the **hypoconulid** (posterior).

The evolution of the tribosphenic molar has been much discussed. Therians (marsupials and placentals) share the tribosphenic molar (Box 10.3), and at one time the modern monotremes were treated as quite distinct, perhaps with a separate origin deep in the Triassic, because they show a more linear arrangement of cusps in adult molars. Palaeontologists tried to divide the teeth of the various Mesozoic forms (see Section 10.3.1) into linear and tribosphenic patterns.

Then, a number of Cretaceous teeth from Australia, assigned to Ausktribosphenidae (see Section 10.3.3), appeared to show a kind of tribosphenic pattern and were placed variously on the line to Monotremata or to Theria. The resolution (Luo *et al*., 2002, 2003; Davis, 2011) appears to be that crown-group mammals divide into two clades that diverged in the Jurassic, the Australosphenida based in the southern hemisphere, and the Boreosphenida based in the northern hemisphere. Each clade evolved a kind of tribosphenic tooth, but these tooth types differ in details, and the basal members of each clade had more simple teeth.

10.3.3 Australosphenida: monotremes and relatives

The division of modern mammals into three clades is well established, and reflects their fundamental reproductive modes. Monotremes lay eggs, marsupials give birth to tiny young that finish developing in a pouch, and placentals retain their young in the uterus to a more advanced stage.

The monotremes, represented today by the platypus of Australia and the echidnas of Australia and New Guinea (Figure 10.14(a,b)), share many plesiomorphic features, such as egg-laying, and two large coracoids in the shoulder girdle on each side, with a single interclavicle lying between them, ventral to the sternum. Neither monotreme has teeth in the adult, although the juvenile platypus has unerupted molars (Figure 10.14(c)) that are soon replaced by horny plates.

The fossil record of monotremes used to extend back only to the middle Miocene (c. 15 Myr ago), which was frustrating as monotremes were supposed to be the most plesiomorphic living mammals. Several monotreme jaw fragments have since been reported from the Early Cretaceous of Australia (Archer *et al*.,

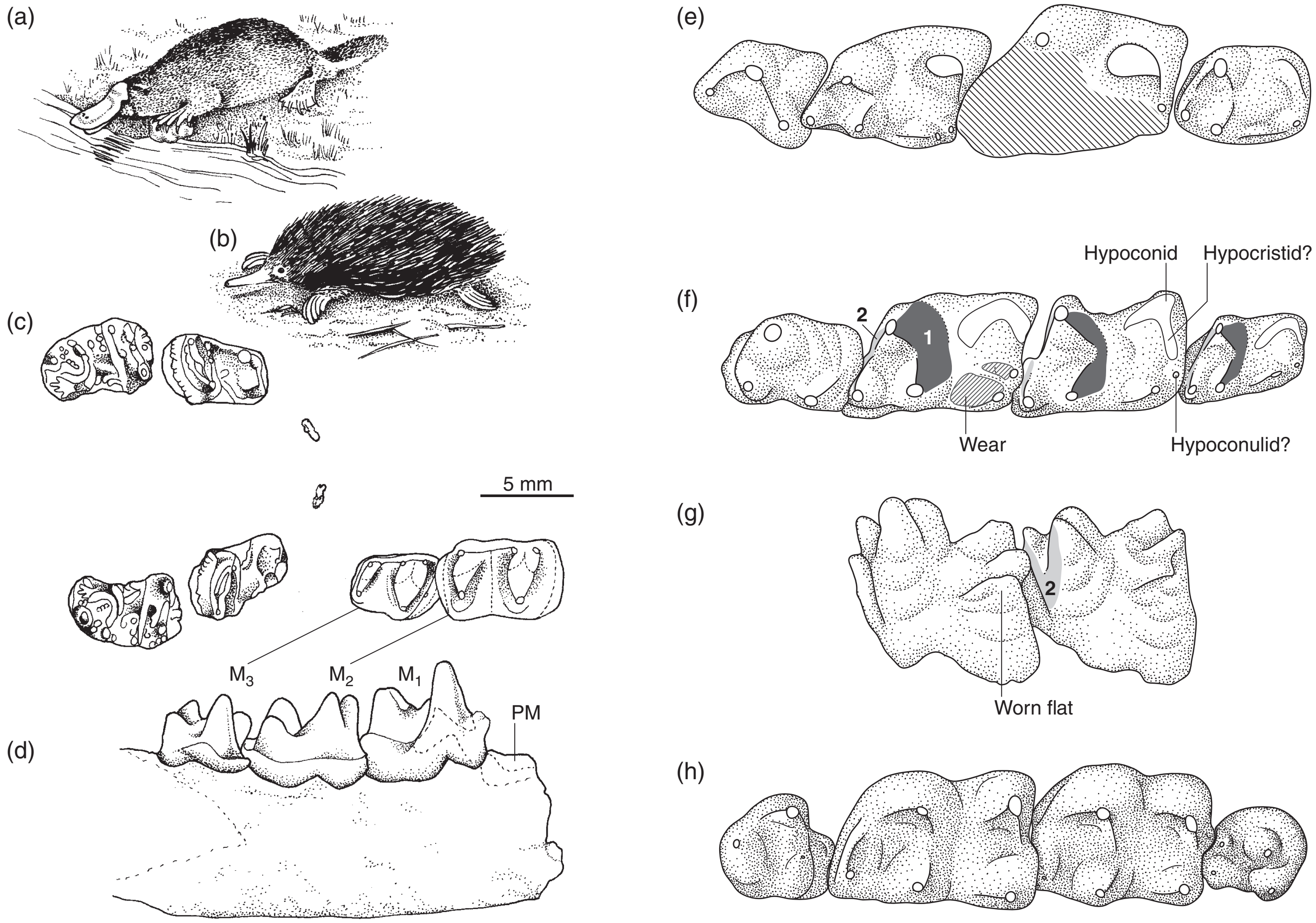


Figure 10.14 Boresophenida, including monotremes (a–d) and ausktribosphenidans (e–h): (a) *Ornithorhynchus*, the duck-billed platypus; (b) *Tachyglossus*, the echidna; (c) the temporary upper molars of a juvenile *Ornithorhynchus*, in occlusal view of both sides; (d) jaw fragment of *Steropodon*, an Early Cretaceous monotreme, in lateral and occlusal views; (e,f) occlusal view and wear facets in lower last premolar and molars 1–3 of *Bishops* (e) and *Ausktribosphenos* (f); (g) external view of upper molars 1–2 of *Ausktribosphenos*; (h) occlusal view of lower last premolar and molars 1–3 of the hedgehog *Erinaceus*, true tribosphenic teeth, for comparison. Abbreviations: M$_1$–M$_3$, molars 1–3; PM, premolar. Source: (a–c) Adapted from Young (1981). (d) Adapted from Archer *et al*. (1985). (e–h) Davis (2011). Reproduced with permission from Springer Science + Business Media.

1985; Rowe *et al*., 2008). One of these, *Steropodon*, has lower molars (Figure 10.14(d)) that are like those of the Miocene toothed platypus in the very short V-shaped array of cusps and the height of the transverse ridges, but which also show some approaches to the tribosphenic condition. If *Steropodon* and *Teinolophos*, another Early Cretaceous form, are platypuses, this would suggest a very ancient phylogenetic split between platypuses and echidnas (Rowe *et al*., 2008). However, molecular information suggests that echidnas diverged from platypuses rather late, in the mid Cenozoic (Phillips *et al*., 2009), and so the Cretaceous taxa are on the stem to the crown clade.

Platypus teeth have also been found in the Palaeocene of Argentina. This suggests a Gondwanan origin for the group and fits with a suggestion that monotremes arose in Australia, and that some of them migrated across Antarctica to South America, where they existed perhaps for only a short time.

The origin of monotremes has long been debated. The discovery of teeth and jaw fragments in the Middle Jurassic of Madagascar (*Ambondro*) and South America (*Asfaltomylos*), and the Early Cretaceous of Australia (*Ausktribosphenos, Bishops*), have clarified the situation. These teeth, many of which are superficially tribosphenic (see Section 10.3.2), are assigned to Ausktribosphenidae, and they and Monotremata to Australosphenida (Luo *et al*., 2002, 2003; Davis, 2011). These show molar occlusal surfaces whose facets are limited to a shearing function and do not appear to be present within the talonid basin (Figure 10.14(e–h)), as in the true tribosphenic tooth of Boreosphenida.

10.3.4 Multituberculates

The largest group of Mesozoic mammals, the 125 species of multituberculates, are part of Theriimorpha, the clade that includes modern marsupials and placentals (see Box 10.3). Multituberculates emerged in the Middle Jurassic, and they have the distinction of having survived at high diversity until the end of the Eocene (Kielan-Jaworowska and Hurum, 2001; Kielan-Jaworowska *et al.*, 2004; see Chapter 8). Multituberculates are best known from the Late Cretaceous and Paleogene of North America and central Asia, but new finds have extended their range to Africa and Australia, and especially to South America, where the group radiated in partial isolation in the Late Cretaceous. Indeed, the clade underwent a substantial diversification 20 Myr before the KPg mass extinction, represented by increases in diversity, range of body sizes, and dental complexity (Wilson *et al.*, 2012).

The first multituberculates, such as *Rugosodon* from the Late Jurassic of China (Yuan *et al.*, 2013), were small animals, 25 cm long, with limbs adapted for locomotion on the ground, and teeth that may have functioned in consuming a mixed diet. The lower premolars combine to form a bladelike structure that may have been used in cutting arthropod cuticles, whereas the upper and lower first molars have broad multicusped occlusal surfaces that would have been ideal for shearing plant material.

Later multituberculates showed stronger specialization on a tough herbivorous diet and possibly also for tree climbing. *Kamptobaatar* from the Late Cretaceous of Mongolia has a broad flat skull (Figure 10.15(a–c)) with large eyes that appear to have faced forwards over a short snout. There are large rodent-like incisors, generally no canines and a long gap in front of the cheek teeth, as in rodents. The last lower premolar forms a large shearing blade, a feature not seen in rodents. *Nemegtbaatar*, a relative (Figure 10.15(d)), shows the superficially rodent-like specializations.

During feeding, the lower jaw slid back and the long incisors may have been used for puncturing and snipping tough vegetation, or even for picking up and killing insects or other prey. The chewing stroke was nearly horizontal and it was operated by a number of muscles, principally divisions of the masseter. The lower jaw was pulled back about one-quarter of the length of the tooth row, so that the lower incisors lay below the upper premolars. The effect of this chewing stroke would have been to shear vegetation, or other food material, along the blade-like lower premolar 4 and grind it between the molar teeth.

Ptilodus from the Palaeocene of Canada (Figure 10.15(e)) may have been arboreal because it has a long prehensile tail for grasping branches, a reversible foot as in squirrels, which allows it to descend a tree trunk head-first, and flexible elbow and knee joints (Krause and Jenkins, 1983).

Two unexpected little bones were found attached to the front of the pelvis in *Ptilodus* (Figure 10.15(e)), interpreted as **epipubic** bones. These appeared first in tritylodonts and are known from several Mesozoic mammal groups. They are retained by modern monotremes and marsupials and are known in some early placentals, although they are absent in living placentals. The epipubic bones were once thought to support the marsupial pouch, but studies of living opossums (Reilly and White, 2003) show that they function as small levers to stiffen the trunk

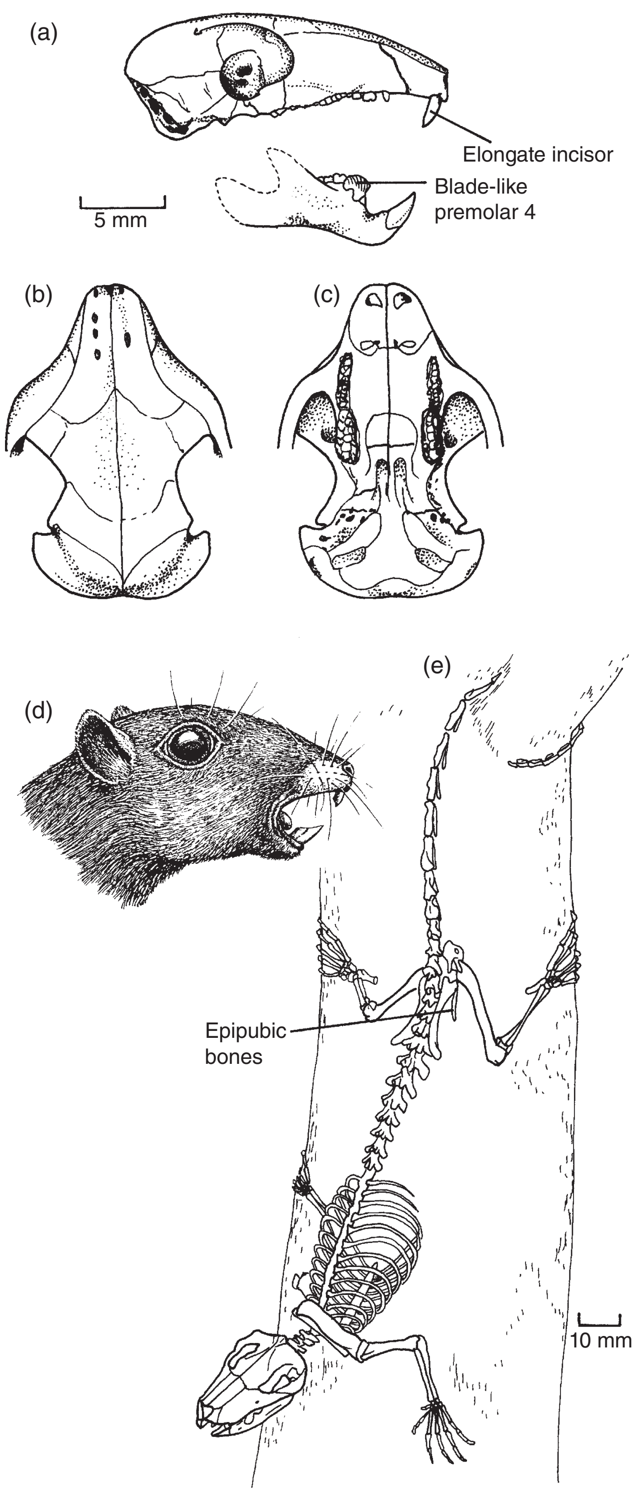


Figure 10.15 The multituberculates: (a–c) skull of *Kamptobaatar* in lateral, dorsal and ventral views; (d) restored head of *Nemegtbaatar*; (e) reconstructed skeleton of *Ptilodus* descending a tree trunk. Source: (a–c) Adapted from Kielan-Jaworowska (1971). (d) Z. Kielan-Jaworowska, formerly, Institute of Paleobiology, Warsaw, Poland. Reproduced with permission. (e) Adapted from Krause and Jenkins (1983).

during walking when one hindlimb and the diagonally opposite forelimb are pointing forward and the others back. Epipubic bones were probably lost in placentals because they would interfere with the expansion of the abdomen during pregnancy, and perhaps also with the type of galloping gait of large mammals. This might also explain why epipublic bones were also lost in the dog-like marsupials, the recently extinct thylacines of Australia, and the diverse borhyaenids of South America.

10.3.5 Boreosphenida: Cretaceous therian outgroups

The Theriiformes, comprising multituberculates, symmetrodontans, and dryolestoids (see Sections 10.3.1, 10.3.4) and the prototribosphenids (see Box 10.3) were a largely northern hemisphere clade that sent subclades south from time to time. Here we will consider a few Cretaceous mammals that come close to the roots of Theria, but fall just outside that clade.

Vincelestes from the Early Cretaceous of Argentina (Hopson and Rougier, 1993; Macrini *et al.*, 2007) is known from several skulls and skeletons (Figure 10.16(a)). It does not have the tribosphenic molar of Boreosphenida, but it shares with them a broad contact between the alisphenoid and the frontal, and a **cochlea** that is elongated and coiled up to 360°. The cochlea is a coiled structure in the inner ear of therian mammals (see Box 10.2, illustration II(b)), homologus with the uncoiled lagena of other tetrapods, that helps detect sound vibrations received through the three auditory ossicles, and passes them to the brain for interpretation. *Sinoconodon*, *Morganucodon*, eutriconodontans and multituberculates have uncoiled cochlear canals and monotremes have half a coil.

The eupantotheres are hard to position phylogenetically, consisting as they do of taxa largely based on isolated teeth and jaws. They include the Peramuridae and Amphitheriidae, two families focused around classic materials from the Late Jurassic and Early Cretaceous of England, with relatives in the Late Jurassic of Africa (Kielan-Jaworowska *et al.*, 2004; see

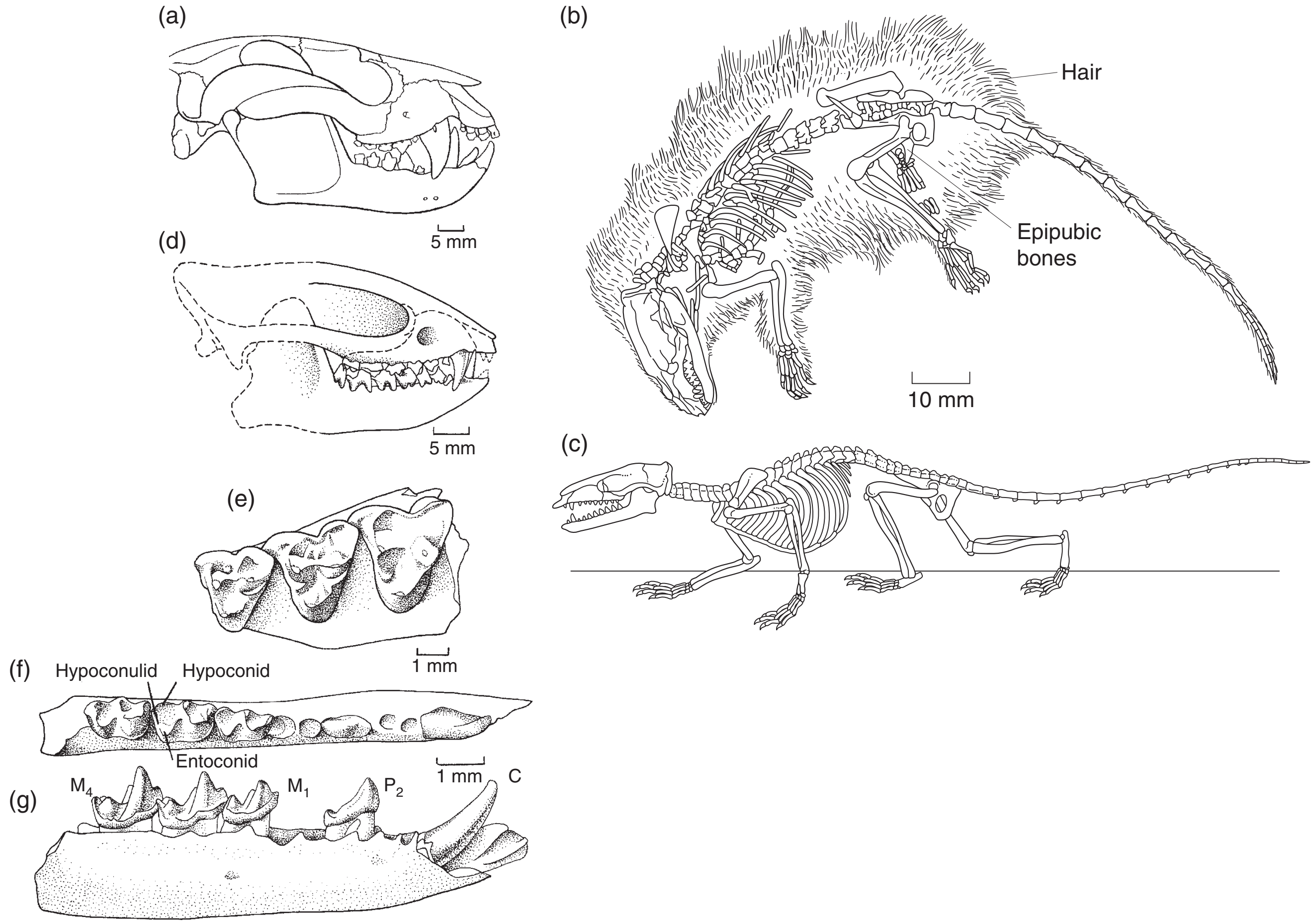


Figure 10.16 Cretaceous pre-therians (a–d) and metatherians (e–g): (a) skull of *Vincelestes* from the Early Cretaceous of Argentina; (b,c) skeleton as preserved with fur 'halo' and restoration of *Eomaia* from the Early Cretaceous of China; (d) skull of *Deltatheridium* from the Late Cretaceous of Mongolia; (e–g) jaw fragments of the marsupial *Alphadon* from the Late Cretaceous of North America, maxillary fragment in occlusal view, lower jaw in occlusal and lateral views. Abbreviations: C, canine; P_2, premolar; M_1, M_4, molars. Source: (a) Adapted from Hopson and Rougier (1993). (b,c) L. Zhe-xi, Field Museum of Natural History, Chicago, IL, USA. Reproduced with permission. (d–g) Adapted from Kielan-Jaworowska *et al.* (2004).

Chapter 10; Davis, 2012). Peramurids are more derived than dryolestoids (Figure 10.11(f)), but lack the tribosphenic molars of boreosphenidans.

The major clade Boreosphenida, members of which have tribosphenic molar teeth (see Section 10.3.2), emerged by the Middle Jurassic, as indicated by the oldest eutherian *Juramaia* (see Section 10.3.7). The most complete basal boreosphenidan is *Eomaia* ('dawn mother') from the Early Cretaceous Yixian Formation of China. When it was first reported (Ji *et al.*, 2002), *Eomaia* was interpreted as a placental mammal, a remarkable find that extended the range of placentals by some 40 Myr. However, new phylogenetic analyses (e.g. Luo *et al.*, 2003) place it as a member of Boreosphenida, and sister to Theria (see Box 10.3). *Eomaia* is a shrew-sized animal, some 16 cm long that weighed perhaps 20 g. The exceptionally well-preserved fossil (Figure 10.16(b,c)) shows that *Eomaia* had hair, which is not a surprise. It also retains the epipubic bones that are typical of modern monotremes and marsupials, but are lost in modern placentals (see Section 10.3.4). *Eomaia* was an agile little animal and it might have been a climber – its finger and toe bones are long and the claws are strongly curved and laterally compressed, features that help in grasping twigs.

10.3.6 Metatheria: Cretaceous marsupials

The marsupials are part of a wider clade Metatheria that accommodates more than 60 Cretaceous species in total (Vullo *et al.*, 2009; Williamson *et al.*, 2012). Among non-marsupial metatherians, *Sinodelphys* from the Early Cretaceous of China (Luo *et al.*, 2003) appears to be the oldest, sharing characters of the ankle, forelimb and dentition with other Metatheria. It was a small, 140-mm-long tree-climber, superficially similar to an opossum. More complete materials are known for Deltatheroida, a Late Cretaceous group known best from Mongolia. *Deltatheridium* from the Late Cretaceous of Mongolia (Figure 10.16(d)) was a short-snouted animal with well-developed carnivorous cheek teeth. Deltatheroida are allied with marsupials (e.g. Luo *et al.*, 2002; Vullo *et al.*, 2009) because they display marsupial-like tooth replacement and cranial vascularization (see Box 10.3).

There was then a substantial diversification of metatherians in the mid-Cretaceous, mainly in North America with forms such as *Kokopellia* and *Dakotadens*, and in Europe with *Arcantiodelphys* (Vullo *et al.*, 2009; Williamson *et al.*, 2012). These all suggest an origin of Metatheria in the northern hemisphere, perhaps in Asia, with dispersal over Europe and North America.

In the Late Cretaceous, metatherians were most diverse in North America, with some 45 species assigned to three families, the Alphadontidae, Pediomyidae and Stagodontidae, and with rare forms in Asia, and South America. These Late Cretaceous forms ranged in body size from about 20 g to 1700 g for *Didelphodon*, and they show adaptations for a variety of diets, feeding on insects, larger prey, fruit, tough vegetation, and omnivory. *Alphadon* (Figure 10.16(e–g)) from the Late Cretaceous of North America is superficially like the living opossum, but is generally classed as a stem metatherian, outside Marsupialia. The teeth show the typical metatherian character of three premolars and four molars (placentals have four or five premolars and three molars). The upper molars (Figure 10.16(e)) are not as wide as typical placental molars of the same length (cf. Figure 10.18(d)) and they have several large cusps on an external shelf. In lower molars (Figure 10.16(f,g)), two of the cusps, the entoconid and hypoconulid, are very close together and more distant from the hypoconid than in placental mammals of the same age.

Metatherian teeth and nursing habits are linked. Only the last premolar is replaced, and the anterior dentition is not replaced because of the extended nursing of highly altricial young that attach in the pouch to the mother's teats, often, but not always, contained within a pouch. This metatherian character can be traced to the Cretaceous forms such as *Alphadon*.

10.3.7 Eutheria: Jurassic and Cretaceous placentals

Modern placental mammals are part of the wider clade Eutheria. The timing of eutherian origins was altered dramatically by the report of *Juramaia* from the Middle-Late Jurassic Tiaojishan Formation of China (Luo *et al.*, 2011). The previous oldest eutherian had been *Eomaia* from the Early Cretaceous Yixian Formation of China, but this has been reassigned to nontherian Boreosphenida (see Section 10.3.6). *Juramaia* shifts the origin of Eutheria, as well as all boreosphenidan nodes downwards by some 35 Myr (see Box 10.3). *Juramaia* is known from a skull and front half of the skeleton (Figure 10.17(a)). The molars (Figure 10.17(b,c)) are tribosphenic, so the fossil is assigned to Boreosphenida, and it shows diagnostic characters of Eutheria in the distinctive paraconule, incipient metaconule (M2 only), long preprotocrista past the paracone, and long postprotocrista past the metacone. The forelimb shows evidence for climbing in the grasping hand, a feature shared in common with other early therians.

There is a substantial gap in time before the next rare eutherians reported from the late Early Cretaceous. There are two genera of similar age, *Acristatherium* from the Yixian Formation of China (Hu *et al.*, 2010), known from a partial skull, and *Sasayamamylos* from the Sasayama Group of Japan (Kusuhashi *et al.*, 2013), known from jaw remains. These show reductions in the numbers of incisors (four to three) and premolars (five to four), features of more derived eutherians.

Eutheria are then represented by ten or more families in the Late Cretaceous of North America, Uzbekistan and Mongolia. One of the first such clades to radiate were the Zhelestidae, comprising about 12 species initially from the early Late Cretaceous of central Asia, and then later from Europe and North America as well (Archibald and Averianov, 2012). The zhelestids were small animals, with skulls perhaps 10–30 mm long, which are known from teeth, jaws and bones from the ear region. These were initially classed as ungulates, early relatives of modern

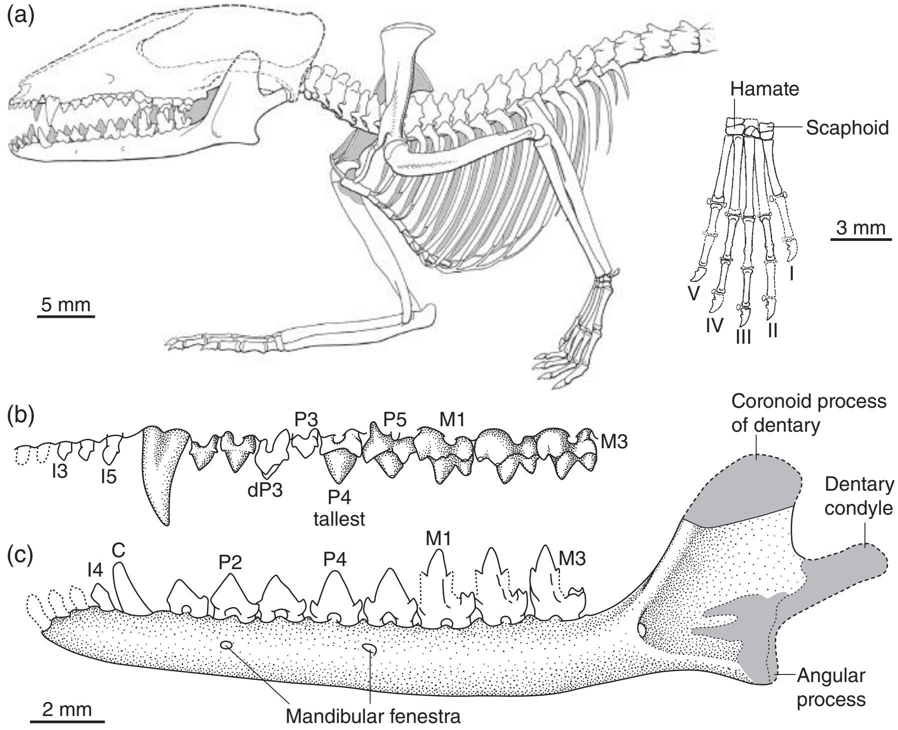


Figure 10.17 The Jurassic eutherian *Juramaia* from China: (a) partial skeleton and skull, and restored hand in ventral view; (b) occlusal view of the right upper premolars and molars; (c) lateral view of the upper and lower jaw dentitions, viewed from the left. Source: Luo *et al.* (2011). Reproduced with permission from Nature Publishing Group.

artiodactyls and perissodactyls, and so enormously important in our understanding of the origins of modern placental mammals. However, newer phylogenetic analyses (Wible *et al*., 2007, 2009; Archibald and Averianov, 2012) assign Zhelestidae to a position low among non-placental eutherians.

Another non-placental eutherian family, Zalambdalestidae, was important in the Late Cretaceous of central Asia. *Zalambdalestes* (Kielan-Jaworowska *et al.,* 2004; see Chapter 13; Wible *et al*., 2004) is an agile hedgehog-sized animal with a long-snouted skull (Figure 10.18(a–e)). The zygomatic arch is slender and there is no bony bar between the orbit and the temporal region. The braincase (Figure 10.18(c)) is small. There are typical numbers of teeth for a placental (Figure 10.18(d,e)), four premolars and three molars. The molars are broad and they lack the specializations of marsupial molars. All teeth appear to be replaced once, apart from the molars, whereas in marsupials there is only one set of teeth, except for the third premolar, which is replaced.

In the skeleton, the vertebrae of the neck are broad, low-spined elements. The atlas forms a fused ring (Figure 10.18(f)) with broad facets on either side for the two occipital condyles, and the axis has an unusual long spinal process.

The shoulder girdle is only incompletely known (Figure 10.18(a)), but it shows evidence of the mobile structure seen in modern marsupials and placentals. Derived features include the loss of the coracoid bones and the interclavicle. The scapula also takes on an entirely new form, better seen in a modern therian mammal (Figure 10.18(g)). The scapular blade is divided in two by a sharp ridge or spine that ends in the **acromion process** to which the clavicle is attached. The fields in front of the spine and behind it bear major new muscles that move the arm back and forwards with the elbows tucked well in. Further features that relate to erect gait are that the humerus head fits into a glenoid that faces downwards instead of outwards as in early mammals, and the elbow joint is hinge-like. The hand (Figure 10.18(h)) has long digits.

Although the zalambdalestid arm shows many new features, the hindlimb is rather like that of earlier mammals. It seems that erect gait was achieved in the hindlimb by derived cynodonts in the Triassic, but in the forelimb only much later by Late Cretaceous marsupials and placentals. The foot of *Zalambdalestes* is long. In the ankle, the calcaneum has a long ‘heel’ (Figure 10.18(i)) and the astragalus sits on top of it, out of contact with the ground, as in modern placentals. The fibula is reduced to a thin splint and is largely fused to the tibia. *Zalambdalestes* is interpreted as a specialized **ricochetal** mammal that made great leaps using its powerful hind legs.

The origin of Placentalia, the crown group including modern placental mammals and their ancestors, is a much-discussed question (see Section 10.4), but there is little evidence for pre-Cenozoic placental mammal fossils (Wible *et al*., 2007, 2009). As noted, zhelestids had been classed as early ungulates, and the other Late Cretaceous eutherians have from time to time been assigned to modern placental clades. This is easy to do, with

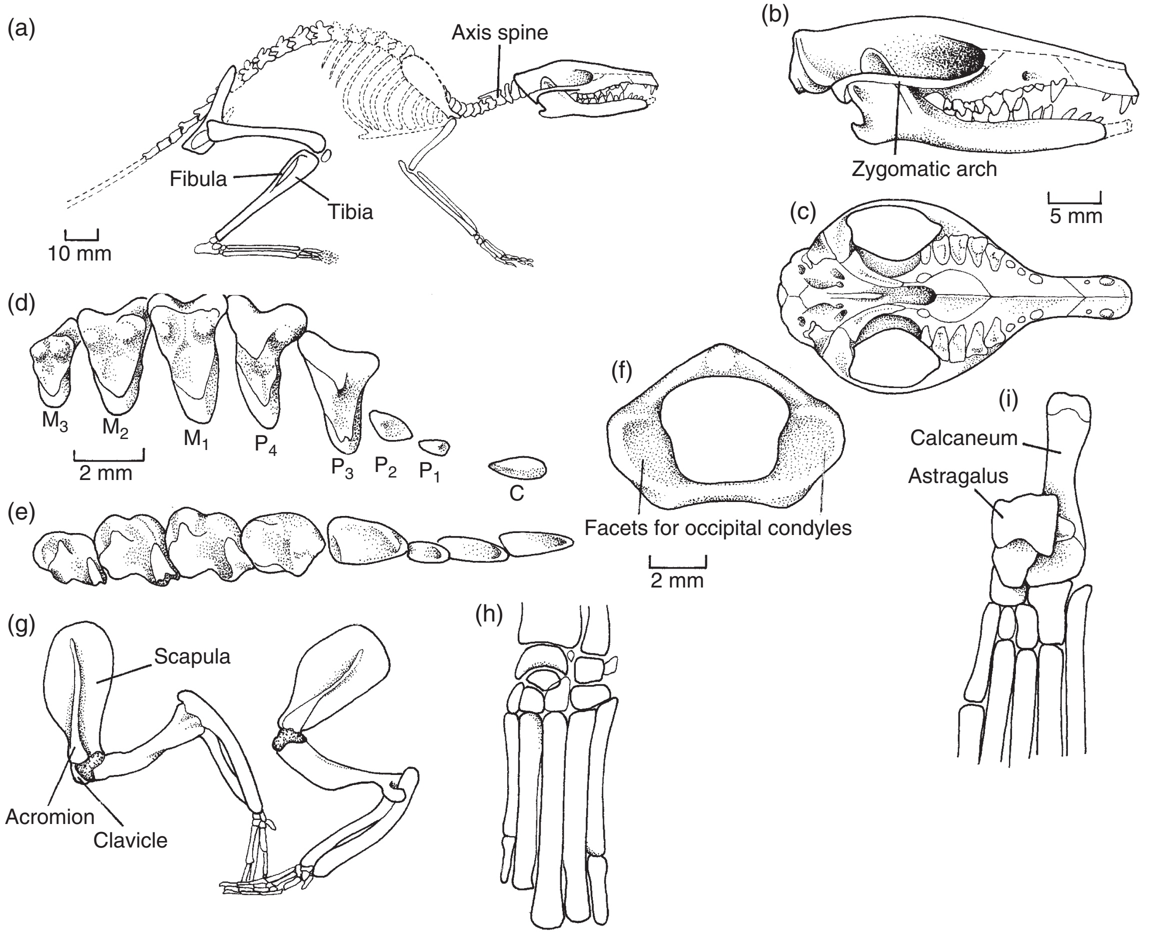


Figure 10.18 The Late Cretaceous placental mammals (a–e, i) *Zalambdalestes* and (f,h) *Barunlestes*: (a) restored skeleton; (b,c) skull in lateral and ventral views; (d) upper dentition in occlusal view; (e) lower dentition in occlusal view; (f) atlas vertebra in anterior view; (g) two positions of the forelimb of the living opossum *Didelphis* during a stride; (h) hand; (i) foot. Abbreviations: C, canine; P_2, premolar; M_1, M_4, molars. Source: (a–f,h,i) Adapted from Kielan-Jaworowska *et al.* (2004). (g) Adapted from Jenkins (1971b).

often incomplete fossils, and an optimistic desire to find the 'oldest primate' or the 'oldest rodent', for example.

10.3.8 Mammals and the KPg mass extinction

Mammals famously survived the KPg mass extinction (see Section 8.11), but many of the Cretaceous clades died out. The three modern clades, Monotremata, Metatheria, and Placentalia clearly survived, as did Meridiolestida and Multituberculata (see Sections 10.3.1, 10.3.4).

Little can be said of monotreme survival or selectivity because no fossils are known close to the boundary. Metatherians, however, showed substantial losses. More broadly among metatherians, Deltatheroida survived to the KPg boundary and the last species disappeared at that time. Among Metatheria, Williamson *et al.* (2012) show 36 lineages reaching the boundary, of which 18 died out and 18 survived. The extinctions were phylogenetically selective, including all Stagodontidae, Pediomyidae, and the *Alphadon-Turgidodon-Nortedelphys* assemblage. Some genera such as *Thylacodon* and *Swaindelphys* just crossed the KPg boundary and then died out, but only the Herpetotheriidae and Peradectidae survived substantially into the Paleogene. Williamson *et al.* (2012) estimate that a minimum of four marsupial lineages crossed the KPg boundary, and no more than a dozen species existed throughout the Palaeocene in North America. Overall, the KPg mass extinction severely affected the marsupials.

A similar pattern has been identified in studies of mammalian faunal dynamics through the Maastrichtian of the Hell Creek Formation, considering metatherians and eutherians together. In the last 1.8 Myr of the Maastrichtian, mammalian species originated and died out in an unremarkable way, and then 22–27 families died out abruptly just at the KPg boundary (Wilson, 2005). Further, Wilson (2013) explored patterns of selectivity among mammals across the KPg boundary, and found evidence for selectivity against larger-bodied dietary specialists, especially strict carnivores and herbivores in general. Phylogenetically speaking, Wible *et al.* (2007, 2009) class all the extinct eutherians as non-placentals, and they find the first fossil evidence of the key placental clades emerging in the Paleogene. The KPg mass extinction evidently had a more profound impact on mammalian evolution than had sometimes been acknowledged.

10.4 EVOLUTION OF MODERN MAMMALS

There are over 5400 species of mammals alive today, comprising five species of monotremes, 334 species of marsupials, and over 5100 species of placentals. The major subdivisions of each clade have been evident really since Victorian times: everyone can tell what is a kangaroo or not a kangaroo, a whale, or a bat, or a rodent. Indeed the divisions of modern mammals presented by Simpson (1945) in his classic summary have changed little since then. The difficulty was in determining the relationships between the mammalian clades, traditionally the orders of mammals.

In earlier works (e.g. Simpson, 1945; Novacek *et al.*, 1988; McKenna and Bell, 1997), the Xenarthra (sloths and kin) were generally identified as a basal clade among Placentalia, and various combinations of smaller placental clades were discovered on the basis of morphological characters, such as the Paenungulata/Tethytheria (hyracoids, sirenians, proboscideans), Glires (rodents, lagomorphs) and Archonta (scandentians, primates, dermopterans, chiropterans). These have been confirmed by the new molecular work, and the more fundamental patterns have also been determined to wide approval.

The revolution began in 1997, when Springer *et al.* (1997) identified the clade Afrotheria. This weird association of elephants, tenrecs, golden moles, sirenians, and others seemed at first unbelievable, and hard to associate with any diagnostic morphological characters, but every phylogenomic study since then has confirmed the reality of Afrotheria (Springer *et al.*, 2004; Murphy *et al.*, 2007; Meredith *et al.*, 2011; dos Reis *et al.*, 2012; O'Leary *et al.*, 2013). With Xenarthra and Afrotheria determined as basal clades, the remainder are assigned to the third and largest clade, Boreoeutheria (see Box 10.5). The only continuing debates concern the exact placement of some marsupial clades and some placental clades (e.g. Tubulidentata, Chiroptera).

The major clades of marsupials and placentals then map onto major geographic realms (Fig. 10.19(a)), namely South America and Australia for the marsupials. For placentals, the Xenarthra and Afrotheria represent placental mammalian radiations in South America and Africa respectively, and the Boreoeutheria in the northern hemisphere – North America, Europe, and Asia.

There are two alternative views on the relationships of the three major placental clades, and these have biogeographic consequences (Teeling and Hedges, 2013). Many analysts (e.g. dos Reis *et al.*, 2012) find evidence to pair Xenarthra and Afrotheria, as Atlantogenata, and this implies a southern–northern hemisphere split early in the evolution of Placentalia, between Atlantogenata (Gondwana) and Boreoeutheria (Laurasia). The more traditional view is also supported (e.g. O'Leary *et al.*, 2013), in which Xenarthra splits off first, perhaps matching the early isolation of South America, and Afrotheria and Boreoeutheria divide later.

As with birds (see Section 9.4.3), there has been a long-rumbling debate about the timing of these fundamental splits in the phylogeny of modern mammals. In early studies (e.g. Hedges *et al.*, 1996), the fundamental splitting dates between placental orders were in the range 95–115 Myr, some 30–50 Myr before the KPg boundary and the first fossils. As in the birds case, scientists can either accept these discrepancies, or reason about why one or other data set, or both, might be erroneous. Certainly, the molecular divergence dates should always predate the first fossil in the clade in question, but a 30–50 Myr gap is probably unacceptably large, as argued early in the debate (e.g. Benton, 1999; Foote *et al.*, 1999). Such a gap implies an enormous amount of missing data, and through a time span (the Late Cretaceous), when several localities in North America and Asia were producing exquisite specimens of tiny mammals, but just the pre-marsupial and pre-placental clades.

There are three possible models for the radiation of modern mammal groups, primarily Placentalia (Archibald and Deutschman, 2001): (1) the **explosive model**, in which the clade diversified in the Paleogene after the KPg event; (2) the **long-fuse model**, in which the ancestor of Placentalia emerged about 100 Myr ago, but ordinal diversification happened only in the Paleogene; and (3) the **short-fuse model**, in which placental orders diversified in the Late Cretaceous, but their fossils have yet to be found. In resolving which of these three models might be correct, it is important to note that earlier reports of ancient representatives of modern placental clades have been rejected (Asher *et al.*, 2005; Wible *et al.*, 2007, 2009; Goswami *et al.*, 2011).

The debate continues, with more recent studies still pointing to dates of origin of modern placental orders about 100 Myr ago (e.g. Meredith *et al.*, 2011). However, the question may now be resolved. In a comprehensive study, taking special care over the use of fossils as calibrations, and assessing huge amounts of phylogenomic data, dos Reis *et al.* (2012) find divergence dates more in accordance with the fossil record. They estimate that metatherians diverged from eutherians 168–178 Myr ago, and crown Marsupialia diverged 64–84 Myr ago. Placentalia diverged 88–90 Myr ago, and present-day placental orders (except Primates and Xenarthra) originated in a 20 Myr window (45–65 Myr ago) after the KPg extinction. These authors present a reconciliation of molecular and fossil data, rejecting both the explosive and short-fuse models. Placentals originated earlier than the oldest currently known fossils, but persisted at low diversity and low abundance until the KPg mass extinction provided the opportunity for explosive diversification of modern marsupial and placental orders.

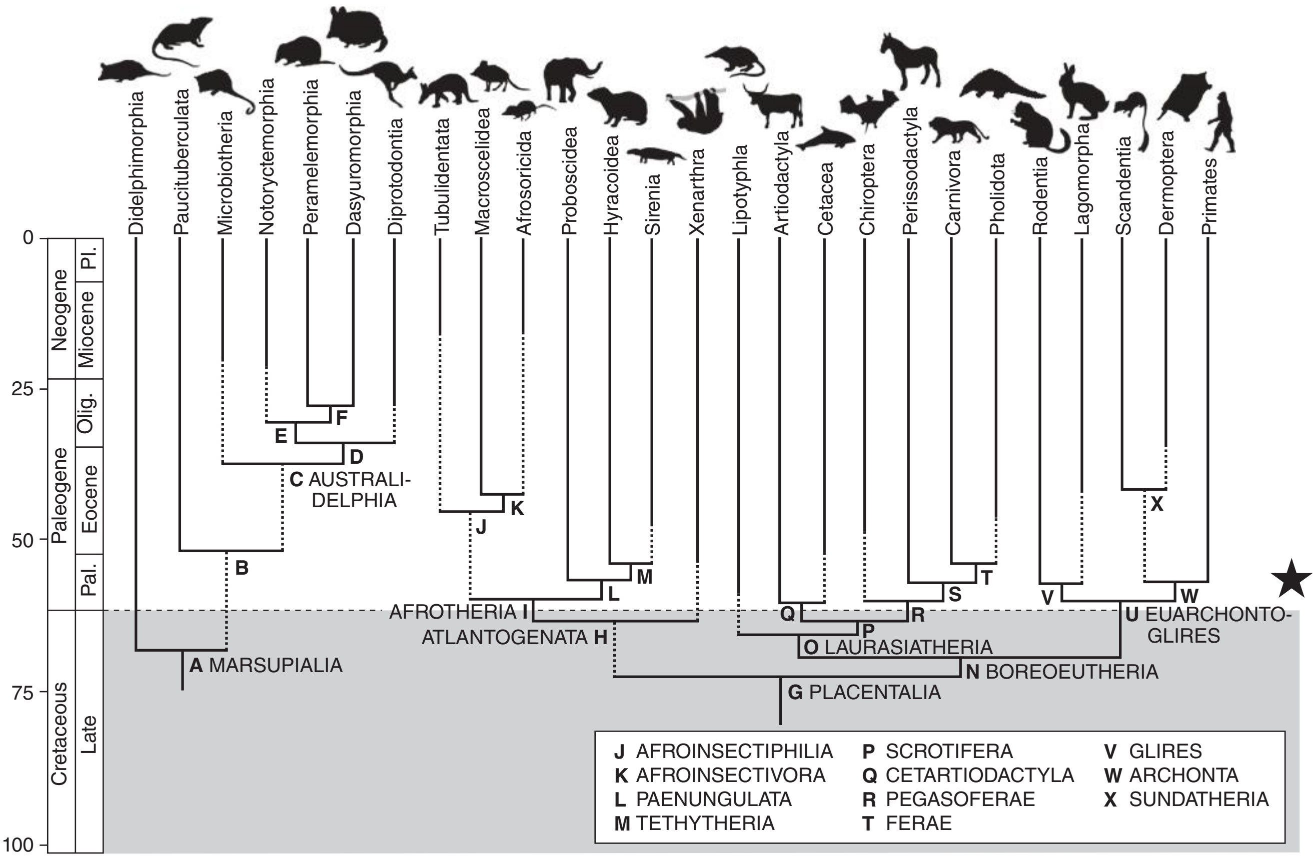
Evolution of all organisms, and especially of mammals, has been affected by continuing cooling of climates through the Cenozoic (Figure 10.19(b)). It is likely that rising temperatures through the Paleogene favoured certain early mammalian groups (see Section 10.8), then falling temperatures and continental

BOX 10.5 THE PHYLOGENY OF MODERN MAMMALS

The phylogeny of modern mammals has undergone a substantial revolution thanks to new phylogenomic analyses. These have more or less confirmed cladograms of Marsupialia based on morphological characters, except that the older split into Ameridelphia and Australidelphia is not generally supported on the basis of molecular and combined evidence. The current consensus (Asher *et al*., 2004; Meredith *et al*., 2008; Horovitz *et al*., 2009) recognizes the Australian clade, and the South American taxa form outgroups to that.

The phylogeny of placental mammals has been substantially overturned by the application of molecular phylogenetic techniques. These determined the major mammalian clades Afrotheria, Xenarthra, and Boreoeutheria, which have been confirmed repeatedly (Springer *et al*., 2004; Murphy *et al*., 2007; Meredith *et al*., 2011; dos Reis *et al*., 2012; O'Leary *et al*., 2013). Within Boreoeutheria are the two clades Euarchontoglires (=Glires [rodents, rabbits] + Archonta [primates, treeshrews, flying lemurs]) and Laurasiatheria (insectivores, bats, carnivores, ungulates).

The project on placental phylogeny, led by Maureen O'Leary (O'Leary *et al*., 2013), is documented in massive detail, with listings of taxa, characters, molecular and morphological data, and illustrations of all character codings, at: http://www.morphobank.org/index.php/Projects/ProjectOverview/project_id/773.



Cladograms showing the postulated relationships of the placental mammals. The outlines of the tree are founded on recent molecular analyses, and morphological synapomorphies are taken from Horovitz and Sánchez-Villagra (2003) for marsupials, and Novacek *et al*. (1988), Asher *et al*. (2009), O'Leary *et al*. (2013), and other sources for placentals. Naming the new clades has become an active field (Asher *et al*., 2009). Animal silhouettes are mostly from the PhyloPic website, and we acknowledge the work of Pearson Scott Foresman, Chris Huh, Mo Hassan, T. Michael Keesey, David Orr, Steven Traver and Sarah Werning. Synapomorphies for many nodes have yet to be discovered: **A MARSUPIALIA**, proximal extension of trochlea and capitulum in humerus equal, tibia posterior shelf extends beyond medial astragalotibial facet, calcaneal sustentacular facet oriented dorsally, alisphenoid tympanic wing poorly developed, transverse canal foramen anterior to carotid foramen, palatal vacuities present and restricted to palatine bones; **B**, suture between rib and axis visible, cuboidcalcaneal facet outer shelf present, alisphenoid tympanic wing moderately developed; **C AUSTRALIDELPHIA**, calcaneal sustentacular facet and posterior calcaneoastragalar facets merged; cuboid medial plantar process forms groove, three lower incisors; **D**, no synapomorphies identified; **E**, no synapomorphies identified; **F**, no synapomorphie sidentified; **G PLACENTALIA**, chorioallantoic placenta, prolonged gestation in uterus, median vagina, epipubic bones and pouch absent, shell membrane absent, narrow stylar shelves on upper molars, optic foramen widely separated from sphenorbital fissure; **H ATLANTOGENATA**, late dental eruption, infant precociality, amniogenesis by cavitation; **I AFROTHERIA**, more than 19 thoracolumbar vertebrae, testicondy (non-descended male gonads adjacent to the kidneys, four-lobed morphology of the allantois;

J AFROINSECTIPHILIA, two frontoturbinals and three ethmoturbinals in the nasal cavity; **K AFROINSECTIVORA,** anteriorly downturned rostrum, anterior semicircular canal is amply undulate, crista falciformis is thickened, cochlear canal is voluminous with respect to volume of inner ear, capitular tail on humerus; **L PAENUNGULATA**, short (retracted) nasal bones, amastoidy (mastoid process concealed by expansion and overlap of squamosal), jugal extends posteriorly as a prominent ventral crest to anterolateral border of the glenoid fossa, carpals dorsoventrally compressed and serially arranged; **M TETHYTHERIA**, bilophodont cheek teeth with tendency to form additional lobe on posterior part of cingulum, forward displacement of orbits, infraorbital canal very short, zygomatic process of squamosal robust and extends dorsally and laterally, premaxilla with strong posterior process extending around reduced nasals and nearly contacting frontals, ventrally protruding coracoid process on the scapula, medial tubercle on the astragalus; **G**, no synapomorphies identified; **N BOREOEUTHERIA**, cochlear canaliculus length greater than width of the fenestra cochleae, presence of a muscular process on the stapes, thryohyoid with a tapered distal end, spatulate upper I2, upper P2 with only one cusp; **O LAURASIATHERIA**, small coracoid process, allantoic vessels of large to moderate size; **P SCROTIFERA**, descended testicles and scrotum; **Q CETARTIODACTYLA**, trochlea (groove) on navicular bone in ankle, narrow calcaneum and elongate heel process; **R PEGASOFERAE**, no synapomorphies identified; **S**, no synapomorphies identified; **T FERAE**, caudal tympanic process mediolaterally narrow, median furrow bar of bone absent, mastoid foramen absent, carnassial shear anywhere on toothrow, stylar shelf on M2, angle between lateral calcaneus and sustentaculum 180 degrees, astragalar neck long, 1st metatarsal greater than or equal to 50% length of 3rd metatarsal, ventral border of distal phalanges curved inferiorly; **U EUARCHONTOGLIRES**, contact between exoccipital and auditory bulla, absence of cranial foramina for temporal rami, pterygoid shelf on ramus of dentary, absence of parastylar and metastylar cusps on M1; **V GLIRES**, posterior process of premaxilla long and contacts frontal, maxilla does not contact frontal, premaxilla and maxilla equally exposed in palate, glenoid fossa (jaw joint) set well dorsally of basicranium, upper and lower first incisor teeth absent, ever-growing incisors; **W ARCHONTA**, sustentacular facet of astragalus in distinct medial contact with distal astragalar facets, pendulous penis suspended by reduced sheath between genital pouch and abdomen; **X SUNDATHERIA**, fused premaxillae, lacrimal extending along the entire orbital rim, anteroposteriorly elongate facial process, flat glenoid fossa on the squamosal, absence of a tympanic incisura, scapholunate fusion, absence of articulation between the magnum and scaphoid, digitigrady, presence of a prehallux, presence of an entotympanic. Abbreviations: Ol, Oligocene; Pal, Paleocene; Pl, Pliocene/Pleistocene. Dashed lines and star symbols indicate extinction events.

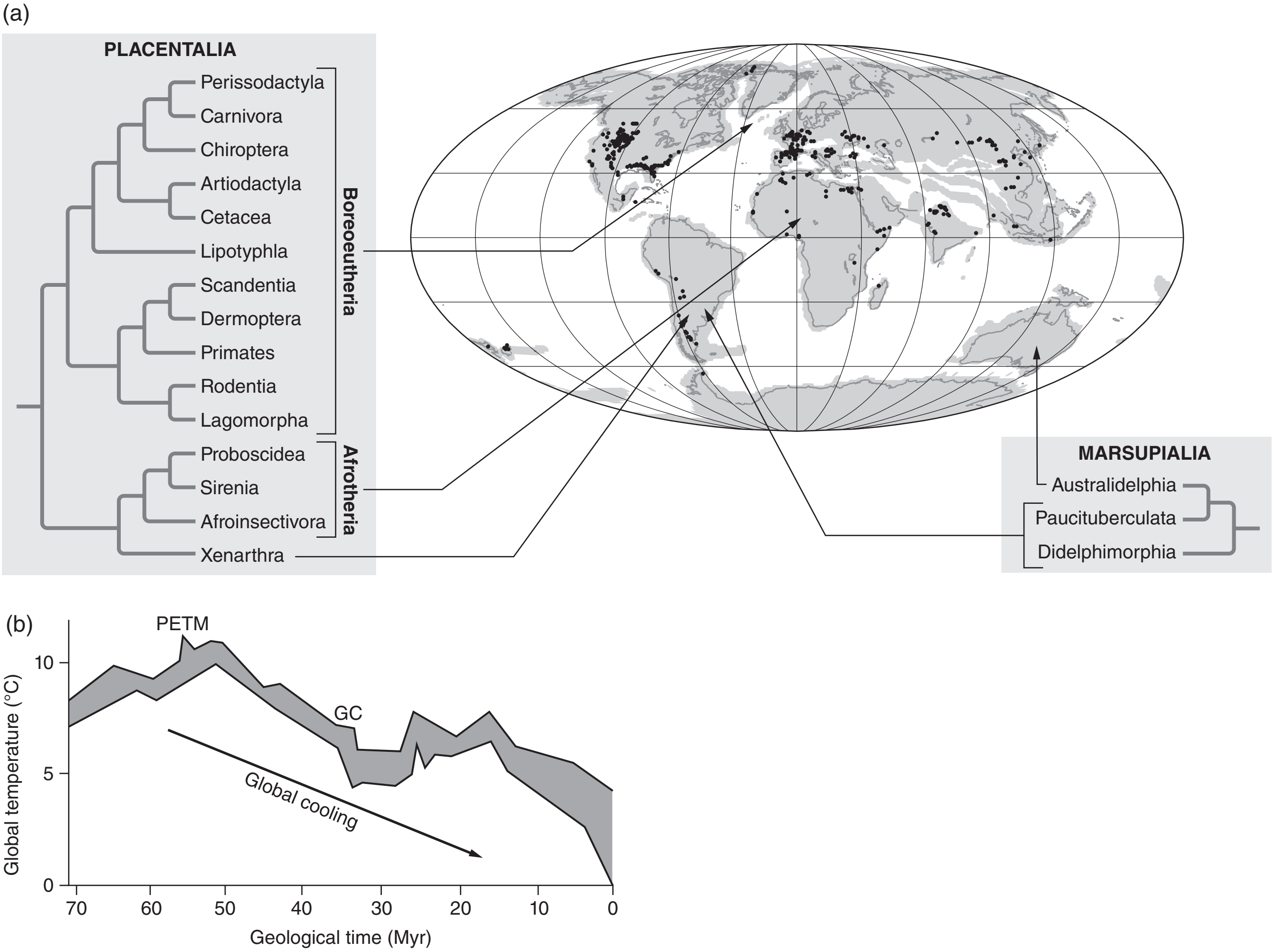


Figure 10.19 Mammals and climates through the Cenozoic. (a) Simplified phylogenies of Placentalia (left) and Marsupialia (right), showing major biogeographic divisions and locations on a Paleogene world map, which shows ancient coastlines and major mammal fossil localities; (b) global temperature ranges through the past 80 Myr. Two events are noted, the Palaeocene-Eocene Thermal Maximum (PETM), a sudden peak in temperature worldwide, and the Grand Coupure (GC), at the Eocene-Oligocene boundary, associated with a sudden drop in temperature. Source: Adapted from various sources and Alroy (2013).

movements led to the spread of grasslands in the Oligocene and Miocene, which had major effects on mammalian feeding and locomotion (see Sections 10.10.4, 10.11.2), and then continuing falls in temperature, culminating in the Pleistocene ice ages (see Section 10.14) had further major effects on mammalian distributions and body sizes.

Next we consider the modern mammalian clades, dividing them broadly geographically, and considering first the marsupials of Australia, then the unusual marsupials and placentals of South America, then the Afrotheria from Africa, and finally the Boreoeutheria from northern continents.

10.5 MARSUPIALS DOWN UNDER

Metatherians, including marsupials, probably arose in the Early Cretaceous of Asia (see Section 10.3.6), and spread from there across Europe to North America and then to South America and Australasia (Vullo *et al*., 2009; Williamson *et al*., 2012). The Australasian marsupials, Australidelphia, are a distinct clade nested within a wider clade that includes the South American marsupials as outgroups (see Box 10.5), which is confirmed by morphology and molecules (Asher *et al*., 2004; Meredith *et al*., 2008; Horovitz *et al*., 2009). For years, the split distribution of marsupials was a mystery and numerous biogeographical theories were proposed about how they could have travelled from the Americas to Australasia.

10.5.1 Geography and marsupial migrations

Marsupials migrated from Asia to Europe and the Americas in the Late Cretaceous (see Section 10.3.6), but there was a break at the KPg boundary when most Cretaceous groups went extinct. Then, didelphid marsupials, which had survived the KPg mass extinction in North America, apparently migrated back to Eurasia (Figure 10.20), where they survived until the Miocene, and Africa. In North America, the didelphids became extinct in the Miocene, but they reinvaded from South America much more recently. Marsupials are known in Australia from the early Eocene onwards.

The present split distribution of marsupials has been a classic theme of enquiry for biogeographers. Before 1960, when biogeographers assumed that the arrangement of the continents had never changed, a northern dispersal route was generally favoured, with the early marsupials travelling across Asia from North America to Australia in the Paleogene, but no evidence of marsupials had been found in Asia up to that point. With the acceptance of continental drift (see Section 2.3.2), most people preferred a southern dispersal route from South America to Australia via Antarctica. Now, several South American types of marsupial have been found in the Paleogene of Antarctica and these confirm the likelihood of the southern dispersal route.

Which way did modern marsupials migrate? It might seem obvious that they went from the Americas (where marsupials had had a long Cretaceous history; see Section 10.3.6) to Australia, via Antarctica. But is this so? Evidence for the America to Australia route might be the discovery that the modern South American monito del monte (*Dromiciops*), and its extinct relatives (Microbiotheria), are members of Australidelphia (Meredith *et al*., 2008). Fossils date Microbiotheria back to the early Miocene, with questionable Paleocene representatives. This could be taken as evidence that the Australidelphia arose in South America and then migrated to Australasia, leaving the microbiotheres behind. However, the oldest Australian marsupial, *Djarthia*, is more plesiomorphic than the microbiotheres (Beck *et al*., 2008), so the direction of movement could have been the reverse, with some australidelphians trekking back across Antarctica to re-populate South America. Further, the discovery of a non-australidelphian calcaneum in Australia (Beck, 2012)

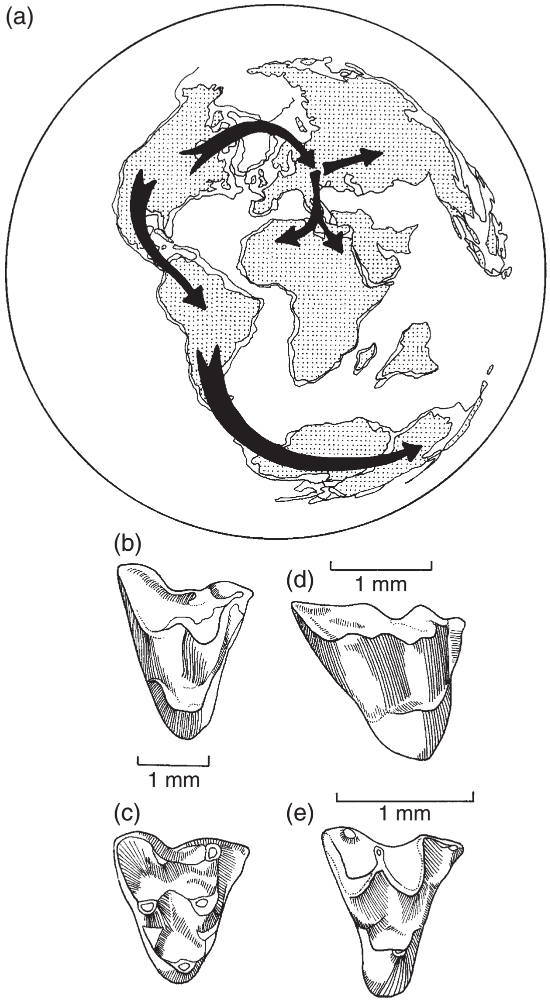


Figure 10.20 (a) The migration of the didelphid marsupials (opossums) from an origin in the Late Cretacous of North America, into South America, Antarctica and Australasia, and into Europe, North Africa and Asia. (b–e) Typical opossum-like marsupial molars from all parts of the world: (b) *Amphiperatherium* from Europe; (c) *Alphadon* from North America; (d) cf. *Peratherium* from Kazakhstan, central Asia; (e) *Garatherium* from Algeria, North Africa. Source: Adapted from various sources.

suggests that the distribution of marsupials in Gondwana cannot be explained by a single dispersal event. Either there were multiple dispersals, in one or both directions, or there may have been a broadly similar metatherian fauna occupying southern South America, Antarctica and Australia during the Late Cretaceous and early Paleogene.

10.5.2 The Australian marsupials

The Australian marsupials, Australidelphia, differ from the South American marsupials (see Section 10.6.2) in characters of the astragalus. The American marsupials show the plesiomorphic lower ankle joint pattern, with two facets on the calcaneum for articulation with the astragalus, and a single calcaneocuboid facet at the other end of the calcaneum for articulation with the cuboid (distal tarsal). Australidelphians show derived states of these characters, in which the facets on the calcaneum for articulation with the astragalus combine as one, and the calcaneocuboid facet is divided into three distinct facets.

Convergence between Australian marsupials and placentals from other parts of the world is often striking. For example, the recently extinct thylacine, or marsupial 'wolf', *Thylacinus* has a skull that seems at first sight to be identical to that of the dog or fox (Figure 10.21(a, b)). It differs in details, however; the molars of *Thylacinus* have both shearing and grinding surfaces, whereas in *Canis* meat is cut and bones crushed by separate teeth. The skull is also rather more delicately built, and has characteristic marsupial signatures, such as an inturned angle of the dentary, and more incisors (four uppers and lowers on each side, while no placental has more than three). Similar convergences may be found in the marsupial moles, ant-eaters, climbing insectivores, leaf-eaters and even grazing ungulates (even though a kangaroo at first looks very different from a deer or antelope, the head is similar and it lives in roughly the same way).

The fossil record of Australian marsupials extends back to the early Eocene (Beck *et al*., 2008), with more substantial remains from the late Oligocene onwards. Two times are extensively sampled, first the Oligocene and Miocene in the Riversleigh area, Queensland, source of more than 60 genera of monotremes and marsupials, as well as fishes, frogs, reptiles, birds, and bats. Secondly, equally spectacular faunas are known from the Pleistocene, when giant diprotodonts, kangaroos and others lived with giant echidnas and the heavily armoured turtle *Meiolania* (see Section 8.7.2), as well as the cow-sized varanoid lizard *Megalania* and the redoubtable snake *Montypythonoides*. The scene (Figure 10.21(c)) was dominated by great herds of the bison-sized diprotodontid *Diprotodon* and its smaller relatives, the giant kangaroo *Procoptodon* and *Thylacoleo*, the marsupial lion. The extinction of these spectacular faunas has been blamed on the arrival of humans in Australia or on climate change (see Section 10.14).

The Australian marsupials radiated into four major clades (Asher *et al*., 2004; Meredith *et al*., 2008; Horovitz *et al*., 2009). The Dasyuromorphia includes 70 or so species of marsupial mice and rats, dasyures (cat-like animals), the Tasmanian devil and the Tasmanian wolf *Thylacinus* (Figure 10.21(a)). The thylacine became extinct in 1936 when the last captive individual, named Benjamin, died in Hobart Zoo. The Peramelemorphia includes some 20 species of bandicoots and bilbies, the oldest bandicoot being late Oligocene in age. The Notoryctemorphia contains the two living species of marsupial moles, with oldest fossils from the early Miocene.

The Diprotodontia is represented today by 117 species of possums, gliding phalangers, wallabies, kangaroos, koalas and wombats (Meredith *et al*., 2009). They are characterized by diprotodonty (= 'two front teeth'), possessing a pair of large, procumbent incisor teeth on the lower jaw, instead of four or six. Diprotodontians share with bandicoots the feature of

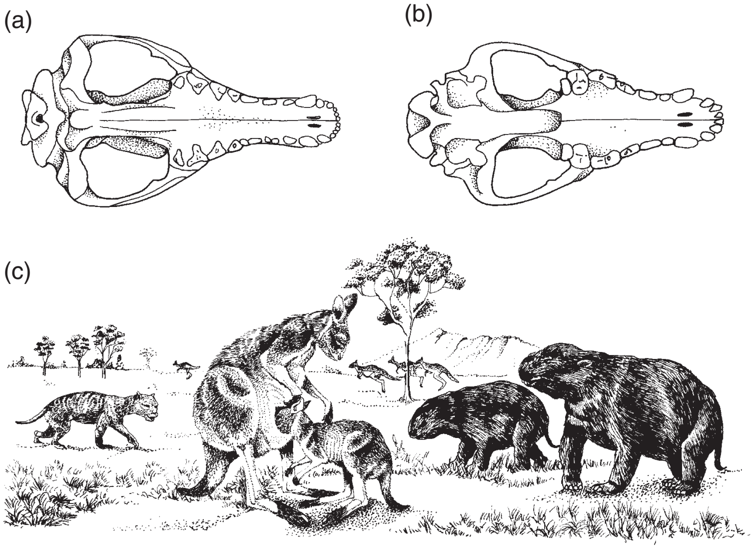


Figure 10.21 Convergent evolution of a dog-like form of the skull (ventral view) in (a) the marsupial thylacine *Thylacinus* and (b) the placental dog *Canis*; (c) scene in the Pleistocene of Australia, with the marsupial 'lion' *Thylacoleo* on the left, a mother and juvenile giant kangaroo *Procoptodon*, and two giant diprotodontids *Diprotodon*. Source: (a,b) Adapted from various sources. (c) Adapted from a painting in Benton (1986), © Grisewood & Dempsey Ltd., 1986.

syndactyly in the hind foot, where the fourth toe is the major element, and toes two and three are tiny and bound together to form a grooming claw. Four diprotodontian subclades are generally recognized.

Most basal are the Vombatiformes, wombats and koalas, whose fossil record dates back to the late Oligocene. Among extinct relatives, the marsupial lion, *Thylacoleo*, may seem unlikely. It is a well-known Pleistocene predator that fed on most mammals, although adult diprotodontids and giant kangaroos were probably safe from its attentions. The heavy, 250-mm-long skull of *Thylacoleo* (Figure 10.22(a)) has strong canine-like incisors and exceptionally long flesh-cutting blades extending across two teeth. More obviously wombat-like are the extinct Diprotodontidae. They arose in the mid-Miocene and survived into the Holocene: perhaps the last ones were hunted by early Australian aboriginals. *Diprotodon* (Figure 10.22(b)) has heavy limbs with broad plantigrade feet to bear its weight. The feet have powerful digits and deep claws and they may have functioned in scratch digging for food. This gentle giant has a massive skull and its upper and lower jaws are armed with a pair of tusk-like incisor teeth at the front, and broader crushing molars set well back.

Next come the Petauroidea, the ringtailed possums and gliding possums, most of which are arboreal, and feed on leaves. Some have flaps of skin down the sides of their bodies to enable them to glide short distances. Fossils are known from the late Oligocene and early Miocene.

The Phalangeroidea are more possums and phalangers, and these are also small to medium-sized tree-dwellers. Possums generally feed on plants, some are omnivores, and individual species specialize on diets of nectar or insects, while the phalangers are largely nocturnal leaf-eaters. Fossil forms date back to the late Oligocene.

Finally, the Macropodiformes, kangaroos and wallabies, arose in the late Oligocene. Some extinct kangaroos, the Sthenurinae, were the dominant forms of large kangaroos in the Pleistocene, most being larger than the largest kangaroos today. They had short and deep faces, teeth indicative of browsing, arms that were longer and stronger than in modern kangaroos, and had reduced the hind foot toes to a single digit. Some of these forms achieved very large sizes: *Procoptodon* (Figure 10.22(c)) had an estimated mass of 250 kg, more than three times the size of a big male red kangaroo. At these large body sizes their mode of locomotion is debatable, as they may have been too large to hop. On the other hand, almost all extant kangaroos move by hopping on enlarged back legs, with an extremely enlarged fourth toe, and a reduced fifth one (Figure 10.22(d)). Kangaroos are familiar to us as the large grey and red kangaroos that are highly proficient hoppers, who can achieve racehorse speeds of 45–55 km h^{-1} over short distances, but with much less energy expenditure than a horse. But kangaroos are a diverse group, including little potoroos, tree kangaroos, and a large variety of small wallabies.

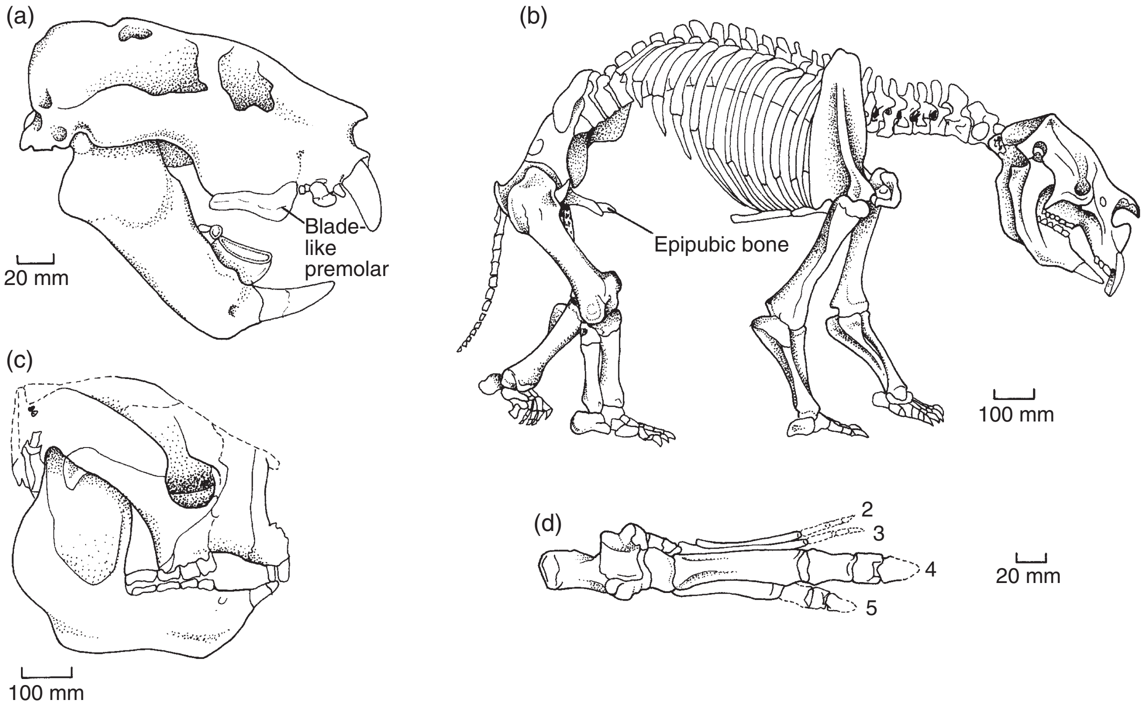


Figure 10.22 Australian fossil marsupials: (a) skull of the marsupial 'lion' *Thylacoleo*, showing the blade-like cheek teeth; (b) skeleton of the diprotodontid *Diprotodon;* (c) skull of the kangaroo *Procoptodon*; (d) foot of the kangaroo *Protemnodon*, showing the dominant fourth toe. Source: (a) Adapted from Nicholson and Lydekker (1889). (b) Adapted from Flower and Lydekker (1891). (c) Adapted from Tedford (1966). (d) Adapted from Flannery (1982).

10.6 SOUTH AMERICAN MAMMALS – A WORLD APART

For most of the Cenozoic, South America was an island, isolated from all other parts of the world. As in Australia, a spectacular **endemic** (geographically restricted) fauna of mammals evolved that shows little taxonomic similarity to those of other parts of the world. South America had its own families of marsupials, some of which mimicked dogs, bears, sabre-toothed cats and others in an uncanny way. The herbivores for most of the Cenozoic were rodents, some as large as deer, or larger (see Section 10.12.2), native South American ungulates, including horse-mimics and rhinoceros-mimics, and the armadillos and sloths (edentates). Where did these remarkable mammals come from and what has happened to them now?

10.6.1 The Mesozoic mammals of South America

For much of the Mesozoic (252–66 Myr ago), South America was linked to Africa (see Section 2.3.2), but this connection was lost during the Cretaceous when the South Atlantic Ocean began to open up. There may have been a geologically brief land bridge formed to Central and North America about 70 Myr ago when mammals were able to cross both ways.

Mesozoic mammals from Argentina include *Vincelestes* from the Early Cretaceous (see Section 10.3.5) and a diverse mammalian assemblage from three Late Cretaceous formations, the Los Alamitos, La Colonia, and Allen, all of similar Campanian-Maastrichtian age (Rougier *et al*., 2009; Woodburne *et al*., 2014). The mammalian faunas are associated with dinosaurs and crocodilians, and they are dominated by diverse dryolestoids (see Section 10.3.1), with a triconodontan and a symmetrodontan, as well. Rare examples of the bizarre ferugliotherids and sudamericids are also known; these two groups have been combined as the clade Gondwanatheria, known only from isolated teeth and some jaws primarily from the Late Cretaceous and Paleogene of South America, with some materials from Antarctica, Madagascar, and India. Molars attributed to gondwanatherians are unique among all Mesozoic and early Cenozoic mammals in possessing lophs of enamel, separating areas of exposed dentine. Ferugliotheriids have low teeth, whereas as sudamericids have high-crowned teeth, possibly reflecting diets of, respectively, soft vegetation or insects and tough vegetation. The affinities of gondwanatheres have been much debated (this is often the case with taxa represented by little more than teeth; the less the evidence, the wider the debate), but they seem most plausibly (Gurovich and Beck, 2009) to be a unique Gondwanan side-branch of the multituberculates (see Section 10.3.4).

After the KPg event, the basal mammalian groups and many of the marsupials disappeared elsewhere in the world. But South America was now an island again and the marsupials and placentals evolved there in isolation, together with late-surviving Cretaceous nontherian mammals such as dryolestoids and gondwanatherian multituberculates. An early Palaeocene fauna from Tiupampa, Bolivia, includes 19 genera, of which 12 are marsupials, mostly showing similarities to later uniquely South American groups. The placentals mostly show relationships to North American forms (cimolestans, mioclaenids, pantodonts), but some (notoungulates) are unique to South America. Ecologically, the majority of these mammals are small insectivores weighing less than 50 g, with smaller numbers of medium-sized browsing herbivores. None of the 19 Tiupampan mammals can be related to the latest Cretaceous faunas from Los Alamitos and other formations, so they must have migrated over the long route from North America to Argentina either just before or just after the KPg event (Woodburne *et al*., 2014).

10.6.2 South American marsupials

Marsupials radiated in South America to a lesser extent than they did in Australia, but they dominated as insectivores and included major carnivore groups and some small herbivores. The 15 families of extinct insectivorous and carnivorous marsupials show striking convergences with placental shrews, cats, sabre-tooths and dogs. The South American marsupials comprise four clades that are generally outgroups to Australidelphia (see Box 10.5). The Didelphimorphia, essentially the opossums, are well known from the Palaeocene of South America (Muizon and Cifelli, 2001). Didelphids survived through the Cenozoic in South America, although they died out in North America in the Miocene. They radiated in Europe in the Eocene to middle Miocene, and isolated taxa reached North Africa and Central Asia. Didelphids re-entered North America at the time of the Great American Interchange (see Section 10.6.6).

The Paucituberculata includes six living species of shrew opossum, as well as 50 extinct species, spanning the Cenozoic (Abello, 2013). The caenolestids, such as the living *Caenolestes* and *Palaeothentes* from the late Oligocene and early Miocene, were small insectivores or omnivores with an elongate lower incisor and blade-like cheek teeth (Figure 10.23(c)).

The relationships of the third clade, the extinct Polydolopimorphia, are debated (Goin *et al*., 2009; Abello, 2013). It was generally regarded as close to Paucituberculata, but some evidence links Polydolopimorphia with the microbiotheres, and so would make it part of Australidelphia (see Section 10.5.2). One polydolopimorphian that used to be assigned to Paucituberculata is *Roberthoffstetteria* (Figure 10.23(a,b)), a small insect-eater (Goin *et al*., 2009). A possible relative is the kangaroo rat lookalike *Argyrolagus* (Figure 10.23(d)), which has a narrow snout and broad cheek teeth for crushing tough plant food. The hindlimbs are long and powerful, which suggests a hopping mode of locomotion.

The fourth clade, the extinct Sparassodonta, consists of two groups of larger animals, both carnivorous (Prevosti *et al*., 2013). The borhyaenids, known from the Palaeocene to the Pliocene, such as *Prothylacynus* (Figure 10.23(e)), have short limbs and rather dog-like skulls, but with substantial biting forces (Blanco *et al*., 2011). Their later relatives, the late Miocene

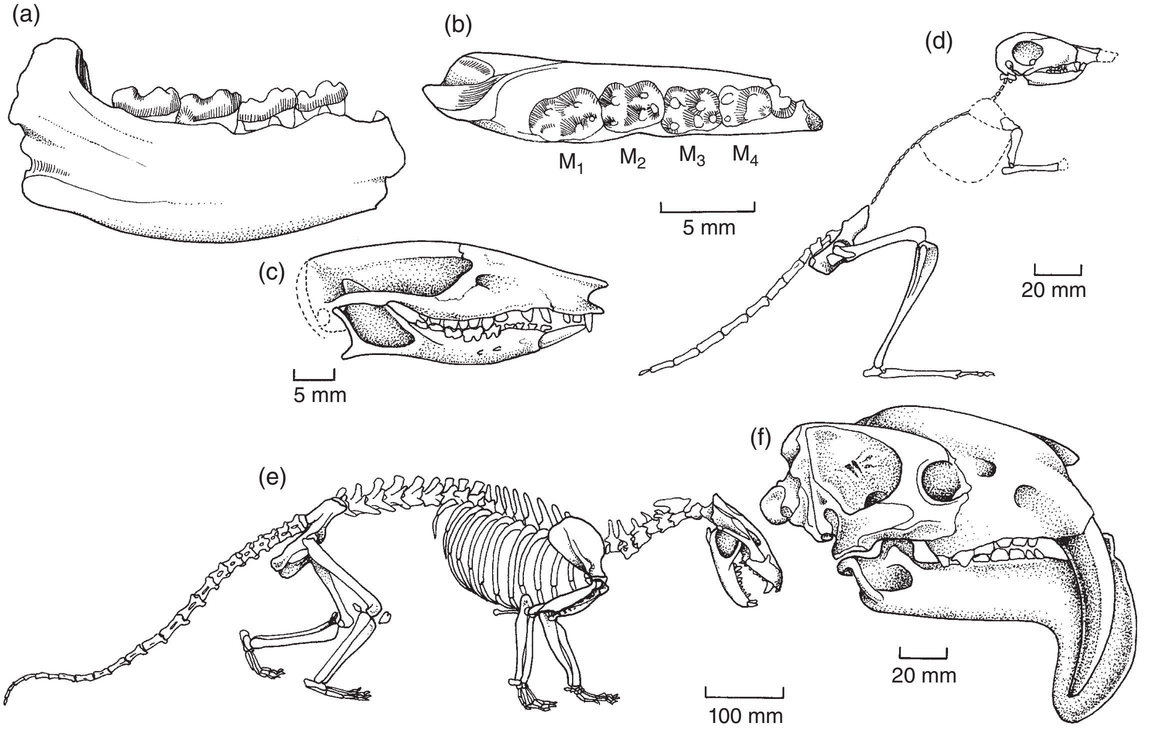


Figure 10.23 South American fossil marsupials: (a,b) the Palaeocene caroloameghinid *Roberthoffstetteria*, lower jaw fragment in lateral and occlusal views (c) the Oligocene to early Miocene caenolestid *Palaeothentes*; (d) the Pliocene argyrolagid *Argyrolagus*; (e) the early Miocene borhyaenid *Prothylacinus*; (f) the sabre-toothed Pliocene thylacosmilid *Thylacosmilus*. Abbreviations: M_1–M_4, molars. Source: (a,b) Adapted from Marshall and Muizon (1988). (c) Adapted from Marshall (1980). (d) Adapted from Simpson (1970). (e) Adapted from Sinclair (1906). (f) Adapted from Riggs (1934).

and Pliocene thylacosmilids, have skulls (Figure 10.23(f)) that are very similar to those of the sabre-toothed (placental) cats that lived in North America at the same time. The upper canine tooth is very long and it grew continuously, unlike the canine of true cats. It was presumably used for puncturing the thickened hides of the large thick-skinned South American notoungulates, but used a different method from the placental *Smilodon* (see Box 10.6).

10.6.3 Xenarthra: armadillos, sloths and ant-eaters

Some of the most characteristic mammals of South America are the Xenarthra, which include today 30 species of armadillos, tree sloths and anteaters (Vizcaíno and Loughry, 2008). This group has had a spectacular history, which is not evident from the living forms (Simpson, 1980; Fariña *et al.*, 2013). The name Xenarthra (literally 'strange joints') refers to supplementary articulations between some of the trunk and tail vertebrae (Figure 10.24(h)). In addition, they have a peculiar arrangement in the hip girdle in which the ischium, as well as the ilium, is fused to the anterior caudal vertebrae (Figure 10.24(c)). Thirdly, the teeth are much reduced: xenarthrans have few or no incisors and the anteaters have no teeth at all. Two further characters are that the males have internal testicles, and xenarthrans have the lowest metabolic rates among modern mammals.

The armadillos (Dasypodidae) first appear in the fossil record in the late Palaeocene, but the remains are only armour scutes. They radiated in the Oligocene and Miocene when a variety of small and large forms appeared. Like the modern *Dasypus* (Figure 10.24(a)), they all have a bony shield over their heads and body armour that is partly fixed and partly formed of movable rings and a bony tube over the tail.

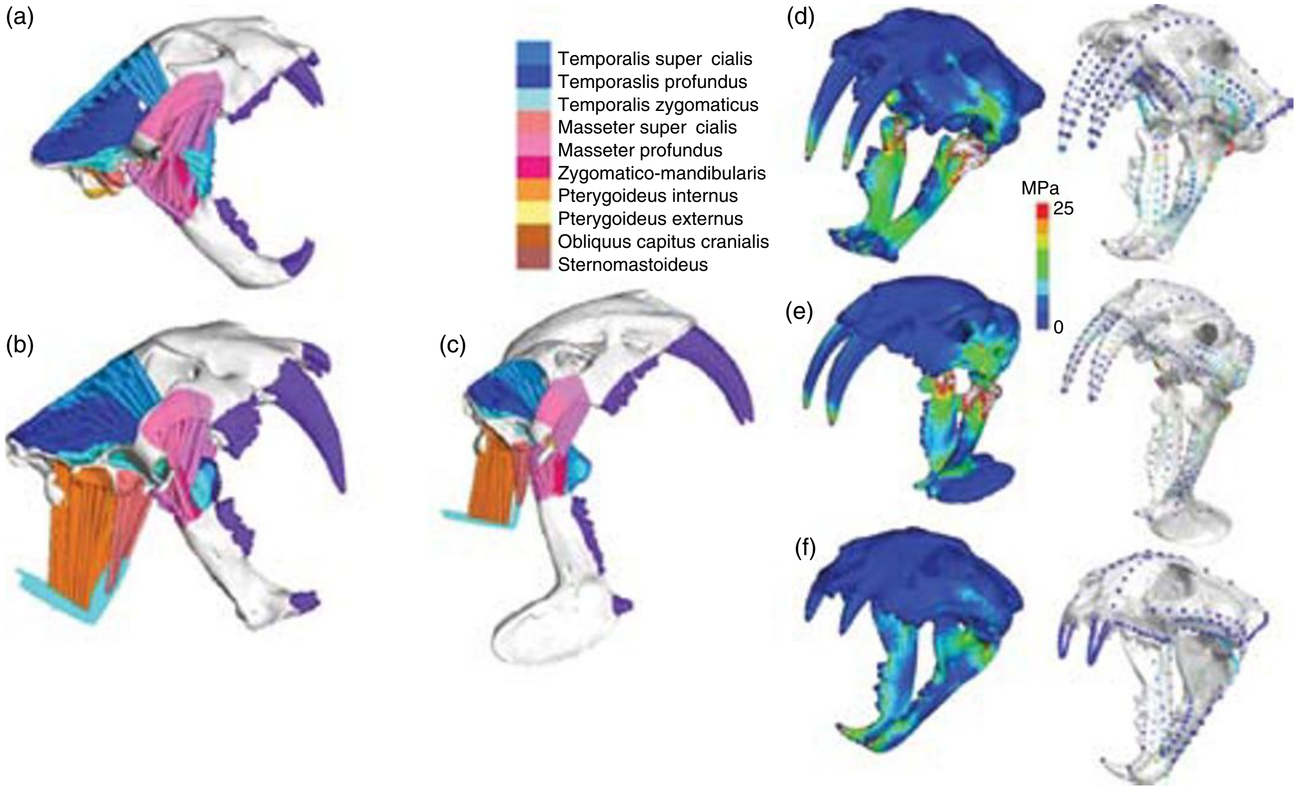
The most spectacular relatives of the armadillos were the glyptodonts (Figure 10.24(b,c)), which reached very large sizes in the Pliocene and Pleistocene (Vizcaíno *et al.*, 2010; Fernicolo and Porpino, 2012). The heavy armour, weighing as much as 400 kg in a 2-tonne animal, is clearly proof against voracious predators such as the sabre-toothed marsupials (see Section 10.6.2). The skull is short and deep (Figure 10.24(c)) and the massive jaws accommodate long, continuously growing cheek teeth that were used to grind up abrasive grasses. The short tail is flexible and in some forms bears a spiked club (Figure 10.24(e)) that was probably used to whack sabre-tooths. How effective was it? In classic biomechanical work, Alexander *et al.* (1999) found that a large *Glyptodon* with a 40-kg tail club could move the tip at up to 12 m s^{-1}, using some 3000 joules of energy. This is equivalent to the speed achieved by a shot-putter hurling the metal shot, and the power of the blow was sufficient to shatter glyptodont armour in intraspecific fights. But there is danger in having such a formidable weapon, that the animal might cause itself some injury if it is used ineffectively. Calculations of the

BOX 10.6 BITING MECHANICS OF MARSUPIAL AND PLACENTAL SABRE-TOOTHS

The sabretooths *Smilodon* (a placental) and *Thylacosmilus* (a marsupial) look superficially remarkably similar. These two represent extremes of their kind, on the one hand a large true cat, and on the other the largest thylacosmilid sparassodont marsupial, and both with the largest sabre teeth. There has been much debate about how these top carnivores used their massive canines, whether to puncture the thick skin of large herbivores and leave them to bleed, or to bite and remove chunks of flesh (see Section 10.11.5).

Using finite element analysis, Wroe *et al*. (2013a) assessed the mechanical performance in three dimensions of scanned skulls of the marsupial *Thylacosmilus* and the placental *Smilodon*, and compared these with the modern leopard, *Panthera pardus*. Their first finding was that the two sabre-toothed animals shared much more in common in terms of their biomechanics than did *Smildon* with its close relative *Panthera*. Compared to modern big cats, the two extinct sabre-tooths did not rely so much on biting forces generated by the jaw adductor muscles, but more on the power of massive neck muscles that drove the teeth down into the prey.

The FEA study also revealed differences between the two sabre-tooths that point to their respective killing mechanisms. First, *Smilodon* used both its jaw adductor and neck depressor muscles in delivering the killing bite. The mechanism was rather different in *Thylacosmilus*, which Wroe *et al*. (2013) characterize as showing 'a more complete commitment to the already extreme saber-tooth 'lifestyle'.' This is because they were able to show that its skull was better adapted to resist stress caused by the head-depressor muscles of the neck, whereas the jaw adductors probably played only a small part in delivering the killing bite.



Jaw mechanics of the placental sabre-tooth *Smilodon*, the marsupial sabre-tooth *Thylacosmilus*, and the modern conical-toothed leopard, *Panthera*. (a–c) Jaw adductor muscles in *Panthera* (a), and reconstructed jaw adductor and head depressor muscles in *Smilodon* (b), and *Thylacosmilus* (c). (d–e) Stress distributions for bites powered by the jaw adductor muscles, showing the intensity of stresses by the hotness of the colour, in *Panthera* (d), *Thylacosmilus* (e), and *Smilodon* (f). See Colour plate 10.3. Source: Wroe *et al*. (2013a). Reproduced with permission.

ideal centre of percussion (equivalent to the 'sweet spot' on a tennis racket or baseball club) shows that spikes on the club were located in precisely the right place for maximum energy of strike combined with greatest efficiency and safety for the glyptodont batsman (Blanco *et al*., 2009).

The sloths date back to the Oligocene and they had a broad radiation, even though only six species of tree sloths survive today (Pujos *et al*., 2012). A Miocene sloth, *Hapalops* (Figure 10.24(d)) is a small semi-arboreal animal that has only four or five cheek teeth in the jaws. Sloth evolution followed two

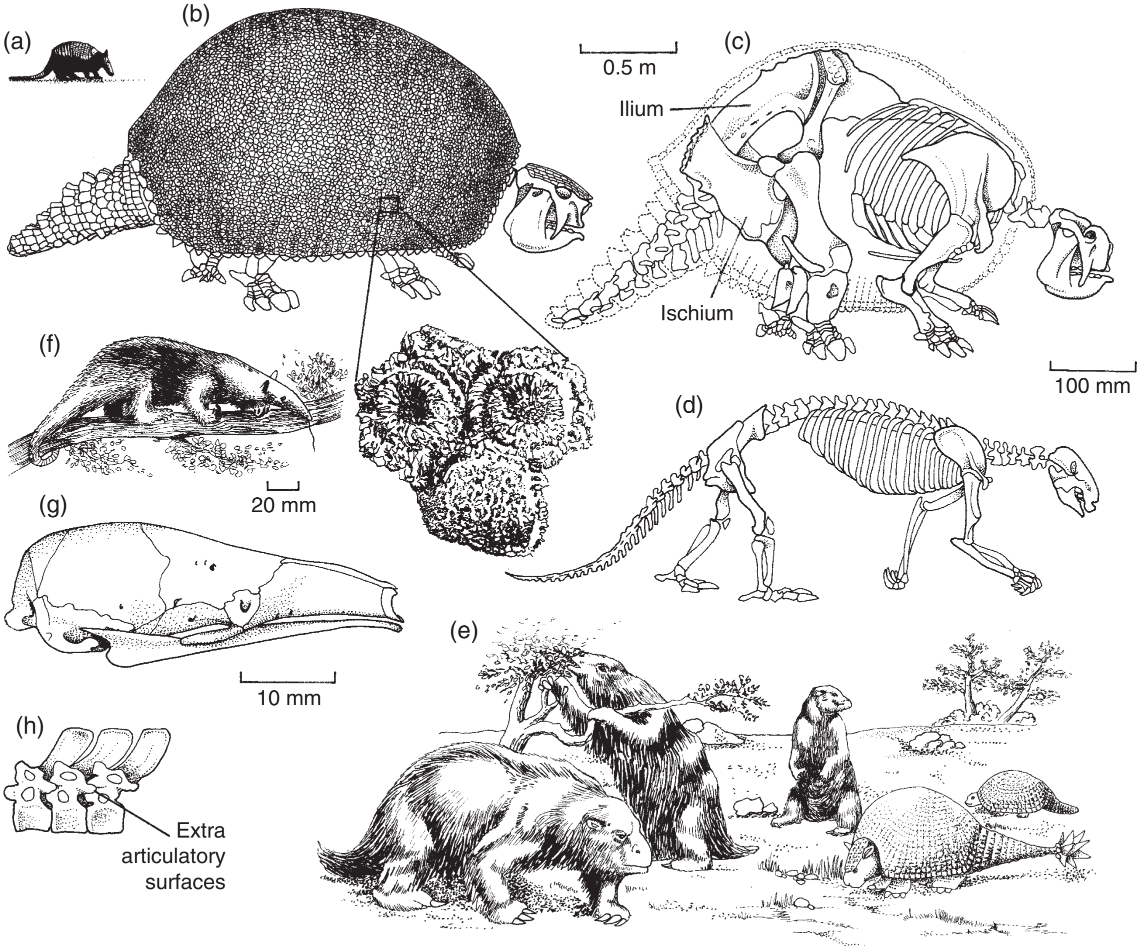


Figure 10.24 South American xenarthrans: (a) the modern armadillo *Dasypus* drawn to scale with (b) and (c) the Pleistocene glyptodont *Glyptodon*, showing the armour covering, a detail of the armour and the skeleton; (d) the Miocene sloth *Hapalops*; (e) a Pleistocene scene in South America showing the ground sloth *Megatherium* (left) and the glyptodont *Doedicurus*; (f,g) the living ant-eater *Tamandua*, life appearance and skull in lateral view; (h) dorsal vertebrae of the ant-eater *Myrmecophaga* to show extra articulating surfaces, the xenarthran condition. Source: (a–c,f) Adapted from Flower and Lydekker (1891). (d) Adapted from Matthew (1918). (e) Based on a painting by Charles Knight.

main ecological lines from the Miocene onwards. Some remained small and became adapted to life in the trees, like the modern tree sloths (Bradypodidae, some Megalonychidae), and the ground sloths (Megatheridae, Mylodontidae, some Megalonychidae), achieved giant size.

Megatherium, the largest ground sloth at 6 m in length, was a massive animal that may have fed on the leaves of tall trees (Figure 10.24(e)). It could rear up on its hind legs, and resting on the short tail and massive bowl-like pelvis, pull branches to its mouth with its long, hooked claws. The giant ground sloths ranged widely over South, Central and North America in the Pleistocene, and they died out only 11,000 years ago. Their extinction cleared a niche that has remained empty. The giant ground sloths were no doubt encountered by early humans: were they hunted to extinction? Specimens found in caves often have clumps of their yellowish and red hair still preserved, and thick accumulations of their dung in some South American caves have been known to ignite and to burn for months. Ancient DNA can be recovered from some specimens of dung (remains of the megathere's gut lining) and from bones preserved in cool, dry caves of the Andes (Shockey *et al*., 2009).

The anteaters (Myrmecophagidae) have a much poorer fossil record than the armadillos or sloths. There are three living genera, *Cyclopes* and *Tamandua* (Figure 10.24(f,g)), which live in trees, and the terrestrial *Myrmecophaga* (Figure 10.24(h)). The snout is long and toothless and it houses a long sticky tongue rooted far down the throat about level with the sternum that can be shot out to capture small insects (Figure 10.24(g)).

10.6.4 Meridiungulata: South American ungulates

There were five uniquely South American ungulate ('hoof-bearing') clades dating from the Palaeocene to the Pleistocene, the Litopterna, Notoungulata, Astrapotheria, Pyrotheria, and Xenungulata. There is some evidence that all five may be divisions

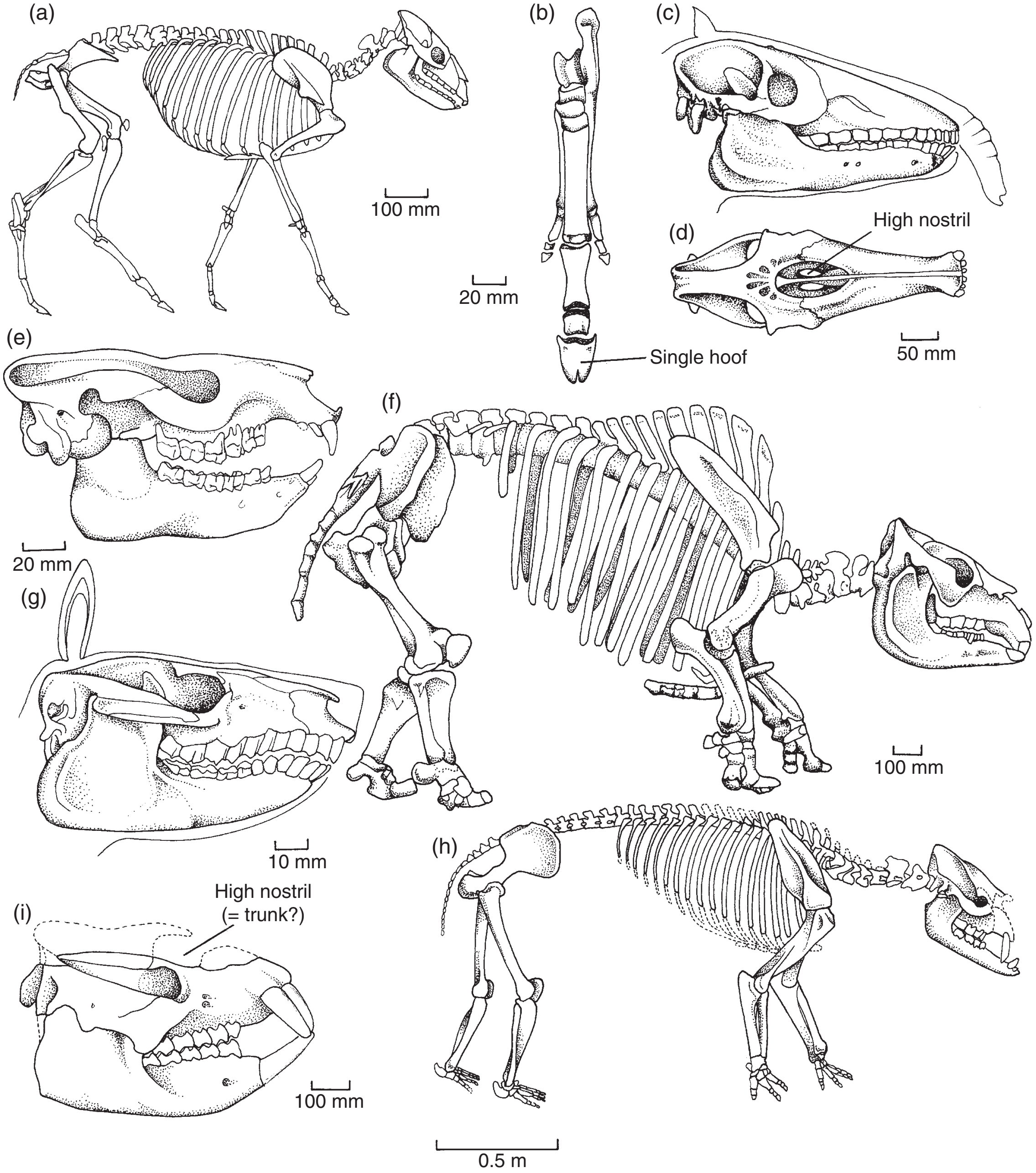


Figure 10.25 South American ungulates: (a,b) the Miocene litoptern *Diadiaphorus*, skeleton and foot in anterior view showing the horse-like single hoof; (c,d) the Pleistocene litoptern *Macrauchenia*, skull in lateral view with restored trunk and in dorsal view; (e) the Eocene notoungulate *Notostylops*; (f) the Pleistocene notoungulate *Toxodon*; (g) the Oligocene notoungulate *Protypotherium*; (h) the Oligocene and Miocene astrapothere *Astrapotherium*; (i) the Oligocene pyrothere *Pyrotherium*. Source: (a–d) Adapted from Scott (1910). (e,f) Adapted from Simpson (1948). (g) Adapted from Flower and Lydekker (1891). (h) Adapted from Riggs (1935). (i) Adapted from Loomis (1914).

of a single clade Meridiungulata (McKenna and Bell, 1997), but this is much discussed.

The litopterns include a range of rabbit-, horse- and camel-like forms. *Diadiaphorus* from the Miocene and Pliocene (Figure 10.25(a)) is a lightly built animal with many striking convergences with horses. The legs are long and only the middle toe (hoof) remains (Figure 10.25(b)). Some litopterns have the nostrils set well back in the skull roof, which almost certainly indicates the presence of a tapir-like trunk, as is seen in the superficially camel-like *Macrauchenia* from the Pleistocene (Figure 10.25(c,d)).

The notoungulates are by far the most diverse of the South American herbivore groups, with well over 100 genera known from the late Palaeocene to the Holocene. Their ear region is greatly expanded, with additional chambers above and below the normal middle ear cavity; they also have a particular pattern of ridges on their molar teeth, and a number of them evolved ever-growing (hypselodont) cheek teeth, as seen today in sloths, rabbits, and many rodents. Most notoungulates retain the plesiomorphic total of five fingers and five toes on each foot.

There were a number of early forms, and then the major subclades Toxodontia and Typotheria (Billet, 2011). The early notoungulates, forms such as *Notostylops* from the Eocene (Figure 10.25(e)) have a diastema, or gap, between the large nipping incisors at the front and the cheek teeth behind. Already, in this early form, the incisors are enlarged and the canines reduced. In later notoungulates, the canines often disappear and the incisors become ever-growing, like the gnawing teeth of rodents (see Section 10.12.1).

The largest notoungulate, the toxodont *Toxodon* (Figure 10.25(f)), was first collected by Charles Darwin in the Pleistocene of Argentina. He described it as 'perhaps one of the strangest animals ever discovered'. As in the notoungulates, the roots of the teeth remained open thoughout life so that they continued to grow to keep up with the wear produced by their abrasive diet of grass, and accidentally ingested grit. Some toxodonts, the notohippids, were superficially rather horse-like.

Many of the typotheres, such as *Protypotherium* from the Oligocene (Figure 10.25(g)), were rabbit-like animals, although some became as large as bears. *Protypotherium* has a continuous battery of shearing teeth, with no sign of a diastema. The typotheres include forms with reduced numbers of digits, down to two toes and three fingers in some species.

The astrapotheres, known from the Palaeocene to the late Miocene, are diagnosed by tusk-like canine teeth and some molar and ankle characters (Kramarz and Bond, 2009). Early forms are modest in size, but *Astrapotherium* from the Oligocene and Miocene (Figure 10.25(h)) is as large as a rhinoceros. It has a long body and short legs. The lower incisors stick out straight in front and may have been used in digging for water plants and roots.

The pyrotheres from the Eocene and Oligocene are also large long-bodied animals with trunks (Billet, 2010). The skull (Figure 10.25(i)) is short, and bears broad tusk-like incisors. The xenungulates are a poorly known group from the Palaeocene that might be related to pyrotheres because of their shared bilophodont cheek teeth.

Is the Meridiungulata real or not? Several analysts find relationships between pairs of the five South American ungulate clades. For example, Billet (2010) suggests that pyrotheres may be included among the notoungulates. The alternative to monophyly of Meridiungulata is to divide it into two clades, each with distinct northern hemisphere ancestry, one comprising the South American mioclaenids, didolodonts, litopterns, and notoungulates, and a second including the pyrotheres, astrapotheres, and xenungulates (Muizon and Cifelli, 2000).

10.6.5 South American waifs

Several smaller groups of placental mammals invaded South America during the Cenozoic. For example, rodents appeared in the Eocene and bats arrived at least by the late Oligocene. The South American rodents became important elements of the faunas and some reached large size (see Section 10.12.2). Primates also reached South America in the Oligocene and gave rise to a radiation of marmosets and monkeys (see Section 11.2.3). The invaders are termed 'waifs' because the first bats, rodents, and primates to reach South America were probably small populations that had arrived by chance dispersal events, most likely from Africa.

10.6.6 The Great American Biotic Interchange

All of the South American ungulates have gone, as have the larger carnivorous marsupials, glyptodonts and ground sloths. These extinctions in the Pliocene and Pleistocene were once explained as a consequence of the opening of the Central American land bridge (Figure 10.26), the Great American Biotic Interchange (GABI; Webb, 2006; Woodburne, 2010). Mammals headed south across the landbridge, and these 'superior' northern migrants supposedly wiped out the weaker southern mammals by intensive competition.

Full formation of the Isthmus of Panama happened 3 Myr ago, but there were already islands across the Central American area by 12 Myr ago, and some mammals headed across by island hopping as early as the late Miocene. North American mammals such as raccoons, rabbits, dogs, horses, deer, camels, bears, pumas and mastodonts headed south, while South American opossums, armadillos, glyptodonts, ground sloths, ant-eaters, monkeys and porcupines headed north.

Can the extinctions of South American native mammals be explained by this competitive model? In an early statistical study, Marshall *et al*. (1982) showed that, at generic level, the GABI was balanced in terms of relative land areas. The classic story at first seems to be confirmed: 50% of the present-day mammal genera in South America are derived from members of immigrant North American families, whereas only 21% of the present-day mammal genera in North America had their origins in South America. The total number of mammal genera in South America, however, increased markedly after the land-bridge appeared (Figure 10.26), and this increase consisted of North American immigrants that 'insinuated', that is, they exploited additional niches without competing and causing extinctions among the genera already present. South America and North America show similar levels of extinction of invading genera immediately after the formation of the land bridge.

The major extinctions affected South American ungulates and xenarthrans. Were they inferior to the horses and deer from North America? The litopterns and notoungulates were already declining before the invaders arrived, and the surviving

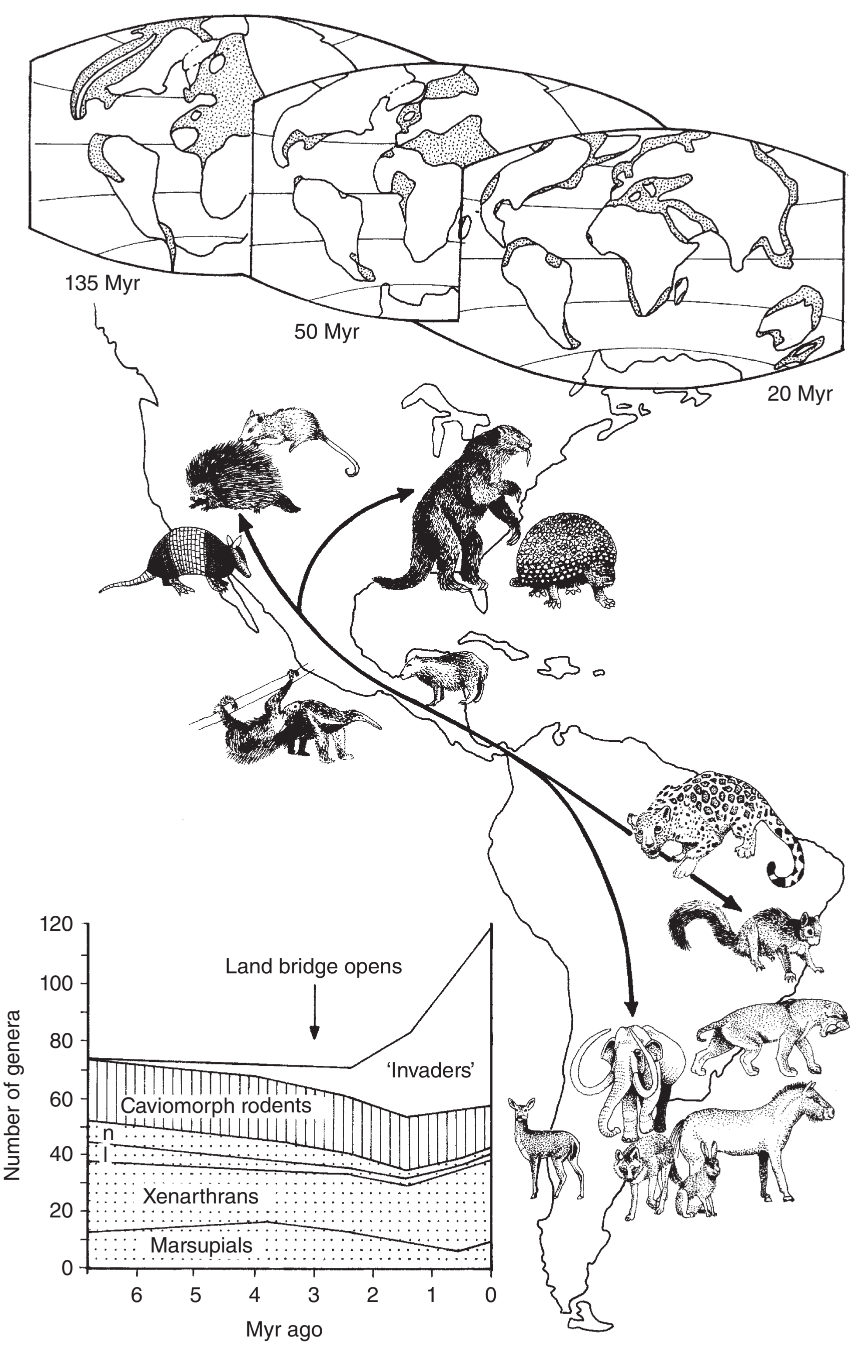


Figure 10.26 The biogeographical history of South America, the land bridge and the Great American Interchange. Maps showing the position of South America in the Early Cretaceous (135 Myr ago), middle Eocene (50 Myr ago) and early Miocene (20 Myr ago) across the top. Movements of major groups after the formation of the land bridge 3 Myr ago: sloths, ant-eaters, caviomorph rodents, armadillos, porcupines, opossums, ground sloths and glyptodonts head north, and cats (including sabre-tooths), squirrels, proboscideans (gomphotheres), deer, peccaries, tapirs, foxes, rabbits and horses head south. The graph (bottom left) shows how northern invaders to South America depressed the diversity of South American groups a little, but mainly added to the overall diversity by insinuation. Abbreviations: l, litopterns; n, notoungulates. Source: Adapted from Marshall *et al.* (1982), Marshall (1988) and various other sources.

lines died out much later along with their supposed competitors, the invading mastodonts and horses. Further, the glyptodonts, ground sloths and toxodonts were so different from the North American forms in terms of ecology that it is hard to see how they could have competed. Fourthly, when all of the genera of large herbivores are added together, it is clear that no gradual replacement took place – the numbers of genera of South American forms went down from 26 to 21 after the interchange and then rose to 26 again. The Pleistocene extinctions in South America (see Section 10.14) were distinct from the GABI, 2.5 Myr before.

10.7 AFROTHERIA AND THE BREAK-UP OF GONDWANA

All key southern hemisphere continents had their unique mammalian faunas, and Africa is no exception. A fundamental division of placental mammals was into Atlantogenata and Boreoeutheria, the Atlantogenata comprising Xenarthra and Afrotheria (see Section 10.14). Afrotheria, including modern mammals as different as elephants, golden moles, tenrecs and aardvarks, all share a common ancestry. Evidence for Afrotheria was initially phylogenomic, but the clade is now supported by morphological data from living forms, and especially by fossil finds in northern Africa and the Middle East (Tabuce *et al.*, 2007, 2008; Asher *et al.*, 2009, 2010; Benoit *et al.*, 2013a,b).

10.7.1 Aardvarks, tenrecs and elephant shrews

The first division of the Afrotheria is Afroinsectiphilia, comprising the aardvark, tenrecs, golden mole, and elephant shrews (see Box 10.5). The aardvark, *Orycteropus*, is the sole living representative of the Tubulidentata (Figure 10.27(a)). It is a bulky animal with a tubular snout and reduced teeth that lives in burrows and digs for termites. Fossil aardvarks date back to the Miocene (Lehmann, 2009).

There has been some debate about relationships between aardvarks and the other afroinsectiphilians, but it seems likely that Tubulidentata are sister to Afroinsectivora, the Afrosoricida and Macroscelidea. Afrosoricida includes the tenrecs and golden moles. There are 30 species of living tenrecs (Tenrecidae), insect-eating mammals that are found mainly in Madagascar, and some in west Africa. Many are small, but some range up to cat-sized and some are semi-aquatic. Many have spines and they look generally hedgehog-like (Figure 10.27(b)), so it is no wonder they were previously classified in the Lipotyphla, with the other insectivorous mammals. The oldest fossil tenrecs are Miocene.

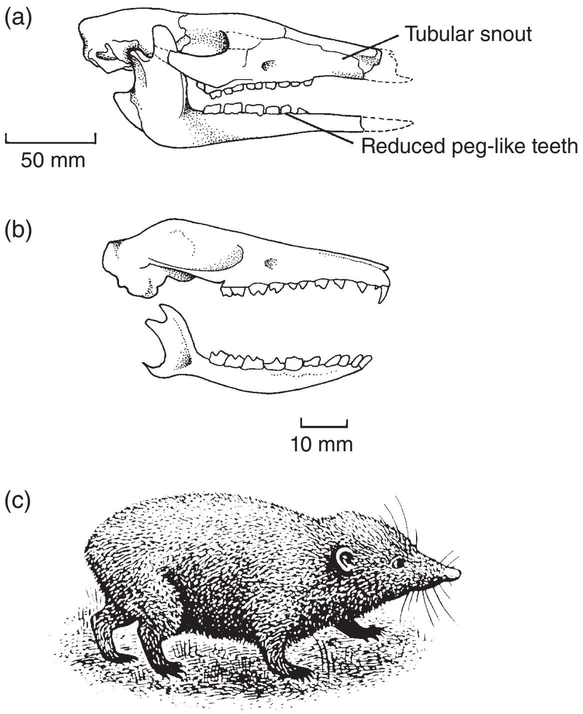


Figure 10.27 Diverse afrotheres: (a) the Miocene aardvark *Orycteropus gaudryi*; (b) the tenrec *Tenrec*; (c) skull of the living elephant shrew *Elephantulus*. Source: (a) Adapted from Andrews (1896). (b,c) Adapted from Young (1981).

Golden moles (Chrysochloridae), 21 species from southern Africa, are small insect-eaters that burrow using both fore and hind paws and a leathery pad on the nose. They show some remarkable features, such as three long bones in the forearm, massively enlarged middle ear ossicles, and a hyoid-mandible articulation (Asher *et al.*, 2010). The oldest fossils are Miocene.

The sister group of Afrosoricida is the Macroscelidea, the elephant shrews or sengis. The rare elephant shrews, some 17 living species, have a skull (Figure 10.27(c)) that is superficially shrew-like, the snout bears a flexible proboscis, and the limbs are relatively long. The macroscelidean fossil record dates back to *Chambius* from the Eocene of Tunisia and Algeria in North Africa (Tabuce *et al.*, 2007; Benoit *et al.*, 2013b). There was, however, an unexpected radiation of early relatives of Macroscelidea, and hence members of Afrotheria, in Europe and North America in the Palaeocene and Eocene, comprising groups such as the Louisinidae, Apheliscidae, Amphilemuridae, and Adapisoricidae (Tabuce *et al.*, 2007; Hooker and Russell, 2012; Rose, 2012). An example is *Macrocranion*, a tiny, 5-cm long, insect-eater, known from exquisite specimens preserving fur from the famous Early Eocene site, Messel in Germany (see Box 10.8), as well as from Wyoming, USA. Stomach contents show that *Macrocranion* ate ants, and its long legs may have been used in bounding locomotion like a modern kangaroo rat.

10.7.2 Paenungulata: elephants and their relatives

Modern elephants, seacows (sirenians) and hyraxes may seem strange bedfellows. Relationship between the relatively hairless elephants and seacows might seem faintly plausible, but hyraxes look superficially more like rabbits than elephants. To ancient peoples, hyraxes and elephants were at opposite ends of the spectrum; in the Bible, hyraxes (called conies), are referred to as ‘but a feeble folk, yet make their houses in the rocks’, whereas elephants were engines of war that provided ivory for rich decoration. Despite their substantial physical differences, the phylogenetic association of these three clades was recognized by Simpson (1945) as Paenungulata, within which Hyracoidea is the outgroup of Tethytheria, which consists of Sirenia and Proboscidea. A number of extinct groups are also assigned to Paenungulata (Gheerbrandt *et al.*, 2005).

Paenungulates are diagnosed by posterior extension of the jugal to the front margin of the jaw joint and by serial arrangement of the wrist bones. Tethytheres share a forward position of the orbit over the anterior premolars, and bilophodont molars (cusps arranged opposite each other transversely), amongst other characters (see Box 10.5).

10.7.3 Hyracoidea and Sirenia: hyraxes and sea cows

The hyraxes (sometimes called dassies or conies) are rabbit-sized animals (Figure 10.28(a)) that live in Africa and the Middle East, feeding on a mixed vegetable diet. They have short

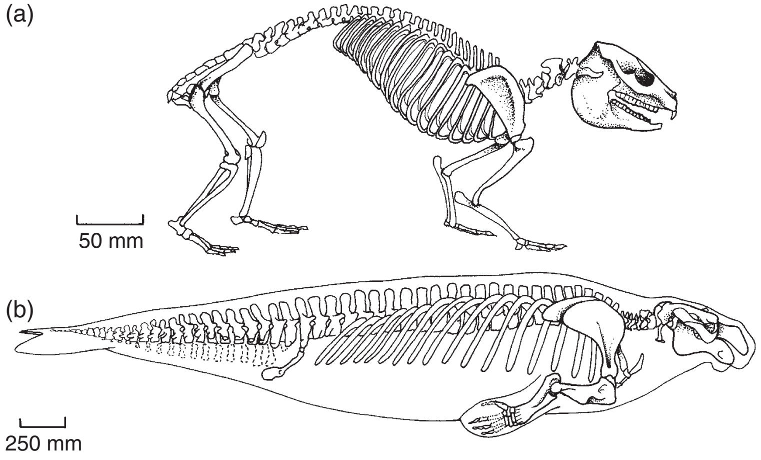


Figure 10.28 Proboscidean relatives: (a) the modern hyrax *Heterohyrax*; (b) the Miocene dugong *Dusisiren*. Source: (a) Adapted from Young (1981). (b) Adapted from Domning (1978).

limbs, four-fingered hands and three-toed feet. They are adept climbers, and can run up impossibly steep rock faces without slipping, perhaps thanks to sweat glands in their foot pads. Fossil hyraxes are known from Europe, the Middle East and Africa from the Eocene, and the group radiated to over 20 species in the Oligocene and Miocene, before declining to its present diversity of four species. Hyraxes today defecate in communal middens, and such middens have been preserved through the Pleistocene of southern Africa, where they preserve rich records of pollen, charcoal, biomarkers, stable isotopes, and ancient DNA, all useful in reconstructing climate change in detail (Chase *et al*., 2012). Despite their rather cute appearance, they are fierce little beasts, and have been observed staring down juvenile leopards.

Sirenia includes today four species, the dugong and three species of manatees that live in tropical coastal waters of the Pacific, Atlantic, and Indian Ocean. These are fat animals, 2.5–4.0 m long, that live in coastal seas or freshwaters of tropical regions and feed on water plants. They arose in the early Eocene, probably in Africa (Benoit *et al*., 2013a) and radiated during the Eocene to Miocene. An early sirenian, *Pezosiren* (Domning, 2001) from the Eocene of Jamaica, has short legs for walking on land, and the group adapted from terrestrial ancestors to life in brackish lakes and shallow seas. Later forms, such as the Miocene dugong *Dusisiren* (Figure 10.28(b)), show the strange down-turned snout and the reduced dentition (only four cheek teeth on each side), as well as aquatic adaptations in the broad thickened ribs (for extra weight during diving), front paddles, reduced hindlimbs and a whale-like tail. The spectacular Steller's sea cow, 8–9 m long, fed on kelp around Arctic shores in the North Pacific, but was hunted to extinction by 1768 by early seafarers.

Three extinct groups may be part of Tethytheria. The anthracobunids were medium-sized herbivores, 1–2 m in length, from the Eocene of India and Pakistan, with molar teeth that share many features with those of early elephants (Gheerbrant, 2009). The desmostylians were large, ungainly semi-aquatic animals found in marine beds of the Oligocene and Miocene, and restricted to the northern Pacific rim. They may have evolved their aquatic adaptations independently of Sirenia, some specializing in walking along the seabed, and others using their massive forelimbs to paddle along, superficially like a polar bear (Hayashi *et al*., 2013). The embrithopods include three or four species of palaeoamasiids from southeastern Europe and Turkey, and the massive, elephantine, horned herbivore *Arsinoitherium* from the Oligocene of Egypt. These show the paenungulate characters of a concealed mastoid and the serial carpal arrangement, as well as the tethythere ventrally protruding coracoid process on the scapula and the medial tubercle on the astragalus.

10.7.4 Proboscidea: elephants and relatives

Proboscideans are diagnosed by a number of features (Shoshani and Tassy, 1996, 2005): a reduced jugal and orbit that opens in the maxilla, enlarged second upper incisors (these become the tusks in most later forms), lower canines and first premolars absent, broad molar teeth with thickened cusps and ridges and adaptations of the limbs for weight-supporting.

The early evolution of the group took place mainly in Africa. Close to the origin of Proboscidea is *Eritherium*, known from incomplete jaw remains from the late Palaeocene of Morocco, a generalized herbivore, about 0.5 m long. It shares several dental features with Proboscidea, as well as more plesiomorphic features with anthracobnunids and embriothopods. This is all taken as evidence that *Eritherium* lies close to the rapid basal divergence of Paenungulata, but it already on the lineage to Proboscidea (Gheerbrant, 2009). The oldest proboscidean is *Phosphatherium* from the early Eocene of Morocco, also known from incomplete materials. The oldest, relatively completely known proboscidean is *Moeritherium* from the late Eocene and Oligocene of North Africa (Figure 10.29(a,b)), which has a deep skull with the upper and lower second incisors enlarged as short projecting tusks. The skeleton indicates a long-bodied animal that was about 0.7 m tall and probably lived in freshwaters, rather like a small hippo.

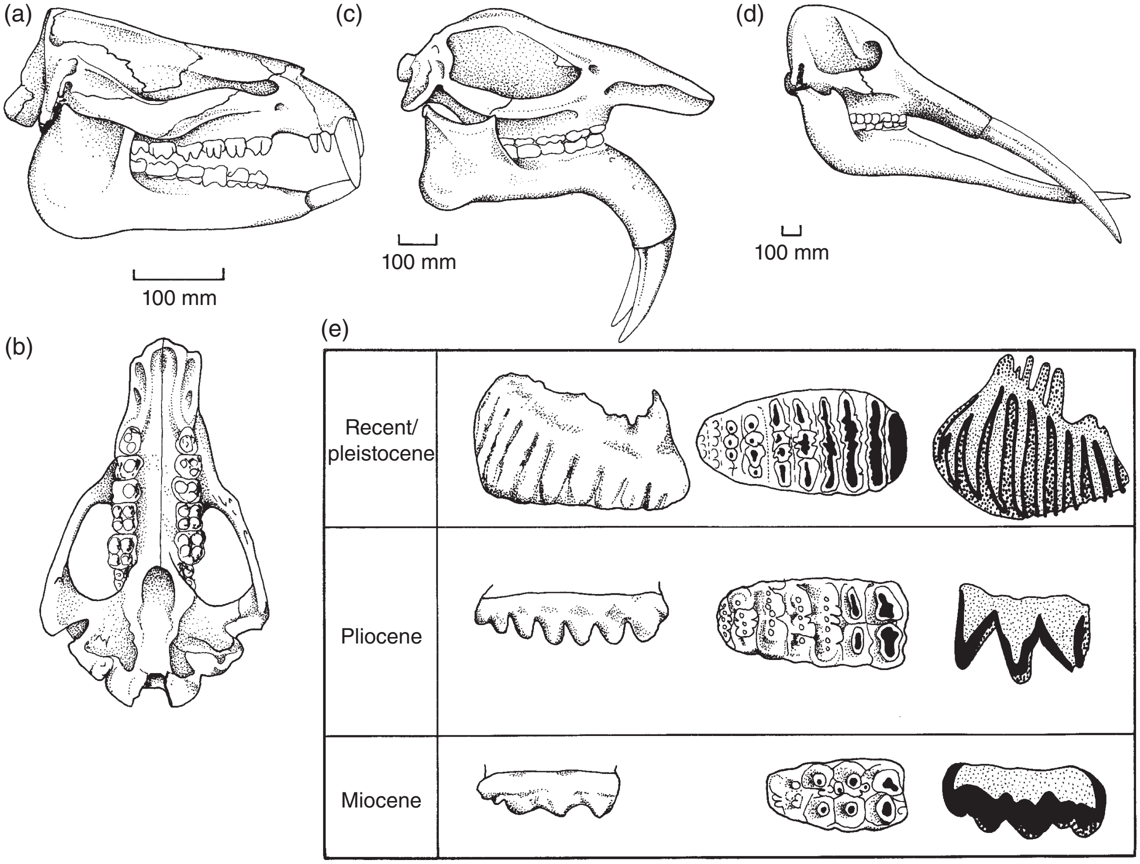


Figure 10.29 Proboscidean diversity: (a,b) early Eocene *Moeritherium*; (c) Miocene *Deinotherium*; (d) Miocene *Gomphotherium*; (e) evolution of elephant molars from the low mounded teeth of the Miocene *Gomphotherium* (bottom), through the more incized teeth of the Pliocene *Stegodon* (middle), to the deeply ridged teeth of the living *Elephas*; teeth are shown in lateral, occlusal and section views; enamel is black, cementum heavy stipple and dentine light stipple. Source: (a,b,d) Adapted from Andrews (1906). (c) Adapted from Flower and Lydekker (1891). (e) Adapted from Savage and Long (1986).

There were several further Eocene proboscideans in North Africa, before a split into the deinotheres and the elephantiforms (Shoshani and Tassy, 2005). The deinotheres lived from the late Oligocene to the mid-Pleistocene in the Old World. They have a pair of lower tusks curling under the chin from the lower jaw (Figure 10.29(c)), which may have been used in scraping the bark from trees. The upper tusks have been lost.

The Elephantiformes include two early forms, *Palaeomastodon* and *Phiomia* from the late Eocene and early Oligocene of Egypt, and Elephantimorpha. Elephantimorphs show many modifications in the skull (Shoshani and Tassy, 2006), including the loss of more premolars, modification in the shape of the molars to become long and replacement of the teeth from the back with wear. The elephantimorphs diversified rapidly during the early Miocene and they include several distinctive groups, a paraphyletic assemblage sometimes known as mastodonts, the Mammutida, the gomphotheres and the stegodontids. All of these groups died out in the Pliocene or Pleistocene. The other elephantimorph clade, the Elephantida, arose in the late Miocene and of these the Elephantidae survives.

Some Plio-Pleistocene lineages of mammutids retained the plesiomorphic pattern of rounded mound-like cusps on the cheek teeth. Mastodonts arose perhaps in central Asia and they spread rapidly over Asia, Europe and Africa, and reached North America in the early Miocene. The Miocene gomphotheres (Figure 10.29(d)) have four short tusks. They spread from Africa to Europe, Asia, North America and even South America, and survived to the end of the Pleistocene in many parts of the world. At one time, gomphotheres were thought to have entered South America as part of the GABI (see Section 10.6.6), but the presence of a late Miocene form in Peru suggests they island-hopped there rather earlier (Mothé *et al*., 2013).

What was the origin of the elephant's trunk? The earlier proboscideans probably had no trunk, or only a short, flexible proboscis. In his 'Just So Stories', Rudyard Kipling suggested that the elephant got his trunk during a tug-of-war between a young elephant and a crocodile. In fact, the trunk probably evolved as part of a coupled set of trends among elephants in the Neogene: increasing height, reduction in the number of functioning teeth at any time, tusks, and the trunk. As the elephantimorphs became taller (modern elephants are up to 3.5 m at the shoulder), the head became heavier not least because of the large tusks. The vast head is supported on a very short neck and so the modern elephant cannot reach the ground with its mouth. Hence, the short trunk of the early proboscideans became much longer.

But what about the replacement of functioning molars? Modern elephants have long lives, up to 60 years, and this leads to problems of tooth wear by abrasive plant material. Whereas *Moeritherium* had all six cheek teeth in each jaw, as in other mammals, the modern elephant has only one or two in place in each jaw at a time. They still have six cheek teeth in each jaw sector, but the first three are milk molars, occurring in the young animal up to age 15. The remaining three adult molars come into use as follows: number 4 at ages 18–28, number 5 at ages 40–50 and number 6 at ages 50 and onwards. This final tooth remains in the mouth and old elephants die when this last tooth is worn to the bone. The teeth are replaced by a process of drift, whereby teeth push forward in the jaw as they erupt, over many years, a modification of the normal mammalian cycle in which the adult molar set erupts over a short time.

The elephantids (mammoths and elephants) elaborated their teeth to enhance their efficiency in grinding tough plant food (Figure 10.29(e)). The ridges and valleys, covered by hard crystalline enamel, become extremely deep, and they increase in number to 10–30 transverse lines of fused cusps. The valleys between the cusp rows are filled with cementum, a type of bone used in all animals to anchor the tooth to the jaw, so that a worn tooth is made from an alternating series of transverse lines of enamel, dentine, enamel, cement, enamel, dentine and so on. The hard enamel forms ridges and the whole tooth appears like a row of parallel shears for cutting vegetation.

Mammoths spread from Africa over much of Europe and Asia, and later, North America (Lister, 2001; Lister and Bahn, 2007). These most iconic of the Ice Age mammals appear to form a monophyletic group and to be most closely related to the African elephant, based on molecular analysis of preserved DNA (Miller *et al*., 2008). The woolly mammoth is known from many bones, as well as near-complete carcasses preserved for thousands of years in the frozen tundra of Siberia and Alaska. These show a 2.8-m-tall elephant, covered with an 80-mm-thick fat layer and shaggy hair, sometimes preserved black, sometimes ginger – but what colour were they really (see Box 10.7)? The broad sweeping tusks may have been used in fighting, in breaking through the ice to get water, or to clear snow from the grasses and low plants that they ate. It is sometimes said that the flesh of mammoths can still be eaten, but this is unlikely. Nevertheless, the preservation is often good enough to yield the remnants of their last meal in the stomach or even in the mouth. Mammoths lived side-by-side with early humans, and died out 12,000 years ago in Europe and 10,000 years ago in North America, with some late-surviving dwarf mammoths on Wrangel Island in the Russian Arctic 4000 years ago. These last mammoths (which lived at the same time as the Middle Kingdom pharaohs were uniting Upper and Lower Egypt) existed in a population of about 500 and they showed full genetic variability in their DNA to the very end (Nyström *et al*., 2012).

BOX 10.7 THE GENES FOR MAMMOTH HAIR COLOUR

Many Siberian mammoths preserve hair. This can cover the entire carcass, in great shaggy clumps, individual hairs being thick and tough, and feeling as strong as plastic fishing line. Most commonly, the preserved hair is orange, but in some specimens it is blond, brown, or even almost black. These colours probably reflect discolouration during burial, and it is unclear what the original colour was (Lister and Bahn, 2007).

An unexpected piece of work using modern genomic laboratory techniques has shed light on the question. Workman *et al*. (2011) used population genotyping approaches to study populations of mammoths with preserved flesh and to explore their likely original colours. By determining the relative proportions of alleles of the *Mc1r* gene, they concluded that light-coloured mammoths were very rare, or did not exist.

The melanocortin receptor 1 (*Mc1r*) is one of the key proteins that controls hair and skin colour in mammals. It is a receptor protein that is located on the cell membrane of melanocytes, the specialized cells in the skin that produce the pigment melanin. There are two forms of melanin, phaeomelanin, which produces ginger colours, and eumelanin, which produces black and dark brown colours, the key forms of melanin in mammals, birds, and dinosaurs (see Box 9.1). *Mc1r* is activated by melanocyte-stimulating hormone and produces a complex signalling cascade that leads to the production of eumelanin. This process can be antagonized by agouti signalling peptide (ASIP), which switches the melanocyte back to producing phaeomelanin. Phaeomelanin is also produced in red-headed people (including Neanderthals), and in mutant yellow-orange mice, where the *Mc1r* receptor is not functioning.

Pigmentation genetics in mammals is well studied. Mutations of the *Mc1r* gene can stimulate continuous functioning of the *Mc1r* protein, which signals constantly even when not stimulated, or mutations can lower the activity level of the receptor. Alleles for constant signalling are inherited dominantly and result in black or dark brown coat colours, whereas alleles for dysfunctional *Mc1r* are recessive and result in a light coat colour.

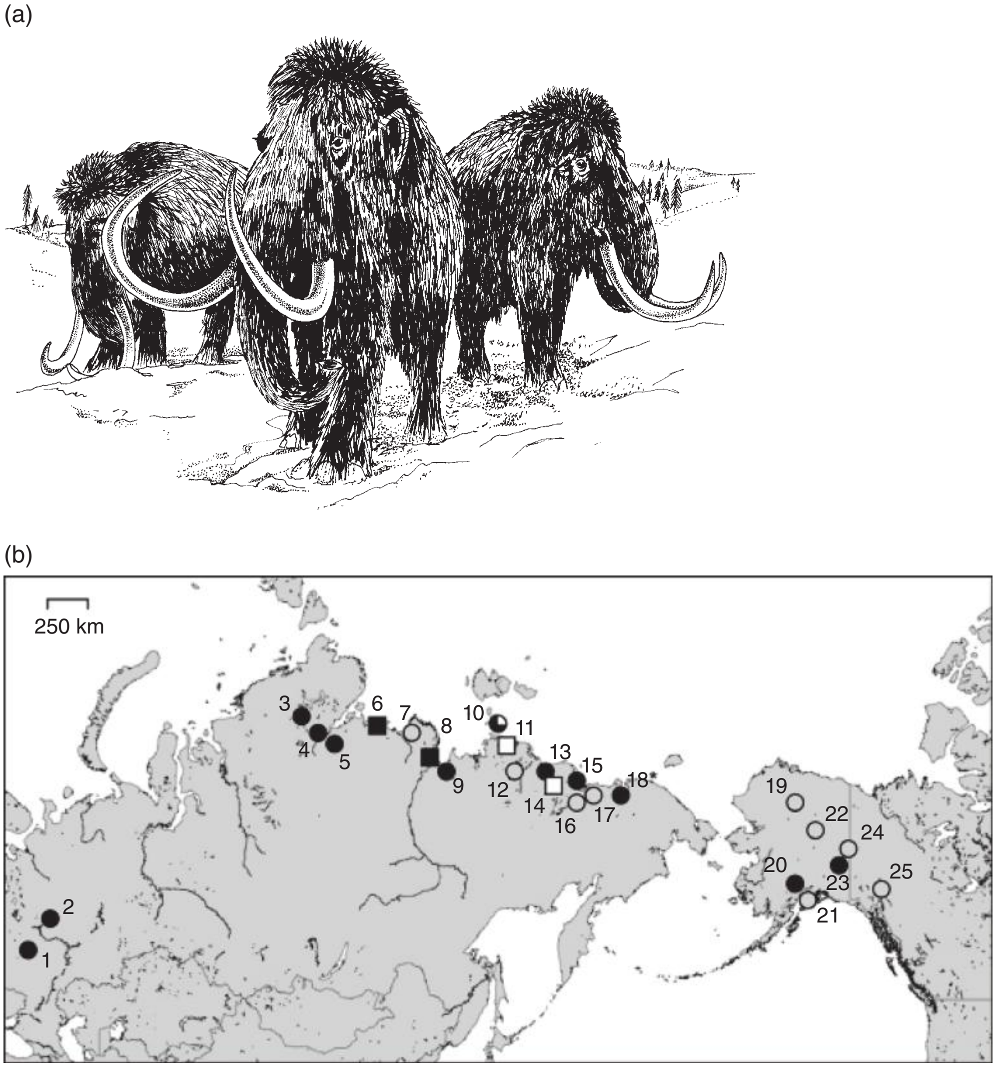
The *Mc1r* gene exhibits two alleles in mammoths: allele 1 is represented by the amino acid triplet threonine^{31}-arginine^{67}-arginine^{301}, and allele 2 by alanine^{31}-cysteine^{67}-serine^{301} (the superscript numbers mark positions in the genotype). Rompler *et al*. (2006) showed that allele 1 determines darker coat colours, and allele 2 reduces function, and in its homozygotic state determines pale coat colour, as in other mammals. They estimated that blonde colours were relatively frequent (25%).

Continued

This was not confirmed by Workman *et al*. (2011). They investigated a much larger sample of bones, teeth, and tusks of 108 mammoth specimens from Siberia, European Russia, and Alaska, and they were able to extract DNA from 47 of them. This kind of work requires a dedicated ancient DNA laboratory where no modern samples are handled, to avoid the risk of contamination, the laboratory is sterilized every night, and each sample is run numerous times to cross check. Because samples were tiny, standard polymerase chain reaction (PCR) methods were used to amplify the DNA, and sequences were compared with known sequences of the *Mc1r* gene in modern human, cow, and mouse.

The analysts were surprised to find that the mutant blonde allele occurred only once in the 47 samples, and with an overall frequency of 1%. It was not associated with any geographic location, population affiliation, or particular body size. If mammoths shared the genetics of other mammals, then the blonde allele would be recessive, and would be expressed only in homozygous individuals; heteroyzgotes and homozygotes for the normal allele would all exhibit dark coat colours.

Mammoths are always pictured against a wintery landscape, where pale colours might be thought to be advantageous for two reasons: camouflage and thermal reflectance. However, for much of the year they presumably trekked over stony, black landscapes seeking food, and so darker colours may have been satisfactory. In any case, only juveniles were seriously threatened by predators. More investigation will be needed to determine whether coat colour in mammoths varied with latitude, and whether juveniles were more often pale in colour.



Memories of the Ice Age. (a) Three woolly mammoths in a typical Ice Age scene; (b) Geographical distribution of mammoths, indicating sites sampled for genotyping studies by Rompler *et al*. (2006), shown as squares, and Workman *et al*. (2011), shown as circles. Open circles, particularly in Alaska, did not yield usable DNA. Filled circles show the frequency of the wild-type (dark colour) allele of the Mc1r gene, and the circle at locality 10 indicates the rare occurrence of the mutant (blonde) allele. Source: (a) Adapted from a painting by J. Long in Savage and Long (1986). (b) Workman *et al*. (2011). Reproduced with permission from Elsevier.

10.8 BOREOEUTHERIAN BEGINNINGS: THE PALAEOCENE IN THE NORTHERN HEMISPHERE

After considering the evolution of Xenarthra in South America and Afrotheria in Africa, and their subsequent histories, we come now to Boreoeutheria, the large northern hemisphere clade of placental mammals (see Box 10.5). The clade may have originated in the Late Cretaceous or earliest Paleogene (see Section 10.4), but it diversified in rather bewildering fashion in the Palaeocene (66–56 Myr ago), with the first representatives of most modern orders, as well as numerous other apparently short-lived clades.

The death of the dinosaurs must have left the land surface strangely empty of large land animals. The 10 Myr after the KPg event has always been seen as a time of opportunity for mammals, a time when many clades experimented with new modes of life. The huge diversity can be hard to comprehend, and it is hard at present to assign many of the extinct clades to modern placental clades (Rose, 2006).

10.8.1 Small Palaeocene mammals

The leptictids are small shrew-like insectivorous forms that existed from the early Palaeocene to Oligocene in Asia, Europe and North America. *Leptictis*, a late form, has a long snout lined with small sharp teeth (Figure 10.30(a)), evidently adapted for puncturing the skin of insects. The leptictids are plesiomorphic in many characters: for example, they retain the jugal, a bone lost in true insectivores. The hindlimbs, however, are specialized for fast running and even jumping: they are elongate and the tibia and fibula are fused. Leptictids were once tracked back to the latest Cretaceous, but the clade seems entirely Paleogene, and is near the root of crown Placentalia, associated either with Lipotyphla or Afrotheria (O'Leary *et al*., 2013).

The pantolestids are otter-like animals with skulls up to 150 mm long, known from the Palaeocene to Oligocene of North America and Europe (Boyer and Georgi, 2007; Rose, 2012). They have broad, thickly enamelled molars that may have been used in crushing shellfish, and large powerful canines (Figure 10.30(b)). Fish remains have been found in the gut region of *Buxolestes* and perhaps the pantolestids lived like seals or otters.

The apatotheres or apatemyids are another small group of insect-eaters, known from the Palaeocene to Oligocene of North America and Europe. *Sinclairella* (Figure 10.30(c)) shows the strange dentition, part insectivore and part rodent, that characterizes the group. The cheek teeth are adapted for puncturing insect skins, and the incisors are extremely long and projecting, rather like the front piercing teeth of the aye-aye lemur, and like the aye-aye they also have modified slender fingers (one on each hand in the aye-aye, two in the apatamyids) for digging grubs

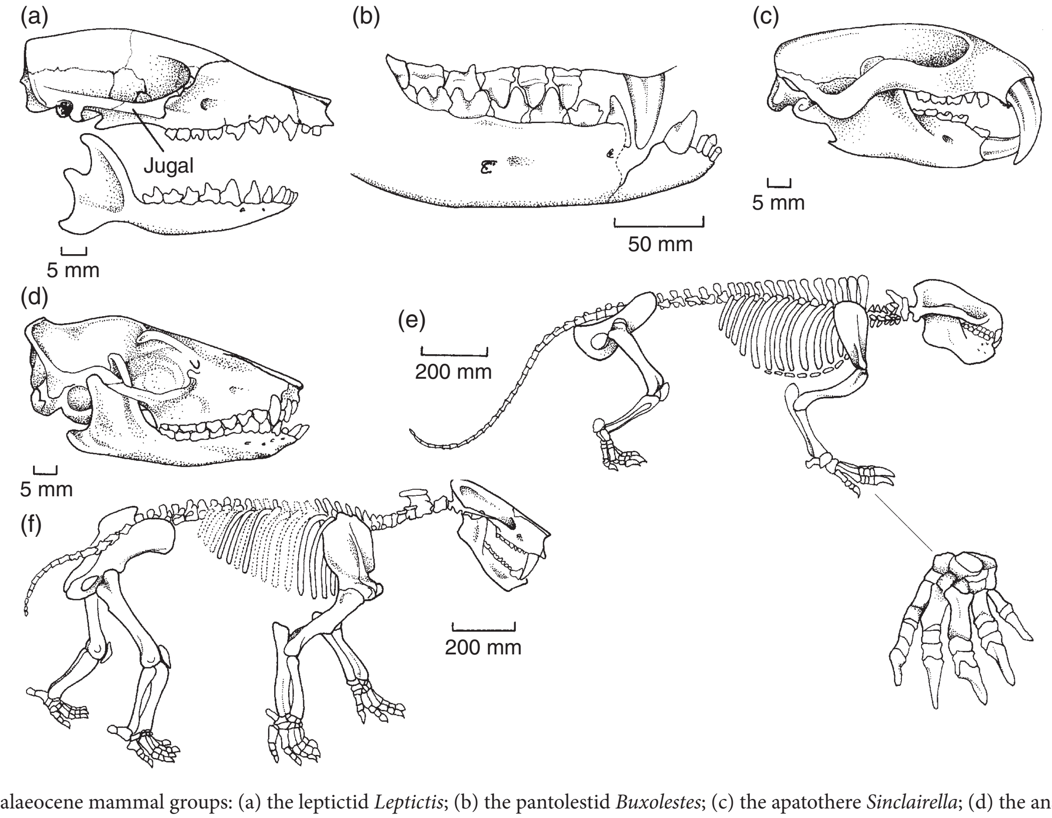


Figure 10.30 Palaeocene mammal groups: (a) the leptictid *Leptictis*; (b) the pantolestid *Buxolestes*; (c) the apatothere *Sinclairella*; (d) the anagalid *Anagale*; (e) the taeniodont *Stylinodon*; (f) the pantodont *Titanoides*. Source: (a–c) Adapted from Scott and Jepsen (1936). (d) Adapted from Simpson (1931). (e) Adapted from Schoch (1986). (f) Adapted from Simons (1960).

out from underneath bark. Relationships are problematic, but apatotheres may be early euarchontoglirans (Silcox *et al*., 2010; Rose, 2012).

The anagalids dominated Asian Palaeocene faunas. Their broad molars indicate a diet of plant food and the anagalids are reconstructed as being rather rabbit-like in habits and appearance. They are plesiomorphic in retaining a postorbital process behind the orbit (Figure 10.30(d)), but the tooth row of the lower jaw is set well below the jaw joint. The anagalids have been said to be close to the origin of rodents and rabbits, but that is uncertain.

10.8.2 Early rooters and browsers

The taeniodonts were a small group of North American Palaeocene and Eocene herbivores that ranged up to pig-size, some of the first reasonably large mammals to emerge after the KPg event. *Stylinodon* (Figure 10.30(e)) has short limbs and these are rather odd in that the forelimb and hand are larger than the hindlimb and foot. The claws are narrow and curved and they were probably used for digging up succulent roots and tubers. Taeniodonts may have originated in the latest Cretaceous, and they appear to be stem placentals (Rook and Hunter, 2014).

The tillodonts, from the Palaeocene and Eocene of Asia, Europe and North America, are a second small group of herbivores whose relationships are as much a mystery as are those of the taeniodonts. They were up to bear-sized and most fed on a diet of tough plant material like the taeniodonts.

The pantodonts, from the Palaeocene to Oligocene of Asia and North America, may be related to the tillodonts. They were rooting and browsing forms that ranged in size and appearance from pig to hippo, and some even looked superficially like ground sloths. *Titanoides*, a pig-like animal (Figure 10.30(f)), has massive limbs, plantigrade feet (soles flat on the ground) and digging claws on its hands. Later forms may have been semi-erect.

The arctocyonids include *Arctocyon* from the Palaeocene of Europe and North America (Figure 10.31(a)), a sheep-sized animal that would have looked rather like a modern dog. Its molars are broad and adapted for crushing plant food, rather than slicing flesh. Some arctocyonids have a skeleton adapted for climbing: strong bony crests and processes on the limb bones for the attachment of powerful muscles, highly mobile arm and ankle joints, curved claws and a possibly prehensile tail. Arctocyonids appear to be a paraphyletic assemblage of species that all lie low in the cladogram, close to condylarths (De Bast and Smith, 2013), and some may lie on the stem to Cetartiodactyla.

The ‘condylarths’ are an assemblage of five or six distinct lineages that all probably lie at the base of Laurasiatheria (O’Leary *et al*., 2013). The periptychids, such as *Ectoconus* (Figure 10.31(b)), were common in the Palaeocene. The massive crushing teeth indicate a pig-like omnivorous diet and the skeleton is generally plesiomorphic: the hands and feet each retain five digits and all the wrist and ankle bones are present. The hyopsodontids, such as *Hyopsodus* (Figure 10.31(c)), arose in the Palaeocene and were abundant in the early Eocene (Zack *et al*., 2005). These were small, short-limbed animals that may have lived semi-arboreally.

The phenacodonts of the Palaeocene and early Eocene, such as *Phenacodus* (Figure 10.31(d)) are sheep-sized and the limbs are short and plesiomorphic. The outer toes are shorter than the middle three and the cheek teeth have broad surfaces for crushing fruit and slicing leaves, as is seen in early horses (see Section 10.11.2). The early Palaeocene *Tetraclaenodon* showed none of the cursorial adaptations of later forms (Kondrashov and Lucas, 2012). Phenacodonts may be related, with hyopsodontid ‘condylarths’, to basal laurasiatherians (O’Leary *et al*., 2013) or to perissodactyls.

The largest mammals in the late Palaeocene and early Eocene were the dinoceratans, or uintatheres, of North America and Asia. *Uintatherium* (Figure 10.31(e,f)), a late-appearing mid-Eocene form, is as large as a rhinoceros and has bony protuberances on its head. Males have canine teeth 150 mm long, which may have been used in fighting, a possible explanation of the bony head bumps. Uintatheres have small, tapir-like cheek teeth that were used to deal with plant food, and their brains are unusually small (Figure 10.31(f)).

10.8.3 Palaeocene flesh-eaters

The largest mammalian meat-eaters in the Palaeocene to early Oligocene were the mesonychians, a group that originated in Asia, and migrated to Europe and North America. Early forms such as *Mesonyx* (Figure 10.32(a)) are about wolf-sized and have pointed molar teeth adapted for cutting flesh, just like those of a dog; the molars are still broad and may also have been used for crushing bones. One of the later mesonychians, *Andrewsarchus* from the late Eocene of Mongolia, has a vast skull, 830 mm long and 560 mm wide, larger than any other known terrestrial carnivore, and in life it must have been a terrifying 5–6 m or more long. Mesonychians have frequently been regarded as early members of Cetacea or Cetartiodactyla, but they may fall in a more stemward position within Laurasiatheria (Spaulding *et al*., 2009; O’Leary *et al*., 2013).

The ‘creodonts’ were the main meat-eaters in North America, Europe and Asia in the Paleogene; they appear to form two independent lineages, Hyaenodontidae and Oxyaenidae (Rose, 2006; Solé *et al*., 2009). Among the hyaenodontids, *Sinopa* was an early fox-like form (Figure 10.32(b)) with a low skull and all of its cheek teeth sharpened for cutting flesh. Its later relative, *Hyaenodon* (Figure 10.32(d)), was larger, and some of its relatives reached bear size. This wolf-like animal was the only creodont to survive the late Eocene, living in Africa and Asia until the late Miocene. The oxyaenid *Oxyaena* (Figure 10.32(c)), a rather cat-like animal, has a long body and short limbs, retaining five toes on each plantigrade foot. Hyaenodontids and oxyaenids are further early members of Laurasiatheria, and possibly include relatives of the modern Carnivora (see Section 10.11.5).

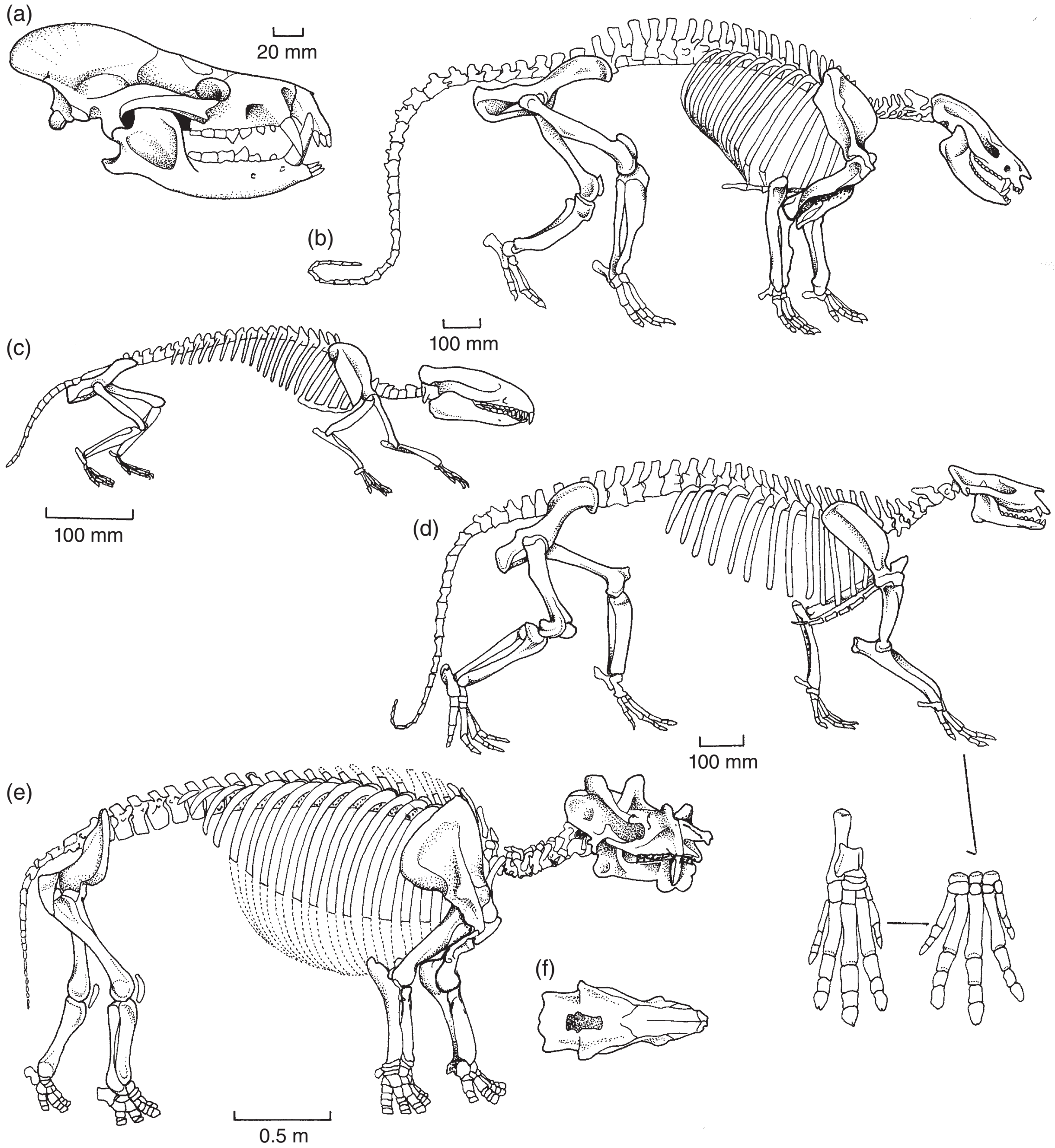


Figure 10.31 Palaeocene herbivores: (a) the arctocyonid *Arctocyon*; (b) the periptychid 'condylarth' *Ectoconus*; (c) the hyopsodontid 'condylarth' *Hyopsodus*; (d) the phenacodontid 'condylarth' *Phenacodus*, with anterior views of the foot and hand; (e,f) the dinocerate *Uintatherium*, skeleton and dorsal view of the skull, showing the area occupied by the brain shaded. Source: (a) Adapted from Russell (1964). (b) Adapted from Gregory (1951). (c) Adapted from Gazin (1968). (d) Adapted from Osborn (1910). (e,f) Adapted from Flower and Lydekker (1891).

10.8.4 The Palaeocene placental explosion

The diversification of mammals in the first 10 Myr after the KPg mass extinction is the classic example of an **adaptive radiation** (e.g. Simpson, 1945). Study of this event had been put on hold while palaeontologists and phylogenomicists debated the timing of the origin of Placentalia. However, there is now sufficient evidence for a long-fuse model (see Section 10.4; Meredith *et al.*, 2011; dos Reis *et al.*, 2012), with placental origins deep in the Cretaceous, but diversification of crown placentals after the KPg event (Wible *et al.*, 2007), including the earliest members of all living orders, as well as the various hard-to-place Paleogene clades just reviewed (see Sections 10.7.1–3).

The record of early Palaeocene mammals, especially in North America, is rich and it has been heavily studied, but there have also been investigations of the same patterns in other continents. Rose (2006) notes that 52 families of mammals are reported from the early Palaeocene, that is the first 4.5 Myr of the Paleogene, of which only eight had survived from the Late Cretaceous. Regional-scale studies in North America have

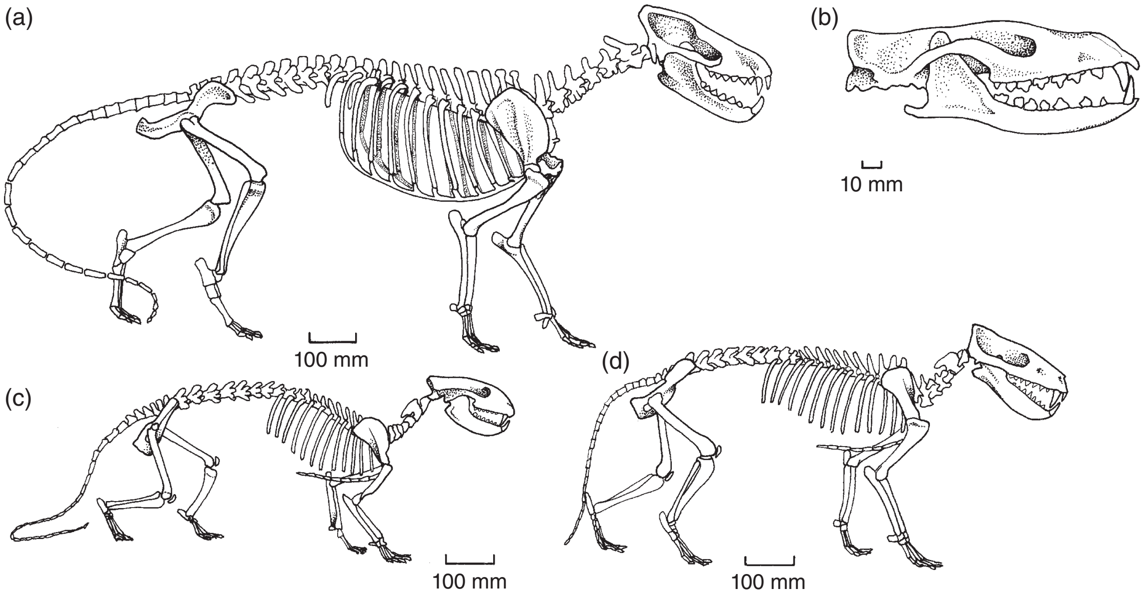


Figure 10.32 Palaeocene flesh-eaters: (a) the mesonychian *Mesonyx*; the creodonts (b) *Sinopa*, (c) *Oxyaena* and (d) *Hyaenodon*. Source: Adapted from Osborn (1910).

confirmed the devastating reductions in mammalian numbers through the KPg event, and the apparently rapid proliferation of new forms in the immediate aftermath (see Section 10.3.8; Wilson, 2005, 2013; Williamson *et al.*, 2012).

After 10 Myr of evolution through the Palaeocene, there was an abrupt heating event, the Palaeocene-Eocene Thermal Maximum (PETM) 56 Myr ago (see Figure 10.19(b)), when massive amounts of methane were released from deep ocean sources and caused a sharp temperature increase, and then dramatic changes in plants and animals on land and in the sea. At this point, some Palaeocene clades disappeared, and the first perissodactyls, artiodactyls, euprimates, and hyaenodontid creodonts appeared abruptly.

There was a further faunal turnover near the Eocene/Oligocene boundary, 34 Myr ago, when global temperatures continued their downward trajectory from a mid Eocene peak (the Early Eocene Climatic Optimum, EECO) at around 51 Myr ago, with a fairly sudden drop. This has long been termed the Grande Coupure (= 'great break') in Europe, a rather long span of time when 50% of the native mammals died out and were replaced especially by immigrants from Asia. At the beginning of the Paleogene, major continents such as North America and Africa were divided in two by major seaways, and Europe was separated from Asia by another seaway. During the Paleogene, sea levels fell as temperatures cooled, and movement of terrestrial mammals between Asia and Europe, and Europe and North America became possible (see Figure 10.19(a)).

One key question about the Paleogene diversification of placental mammals concerns the process: was the expansion of the clade driven primarily by the opportunity to fill niches that had been emptied by the extinction of dinosaurs and of Late Cretaceous mammals, or was the expansion driven by changes in climate and palaeogeography? Smith *et al.* (2010) conclude that it was a bit of both. They explored mean and maximum body sizes through the Paleogene, and found that on each continent the maximum size of mammals levelled off at about 18 tonnes in the middle to late Eocene, after 25 Myr of evolution (Figure 10.33). Several clades vied with each other during this time to produce the largest mammal, and the torch passed from condylarths in the early Palaeocene (90 kg) to pantodonts in the late Palaeocene (800 kg), then to uintatheres in the middle Eocene (1.5 tonnes), then perissodactyls in the late Eocene and Oligocene (10–18 tonnes), and finally proboscideans in the Miocene (10–18 tonnes). The patterns of size increase were similar on the different continents, even though the particular clades at any time were often different. From these observations, Smith *et al.* (2010) conclude that the primary driver for the evolution of giant mammals was diversification to fill ecological niches ('ecological release'). Slater (2013) confirmed this result with a direct test of evolutionary models among mammals: he found that Mesozoic mammals were constrained in body size (Ornstein-Uhlenbeck model), but that this constraint was released following the KPg mass extinction, and post-extinction mammalian evolution was unconstrained, but passive in terms of size change (Brownian motion model).

The Paleogene diversification of mammals was assisted by generally equable temperatures worldwide, and the temperatures and available land areas probably acted as constraints to limit the maximum size that could be achieved. Raia *et al.* (2013) confirmed the rapid, almost exponential increase of mammalian body size during the Paleogene, and that maximum rates of change in body sizes were correlated with rates of speciation. This confirms that mammals were rapidly diversifying, filling

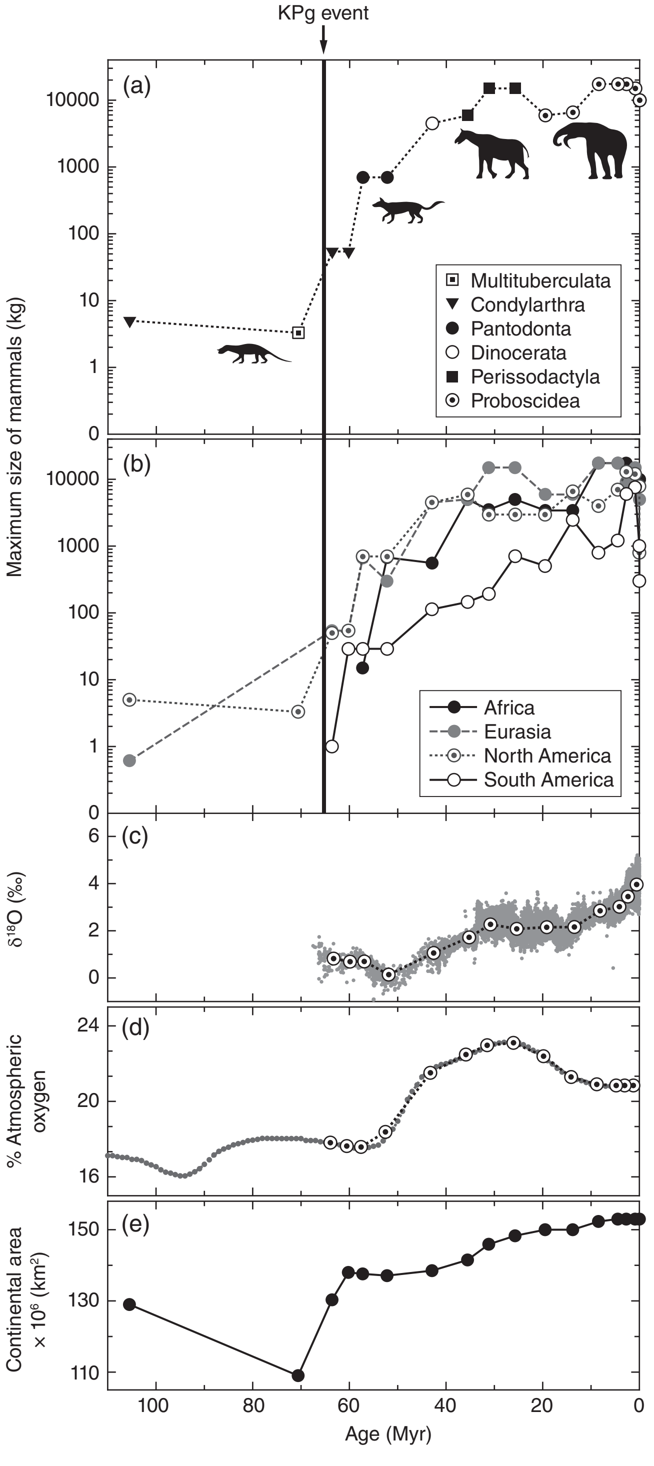


Figure 10.33 Body size evolution among mammals: (a,b) Maximum body mass of terrestrial mammals over the past 110 million years, for the world (a), and for individual continents (b); note the massive rise in the Paleogene, and the fact that maximum size passes from clade to clade through time. (c–e) Comparison of maximum body size (a,b) with oxygen isotopes (d), percentage atmospheric oxygen (e), and continental area (f); palaeodiversity shows good correlation with all these physical environmental time series. Source: Smith *et al.* (2010). Reproduced with permission from the American Association for the Advancement of Science.

niches, and expanding their range of body sizes, but that the process of expansion ended after 25 Myr.

The wider impact of intrinsic (i.e. internal, population interactions) versus extrinsic (i.e. external, environmental factors) drivers on Cenozoic mammalian evolution has been much discussed. Understanding how much of the diversity and body size distributions of mammals are the result of instrinsic and extrinsic factors is of course important for considerations of modern biodiversity and future climate change. Mammal palaeontologists have argued against (e.g. Prothero, 2004) and for (e.g. Figuerido *et al.*, 2012) extrinsic drivers. In their study, Figuerido *et al.* (2012) find six consecutive mammalian chronofaunas through the North American Cenozoic, and these show correlation with the oxygen isotope curve, and so with rises and falls in temperature. Therefore, climate change has had a substantial role in driving the palaeodiversity of

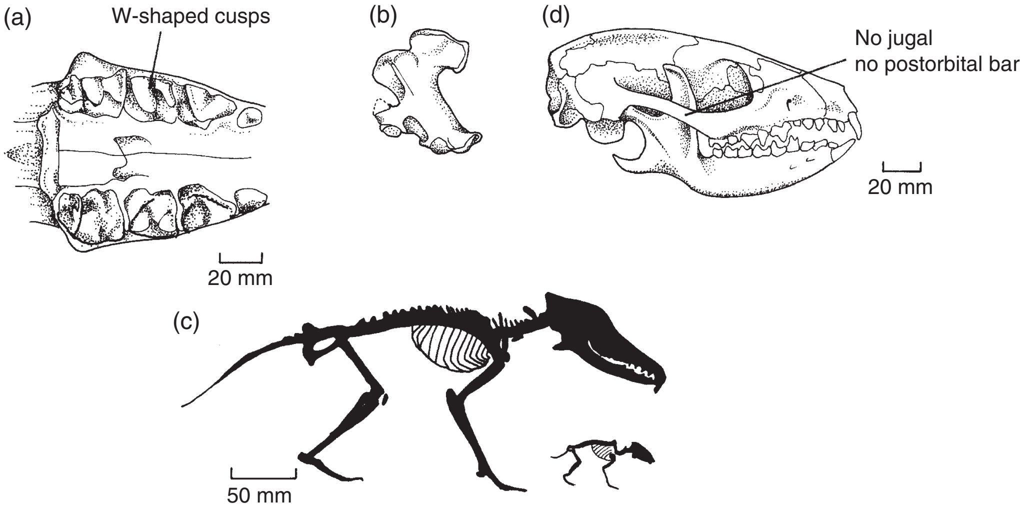


Figure 10.34 Lipotyphla: (a) palate of *Domnina*, an Oligocene shrew; (b) the broad humerus of the living mole *Cryptoproctes*; (c) the giant Miocene hedgehog *Deinogalerix* drawn in proportion to the living *Erinaceus*; (d) skull of *Erinaceus*. Source: (a) Adapted from McDowell (1958). (b,d) Adapted from various sources. (c) Adapted from Butler (1981).

mammals, but it is harder to determine the relative roles of intrinsic drivers.

10.9 BASAL LAURASIATHERIANS: LIPOTYPHLA

The Laurasiatheria, one of the two clades within Boreoeutheria, includes insectivores as sister group to the clade Scrotifera, which includes cetartiodactyls, bats, perissodactyls, carnivores and pholidotans (Tsagkogeorga *et al*., 2013; see Box 10.5).

The boreosphenidian insectivorous mammals are generally called Lipotyphla or Eulipotyphla to recognize the fact that the old clade Insectivora also included other taxa, such as the afrosoricids and macroscelideans, which are now removed to Afrotheria (see Section 10.7.1), and the tree shrews, now removed to the Euarchonta (see Section 10.13.1). Lipotyphla includes two main clades, Soricomorpha (Soricidae, Talpidae, Solenodontidae, Nesophontidae) and Erinaceomorpha (Erinaceidae), and 365 living species altogether.

The soricomorphs arose in the mid-Palaeocene, with several extinct clades such as geolabidids, nyctitheriids, and apternodontids (Rose, 2006). The palate of the Oligocene shrew (soricid) *Domnina* (Figure 10.34(a)) shows the W-shaped pattern of ridges on the upper molar teeth, typical of the group. The moles (talpids) arose in the Eocene. Their forelimbs, which are used in burrowing or in swimming (the desmans), are broad and paddle-like, and the mole humerus (Figure 10.34(b)) is a very characteristic broad bone with large processes for the attachment of powerful muscles. The other two soricomorph families include one living, and one recently extinct. The solenodontids comprise one living genus, *Solenodon*, a venomous, nocturnal, burrower from Cuba and Hispaniola. The related nesophontids, represented by species of *Nesophontes*, were abundant in the West Indies, but died out in the 15th century when European seafarers arrived.

The hedgehogs and moonrats (erinaceomorphs) arose in the Eocene. The most spectacular hedgehog was *Deinogalerix*, a long-limbed dog-sized animal (Figure 10.34(c)) from the late Miocene, which was probably covered with stiff hair rather than spines (modified hairs). *Deinogalerix* was five times as long as the European hedgehog *Erinaceus* and it must have been a dramatic sight as it charged about the hot grasslands of southern Italy (Villier and Carnevale, 2013). The skull of *Erinaceus* (Figure 10.34(d)) shows some derived characters of the Insectivora, such as the loss of the jugal and the absence of a postorbital process (present in most placentals). Erinacids are now only known from the Old World, but for much of the Cenozoic they were also common in North America.

10.10 CETARTIODACTYLA: CATTLE, PIGS AND WHALES

The pairing of artiodactyls and whales may seem at first startling, but evidence for such a relationship is overwhelming. Molecular data includes whales entirely within Artiodactyla, as a sister group of hippos (Price *et al*., 2005; O'Leary and Gatesy, 2008; Zhou *et al*., 2011; Hassanin *et al*., 2012), and there are some morphological characters that suggest a special relationship to hippos, such as the absence of paraconules on upper molars, and the absence of a crest between the hypoconid and entoconid on lower molars (Geisler and Uhen, 2003, 2005; O'Leary and Gatesy, 2008). Whales and hippos today share their hairless thick skin and absence of sebaceous glands, but these features probably arose convergently as the ancestors of both clades were not aquatic.

An older view had been that the flesh-eating mesonychians (see Section 10.8.3) were the closest extinct sister group to whales because of similarities in their skulls and teeth. However, there are synapomorphies in the skeletons of whales and artiodactyls, most notably the 'double-pulley' astragalus, previously thought to be unique to artiodactyls, and then discovered in early, limbed whales (Gingerich *et al.*, 2001; Thewissen *et al.*, 2001), but not in mesonychians.

10.10.1 Artiodactyla: cattle, deer and pigs

The even-toed ungulates, the artiodactyls, comprise nearly 250 species today, and they are diagnosed by having an even number of toes, two or four, unlike the perissodactyls, which have an odd number (1, 3, or 5). There were some basal artiodactyls in the Eocene, and then later forms fall into several clades, the Suina, the pigs the Tylopoda, camels, the Ruminantia, cattle, deer, giraffes, and antelopes, and Whippomorpha, hippos and whales (Prothero and Foss, 2007).

The oldest artiodactyls were small, rabbit-sized animals that fed on fruit, seeds and leaves, and had toes 3 and 4 enlarged to bear most of the weight of the body. *Diacodexis* from the early Eocene of North America, Europe and Asia (Rose, 1982, 2006) is a slender long-limbed animal (Figure 10.35(a)) that has the key cetartiodactyl feature, the 'double pulley' astragalus, which allows controlled bending between the lower leg and the ankle and restricts movement to a vertical plane. Further excellent materials of early artiodactyls are known from the world-famous middle Eocene site of Messel in Germany (see Box 10.8).

The limbs are long and slender, and *Diacodexis* may have moved by leaping. The limbs are otherwise plesiomorphic: the fibula is still present, although reduced, the ulna is also retained, as is the clavicle in the shoulder girdle. *Diacodexis* has five fingers on the hand and four toes, but the main weight of the body is expressed through digits 3 and 4, which each bear small hooves.

Diacodexis shows unique artiodactyl characters in the skull: the facial portion of the lacrimal is enlarged, the orbitosphenoid is expanded and separates the frontal from the alisphenoid, and in the lower molar teeth the trigonid is narrow because the paraconid and metaconid are placed close together.

Basal artiodactyls continued into the Oligocene, but a major radiation of new forms occurred in the late Eocene, the first members of the Suina, Tylopoda, Ruminantia, and Whippomorpha (Rose, 2006).

10.10.2 Suina: pigs and peccaries

Pigs and hippos used to be classed together in the clade 'Suiformes', together with the extinct entelodonts and anthracotheriids. However, molecular phylogenetic studies show that these fossil groups, together with the hippos are close relatives of the whales, and members of the clade Whippomorpha (see Section 10.10.5).

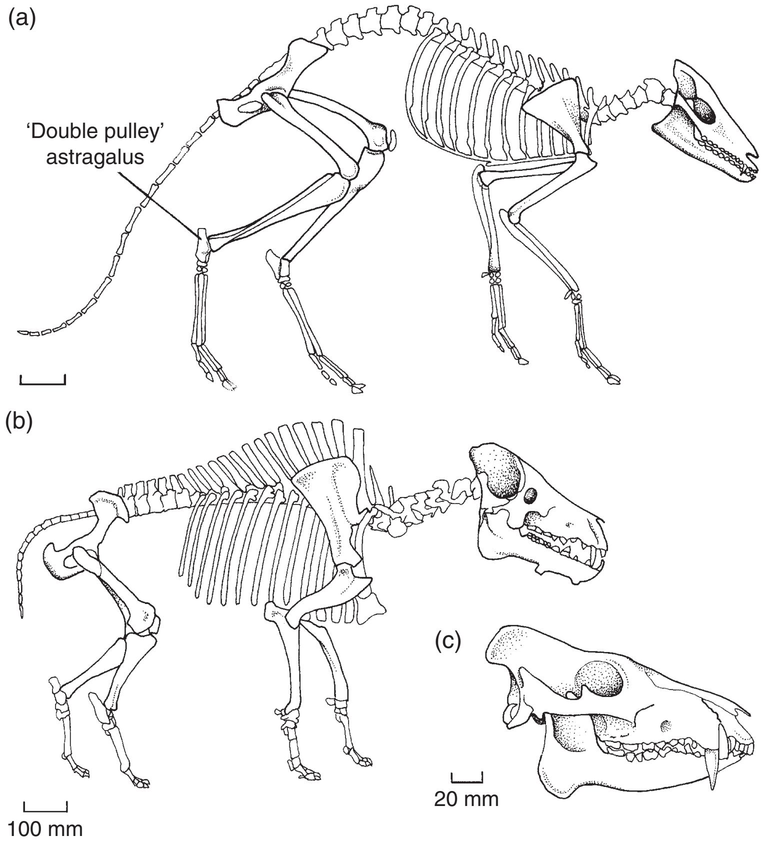


Figure 10.35 Early artiodactyls and pigs: (a) the basal Eocene artiodactyl *Diacodexis*; (b) the Oligocene entelodont *Dinohyus*; (c) the Oligocene peccary *Perchoerus*. Source: (a) Adapted from Rose (1982). (b,c) Adapted from Gregory (1951).

BOX 10.8 MESSEL WORLD – EOCENE LIFE

Some of the most astounding mammal fossils have been found in the middle Eocene (c. 49 Myr ago) oil shales at Messel, near Frankfurt, Germany (Schaal and Ziegler, 1992; Rose, 2012). All details of their hair, stomach contents and even internal organs are preserved in some cases.

The Messel deposits contain abundant plant remains – laurel, oak, beech, citrus fruits, vines and palms, with rare conifers, and ponds covered by water lilies, which indicate a humid tropical or subtropical climate. Invertebrate fossils include snails and insects, and fishes account for 90% of the vertebrate fossils. Rare frogs, toads and salamanders have been found, as well as six genera of crocodilians, several tortoises and terrapins, and some large lizards and snakes. The birds include dozens of species spanning most modern groups except passerines (Mayr, 2009).

The mammal fossils, although constituting only 2–3% of vertebrates found, have attracted most attention. They include 46 species belonging to 13 orders (Rose, 2012), ranging from opossums and pantolestids to lemur-like primates and rodents. The smaller mammals include eight species of bats, some of which have scales from butterfly wings and beetle exoskeletons preserved in their stomachs, and four genera of squirrel-like rodents. Carnivorous mammals include a ‘creodont’ and two miacids (see Section 10.11.5). The most famous (or infamous) fossil from Messel must be *Darwinius*, one of three genera of lemur-like primates (see Section 11.2.2).

An unusual small mammal is *Leptictidium*, a biped, standing only 200 mm tall, that dashed about like a long-tailed leprachaun (see illustration I). Several nearly complete skeletons (Storch and Lister, 1985) show that it has a long tail, a strong but short trunk and relatively long hindlimbs and short forelimbs. The long tail suggests a balancing function, as in bipedal dinosaurs, and the short strong trunk also points to an ability to balance. *Leptictidium* was probably a facultative biped: it ran and walked on its hindlegs, perhaps even jumping like a kangaroo rat, but could have adopted a quadrupedal posture for slow locomotion and standing.

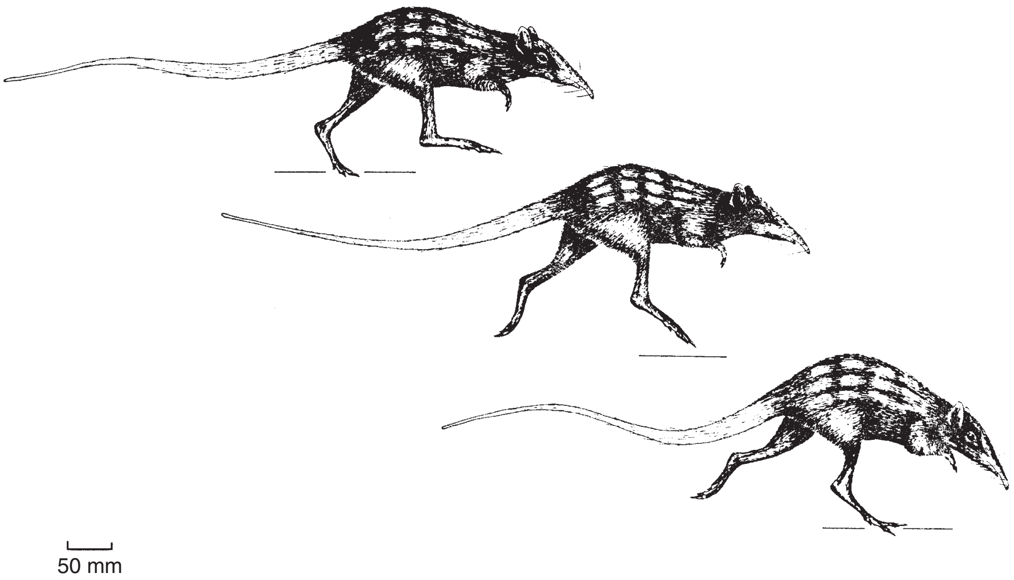
The extraordinary conditions of fossilization at Messel have allowed detailed studies of the diet of *Leptictidium*. In one specimen, several dozen pieces of bone were found, some of which could be identified as limb bones and vertebrae of a small reptile, possibly a lizard. A second skeleton contained bones of a small mammal and another contained fragments of chitin from the exoskeletons of large insects. The gut regions also show a variety of plant fragments, so that *Leptictidium* had a very varied diet.

Ground-dwelling herbivores include a ‘condylarth’ (see Section 10.8.2), three artiodactyls, and six perissodactyls. The Messel artiodactyls are dichobunids, a clade that includes *Diacodexis* from North America (see Section 10.10.1). *Messelobunodon* from Messel was a rabbit-sized, long-limbed animal that fed nervously on leaves in the subtropical German forests. The horse-like palaeothere *Propalaeotherium* preserves stomach contents that confirm it fed on leaves and berries.

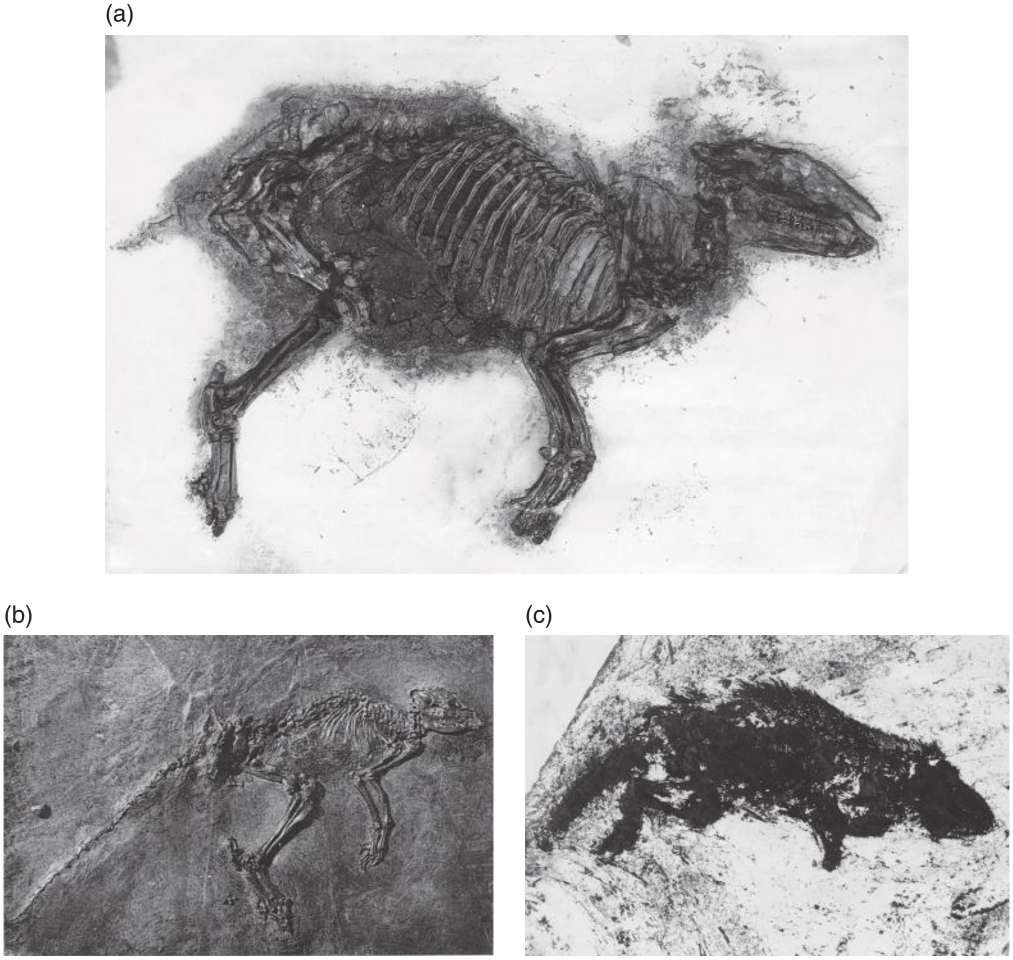
Some of the Messel mammals provide evidence for major migrations. For example, the small spine-covered insect-eater *Macrocranion*, formerly assigned to Lipotyphla, now seems to belong to Macroscelidea (see Section 10.7.1), and so is part of Afrotheria. The same may be true of *Pholidocercus*, which was also covered with spines and had a helmet-like structure of scales on its head. So, mammals were somehow able to move between Africa and Europe, perhaps hopping over chains of islands. Two further mammals, the pholidotamorphs *Eurotamandua* and *Eomanis*, provide evidence of linkages with southeast Asia. Their modern relatives, the pangolins (see Section 10.11.7) occur in southeast Asia and Africa, and the fossils from Messel provide evidence of a formerly more widespread distribution.

The Messel site seems to represent an Eocene lake that filled with organic matter periodically. Cadavers of land animals were washed in and birds and bats fell into the lake and sank to the bottom. The anoxic bottom waters prevented putrefaction and scavenging and the corpses were slowly covered by organic clays and preserved as near-perfect fossils (illustration II).

The official Messel site web page (auf Deutsch) is: http://www.grube-messel.de/, and the UNESCO description, with videos, is at: http://whc.unesco.org/en/list/720/. A brief documentary on the site, with Jørn Hurum and Jens Franzen is at: http://www.revealingthelink.com/the-discovery/messel-pit, and a walk-through of the spectacular Messel exhibition in the Senckenberg Museum in Frankfurt, where most of the research is carried out, is here (auch auf Deutsch): http://www.senckenberg.de/messelaust/143smf_2005/_AusstellungME2005.htm.



(I) The tiny bipedal insectivorous mammal *Leptictidium* from the Messel deposits, restoration of its running style. Source: Adapted from Storch and Lister (1985).



(II) Exceptional preservation of mammalian fossils in the Messel deposits, Germany: (a) the early horse-like animal *Propalaeotherium parvalum*, shoulder height 350 mm; (b) the dichobunid artiodactyl *Messelobunodon schaefferi*, shoulder height 220 mm; (c) the insect-eating *Pholidocercus hassiacus*, length of head and trunk 190 mm, showing a clear silhouette of the fur. Source: J. Franzen, Senckenberg Institute, Frankfurt, Germany. Reproduced with permission.

The Suidae, pigs, arose in the late Oligocene of Europe, and the Tayassuidae, peccaries, date from the late Eocene of North America and Europe. Pigs never made it to the Americas, and today peccaries are only found in North and South America. *Perchoerus*, an early peccary (Figure 10.35(c)) from the Oligocene of North America, has long canines, used in feeding and in fighting, as in other suoids. Both pigs and peccaries tend to have long, tusk-like upper canines in the males, used for fighting, but while the tusks of peccaries point downwards, like the upper canines of most mammals, those of pigs recurve upwards.

10.10.3 Tylopoda: camels and relatives

Relationships of the tylopods and ruminants are debated. They share specialized cheek teeth (Figure 10.36(a)) that show the **selenodont** pattern: the molars are square in outline and the cusps form pairs of crescent-shaped ridges (selenodont means ‘crescent-moon tooth’) that were durable grinders, effective for side-to-side chewing of leaves. Camelids and ruminants share a number of other characters: the upper incisors are reduced or missing (or may be enlarged into sabre-like structures for display in the males, especially hornless species), the lower incisors and canines are small, spatulate and procumbent (they stick out forwards), the feet have two main toes, the metacarpals and metatarsals are fused into cannon bones in derived forms (made from metapodials 3 + 4) and the stomach is compound and adapted for fermenting the food.

Although the selenodont teeth and these other characters suggests a close relationship, molecular studies put ruminants and suoids together as sister taxa, with tylopods relegated to a basal position. But ‘tylopods’ are just an assemblage of selenodont artiodactyls that are not ruminants, nor necessarily closely related to camelids or even to each other. As well as the

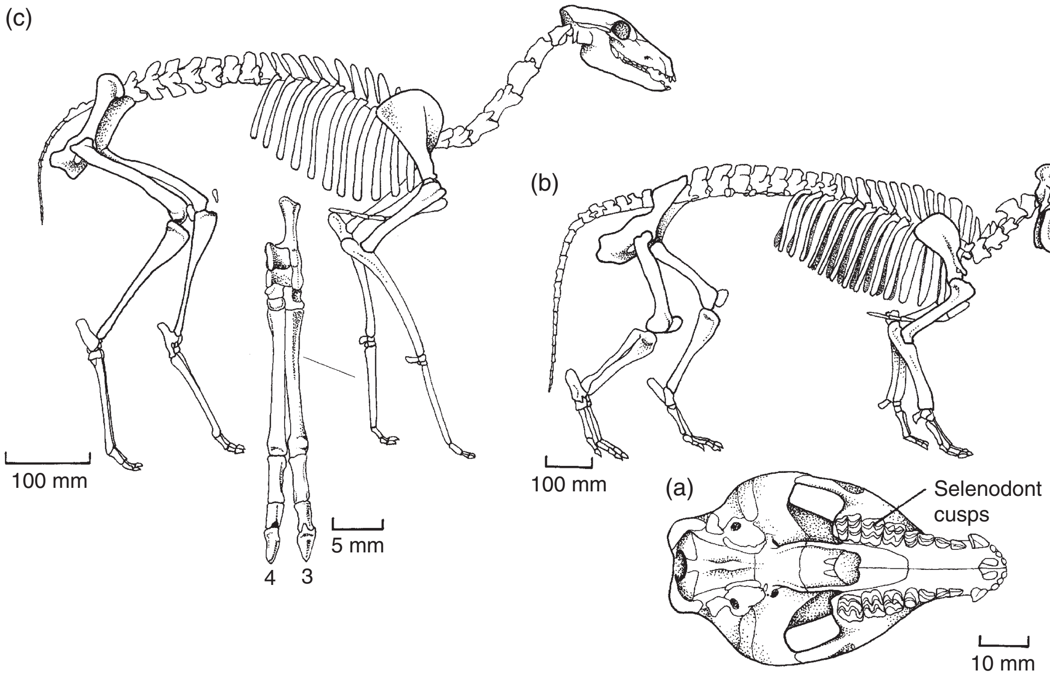


Figure 10.36 Tylopods: (a) ventral view of the skull of the late Eocene oreodont *Bathygenys*; (b) the Oligocene oreodont *Merycoidodon*; (c) the late Eocene camel *Poebrotherium*, skeleton and hindfoot in anterior view, showing the divergent toes 3 and 4. Source: (a) Adapted from Wilson (1971). (b,c) Adapted from Gregory (1951).

protoceratids and oreodonts discussed below, from the late Eocene through the Oligocene there were seven families of small to medium-sized endemic selenodont ruminants in Europe that have been grouped with 'tylopods': these include the rabbit-like cainotheres (which survived into the early Miocene), the llama-like xiphodontids, and the pig-like cebochoerids (Prothero and Foss, 2007).

Tylopods (camels, protoceratids) share some diagnostic characters of the teeth, jaws, vertebrae and ankle. Oreodonts (Merycoidodontidae and Agriochoeridae) were exclusively North American forms, ranging from the late Eocene through most of the Miocene, but most common in the Oligocene. These low, pig-sized animals (Figure 10.36(b)) have four toes on each foot and were probably not very fast moving. Large numbers of oreodonts have been collected in the Big Badlands of South Dakota, where they lived in huge numbers as denning burrowers, browsing on low bushes, and scuttling for safety when threatened.

The protoceratids were also exclusively North American, from the late Eocene to the Pliocene. They were rather deer-like forms, but with shorter legs, and are distinguished by evolving horns convergently with the Ruminantia – not only above the eyes but also in the form of a single, sling-shot shaped horn on the nose.

The camelids include camels, as well as llamas, alpacas, and vicuñas. Camels are especially known for their feats of endurance, living for days without water or food in the deserts of Asia and Africa. Camelids all have a broad pad on each foot (tylopod means 'padded foot'), useful for walking over moving sand, but also for the South American forms in climbing rocky slopes. An early camel, *Poebrotherium* from the late Eocene of North America (Figure 10.36(c)), is a slender, goat-sized animal. Like all camels, it has a long neck, long limbs and two toes (3 and 4). It still has hooves on these toes, but by Miocene times, camels had become secondarily digitigrade, with the hooves essentially replaced by broad pads as in modern forms. It is an unexpected fact that camels originated in North America, and they then migrated over two new land bridges in the late Miocene and Pliocene. Camels crossed the Bering Strait to Asia, and eventually the Middle East and Africa, while llamas and vicuñas passed into South America across the Isthmus of Panama during the GABI (see Section 10.6.6). They became extinct in North America at the end of the Pleistocene.

10.10.4 Ruminantia: cattle, sheep, deer and giraffe

The main artiodactyl group is Ruminantia, cattle, sheep, antelope, giraffe, deer and mouse deer (Fernández and Vrba, 2005; DeMiguel *et al*., 2014), so-called because they all **ruminate**, or regurgitate their food. The cow, like most living ruminants, has a four-chambered stomach. A mouthful of grass enters the rumen and part of the reticulum, where it is partially broken down by bacteria (foregut fermentation). The food is returned to the mouth for rumination or 'chewing the cud' and it then passes through the other two stomachs, which allows a cow to extract the maximum nutritive value from its food. Camels also have a ruminating system, perhaps evolved convergently, but

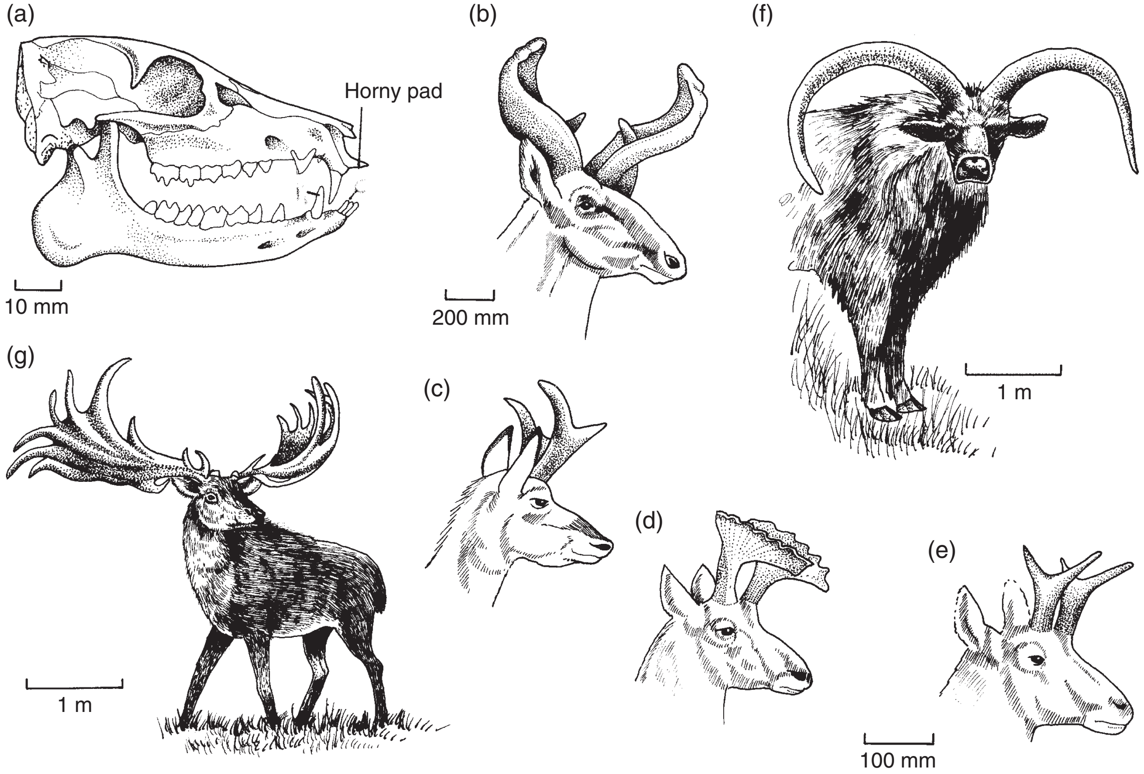


Figure 10.37 The ruminant artiodactyls: (a) the Oligocene *Hypertragulus*; (b–e) restored heads and horns of (b) the Pliocene giraffe *Sivatherium*, (c) the modern pronghorn *Antilocapra*, (d,e) the Miocene pronghorns *Ramoceros* and *Meryceros*; (f) the giant Pleistocene sheep *Pelorovis*; (g) the giant Pleistocene deer *Megaloceros*. Source: (a) Adapted from Scott (1940). (b–e) Adapted from various sources. (f,g) Adapted from Savage and Long (1986).

other plant-eaters, such as pigs, rhinos and horses, lack the two-stage fermentation process.

In addition to their specialized digestion, ruminants can be diagnosed by a derived feature of the ankle joint, the fusion of the cuboid and navicular bones, forming an L-shaped pattern. Further, they have reduced or lost their upper incisors and have only a horny pad against which the lower incisors nip off food items. *Hypertragulus*, an early form from the late Eocene and Oligocene of North America, is a small, rabbit-sized animal that shows the ruminant horny pad (Figure 10.37(a)). Its lower canine teeth look like incisors and the first premolars have taken on the canine role.

The early ruminants, the traguloids (a paraphyletic assemblage including the relatives of the modern mouse deer) were small, hornless animals that were fairly common until the early Miocene when the modern groups radiated (Prothero and Foss, 2007; Bibi, 2013; DeMiguel *et al.*, 2014). These, the pecoran ruminants, deer, giraffes, cattle and antelopes, nearly all have horns of one kind or another (Figure 10.37(b–g)), usually in the males alone or, if in both sexes, the horns in the males are larger: a bony horn core that is surrounded by a permanent horny sheath (cattle), a bony structure that is shed annually (deer antlers), permanent bony horns covered with skin (giraffes), or a bony nose prong whose outer sheath is shed (pronghorns, which are often called 'antelope' but are actually in their own family). These types of horns probably evolved independently in the three main groups of ruminants as fighting structures. Males of the ruminant groups use their horns in head-butting (sheep), or 'antler-wrestling' (deer), which may follow displays establishing social dominance rank, winning females and patrolling feeding territories. Other plant-eaters such as horses or camels do not have horns or antlers because they live in open grasslands and eat less clumped food resources, so that territories are unnecessary (Janis, 2007).

Ruminants are by far the most succesful large herbivores today, with 217 species, compared to only 17 species of perissodactyls (see Sections 10.11.2–4). And yet this was not always the case. The late Eocene woodlands of North America and Asia were dominated by horses, rhinos and brontotheres, but then, from the mid-Miocene onwards, the camels, pigs and ruminants rose to prominence. However, this was not a simple one-for-one replacement, that might then be interpreted as providing evidence that the hindgut digestion of perissodactyls is inferior to the ruminating foregut digestion of the selenodont artiodactyls in all situations (Janis, 2007). Both groups responded to the major climatic and vegetational changes that were underway during the Cenozoic, for example switching from browsing (feeding on leaves from bushes and trees) to grazing (feeding on grass) as climates cooled and grasslands expanded in the Oligocene and Miocene. Because ruminants retain their food for multiple phases of digestion, they need less fodder than perissodactyls of the same body weight, so they may have been more successful as climates became cooler and more seasonal, with consequent times of food shortage in winter. However, perissodactyls continue to do well in situations where they can bulk feed on food that is of such low quality that it would take a ruminant too long to digest: horses, zebras and asses living in arid steppes and plains eat dry grass, and tapirs living in tropical forests eat the kinds of tough evergreen plants that otherwise appear to be palatable only to house cats.

Despite the advantages that artiodactyls may have had through the Neogene, they never reached the truly large sizes of some perissodactyls and proboscideans. Indeed, the largest artiodactyls, such as some extinct camelids and sivatheriine giraffes, weighed less than 2 tonnes, whereas brontotheres and indricothere rhinos (see Sections 10.11.3–4) weighed 5–6 and 12–15 tonnes respectively, and extinct uintatheres and proboscideans equalled these weights also (see Figure 10.33). The explanation may be to do with the relationship between body size, gut size, and retention time (Janis, 2007). In ruminants, the retention time of food increases with body and gut size. At a body mass of 1 tonne, the food is retained for 60–70 hours, which is the maximum time needed to completely digest the plant material. Therefore, at body masses over 1 tonne, there is no further advantage for a ruminant in retaining its food any longer. Indeed, if it does, bacteria convert the digestive products to methane and carbon dioxide, so causing loss of useful materials and excess gas.

10.10.5 Whippomorpha: hippos, whales and extinct relatives

Somehow, fossil hippos never had the cachet of other important transitional fossils, but their new role in bridging phylogenetically between artiodactyls and whales has led to a flurry of interest (e.g. Geisler and Uhen, 2003, 2005; Thewissen *et al*., 2007, 2009; Orliac *et al*., 2010; Boisserie *et al*., 2011). Among close relatives of hippos and whales, the raoellids, a small family of semiaquatic artiodactyls from Eocene of Asia, may actually be whales (Thewissen *et al*., 2007) or the sister group of Cetacea (Boisserie *et al*., 2011). The whale-hippo clade has the excellent name Whippomorpha.

Hippos date back to the early Miocene of Uganda and Kenya (Orliac *et al*., 2010). Two species survive today, *Hippopotamus* itself, a semi-aquatic grazer, and the pigmy hippo, *Choeropsis*, a forest browser, both restricted to Africa south of the Sahara.

Two extinct groups of superficially pig-like animals are whippomorphs. The anthracotheriids, known from the Eocene to Pliocene, originated in Asia and later spread to Europe, North America and Africa. The first anthracotheriids were small, but later ones became as large as pigmy hippos. From the late Eocene to the early Miocene, North America and Asia were populated by giant pig-like animals, called entelodonts. These animals, up to 2–3 m long, had long heavy skulls (Figure 10.35(b)) and they may have fed on a broad range of plants (? and animals). The deep lappets on the zygomatic arch and the knobs beneath the lower jaw may have been associated with sexual display activity.

10.10.6 Cetacea: evolution of the whales

The whales (Cetacea) are some of the most spectacular living mammals, including 85 species of dolphins, porpoises, and whales today. Looking at a great blue whale, 30 m long, or a fast-swimming dolphin, it is hard to imagine how they evolved from terrestrial mammal ancestors, and yet that is what happened (Thewissen *et al*., 2009; Uhen, 2010). The close relationships of whales and hippos that emerged from phylogenomic study has been confirmed by the discovery of unexpected artiodactyl characters in the hindlimb of early whales (see Section 10.10, introduction).

The earliest whales are a dozen genera in three families, Pakicetidae, Ambulocetidae, and Remingtonocetidae from the early and middle Eocene of Pakistan and northern India; these and other Eocene whales are sometimes collectively termed 'archaeocetes'. The pakicetids include *Pakicetus*, which has a long-snouted skull with plesiomorphic carnivorous teeth lining its jaws (Figure 10.38(a)). The skeleton of *Pakicetus* is incompletely known, and an early tentative reconstruction (Figure 10.38(b)) showed a semi-aquatic coast-dwelling carnivore. This was debated, and some more terrestrial reconstructions were presented, on the basis of the extensive retention of adaptations such as the typical artiodactyl double-pulley astragalus. In reviewing the evidence, Madar (2007) concluded that pakicetids were capable of walking on land, but not sustained running, and that they spent more time in the water, moving around by bottom walking, paddling, and undulatory swimming.

The ambulocetids such as *Ambulocetus* have limbs adapted for swimming (Figure 10.38(c)), with short upper elements and paddle-like hands and feet. *Ambulocetus* could walk on land, even though its posture would have been rather crouched. Sedimentological and isotopic evidence indicates that pakicetids and ambulocetids were primarily freshwater, perhaps living near the edges of lakes and rivers, and rushing into the water to seize prey. The remingtonocetids are less well known, but were low-bodied, marine animals, perhaps looking and acting something like 'mammalian crocodiles' (Uhen, 2010).

More derived than these three families were the Protocetidae, which arose in Indo-Pakistan in the early middle Eocene, and then spread across much of the world. These were much more fully aquatic animals, entirely marine, with reduced limbs that could be used to move on land, perhaps like modern seals. They may still have given birth on land. Protocetids form a paraphyletic stem radiation to the later whales: some more primitive forms still retain a connection of the hind leg and pelvis to the vertebral column, while this is lost in more derived forms.

All remaining whales are members of Pelagiceti, marking the permanent switch to purely aquatic adaptations (Uhen, 2010). These derived whales had much reduced hindlimbs, a rotated

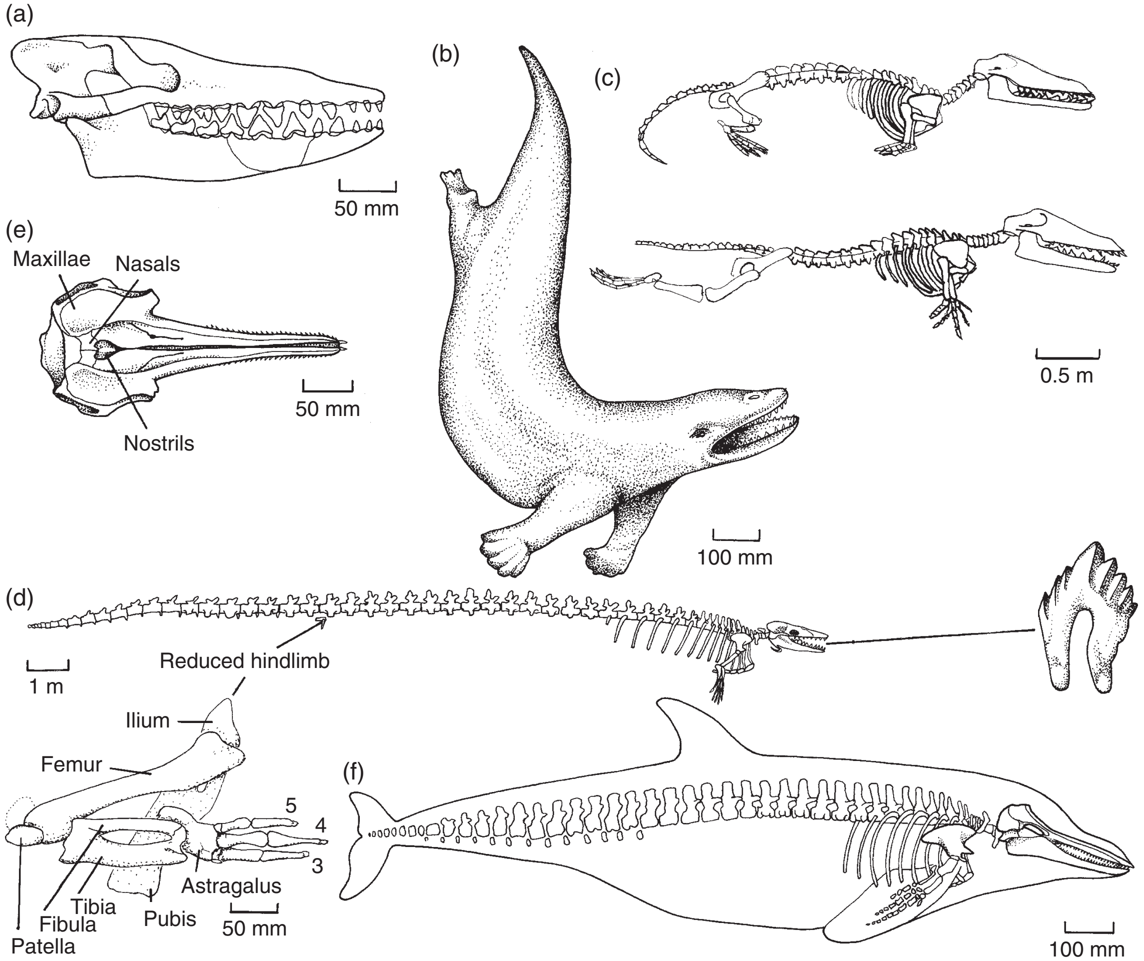


Figure 10.38 The whales: (a,b) one of the first whales, *Pakicetus* from the early Eocene, reconstructed skull in lateral view and tentative life restoration; (c) a whale with limbs, *Ambulocetus* from the middle Eocene, in walking (top) and swimming (bottom) postures; (d) the first giant whale, *Basilosaurus*, skeleton, detail of reduced hindlimb and typical triangular-crested tooth; (e) telescoping of the skull elements in a dorsal view of the skull of *Kentriodon*; (f) skeleton of *Kentriodon*, a Miocene dolphin. Source: (a) Adapted from Gingerich and Russell (1981). (b) Adapted from Savage and Long (1986). (c) Adapted from Thewissen *et al.* (1994). (d–f) Adapted from Kellogg (1936) and Gingerich *et al.* (1990).

pelvis that was no longer weight-supporting, and compressed caudal vertebrae associated with the evolution of a broad, horizontal tail fin, the famous whale flukes, that are essential for their undulatory swimming mode in which the muscular tail and posterior trunk beat up and down.

An early pelagicetid is the late Eocene *Basilosaurus* (Figure 10.38(d)), which is over 20 m long and, unlike modern whales, must have looked like a classic sea serpent because of its tiny head and long, thin body. This explains its odd name: the suffix 'saurus' refers to a reptile, and its remains were originally thought to belong to a sea serpent. Its hindlimbs are much reduced, but still present, with all elements in place. The pelvis has lost contact with the backbone and the lower limb and ankle are largely fused. This hindlimb would have been useless in swimming, but it may have been used as a copulatory guide. The head is relatively small and the teeth have a comb-like pattern of small pointed cusps. A contemporary of *Basilosaurus* is the more dolphin-like *Dorudon*, which was closer to the ancestry of the modern whales.

After the Eocene, following the extinction of numerous limbed and serpentine cetaceans, whales radiated into two clades, together the clade Neoceti, the toothed whales, such as dolphins and porpoises (Odontoceti), and the baleen whales such as the blue whale and humpback (Mysticeti). There have been many morphological and molecular phylogenetic studies of extant whales, and debates about whether, for example, the sperm whale, the largest living whale to retain teeth, is an odontocete or a mysticete. These now converge (Geisler *et al.*, 2011) on the view that the sperm whale is an odontocete.

In all modern whales, the bones of the top of the snout (premaxilla, maxilla, nasal) have moved right back over the top of the skull (Figure 10.38(e,f)), independently and convergently in each clade. This is associated with a backwards move of the nostrils to lie above the eyes (the blowhole), an adaptation for breathing at the surface, which has had the effect of telescoping the rest of the skull elements backwards.

Odontocetes radiated in the Miocene and dozens of fossil dolphin-like forms are known (Figure 10.38(e,f)), with up to 300 simple pointed, peg-like teeth. The toothed whales show a second major adaptation in developing an echolocation system. The splayed bowl-like nasal region over the snout houses a fatty cushion-like mass that focuses whistles, clicks and squeaks produced in the nasal passages and sends them out as a directed beam of sound. The echoes are picked up in the narrow lower jaw and transmitted through bone to the ear.

Mysticetes have lost their teeth and have instead baleen, or whalebone, a modified protein akin to horn, which is used for filtering planktonic organisms out of the seawater. The first mysticetes still had teeth and many were small (Fitzgerald, 2006; Déméré and Berta, 2008); baleen evolved in the late Oligocene, and since then their combination of large body size, baleen, and bulk filter feeding was established. Whales today, and in the past, form unique habitats when they fall dead to the bottom of the ocean (see Box 10.9).

Whales require huge amounts of food, and so can live only in highly productive oceans. The modern clades arose in the late Eocene and became particularly diverse in the middle and late Miocene. This is best explained by variations in the diversity if diatoms and by declining ocean temperatures (Marx and Uhen, 2010). Diatoms are planktonic organisms that are the base of the food chain for krill, the small shrimp-like crustaceans that form the bulk of the diet of mysticetes, as well as of fishes. Perhaps the establishment of the Antarctic Circumpolar Current in the early Oligocene and the freezing of Antarctica in the mid Miocene provided the boost in marine productivity, as cool bottom waters rose around the southern oceans, causing ocean mixing.

BOX 10.9 DEAD WHALES AS LONG-TERM FEEDING STATIONS

When a whale falls to the deep ocean floor, there is a feeding bonanza. Isopods, crabs, bristleworms, hagfish, and sharks are on the scene within minutes, and the tonnes of flesh can be stripped and consumed in a few months. The initial reaction is fast, because such a vast amount of food is rarely encountered in the cold, dark abyssal depths of 2 km or more, but the scavengers have evolved to survive long periods of starvation, and they make these bonanzas last. Indeed, the final stages, where worms eat their way through the bones to extract every last atom of nourishment, may last 100 years or more.

Ecosystems on the whale carcass change as the feeding modes change (Smith and Baco, 2003; Little, 2010). There are four stages.

1 *Mobile scavengers* such as hagfish and sleeper sharks tear and twist the flesh from the carcass. This can be hard work at first, as they break through the thick hide, and it may take them two months or more to remove the mouldering flesh from the bones.

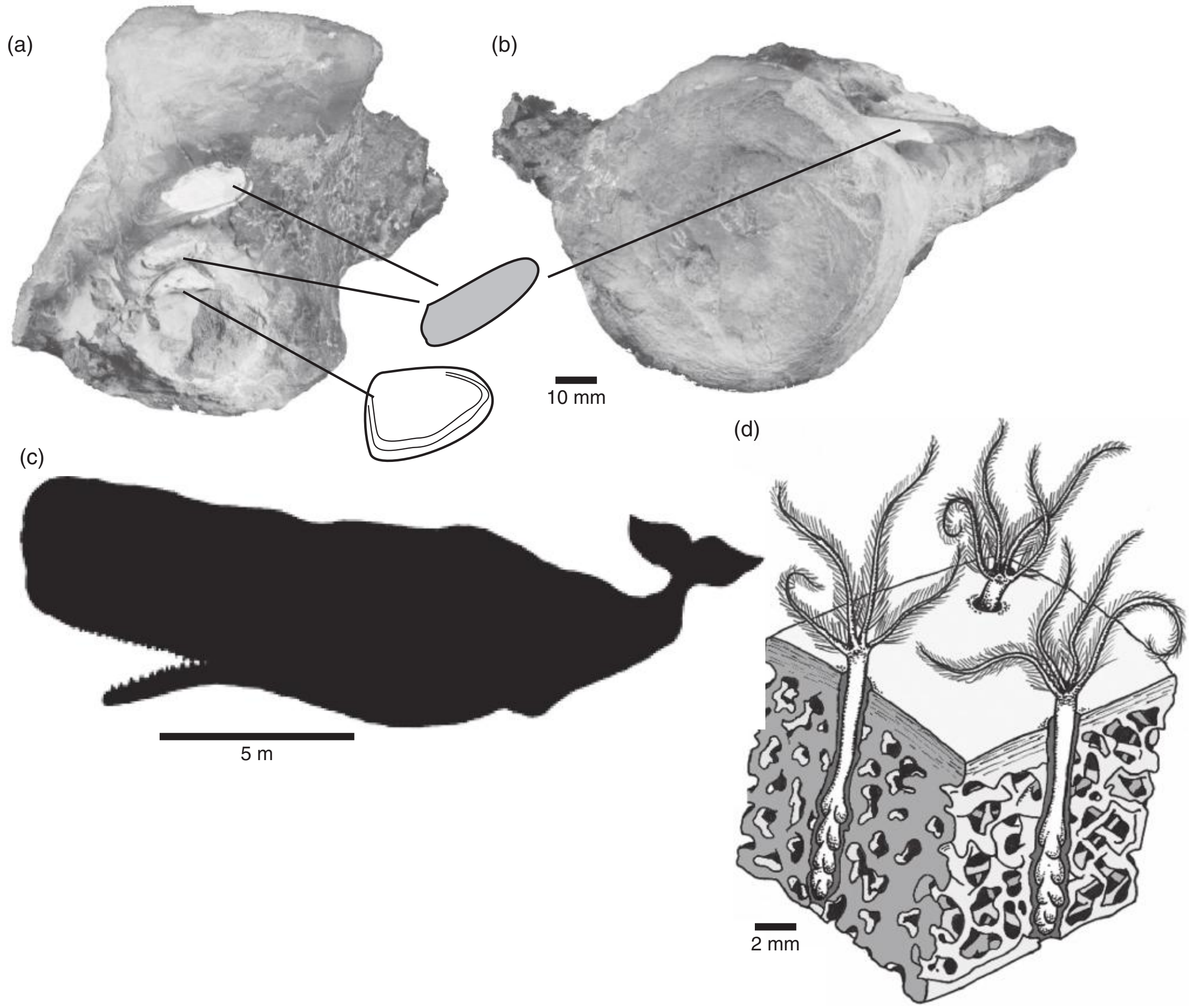
2 *Opportunistic species* then occupy the bones and a considerable area around the carcass, where body fluids, fats, and other organic matter have seeped out. These opportunists, today, and in the Miocene, include specialist bivalves that feed on the lipids and collagen of the decaying bone (see Illustrations (a,b)).

3 *Anaerobic processes* continue for up to a century when bacteria occupy the bones and break down the fats within the bones, turning sulphate into hydrogen sulphide, and these sulphophilic bacteria in turn provide nourishment for mussels, clams, limpets and snails that otherwise can occupy mid-ocean ridge black smokers.

4 Finally, when all nourishment has been extracted from the carcass, most carcasses are covered by sediment, but some can remain as a *long-term reef*, perhaps for thousands of years. On a muddy sea floor, any rock or bone is a bonanza for organisms that require clear water for feeding or for releasing larvae, and numerous encrusters cover the bones.

The most gruesome aspect of the new science of deep ocean whale falls was the report in 2004 of a new genus of worm, the bone-eater *Osedax*, fished up first from the bones of a decaying grey whale off California. The worm sits on the surface of the bone, and sends a root-like structure downwards, using acids to dissolve the apatite (see Illustration (d)). The worm breaks down proteins and oils deep within the bones and turns them into nutrient. Twenty or more species of *Osedax* have been identified in different oceans around the world, feeding on different carcasses, and it is still poorly understood how these so-called ‘zombie worms’ locate a fresh carcass, and indeed what they do when there is no carcass within reach.

These grisly scavengers who lurk about on the sea bed may have existed for longer than the whales. Many will transfer their attentions to turtles, fish skeletons, or even bundles of cow bones left by scientists (and probably also the scientists), and it is likely that marine reptile carcasses were subject to similar treatment in the Mesozoic. Fossil whale carcasses from the Eocene onwards show evidence of invasion by diverse organisms, including molluscs that specialize on sulphophilic bacteria. Borings attributed to *Osedax* have also been found to be relatively common, as for example in a whale carcass from the Pliocene of Italy (Higgs *et al.*, 2012), where borings are 0.5–0.7 mm in diameter, and expand within the bone as chambers where bone has been removed. Tasty.



Whale falls as feeding opportunities. (a,b) Two views of a whale vertebra from the Morozaki Group (middle Miocene) of Japan, showing attached bivalves *Calyptogena* (shaded outline) and *Vesicomya* (unshaded outline). (c) Silhouette of sperm whale, *Physeter*, found offshore around Japan today. (d) Stylized reconstruction drawing of *Osedax* bone worms in a block of fossil whale bone; the vertical burrows are probably too regular and should expand and amalgamate inside the bone. Source: (a,b) K. Amano, Joetsu University of Education, Joetsu, Japan. Reproduced with permission. (c) Adapted from http://www.shutterstock.com/pic-113201656/stock-vector-sperm-whale-silhouette.html (d) R. Esperante, Geoscience Research Institute, Loma Linda, CA, USA. Reproduced with permission.

10.11 PEGASOFERAE: BATS, HORSES, CARNIVORES AND PANGOLINS

The clade Pegasoferae brings together animals as diverse as bats, horses, and carnivores, which were traditionally assumed to be unrelated. The unusual name refers to Pegasus, the flying horse in Greek mythology (i.e. Chiroptera + Perissodactyla) and Ferae is a term that had been long applied to the clade Carnivora + Pholidota. The clade was identified by Nishihara *et al*. (2006) and confirmed by dos Reis *et al*. (2012), but others find different relationships among the clades, assigning Perissodactyla to a close association with Cetartiodactyla (as Euungulata; O'Leary *et al*., 2013), and Chiroptera as sister to Cetartiodactyla, and various combinations of laurasiatherians. Tsagkogeorga *et al*. (2013) find a clade Ungulata (Cetartiodactyla + Perissodactyla), paired with Carnivora (as Fereungulata), and this paired with Chiroptera (as Scrotifera).

The perissodactyls, such as horses, tapirs and rhinoceroses, are distinguished from the artiodactyls, or even-toed ungulates (2 or 4 toes), by having an odd number of toes (1, 3, or 5).

Perissodactyls diversified in the early Eocene, replacing basal placental groups (see Section 10.8.2) as dominant browsing herbivores.

10.11.1 Chiroptera: bats

Bats include 1240 species, just under one quarter of all living mammals, and they appear to owe their success to their advanced flying and hunting capabilities that make them effectively 'birds of the night' (Altringham, 2011; Gunnell and Simmons, 2012). There are two groups of bats, the megachiropterans or fruit bats and the more abundant microchiropterans, the small insect-eaters

Bat remains have been found in the latest Palaeocene, and excellent materials are known from the Eocene: several species are known from the early Eocene Vastan local fauna in India, some of which are related to the eight bat species from the middle Eocene Messel site in Germany (see Box 10.8). Two particularly intensively studied early bats come from the early Eocene of Wyoming, *Icaronycteris* and *Onychonycteris* (Figure 10.39). These already show all the key microchiropteran features: the humerus, radius (and fused ulna) and digits are all elongated, and the flight membrane is supported by the spread fingers 2–5 (digit 1, the thumb, is much shorter). The shoulder girdle is modified to take the large flight muscles on the expanded scapula on the back and the broad ribs and sternum on the front. The hindlimbs are strong, and the feet are turned backwards so that these early bats could hang upside down as modern bats do.

There is a key difference in the sensory systems of these two early bats, however, and this gives clues about the evolution of echolocation. Modern microbats emit high-pitched squeaks from the throat (larynx), generally above the normal human hearing range, and they hear the echoes in such a way that they can build up a sound picture of the surrounding habitat, allowing them to 'see' in the dark. *Icaronycteris*, like all the other Eocene microbats, could echolocate: it has an enlarged cochlea, an enlarged orbicular apophysis on the malleus, and a stylohyal element with an expanded, paddle-like cranial tip, all of which are features of the ear that help enhance the echoes. *Onychonycteris* lacks these three indicators of echolocation capability (Simmons *et al*., 2008). It is also more plesiomorphic than any other known bat in its relatively short fingers and retention of claws.

The evolution of echolocation in bats has been hard to resolve. Most phylogenetic analyses do not split bats into Megachiroptera (the non-echolocating fruit bats, Pteropodidae) and Microchiroptera (the echolocating, regular microbats), as had been assumed traditionally, and which would indicate that laryngeal echolocation arose once only. Instead, Pteropodidae are nearly always paired with the Rhinolophoidea (horsehoe bats), as clade Yinpterochiroptera (Teeling *et al*., 2005). This implies that echolocation arose once only among earliest bats and was later lost in fruitbats, or that it arose twice, independently in Rhinolophoidea and in the other microbats, the Yangochiroptera (Teeling, 2009). Interestingly, in a species-level gene tree of bats, Agnarsson *et al.* (2011) found mixed results, with most analyses supporting the Yin/Yang tree, but some retrieving the older Mega/Micro division of bats; Tsagkogeorga *et al.* (2013) find the Yin/Yang split. This is an interesting case that shows the importance (and difficulty) of determining true phylogenies and their implications on evolutionary assumptions.

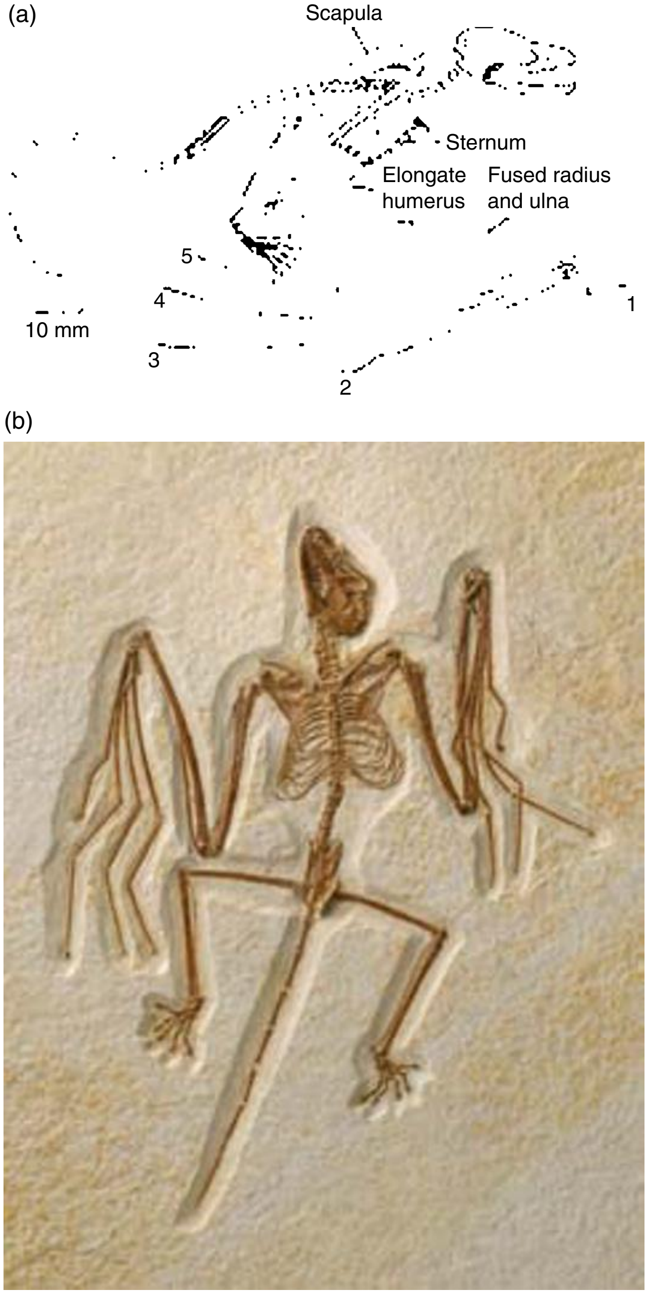


Figure 10.39 The oldest reasonably complete bat fossils, *Icaronycteris* (a) and *Onychonycteris* (b) from the Green River Formation (early Eocene) of Wyoming. See Colour plate 10.4. Source: (a) Adapted from Jepsen (1970). (b) Simmons *et al.* (2008). Reproduced with permission from Nature Publishing Group.

10.11.2 The evolution of horses

Some of the first perissodactyls were horses, no larger than a terrier admittedly, but the first in what has come to be regarded as a classic story of evolution since the days of Edward Cope and Thomas Henry Huxley (MacFadden, 1992; Franzen and Brown, 2010). Major changes may be observed during the history of the horses (Figure 10.40): increase in body size; reduction in the number of toes from four (front) and three (back) in the first horse *Hyracotherium*, to three in *Mesohippus* and one in *Pliohippus* and, independently, in modern *Equus*; and a deepening of the cheek teeth from small leaf-crushing molars, to the high-crowned (**hypsodont**) grass-grinders of modern horses. Grass contains a high proportion of silica, is very abrasive and feeding on grasses also introduces grit and soil into the mouth. Grazers need high-crowned teeth that last for a long time, and they usually have complex infoldings of enamel and dentine to provide a better grinding surface.

These changes may have been driven by a major environmental change that took place during the late Oligocene and early Miocene: the spread of grasslands in North America. Early horses, such as *Hyracotherium* and *Mesohippus*, were rather secretive forest-dwellers, browsers that fed on leaves from bushes and low trees. As the forests retreated and grasslands spread, new horse lineages, such as *Merychippus* and *Hipparion*, stepped out onto the plains and put their hypsodont molars to work (Damuth and Janis, 2011; Mihlbachler *et al.*, 2011). This radiation happened relatively rapidly, about 17–15 Myr ago (early mid-Miocene) in North America and rather later elsewhere, as *Hipparion* migrated into the Old World in the late Miocene (10 Myr ago) and eventually in South America when *Hippidion* entered 3.5 Myr ago during the GABI (see Section 10.6.6).

The classic story of grass = hypsodonty may be a little simplistic: there is a mismatch in timing between the spread of grasslands 26–22 Myr ago in North America and the acquisition of partial hypsodonty in horses and rodents 31–29 Myr ago, and full hypsodonty 17–15 Myr ago. Palaeobotanical evidence does not support the idea of extensive grasslands 31–29 Myr ago, so hypsodonty probably arose as a defence against the ingestion of grit, which inevitably happens when herbivores feed from the ground, as much as a defence against the silica in grasses (Jardine *et al.*, 2012; Strömberg *et al.*, 2013).

In more detail, the evolution of horses, and their close relatives the palaeotheres, show different patterns in different continents. They were both known across the northern hemisphere in the early Eocene: the horses (hyracotheres) diversified in North America and the palaeotheres in Europe, both browsers in the tropical forests that covered the higher latitudes in warmer Eocene times. However, the cooling and drying climatic events in the late Eocene had a devastating effect on these early browsers. The hyracotheres declined and were extinct before the end of the Eocene; and while the palaeotheres became larger and more specialized at this time, they did not survive the Oligocene. Only in North America did horse-like forms survive these climatic changes, with the appearance of the first anchitheriine horse, *Mesohippus*, in the late Eocene of North America. Anchitherines

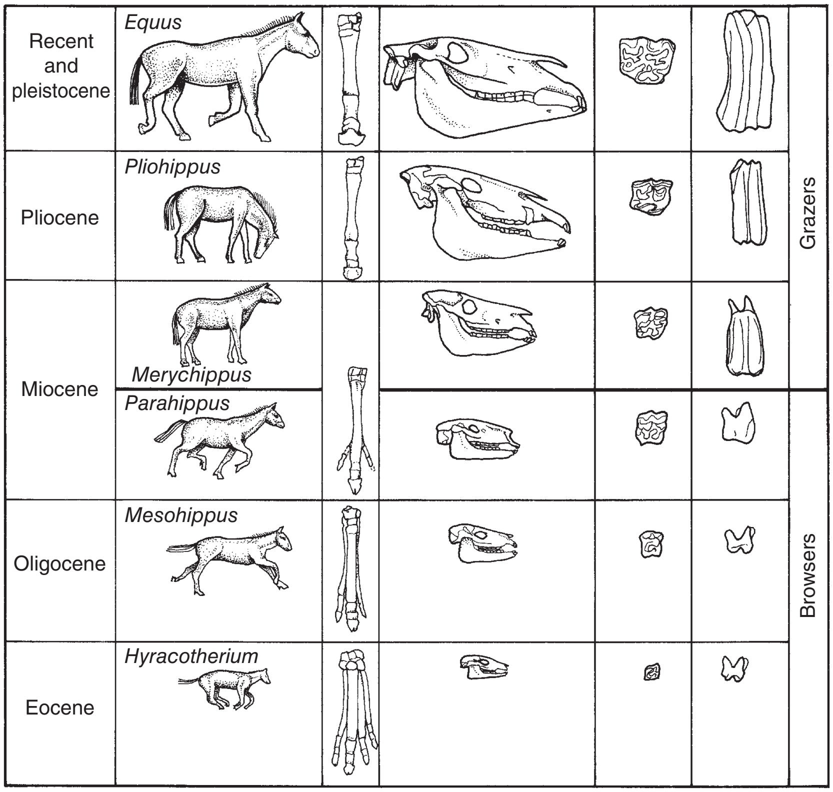


Figure 10.40 Horse evolution: sketches of body form, front limb, skull and upper molar in occlusal and lateral views. The whole-body restorations, skulls and teeth are drawn to scale, and the legs are drawn to a standard length. Note the major changes in the skull and teeth when dietary habits changed from browsing to grazing. Source: Adapted from Savage and Long (1986) and other sources.

had more specialized limbs and teeth than the hyracotheres, and eventually gave rise to the modern types of horses, the equines. All horses found in the Old World after the Oligocene represent immigrations from the subsequent evolution of horses in North America: large, browsing anchitherines in the early Miocene (extinct by the Pliocene); three-toed, hypsodont hipparionines in the late Miocene (extinct in the Pleistocene), and the single-toed, extant genus *Equus* in the Pleistocene. Horse diversity plummeted since the late Miocene, with seven species today, all members of the genus *Equus*, which includes horses, zebras, the ass, donkey, and recently extinct quagga.

10.11.3 Tapirs and rhinoceroses

The other living perissodactyls, the four species of tapirs of Central and South America and south-east Asia, and the five species of rhinoceroses of Africa and India, form a clade Ceratomorpha on the basis of morphology and molecules (Steiner and Ryder, 2011). Early tapirs, such as *Heptodon* from the Eocene of North America (Figure 10.41(a)) probably looked rather like the contemporaneous horses. The tapirs radiated in Eocene times, but became restricted to a single lineage after that (Holbrook, 2001). The main evolutionary change was the development of a proboscis or short trunk (Figure 10.41(b)).

The rhinoceroses had a much more varied history, with a variety of spectacular families, now extinct, in the Oligocene and Miocene of North America and Asia in particular (Prothero, 2005, 2013). The Eocene and Oligocene rhinoceroses, such as *Hyracodon* (Figure 10.41(c)), were moderate-sized hornless running animals, not unlike the early horses and tapirs. *Paraceratherium* (= *Indricotherium* or *Baluchitherium*), the largest land mammal of all time (Figure 10.41(d)), was 5.4 m tall at the shoulder and probably weighed 15 tonnes (the largest elephants today weigh 6.6 tonnes). The horned rhinoceroses radiated widely in the Miocene. A variety of rhinos lived in the Old World during the Pleistocene, including the extinct woolly rhino *Coelodonta* of Europe and Russia.

10.11.4 Brontotheres and chalicotheres

Two other lines of unusual perissodactyls, the brontotheres and the chalicotheres, arose in the Eocene, but are now extinct. The brontotheres, or titanotheres, were often large (Mihlbachler *et al*., 2004). *Brontops* from the late Eocene of North America (Figure 10.42(a)) is a heavily built animal, 2.5 m high at the shoulder and with a horn on its snout like a thickened catapult. The horn was probably covered with skin in life and it may have been a sexual display structure. Brontotheres were browsers and they may also have fed on fruit. They died out at the end of the Eocene, although in Asia some may have survived into the Oligocene.

The chalicotheres, which died out in the Pleistocene, are even odder-looking than the brontotheres (Anquetin *et al*., 2007). *Chalicotherium* (Figure 10.42(b)), looks rather like a cross between a horse and a gorilla! The head is horse-like, but the forelimbs are very long and hindlimbs short. The pelvis is low and broad and it is likely that *Chalicotherium* could stand bipedally and pull down leaves from high branches. The fingers bear small 'hooves' and the toes small claws that may have been useful in digging for roots. It seems that *Chalicotherium* walked with its hands curled up, a kind of knuckle-walking seen elsewhere only in chimps and gorillas.

Brontotheres and chalicotheres were often placed together in a clade, but morphological evidence (Hooker and Dashzeveg, 2004) suggests that brontotheres are a rather deep outgroup to the modern clades (Euperissodactyla), and chalicotheres (together with the Eocene isectolophids (small, North American forms) and lophiodontids (larger, European tapir-like animals), forming the clade Ancylopoda) are sister group to Euperissodactyla.

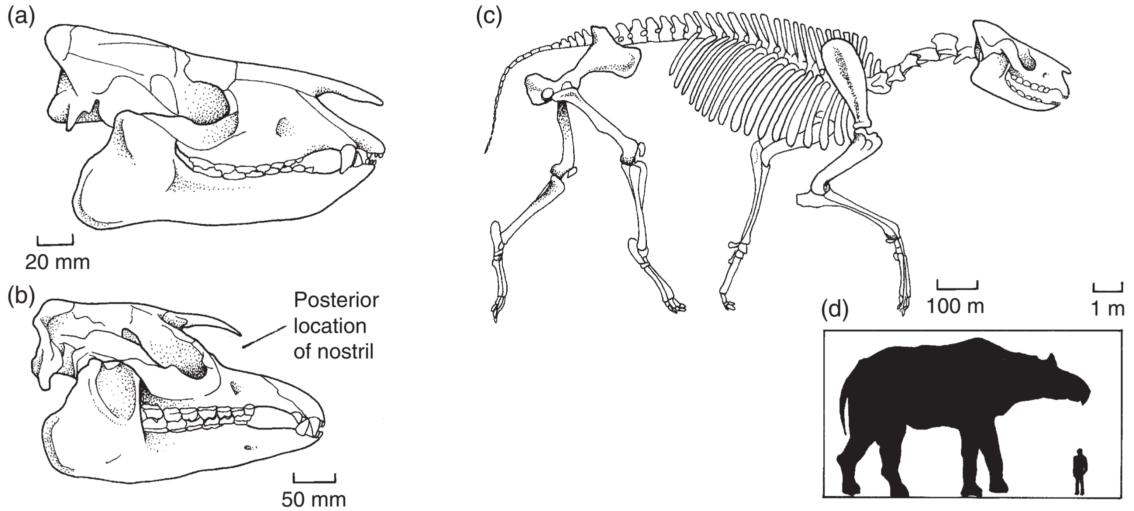


Figure 10.41 Tapirs and rhinoceroses: (a) the Eocene tapir *Heptodon*; (b) the modern *Tapirus*; (c) the Oligocene rhinoceros *Hyracodon*; (d) the giant Oligocene rhinoceros *Paraceratherium* in silhouette, and to scale with a human. Source: (a,b) Adapted from Radinsky (1965). (c) Adapted from Scott (1941). (d) Adapted from Savage and Long (1986).

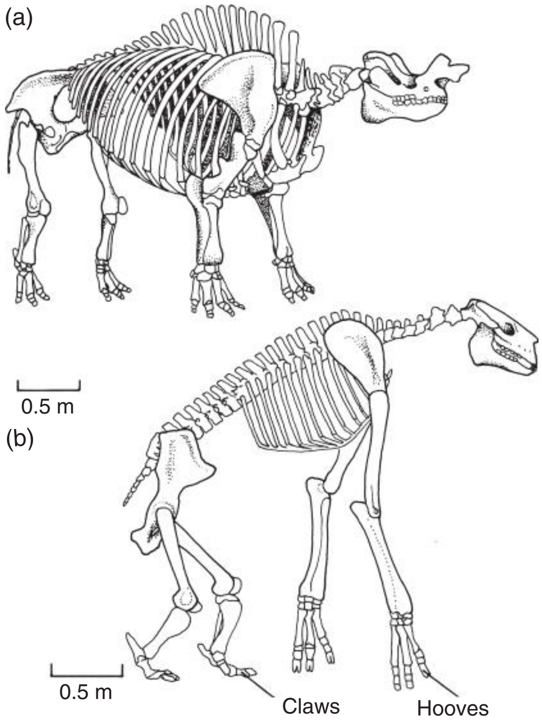


Figure 10.42 Brontotheres and chalicotheres: (a) the late Eocene brontothere *Brontops*; (b) the Miocene chalicothere *Chalicotherium*. Source: (a) Adapted from Woodward (1898). (b) Adapted from Zapfe (1979).

10.11.5 Carnivora: terrestrial carnivores

The 280 species of living meat-eaters, cats, dogs, hyaenas, weasels and seals are members of the clade Carnivora (Goswami and Friscia, 2010). These animals are diagnosed by the possession of a pair of **carnassial** teeth on each side of the jaws: the upper premolar 4 and the lower molar 1 are enlarged as longitudinal blades that shear across each other like a powerful pair of scissor blades (Figure 10.43(a,b)). Certain forms that crush bones, such as hyaenas, have broad premolars with thick enamel and powerful jaw adductors. Extinct bone-crushing dogs had broad molars. The canine teeth are generally long and used in puncturing the skin of prey animals, whereas carnivores use their incisors for grasping and tearing flesh, as well as for grooming.

Modern carnivores are members of a wider clade Carnivoramorpha, whose sister group may be Creodonta, as long suspected (see Section 10.8.3). Basal carnivoramorphans include various extinct clades (Wesley-Hunt and Flynn, 2005; Rose, 2006; Spaulding and Flynn, 2012), including viverravids and miacids from the late Palaeocene and early Eocene. The miacid *Vulpavus* has a long skull (Figure 10.43(c)) and probably hunted small tree-living mammals. Miacids (Solé *et al.*, 2014) were small cat-like tree- and ground-dwellers, with short powerful limbs and plantigrade feet. The auditory region of miacids was presumably covered by connective tissue, without an ossified **auditory bulla**, as in many plesiomorphic mammals of the

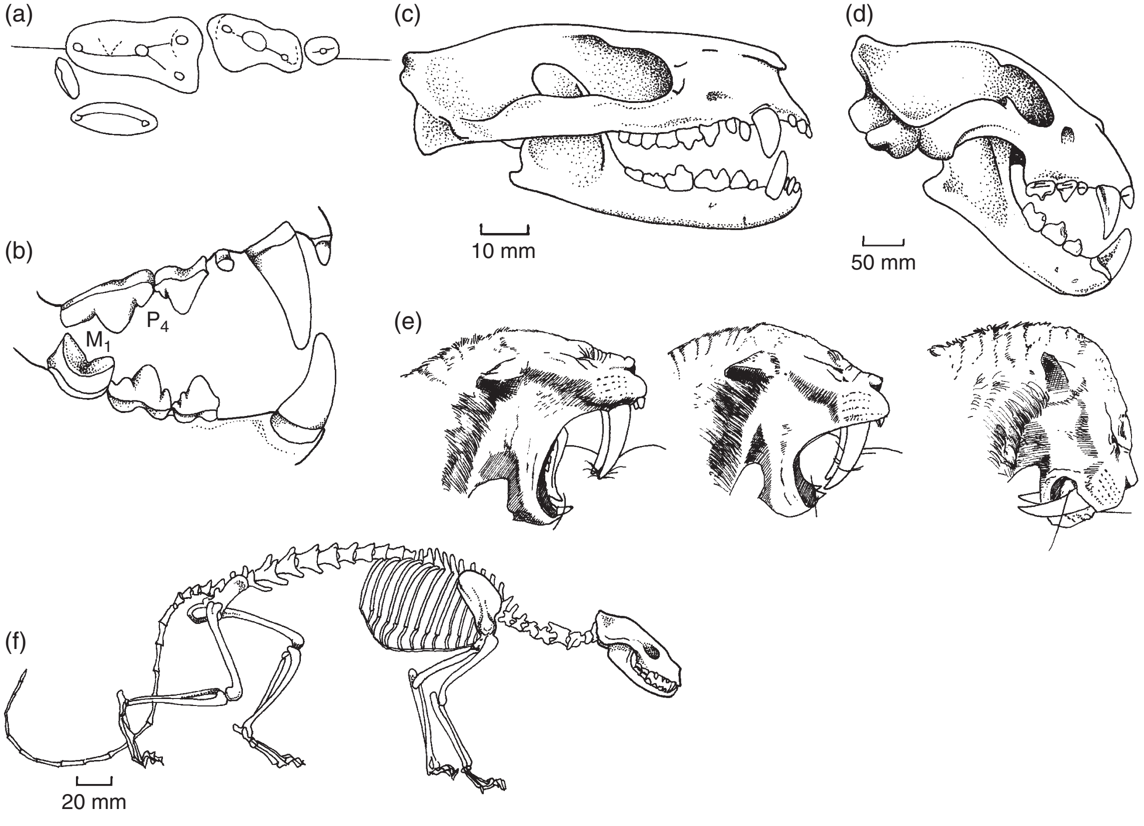


Figure 10.43 Carnivore teeth and jaws: (a,b) teeth of the modern cat *Felis* in occlusal and lateral views, showing the carnassials (upper premolar 4 (P^4) and lower molar 1 (M_1)); (c) skull of the Eocene miacid *Vulpavus*; (d) the modern tiger *Panthera*; (e) piercing and tearing flesh by the Pleistocene sabre-tooth *Smilodon*; (f) the late Eocene dog *Hesperocyon*. Source: (a,b,d) Adapted from Savage and Long (1986). (c,f) Adapted from Gregory (1951). (e) Adapted from Akersten (1985).

Palaeocene and Eocene. The nimravids, from the Eocene to Miocene of Europe, Asia, Africa and North America (Peigné, 2003), were extremely cat-like in form and generally have sabre teeth.

Modern carnivores began to diverge in the late Eocene and early Oligocene (Rose, 2006; Agnarsson *et al.*, 2010; Spaulding and Flynn, 2012). Their auditory bulla has become ossified, but in two different ways, and these define two major lines of carnivore evolution. In Feliformia, a main component of the auditory bulla is the ectotympanic, the bony ring that plesiomorphically supported the ear drum (see Box 10.2). In Caniformia, the auditory bulla is formed mainly from **entotympanics**, new bony structures. In addition, feliforms have intrabullar septa, which caniforms lack.

Feliformia includes cats, civets, mongooses, and hyaenas. Civets (Viverridae) date back to the late Eocene, and mongooses (Herpestidae) to the late Oligocene. They are abundant today in tropical Africa and Asia and feed on a mixed diet of insects, small vertebrates and fruit. Early viverrids are close to the ancestry of hyaenas (Hyaenidae), which arose in the Miocene, and cats (Felidae) in the early Oligocene. The evolutionary history of cats is characterized by two major episodes of morphological divergence, one marking the separation between sabre-toothed and conical-toothed cats, including all modern forms, in the early Miocene, the other marking the split between large and small-medium conical-toothed cats, in the middle to late Miocene (Sakamoto and Ruta, 2012). An astonishing cat mimic can be found in the fossa (*Cryptoprocta*) of Madagascar, which is actually a type of viverrid.

During the evolution of the nimravids and sabre-toothed cats, scimitar-like and sabre teeth arose independently several times (Turner and Anton, 1997; Naples *et al.*, 2011; Sakamoto and Ruta, 2012; Christiansen, 2013), and most of the extinct forms have larger canines than in modern lions and tigers (Figure 10.43(d,e)). The sabre-toothed cats of North America and Europe are similar to the unrelated marsupial sabre-tooths of South America (see Box 10.6), which share specific predatory adaptations: the lower jaw can be dropped very low; the sabre, up to 150 mm long, has a backwards curve; and it is flattened like a knife blade, rather than being round.

The most famous sabre-toothed cat, *Smilodon*, fed on the carcasses of elephants and other large herbivores in the Pleistocene. It probably used its sabres for cutting out chunks of flesh from its prey, rather than stabbing (Akersten, 1985). *Smilodon* attacked a vulnerable young elephant, say, by sinking its teeth in superficially, closing the jaws and levering a chunk of flesh off using its powerful neck muscles (Figure 10.43(e)). The prey was left to bleed to death. The jaws were powered as much by the jaw adductors, as in modern cats, as by the massively reinforced neck muscles (Wroe *et al.*, 2013a). Huge collections of *Smilodon* and other large carnivores, such as coyote, dire wolf, American lion, bobcat, puma and lynx, have been found in the Rancho La Brea tar pits in California, USA. It has been debated whether times were getting tougher for sabre tooths through the Pleistocene. Binder and Van Valkenburgh (2010) note that *Smilodon* show significantly more broken teeth than in living large carnivores, which could indicate that they were competing more actively for prey. However, there is no evidence that sabre tooths increased the utilization of carcasses by scraping at bones or otherwise changing their feeding modes towards the end of the late Pleistocene (DeSantis *et al.*, 2012). Nonetheless, when the abundant larger prey animals died out at the end of the Pleistocene, the sabre tooths also disappeared.

The second carnivore group, Caniformia, includes the dogs (Canidae) and the arctoids, the bears, raccoons, weasels and seals (Delisle and Strobeck, 2005). Skunks were once included with the weasels in the Mustelidae, and the red panda with the racoons in the Procyonidae, but are now placed in their own separate families, respectively. The caniforms are largely a North American and European radiation, while the feliforms are more predominant in Africa and Asia. Cats, dogs, procyonids and otters (mustelids) have all had a rapid and successful radiation in South America following the GABI.

Like camels and horses, dogs were largely a North American radiation through their history. A typical early dog, *Hesperocyon* (Figure 10.43(f)), has long limbs and digitigrade feet (only the toes touch the ground), but it was probably not a fast runner. Dogs of the modern Caninae did not become the dominant predators until the Plio-Pleistocene. The extinct Miocene Borophaginae included large, hyaena-like forms with bone-crushing teeth. Members of the Caninae first appeared in the Old World at the end of the Miocene and, perhaps not coincidentally, the more dog-like of the hyaenas disappeared at the same time. Dogs today include many domesticated breeds, whose history is still contentious (see Box 10.10).

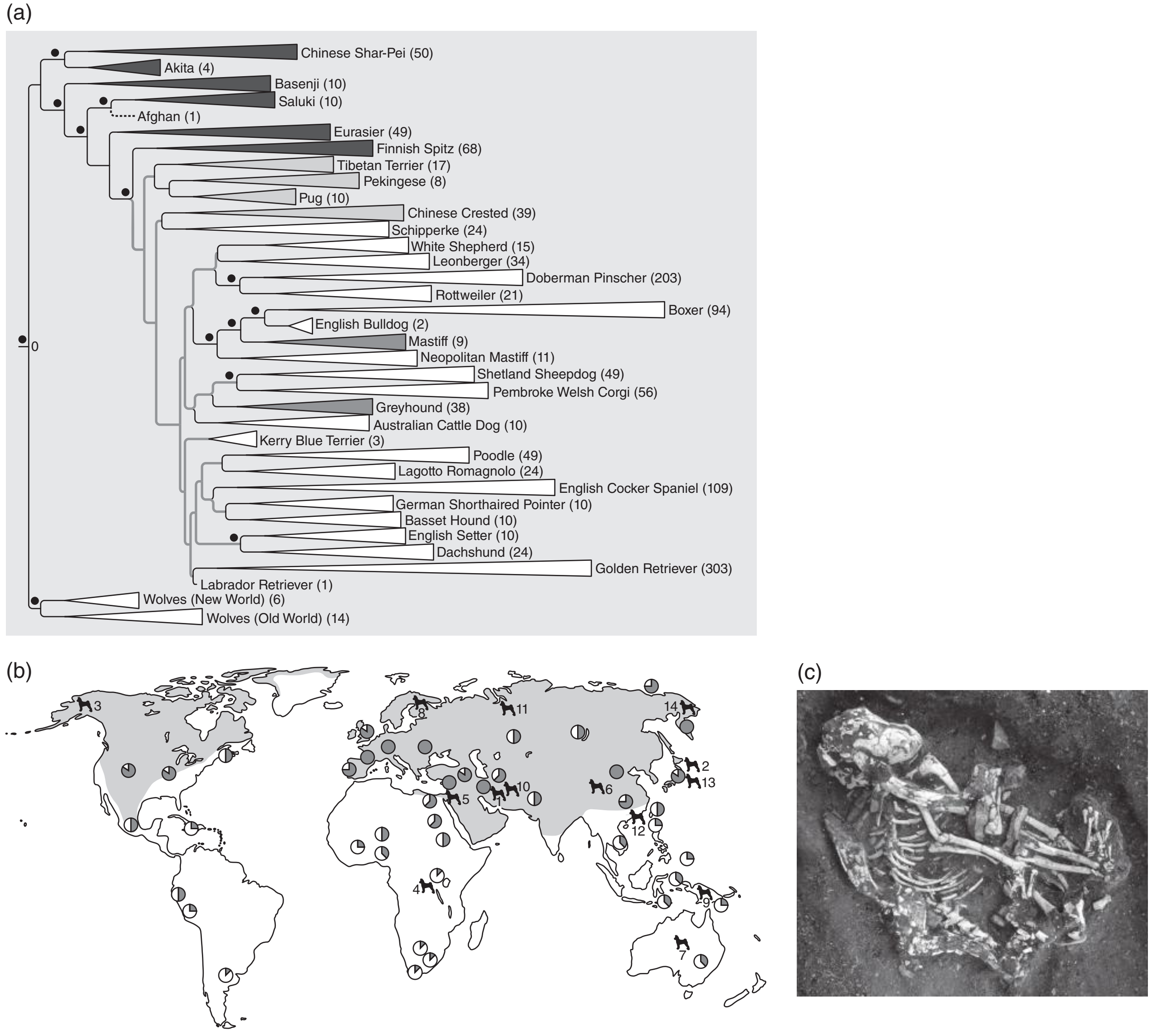
BOX 10.10 DOGS: DOMESTICATED WOLVES, OR WHAT?

Dogs are probably the most popular pets worldwide, and yet the timing and nature of their domestication are uncertain. Also, the reasons for their amazing range of sizes and forms, especially when compared to cats, are mysterious. Everyone since Charles Darwin has considered these questions; indeed, Darwin argued that because modern dogs show such a vast range of breeds, they must stem from a number of ancestors. One thing is for sure: all domesticated dogs had a single ancestor, and this was the grey wolf, *Canis lupus*.

Archaeological evidence shows that dogs were domesticated before settled agriculture emerged, but it becomes harder and harder to distinguish wolves from dogs in ancient archaeological sites because the unique characters of the teeth, skull, and skeleton seen in domesticated breeds had not yet appeared. It is likely that the first canids to associate with humans were wolves and foxes foraging for waste food. There are claims for very early domestication of dogs from sites in Belgium the Czech Republic, and south-western Siberia, with some examples as old as 33,000 years ago. However, the first widely convincing archaeological evidence (illustration (c)) comes from sites dated at about 14,000 years ago in the Levant, Cyprus, Iraq, northern China, and the Kamchatka Peninsula in the far west of Russia (Larson *et al*., 2012).

Early genomic studies of dogs sometimes pointed to origins over 100,000 years ago, completely out of the range suggested by archaeology. However, more recent studies, using more appropriate calibration methods, have found dates more in line with the archaeological sites, fcusing on the time range from 11-16,000 years ago (Freedman *et al*., 2014). However, the story is not as simple as might have been hoped. In one of the largest studies to date, Larson *et al*. (2012) analysed genomic data on 121 dog breeds, as well as New World and Old World wolves. They identified 14 'ancient breeds' that branched early (illustration (a)). However, they show that this is not a helpful concept, as none of these supposedly 'ancient breeds' came from regions where the oldest archaeological remains have been found (illustration (b)). Indeed, three (Basenjis, Dingoes, and New Guinea Singing Dogs) come from regions outside the natural range of *Canis lupus*, and only the Finnish Spitz and Israeli Canaan Dog occur in areas (Europe, Middle East) that have yielded ancient examples of canine domestication.

A study such as this is made complex by the amount of human movement around the world in the past 10,000 years. Migrations of humans and their pets have led to considerable interbreeding of the dogs, and added complexity to determining their phylogeny. Perhaps the so-called 'ancient' forms are simply those that have been isolated and have not interbred with other dogs, and so they may not reliably indicate ancestral forms (Larson *et al*., 2012). Most dog breeds have been created in the past 150 years by intensive breeding programmes, but establishing their deeper phylogeny requires much more genomic data and analysis.



Evolution of the domestic dog: (a) Phylogenetic tree of domestic dogs, and two wolf populations as outgroups. The analysis shows 35 dog breeds (and sample sizes), and robust nodes are marked by black dots. The so-called 'ancient breeds' are given first, from Chinese Shar-Pei to Finnish Spitz. Some of the relationships reflect known interbreeding recently, and conceal aspects of the deeper phylogeny. (b) World map showing the maximum range of grey wolves (grey shading), together with archaeological sites of domestic dogs (circles, with infill representing age, in 1500-year segments), and dog symbols indicate the eight 'ancestral breeds'. (c) An excavated domestic dog, from Skateholm, Sweden, dating to 7000 years ago, one of the oldest from Europe. Source: (a,b) G. Larson, Durham University, Durham, UK. Reproduced with permission. (c) L. Larson, Lund University, Lund, Sweden. Reproduced with permission.

The weasels (Mustelidae) and raccoons (Procyonidae) are known first from the early Miocene and late Oligocene respectively. The amphicyonids, extinct medium- to very large dog-like animals, are best known from the late Eocene to late Miocene of North America, with representatives also in Africa and Eurasia. The bears (Ursidae) arose in the late Eocene and they were particularly successful in the northern hemisphere. Early forms were rather dog-like. The large extinct Pleistocene cave bear of Europe is known from extensive remains in the caves it used as a refuge from the icy plains over which it hunted. The most unusual bear, the giant panda, has adapted to survive on bamboo shoots, and it lives a slow, but highly endangeredlife in western China (Lindburg and Baragona, 2004).

10.11.6 Pinnipedia: aquatic carnivores

Seals, sealions and walrus (Pinnipedia) form a part of the arctoid clade within Caniformia (see Section 10.11.5), but they are considered separately here because of their unique aquatic adaptations (Berta, 2012). All the evidence suggests Pinnipedia is a clade, and adapted to the water once, perhaps in the Oligocene.

The oldest pinnipeds include two extinct families, the enaliarctids and the desmatophocids. *Enaliarctos* (Figure 10.44(a–c)) from the late Oligocene and early Miocene of California retains some features of its terrestrial bear-like ancestors, such as distinctive carnassial teeth (Berta *et al*., 1989). The teeth are somewhat simplified, and *Enaliarctos* has flippers with shortened limb bones and elongated digits, although the bones are not so flattened as in later pinnipeds. It was the size of a modern harbour seal, about 1.5 m long. *Allodesmus* (Figure 10.44(d)), a desmatophocid, also from the early Miocene of California is seal-like in many respects. It is 2 m long, has broad paddle-like flippers, a very reduced tail, large eyes and possibly some ability to detect the direction of sound underwater.

It has been hard to determine from modern taxa whether the arctoid ancestor of pinnipeds was bear-like or weasel-like. *Puijila*, an early Miocene enaliarctid from Arctic Canada (Rybczynski *et al*., 2009), shows some superficial similarities to modern otters, so suggesting a possible ecological sequence of pinniped ancestry, and alliance with musteloids rather than ursids.

The 34–36 species of modern pinnipeds are divided into three families (Arnason *et al*., 2006; Dasmahapatra *et al*., 2010; Berta, 2012), the Otariidae (fur seals and sealions), Odobenidae (walruses) and Phocidae (seals). These groups arose in the early and mid-Miocene. *Thalassoleon*, an early sea lion (Figure 10.44(e)), has **homodont** teeth (undifferentiated single-cusped cheek teeth) and large orbits. Initially, the otariids and odobenids were essentially Pacific forms, and the phocids lived mainly in the Atlantic and Mediterranean area. With climatic deterioration during the Pliocene and Pleistocene, all three families extended their ranges, and the seals acquired their modern worldwide distribution.

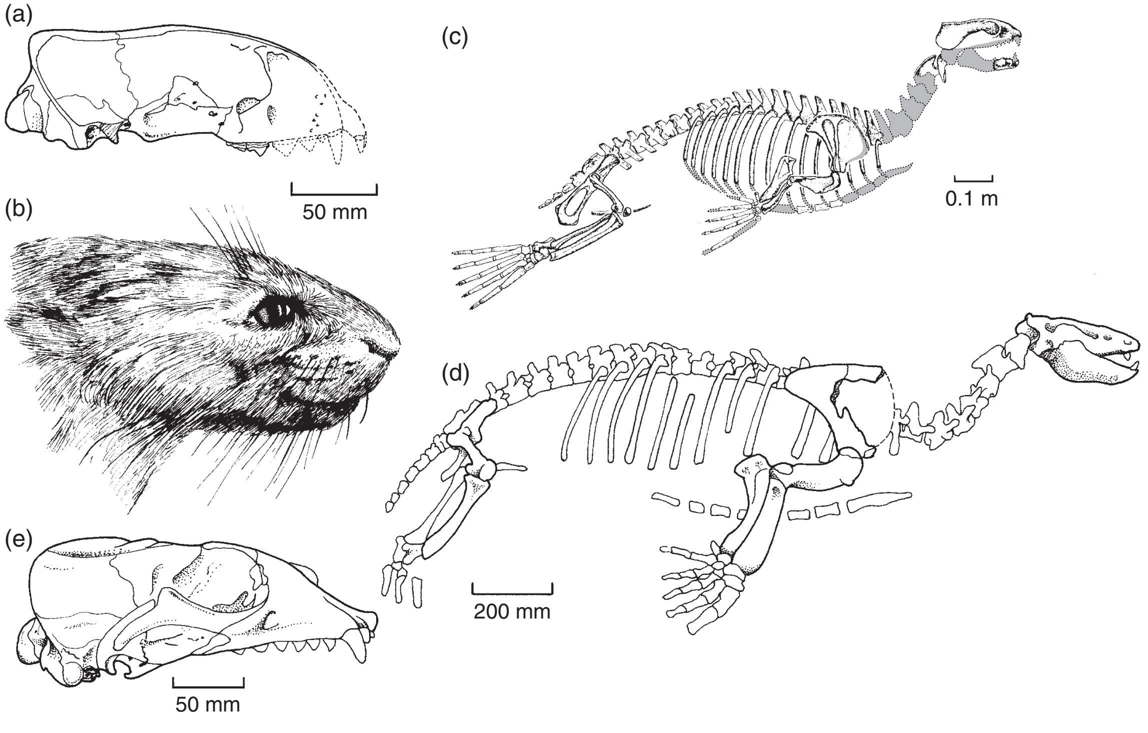


Figure 10.44 Fossil pinnipeds: (a–c) skull, restored head and skeleton of the late Oligocene and early Miocene enaliarctid *Enaliarctos*; (d) skeleton of the early Miocene desmatophocid *Allodesmus*; (e) skull of the late Miocene sealion *Thalassoleon*. Source: (a,b) Adapted from Mitchell and Tedford (1973). (c) A. Berta, San Diego State University, San Diego, CA, USA. Reproduced with permission. (d) Adapted from Mitchell (1975). (e) Adapted from Repenning and Tedford (1977).

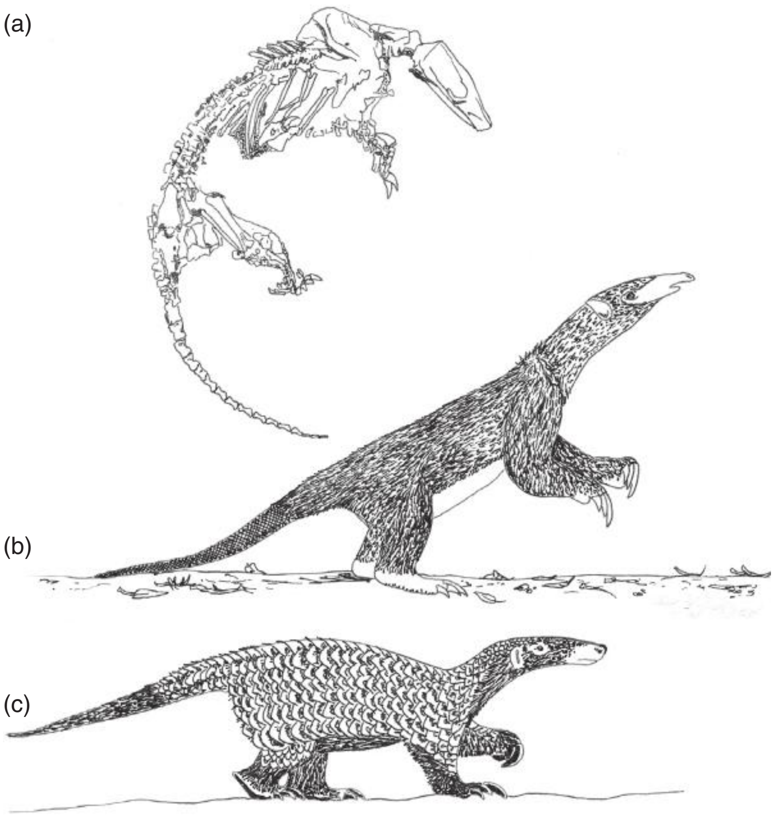


Figure 10.45 The oldest pangolins, from the early Eocene Messel locality in Germany: (a,b) *Eurotamandua*, original skeleton (a) and restoration (b); (c) *Eomanis*, in life mode. Source: D. Naish, University of Southampton, Southampton, UK. Reproduced with permission.

10.11.7 Pholidota: odd ant-eaters

The pangolins, Pholidota, are ant-eaters and not very obvious relatives of the Carnivora. Indeed, systematists have wrestled with pangolins for two centuries: they have been placed as relatives of pantolestans and creodonts, but were generally paired with Xenarthra, partly because of their toothlessness and general resemblance to ant-eaters and armadillos. Their position as allies of Carnivora and within Laurasiatheria has been repeatedly confirmed (see Box 10.5).

Pangolins have a skull that is reduced to a tubular structure with a narrow lower jaw and no teeth. The tongue is immensely long, longer than the head, and can be shot out and looped round corners to extract ants from obscure locations. Pangolins are heavily armoured with broad overlapping 'scales' and they resemble nothing so much as animated globe artichokes. The eight extant species of pangolins live in Africa and south-east Asia, but their ancestry has been surprisingly disputed.

The modern Pholidota are part of a wider clade Pholidotamorpha (Gaudin *et al*., 2009; Rose, 2012) that includes the extinct palaenodonts, known mainly from the early Palaeocene to early Oligocene of North America. These were prairie-dog-sized animals with powerful digging claews on their hands, and appear to have burrowed actively (Rose, 2006). The first fossil pangolins come, surprisingly, from the early Eocene of Messel (see Box 10.8), the genera *Eomanis*, *Euromanis*, and *Eurotamandua*. These are surprisingly modern-looking forms (Figure 10.45), with tubular-shaped heads, toothless jaws, and massive claws for digging into ant and termite mounds. *Eurotamndua* (Figure 10.45(a,b)) had stiff hair, whereas *Eomanis* already had the keratinous scale-like structures seen in modern pangolins.

10.12 GLIRES: RODENTS, RABBITS AND RELATIVES

The Euarchontoglires is the second major subclade of Laurasiatheria, and includes Glier and Archonta (see Box 10.6). The Glires, comprising rodents and rabbits share numerous derived characters of the skull and dentition, such as the large open-rooted incisor teeth.

The success of the rodents is legendary. They are a diverse and widespread order of mammals with just over 2250 living species (over 40% of all living mammals). Their adaptability seems to know no bounds, as can be seen from the way in which mice, rats and squirrels have modified their behaviour in order to exploit and annoy humans. However, with a few notable exceptions, such as the capybara today, and a handful of extinct forms, rodents remain as small mammals. Rodents are diagnosed by their extaordinary teeth and jaws, which formed the basis of their rapid evolutionary radiation.

10.12.1 Rodent teeth and jaws

Rodents have deep-rooted incisor teeth, one pair in the upper jaw and one in the lower, which grow continuously throughout life, an unusual feature among mammals. In cross-section a typical rodent skull (Figure 10.46(a)) seems to be largely occupied by the deep open roots of the incisors that curve back round the snout region and fill up most of the lower jaw. The incisors are used to gnaw wood, nuts, husks of fruit and so on. They are triangular in cross-section and bear enamel only on the front face, so that the dentine behind wears faster and gives a sharp enamel cutting edge. Behind the incisors is a long diastema, a gap representing the missing second and third incisors and a canine, followed by at most a single premolar and three molars. In many forms the molars are hypsodont (high crowned) or hypselodont (ever-growing).

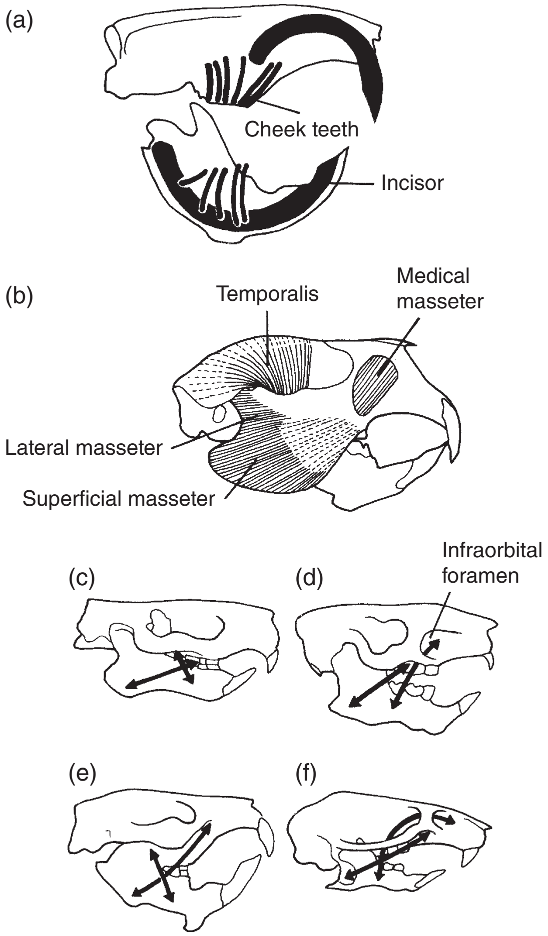


Figure 10.46 Rodent teeth and jaw muscles: (a) cross-section of a beaver skull showing the deeply rooted cheek teeth and ever-growing incisors in black; (b) main jaw muscles of the living porcupine *Erethizon*, showing the temporalis muscle and the masseter muscle, which falls into three main portions; (c–f) the main lines of action of the segments of the masseter muscle in rodents with the (c) protrogomorph, (d) hystricomorph, (e) sciuromorph and (f) myomorph patterns; in the last three, the medial masseter invades further and further forwards on the side of the snout. Source: Adapted from various sources.

The main jaw actions of rodents are **proal**, that is, the lower jaw may be protruded for gnawing, and the cutting action is from back to front. Forward movements are produced by the pterygoideus muscle, which runs from the palate to the inside of the jaw and the masseter muscle, whose main portions originate generally in the snout area and run back to the outside of the lower jaw (Figure 10.46(b)). The strength and effectiveness of the propalinal movements depends on the size and angle of the masseter muscle in particular. Four patterns occur in rodents (Figure 10.46(c–f)).

1 **Protrogomorph**, seen in early forms, in which the middle and deep layers of the masseter attach to the zygomatic arch.
2 **Hystricomorph**, seen in porcupines and the South American caviomorphs, in which the deep masseter passes through the infraorbital foramen to attach to the side of the snout in front of the eye.
3 **Sciuromorph**, seen in squirrels and others, in which the middle masseter attaches in front of the eye.
4 **Myomorph**, seen in rats and mice, in which the middle masseter is attached in front of the eye (as in sciuromorph) and the deep masseter passes up into the orbital area and through the infraorbital foramen.

The four muscle patterns appear to have arisen independently several times and (except for myomorphs) they do not characterize unique monophyletic groups. Analysis of bones and jaw muscles using finite element analysis (Cox *et al.*, 2012) suggests that the three derived jaw modes among modern rodents arose in line with particular feeding specializations: guinea pigs (hystricomorphs) specialize as chewers, squirrels (sciuromorphs) as gnawers, and rats (myomorphs) as high-performance generalists, which helps explain their overwhelming success as a group.

10.12.2 Rodent evolution

Equipped with their ever-growing incisors and powerful low-angle masseters, the rodents have chewed their way through wood, tough plant fibres and nuts for the past 60 Myr. The first rodents, the ischyromyids of the late Palaeocene and Eocene of North America and Eurasia, such as *Paramys* (Figure 10.47(a)), show plesiomorphic characters in the protrogomorph jaw muscle pattern and in the teeth. The cheek teeth (Figure 10.47(b)) still have mound-like cusps instead of the ridges of some later rodents (Figure 10.47(c)) and the last molar is not fully part of the grinding dental battery.

The oddest rodents were the mylagaulids of the Miocene of the Great Basin, USA (Calede and Hopkins, 2012). *Epigaulus* (Figure 10.47(d)) has broad paddle-like hands with long claws, used in digging, and small eyes, so it probably lived underground in burrows. It has a pair of small horns on the snout just in front of the eyes, whose function is a mystery, unless they were used in pre-mating fights; not all specimens have the horns, so they may have been restricted to males only. Alternatively, the horns might have been used for digging.

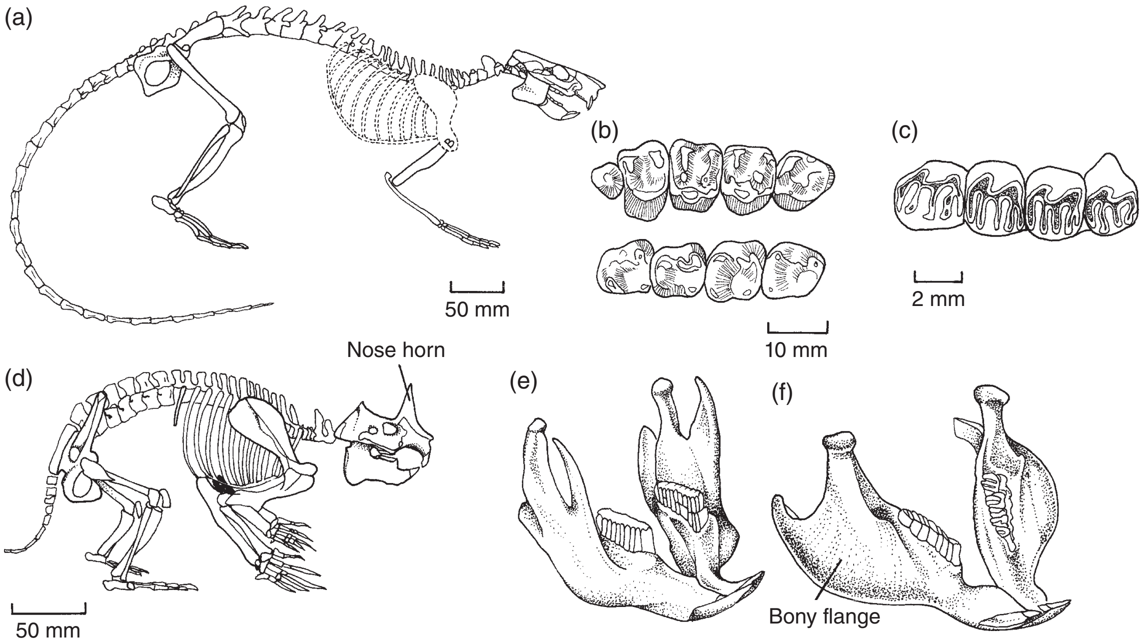


Figure 10.47 Early rodents: (a, b) the early Eocene ischyromyid *Paramys*, skeleton and cheek teeth from the upper (top) and lower (bottom) jaws, seen in occlusal view; (c) upper cheek teeth of the modern mouse *Theridomys* in occlusal view; (d) the horned Miocene mylagaulid *Epigaulus*; (e) the sciurognathous lower jaw with vertical sides; (f) the hystricognathous jaw, with a deflected horizontal bony flange. Source: (a,b) Adapted from Wood (1962). (c,e,f) Adapted from Savage and Long (1986). (d) Adapted from Osborn (1910).

Paramys, and most other Eocene rodents, have the plesiomorphic rodent jaw arrangement in which the area of attachment of the masseter muscle on the dentary is a vertical surface in the same plane as the incisor tooth. This is the **sciurognathous** jaw pattern (Figure 10.47(e)). A second pattern is seen in porcupines and the South American rodents (caviomorphs) in which the masseter insertion is deflected outwards, the **hystricognathous** (Figure 10.47(f)) condition, which arose once only in the South American clade.

Rodent phylogeny has been much discussed and there has been a broad range of viewpoints. Most current analyses (Blanga-Kanfi *et al.*, 2009; Churakov *et al.*, 2010; Fabre *et al.*, 2012) find three clades.

1 **Squirrel-related clade**, comprising squirrels (Sciuridae) and dormice (Gliridae).

2 **Mouse-related clade**, comprising mice, rats, hamsters, and gerbils (Myoidea), jumping mice and jerboas (Dipodoidea), scaly-tailed flying squirrels and springhare (Anomaluromorpha), beavers (Castoridae), pocket gophers (Geomyidae), and kangaroo rats (Heteromyidae).

3 **Ctenohystrica**, comprising gundis (Ctenodactylidae) and hystricognathous groups, including Old World porcupines (Hystricidae), African dassies, cane rats and relatives (Phiomorpha), and the South American cavies and guinea pigs (Caviomorpha).

In the first clade, the oldest squirrels are from the early Eocene, and they diversified from the Miocene onwards.

The mouse-related clade is by far the largest today. It arose in the early Eocene and diversified dramatically from the Miocene onwards. Among these mouse-like forms, beavers today are noted for their dam-building and tree-felling activities. This is seen also in some fossil forms. Large helical burrows named *Daimonelix* have been known for some time from the Oligocene and Miocene of Nebraska, USA. They extend to 2.5 m deep and have an upper entrance pit, a middle vertical spiral and a lower living chamber (Figure 10.48(a)). The burrow diameter is constant and the helix may be dextral or sinistral in the same locality. These burrows have been ascribed to *Palaeocastor* (Figure 10.48(b)), an early beaver, on the basis of complete and incomplete skeletons found in the living chamber (Martin and Bennett, 1977).

Among other mouse relatives, eomyids were important forms in the middle Eocene to Pleistocene of Europe, Asia and North America (Korth, 1994; Rose, 2006). Fossils from the oil shales of the Oligocene locality Enspel in Germany include perfectly preserved examples of *Eomys* with skin and hair, and these show that it was a glider (Figure 10.48(c)) with a narrow skin membrane along the side of the body and between the hindlegs (Storch *et al.*, 1996). This is not the only gliding rodent group: others include certain modern squirrels (Sciuridae), scaly-tailed flying squirrels (Anomaluridae) and dormice (Gliridae). But for its exceptional preservation, there would have been little clue that *Eomys* was a glider too.

Most of the later myomorph radiation consisted of mice and rats, the Family Muridae, which rose from its origins in the Eocene to over 700 living species. Much of the dramatic radiation of murids happened in the Pleistocene. Detailed studies of their superb fossil record have shown high rates of evolution: 217 species and subspecies of *Microtus* in North America in the past 1.5 Myr, 180 species of cricetines (voles) in South America in the past 3.5 Myr, over 100 species of murines in Africa during the past 10.5 Myr (Korth, 1994). These dramatic evolutionary rates are confirmed by molecular studies.

Members of the third rodent clade, the Ctenohystrica, all show the hysrtricognathous jaw condition (Figure 10.47(f)), and they diversified in southern continents, with Ctenodactylidae, Phiomorpha, and Hystricidae radiating initially in Africa. The early porcupine, *Sivacanthion* (Figure 10.48(d)) from the mid-Miocene, is unusual in that it occurs outside Africa, in Pakistan. The largest ctenohystrican clade is the Caviomorpha, the South American guinea pigs, capybaras, chinchillas and New World porcupines. The largest living caviomorph, the capybara, weighs 50 kg and fills an ecological niche more akin to a warthog than a rat or squirrel. But it is a midget compared with some of the giant caviomorphs of the past. *Telicomys* from the late Miocene and Pliocene (Figure 10.48(e)) reached the size of a small rhinoceros and

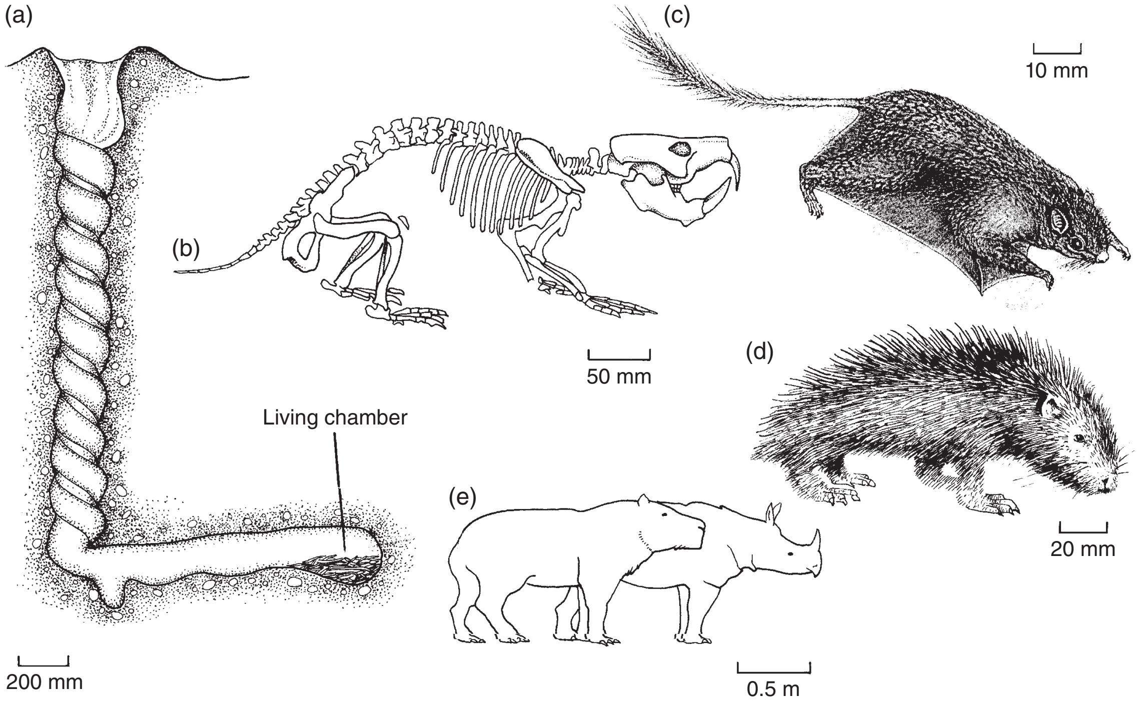


Figure 10.48 Diverse rodents: (a) spiral burrows, termed *Daimonelix*, made by (b) the Miocene beaver *Palaeocastor*; (c) restoration of the Oligocene gliding myomorph *Eomys*; (d) restoration of the Miocene porcupine *Sivacanthion*; (e) relative size of the giant caviomorph *Telicomys* and a small rhinoceros. Source: (a) Adapted from Martin and Bennett (1977). (b) Adapted from Zittel (1925). (c) Adapted from Storch *et al.* (1996). (d,e) Adapted from Savage and Long (1986).

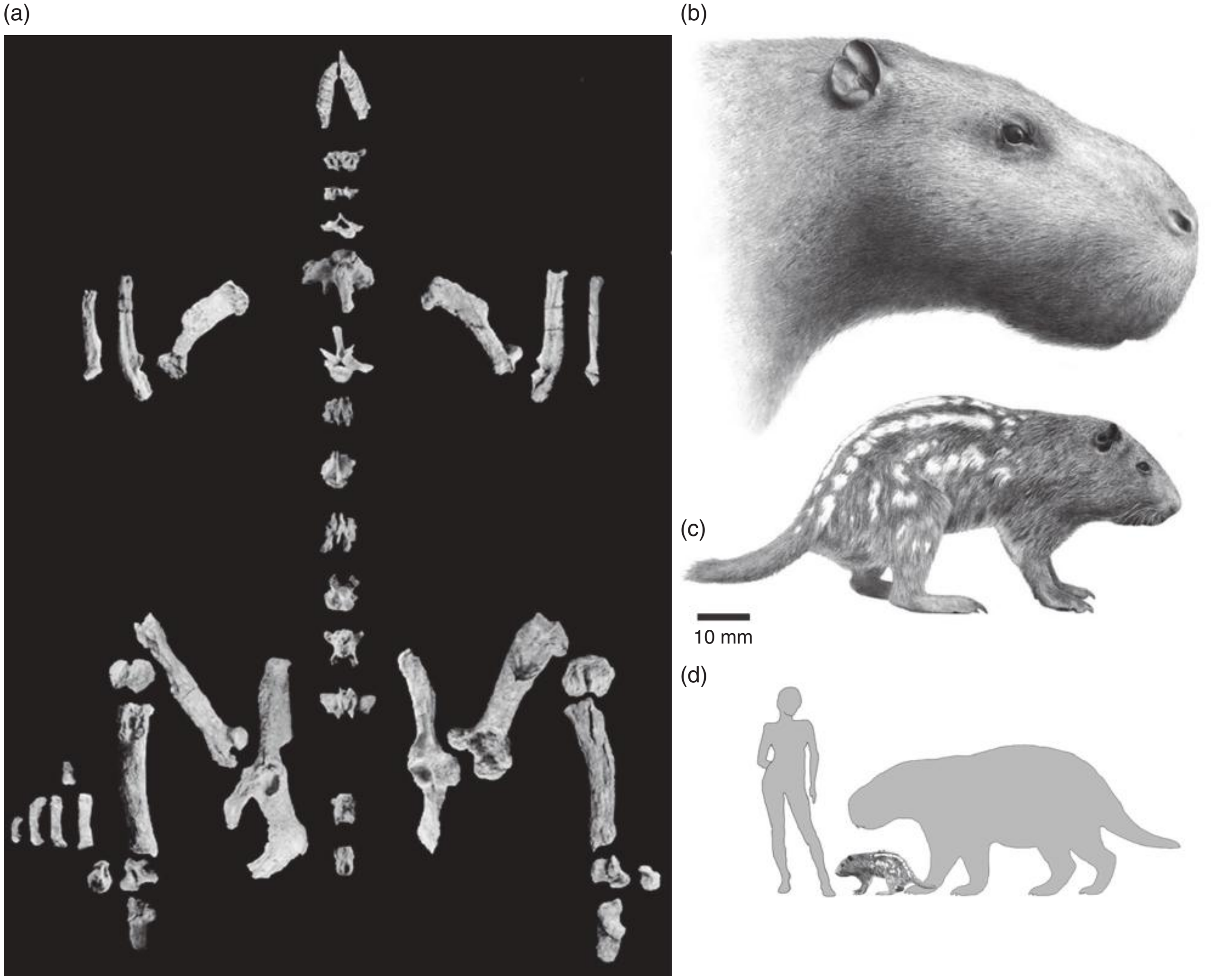
BOX 10.11 WILL THE LARGEST RODENT PLEASE STAND UP?

South America has become well known for its giant rodents, but which one was really the largest? Palaeontologists love to report the oldest, latest, largest, or smallest, and yet when it comes to body sizes, lengths may be reliable, but estimated body masses less so. When Sánchez-Villagra *et al.* (2003) reported a new complete specimen of *Phoberomys*, this seemed to beat all comers. Their specimen (illustration (a)) came from a rich locality of fossil vertebrates in the Late Miocene of Venezuela. *Phoberomys* was 3 m long and it stood 1.3 m at the shoulder. It weighed an estimated 700 kg, more than ten times the mass of the largest living rodent, the capybara, and 700 times the mass of a guinea pig. At the time of discovery, it was said that ‘if you saw it in the distance on a misty day, it would look much more like a buffalo than a rodent’.

Then, five years later, Rinderknecht and Blanco (2008) trumped the 700 kg *Phoberomys* with the 1000 kg (yes, 1 tonne) *Josephoartigasia*, known only from its huge skull, over half a metre in length, from the late Pliocene or early Pleistocene of Uruguay (illustrations (b–d)). The body mass was estimated by comparison with living South American rodents, and various measurements of the skull. Relative proportions of various measures of skull width and length indicate body masses in the range 468–2586 kg, and a mean of 1211 kg.

Estimating body mass is tricky, especially when the animal is so much larger than living relatives. Investigators look for a correlation of some measure (e.g. skull length, femur width) in living forms with body mass, and then fit the fossil onto the line. In criticizing these rodent size estimates, Millien and Bovy (2010) used different correlations, and recalculated *Phoberomys* as having weighed perhaps 220–280 kg, and *Jospheoartigasia* as perhaps 350 kg. At present, it is not clear which weight estimates, low or high, are nearer the truth.

Phoberomys and *Josephoartigasia* were probably semi-aquatic, like the capybara, and foraged for reeds and other tough aquatic plants along the river bed. Both these rodent giants lived in a lush, warm habitat, in rivers that teemed with crocodiles, catfish and enormous turtles. With their vast bulk and shortish forelimbs, these giant rodents probably could not move very fast. Predators included crocodiles up to 10 m long, the flesh-eating flightless bird *Phorusrhacos* (see Box 9.7) and large marsupial 'cats' (see Box 9.6). Probably neither *Josephoartigasia* nor *Phoberomys* could flee from these predators, nor could they squeeze into a small hole in the river bank. This vulnerability to predation, together with cooling climates in the late Miocene, may have contributed to the demise of the truly giant South American rodents.



Skeletons of giant, and even more giant, rodents: (a) *Phoberomys*, showing the skull and major bones of the skeleton laid out; (b) *Josephoartigasia* reconstructed head, by G. Lecuona; (c) the living pacarana, *Dinomys branickii*; (d) human, *Josephoartigasia*, and pacarana, to scale. Source: (a) M. Sánchez-Villagra, ETH, Zürich, Switzerland. Reproduced with permission. (b–d) A. Rinderknecht, Museo Nacional de Historia Natural, Montevideo, Uruguay. Reproduced with permission.

even that has been exceeded by *Phoberomys* from Venezuela (see Box 10.11).

The origin of South American rodents has been disputed, and they might have migrated in from Africa or from North America. Phylogenetic results have always pointed to an origin from Africa, because of the close relationships between Caviomorpha and Phiomorpha. Fossil evidence of the oldest South American caviomorphs in the middle Eocene of Peru

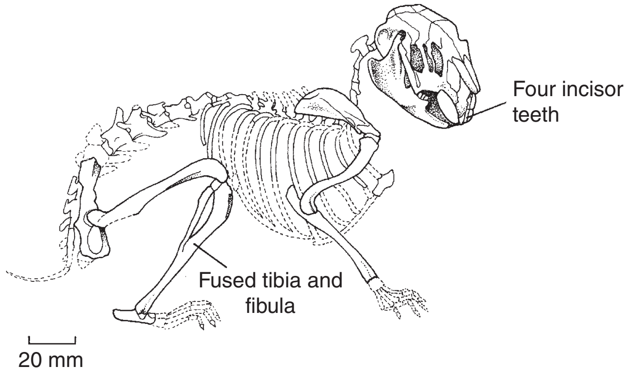


Figure 10.49 The Oligocene rabbit *Palaeolagus*. Source: Adapted from Wood (1957).

confirm the links to Africa, and suggest that rodents hopped and squeaked their way across from Africa at the time of the middle Eocene climatic optimum (Antoine *et al.*, 2012).

10.12.3 Lagomorpha: rabbits, hares and pikas

Rabbits and their relatives (Lagomorpha) have generally been grouped close to the rodents, not least because both groups share long ever-growing incisor teeth. Lagomorphs include two living clades, the leporids (rabbits and hares) and the ochotonids (short-eared and short-legged pikas). Lagomorphs have a second small pair of incisors in the upper jaw while rodents have only one, and they use transverse jaw movments to chew rather than proal ones, but the similarities in the skull otherwise are very striking.

The rabbit fossil record extends back to the early Eocene, where the oldest fossils so far have been reported from India. Even older is the stem lagomorph *Gomphos*, a small, long-limbed runner, from Mongolia, close to the Palaeocene-Eocene boundary (Asher *et al.*, 2005). *Palaeolagus* from the Oligocene of North America (Figure 10.49) is very like a modern rabbit. The tail is short, the hindlimb is long (for the characteristic bounding mode of locomotion in rabbits) and the limb girdles are strong (to take up the impact of landing). The long incisors are used for nipping grass and leaves from bushes, and the broad cheek teeth are adapted for side-to-side grinding.

10.13 ARCHONTA: PRIMATES, TREE SHREWS AND FLYING LEMURS

The primates (see Chapter 11), tree shrews, and flying lemurs constitute Archonta, the second major subclade within Euarchontoglires (see Box 10.5). This was hypothesized based on morphological data, and has been confirmed by numerous molecular phylogenetic analyses. Morphological support comes from characters of the ankle, ear region, and the fact that male archontants all have a 'pendulous penis suspended by a reduced sheath between the genital pouch and the abdomen'. Most evidence indicates that Primates are outgroup to Sundatheria, a clade that comprises Scandentia and Dermoptera (Asher *et al.*, 2009; O'Leary *et al.*, 2013).

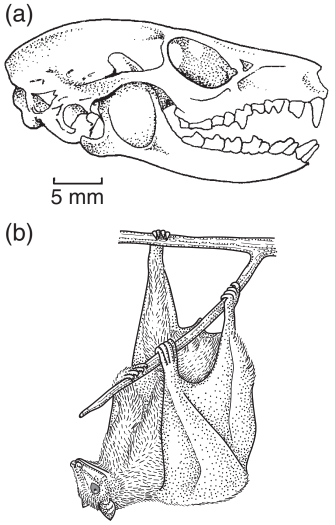


Figure 10.50 Archontan mammals: (a) skull of the modern tree shrew *Ptilocercus*; (b) the dermopteran *Cynocephalus*. Source: (a) Adapted from Young (1981). (b) Adapted from various sources.

10.13.1 Scandentia: tree shrews

The 20 extant species of tree shrews of south-east Asia look rather like small squirrels with pointy noses, and yet their relationships have generally been sought either with the insectivores or the primates (Roberts *et al.*, 2011). The skull (Figure 10.50(a)) is plesiomorphic in many respects, but superficially primate-like in the enlarged brain and large eyes. Fossil tree shrews include possible examples from the Eocene of China and unequivocal material from the Miocene of India.

10.13.2 Dermoptera: flying lemurs

The flying lemurs are represented today by two species of the colugo *Cynocephalus* of south-east Asia (Figure 10.50(b)), which has a gliding membrane between its limbs, body and tail, a broad flap of skin that allows it to leap for up to 100 m between trees. It has a reduced ulna and fibula, broad cheek teeth and comb-like middle incisors. It is nocturnal and feeds on leaves and fruit. The dermopteran fossil record is limited to isolated teeth and jaws from the middle Eocene to late Oligocene of Thailand, Myanmar, and Pakistan (Marivaux *et al.*, 2006). The extinct plagiomenids of the Palaeocene and early Eocene of North America may be relatives of Dermoptera.

10.14 ICE AGE EXTINCTION OF LARGE MAMMALS

Many fossil mammals of the Pleistocene are regarded as typical of the Ice Ages that affected large parts of the world – animals such as the mammoth, woolly rhinoceros, giant Irish deer, giant cattle and cave bear. These all disappeared, however, in relatively recent times and there is considerable interest in trying to establish just what happened and why (Martin and Klein, 1984; Martin, 2007; Haynes, 2009).

The Pleistocene Epoch (2.59–0.01 Myr ago) is marked by many ice ages, during which the ice sheet covering the North Pole advanced southwards and blanketed Europe as far south as Germany and England, northern Asia, and Canada. Ice also advanced outwards from the Himalayas and the Alps, and there were major climatic changes throughout the rest of the world, including drying episodes as so much water was locked up in the ice. Between the ice ages, there were intervals of warmer weather, the main ones being interglacials, during which elephants and hippos roamed around England. The last ice age ended about 11,000 years ago.

Some time between 15,000 and 10,000 years ago, the mammalian faunas of most continents underwent major changes, although extinctions in Australia had already happened before 20,000 years ago (Koch and Barnosky, 2004). In North America, for example, 73% of the large mammals (35 genera) died out, including all of the proboscideans (mammoths, mastodonts), the horses, tapirs, camels, ground sloths and glyptodonts, as well as various predators and deer (Figure 10.51). In South America, 50 genera died out (80%), including species of edentates, rodents, carnivores, peccaries, camels, deer, litopterns, notoungulates, horses and mastodonts. In Australia, 21 genera disappeared, including echidnas, marsupial carnivores, wombats, diprotodonts, kangaroos and wallabies. In Eurasia, on the other hand, the losses were less severe. True, nine genera including the woolly rhino, mammoth and giant deer died out, but others, such as the horse, hippo, musk ox, hyaena and saiga antelope, simply contracted their ranges to other parts of the world. In Africa, ten genera disappeared, but over a long time span.

There are two competing killing models, environmental change or overkill (Koch and Barnosky, 2004). The climate change models identify long-term warming as the ice sheets retreated northwards, and then sharp climate cooling in the Younger Dryas Cooling Event (YDCE), 12,800 years ago. If the cold-adapted megafauna were not finished off by warm summers, the then sharp YDCE hit them hard. Whether the YDCE was caused by an extraterrestrial impact (Firestone *et al.*, 2007; Wittke *et al.*, 2013) or not is hotly debated. The overkill hypothesis, or Blitzkrieg (Martin, 2007), is that spreading human populations exerted pressure on the larger mammals in particular, and these mammals were wiped out by hunting or disease, or both.

The 'overkillers' point out how the spread of human populations seems to correlate with the extinctions, and also that virtually the only organisms to suffer extinction were large mammals, attractive prey for hunting. This is particularly compelling in North America, where the timing of megafaunal extinction was rapid, from 13,800 to 11,400 years ago (Faith and Surovell, 2009), coinciding closely with the arrival and spread of human populations. Overkillers argue that if there were major climatic

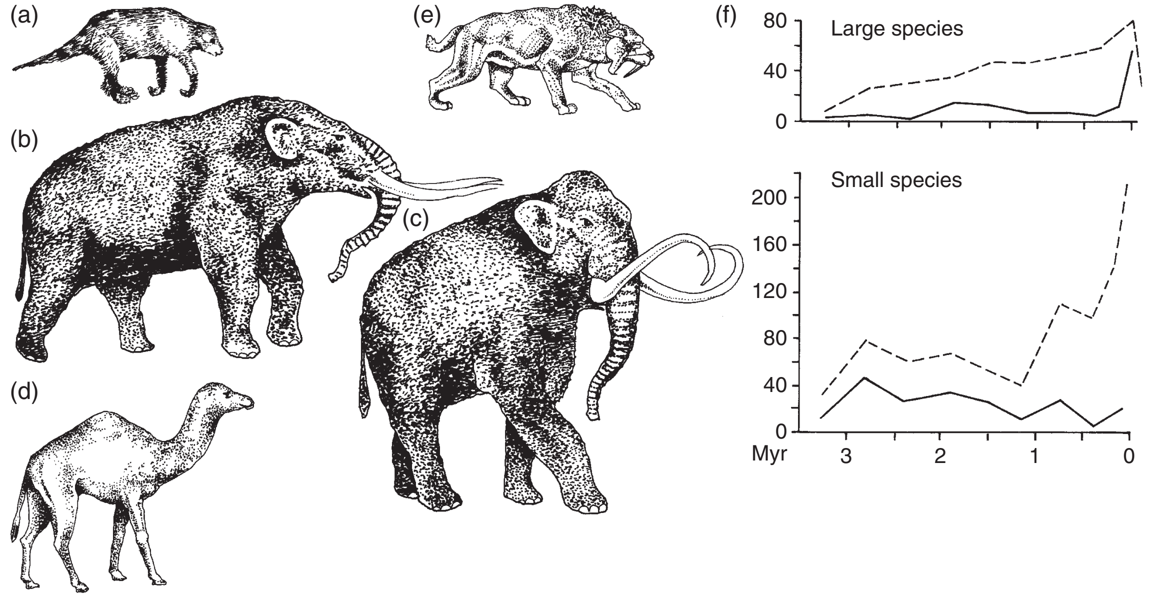


Figure 10.51 Pleistocene extinctions in North America: (a–e) typical large North American mammals before the extinctions: (a) the Shasta ground sloth *Nothrotheriops*, (b) the American mastodon *Mammut*, (c) the Columbian mammoth *Mammuthus*, (d) the camel *Camelops* and (e) the sabre-toothed cat *Smilodon*; (f) patterns of diversity (dashed line) and extinction (solid line) of mammals in North America during the past 3 Myr: large species show more dramatic extinctions in the Late Pleistocene than do small species. Source: (a-e) J. Fuller (artist). Reproduced with permission. (f) Adapted from Martin and Klein (1984).

and environmental changes, then there ought to have been extinctions among the smaller animals and plants as well.

'Climatists', on the other hand, point to the lack of archaeological evidence of kill sites. Further, they note mismatches between the times of arrival of humans on different continents, and the fact that sometimes megafauna had already become extinct before contact with humans, especially in South America. In other cases, for example Australia, humans arrived around 50–45,000 years ago, long before the bulk of the extinctions took place (Wroe *et al*. 2013b). Likewise, humans had been present throughout Africa and Eurasia for long spans of time before the end-Pleistocene megafaunal extinctions. A third criticism of overkill is that many species died out that were seemingly never hunted.

It is evident that neither climate nor overkill alone can account for all end-Pleistocene mammalian extinctions (Koch and Barnosky, 2004). Many large mammals succumbed to long-term climate warming, some perhaps to the sharp cooling of the YDCE, and others must have been hunted to extinction – humans do that, as is well attested by the tragic history of moas in New Zealand, and numerous cases of more recent human-caused extinction. Combined climate-human models have been confirmed as the most informative in numerical simulations of extinction scenarios on all five continents (Prescott *et al*., 2012), and current thinking is that each large mammal species owed its extinction to either major climate change and range contraction or human hunting, or some of both. To try to assert dominance of one model over the other would be unrealistic.

10.15 FURTHER READING

There are numerous books about the evolution of mammals. Savage and Long (1986) and Wallace (2005) are excellent illustrated books, Kemp (2005) is a broad-based evolutionary account, and Ungar (2010) focuses on the evolution and diversity of mammalian teeth. Feldhamer *et al*. (2007) and Vaughan *et al*. (2014) are good textbooks on mammalogy, and Macdonald (2009) is a comprehensive overview of all living mammals. McKenna and Bell (1997) offer a complete listing and classification of mammals living and extinct. Permo-Triassic synapsid evolution is reviewed by Kemp (1982), Chinsamy-Turan (2011), and Kammerer *et al*. (2014), and Mesozoic mammals by Kielan-Jaworowska *et al*. (2004). Kielan-Jaworowska (2013) is a fascinating overview of Mesozoic mammals, with stories of heroic collecting in Mongolia by one of the doyens of the field. Prothero (2006) and Rose (2006) describe the mammals in the Cenozoic. The volumes edited by Szalay *et al*. (1993) include papers on the phylogeny of mammalian groups, and Rose and Archibald (2004) update these with an authoritative overview of the phylogeny of placental mammals.

Mammalian faunas are summarized by Savage and Russell (1983). Mammalian evolution in different continents has been reviewed by Agusti (2005) on the Cenozoic mammals of Europe, Turner and Anton (2007) and Werdelin and Sanders (2010) on the Cenozoic mammals of Africa, Wang *et al*. (2013) on the Cenozoic mammals of Asia, Woodburne (2004) and Janis *et al*. (1998, 2008) on the Late Cretaceous and Cenozoic mammals of North America, and Farina *et al*. (2013) on the Pleistocene mammals of South America.

Many books deal with individual mammal groups. Hoelzel (2002) surveys all the marine mammal groups, and Berta (2012) provides a broad perspective on the evolution of marine mammals. Shoshani and Tassy (1996) includes everything about proboscideans, Prothero and Schoch (2003) is a broad overview of ungulates, Prothero and Schoch (1989) covers all aspects of the evolution of perissodactyls, Prothero and Foss (2007) the evolution of artiodactyls, Franzen and Brown (2010) review the evolution of horses, while Prothero (2013) introduces the giant rhinoceroses. Goswami and Friscia (2010) provide an overview of the evolution of Carnivora, Turner and Anton (1997) and Anton (2000) are excellent introductions to fossil cats, and Wang and Tedford (2010) to dogs and their fossil relatives. Altringham (2011) and Gunnell and Simmons (2012) provide excellent overviews of everything chiropteran. Pleistocene megafaunal extinctions are discussed by Haynes (2009), and the overkill hypothesis by Martin (2007).

QUESTIONS FOR FUTURE RESEARCH

1 How did Late Permian and Triassic cynodonts acquire the key adaptations of mammals, and which were the most important in evolution?

2 Was the transition from reptile to mammal driven by external factors (e.g. Permo-Triassic mass extinction; Triassic climate change) or by internal factors (acquisition of new adaptations)?

3 What were the key morphological changes and adaptive steps through derived probainognathians to the basal mammals (mammaliaforms)? These animals were tiny, and many key specimens are incomplete; more materials are needed for tritherledonts, tritylodonts, brasilodonts, and pre-morganucodontid mammals.

4 How are the ausktribosphenids and Cretaceous monotremes interrelated, and what happened to this clade during the long gap in its fossil record from Late Cretaceous to Oligocene?

5 What are the relationships of poorly defined Mesozoic mammalian taxa such as symmetrodontans, eutriconodonts, eupantotheres, and dryolestoids? Further astonishing specimens from the Chinese Jurassic and Cretaceous are required; but also from other parts of the world.

6 What were the faunal dynamics of mammals in different parts of the world before and after the KPg mass extinction?

7 What were the major events in metatherian evolution, including the palaeobiogeographic moves of the various marsupial clades? More, and more complete, specimens are required from the Americas, Antarctica, and Australia from the Late Cretaceous and Paleogene.

8 Do the fundamental phylogenetic divisions in Placentalia reflect a south-north geographic division? When did placentals evolve and when did the major splits occur? Resolution of the early vs. late origins debate is urgently required.

9 How and where did Afrotheria evolve? New specimens from Africa apparently confirm African origins for most clades, but more detailed resolution of the relationships of the living and extinct Paleogene clades is required, especially a detailed cladistic study of whether louisinids, apheliscids, amphilemurids, adapisoricids, anthracobunids, desmostylans, and embrithopods are afrotherians, and if so, how they are all related, and what this says about geographic moves and functional changes.

10 What happened in the northern hemisphere Palaeocene, as mammals diversified? Is this a classic Simpsonian 'adaptive radiation', characterized by an early burst of disparity and diversity? How endemic and cosmopolitan were the new forms? How did body size and ecosystem occupancy increase?

11 How did various mammal clades – Cetacea, Pinnipedia – enter the oceans, how did they adapt, and share niches with each other and with marine birds?

12 Were changes in major herbivore clades on land – especially between artiodactyls and perissodactyls – driven by their specific adaptations or by climate change, or by both?

13 Why are there no sabre-toothed predators today?

14 To what extent did early humans cause the end-Pleistocene megafaunal extinctions?

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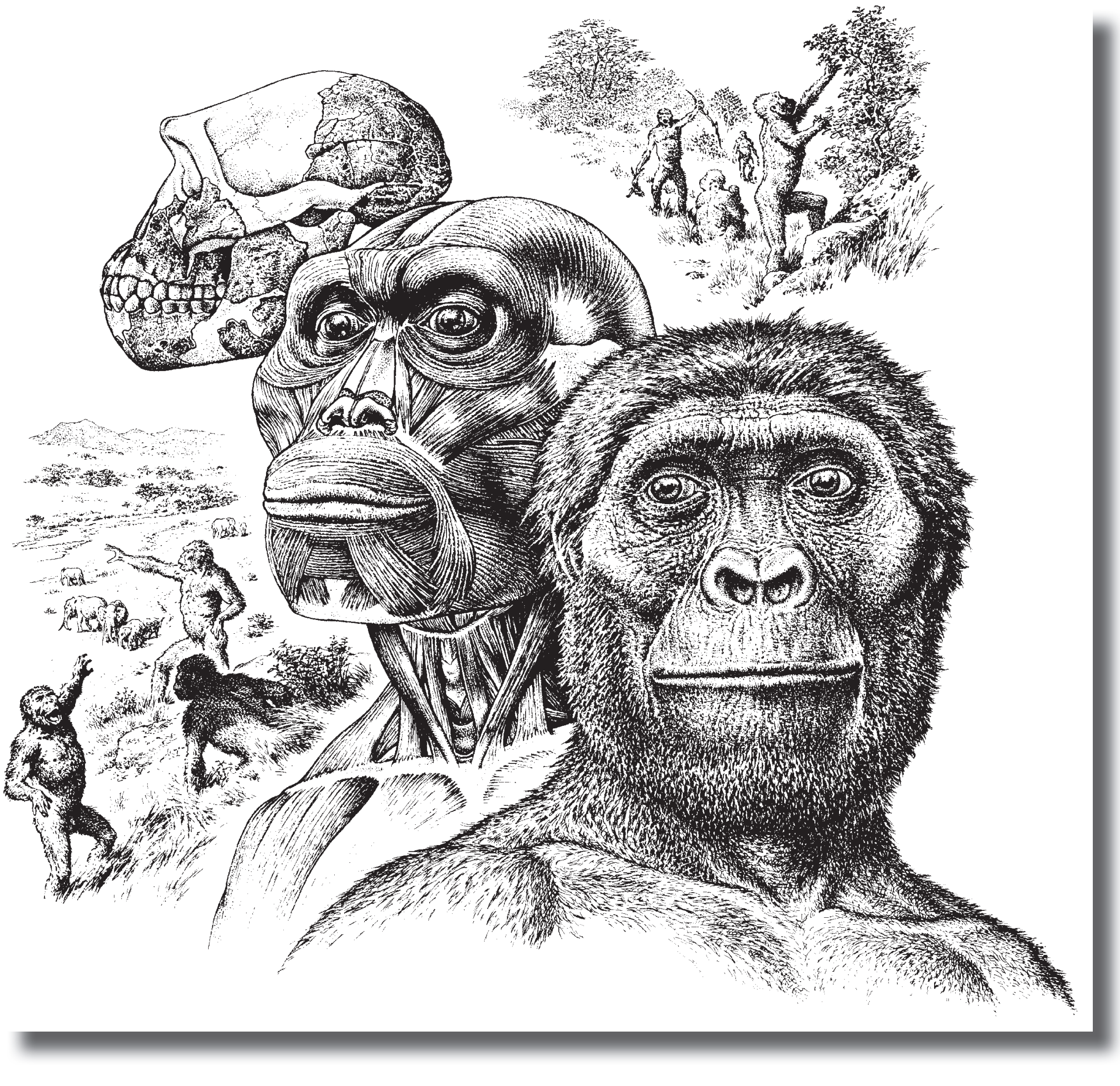
CHAPTER 11

Human Evolution



Vertebrate Palaeontology, Fourth Edition. Michael J. Benton.

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KEY QUESTIONS IN THIS CHAPTER

1 What are the oldest primates?
2 Does the old division of modern primates into prosimians and anthropoids make sense?
3 How do the diverse Eocene primates such as adapiforms and omomyids relate to modern primates?
4 How long have the Old World and New World monkeys had a separate existence?
5 What is the oldest ape, and what were the Miocene apes like?
6 How do humans differ from the other apes?
7 What came first – bipedalism or the large brain?
8 What is the oldest human being, and why is it so difficult to gain agreement among experts?
9 How do palaeoanthropologists reconstruct the appearance and palaeobiology of the early hominids?
10 To what extent were the Neanderthals our ancestors?
11 Are all the modern human races closely related, and when did they split apart?
12 How and when did humans populate the world?

INTRODUCTION

A key theme in palaeontological research is human origins. Indeed, this goes much deeper, because people have been intrigued about the origins of humanity for thousands of years, and it could be counted as one of the core questions any intelligent person might ask. Unfortunately, the fossil evidence for human evolution is patchy. There has been a great deal of controversy over primate and human relationships, partly because of the limited number of good fossils, but also because of the numbers of researchers involved, and the high stakes associated with each new discovery. There are almost as many palaeoanthropologists as there are good fossils, and each researcher of course has his or her own theories!

In this chapter, the fossil evidence for primate evolution is presented, with critical assessments of the key fossils and some of the major controversies over relationships.

11.1 WHAT ARE THE PRIMATES?

There are over 430 species of living primates, classified in 16 families, of which modern humans, *Homo sapiens*, are but one. Primates include a wide array of morphological types, from bush babies and tarsiers to gorillas and humans (Figure 11.1), and they range in size from the pygmy mouse lemur weighing 30 g to the gorilla at more than 175 kg. Primates are diagnosed by 30 or so characters that relate to three major sets of adaptations: (1) agility in the trees; (2) large brain and acute daylight vision; and (3) parental care (Kirk, 2013).

Primates are essentially tree-dwellers, although many lack the remarkable agility seen in certain South American monkeys and the gibbons. Anatomical changes to permit this kind of activity include grasping hands and feet in which the big toe may be opposable, flat nails instead of claws and sensitive tactile pads on all digits, and in hominoids, a very mobile shoulder joint and elbow so that the arm can be rotated in a complete circle.

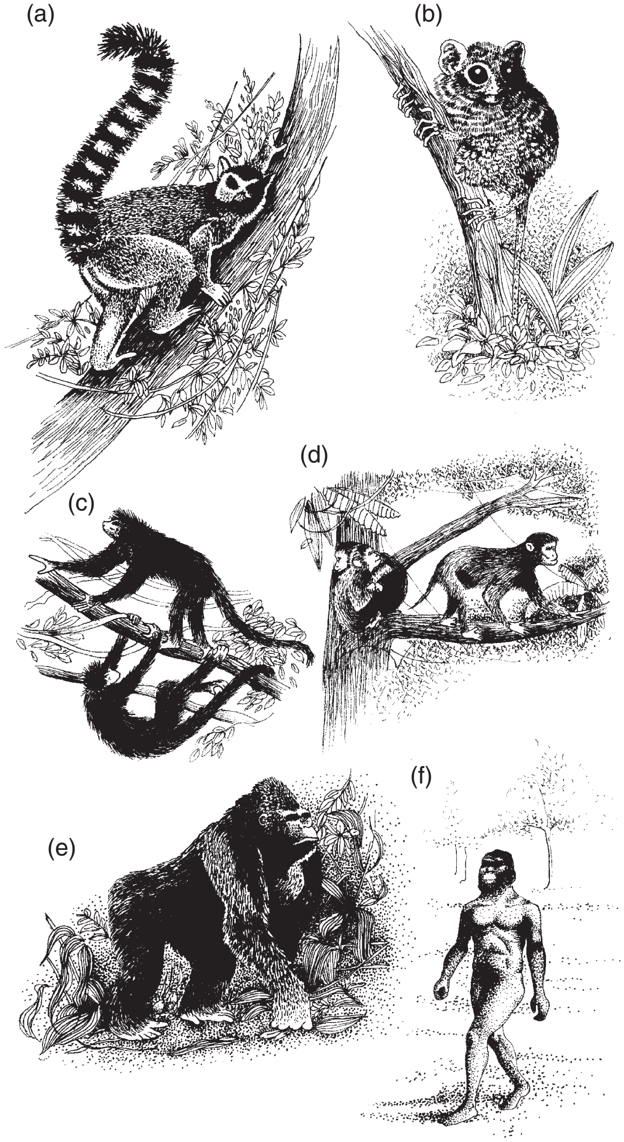


Figure 11.1 A selection of modern primates shown in their natural habitats: (a) the ring-tailed lemur, *Lemur catta*; (b) the spectral tarsier, *Tarsius*; (c) the spider monkey, *Ateles*; (d) the rhesus monkey, *Macaca*; (e) the gorilla, *Gorilla*; (f) the early hominin *Australopithecus*.
Source: Adapted from various sources.

Primates have larger brains, in proportion to body size, than all other terrestrial mammals. In addition, their eyes are generally large and close together on the front of the face, and the snout is reduced. The flattened face of most primates allows them to look forwards and to have a large amount of overlap between the fields of vision of both eyes, which makes stereoscopic, or three-dimensional, sight possible. Primates use their binocular vision to judge distances when they leap from branch to branch, and the enlarged brain allows them to cope with the variety of forest life and social interactions.

Turning to the cranium, primates have a postorbital bar (see Figure 11.4(a,b)), a strut between the orbit and lower temporal fenestra (= fossa), which is absent in related mammals (see Section 10.13). Furthermore, the auditory bulla, the bony capsule that encloses the middle ear and other structures (see Figure 11.4(d)) in primates, is large and it is composed of the petrosal bone (see Section 10.2.1).

The third set of derived characters of the primates relates to improved parental care of their offspring. Primates usually have only one baby at a time, the foetus is retained longer in the womb than in other mammals of the same body size, and there is an extended period of parental care of the offspring. In addition, primates usually have only two mammary glands. Sexual maturity comes late and the total life span is long relative to other similar-sized mammals. Primates have opted for high parental investment, which may have been essential so that the young could learn the complexities of forest life.

There have been many suggestions about why primates adopted their tree-climbing characteristics. For at least 100 years, primatologists have emphasized that primates reduced the sense of smell that is typical of most other mammals, and noted the improvements in their vision, brains, and branch-grasping abilities, all of which form parts of the 'arboreal theory' for primate origins. This has been extended (Sussman *et al.*, 2013) as the 'primate/angiosperm coevolution theory', that the earliest primates, presumably in the latest Cretaceous, and certainly in the early Palaeocene, made their move into the trees to exploit a unique new food source, the fruits and flowers of angiosperms. In order to do this, they had to become especially adept at manoeuvering themselves to the ends of the thinnest branches of trees to snatch the flowers and berries, hence their tiny body sizes, long, slender limbs, sensitive, grasping fingers, and excellent binocular vision.

11.2 THE FOSSIL RECORD OF EARLY PRIMATES

The fossil record indicates that primates radiated in the Palaeocene and Eocene. Older records from the Cretaceous are doubtful, although molecular evidence (see Section 10.4) suggests that the order might have originated in the latest Cretaceous. Could our distant ancestor, a small squirrel-like animal, have seen the last dinosaurs as it peered nervously from behind some branches?

The earliest primates include plesiadapiforms (possibly), adapiforms, omomyids, and tarsiids. The relationships of these 'pre-monkey' primates are currently hotly debated: are plesiadapiforms primates at all, are adapiforms on the line to humans or lemurs, and how do lemurs and tarsiers relate to each other?

11.2.1 Plesiadapiforms

Plesiadapiformes are a group of eleven families that radiated in the Palaeocene and Eocene of North America, western Europe, and Asia (Rose, 2006; Bloch *et al.*, 2007; Sussman *et al.*, 2013). Their oldest representative is *Purgatorius*, known from teeth and jaw fragments from the early Palaeocene. A supposed Late Cretaceous record, once billed as the first true primate, is discounted now. The best known plesiadapiform is *Plesiadapis* itself from the late Palaeocene of North America and France (Figure 11.2), a squirrel-like animal with strong claws on its digits and adaptations for tree-climbing. The eyes are large, but face sideways, a plesiomorphic character suggesting this animal did not have binocular vision. The long snout bears large rodent-like incisors, with large gaps behind and broad cheek teeth for grinding plant food.

Plesiadapiforms have brachiated in and out of the primate tree over the years, but recent cladistic analyses (e.g. Seiffert *et al.*, 2005; Rose, 2006; Bloch *et al.*, 2007; Gunnell and Silcox, 2010) generally confirm that they are sister clade to all other primates. However, this is opposed by a comprehensive phylogenetic

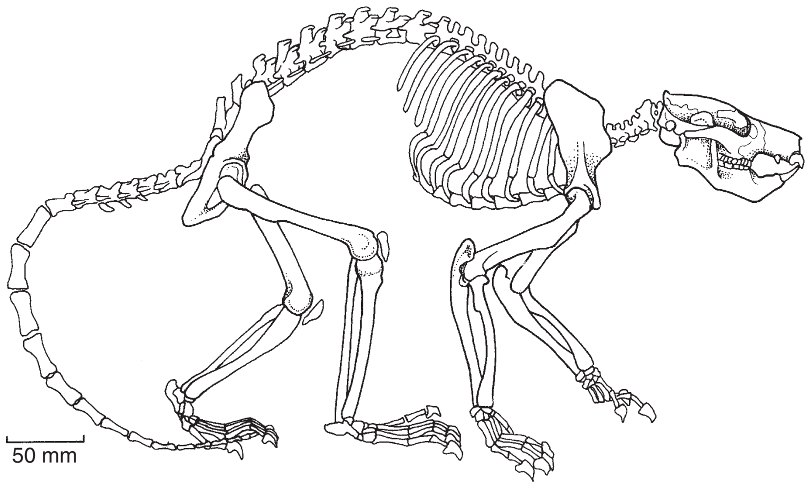


Figure 11.2 Skeleton of the early Eocene plesiadapiform *Plesiadapis*. Source: Adapted from Tattersall (1970).

study by Ni *et al*. (2013), who place plesiadapiforms within Archonta, but between Scandentia and Dermoptera.

11.2.2 Strepsirhini: lemurs and their kin

All other primates belong to the clade Euprimates (see Box 11.1), which radiated extensively during the early Eocene (Rose, 2006; Hartwig, 2008). Euprimates are divided into Strepsirhini, lemurs and lorises, and Haplorhini, the tarsiers, monkeys and apes, and among the most abundant Eocene euprimates, the adapiforms are strepsirhines and the omomyids are haplorhines.

The most abundant of the early primates were the lemur-like adapiforms. The adapiforms arose in the early Eocene and survived until the late Miocene, and during that time they spread from Europe and North America to Africa and Asia. *Smilodectes* from the mid-Eocene of North America (Figure 11.3(a,b)) has a long snout and small orbits, distinguishing it from the contemporary omomyids. The long hindlimbs, grasping hands and feet and long tail were presumably used for balancing during climbing. The teeth of adapiforms suggest a diet of fruit and leaves.

The most famous, or infamous, adapiform is *Darwinius* from the middle Eocene Messel Formation in Germany (see Box 10.8). This little primate is known from a complete specimen preserved as slab and counter-slab, originally found in 1982. In 2007, one of the slabs was sold for $1 million to the Oslo Natural History Museum in Norway, amidst enormous publicity and claims that it was the definitive 'missing link' in human evolution. *Darwinius* is 58 cm long, with a 34 cm tail, and was clearly adapted for scampering around in trees (Figure 11.3(c); Franzen *et al*., 2009). She lacks a baculum, or penis bone, and so was identified as female, and nicknamed 'Ida'. Her teeth, with sharp edges on the molars, were adapted for a diet of leaves and fruit, as confirmed by her stomach contents.

There has been an active debate about the phylogenetic position of *Darwinius* and the adapiforms, with strong claims that they are haplorhines, and hence on the line to humans (Franzen *et al*., 2009). However, most cladistic analyses (Seiffert *et al*., 2009; Maiolino *et al*., 2012; Ni *et al*., 2013) unequivocally identify adapiforms as strepsirhines. For example, adapiforms share an unusual feature with modern lemurs and lorises (Maiolino *et al*., 2012), the grooming or toilet claw on their second toe, which is used for raking through the fur to remove plant debris and dead skin, and for scratching. The living forms also have a toothcomb composed of the incisors and canines, which are narrow and point forwards, and these are also used for feeding and for grooming the fur.

The extant lemurs and lorises branched from adapiforms early in the Paleogene. A fossil from the early Eocene of Tunisia, *Djebelemur*, appears to be on the stem to both modern groups, and suggests these animals originated in Africa (Marivaux *et al*., 2013). *Djebelemur* was a nocturnal animal that walked on all fours through the trees, feeding primarily on insects. Its anterior teeth pointed forwards and may have been used in grooming the fur, but this is not a full tooth-comb as seen in modern lemurs.

There are 100 living species of lemuriforms, which include the lemurs, indriids and the aye-aye, all restricted now to Madagascar. Most of these are cat-sized, but a few are mouse-sized. They have long bushy tails, often striped black and white (see Figure 11.1(a)). Different species of lemurs are diurnal or nocturnal, feeding on insects, small vertebrates and fruit. The incisors and canines of the lower jaw point forwards and form a comb that is used for scooping out soft fruit and for grooming the fur. The indrisids include the woolly lemur, which is nocturnal and lives in trees, whereas the indri and the sifaka are diurnal animals that live in troops and may move about bipedally by leaping along the ground. The aye-aye (*Daubentonia*) is a cat-sized nocturnal animal that probes for insects in tree bark with its slender elongated fingers.

Until the arrival of humans in Madagascar some 2000 years ago, the island was populated by a remarkable array of giant lemurs, ranging up to 200 kg in weight. In the absence of artiodactyls and perissodactyls, the lemurs took on a very wide array of ecological roles, many feeding in the trees, but others chomping vegetation on the ground like horses or cattle. These include the giant lemur, *Megaladapis*, with an elongate almost horse-like skull measuring 0.3 m in length (see Figure 11.3(d)). This would suggest an original body length of 1.3–1.5 m, several times larger than the largest living lemur. Another subfossil lemur, *Hadropithecus*, was baboon-sized, and may have grazed on grass that it grabbed in its hands. The 17 species of giant lemur died out as a result of hunting – there are several sites where butchered lemur bones show they were eaten by humans – and through competition with pigs and other mammals brought by the people. The last giant lemur disappeared about the year 1450 (Crowley *et al*., 2012). It had been thought that there was fossil evidence for earlier evolution of lemurs in Asia: an enigmatic strepsirhine from the Oligocene of Pakistan, *Bugtilemur*, was interpreted as a lemuriform, by far the oldest of the clade (Marivaux *et al*., 2001), but this may in fact be an adapiform (Godinot, 2006).

The lorisiforms, 30 species of lorises and galagos (bushbaby) from Africa and southern Asia, have a more substantial fossil record, with teeth and jaw remains representing a galago and a possible loris from the middle Eocene of Egypt (Seiffert *et al*., 2003). Later fossil lorises include Miocene forms from East Africa and from Pakistan.

11.2.3 Tarsiiformes: tarsiers and their kin

The living tarsier (see Figure 11.1(b)) is a small nocturnal animal that leaps from tree to tree in the forests of south-east Asia, feeding on insects, lizards and small birds. Long classed with lemurs and lorises as a 'prosimian', tarsiers are part of the clade Haplorhini, together with the anthropoids (see Box 10.1). Within Haplorhini, tarsiids are part of the clade Tarsiiformes, which also includes the extinct omomyids.

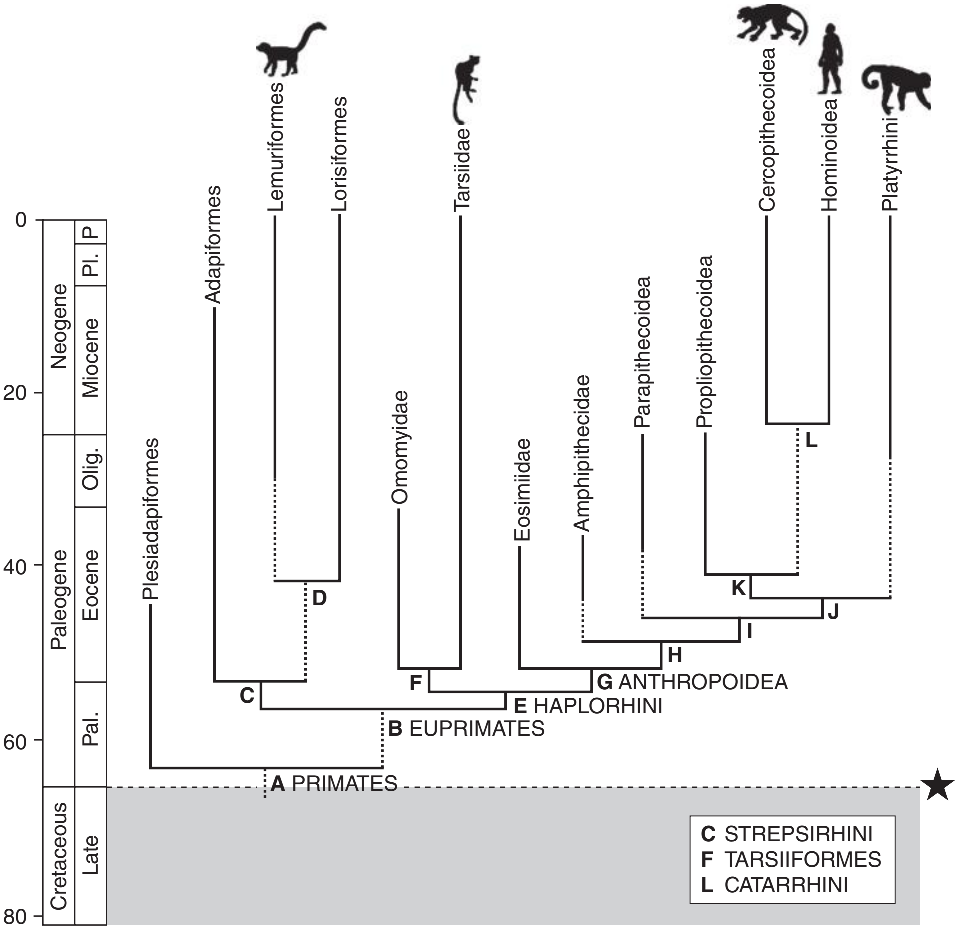
The omomyids, some 50 genera from the Eocene of North America, Europe, Asia, and possibly north Africa (Szalay, 1976),

BOX 11.1 RELATIONSHIPS OF THE BASAL PRIMATES

The traditional classification of the Order Primates was simple: the lemurs, lorises and tarsiers were grouped in the Suborder Prosimii, and the monkeys and apes in the Suborder Anthropoidea. However, the Prosimii were clearly paraphyletic, and they could be diagnosed only with respect to the Anthropoidea, in other words, by the absence of characters. A phylogenetic approach then is bound to break up the classic Prosimii.

There is wide agreement that the old 'prosimians' are divided into lemurs and lorises on the one hand, which together form the clade Strepsirhini, and the tarsiers and anthropoids on the other, which form the clade Haplorhini, distinguished from each other by characters of the nostrils and skeleton. Among Haplorhini, tarsiers are outgroup to Anthropoidea, comprising the Catarrhini and Platyrrhini (New World monkeys). The Catarrhini comprise two extant subclades, the cercopithecoids (Old World monkeys) and hominoids (apes, including humans).

There are numerous extinct clades of primates, and we include only some major clades here. Adapiformes is a large clade, generally assigned to Strepsirhini, and so close relatives of lemurs and lorises (Seiffert *et al*., 2005; Rose, 2006; Ni *et al*., 2013). A second large clade of early primates, the Omomyidae, is widely classed as sister group to Tarsiidae, forming together with them the clade Tarsiiformes (Seiffert *et al*., 2005; Rose, 2006; Ni *et al*., 2013). There then follow a number of stem anthropoid clades, the Eosimiidae, Amphipithecidae, and Propliopithecoidea, among many smaller clades, probably outgroups to crown Anthropoidea (Seiffert *et al*., 2005; Rose, 2006).



Cladogram showing postulated relationships of the major primate clades. Animal silhouettes are mostly from the PhyloPic website, and we acknowledge the work of Gareth Monger, T. Michael Keesey, Smokeybjb, Mateus Zica, and Sarah Werning. Synapomorphies from Kay *et al*. (1997), Seiffert *et al*. (2005), and other sources: **A PRIMATES**, postorbital bar, large orbits, orbits are located close together and on the front of the face, large braincase, modifications of the elbow to allow extra flexibility, modifications of the tarsus, opposable thumb; **B EUPRIMATES**, petrosal bulla, nails on the digits and terminal tactile pads, grasping hind feet; **C STREPSIRHINI**, ring-shaped tympanic bone enclosed within the tympanic cavity, posterolateral and dorsal position of the posterior carotid foramen, as well as characters of the hand and foot such as the grooming claw on the second toe; **D**, grooming claw on second toe, dental tooth comb made from forwards-projecting lower incisors and canines; **E HAPLORHINI**, haplorhine nose (nostrils have complete margins and are not slit-like), short face placed largely below the braincase, narrow and simplified bony bar between orbits, olfactory lobes of brain reduced and optical lobes enlarged, haemochorial placenta (invades uterine wall and chorion directly bathed by maternal blood); **F TARSIIFORMES**, greatly enlarged orbits, tubular ectotympanic bone (external auditory meatus), elongate tarsal bones, closely apposed tibia and fibula; **G ANTHROPOIDEA**, large inferior orbital fissure, large sinuses in the maxilla and sphenoid, fused mandibular symphysis, expanded quadratic molars, molarization of the premolars (especially P_4), strong development of the hypocone, canine occlusion, relatively large canines compared with incisors, lateral incisors larger than central incisors; **H**, no synapomorphies; **I**, no synapomorphies; **J**, no synapomorphies; **K CATARRHINI**, orbits small, forward facing and convergent, bony lamina separates orbit from adductor fossa, tympanic bone fused to bony sidewall of middle ear, relatively deep mandible; **L CROWN CATARRHINI**, two premolars, sexual dimorphism is marked, males have larger canines than females. Abbreviations: Olig, Oligocene; P, Pleistocene; Pal, Paleocene; Pl, Pliocene. Dashed lines and star symbols indicate extinction events.

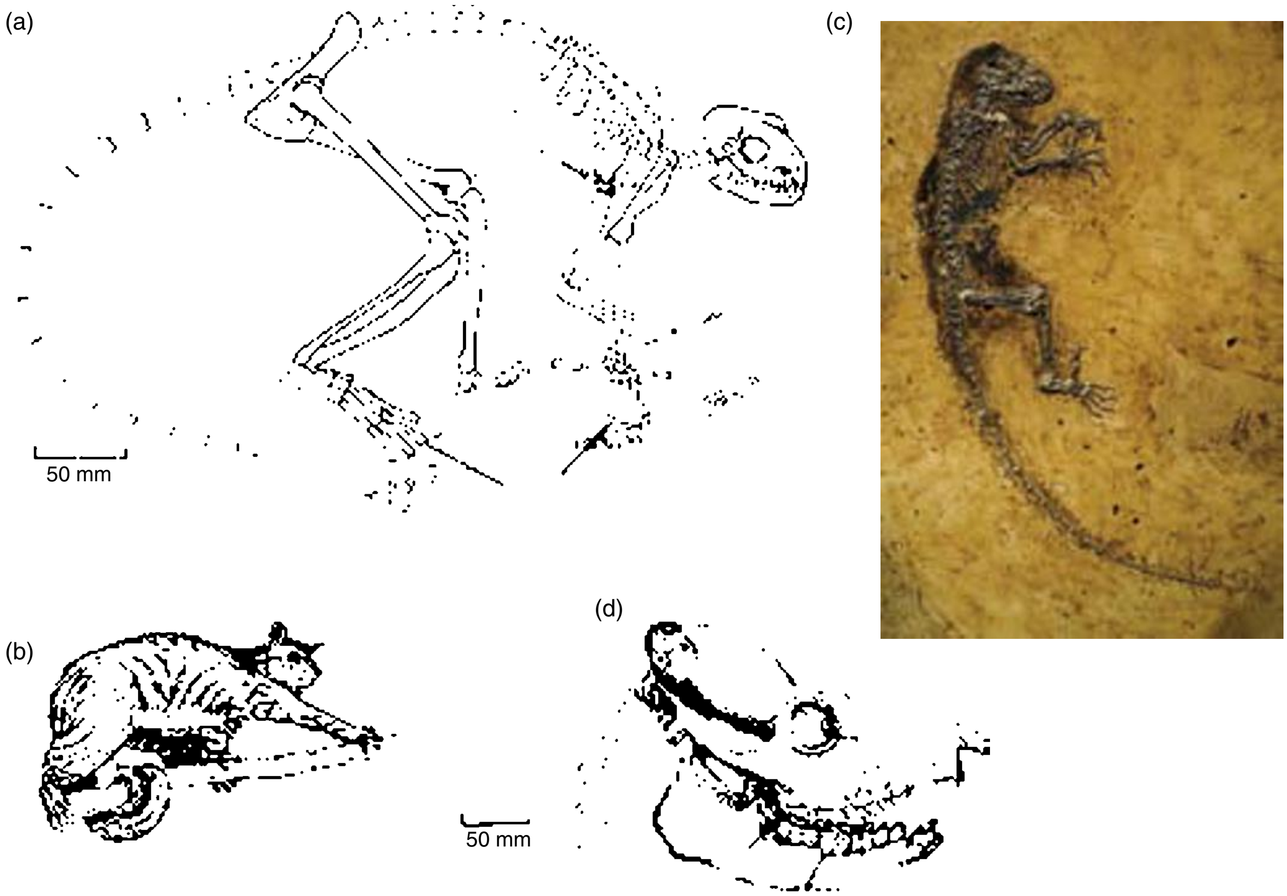


Figure 11.3 Fossil strepsirhine primates: (a b) the middle Eocene adapiform *Smilodectes*, skeleton and restoration of life appearance; (c) the type specimen of the adapiform *Darwinius*; (d) the Pleistocene giant lemur *Megaladapis*, lateral view of skull. See Colour plate 11.1. Source: (a) Adapted from Simons (1964). (b) Adapted from Rose (2006). (c) © Jens L. Franzen, Philip D. Gingerich, Jörg Habersetzer1, Jørn H. Hurum, Wighart von Koenigswald, B. Holly Smith/CC-BY-SA-2.5/GFDL. (d) Adapted from Zapfe (1963).

were all small tarsier-like tree-dwellers, mostly weighing less than 500 g, but some later forms reached 2.5 kg. They generally have large orbits, shortened snouts and tooth rows, loss of the anterior premolars in later forms, and cheek teeth adapted for insect- and fruit-eating diets. For example, *Tetonius* (Figure 11.4(a–c)) has a short snout, a bulbous braincase and an obvious postorbital bar. The orbits face forwards and it is likely that these early primates already had stereoscopic vision. Another omomyid, *Shoshonius* from Wyoming, USA, known from several tiny crania (Figure 11.4(d)), also has very large orbits and a short snout. Omomyids show adaptations in their limb skeletons for climbing, grasping branches with thumbs and large toes and leaping from branch to branch (Rose, 2006).

The tarsiids until recently had a limited fossil record. At times, omomyids such as *Shoshonius*, were assigned to Tarsiidae, but the oldest accepted tarsier records include fossils from middle Eocene cave sediments from China, a jaw named *Xanthorhysis* and teeth assigned to *Tarsius*, the living genus (Rose, 2006). Further, a supposed tarsier from the early Oligocene of Egypt, *Afrotarsius*, is more likely a stem anthropoid. This means the tarsiids had an exclusively Asian history. This is confirmed by a remarkable tarsier fossil from the early Eocene of China, *Archicebus* (see Box 11.2).

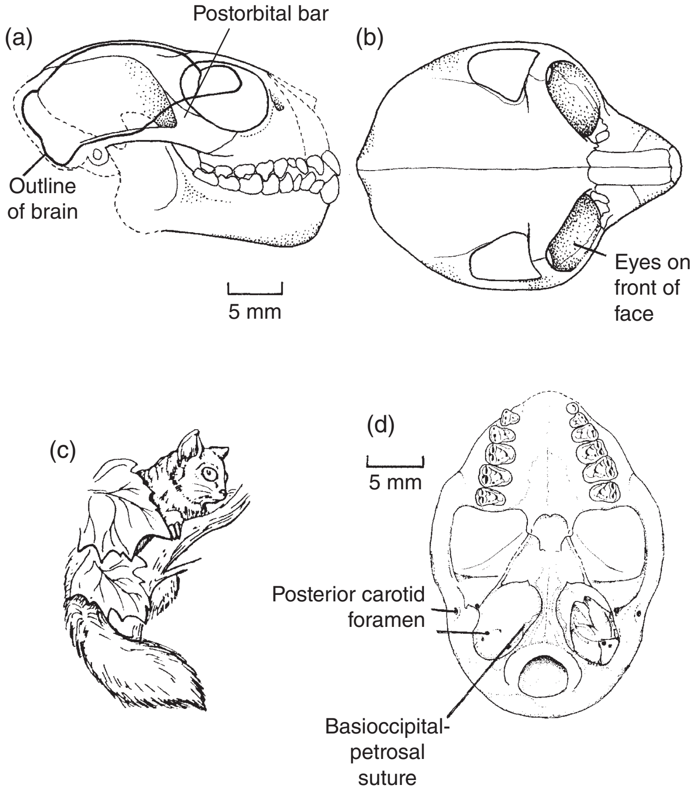


Figure 11.4 Tarsiiform primates: (a–c) the early Eocene omomyid *Tetonius*, skull in lateral and dorsal views, and restoration of life appearance; (d) the early Eocene omomyid *Shoshonius*, ventral view of skull. Source: (a,b) Adapted from Szalay (1976). (c) Adapted from Rose (2006). (d) Adapted from Beard *et al.* (1991).

BOX 11.2 THE WORLD'S FIRST TARSIER

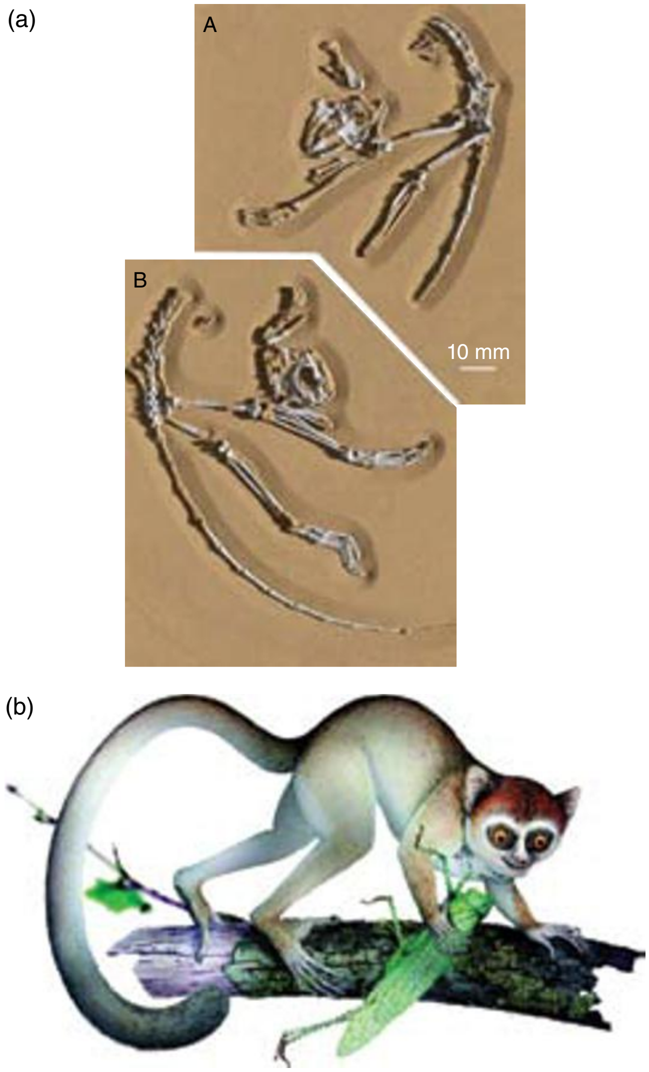
Occasionally, a single complete fossil can resolve decades of debate. The relationships of a broad array of Eocene primates had been hotly debated since the 1960s, and the discussions focused on the adapiforms and omomyids, and the old split of the Order Primates into so-called 'prosimians' and anthropoids, or strepsirhines and haplorhines (see Box 11.1). Humans are haplorhines, and we trace our ancestry back to Eocene forms such as *Eosimias* and *Amphipithecus* (see Section 11.3.1). But what of the highly abundant early and middle Eocene adapiforms and omomyids?

According to some cladistic analyses (e.g. Franzen *et al*., 2009), adapiforms were haplorhines and so in some way ancestral to humans. On the other hand, other recent phylogenetic analyses (e.g. Seiffert *et al*., 2009; Maiolino *et al*., 2012; Ni *et al*., 2013)have shown a great deal of convergence among the different Eocene clades, and that adapiforms are strepsirhines (see Section 11.2.2) and omomyids are tarsiiforms (see Section 11.2.3).

The discovery of the oldest essentially complete primate skeleton in the early Eocene of China then caused a sensation. Not only can it tell us about the adaptations and mode of life of an early primate, it can also help resolve these long-running phylogenetic debates. *Archicebus* is known from a skeleton preserved on slab and counterslab (Ni *et al*., 2013). It was tiny, weighing an estimated 20–30 g, the size of the modern mouse lemur, or indeed the size of a mouse. Its large canine teeth and pointed premolars show it fed mainly on insects. Its eyes are close together, and so *Archicebus* may have had binocular vision, but the eyes are not enlarged, as in most tarsiiforms, so it probably operated in daylight.

In the skeleton *Archicebus* shows adaptations for leaping among tree branches, its long legs, the semi-cylindrical femoral head with a stout and less oblique femoral neck, the tall knee, and the closely apposed tibia and fibula. However, it shows primitive limb features that made it less adept in the trees than modern galagos and tarsiers, such as the long cornoid process of the scapula, the moderately rounded humeral head, the long and straight ischium, the high crural index (ratio of tibia to femur), and the long metatarsals and toes. *Archicebus* likely walked along branches and jumped, but could not cling to vertical trunks.

The importance of *Archicebus* is especially in what it says about early primate phylogeny. Cladistic analysis (Ni *et al*., 2013) places this new form firmly at the base of Tarsiiformes, and Tarsiiformes as sister clade to Anthropoidea (see Box 11.1). Adapiforms are strepsirhines and omomyids are tarsiiforms. The new fossil pushes the age of the Tarsiiformes-Anthropoidea and the Strepsirhini-Haplorhini splits down to the early Eocene, or older.



The oldest haplorhine primate, the tarsiiform *Archicebus* from the early Eocene of Hubei, China: (a,b) dorsal and ventral views of the skeleton, showing the long tail, hindlimbs, partial trunk and forelimb, and skull, a composite image based on CT scans of the fossil, showing fossil bones (light grey) and restored elements based on impressions in the rock (dark grey); (b) life restoration. See Colour plate 11.2. Source: (a,b) Adapted from Ni *et al*. (2013).

11.3 ANTHROPOIDEA: MONKEYS AND APES

The 'higher' primates, the monkeys and apes, form a clade, the Anthropoidea ('human-like'), which today comprises two groups that evolved separately in the New World (mainly South America) and the Old World (Africa, Asia, Europe). The New World monkeys, the platyrrhines (literally 'broad nose') have broadly spaced nostrils that face forwards, and some have a prehensile tail. The catarrhines (literally 'hooked nose'), or Old World monkeys and apes, have narrow snouts and non-prehensile tails.

Anthropoids have the rounded nostrils of all haplorhines (tarsiiforms and anthropoids), as well as large canines that occlude with the opposite canine and first premolar, the premolars are rather molar-like, and the molars are broad and square. Anthropoids originated surprisingly early, even by the late Palaeocene, and there were several Eocene and Oligocene clades along the stem lineage to the modern monkey groups (see Box 11.1).

11.3.1 Anthropoid adaptations

Anthropoids are distinguished from strepsirhines and tarsiers by numerous features of their body size, diet, locomotion, senses, and brain size (Williams *et al*., 2010). In terms of size, most modern monkeys and apes weigh more than 1 kg (exceptions are the marmosets, tamarins, and squirrel monkeys), whereas some of the Eocene anthropoids were tiny. This affected their diet. Tiny animals can rarely obtain enough nourishment from leaves alone, and so most of the Eocene primates, including the early anthropoids, relied on insects as their main source of protein. As anthropoids became larger (over 500 g), they could become entirely vegetarian, relying on leaves as their main diet.

Eocene primates were all arboreal, even if many were not as agile as some living forms. The first anthropoids show adaptations to a variety of locomotory modes, most being capable of walking quadrupedally along branches, and leaping from tree to tree. Larger forms were probably slower moving.

Anthropoids show many modifications to their visual system. For example, their cornea is smaller than in lemurs, lorises, and most other mammals, giving them a longer focal length, and so improved visual acuity. Such a reduced cornea means that less light can enter the eye, and so this adaptation must have arisen in diurnal species, whereas strepsirhines are primarily nocturnal. Tarsiers, although primarily nocturnal and equipped with enlarged eyes, share other features of the eye (the retinal fovea and a macula lutea) with anthropoids, and so probably became secondarily nocturnal. Anthropoids and tarsiers have postorbital septa, bony divisions between the back of the eye socket and the temporal fossa. This bony barrier separates the eyeball from the adductor jaw muscles, and may have evolved as the haplorhine face flattened, and the eyes converged on the midline. Anthropoids have colour vision and many strepsirhines do not, but the anthropoids resemble other mammals, and lorises and bushbabies with monochromatic vision have seemingly lost the ability. Catarrhines (Old World monkeys, apes, humans) stand out as having three cone types (other mammals, including other anthropoids have two cone types). Catarrhines again show unique aspects of the loss of the sense of smell (Williams *et al.*, 2010); indeed all haplorhines have reduced olfactory lobes of the brain, but tarsiers and platyrrhines retain a large number of functional olfactory receptor protein genes that are lost in catarrrhines.

The final anthropoid characteristic, when compared to tarsiers and strepsirhines, is a step-change in brain size (Williams *et al.*, 2010). Eocene anthropoids had brains in the size range (when corrected for body mass) of living strepsirhines. However, in these early forms, the visual cortex had increased in size, matching the assumed improved visual acuity. Further, in modern monkeys and apes, the neocortex is expanded when compared to tarsiers and lemuriforms. The neocortex is the outer layer of the cerebral hemispheres, the part of the brain associated with sensory perception, the generation of motor commands, spatial reasoning, conscious thought, and language. This is a further step along the road from the initial expansion of the brain when Primates originated (see Section 11.1), and precedes further brain expansions on the line to modern humans (see Section 11.5.2).

11.3.2 The first anthropoids

The prize for the oldest confirmed primate, and perhaps the oldest anthropoid, may go to *Altiatlasius*, based on ten isolated cheek teeth and a dentary fragment of a juvenile from the late Palaeocene of Morocco (Sigé *et al.*, 1990). The teeth (Figure 11.5(a)) show resemblances to plesiadapiform dentitions,

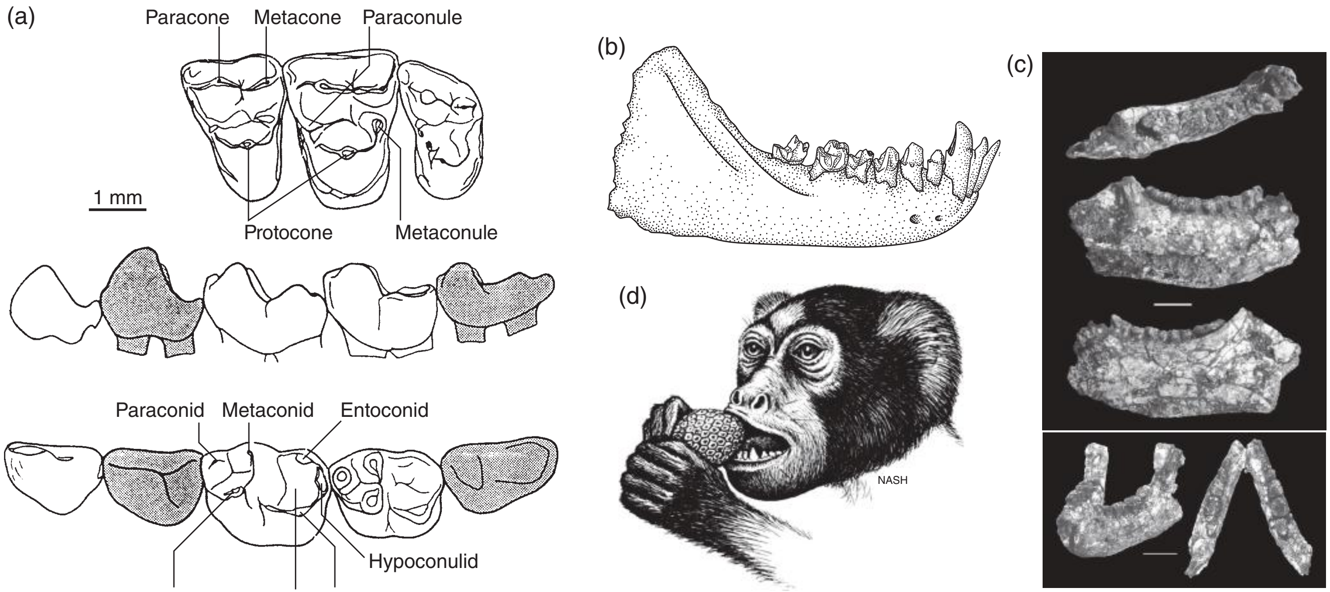


Figure 11.5 Early anthropoids: (a) upper molars 1–3 and lower cheek teeth of *Altiatlasius*, the oldest known primate, from the upper Palaeocene of Morocco; (b) mandible and lower jaw dentition of *Eosimias* from the middle Eocene of China; (c) lower jaw of *Pondaungia*, the original specimen found in 1923, and outline of a second specimen found in 1977; (d) restoration of the head of *Amphipithecus*. Source: (a) Adapted from Rose (2006). (b) Beard and Wang (2004). Reproduced with permission from Elsevier. (c,d) R. Ciochon, University of Iowa, Iowa City, IA, USA. Drawing by S. Nash, Denver Museum of Nature and Science, Denver, CO, USA. Reproduced with permission.

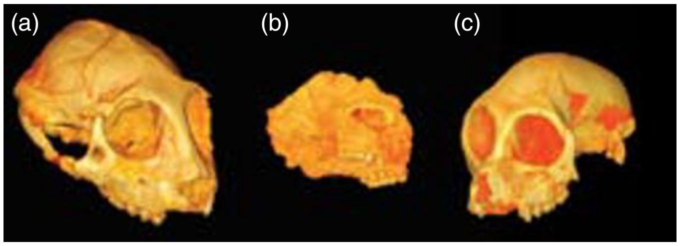


Figure 11.6 Crania of (a) the early Oligocene parapithecid anthropoid *Parapithecus grangeri*; (b) the late Eocene stem catarrhine *Catopithecus browni* (a substantially distorted skull); and (c) the early Oligocene stem catarrhine *Aegyptopithecus zeuxis*. See Colour plate 11.3. Source: Seiffert (2012). Reproduced with permission from John Wiley & Sons.

but *Altiatlasius* was initially identified as an omomyid (Sigé *et al*., 1990). It has since been assigned many phylogenetic positions, but is generally accepted as the first euprimate, and perhaps even the first anthropoid (Seiffert *et al*., 2005; Beard, 2006; Rose, 2006; Tabuce *et al*., 2009). *Altiatlasius* was a tiny animal, about the size of a modern mouse lemur, and weighed perhaps 50–100 g.

Discoveries of early anthropoids during the past twenty years have fostered a heated debate about the geographic area of origin of the clade, whether in Africa or Asia. *Altiatlasius* is too incomplete to be placed confidently in the cladogram, whereas the Eosimiidae from China, Myanmar, and possibly from India (Bajpai *et al*., 2008) are definitively basal anthropoids (see Box 11.1). *Eosimias* is known from several lower jaws with full dentitions (Beard and Wang, 2004) from the middle Eocene of China. The animal was tiny, weighing perhaps 90–180 g, and small enough to sit on the palm of your hand, and its teeth indicate a probable mixed diet of fruit and insects. The lower jaws (Figure 11.5(b)) show anthropoid characters in the small incisors, large canines, obliquely oriented premolars 3 and 4, molars with broad trigonids, and the relatively deep dentary. Tarsal bones assigned to *Eosimias* suggest anthropoid affinities, the most widely accepted view (Beard and Wang, 2004; Bajpai *et al*., 2008; Seiffert *et al*., 2009; Williams *et al*., 2010; Ni *et al*., 2013).

Next in the cladogram (see Box 11.1) are the Amphipithecidae, another Asiatic anthropoid family, comprising five or six genera mainly from the middle Eocene of Myanmar (Beard *et al*., 2009), as well as from the late Eocene of Thailand. Some of these taxa, such as *Pondaungia* and *Amphipithecus* had been named in the 1920s and 1930s, and there are several new forms such as *Siamopithecus*; most are known only from isolated teeth, jaws, and a few other fragments. These were medium-sized to large animals, weighing 5–10 kg, mostly frugivores, and the tooth morphology of *Pondaungia* and *Amphipithecus* (Figure 11.5(c,d)) suggests that they also ate harder food such as nuts and seeds. Other amphipithecids may have fed on leaves, and some smaller animals may have relied on insects. These primates have long been regarded as anthropoids, although some have argued that they were related to adapiforms or omomyids. The anthropoid position has been confirmed in most recent studies, however (e.g. Beard *et al*., 2009; Seiffert *et al*., 2009; Coster *et al*., 2013; Ni *et al*., 2013), based on similarities in the teeth and jaws, and in the tarsal bones, of the amphipithecids to living anthropoids.

Except for the enigmatic, and unusually early, *Altiatlasius*, the earliest anthropoids come from south-east Asia. The first definitively African clade is the Parapithecoidea from the late Eocene and early Oligocene of Egypt (Seiffert *et al*., 2005, 2012). These include three species of *Biretia* from the late Eocene, all of which are tiny (<300 g), and may show evidence for enlarged orbits and nocturnality, although this is debated (Seiffert *et al*., 2005; Seiffert, 2012). Other parapithecoids from the same rock successions in Egypt were diurnal fruit-eaters that moved about in the tropical forest trees by a combination of quadrupedal walking and leaping. *Parapithecus* is known from a reasonably complete skull (Figure 11.6(a)) from the early Oligocene of Egypt, whose small orbits indicate diurnal habits, and size differences in the jaws and teeth may indicate sexual dimorphism between males and females (Simons, 2001). The brain size was smaller than in modern anthropoids of the same size.

11.3.3 Catarrhines: the Old World monkeys

After a to-and-fro between Asiatic and African stem-group anthropoids, the crown-group anthropoids split into Old and New World monkeys in the late Eocene or Oligocene, and the early history of catarrhines is documented by some intriguing, but inevitably controversial, fossils.

Catarrhines share a number of characters. They have only two premolars in each jaw and they generally show considerable sexual dimorphism: males are larger than females and their canine teeth are almost always larger than those of females. The Old World monkeys, the Cercopithecoidea, have long molars with crests (**lophs**) linking transverse pairs of cusps, the bilophodont condition.

Among probable stem catarrhines are a number of small clades, including oligopithecids and propliopithecids. For example, *Catopithecus*, an oligopithecid from the late Eocene of Egypt (Simons, 1995) is relatively completely known. It has two premolars, large upper canines and flattened spatulate incisors. *Catopithecus* specimens show pronounced sexual dimorphism, with males apparently twice the size of females and equipped with much larger canine teeth (Figures 11.6(b), 11.7(a)). *Aegyptopithecus*, a propliopithecid from the Oligocene of Egypt (Figures 11.6(c), 11.7(b,c)), was about the size of a gibbon, with a short snout, large forward-facing eyes and an enlarged braincase. The heavy jaw and broad cheek teeth suggest a diet of fruit, and the limb bones show that *Aegyptopithecus* probably climbed trees and ran along stout branches. *Saadanius* from the Oligocene of Saudi Arabia is close to the split of crown catarrhines (Zalmout *et al*., 2013).

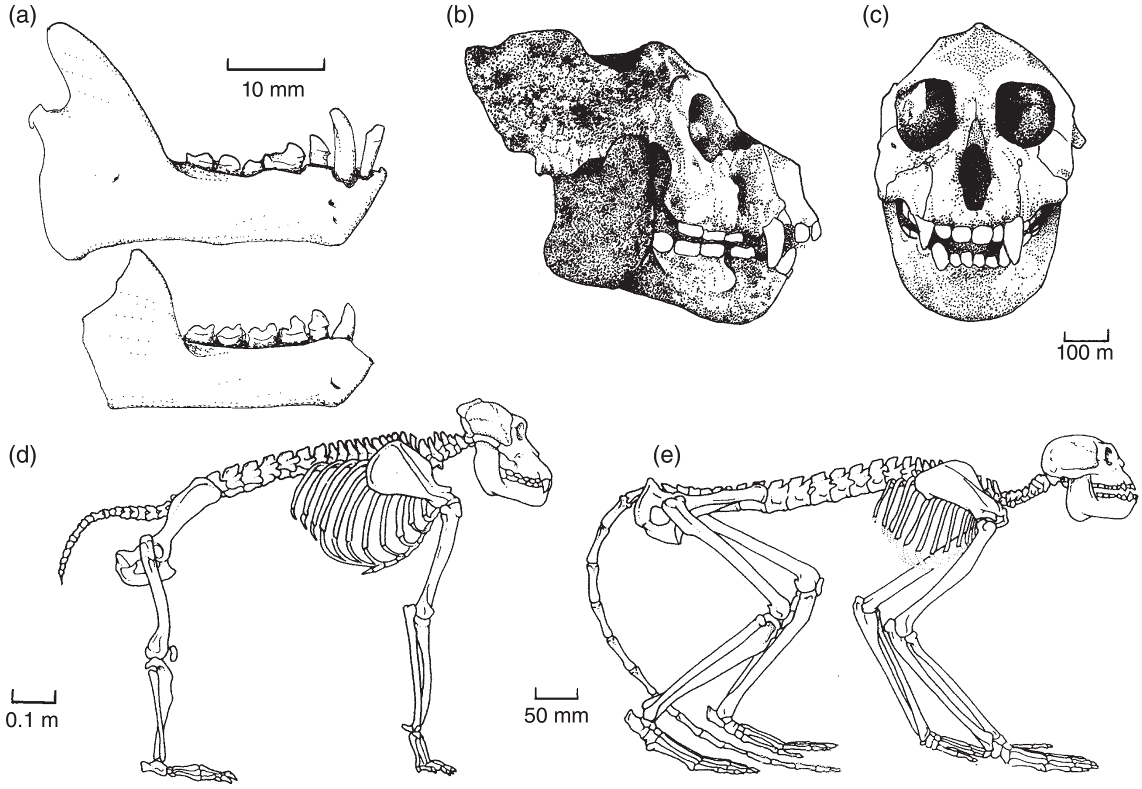


Figure 11.7 Early monkeys: (a) lower jaws of a male and female *Catopithecus*, an early catarrhine, from the upper Eocene of Egypt; (b,c) the skull of *Aegyptopithecus* from the Oligocene of Egypt, in lateral and anterior views; (d) skeleton of the giant baboon *Theropithecus oswaldi* from the Pleistocene of East Africa; (e) skeleton of the tree-dwelling cercopithecoid monkey *Mesopithecus pentelicus* from the upper Miocene of Greece. Source: (a) Adapted from Simons (1995). (b,c) Adapted from Simons (1967). (d,e) E. Delson, CUNY, New York, NY, USA. Reproduced with permission.

The 140 species of modern cercopithecids divide into two groups, the cercopithecines, such as the macaques (see Figure 11.1(d)) of Africa, Asia and Europe (the barbary ‘ape’ of Gibraltar) and the terrestrial baboons and mandrills, and the colobines, the leaf-eating colobus monkeys and langurs. The oldest fossil evidence of cercopithecids is from the late Oligocene of Africa, a lower third molar (Stevens *et al*., 2013). More completely known is *Victoriapithecus*, a cercopithecid from the middle Miocene (15–14 Myr ago) of Kenya, which has bilophodont molars and probably fed on fruit (Miller *et al*., 2009). By the late Miocene, cercopithecids had extended their range across the Old World, as far as China and Java and Europe, and in the Pleistocene such monkeys reached as far north as England. As many as ten cercopithecid lineages took to the ground and they replaced the ground-dwelling apes in parts of Africa.

Modern genera of cercopithecines appeared in Africa during the Pliocene and Pleistocene. The living gelada, *Theropithecus*, a specialized ground-dweller related to the baboon, lives in the Ethiopian highlands and feeds on grass and seeds. Pleistocene relatives were larger than the modern species, some of them much larger (Figure 11.7(d)), and they are common at East African fossil sites and their range extended as far as India and Spain.

Fossils of colobine monkeys also appear first in the Miocene. Colobines entered Asia and Europe before the cercopithecines and diverged into distinctive groups in those continents. *Mesopithecus* from the upper Miocene and Pliocene of Europe and the Middle East (Figure 11.7(e)), is a short-faced form, similar to modern langurs. It has a deep lower jaw, as in all colobines, an adaptation for chomping huge amounts of leaves and other plant material.

11.3.4 Platyrrhines: the New World monkeys

The 130 species of living platyrrhines are divided into three families, the Pitheciidae (titis, saki monkeys and uakaris), the Cebidae (capuchin and squirrel monkeys, tamarins and marmosets) and Atelidae (howler and spider monkeys, owl monkeys; see Figure 11.1(c)). All of these are confirmed tree-dwellers, and they are either herbivores, feeding on fruit and leaves, or omnivores, with the addition of insects and small vertebrates to their diet. Most are small, including the world’s smallest monkey, the 120–190 g pygmy marmoset.

Platyrrhine fossil remains are sparse (Perez *et al*., 2013; Schrago *et al*., 2013). The oldest fossil platyrrhine is *Branisella* from the late Oligocene, and then good quality fossils of taxa such as *Dolichocebus*, *Tremacebus*, and *Chilecebus* are known from the early Miocene, dating to approximately 20 Myr ago. Some Pleistocene platyrrhines, *Protopithecus* and *Cartelles*, were larger than any living atelid, weighing an estimated 25 kg

(Halenar and Rosenberger, 2013). With longer arms than legs, these large frugivores swung themselves through the trees. *Protopithecus* was named in 1836, based on partial remains from a cave in Brazil; this was the first ever fossil primate to be named.

The platyrrhines probably split from the catarrhines in the Eocene or Oligocene, and they may have reached South America direct from Africa, crossing the opening South Atlantic Ocean. It is currently debated whether the Oligocene and Miocene fossils are part of the modern radiation, or whether they lie on the stem lineage; if the latter is true, then the crown clade, comprising all the living forms, would have diversified only about 20 Myr ago. Molecular evidence strongly supports the multiple expansions model, and a relatively recent diversification of the crown clade (Schrago *et al.*, 2013).

11.4 HOMINOIDEA: THE APES

The apes, Hominoidea, today include the gibbons and orang-utan of southern and eastern Asia, the gorilla and the chimpanzee from Africa, and humans (see Figure 11.1(e,f)). The limited number of living species of ape gives little idea of their great diversity in the past, especially in the Miocene of Africa. For a long time, the timing of divergence of cercopithecoids and hominoids was unclear, but *Nsungwepithecus* and *Rukwapithecus* from the late Oligocene of Tanzania, both based on limited remains, are diagnostic of cercopithecoids and hominoids respectively (Stevens *et al.*, 2013).

11.4.1 Early ape evolution

In the early Miocene of East Africa (23–16 Myr ago), apes were more abundant than anywhere today. Most of these belong to the Proconsulidae, including genera such as *Nyanzapithecus*, *Rangwapithecus* and *Turkanapithecus*. Best known is *Proconsul* (Walker *et al.*, 1983; Walker and Shipman, 2005), which was named in 1933 on the basis of some jaws and teeth from Kenya. The name refers to a chimp named Consul who then lived at London Zoo and entertained visitors with his bicycle riding and pipe smoking. Since the 1930s, evidence of most of the skeleton has been found, including several well-preserved associated skeletons (Figure 11.8). There are four species that differ mainly in body size.

Proconsul has a long monkey-like trunk and the arm and hand bones share the characters of modern monkeys and apes. Many different modes of locomotion have been proposed, ranging from nearly fully bipedal walking (when it was thought to be closer to human ancestry), through knuckle walking, as seen in modern chimps and gorillas, to full **brachiation**, swinging hand over hand through the trees as in modern gibbons. The present view is that *Proconsul* could move on the ground on all fours and run quadrupedally along heavy branches. The elbow and foot anatomy of *Proconsul* is fully ape-like, but the head is primitive, with small molar teeth and long projecting canines (Figure 11.8(b)). Its diet was probably soft fruit.

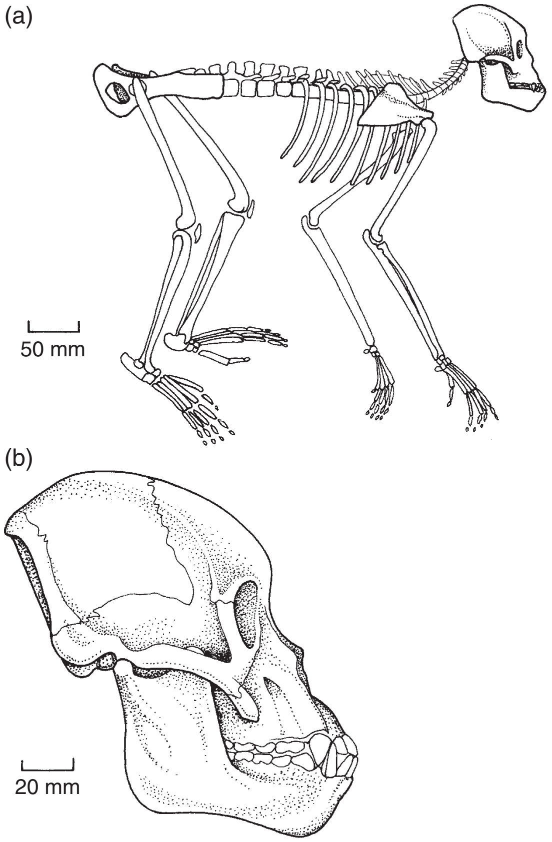


Figure 11.8 Miocene apes: (a,b) *Proconsul* skeleton (a) and skull (b). Source: (a) Adapted from A. Walker in Lewin (2005). (b) Adapted from Walker *et al.* (1983).

Proconsul is regarded as a true ape because it shows a number of derived characters shared with the modern forms, such as the absence of a tail and the relatively large brain size (150 cm^3). In addition, *Proconsul* shows a number of other ape-like characters of the teeth and modifications to strengthen the elbow joint for brachiation.

The story of ape evolution continued in Africa during the mid- and late Miocene (16–5 Myr ago), but some lines branched off and evolved separately in Europe and Asia. The gibbons, 14 species of Hylobatidae, are the most plesiomorphic of living apes, and they appear to have branched off the line to the great apes, the Hominidae, before the late Miocene, when Yuanmoupithecus is known from China, and isolated fossils are known from the Pliocene, Pleistocene, and Holocene of numerous sites across southern China (Jablonski and Chaplin, 2010).

11.4.2 Hominidae: first forms and orang-utan evolution

The living Hominidae fall into two subfamilies, the Ponginae, the two species of orang-utan and its fossil relatives, and the Homininae, five species of chimps, gorillas, and humans and their fossil relatives (see Box 11.3). This split marks a divergence in modes of locomotion from a generalized tree-climbing ancestor: the orang-utans specialized in suspension (brachiation) and slow climbing, whereas the African great apes specialized in terrestrial quadrupedalism (chimps, gorilla) and bipedalism (humans).

The first hominids (Moyà-Sola *et al*., 2009; Begun, 2010; Harrison, 2010) are the Afropithecidae, probably a paraphyletic group, including taxa such as *Kenyapithecus*, *Griphopithecus*, *Equatorius*, *Anoiapithecus* and *Afropithecus*, known mainly from eastern Africa, but also from Turkey, central Europe and perhaps Namibia, from 20 to 14 Myr ago. *Kenyapithecus*, named on the basis of teeth and jaws from Kenya, was a 1-m-tall animal that climbed trees and lived on the ground. The afropithecids were the first hominoids to spread over much of the Old World, and they may have relied on their powerful jaws and teeth to exploit a wide variety of food.

The Ponginae (orang-utans) diverged next, and they have had a long history in south-east Asia from 16 to 13 Myr ago. Close relatives of modern orang-utans include *Lufengpithecus*, known from a few skulls and huge numbers of teeth and jaws from the late Miocene of China (Chaimanee *et al*., 2003), and *Khoratpithecus*, known from a lower jaw from the late Miocene of Thailand (Chaimanee *et al*., 2004).

The Sivapithecinae are a major pongine subclade from the middle and late Miocene. The best known is *Sivapithecus* (Figure 11.9(a)) from Turkey, northern India, Pakistan and China. There were three species, ranging in size from 45 to 95 kg. *Sivapithecus* was rather like the modern orang-utan, with heavy jaws and broad cheek teeth covered with thick enamel, all of which suggest a diet of tough vegetation. There is a specialized pattern of cusps on the molar teeth (Figure 11.9(b)): there are five cusps, separated by deep grooves in a Y-shape, the so-called 'Y-5 molar'. When it was first reported in 1910, *Sivapithecus* was hailed as a 'missing link' between apes and humans, a view confirmed by a superficial comparison of palates (Figure 11.9(c–e)). Apes have a rectangular dental arcade, humans have a rounded tooth row, and the palate of *Sivapithecus* seems to form a perfect intermediate; it is definitively a pongine, based on numerous other anatomical features.

There is disagreement over the modes of locomotion of *Sivapithecus*. Perhaps it was a generalist that moved on all fours both in trees and on the ground, or perhaps some species were adapted for climbing and suspension, and others for quadrupedal locomotion. Some wrist bones even hint at knuckle walking (Begun and Kivell, 2011), which, if it is true, would imply an independent origin of a mode of locomotion seen otherwise only in gorillas and chimps.

The most remarkable sivapithecine is *Gigantopithecus* from the late Miocene of India and the Pleistocene of China. This pongine is known only from its massive heavily worn teeth and some jaw bones (Figure 11.9(f)). Such limited remains have allowed anthropologists free rein in estimating the original body size of *Gigantopithecus*. The teeth suggest it was ten times the size of

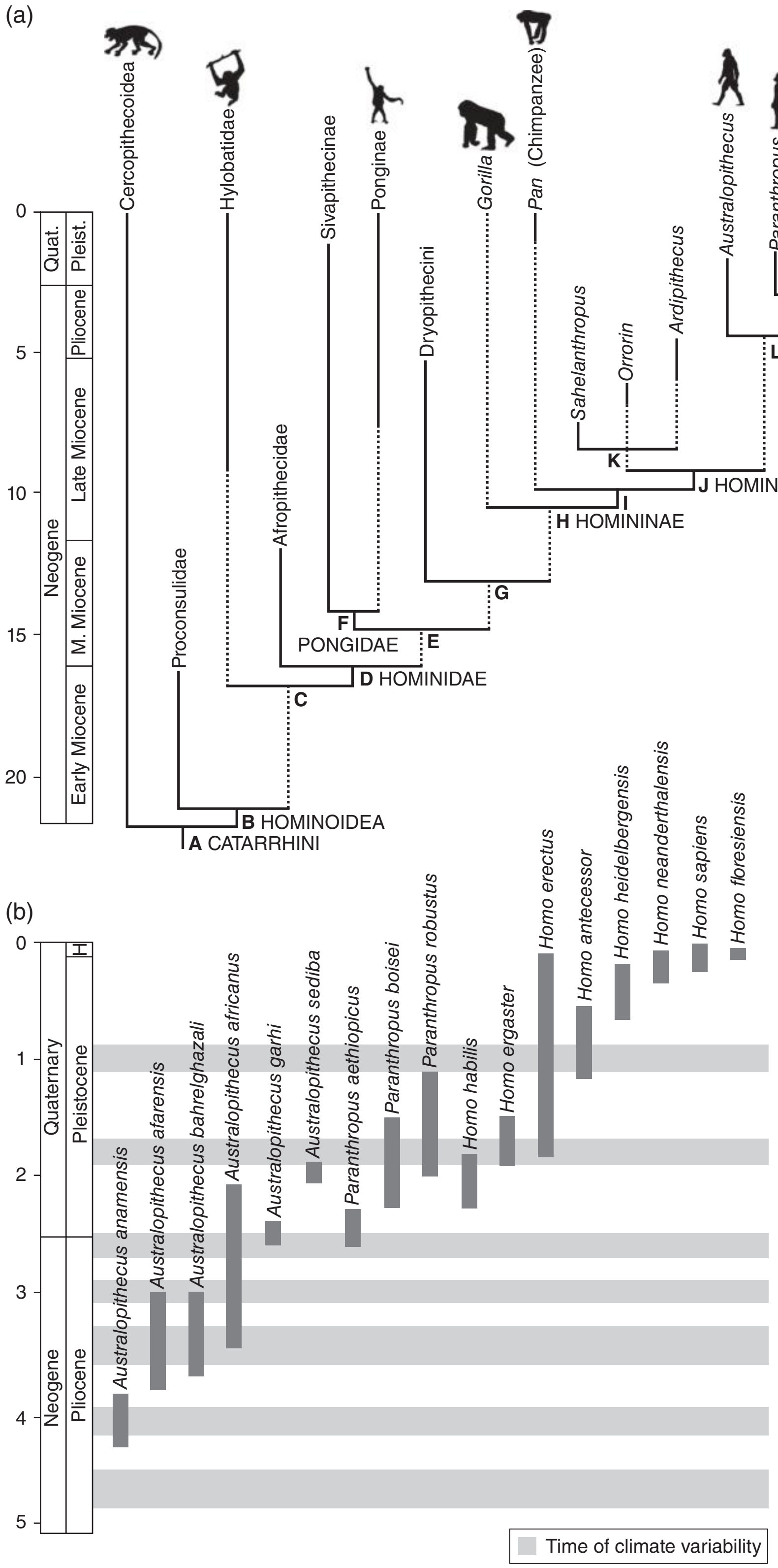
BOX 11.3 RELATIONSHIPS OF APES AND HUMANS

Until about 1980, most anthropologists assumed that humans formed a distinct lineage from the great apes, with forms such as *Sivapithecus* (*Ramapithecus)* being placed on the direct line to humans. The split between apes and humans was dated at 15–25 Myr ago, thus in the late Oligocene or early Miocene.

This view was challenged by the findings of molecular biologists. Early attempts at protein sequencing (see Section 2.5.2) in the 1960s and 1970s showed that humans were much more similar to chimps and gorillas than had been expected, and the branching point was dated at about 5 Myr ago (range of estimates, 9–4 Myr ago). At first, these dates were regarded as gross underestimates by anthropologists, but they were confirmed by later phylogenomic work using DNA sequences. The relatively late split of humans and apes was confirmed in the 1980s and 1990s by restudy of existing ape fossils, and by new specimens of *Proconsul*, *Dryopithecus* and *Sivapithecus* which showed they were side branches from the line to modern apes and humans.

In a cladogram of the apes (figure (a)), most anthropologists accept that Proconsulidae is the basal taxon, followed by the gibbons (Hylobatidae) and then the great apes and humans, Hominidae (Begun, 2010; Harrison, 2010; Williams *et al*., 2010). Within the great ape clade, all evidence confirms that chimps are closest to humans, then gorillas and then the orang-utan. This view is widely accepted, even though there is some morphological support for an African great apes clade: chimps and gorillas share numerous characters that are absent in modern humans, such as thin enamel on the teeth, an enlarged trigonid basin on the lower molars, six sacral vertebrae and ten adaptations for knuckle-walking, but these are presumably convergences or were present in the last common ancestor. Most anthropologists accept that Afropithecidae are basal hominids, perhaps followed by the Pongidae (*Sivapithecus* + orang-utan) and then the dryopithecines, although the latter had also been associated with the Ponginae.

The 17 or more species of human, divided among the genera *Australopithecus*, *Paranthropus*, and *Homo* (figure (b)), are themselves somewhat unstable as regards their content – palaeoanthropologists debate exactly which skulls and skeletons belong to which species – as well as their phylogenetic placement. The figure shows a temporal succession, with presumed close relatives placed close to each other, but no attempt is made to convert this into a cladogram. As an example of the uncertainty, most palaeoanthropologists accept that *Paranthropus* and *Homo* are clades, whereas *Australopithecus* is probably paraphyletic, but some debate, for example, whether *Homo habilis* and *Homo ergaster* are members of *Homo* or could be australopiths (e.g. Wood and Collard, 1999; Cela-Conde and Ayala, 2003; Tattersall and Schwartz, 2009; Harrison, 2010; Wood and Harrison, 2011; Strait, 2013).



Relationships of the living apes and humans: (a) cladogram showing postulated relationships, based on Begun (2010) Harrison (2010), Williams *et al*. (2010), and others. Animal silhouettes are mostly from the PhyloPic website, and we acknowledge the work of Gareth Monger, T. Michael Keesey, Smokeybjb, Mateus Zica, and Sarah Werning. Synapomorphies: **A CATARRHINI**, two premolars, sexual dimorphism is marked, males have larger canines than females; **B HOMINOIDEA**, relatively large brain size, low-crowned lower premolar 3, tail absent, scapula with elongate vertebral border and robust acromion, humeral head rounded and medially oriented; **C**, enlarged sinuses, palate deep, middle incisors spatulate, lower molars broad with low rounded cusps, clavicle elongated, very long arms relative to legs, broad sternum/broad thorax, short olecranon process and reduced styloid process on ulna, ulna shaft bowed, radial head rounded, hand with long curved proximal phalanges with distally-placed flexor insertions, opposable thumb, femur with asymmetrical condyles, iliac blade broad, calcaneum short and broad; **D HOMINIDAE**, maxillary sinus enlarged, orbits higher than broad, lengthened premaxilla, nasals elongate, narrow incisive foramen, subarcuate fossa in petrosal bone absent, incisors enlarged, upper incisor 2 spatulate, canines robust and long, molars with thick enamel, Y-5 molar, ischial tuberosities absent, hindlimbs reduced in length; **E**, zygomatic arch robust with a rugose top and three foramina; **F PONGIDAE**, narrow interorbital pillar, orbits high and narrow, great size discrepancy between upper incisors, alveolar prognathism; **G**, broad thorax, stiff lower back, powerful grasping hands; **H HOMININAE**, facial klinorhynchy (downward bending of the face on the braincase), enlarged continuous supraorbital torus (eyebrow ridge in skull), frontal sinus, adaptations for knuckle-walking, fusion of os centrale in wrist; **I**, premaxillary suture obliterated in adults, premaxillary alveolar process very elongated, nasal premaxilla very short, upper incisors all similar in shape; **J HOMININI**, bipedal posture, relatively long hindlimbs, basin-like pelvis, foramen magnum located forward in skull, large brain relative to body size, small canine teeth, U-shaped dental arcade; **K**, primitive craniofacial pattern; **L**, incisor/ lower canine step absent, canine size dimorphism reduced, thick enamel, molar row elongated, hallux (big toe) in line with other toes; **M**, enlarged brain, similar cranial base. (b) Time chart of human species, with times of climatic variability (dry-wet) indicated as horizontal shaded bands. Abbreviations: H, Holocene; M, Middle; P, Pleistocene; Quat, Quaternary.

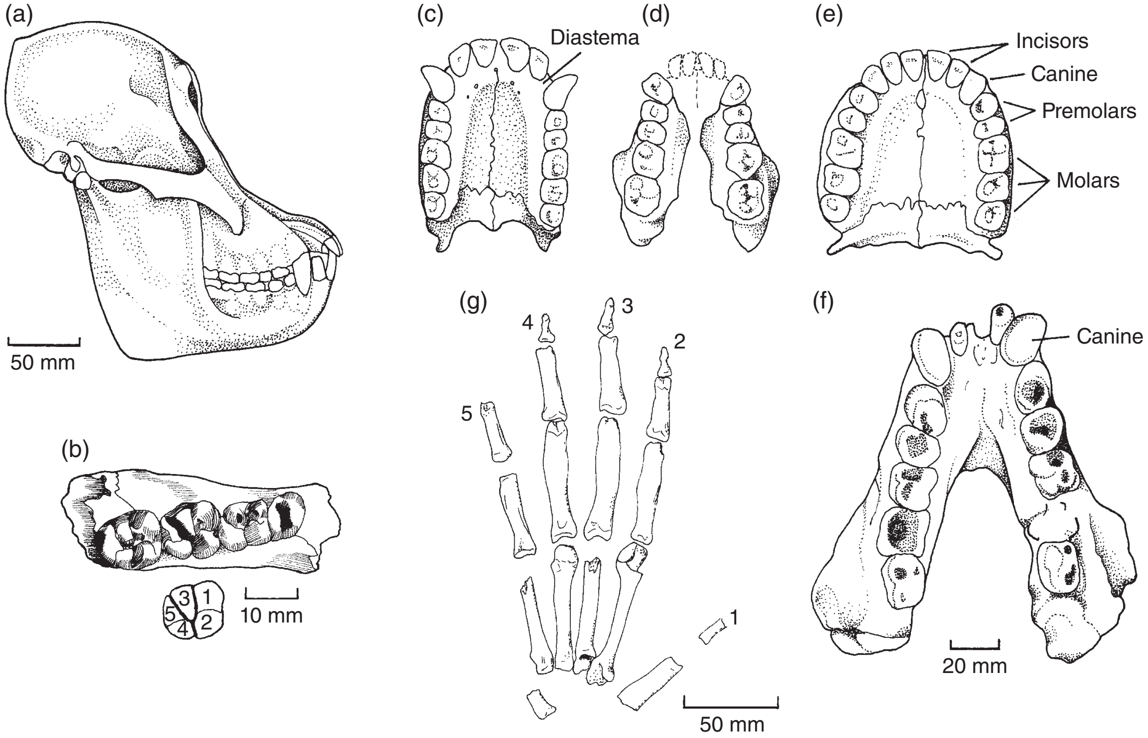


Figure 11.9 Late Miocene apes: (a) skull of *Sivapithecus*; (b) jaw fragment with molar teeth and diagrammatic representation of the Y-5 pattern; palates of (c) the chimpanzee, (d) *Sivapithecus*, and (e) modern human; (f) lower jaw of *Gigantopithecus* in occlusal view; (g) hand of *Dryopithecus*. Source: (a) Adapted from Ward and Pilbeam (1983). (b) Adapted from Gregory and Hellman (1929). (c–e) Adapted from Lewin (2005). (f) Adapted from Simons and Chopra (1969). (g) Adapted from Moyà-Solà and Köhler (1993).

Sivapithecus, and adult males might have reached heights of 2.5 m and weights of 270 kg (others estimate 3 m tall and weighing half a tonne!). This huge animal stalked the forests of south-east Asia from 5 to 0.3 Myr ago and some regard it as the source of stories of yetis in Central Asia and the big foot of North America.

11.4.3 Evolution of European and African hominids

While the pongines were diversifying in south-east Asia, the hominines were evolving in Europe and Africa. The Dryopithecini consist of a number of species of *Dryopithecus* and close relatives that invaded Europe in the middle Miocene. *Dryopithecus* was first reported in 1856 from southern France, the first fossil ape to be found. Since then, further *Dryopithecus* specimens have been found in the late Miocene (12–5 Myr ago) of Europe, from Spain to Hungary (Begun, 2010). *Dryopithecus* was adapted for suspension beneath branches and it probably swung rapidly around the subtropical forests of southern Europe. The arms, and in particular the hands (Figure 11.9(g)), are long, and the thumb and finger bones indicate that there were strong grasping muscles. Other European genera, such as *Pierolapithecus* (13 Myr ago) and *Oreopithecus* (8–6 Myr ago), may be dryopithecines. The Dryopithecini are basal hominines, close to the radiation of African apes and humans (see Box 11.3).

Until recently there was no fossil record for gorillas or chimps, until the report (McBrearty and Jablonski, 2005) of some definitive chimpanzee teeth from the middle Pleistocene of Kenya. These include two spatulate incisors, much thicker antero-posteriorly than human teeth, and a low-crowned molar, all of which have thin enamel, characteristic of *Pan*, and thinner than in *Homo*. The poor fossil record of the African great apes stands in marked contrast to that of their closest relatives, the humans.

11.5 EVOLUTION OF HUMAN CHARACTERISTICS

For centuries, many scientists tried to set humans apart from the animals. There was a heated debate in the 1850s about the features that distinguished *Homo sapiens* from the apes and other mammals, even distinguishing Bimana ('two hands'; humans) from Quadrumana ('four hands'; all other mammals). Even today, many people find it hard to accept the evidence that humans are a very young group that has had a separate evolutionary history for only 5–7 Myr. Two main sets of characters seem to set humans apart from the other apes – bipedalism and large brain size.

11.5.1 Bipedalism: humans as upright apes

Bipedalism, walking upright on the hindlimbs, has led to anatomical changes in all parts of the human body (Figure 11.10). The foot became a flat platform structure with a non-opposable

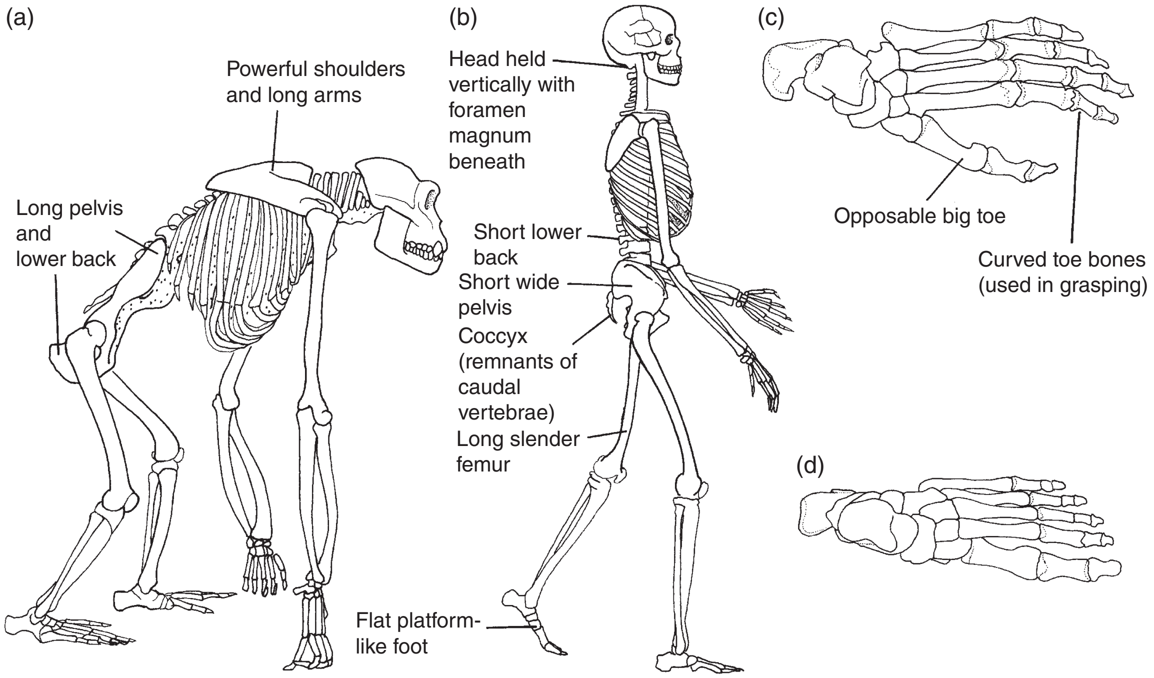


Figure 11.10 Comparison of (a) the skeleton and (c) foot of a gorilla with those (b,d) of a modern human, to show major changes in posture and the anatomical changes associated with bipedalism. Source: Adapted from Lewin (2005).

big toe and straight phalanges in the toes. Apes and monkeys have a grasping foot with curved phalanges and an opposable big toe. The angle of the human knee joint shifts from being slightly splayed to being a straight hinge, and all the leg bones are longer. The hip joint faces downwards and sideways and the femur has a ball-like head that fits into it. The pelvis as a whole is short and bowl-like as it has to support the guts, and the backbone adopts an S-shaped curve. In apes, the pelvis is long and the backbone has a C-shaped curve to brace the weight of the trunk between the arms and legs.

Bipedalism also introduced changes in the skull, as it now sat on top of the vertebral column, instead of at the front. The occipital condyles and the **foramen magnum**, the skull opening through which the spinal cord passes, are placed beneath, rather than behind, the skull roof. This makes it possible for a palaeoanthropologist to identify a bipedal hominid even from a small skull fragment in the region of the foramen magnum.

The evidence for the evolution of bipedalism includes the oldest hominin skeletons, dated as 6–4 Myr old (see Section 11.6.1), and a trackway of footprints in volcanic ash dated as 3.75 Myr old. Bipedalism probably arose 8–5 Myr ago in the hominin line, when it split from the African apes. According to one theory, the forest-dwelling Miocene apes became restricted to the west of Africa, where they gave rise to the gorillas and chimps, after the Great Rift Valley began to open up, and the apes that remained in the east had to adapt to life on the open grasslands.

A key adaptation to life in the open habitats was to stand upright in order to spot dangerous predators. Bipedal movement allowed these apes to carry food and other objects with them. The great majority of early human fossils, remains of this East African ape lineage, come from the eastern region of Africa, in a strip from southern Ethiopia, through Kenya and Tanzania, to Malawi and South Africa. This classic 'savanna hypothesis' for the origin of humans has been very actively debated; many recent authors have pointed out that early human fossils often occur in wooded habitats. However, a reanalysis of the evidence (Dominguez-Rodrigo, 2014) suggests that the rejection was wrong. Savanna habitats were not simply open grassland, but mosaic habits comprising patches of grassland and woodland, and he concludes that this is a highly plausible setting for the early evolution of bipedalism.

11.5.2 Increased brain size

The second key human character was the increase in relative brain size that occurred much later, only about 2 Myr ago with the origin of the genus *Homo*. The early bipedal humans still had rather ape-like heads with brain sizes of 400–550 cm^3, similar to apes, and by no means comparable with modern humans, who have a brain size of 1000–2000 cm^3 (mean, 1360 cm^3), a value approached by some examples of 500,000-year-old fossil *Homo*.

Various anatomical characters changed as a result of the increase in brain size. The back of the head became enlarged to accommodate it, the face became less projecting and placed largely beneath the front of the brain, rather than in front of it. Thus, the projecting face of the apes was lost with increasing brain size in the human line and this led to a shortening of the tooth rows. The rounded tooth row with a continuous arc of teeth and no gap (diastema) between the incisors and canines (see Figure 11.5(d)) is a human character.

Present fossil evidence then suggests that human evolution followed a 'locomotion-first' pattern, with bipedalism arising before 6 Myr ago and the enlarged brain less than 2 Myr ago. During of the first half of the twentieth century, though, many experts held to the more comforting 'brain-first' theory, and the fossil evidence seemed to confirm their view.

11.5.3 'Brain-first' theories of human evolution

The first fossil human specimen was a Neanderthal child's skull found in Belgium in 1828, but its importance was not realized. The first partial skeleton was found in 1856 in Germany, an injured specimen, named Neanderthal man after the Neander Valley where it was found. This poor individual became the type 'cave man', our brutish forebear, coarse of limb, hairy of body and small of brain. He grunted at his fellows, tore raw meat from the bones of prey animals, dragged his wife along by her hair and huddled miserably in caves to keep warm.

Older human remains, found in 1891 in Java, were hailed as the 'missing link' and named *Pithecanthropus erectus* (now *Homo erectus*), a primitive form. Key evidence for the 'brain-first' theory came in 1912 when a remarkable skull was found by an amateur, Charles Dawson, in southern England, at the village of Piltdown. The skull (Figure 11.11(a)) showed a large brain size of modern proportions, but the jaw was primitive, with ape-like teeth. This specimen was a godsend to the leading anthropologists of the day, the true 'missing link', clearly ancient, and yet a brainy forebear. Not only that, he was English!

In 1925, Raymond Dart announced an even more ancient skull from southern Africa, which he named *Australopithecus africanus*. It was a child's skull (Figure 11.11(b)), with a small ape-like braincase. Dart's new fossil was greeted widely with scepticism. Surely it was only a fossil ape, with nothing to do with our ancestry? Piltdown man proved the 'brain-first' model.

During the 1950s, two important chains of events overthrew the received wisdom on our ancestry. First, Piltdown man was shown to be a forgery – a recent human braincase with a modern orang-utan's jaw. The great champions of Piltdown man, the anatomists Elliot Smith and Arthur Keith, and the palaeontologists Arthur Smith Woodward and W. P. Pycraft, had died.

The second set of events took place in southern Africa, where many specimens of *Australopithecus* had been coming to light, and the weight of new material was proving harder to discount by the supporters of Piltdown. The unmasking of Piltdown in 1953 passed without any major public dispute, and scientific attention from that time onwards has focused on African fossils of early, small-brained bipedal humans.

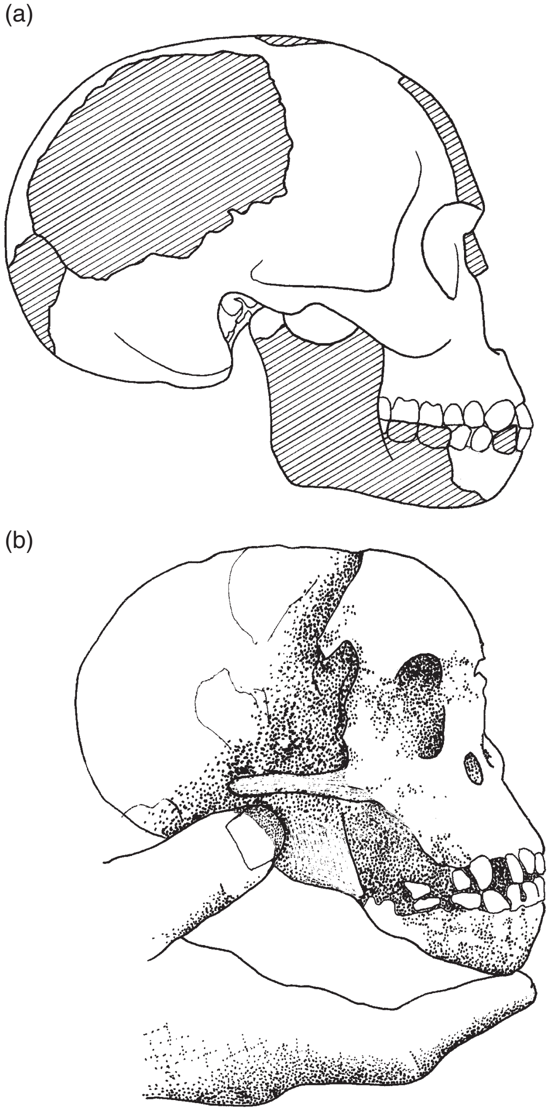


Figure 11.11 Two controversial hominid skulls of the early twentieth century: (a) Piltdown man, found in 1912, and subsequently shown to be a hoax; (b) the first skull of *Australopithecus africanus*, the Taung child, reported in 1925. Source: Adapted from various photographs.

11.6 THE EARLY STAGES OF HUMAN EVOLUTION

The line to modern humans includes as many as 22 species, four species of pre-australopiths, nine species of australopiths and nine of *Homo* (Wood and Harrison, 2011; Strait, 2013). Until 1990, the australopiths were generally all assigned to one genus, *Australopithecus*, but new finds suggest that as many as six genera is a more appropriate division: *Orrorin* and *Sahelanthropus* from the late Miocene, *Ardipithecus* and early species of *Australopithecus* from the Pliocene, and later species of *Australopithecus* and *Paranthropus* from the Plio-Pleistocene. Similarly, after a century of ever more subdivision, most anthropologists had lumped all specimens of *Homo* into three species, but current views indicate perhaps seven, or up to ten by some counts.

11.6.1 The pre-australopiths: *Orrorin*, *Sahelanthropus*, *Ardipithecus*

Until 2000, the oldest humans were Pliocene in age, 4 Myr or younger, but then a series of fossils from different parts of Africa pushed that fossil record back to 6 and 7 Myr ago. These early dates are within the range of molecular estimates for the split of humans from chimps (8–5 Myr ago), but they exceed the favoured estimate of 5 Myr ago derived from genetic analyses.

There are two ancient contenders, both announced in rapid succession by rival teams, and both from the late Miocene of Africa. First is *Sahelanthropus* from 7 Myr-old old sediments in Chad, named by Brunet *et al.* (2002) on the basis of a distorted, but nearly complete cranium (Figure 11.12) and fragmentary lower jaws. The skull shows a mixture of primitive and advanced characters: the brain size, at 320–380 cm^3, is comparable to that of chimpanzees, but the canine teeth are small, more like those of a human, and the prominent brow ridges are of the kind seen only in *Homo*. There has been some dispute about the location of the foramen magnum, whether it lies below the skull (indicating bipedality) or towards the back (ape-like quadrupedality). *Sahelanthropus* has generally been accepted, however, as a basal hominid (Cela-Conde and Ayala, 2003; Strait, 2013), perhaps the closest we will find to the common ancestor of chimps and humans.

Slightly younger is *Orrorin tugenensis*, named by Senut *et al.* (2001) from teeth, jaw fragments and broken limb bones from sediments in Kenya dated at about 6 Myr old. The teeth are rather ape-like, the arm bones indicate some ability to brachiate, but the femora suggest that *Orrorin* was an upright biped. The limited remains led to considerable controversy about the posture and affinities of *Orrorin* (e.g. Cela-Conde and Ayala, 2003), and doubts about the initial claims that it was more closely related to humans than the younger australopiths. Re-study of the *Orrorin* femurs (Richmond and Jungers, 2008) confirm they come from a biped, but not more closely related to *Homo* than to *Australopithecus*.

Equally controversial is *Ardipithecus ramidus* from Ethiopia, dating from 4.4 Myr ago and the older species *Ar. kadabba* from 5.8 to 5.2 Myr ago. *Ar. ramidus* is especially thoroughly known (White *et al.*, 2009; Suwa *et al.*, 2009; Simpson, 2013), being represented by 110 fossils, including a partial female skeleton from an individual that probably weighed about 50 kg and stood about 1.2 m tall (Figure 11.13). Brain size (300–350 cm^3) was no larger than in a modern chimpanzee of the same body mass. The numerous teeth and a largely complete skull show that *Ar. ramidus* had a small face and a reduced canine/premolar complex, suggesting minimal social aggression (modern chimpanzees and gorillas use their long canines in open-mouth threat displays). *Ardipithecus* has relatively large canine teeth, narrow molars, thin enamel and other primitive features, but these teeth are more hominine than in any of the great apes. They indicate a diet mainly of fruit and leaves.

The limb bones of *Ardipithecus* show that it could clamber about in trees, grasping branches and trunks with its hands and feet, but there were no adaptations for brachiation, vertical climbing, or knuckle walking. The limbs and forwardly placed foramen magnum show that *Ardipithecus* was a biped, but less accomplished than *Australopithecus* and *Homo*. In particular, the foot has a stiffened midfoot region and the toe joints were capable of bending upward at the end of a pace. However, the big toe is divergent, as in a modern chimp or gorilla. The foot bones also indicate that *Ardipithecus* placed its weight asymmetrically along the outer margin of the sole of the foot, as chimps do today, rather than evenly across the entire width of the foot sole, as modern humans do.

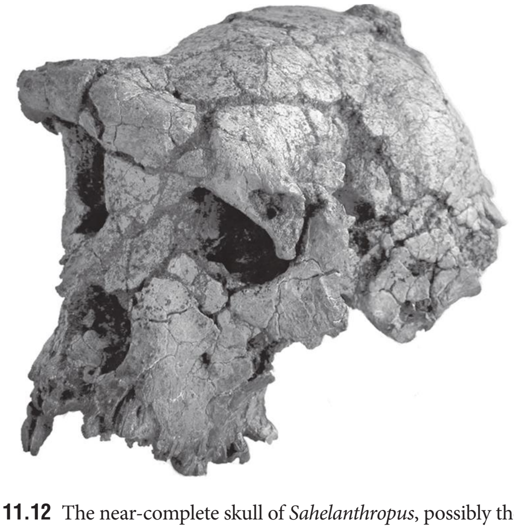


Figure 11.12 The near-complete skull of *Sahelanthropus*, possibly the oldest human ancestor, from the upper Miocene of Chad. Source: M. Brunet, Université de Poitiers, Poitiers, France. Reproduced with permission.

Figure 11.13 The early hominin *Ardipithecus ramidus*, reconstructed CT-scanned skull in anterior view. Source: © T. Michael Keesey/CC BY 2.0.

In sum, *Ardipithecus* shows that the common ancestor of chimps and humans was like neither of the modern forms, and chimps have evolved as many specializations since that point as have modern humans.

11.6.2 Early *Australopithecus*: Lucy and her relations

Basal hominins flourished in the Pliocene. Several species have been named, some of them sometimes assigned to *Praeanthropus*, a genus that had been named in 1948 for a jaw fragment from the Pliocene of Kenya (Cela-Conde and Ayala, 2003). This assignment has not been widely accepted, and most palaeoanthropologists assign these very early hominins to *Australopithecus*, which is then a long-ranging genus, known from 4.2 to 1.4 Myr ago.

Leakey *et al.* (1995) reported an ancient hominin, *Australopithecus anamensis*, from sediments 4.1–3.9 Myr old near Lake Turkana in Kenya, which appears to be an intermediate between *Ardipithecus* and later species. The remains include jaws, a humerus, a tibia and isolated teeth. It has a primitive jaw with a shallow palate and large canines. The tibia shows, however, that *Au. anamensis* was a biped. A further find of *Au. anamensis* from Ethiopia (White *et al.*, 2006) extends the age range back to 4.2 Myr ago, and includes teeth and a femur that confirm assignment to this genus and species.

The most complete, and famous skeleton of a Pliocene hominin, *Australopithecus afarensis*, was discovered by Donald Johanson and colleagues in Ethiopia in 1974. The skeleton was from a young female, nicknamed Lucy, which consisted of 40% of the bones, unusually complete by usual standards (Figure 11.14(a)). Some 240 specimens were found at Hadar in the 1970s, and since then dozens of additional specimens have been found at several localities in Ethiopia, Kenya, Tanzania, and Chad (Kimbel and Delezene, 2009). Lucy is dated as 3.2 Myr old and *Au. afarensis* specimens range from 3.7 to 3.0 Myr in age. Further specimens from Laetoli in Tanzania are dated as 3.7–3.5 Myr old. These include some bones and the famous trackway of bipedal footprints.

Australopithecus afarensis individuals are 1–1.2 m tall, with a brain size of only 415 cm^3 and a generally ape-like face. Other plesiomorphic characters include a small diastema (Figure 11.14(b)), long arms and rather short legs and curved finger and toe bones (Figure 11.14(c–e)). These curved bones imply that Lucy still

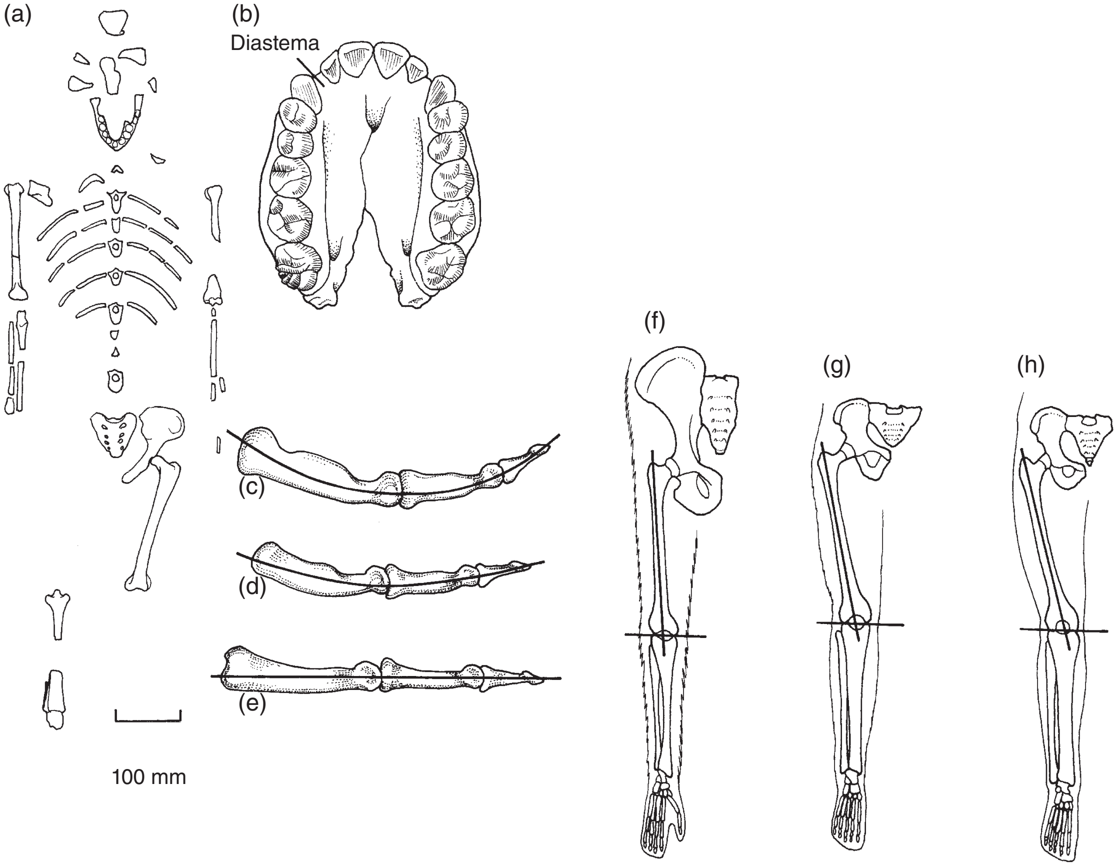


Figure 11.14 The australopiths: (a) skeleton of 'Lucy', the oldest reasonably complete hominid, *Au. afarensis*; (b) palate of 'Lucy'; fingers of (c) an ape, (d) *Australopithecus* and (e) a modern human, showing the loss of curvature, used for grasping branches; the hindlimbs of (f) an ape, (g) *Au. afarensis* and (h) a modern human, showing changes in pelvic shape, limb bone length and angle. Source: (a) Adapted from various photographs. (b,f–h) Adapted from Lewin (2005). (c–e) Adapted from Napier (1962).

used her hands and feet in grasping branches, as apes do. *Au. afarensis* is more human, though, in some significant ways: the tooth row is somewhat rounded (Figure 11.14(b)) and hindlimbs and pelvis are fully adapted for a type of bipedal locomotion (Figure 11.14(f–h)), although there is some dispute over just how 'modern' Lucy's bipedalism was (Kimbel and Delezene, 2009). The fuller collections now available show that *Au. afarensis* was a sexually dimorphic species, with males having jaws 30% larger than females.

The likely diet of *Au. afarensis* has been hotly debated, with evidence coming from tooth shape, enamel thickness, microwear patterns, and palaeoecological analysis of the surrounding sediments, but with little agreement (Kimbel and Delezene, 2009). Stable carbon isotopic analyses of 20 *Au. afarensis* samples from different localities in Ethiopia shows that these individuals had eaten considerable quantities of C_4/crassulacean acid metabolism foods, that is foods derived from grasses, sedges, and succulents, all of which are common in tropical savannas and deserts (Wynn *et al.*, 2013). This marks a major step in hominid evolution. Earlier hominins had fed on leaves, fruits and nuts from trees. With the expansion of grasslands at least 1 Myr earlier, massive new plant food resources had become available, but had not yet been exploited by early humans. In this sense, *Au afarensis* was the first human to take advantage of the richest food resources in its new savanna home.

A further hominin fossil is *Kenyanthropus platyops* from 3.5-Myr-old rocks in Kenya (Leakey *et al.*, 2001), based on a relatively complete cranium. The face is flatter than in *Au. afarensis* and the skull differs in further details, although White (2013) suggests this is most likely a distorted specimen of *Au. afarensis*.

11.6.3 The later australopiths

The australopiths lived on in Africa through the late Pliocene and earliest Pleistocene, from about 3.6 to 1.1 Myr ago, and there were as many as seven species; *Australopithecus africanus*, *Au. sediba*, and *Paranthropus robustus* from southern Africa, *Au. garhi*, *P. boisei* and *P. aethiopicus* from eastern Africa (Ethiopia, Kenya, Malawi) and *Au. bahrelghazali* from Chad (Roberts, 2011; Reed *et al.*, 2013). There were two size classes of australopiths living in Africa at the same time (Figure 11.15), the lightly built, or gracile, *Au. africanus*, which was typically 1.3 m tall, 45 kg in body weight and had a brain capacity of 445 cm^3, and the heavier *P. aethiopicus*, *P. robustus* and *P. boisei*, which were 1.75 m tall, 50 kg in body weight and had a brain capacity of 520 cm^3.

These australopiths show advances over *Australopithecus afarensis* in the flattening of the face, the loss of the diastema and the small canine teeth. They show some specializations that place them off the line to modern humans. For example, the molars and premolars are more massive than in *Au. afarensis* or *Homo*, and they are covered with layers of thick enamel, adaptations in this lineage to a diet of tough plant food. After many years of collecting new remains of *Au. africanus*, ever since 1925 (see Section 11.5.3), palaeontologists have now added new australopithecines to the roster, including *Au. sediba* (see Box 11.4).

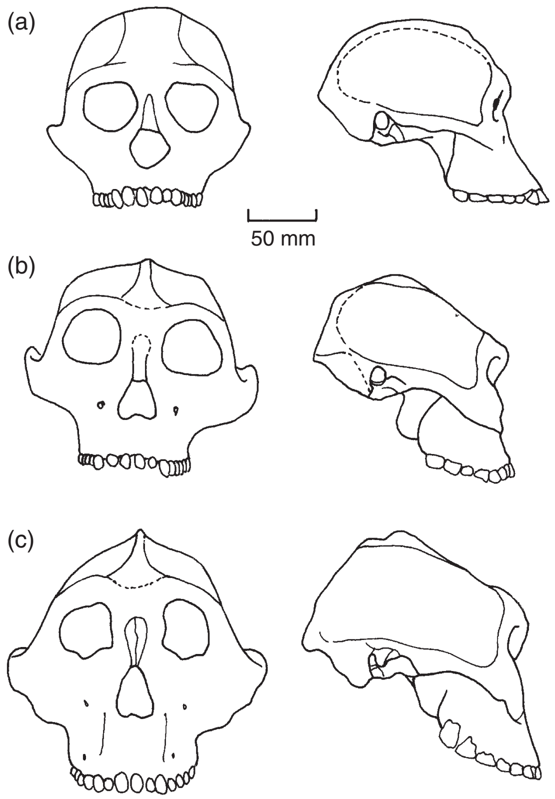


Figure 11.15 Skull proportions of the australopiths: skulls of (a) *Australopithecus africanus*, (b) *Paranthropus robustus* and (c) *P. boisei* in anterior (top) and lateral (bottom) views. Source: Adapted from Tobias (1967).

The robust australopiths, species of *Paranthropus*, have broad faces, huge molar and premolar teeth and a heavy sagittal crest over the top of the skull in presumed males (Figure 11.15(b)). These are all adaptations for powerful chewing of tough plant food. The sagittal crest supports this interpretation because it marks the upper limit of jaw muscles that were much larger than in *Au. africanus* or in *Homo*. The robust australopiths may have fed on tough roots and tubers, and the gracile *A. africanus* perhaps specialized on soft fruits and leaves in the wooded areas.

11.6.4 *Homo habilis* and *H. rudolfensis*: the first of our line?

A lower jaw and other skull and skeletal remains found in 1960 and 1963 in the Olduvai Gorge, Kenya by Louis Leakey and others, could be the oldest species of our own genus, *Homo*. This hominid had a large brain, in the range of 630–700 cm^3, and its hands had the manipulative ability to make tools, hence its name *Homo habilis* (literally 'handy man'). A more complete skull (Figure 11.16) found ten years later near Lake Turkana (formerly Lake Rudolf) in Kenya, by Richard Leakey, was also

BOX 11.4 *AUSTRALOPITHECUS SEDIBA*: TRANSITIONAL FOSSIL

A new australopithecine, *Au. sediba* (Berger *et al*., 2010; Berger, 2013), from the Malapa site in South Africa, dated at just under 2 Myr ago, appears to be in some way intermediate between other gracile australopithecines and *Homo*. The first fossil was found in August 2008, by Matthew Berger, son of Lee Berger, a palaeoanthropologist at the University of the Witwatersrand, Johannesburg, South Africa. Matthew had found a hominid clavicle, and when his father Lee turned over the rock, he reported, 'sticking out of the back of the rock was a mandible with a tooth, a canine, sticking out. And I almost died.'

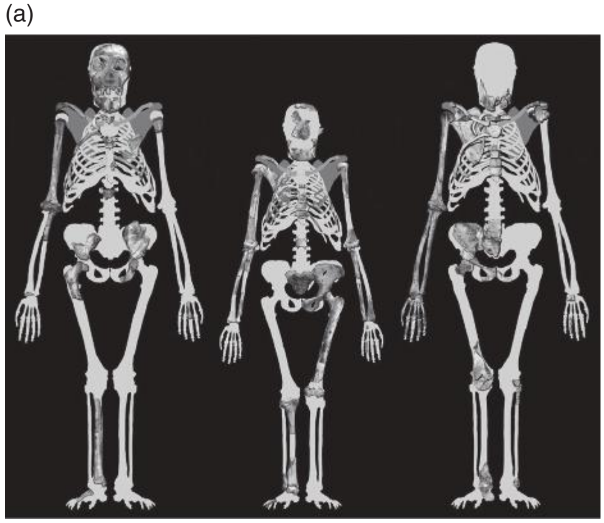
After several subsequent field seasons, Berger and his team extracted remains of six skeletons, an adult male, an adult female, a juvenile male, and three infants. These six early humans were all found together at the bottom of Malapa Cave, where they had apparently all fallen to their death. Because their skeletons lay where they had fallen, the scientists were able to extract a great deal of information about how they had lived. For example, there were tiny plant remains trapped in the dental plaque of some individuals, which pointed to specific parts of their diet.

The *Au. sediba* remains show a mosaic of australopithecine and *Homo* characters (Berger, 2013). For example, the teeth are similar to *Au. africanus*, but the mandibular remains differ in size and shape from that species, and approach *Homo* in some aspects. The arm is more primitive, however, sharing with other australopiths adaptations for arboreal climbing and possibly suspension. The rib cage is rather ape-like in being narrow, quite unlike the broad cylindrical chest of humans, and the shoulders were narrow and high, giving something like the 'shrugged' shoulder appearance of standing African apes. On the other hand, the vertebrae of the lumbar region indicate a long and flexible back as in *Homo erectus,* and unlike *Au. africanus*.

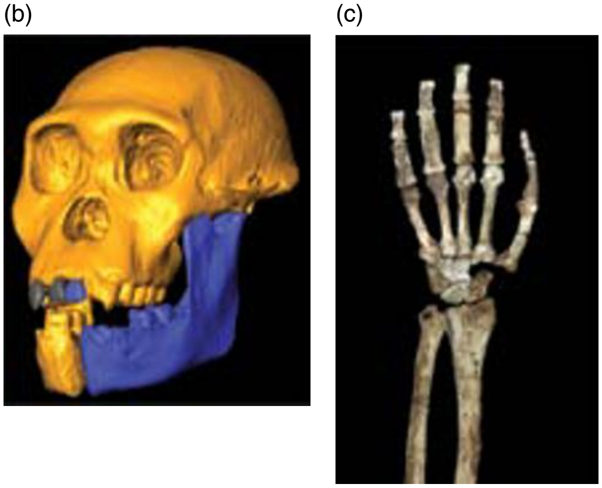
The *Au. sediba* hindlimb is particularly odd. The detailed anatomy of the heel, foot, knee, hip, and back differ from all other hominins, but in combination they suggest bipedal walking, but perhaps with a mode that differs from other species of *Australopithecus* and *Homo*. In detail, perhaps *Au. sediba* walked with a fully extended leg and with an inverted foot during the swing phase of bipedal walking. It probably did not place the foot flat on the ground, as we do, but the lateral side of the foot touched the ground first, and then as the rest of the foot touched down, there was a substantial rotation around the joints of the foot. In particular, there was extreme transfer of the weight of the body in a medial (inwards) direction, termed hyperpronation.

Au. sediba lived on the South African savannah of 2 Myr ago, side-by-side with several other early hominin species, feeding on grasses, as well as fruits and nuts. Its brain size of 420 cm^3 is at the high end of the range for *Au. africanus*, but much less than any *Homo*. Whether this species is truly intermediate between *Australopithecus* and *Homo* is debated, but the six skeletons have offered a remarkable opportunity for highly detailed studies of the anatomy of an early hominin, comparing males, females, and infants.

The detailed descriptions of *Australopithecus sediba* are available as a series of papers in the online edition of *Science*, at: http://www.sciencemag.org/site/extra/sediba/index.xhtml.



Skeleton and skull of *Australopithecus sediba*: (a) the juvenile male, Malapa hominin 1 (MH1) left, Lucy (AL 288-1) centre, and the adult female, Malapa hominin 2 (MH2) right;



(b) reconstruction of the MH1 skull; (c) hand and forearm. See Colour plate 11.4. Source: L.R. Berger, University of the Witwatersrand, Johannesburg, South Africa. Reproduced with permission. (a,c) Image created by P. Schmid, Anthropological Institute, University of Zurich, Switzerland. (b) Reconstruction by K. Carlson, University of the Witwatersrand, Johannesburg, South Africa.

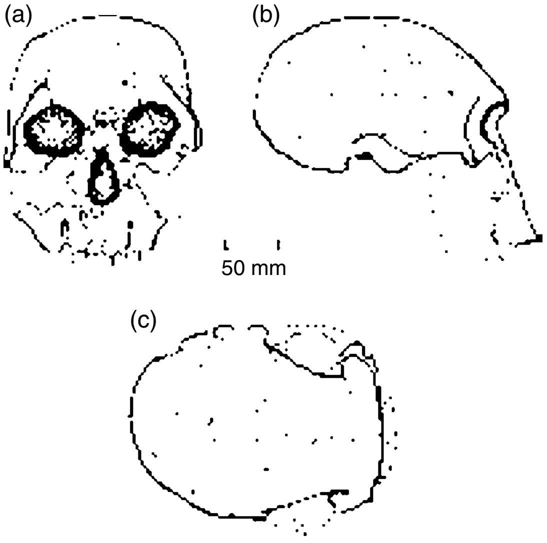


Figure 11.16 The skull of *Homo rudolfensis* in (a) anterior, (b) lateral and (c) dorsal views. Source: Adapted from Day *et al.* (1974).

assigned to *H. habilis*. This specimen showed a brain size of about 700 cm^3.

The identity of these early *Homo* specimens from Olduvai and Lake Turkana has been much debated, whether there were two or more *Homo* species living side-by-side in East Africa, *H. habilis* at Olduvai and Lake Turkana specimens, and *H. rudolfensis* also at Lake Turkana specimens (Leakey *et al.*, 2012), or whether there is serious over-inflation of species names (White, 2013). *H. habilis* and *H. rudolfensis* (Figure 11.16) are distinguished on the basis of a number of characters. *H. rudolfensis* has a larger mean brain size, but appears to be primitive in other skull features (smaller 'eyebrow ridge', palate large). Many palaeoanthropologists question whether these two species are really members of the genus *Homo*, and they emphasize their many australopith characters (e.g. Wood and Collard, 1999; Tattersall and Schwartz, 2009).

The remains of *H. habilis* and *H. rudolfensis* are dated as 2.4–1.5 Myr old and they have been found in association with the remains of various species of australopith. This conjures up the striking notion of four or five different human species living side by side and presumably interacting in various ways.

11.7 THE PAST TWO MILLION YEARS OF HUMAN EVOLUTION

Human beings spread out of eastern and southern Africa perhaps as long ago as 1.9 Myr, seemingly for the first time. Until then, all known phases of evolution of the australopiths and *Homo* seem to have taken place in the part of Africa between Ethiopia and South Africa.

11.7.1 *Homo erectus* – the first widespread human

A new hominin species arose in Africa about 1.9 Myr ago that showed advances over *H. habilis*. The best specimen, and one of the most complete fossil hominid skeletons yet found (Figure 11.17(a)), was collected in 1984 by Richard Leakey and colleagues on the west side of Lake Turkana, Kenya. The pelvic shape shows that the individual is a male and his teeth show that he was about 12 years old when he died. He stood about 1.6 m tall and had a brain size of 830 cm^3. The skull (Figure 11.17(b)) is more primitive than *H. sapiens* because it still has large eyebrow ridges and a heavy jaw with no clear chin. The skeleton seems largely modern and fully bipedal in adaptations.

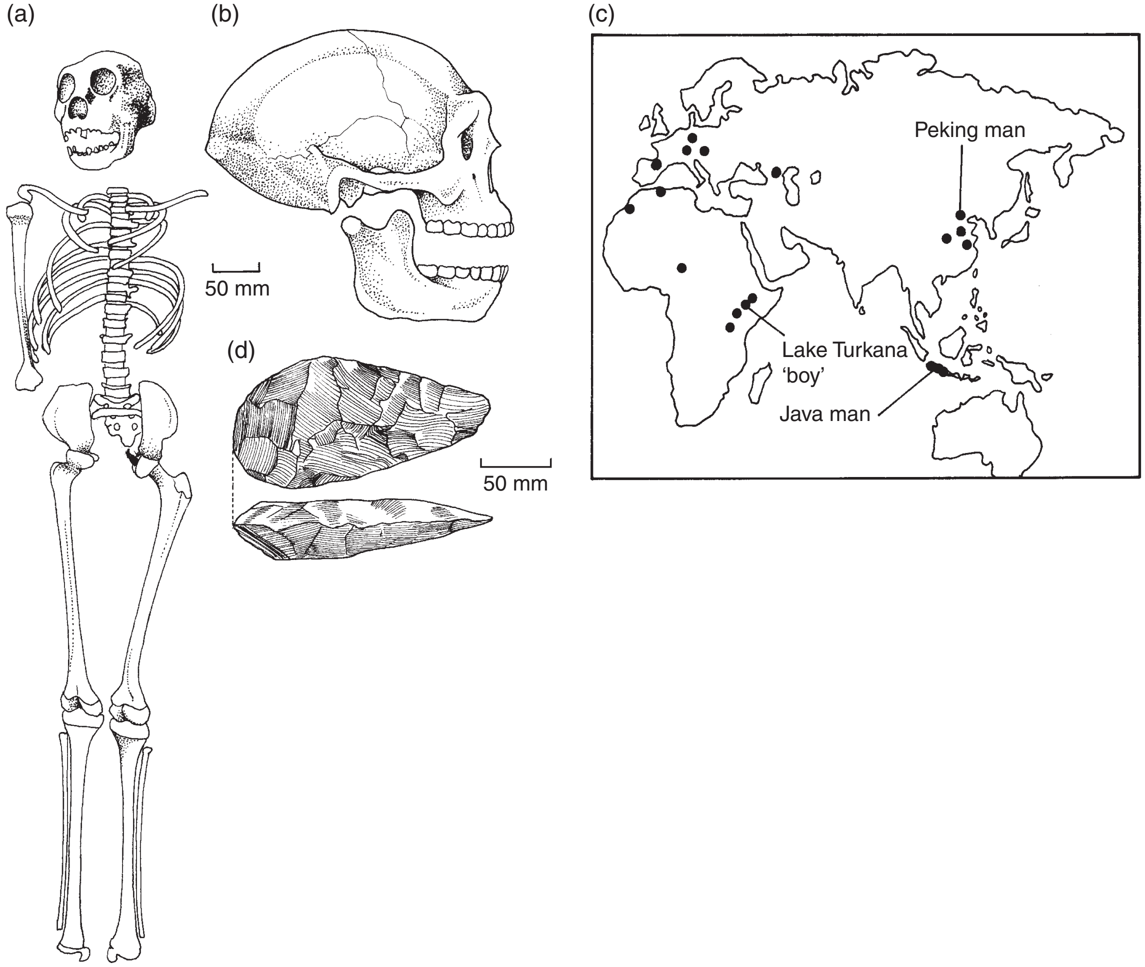


Figure 11.17 Finds of *Homo ergaster* (a) and *H. erectus* (b): (a) the skeleton of a youth from Lake Turkana, Kenya; (b) skull of Peking man; (c) map showing the distribution of finds of *H. erectus* and *H. ergaster*; (d) Acheulean hand axe. Source: (a) Adapted from a photograph. (b) Adapted from Black (1934). (c) Adapted from Delson (1985). (d) Adapted from Savage and Long (1986).

This remarkable early find from Africa was assigned to *Homo erectus*, but it might more appropriately be retained in a separate primitive species, *H. ergaster* (Klein, 2009; Wood, 2012), and the name *H. erectus* is used only for younger and more specialized material. This includes fossils from eastern and southern Africa dating from 1.6 to 0.6 Myr ago, as well as specimens from other parts of the world.

But when did *Homo* first leave Africa? Until recently, the oldest fossils of *H. erectus* from outside Africa were dated at about 1.25 Myr ago, and dates from 1.25 to 0.5 Myr ago were assigned to numerous localities in North Africa, Asia and Europe (Figure 11.17(c)). Then, discoveries from Dmanisi in Georgia, in the Caucasus area east of Turkey, overturned this idea: they were dated at 1.8–1.7 Myr ago. The remains include partial skeletons of females, males, and juveniles, with males 1.5 m tall and with a brain volume of 610–775 cm^3. They were initially assigned to the new species *Homo georgicus* (Vekua *et al.*, 2002), but were later recognized as a subspecies, or even local variant of *Homo erectus* (Lordkipanidze *et al.*, 2005; Tattersall and Schwartz, 2009; Hublin, 2014).

Homo erectus evidently spread across Europe and Asia at about this time. Some Chinese materials are dated at 1.9 Myr, and they comprise isolated teeth and jaw fragments from cave deposits. Re-dating of the famous specimens of Java man have also yielded more ancient dates, in the range 1.6–1.8 Myr ago. If these ages are confirmed, it is evident that *H. erectus* set out from Africa much nearer 2 Myr ago, than 1 Myr ago. Further, the Java *H. erectus* may have survived until very recently, perhaps 50,000 years ago, hence probably overlapping with the first *Homo sapiens* to reach the area (Baba *et al.*, 2003).

One of the richest sites for *H. erectus* is the Zhoukoudian Cave near Beijing in China, the source of over 40 individuals of 'Peking Man' (Figure 11.17(b)). They were found in cave deposits dating from 0.8 to 0.2 Myr ago and seem to show an increase in mean brain size from 900 to 1100 cm^3 during that time. The cave was thought to have provided evidence for a number of major cultural advances, including the use of fire, but the evidence has since been shown to be unreliable. Older evidence for the use of fire by *H. erectus* is reported from a cave site in South Africa dated as 1.5–1.0 Myr ago.

Homo erectus sites elsewhere show that these peoples manufactured advanced tools and that they foraged and perhaps hunted in a cooperative way. *Homo erectus* in East Africa perhaps made the Acheulean tools, which date from 1.5 Myr ago. These show significant control in their execution with continuous cutting edges all round (Figure 11.17(d)). The older Oldowan tools of East Africa, dated from 2.6 to 1.5 Myr ago and generally ascribed to *H. habilis*, *H. ergaster* and *H. rudolfensis*, are simple and rough, consisting of rounded pebbles with usually only one cutting edge. The Oldowan and Acheulean industries were often classed together as early Palaeolithic ('Old Stone Age').

11.7.2 Middle Pleistocene hominins

Palaeoanthropologists have long been puzzled over a series of large-brained humans that lived in the Middle Pleistocene of Africa and Europe, side by side with *Homo erectus*. These forms differ substantially from *H. erectus* and must be assigned to the roots of modern *H. sapiens*, but currently there is little agreement about what to call them or their placement in the phylogeny (Rightmire, 2013).

The first of these to be named was *Homo heidelbergensis*, for a jawbone found in Germany in 1907. Since then, further similar, advanced human remains have been recovered from the middle Pleistocene of Africa and Europe in rocks dated from 0.6 to 0.2 Myr ago. English remains consist of a tibia and some teeth, associated with Acheulean tools. These perhaps indicate a unique radiation of humans in the mid-Pleistocene of Europe that were more derived than *H. erectus*, but ancestral to the Neanderthals. The African specimens, skulls and postcranial remains from Ethiopia, Zambia and South Africa, used to be termed 'archaic *Homo sapiens*'. They date from 0.6 to 0.4 Myr ago. These forms, showing apparently intermediate characters between *H. erectus* and *H. sapiens*, may also belong to *H. heidelbergensis*.

Recent finds from Spain have been interpreted in different ways. The famous Atapuerca sites have yielded jaws and partial skulls from an ancient cave dated as 0.8–1.2 Myr old (Blain *et al.*, 2013). Tools associated with the Spanish fossils indicate a pre-Acheulean industry. These peoples have been named *Homo antecessor*, members of a species that is claimed to include the common ancestors of Neanderthals and modern *Homo sapiens*. However, it is still debated which of the Spanish materials belong to *H. heidelbergensis* or *H. antecessor*, and whether some of the younger (0.4–0.6 Myr) specimens might even represent early populations of *H. neanderthalensis* (Tattersall and Schwartz, 2009; Stringer, 2012b).

11.7.3 The Neanderthal peoples

The first Neanderthal was reported from Germany in 1856 (see Section 11.5.3) and originally regarded as a dim-witted slouching brute, but actually had a larger brain capacity (mean 1450 cm^3) than many modern humans (mean 1360 cm^3). The heavy eyebrow ridges, massive jaws and large teeth compared with modern *H. sapiens* (Figure 11.18(a, b)) could mean little more than that Neanderthals were merely a coarsely-built race of *Homo sapiens*. Indeed, it has been remarked that if a Neanderthal man were shaved and dressed in modern clothes, he would pass unnoticed on a busy city street (Figure 11.18(c))! However, the morphological distinctiveness of Neanderthals suggests they are a distinct

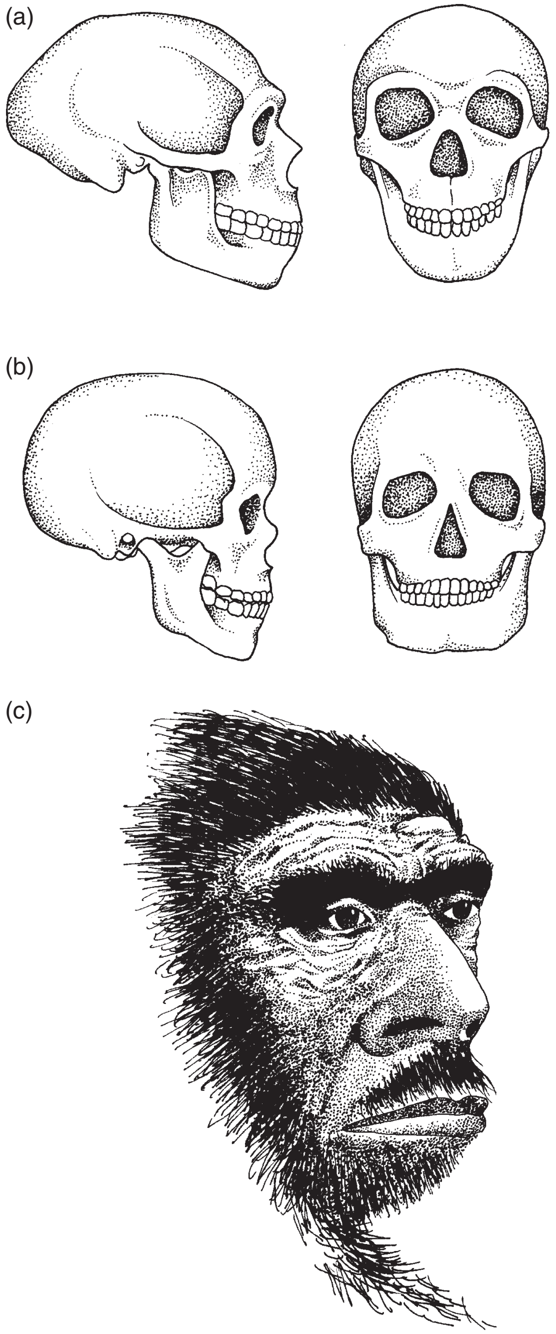


Figure 11.18 Comparing *Homo neanderthalensis* and *Homo sapiens*: skulls of (a) Neanderthal and (b) modern humans, in lateral and anterior views; (c) restoration of the head of a Neanderthal man. Source: (a,b) Adapted from Lewin (2005). (c) Adapted from Savage and Long (1986).

species (Wood and Collard, 1999; Tattersall and Schwartz, 2009; Stringer, 2012b; Wood, 2012), and this was confirmed by an early study of Neanderthal DNA (Krings *et al*., 1997), which showed that Neanderthals separated from modern humans some 0.6 Myr ago. Since 1997, there have been remarkable advances in understanding of the Neanderthal genome (see Box 11.5), and these help resolve the question of how Neanderthals relate to modern humans, and how many Neanderthals lived at any time.

Neanderthals have been found in Europe and Asia as far east as Uzbekistan, and in the Middle East, in sites dated as 200,000–27,000 years old (Tattersall and Schwartz, 2009). The most abundant remains come from France and central Europe and, in their most extreme form, they are associated with phases of the later Ice Ages that covered much of the area. A robust compact body is better able to resist the cold than our generally more slender form.

Neanderthals were culturally advanced in many ways (Finlayson, 2010; Gamble, 2011; Monnier, 2012; Papagianni and Morse, 2013). For example, they made a variety of tools and weapons from wood, bone and stone, the Mousterian (Middle Stone Age, Middle Palaeolithic) culture of Europe. These include delicate spearheads, hand axes, scrapers for removing fat from animal skins and pointed tools for making holes in skins and for engraving designs on bone and stone, a total of 60 or so tool types. Neanderthals also made clothes from animal skins, used fire extensively, lived in caves or bone and skin shelters and perhaps even had ritual. At Le Moustier in France, a teenage boy was buried with a pile of flints for a pillow and a well-made axe beside his hand. Ox bones were nearby, which suggests that he was buried with joints of meat as food for his journey to another world. It is hotly debated whether Neanderthals could have formed words or made language-like sounds.

The Neanderthals disappeared about 27,000 years ago; their last refuge may have been in northern Spain and southwest

BOX 11.5 NEANDERTHAL AND DENISOVAN GENOMICS

At one time it would have seemed an impossible dream, to sequence the entire genome of a fossil species. And yet, since the initial work in 1997, knowledge of the Neanderthal genome has grown exponentially (Hawks, 2013). In that first study, Krings *et al*. (1997) sequenced a 360-base-pair (bp) section of the mitochondrial DNA (mtDNA) of the original 1856 Neanderthal specimen. Thirteen years later, Green *et al*. (2010) reported 5.5 billion bp of nuclear DNA sequence data from six Neanderthals, and partial or complete mtDNA sequences from more than 20 other specimens.

Mitochondrial DNA occurs in the mitochondria of cells, and hence mtDNA is passed down only in the female line. Nuclear DNA (nDNA) is transmitted through the egg and the sperm to any offpsring, but sperm do not transfer mitochondria. Initial studies focused on sequencing mtDNA because the scale is more manageable (human mtDNA contains 16,600 bp and codes for 37 genes, whereas human nDNA comprises 3 billion bp and codes for 20,000 genes) and rates of change are slower, so the analysis is not confused by numerous small population-scale mutations. However, nDNA is the stuff of evolution, and newer work has reported Neanderthal nDNA, the genome of this extinct species (Green *et al*., 2006, 2010; Noonan *et al*., 2006).

Sequencing ancient DNA has always been technically very difficult. In some early efforts, analysts confidently announced DNA from Mesozoic insects, plants, and even dinosaurs. However, all those early studies from the 1990s were flawed by massive contamination. Even a microscopic droplet of sweat, a sneeze, a particle of a modern organism can be multiplied by the polymerase chain reaction (PCR) equipment and entirely invalidate the analysis. There are only a small number of reliable ancient DNA laboratories in the world, and these must carry out no PCR work on modern genomes. The labs are sterilized every night. In fact, ancient DNA can be recovered from specimens only up to a few hundred thousand years, not millions of years, because the DNA rapidly breaks into tiny fragments (Dabney *et al*., 2014).

The new genomic work shows that Neanderthal and modern human genomes are about 0.15% different from each other, and so about 99.85% genetically similar (Green *et al*., 2010; Sankararaman *et al*., 2014). To put this in context, any randomly selected pair of modern human genomes are about 0.1% different, whereas humans and chimpanzees are about 2% different. Among living humans, non-Africans are more similar than Africans to Neanderthals, but overall, the Neanderthal genome is always more different from modern human genomes than the differences between genomes of any modern humans. This all suggests that Neanderthals share some common ancestry with Europeans and Asians, but less with Africans.

Comparison of genomes of contemporary humans can suggest the actual population sizes. Whereas there are 7 billion humans today, all *Homo sapiens*, the genomic variation of Neanderthals suggests population sizes as low as a few hundred corresponding to the Mousterian culture in France, with as few as 10,000 Neanderthals across Europe for most of their existence, and at most 40,000 in the late Palaeolithic across Europe and western Asia (Hawks, 2013).

Ancient human genomes include another, unusual, example, from Denisova Cave in the Altai Mountains in central Siberia, where samples were taken from teeth and isolated finger bones of a juvenile female who lived 41,000 years ago. The genome differs from the Neanderthal and modern human sufficiently to provide evidence for a whole population of ‘Denisovans’, which differ as much genomically from modern humans as do the Neanderthals (Krause *et al*., 2010; Reich *et al*., 2010; Hawks, 2013). The Denisovans show closest relationship to modern indigenous peoples of Australia and New Guinea. These studies have highlighted that genomic data can reveal whole human populations – even species – represented by minimal skeletal material. The Denisovans are fast becoming as much talked about as the Neanderthals, and yet they have no face.

France. It is not clear whether they were seen off by the loss of cold-weather habitat as the ice sheets retreated, or whether they were slaughtered by more modern *H. sapiens* of our own type (Klein, 2003). Although the initial molecular evidence (Krings *et al.*, 1997) suggested that Neanderthals did not interbreed with the interlopers, more recent studies (Green *et al.*, 2010; Pääbo, 2014) have shown that modern European and Asian DNA contains 1–4% Neanderthal genes. Indeed, some of those Neanderthal genes are associated with keratin formation, and so may have survived in Europeans and Asians in cold climates as a means of maintaining hair growth (Sankararaman *et al.*, 2014). This suggests that before Neanderthals became extinct, some, at least, interbred with modern humans.

11.7.4 Modern *Homo sapiens*

When did our own species originate? Undisputed modern *Homo sapiens* fossils were known from several sites in Africa and Israel dated as 195,000–100,000 years old (Figure 11.19). The earliest possible example of *H. sapiens* is the partial cranium Omo 1 from southern Ethiopia (Figure 11.19(d)), dated at 195,000 years ago, although it lacks critical characters of the brow and chin that distinguish *H. sapiens* from other hominin species (Tattersall and Schwartz, 2009). Slightly younger is the 160,000-year-old Herto skull, also from Ethiopia, which shows some very modern features (White *et al.*, 2003), but others are uncertain (Tattersall and Schwartz, 2009). Other skulls from

Figure 11.19 Diverse later Pleistocene Homo crania, in anterior view: (a) Guattari 1, Monte Circeo, Italy; (b) Skull 5, Simo de los Huesos, Atapuerca, Spain; (c) Cro-Magnon 1, Les Eyzies-de-Tayac, France; (d) Cast of Omo 1, Omo Kibish, Ethiopia. See Colour plate 11.5. Source: Tattersall and Schwartz (2009). Reproduced with permission.

Jebel Qafzeh in Israel, include the definitively *H. sapiens* Qafzeh 9 skeleton, dated at 93,000 years. In all such cases, it can be hard to distinguish primate species from limited remains of the skull and skeleton.

Modern *H. sapiens* spread into Europe from 40,000 to 30,000 years ago. The early European forms, often known as the Cro-Magnon peoples (Figure 11.19(c)), brought their advanced Upper Palaeolithic tools and filled the caves of France and northern Spain with paintings and carved objects. They must have seen Neanderthals and much has been made of such possible encounters. A child's skeleton from Lagar Velho in Portugal has been put forward as evidence for hybridization, and DNA evidence (see Box 11.5) suggests that modern Europeans and Asians share some genetic heritage at least with Neanderthals, showing evidence of interbreeding.

Modern *H. sapiens* then spread truly worldwide from about 40,000 years ago (Figure 11.20), reaching Russia and travelling across Asia to the southeast Asian islands and Australia (Diamond and Bellwood, 2003). How these relate to the unique, dwarfed Flores hominins (see Box 11.6) is still much debated. The date of arrival of modern humans in Australia was often reckoned to be 40,000–30,000 years ago, but the Malakunanja

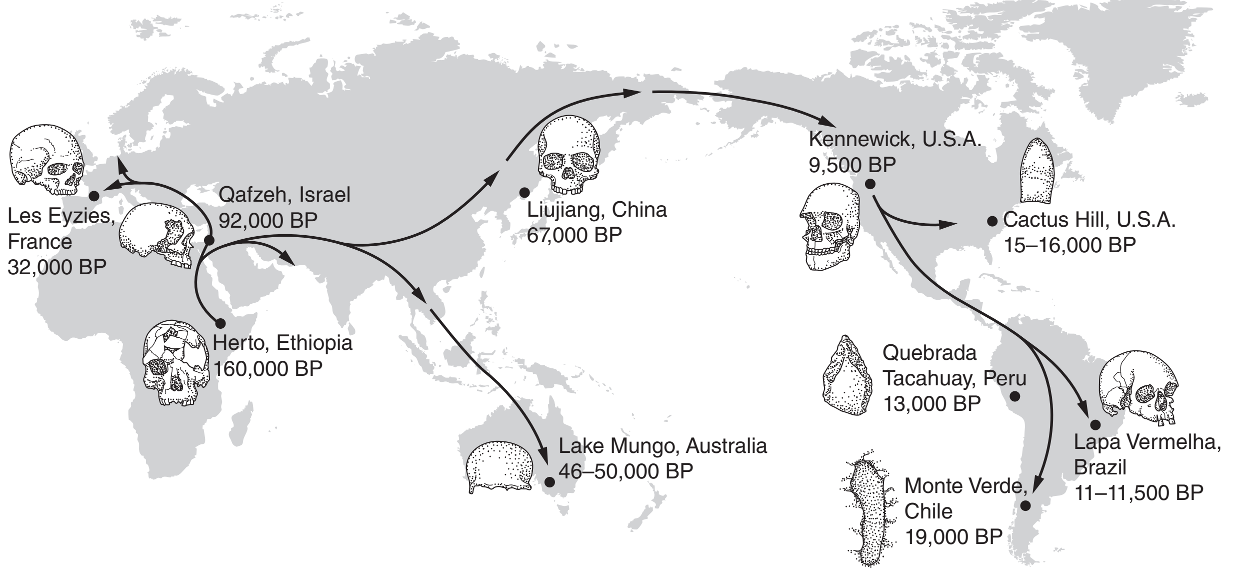


Figure 11.20 The spread of modern *Homo sapiens* out of Africa in the past 100,000 years. Key finds and oldest dates are shown. Source: Adapted from various sources.

BOX 11.6 THE FLORES HOBBIT

One of the most sensational human fossil finds has been Flores man, or the 'hobbit', a population of tiny modern humans from Flores Island, in Indonesia. The first fossils were collected in 2003 by a joint Australian-Indonesian team (Brown *et al*., 2004), and they have proved controversial ever since: are these the remains of a tiny, but distinct human species that lived alongside *Homo sapiens*, or are they a local variant or even diseased population of *Homo sapiens*?

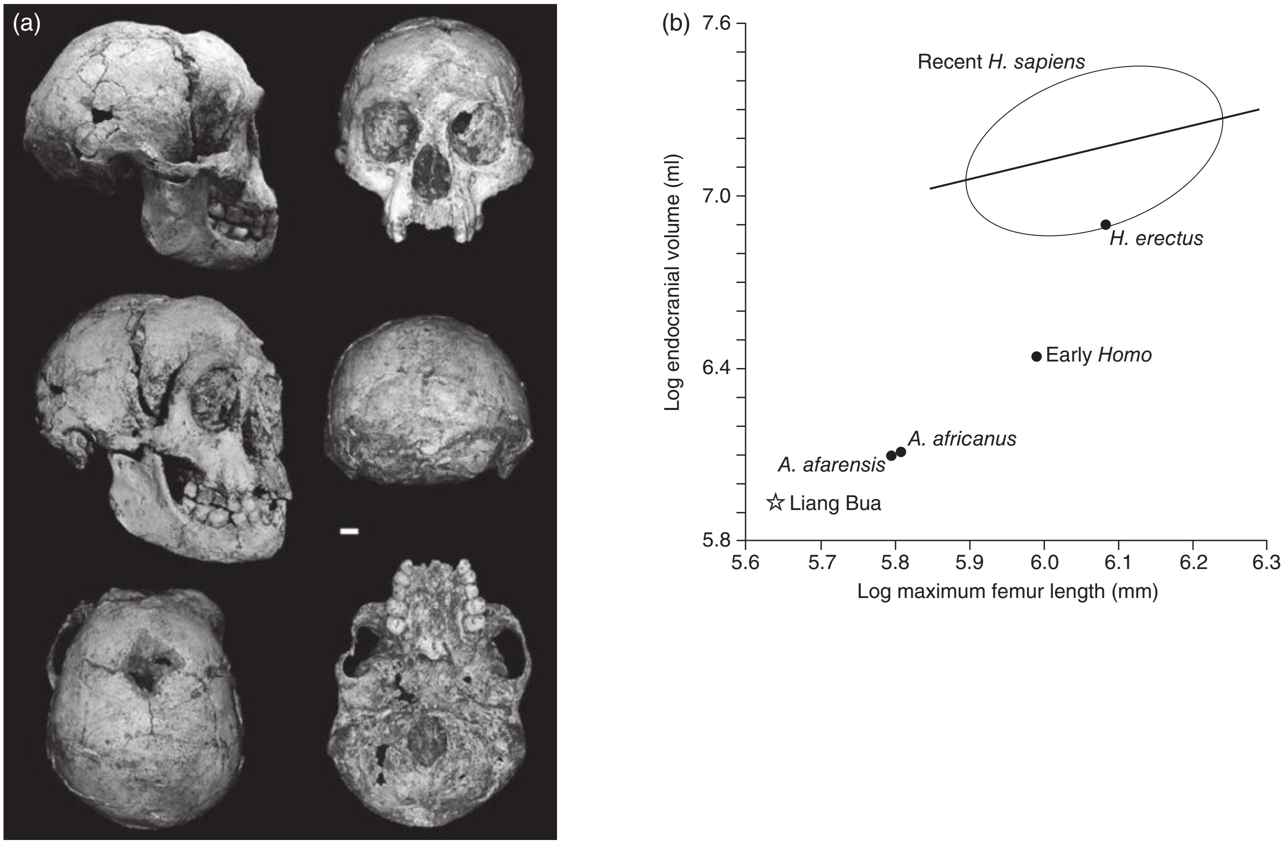
The fossils were found deep below the floor of the Ling Bua cave, comprising remains of eight skeletons, dating from 38,000 to 13,000 years ago. Adult individuals measured 0.9-1.1 m tall, just over half the height of *Homo sapiens* individuals. The skeletons were found associated with sophisticated (but small) stone tools, as well as remains of the elephant *Stegodon*, as well as giant rats, Komodo monitors, and other large extinct lizard species. Other localities show that *Homo sapiens* reached Indonesia 45,000 years ago, so our own species must have encountered their smaller, forest-dwelling relatives for many thousands of years.

In the original description, the hobbit was named *Homo floresiensis*, a definite new species, distinguished from *H. sapiens* by the smaller size, smaller brain capacity, aspects of the teeth, absence of a chin, and differences in the head of the humerus. The body size range of 0.9–1.1 m is definitively less than even the smallest of modern races of *Homo sapiens* (1.4–1.5 m), and body mass estimates suggest an even greater distinction, with *H. floresiensis* estimated at 25 kg adult weight, much smaller than *H. sapiens* (60–80 kg) and even than *H. erectus* (50–60 kg). The brain size of *H. floresiensis* was remarkably small, at 426 cm^3, much less than the modern human range (mean, 1360 cm^3), placing the hobbit in the range of chimpanzees and australopiths, and well below the measure in any other example of the genus *Homo*. Proportional to body size, the relative brain size is just human, but primitive, lying between that of *H. erectus* and the great apes.

Since 2004, there have been scandals about damage to the original specimens and about difficulties of access (once described, fossils should be publicly available for all researchers). More significant though has been the debate about whether the Flores population really represents a distinct species or not. There have been claims that these were in some way an unusual human population, where all individuals were microcephalics (a condition in modern humans where the head size is reduced), or suffered from Laron's syndrome (a genetic disorder that reduces head size), or were endemic cretins perhaps suffering from hypothyroidism caused by a lack of iodine in their diet. All such claims of genetic disorders, diseases, and disordered growth seem unlikely in that all individuals share the morphological features, but also the specific osteological indications of the different diseases have been refuted (Brown, 2012).

The Flores humans have been the subject of lively debate (Aiello, 2010; Montgomery, 2013), and these debates are likely to continue for a while. The stakes are high; this could be the only human species to have survived until relatively recently side-by-side with our own species.

Follow the unfolding story of the discovery and subsequent disputes about *Homo floresiensis* on the *Nature* news pages, here: http://www.nature.com/news/specials/flores/index.html.



Skull and relative size of *Homo floresiensis*: (a) The LB1 skull and mandible, the first-found specimen from an adult female, in lateral and three-quarter views, and the cranium in dorsal, anterior, posterior, and ventral views; (b) Comparison of the relative body size (x-axis) and brain volume (y-axis) for the Flores cranium ('Ling Bua') and various hominins, including modern humans. Source: Brown *et al*. (2004). Reproduced with permission from Nature Publishing Group.

site, in the northwest, source of stone tools and evidence of pigment use, dates back to 60,000 years ago (Bird *et al*., 2013).

The timing of the peopling of North America is highly controversial (Meltzer, 2009). Ice sheets retreated from the area of Beringia (Siberia and Alaska) and there was an ice-free land bridge from Siberia to Alaska from 18,000 to 10,200 years ago. Hundreds of North American archaeological sites with tools of the Clovis industry date from 11,500 years ago, but a human occupation site at Monte Verde in southern Chile dates back to 14,600 years ago, suggesting rapid migration down the length of the Americas long before the makers of the Clovis points. Human faeces from the Paisley Caves, Oregon date to 14,200–14,000 years ago, and other human remains of this age have now been reported (Curry, 2012). Ancient DNA evidence also confirms these dates, showing that humans entered North America after the end of the last glacial maximum, whether they island hopped from Asia to North America, or used boats to work down the coast.

The palaeontological and archaeological evidence then suggests that modern *H. sapiens* has populated the world, from a birthplace in Africa or the Middle East, in the last 60,000 years or so. This would imply that the modern human races have differentiated in this very short time. Confirming evidence has come from molecular studies, which find that there are only minute inter-racial genetic differences. Several studies of human DNA have also suggested an African origin for all human races 200,000–100,000 years ago. In the original study, Cann *et al.* (1987) analysed the mitochondrial DNA (mtDNA) of 147 people from different parts of the world. They found that there was only 0.3–0.4% variation among the mtDNAs of these individuals, regardless of their racial origin, and this low level of variation calibrates to the figure of 200,000 years for the origin of modern *Homo sapiens*. Such studies of mtDNA necessarily concern only the female line of descent, which is why the common ancestor of all modern humans is sometimes called, rather picturesquely, African Eve.

Models for modern human origins have been in constant flux, not least because of the paucity of data. At one time, for example, the modern races were traced back to different geographic variants of *Homo erectus*, so positing an independent history of 1 Myr for modern Africans, Europeans, and Asiatic peoples. However, the combination of fossil, genomic, and cultural evidence has convinced most that modern humans diverged some 200,000 years ago from an African ancestral population, and began their long trek round the globe about 100,000 years ago – termed the 'single, recent origin' or 'Out of Africa' model (Stringer and Andrews, 1988). There is still much uncertainty about the various ancestral *Homo sapiens* fossils from Africa and the Middle East, about the role of interbreeding with Neanderthals and the mysterious Denisovans (see Box 11.5), and the timing of movements of human populations round the world, and how these geographically isolated human populations relate to modern genomic 'clans' (Stewart and Stringer, 2012).

The record of human evolution seems to show an ever-quickening pace of change. Major innovations have occurred ever more rapidly: bipedalism (10–5 Myr ago), enlarged brain (3–2 Myr ago), stone tools (2.6 Myr ago), wide geographical distribution (2–1.5 Myr ago), fire (1.5 Myr ago), art (35,000 years ago), agriculture and the beginning of global population increase (10,000 years ago). The rate of population increase was about 0.1% per annum at that time, rising to 0.3% per annum in the eighteenth century and about 2.0% per annum today. In other words, the total global human population will more than double during the lifetime of individuals born today. In numerical terms at least, *Homo sapiens* has been a spectacularly successful species!

11.8 FURTHER READING

Fuller accounts of modern primate biology and anatomy include Ankel-Simons (2007), Campbell *et al.* (2010), Setchell and Curtis (2011), and Fleagle (2013), and modern primates are surveyed by Redmond (2010) and Petter (2013). Hartwig (2008) gives a detailed survey of fossil primates. Basic texts on human evolution include Lewin and Foley (2003), Lewin (2005), Wood (2005), Klein (2009), Roberts (2011), Stringer and Andrews (2011), Boyd and Silk (2012), Conroy and Pontzer (2012), Stringer (2012a), and Tattersall (2013), and Gibbons (2007) and Reader (2011) tell the often highly colourful stories of the palaeoanthropologists in search of our ancestors, and glory. Two excellent encyclopedias of human evolution, with contributions by the world's leading palaeoanthropologists, are Delson *et al.* (2002) and Begun (2013). Reed *et al.* (2013) explore aspects of the palaeobiology of *Australopithecus*, and an array of recent books deals with Neanderthals (e.g. Finlayson, 2010; Papagianni and Morse, 2013; Pääbo, 2014) and the origins of modern human races (Oppenheimer, 2004; Stringer, 2012a). The definitive account of all hominid fossils is Schwartz *et al.* (2005).

An excellent introduction to everything concerning modern primates is at: http://www.alltheworldsprimates.org/Home.aspx. There are many portals that provide reports and summary diagrams about human evolution, such as: http://www.bbc.co.uk/sn/prehistoric_life/human/human_evolution/, http://www.becominghuman.org/, and http://www.newscientist.com/topic/human-evolution. Some museum offerings on human evolution include: http://www.nhm.ac.uk/nature-online/life/human-origins/ andhttp://humanorigins.si.edu/resources/intro-human-evolution. See a video about the investigation of the early hominin *Ardipithecus* here: http://www.sciencemag.org/content/326/5949/60.2.full. Digital images of hominid fossils may be accessed at: http://paleo.eva.mpg.de/, http://peabody2.ad.fas.harvard.edu/skhul/, http://www.virtual-anthropology.com/3d_data/3d-archive/3d_data/free_data, and https://www.nespos.org/display/openspace/Home.

QUESTIONS FOR FUTURE RESEARCH

1 Are plesiadapiforms primates or relatives of dermopterans or scandentians?
2 How rapidly did Primates diverge in the Palaeocene and early Eocene?
3 What were the relationships and ecological roles of the diverse Eocene primates, including the adapiforms and omomyids?
4 When did lemurs reach Madagascar, and how did these early primates diversify their ecological roles to take over modes of life not normally occupied by primates?
5 What is the early history of anthropoids, including the origins of Old World and New World monkeys?
6 How and when did the platyrrhines reach South America? Was it a single migration, or more, and when did modern forms diversify?
7 Why were apes so diverse in the Miocene, how did they divide up their different ecological roles, and how do they relate to modern hominoids?
8 How did pongids evolve, especially the exctinct sivapithecines and the enigmatic *Gigantopithecus*?
9 Were the major steps in hominid evolution in Africa driven by changes in climate and vegetation?
10 Where do Neanderthals fit into the pattern of evolution of modern humans?
11 How and when did modern human populations reach different parts of the world, and how did these modern forms interact with Neanderthals, Flores persons, and other hominin species they encountered?

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Appendix: Classification of the Vertebrates

The classification given below is a 'conservative cladistic' scheme based upon the cladograms described in this book. The hierarchical ranking (indenting) of the group names gives an indication of the ranking of taxa in the cladogram. There have been proposals to avoid naming the ranks of taxa (e.g. 'Arthrodira', 'Dipnoi'), but rank names are used here (e.g. 'Order Arthrodira', 'Order Dipnoi') in order to provide a broad marker to the relative positions of clades within the hierarchical scheme. The proposal is perfectly reasonable because particular ranks mean nothing in terms of magnitude, history, or comparability, but they provide a ready guide to subordination and are retained here. Further, there is a debate about the use of traditional group names, such as Archosauria or Mammalia, whether they should be used in an inclusive sense to indicate the clade that is closest to the original definition of the name, or in an exclusive sense to refer to the crown-group clade only, that is the minimal clade defined by the closest common ancestor of all living forms. The former usage is generally employed here. Fishes, amphibians, reptiles, birds, and mammals are tabulated separately. All groups named below are monophyletic, except for a very small number of commonly used paraphyletic group names (marked *). All groups have living members, unless they are marked †. Where the sequencing of groups is uncertain, they are indicated as *sedis mutabilis*.

Classifications are based on overviews by Donoghue *et al.* (2000), Janvier (2008), and Heimberg *et al.* (2010) for agnathans; Maisey (1986), Donoghue *et al.* (2000), Brazeau (2009), Davis *et al.* (2012), Swartz (2012), and Zhu *et al.* (2013) for extinct gnathostomes; Coates and Sequeira (2001) and Grogan *et al.* (2012) for chondrichthyans; Hurley *et al.* (2007), Wiley and Johnson (2010), Nakatani *et al.* (2011), Xu and Wu (2012), Near *et al.* (2012), Betancur-R *et al.* (2013), Chen *et al.* (2013) for actinopterygians; Ruta *et al.* (2003a,b), Ahlberg *et al.* (2005), Daeschler *et al.* (2006), Coates *et al.* (2008), and Schoch (2013) for sarcopterygians and amphibians; Hopson and Kitching (2001), Rauhut (2003), Wilson (2005), Langer and Benton (2006), Botha *et al.* (2007), Joyce (2007), Butler *et al.* (2008), Carrano and Sampson (2008), Bronzati *et al.* (2012), Carrano *et al.* (2008), Jones *et al.*, (2103) for reptiles; Mayr and Clarke (2003), Mayr (2011), McCormack *et al.* (2013), and O'Connor and Zhou (2013) for birds; and Luo *et al.* (2002, 2011), Asher *et al.* (2009), Zhou *et al.* (2013), and O'Leary *et al.* (2013) for mammals.

1 CLASSIFICATION OF THE FISHES

- Phylum Chordata
  - Subphylum Tunicata (Urochordata)
  - Subphylum Cephalochordata (Acraniata)
  - Subphylum Vertebrata (Craniata)
    - *Class 'Agnatha'
      - Subclass Myllokunmingiida
      - Subclass Cyclostomata
        - Infraclass Myxinoidea
        - Infraclass Petromyzontida
      - †Subclass Conodonta
      - †Subclass Pteraspidomorphi

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  - Order Astraspida
  - Order Arandaspida
  - Order Heterostraci
- †Order Anaspida
- †Order Thelodonti
- Subclass unnamed
  - †Order Galeaspida
  - †Order Osteostraci
  - †Order Pituriaspida
- Infraphylum Gnathostomata
  - †*Class Placodermi
    - Order Acanthothoraci
    - Order Rhenanida
    - Order Antiarchi
    - Order Petalichthyida
    - Order Ptyctodontida
    - Order Phyllolepida
    - Order Arthrodira
  - †Class Acanthodii
  - Class Chondrichthyes
    - Subclass Elasmobranchii
      - Infraclass unnamed
        - †Family Cladoselachidae
        - †Order Symmoriiformes
      - Infraclass Euselachii
        - †Order Xenacanthiformes
        - †Order Ctenacanthiformes
        - †Order Hybodontiformes
        - Cohort Neoselachii
          - Division Galeomorphi
            - Order Heterodontiformes
            - Order Orectolobiformes
            - Order Lamniformes
            - Order Carcharhiniformes
          - Division Squalea
            - Order Hexanchiformes
            - Order Echinorhiniformes
            - Order Squaliformes
            - Superorder Hypnosqualea
              - Order Squatiniformes
              - Order Pristiophoriformes
              - Superorder Batoidea
    - Subclass Subterbranchialia
      - †Order Petalodontiformes
      - †Order Eugeneodontiformes
      - †Order Iniopterygiiformes
      - †Order Chondrenchelyiformes
      - Superorder Holocephali
      - Class Osteichthyes
    - Subclass Actinopterygii
      - †Family Cheirolepididae
      - Family Polypteridae
      - Infraclass Actinopteri
        - †Family Mimiidae
        - †Family Stegotrachelidae

- †Family Ptycholepididae
- †Superfamily unnamed
  - Family Redfieldiidae
  - Family Amphicentridae
  - Family Dorypteridae
- Superdivision Chondrostei
  - †Family Birgeriidae
  - †Family Saurichthyidae
  - †Family Chondrosteidae
  - Order Acipenseriformes
    - Family Acipenseridae
    - Family Polyodontidae
  - †Order Scanilepiformes
  - Superdivision Neopterygii
    - †Order Pholidopleuriformes
    - †Order Perleidiformes
    - †Family Peltopleuridae
    - †Family Thoracopteridae
    - Division Ginglymodi
      - †Order Semionotiformes
      - Order Lepisosteiformes
    - †Order Pycnodontiformes
    - Division Halecostomi
      - Subdivision Halecomorphi
        - †Family Parasemionotidae
        - Family Amiidae
      - †Family Dapediidae
      - †Family Pholidophoridae
      - †Family Leptolepidae
      - Subdivision Teleostei
        - †Family Pachycormidae
        - †Family Aspidorhynchidae
        - †Family Ichthyodectidae
        - Infradivision Elopocephala
          - Cohort Elopomorpha
            - Order Anguilliformes
          - Cohort Osteoglossomorpha
            - Order Osteoglossiformes
          - Cohort Clupeocephala
            - Subcohort Otocephala
              - Division Clupeomorpha
                - †Order Ellimmichthyiformes
                - Order Clupeiformes
              - Division Ostariophysi
                - Order Gonorhynchiformes
                - Order Cypriniformes
                - Order Characiformes
                - Order Siluriformes
                - Order Gymnotiformes
            - Subcohort Euteleostei
              - Order Salmoniformes
              - Infracohort Neognathi
                - Order Esociformes
                - Division Neoteleostei
                  - Order Stomiiformes

- Subdivision Eurypterygii
  - Order Aulopiformes
  - Infradivision Ctenosquamata
    - Order Myctophiformes
    - Infrasubdivision Acanthomorpha
      - Superorder Paracanthopterygii
        - Order Polymixiiformes
        - Order Percopsiformes
        - Order Gadiformes
        - Order Zeiformes
        - Order Stylephoriformes
      - Superorder Acanthopterygii
        - Series Atherinomorpha
          - Order Beryciformes
          - Order Holocentriformes
        - Series Percomorpha
          - Order Ophidiiformes
          - Order Batrachoidiformes
          - Order Gobiomorpharia
          - Order Scombrimorpharia
          - Order Scombriformes
          - Order Carangimorpharia

- Subclass Sarcopterygii
  - Infraclass Unnamed
    - †Order Onychodontida
    - Order Actinistia
  - Infraclass Dipnomorpha
    - †*Youngolepis*
    - †*Dipterus*
    - Order Dipnoi
  - Infraclass Tetrapodomorpha
    - †*Tungsenia*
    - †*Kenichthys*
    - †Family Rhizodontidae
    - †Family Osteolepididae
    - †*Eusthenopteron*
    - †*Tristichopterus*
    - †*Panderichthys*
    - †*Tiktaalik*
    - Superclass Tetrapoda

2 CLASSIFICATION OF THE EARLY TETRAPODS AND AMPHIBIANS

- Superclass Tetrapoda
  - †Family Elginerpetontidae
  - †*Ventastega*
  - †*Acanthostega*
  - †*Ichthyostega*
  - †*Tulerpeton*
  - †Family Colosteidae
  - †Family Crassigyrinidae
  - †Family Whatcheeriidae
  - †Family Baphetidae
  - Class Neotetrapoda

- Superorder Batrachomorpha
  - †Order Edopoidea
  - †Family Dendrerpetontidae
  - Order Unnamed
    - †Suborder Dvinosauria
    - †Family Branchiosauridae
    - †Family Dissorophidae
    - Infraclass Lissamphibia
      - †Family Albanerpetontidae
      - Order Gymnophiona
      - Order Urodela
      - Order Anura
  - †Order Unnamed
    - Family Eryopidae
    - Family Actinodontidae
    - Family Archegosauridae
    - Family Rhinesuchidae
    - Suborder Capitosauria
    - Suborder Trematosauria
      - Family Trematosauridae
      - Family Metoposauridae
      - Family Plagiosauridae
      - Family Rhytidosteidae
      - Family Brachyopidae
      - Family Chigutisauridae
- Superorder Reptiliomorpha
  - †Order Embolomeri
  - †Family Gephyrostegidae
  - †Order Seymouriamorpha
  - †Superorder Lepospondyli
    - Order Microsauria
    - Order Lysorophia
    - Order Adelospondyli
    - Order Aïstopoda
    - Order Nectridea
  - Order Unnamed
    - †Order Diadectomorpha
    - Series Amniota

3 CLASSIFICATION OF THE EARLY AMNIOTES AND REPTILES

- Series Amniota
  - Class Synapsida
    - †Order Unnamed
      - Family Ophiacodontidae
      - Family Varanopidae
    - Order Unnamed
      - †Suborder Caseasauria
        - Family Eothyrididae
        - Family Caseidae
      - Suborder Unnamed
        - †Family Edaphosauridae
        - †Family Sphenacodontidae
        - Order Therapsida

- †Suborder Biarmosuchia
- †Suborder Dinocephalia
- †Suborder Anomodontia
- †Suborder Gorgonopsia
- †Suborder Therocephalia
- Suborder Cynodontia
  - †Family Procynosuchidae
  - †Family Galesauridae
  - †Family Thrinaxodontidae
  - Infraorder Cynognathia
    - †Family Cynognathidae
    - †Family Diademodontidae
    - †Family Traversodontidae
  - Infraorder Probainognathia
    - †Family Chiniquodontidae
    - †Family Probainognathidae
    - Infrasuborder Mammaliamorpha
      - †Family Tritheledontidae
      - †Family Tritylodontidae
      - Class Mammalia (see below)

- Class Reptilia
  - Subclass Parareptilia
  - †Family Mesosauridae
  - †Family Millerettidae
  - †Family Bolosauridae
  - †Family Procolophonidae
  - Order Pareiasauromorpha
    - †Family Nycteroleteridae
    - †Family Pareiasauridae
  - Subclass Eureptilia
    - †Family Captorhinidae
    - †*Paleothyris*
    - †*Hylonomus*
    - Infraclass Diapsida
      - †Family Araeoscelididae
      - †Family Weigeltisauridae
      - †Order Younginiformes
      - Infraclass Neodiapsida
        - Order Testudinata (Chelonia)
          - †*Odontochelys*
          - †Family Proganochelyidae
          - †Family Australochelyidae
          - †Family Meiolaniidae
          - Suborder Testudines
              - Infraorder Pleurodira
              - Infraorder Cryptodira
                - †Family Pleurosternidae
                - †Family Baenidae
                - Superfamily Chelonioidea
                - Superfamily Trionychoidea
                - Superfamily Testudinoidea
        - Infraclass Lepidosauromorpha
          - Infrasubclass Unnamed
            - †Infraclass Ichthyosauria
            - †Order Thalattosauria

    - Superorder Lepidosauriformes
      - Order Rhynchocephalia
        - Family Sphenodontidae
        - †Family Pleurosauridae
      - Order Squamata
        - Infraorder Gekkota
        - Infraorder Scincoidea
        - Infraorder Lacertoidea
        - Infraorder Amphisbaenia
        - Infraorder Anguimorpha
        - Infraorder Iguania
        - Suborder Serpentes (Ophidia)
  - †Infrasubclass Sauropterygia
    - Order Placodontia
    - Order Eosauropterygia
      - Suborder Pachypleurosauria
      - Suborder Nothosauria
    - Order Plesiosauria
      - Suborder Plesiosauroidea
        - Family Plesiosauridae
        - Family Elasmosauridae
        - Family Cryptoclididae
        - Family Leptocleididae
        - Family Polycotylidae
      - Suborder Pliosauroidea
        - Family Rhomaleosauridae
        - Family Pliosauridae
- Infraclass Archosauromorpha
  - †Family Trilophosauridae
  - †Order Rhynchosauria
  - †Order Protorosauria
  - Division Archosauriformes
    - †Family Proterosuchidae
    - †Family Erythrosuchidae
    - †Family Euparkeriidae
    - Subdivision Archosauria
      - Infradivision Crurotarsi
        - †Order Phytosauria
        - †Family Ornithosuchidae
        - †Family Stagonolepididae
        - †Family Rauisuchidae
        - †Superfamily Poposauroidea
        - Superorder Crocodylomorpha
          - †Family Saltoposuchidae
          - †Family Sphenosuchidae
          - Order Crocodylia
            - †Family Protosuchidae
            - Division Mesoeucrocodylia
              - †Subdivision Thalattosuchia
                - Family Teleosauridae
                - Family Metriorhynchidae
              - †Subdivision Metasuchia
                - †Infradivision Notosuchia
                  - Family Peirosauridae
                  - Family Mahanjungasuchidae

  - Infrasubdivision Ziphosuchia
    - Family Notosuchidae
    - Family Sebecidae
- Infradivision Neosuchia
  - †Family Dyrosauridae
  - †Family Goniopholididae
  - †*Bernissartia*
  - Suborder Eusuchia
    - Family Gavialidae
    - Family Crocodylidae
    - Family Alligatoridae
- Infradivision Avemetatarsalia
  - †*Scleromochlus*
  - Infrasubdivision Ornithodira
    - †Order Pterosauria
      - *Suborder Rhamphorhynchoidea
      - Suborder Pterodactyloidea
    - †Family Lagerpetidae
    - †*Marasuchus*
    - †Family Silesauridae
    - Superorder Dinosauria
      - Order Saurischia
        - †Family Herrerasauridae
        - Suborder Theropoda
          - †Infraorder Coelophysoidea
          - †Infraorder Ceratosauria
            - Family Ceratosauridae
            - Family Abelisauridae
          - Infraorder Tetanurae
            - †Subdivision Megalosauroidea
              - Family Megalosauridae
              - Family Spinosauridae
            - Subdivision Allosauroidea
              - Family Metriacanthosauridae
              - Family Allosauridae
              - Family Neovenatoridae
              - Family Carcharodontosauridae
            - Division Coelurosauria
              - †Superfamily Tyrannosauroidea
              - †Family Compsognathidae
              - Subdivision Maniraptoriformes
                - †Family Ornithomimidae
                - Infradivision Maniraptora
                  - †Family Alvarezsauridae
                  - †Family Therizinosauridae
                  - †Superfamily Oviraptorosauria
                  - Cohort Paraves
                    - †Family Troodontidae
                    - †Family Dromaeosauridae
                    - Class Aves (see below)
        - †Suborder Sauropodomorpha
          - *Thecodontosaurus*
          - Family Plateosauridae
          - Family Riojasauridae
          - Family Massospondylidae

- Infraorder Sauropoda
  - Family Vulcanodontidae
  - Family Mamenchisauridae
  - Family Omeisauridae
  - Division Neosauropoda
    - Subdivision Diplodocoidea
    - Subdivision Macronaria
      - Family Camarasauridae
      - Family Brachiosauridae
      - Infradivision Titanosauria

- †Order Ornithischia
  - *Pisanosaurus*
  - Family Heterodontosauridae
  - Suborder Thyreophora
    - *Lesothosaurus*
    - *Scelidosaurus*
    - Infraorder Stegosauria
    - Infraorder Ankylosauria
      - Family Nodosauridae
      - Family Ankylosauridae
  - Suborder Cerapoda
    - Infraorder Pachycephalosauria
    - Infraorder Ceratopsia
      - Family Psittacosauridae
      - Family Protoceratopsidae
      - Family Ceratopsidae
    - Infraorder Ornithopoda
      - *Hypsilophodon*
      - *Iguanodon*
      - Family Hadrosauridae

4 CLASSIFICATION OF THE BIRDS

- Class Aves
  - †Family Archaeopterygidae
  - †*Jeholornis*
  - Subclass Pygostylia
    - †*Sapeornis*
    - †Family Confuciusornithidae
    - Infraclass Ornithothoraces
      - †Order Enantiornithes
      - Supercohort Ornithuromorpha
        - †*Patagopteryx*
        - †*Hongshanornis*
        - †Family Songlingornithidae
        - †*Apsaravis*
        - Cohort Ornithurae
          - †Order Hesperornithiformes
          - Subcohort Carinatae
            - †Order Ichthyornithiformes
            - Superdivision Neornithes
              - Division Palaeognathae
                - †Order Lithornithiformes
                - Order Ratites

- Division Neognathae
  - Subdivision Galloanserae
    - Order Anseriformes
    - Order Galliformes
  - Subdivision Neoaves
    - Order Columbiiformes
    - Superorder unnamed [‘waterbird assemblage’]
      - Order Gruiformes
      - Order Charadriiformes
      - Megaorder Mirandornithes
        - Order Phoenicopteriformes
        - Order Podicepidiformes
      - Order Muscophagiformes
      - Order Cuculiformes
      - Order Opisthocomiformes
      - Megaorder Aequornithes
        - Order Gaviiformes
        - Order Sphenisciformes
        - Order Procellariformes
        - Order Ciconiiformes
        - Order Pelecaniformes
    - Superorder Strisores
      - Order Caprimulgiformes
      - Order Apodiformes
    - Superorder Telluraves [‘landbird clade’]
      - Family Cariamidae
      - Order ‘Falconiformes’
      - Order Strigiformes
      - Superorder unnamed
        - Order Psittaciformes
        - Order Coliiformes
      - Superorder Picocoriaceae
        - Order Coraciiformes
        - Order Piciformes
        - Order Bucerotiformes
        - Order Trogoniformes
      - Order Passeriformes

5 CLASSIFICATION OF THE MAMMALS

- Class Mammalia* [= Mammaliaformes]
  - †*Adelobasileus*
  - †Family Sinoconodontidae
  - †Order Morganucodonta
  - †Order Haramiyida
  - †Order Docodonta
  - †*Hadrocodium*
  - †*Kuehneotherium*
  - Class Mammalia* [crown Mammalia]
    - Superdivision Australosphenida
      - †Family Ausktribosphenidae
      - Division Monotremata
    - Superdivision Theriimorpha
      - †Family Triconodontidae

- †Order Eutriconodonta
- Division Theriiformes
  - †Order Multituberculata
  - Superlegion Trechnotheria
      - †Order Symmetrodonta
    - Legion Cladotheria
      - †Superfamily Dryolestoidea
      - †*Vincelestes*
      - †’Eupantotheres’
      - Sublegion Boreosphenida
        - †*Eomaia*
        - Infralegion Theria
          - Supercohort Metatheria
            - †Order Deltatheroida
            - Cohort Marsupialia
              - Order Didelphimorphia
                - Family Didelphidae
              - Order Paucituberculata
                - Family Caenolestidae
                - †Family Argyrolagidae
                - †Family Caroloameghinidae
              - Order Sparassodonta
                - †Family Borhyaenidae
                - †Family Thylacosmilidae
              - Magnorder Australidelphia
                - Order Microbiotheria
                - Order Notoryctemorphia
                - Order Peramelemorphia
                - Order Dasyuromorphia
                - Order Diprotodontia
          - Supercohort Eutheria
            - †*Juramaia*
            - †Family Zhelestidae
            - †Family Zalambdalestidae
            - Cohort Placentalia
              - Superorder Atlantogenata
                - Magnorder Xenarthra
                  - Order Cingulata
                    - Family Dasypodidae
                    - †Family Glyptodontidae
                  - Order Pilosa
                    - Family Myrmecophagidae
                    - Family Bradypodidae
                    - Family Megalonychidae
                    - †Family Megatheriidae
                    - †Family Mylodontidae
                - Magnorder Afrotheria
                  - Grandorder Afroinsectiphilia
                    - Order Tubulidentata
                    - Mirorder Afroinsectivora
                      - Order Afrosoricida
                        - Family Tenrecidae
                        - Family Chrysochloridae
                      - Order Macroscelidea
                  - Grandorder Paenungulata

- Order Proboscidea
  - †Family Moeritheriidae
  - †Family Deinotheriidae
  - Suborder Elephantiformes
    - †Family Mammutidae
    - †Family Gomphotheriidae
    - †Family Stegodontidae
    - Family Elephantidae
- Mirorder Tethytheria
  - Order Hyracoidea
  - Order Sirenia
- Superorder Boreoeutheria
  - *Incertae sedis*
    - †Order Leptictida
    - †Order Pantolesta
    - †Order Apatotheria/ Apatemyida
    - †Order Anagalida
    - †Order Taeniodonta
    - †Order Tillodontia
    - †Order Pantodonta
    - †Order Arctocyonida
    - †Order Dinocerata
  - Grandorder Laurasiatheria
    - Grandsuperorder Scrotifera
      - Order Lipotyphla
        - Suborder Erinaceomorpha
        - Suborder Soricomorpha
      - †Superorder ’Condylarthra’
        - †Family Hyopsodontidae
        - †Family Phenacodontidae
      - †Superorder Meridiungulata
        - Order Litopterna
        - Order Notoungulata
        - ?Order Astrapotheria
        - ?Order Pyrotheria
        - Order Xenungulata
      - Superorder Cetartiodactyla
        - †Order Arctocyonia
        - †Family Mesonychidae
        - Order Artiodactyla
          - †Family Dichobunidae
          - Suborder Suiformes (Bunodontia)
            - †Family Entelodontidae
            - Family Suidae
            - †Family Anthracotheriidae
            - Family Hippopotamidae
          - Suborder Selenodontia
            - Infraorder Tylopoda
              - †Family Merycoidodontidae
              - Family Camelidae
            - Infraorder Ruminantia
              - †Family Hypertragulidae
              - Family Tragulidae
              - Family Antilocapridae
              - Family Giraffidae

            - Family Cervidae
            - Family Moschidae
            - Family Bovidae
      - Order Cetacea
        - †Suborder ‘Archaeoceti’
        - Suborder Odontoceti
        - Suborder Mysticeti
    - Superorder Pegasoferae
      - Order Chiroptera
        - Suborder Megachiroptera
        - Suborder Microchiroptera
      - Order Perissodactyla
        - Superfamily Hippomorpha
          - Family Equidae
          - †Family Brontotheriidae
        - Suborder Tapiromorpha
          - †Family Chalicotheriidae
          - Superfamily Ceratomorpha
          - Superfamily Tapiroidea
          - Superfamily Rhinoceratoidea
      - Superorder Ferae
        - †Order Creodonta
        - Order Carnivora
          - †Family Miacidae
          - Suborder Feliformia
            - †Family Nimravidae
            - Infraorder Aeluroidea
              - Family Viverridae
              - Family Herpestidae
              - Family Hyaenidae
              - Family Felidae
          - Suborder Caniformia
            - Family Canidae
            - Family Ursidae
            - †Family Amphicyonidae
            - Family Mustelidae
            - Family Procyonidae
            - Infraorder Pinnipedia
              - †Family Enaliarctidae
              - Family Otariidae
              - Family Odobenidae
              - †Family Desmatophocidae
              - Family Phocidae
        - Order Pholidota
- Grandorder Euarchontoglires
  - Superorder Glires
    - Order Rodentia
      - Suborder Sciurognathi
        - †Superfamily Ischyromyoidea
        - Infraorder Sciuromorpha
        - Infraorder Myomorpha
      - Suborder Hystricognathi
        - Infraorder Hystricomorpha
        - Infraorder Phiomorpha
        - Infraorder Caviomorpha

  - Order Lagomorpha
- Superorder Archonta
  - Grandorder Sundatheria
    - Order Scandentia
    - Order Dermoptera
      - †Family Plagiomenidae
      - Family Galeopithecidae
  - Order Primates
    - †Suborder Plesiadapiformes
    - Unranked Euprimates
      - Suborder Strepsirrhini
        - †Infraorder Adapiformes
        - Infraorder Lemuriformes
          - Family Lemuridae
          - Family Indriidae
          - Family Daubentoniidae
        - Infraorder Lorisiformes
          - Family Lorisidae
          - Family Galagidae
      - Suborder Haplorhini
        - †Family Omomyidae
        - Family Tarsiidae
        - Suborder Anthropoidea
          - †Family Eosimiidae
          - †Family Amphipithecidae
          - †Superfamily Parapithecoidea
          - Unnamed clade
            - Infraorder Platyrrhini
              - Family Cebidae
              - Family Atelidae
            - Unnamed clade
              - †Superfamily Propliopithecoidea
              - Infraorder Catarrhini
                - Superfamily Cercopithecoidea
                  - Family Cercopithecidae
                - Superfamily Hominoidea
                  - †Family Proconsulidae
                  - Family Hylobatidae
                  - Family Hominidae

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Glossary

abrasion Physical wear.

absolute dating Assignment of exact dates, in millions of years, to rocks, usually using measurements of radioactive decay of particular elements in rocks.

acellular Without cells.

acrodont Teeth fused to the jaw bones.

adductor muscles Jaw-closing muscles that run from the skull roof or braincase region to the back of the lower jaw.

aestivation Passing the summer in a state of dormancy.

alignment Matching, or lining up, gene or protein sequences so that the equivalence is maximized.

altricial Remaining in the nest, and dependent on parents.

amniote A tetrapod that produces cleidoic eggs (i.e. a reptile, bird, or mammal).

amphistylic Jaw suspension in which the upper jaw is attached at two points to the cranium.

analogy Comparable biological structures or functions that arose independently.

antorbital fenestra A skull opening between the nostril and the orbit; characteristic of archosaurian reptiles.

aorta Major blood vessel carrying oxygenated blood from the heart to the body.

apatite The crystalline component of bone; calcium phosphate.

appendicular skeleton The limbs and limb girdles.

auditory ossicles The small bones in the middle ear that transmit sound from the tympanum to the inner ear.

autopod The distal part of the arm or leg – the hand and wrist or foot and ankle.

axial skeleton The backbone and ribs.

bicuspid Two-pointed tooth crowns, as seen in living amphibians.

biological species concept The idea that all organisms that interbreed in nature, and which produce fertile offspring, are members of a single species.

biomechanics The application of mathematical/ mechanical principles to organisms.

biota An assemblage of organisms that lived together; often an exceptional assemblage, with soft tissues preserved.

blastopore The hollow portion of the developing embryo at the gastrule stage.

brachiation Locomotion by swinging with the arms.

buccal Of the mouth cavity.

calcified cartilage Cartilage that carries a scattering of apatite crystals, as found in sharks.

calcite Calcium carbonate.

calcrete A calcium carbonate concretion formed in soils as a result of dramatic rainfall followed by rapid evaporation; indicates monsoonal rain in hot climates.

cartilage Non-mineralized skeletal material, often developmentally a precursor of bone.

caudal Of the tail region.

centrum The cotton-reel-shaped lower portion of a vertebra.

cervical Of the neck.

character A describable feature of an organism that may be used in phylogenetic analysis.

choana An opening through bone, usually with a depressed periphery.

cilium (pl. cilia) Hair-like projection from a cell.

clade A monophyletic group.

cladistics Phylogenetic analysis involving the search for monophyletic groups by means of character analysis.

cladogram A dendrogram (tree-like diagram) produced by cladistic analysis, showing the relationships of groups.

claspers Pelvic elements in sharks and some other fishes, found in males and used during mating.

collagen A flexible protein that makes up cartilage, and forms the framework of bone, on which apatite crystals precipitate.

common ancestor The last ancestor shared by two or more taxa.

community A group of organisms that live in close contact and interact with each other.

computed tomography (CT) Three-dimensional imaging of a specimen using X-ray scans.

continental drift The movement of continents over the course of geological time; driven by plate tectonics.

coprolite Fossilized excrement.

correlation Matching of geological strata from locality to locality using evidence of equivalence of age.

cranial nerves The nerves of the head that run directly from the brain to particular sensory structures.

Vertebrate Palaeontology, Fourth Edition. Michael J. Benton.

Companion Website: www.wiley.com/go/benton/vertebratepalaeontology

data matrix (pl. matrices) In cladistics, a tabulation of character states of species/specimens versus characters.

dentine The main constituent of teeth, lying within the enamel crown and root regions.

depressor muscle The muscle that opens the jaws, running from the back of the skull to the retroarticular process of the lower jaw.

dermal Of the skin.

dermal bone Bone formed embryologically in the outer portions of the body, within the skin.

deuterostomes Animals in which, embryologically, the opening at the cup-shaped (gastrula) stage becomes the anus

chordates and echinoderms are the main deuterostome groups.

development The changes in organisms that happen between fertilization of the egg and old age, and the processes that drive those changes; normally refers to embryonic development only (egg to hatchling).

digitigrade stance Posture in which the animal stands only on the tips of its toes.

diphycercal tail Narrow symmetrical tail of an aquatic vertebrate, in which there are only modest fins above and below the middle line.

diphyodont ('Two-type teeth'), having only a milk and an adult dentition, as in mammals, rather than more than two replacements of teeth.

disarticulate To break up; as of a skeleton.

discrete methods Methods for compiling phylogenetic trees from molecular data by using data from the sequences, or from functions derived from the sequences.

disparity Morphological variation.

distance methods Methods for compiling trees from molecular data by attempting to summarize all the distances among all the taxa of interest.

DNA Deoxyribose nucleic acid; the nucleic acid that resides in the nucleus, and which carries the genetic code.

dorsal Of the back.

durophagy Eating hard or tough materials.

ectoderm The outermost of the three primary layers of an embryo; produces the nervous system, the skin and the lining of various body cavities such as the mouth.

ectotherm An animal that uses external means to control its body temperature.

embryology The study of embryos; development from the egg to hatching/birth.

empirical evidence Evidence that may be observed, such as a fossil.

enamel The crystalline material covering the crown of a tooth.

endemic Restricted in distribution to a single area.

endochondral bone Bone formed from cartilage, usually deep within the body.

endoderm The innermost of the germ layers of an embryo that is the source of the lining of the gut and related tissues.

endotherm An animal that uses internal means to control its body temperature.

exponential Accelerating pattern in a curve.

extrinsic 'External', referring to the physical environment (usually contrasted with intrinsic.

faunal province A geographical area that is typified by one or more characteristic species.

fenestra (literally window) A relatively large opening through bone.

finite element analysis An engineering method that models structures, such as buildings or skulls, as three-dimensional meshes with material properties, and that can then be tested for the effects of applied forces.

foramen A small hole in a bone, usually for a blood vessel or nerve.

gastrolith A stomach stone, swallowed by reptiles and birds to aid digestion.

gene An identified coding sequence in a nucleic acid that codes for particular functions or aspects of the anatomy of an organism.

genome The sum of all the genes of an organism as expressed in the chromosomes.

gill arches The rods of cartilage or bone that support and surround the gills.

glenoid The mobile articulation between the shoulder girdle and the arm, and between the lower jaw and the skull.

gnathostome A vertebrate with jaws.

gonads Internal organs that produce eggs (ovaries) or sperm (testes).

hallux The thumb.

heterocercal An asymmetrical aquatic tail, in which the upper portion is larger than the lower.

heterochrony The interplay of development (ontogeny) and evolution (phylogeny), in terms of relative slowing (paedomorphosis) or advancing (peramorphosis) of patterns of developmental change.

heterotroph An organism that feeds on other organisms to gain nourishment.

histology The study of biological tissues.

homeotic Homeotic genes regulate orientation and positional aspects in development (e.g. they specify anterior, and posterior and dorsal and ventral, aspects of the body), as well as the determination of bones and tissues in limb bud development.

homeosis The developmental transformation of one body part into another, generally caused by mutation of Hox genes.

homeotherm An animal with a uniform body temperature.

homocercal A symmetrical aquatic tail, in which both upper and lower portions are equal in size and mirror images of each other.

homology Resemblance in biological structure or function that is the result of shared common ancestry.

hyostylic The jaw suspension of modern fishes, in which the upper jaw bone (palatoquadrate) contacts the cranium in only one place at the front, and moves against the hyomandibular behind.

hypsodont High-crowned, literally 'high-tooth', describing the cheek teeth of mammals (especially perissodactyls, rodents) adapted to consuming abrasive food.

igneous rocks Rocks formed directly from molten material.

interpterygoid vacuity Gap in the palate in the midline, between the pterygoids.

intrinsic 'Internal', referring to biological causes (usually contrasted with extrinsic.

invertebrate An animal with no backbone; term applied to all the animal phyla that fall outside Vertebrata.

isotope Variant of a chemical element, usually differing in atomic mass (e.g. carbon-14, carbon-13, and carbon-12).

kinetic Mobile, in which separate bones may move relative to each other (usually of the skull).

larva A juvenile stage that differs from the adult (e.g. a tadpole).

lateral line A sensory line around the skull and along the side of the body, found in fishes and some aquatic amphibians.

lepidotrichia Small jointed bones in the fins of bony fishes.

lingual Of the tongue; the inside face of the jaw bones.

living fossil An animal with a long history and which has apparently not changed much over millions of years.

lumbar Of the lower back region.

macroevolution Evolution above the species level.

magma Molten rock.

mandible The lower jaw.

metamorphosis Change from a juvenile larva to a rather different adult form.

molecular clock The idea that molecules mutate at a predictable rate.

molecular phylogeny A pattern of evolutionary relationships built up from comparisons of proteins or nucleic acids of different organisms.

monophyletic A group that contains all the descendants of a single common ancestor.

morphological species concept The concept that all organisms that look similar are members of a single species.

morphology Form; physical characteristics of organisms.

motile Capable of movement.

muscle scar A roughened area on the surface of a bone that indicates the site of a muscle attachment.

myomeres The muscle blocks along the length of the body of a chordate.

myotomes The embryonic structures that give rise to then body and eye musculature.

neural arch The upper portion of a vertebra, above the centrum.

neural crest The region of cells in the early vertebrate embryo that forms above the neural tube and which provides precursors for many organ systems of the head region, the nervous system, and pharyngeal gill slits.

neurocranium The braincase bones.

node Branching point in a cladogram.

notochord An elastic rod running the length of the back in chordates, precursor of the spinal column in more derived forms.

nuchal Of the neck region.

nucleic acid The genetic materials, DNA and RNA, that reside in the cells, and are instrumental in synthesizing proteins and in passing on heritable characters.

occlusion Precise meeting of surfaces of interacting upper and lower teeth.

opisthocoelous Posterior articulating face of a vertebra that curves strongly backwards.

oral Of the mouth

orbit Eye socket.

ossify To turn into bone.

osteocyte A bone-building cell.

osteoderm A bony plate set in the skin.

otic capsule The bones enclosing the inner ear region of the braincase.

outgroup In cladistic analysis, the organisms with which one compares the organisms of interest (the ingroup) in order to determine synapomorphies.

oviparity Egg-laying; the condition of animals that lay eggs.

ovoviparity Egg-retention; the condition of animals that lay produce live young from eggs retained and hatched internally.

paedomorphosis The maturation of an organism while retaining juvenile characters of the body (opposite of peramorphosis).

palaeoecology The study of the modes of life of ancient organisms, either singly or in communities.

papilla (pl. papillae) A pimple or rounded structure (often used for the points of attachment of feathers on bones of the bird wing).

paraphyletic A group that arose from a single ancestor, but does not include all of the descendants of that ancestor.

parsimony The principle that a simpler explanation is always preferred to a more complex one, all other factors being equal.

pectoral Of the shoulder region.

pelvic Of the hip region.

pentadactyl Having five fingers and/ or toes.

peramorphosis The maturation of an organism beyond the normal adult condition (opposite of paedomorphosis).

perichondral bone Acellular bone formed by crystallization of apatite around soft tissues such as nerves that pass through cartilage.

phenetics Methods of establishing trees of relationships that are more mathematical than phylogenetic – the methods take account of 'overall similarity', and do not distinguish phylogenetically informative characters from other characters.

phylogenetic comparative methods Numerical methods that explore rates and modes of evolution across phylogenetic trees.

phylogenetic species concept A species is defined as a small clade of diagnosable geographical forms of the same basic kind.

phylogeny An evolutionary tree that indicates closeness of relationships.

pineal opening An opening in the midline of the skull roof, usually between the parietal bones, that lies close to the pineal organ of the brain (the 'third eye').

plate tectonics The processes beneath Earth's crust that produce new crust along mid-oceanic ridges, and cause oceanic and continental plates to move.

pleurodont Teeth set in a groove.

pneumatic (of bones) Hollow, with spaces for air sacs.

poikilotherm An animal with varying body temperature.

polarity The direction of change of a character, from primitive to derived.

polyphyletic A group that arose from several ancestors.

postcranial Those parts of the skeleton lying behind the head.

precocial Leaving the nest immediately on hatching.

presacral In front of the hip (sacral) region.

process A projection on a bone.

protostomes Those animals in which the opening of the gastrula stage in development becomes the mouth (includes everything except the deuterostomes).

pulp cavity The space within a tooth, or a dentine scale, occupied by blood vessels and nerves.

rachis The hollow central shaft of a typical feather.

radials Bony rods within the fins of a fish.

recapitulation A 'throwback', in which a juvenile resembles the adult stage of an ancestral form.

recurved Bending back, referring to teeth that curve back.

relative dating Dating of rocks relative to each other, usually by the use of fossils.

relict An organism that persists in one area long after its relatives have gone extinct elsewhere.

retraction Pulling back.

retroarticular process A process on the lower jaw that extends behind the glenoid articulation.

RNA Ribose nucleic acid, a nucleic acid that occurs in several forms in the cell, and is involved in protein synthesis.

sacral Of the hip region.

sagittal Running along the midline of the head.

sclerotic plates Bony plates in the orbit, supporting the eye ball.

sedimentary rocks Rocks formed from sediments, such as muds, silts, sands, and conglomerates.

sexual dimorphism Variation in morphology and/or behaviour associated with gender.

sigmoid S-shaped, a curve that begins as exponential, and then slows down.

sister group In cladistic analysis, the most closely related pair of outgroups.

spiracle Remnant of an anterior gill slit seen in sharks and some extinct amphibians.

splanchnocranium Bones of the palate, jaws, and branchial area; derived from endoderm.

sprawling gait Mode of locomotion in which the arms and legs are held out sideways from the body, with the elbows and knees bent.

stratigraphy The study of the history of Earth, and especially the dating of rocks.

streptostylic joint A joint in the skull in which the quadrate is mobile.

stylopod The middle part of the arm or leg – the forearm or calf.

synapomorphy A shared derived character, characteristic of a monophyletic group.

synovial A joint that has facets that allow movement of the two bones against each other; typical of limb joints of tetrapods.

synsacrum The fused sacrum of birds and pterosaurs.

taphonomy Study of the processes that affect an organism between death and collection as a fossil.

temporal Of the cheek region, at the back of the side view of the skull.

tessera (pl. tesserae) A small bone plate. Tesserae often formed a kind of chain mail in primitive fishes.

tetrapod A vertebrate with four toe-bearing legs, or descendants of such a vertebrate (effectively a member of the clade Tetrapoda).

thecodont Teeth set in sockets.

thoracic Of the chest region.

till Chaotic mixture of mud, sand and boulders dumped by a glacier.

trace fossil A fossil track or burrow; any non-skeletal evidence of the activity of organisms.

triploblastic Possessing three germ layers in the embryo, endoderm, mesoderm and ectoderm.

trochanter Major processes on the femur; insertion points of major muscles.

tympanum The ear drum.

vane The part of a contour feather on either side of the rachis.

volatile A substance that is readily removed by natural processes.

wear facets Zones of the occlusal surfaces of teeth where enamel and dentine have been worn away by wear on the opposite teeth or on foodstuffs.

zeugopod The proximal part of the arm or leg – the upper arm or thigh.

zygapophysis A process in front of or behind the neural arch of a vertebra, which takes part in linking the vertebrae to each other.

zygomatic arch The bony arch beneath the orbit and temporal fenestra formed from the jugal and squamosal in advanced mammal-like reptiles and mammals.

Index

Note: Page numbers in *italics* refer to figures, those in **bold** refer to boxes

Vertebrate Palaeontology, Fourth Edition. Michael J. Benton.

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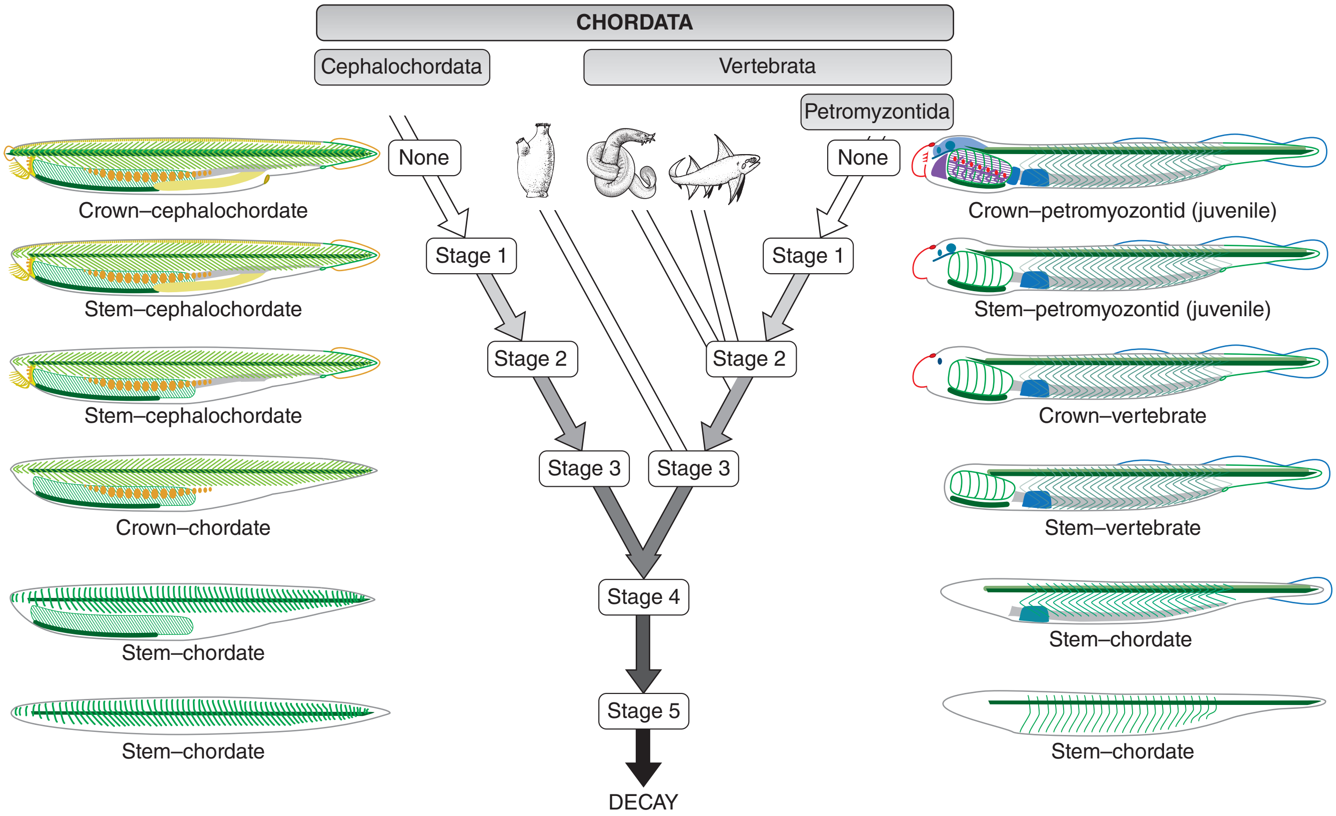

Colour plate 1.1 Morphological decay stages of amphioxus (left) and larval lamprey (right) and the phylogenetic position of each stage if interpreted as a fossil. Rectangles on branches of the phylogeny are morphological characters, their shade indicating the order of loss (white, early; dark, late). As each organism decays, its phylogenetic position moves down the tree; this is evidence for taphonomic bias in the identification of fossil chordates. Characters are colour coded according to the hierarchical level for which they are informative (green, chordate; yellow, cephalochordate; blue, vertebrate; purple, cyclostome and vertebrate; red, petromyzontid). Source: Sansom *et al.* (2010). Reproduced with permission from Nature Publishing Group.

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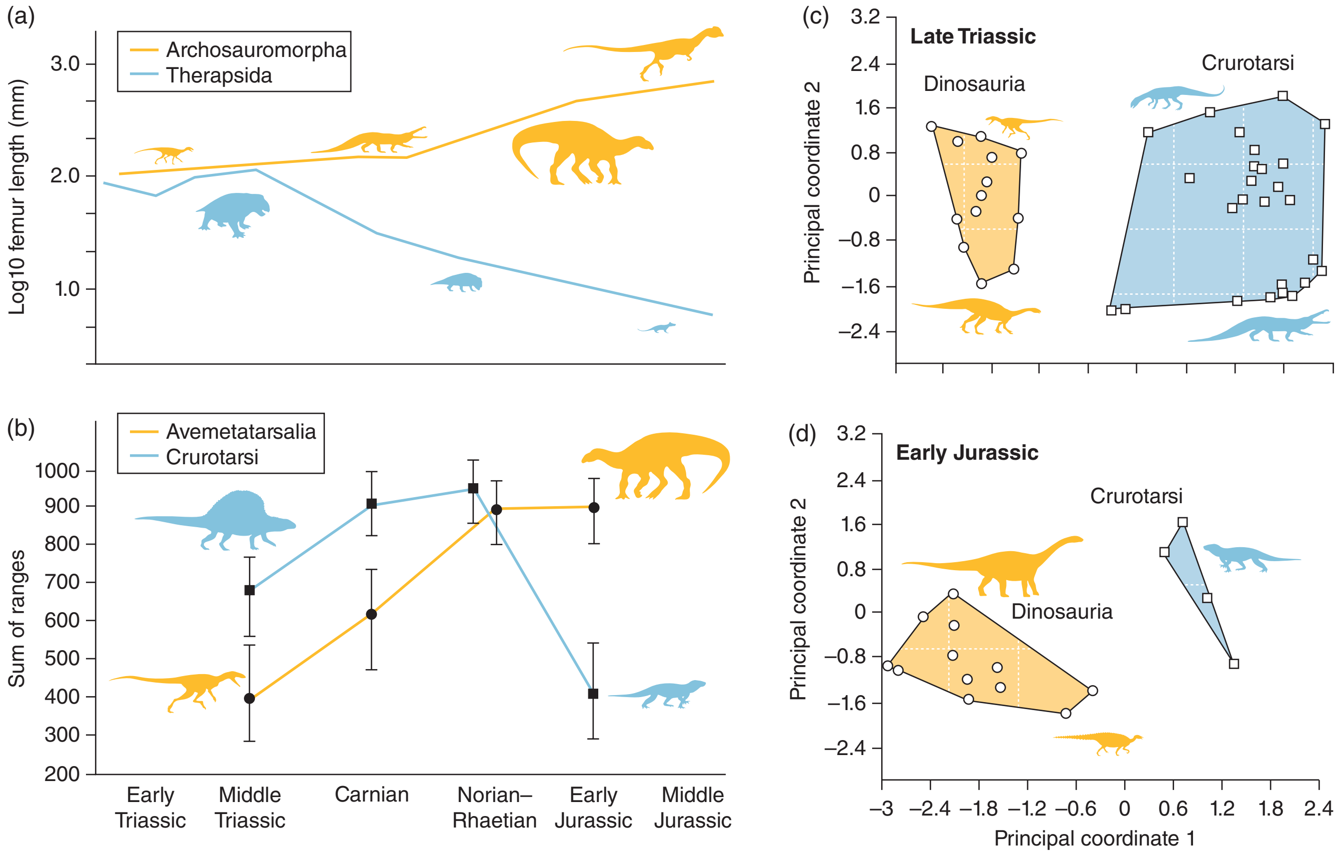
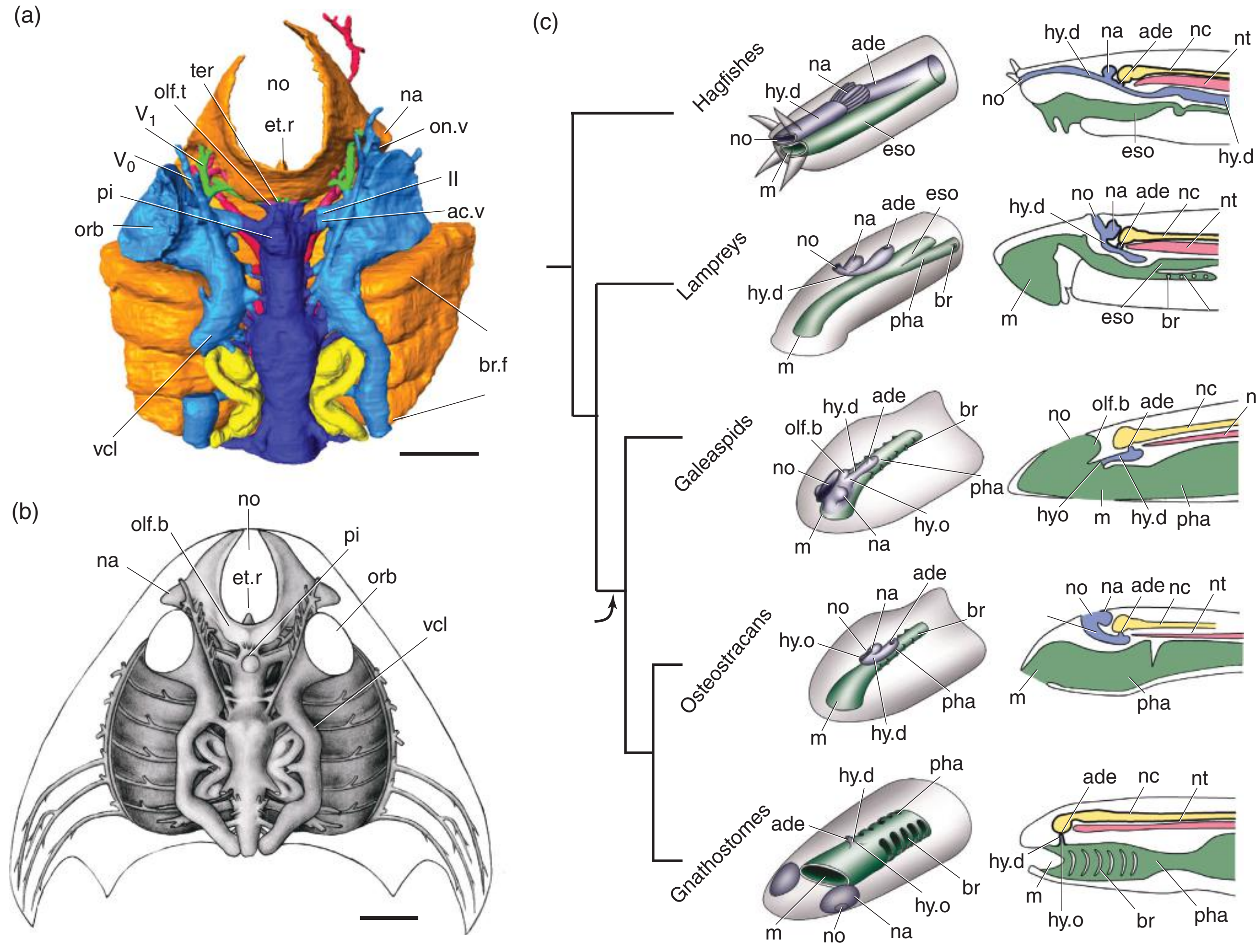
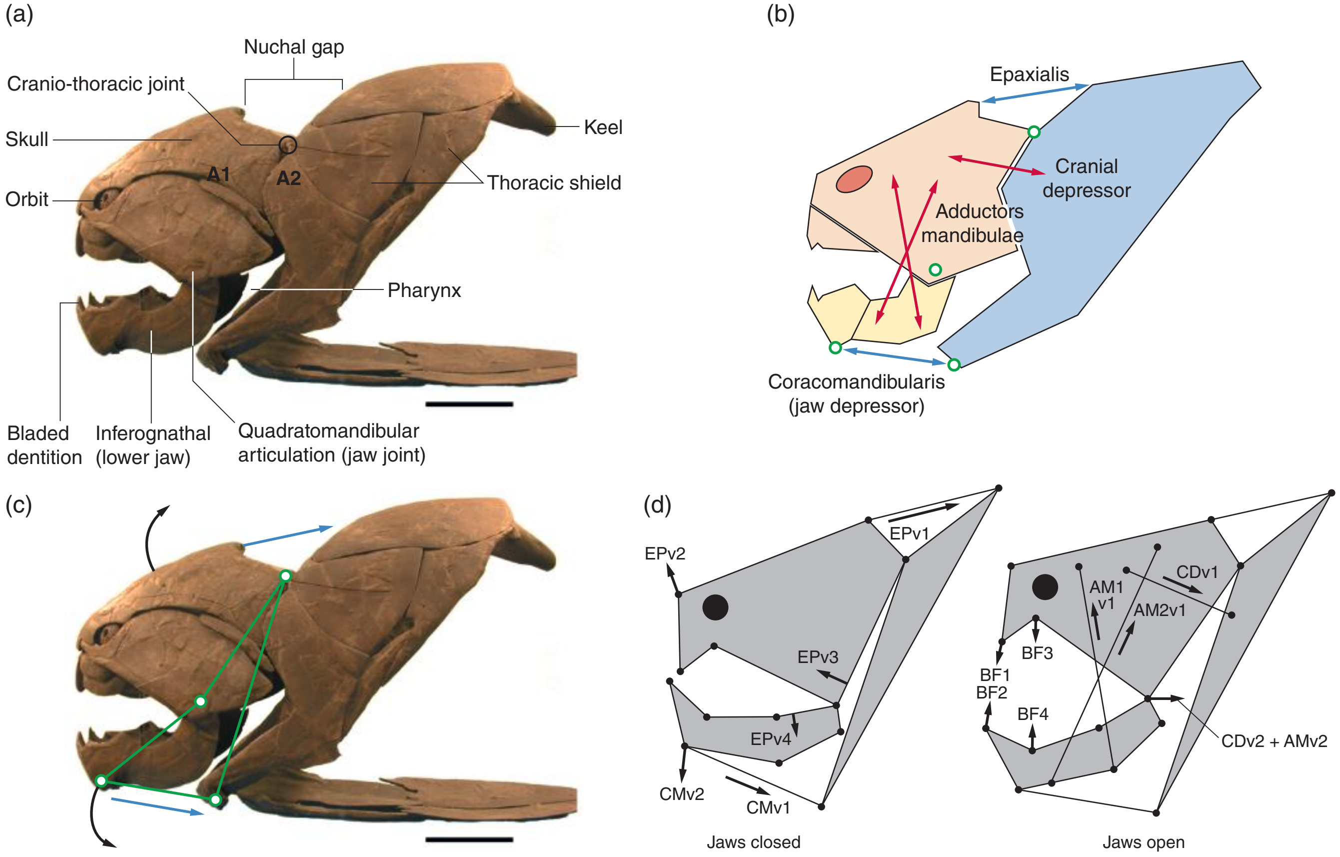


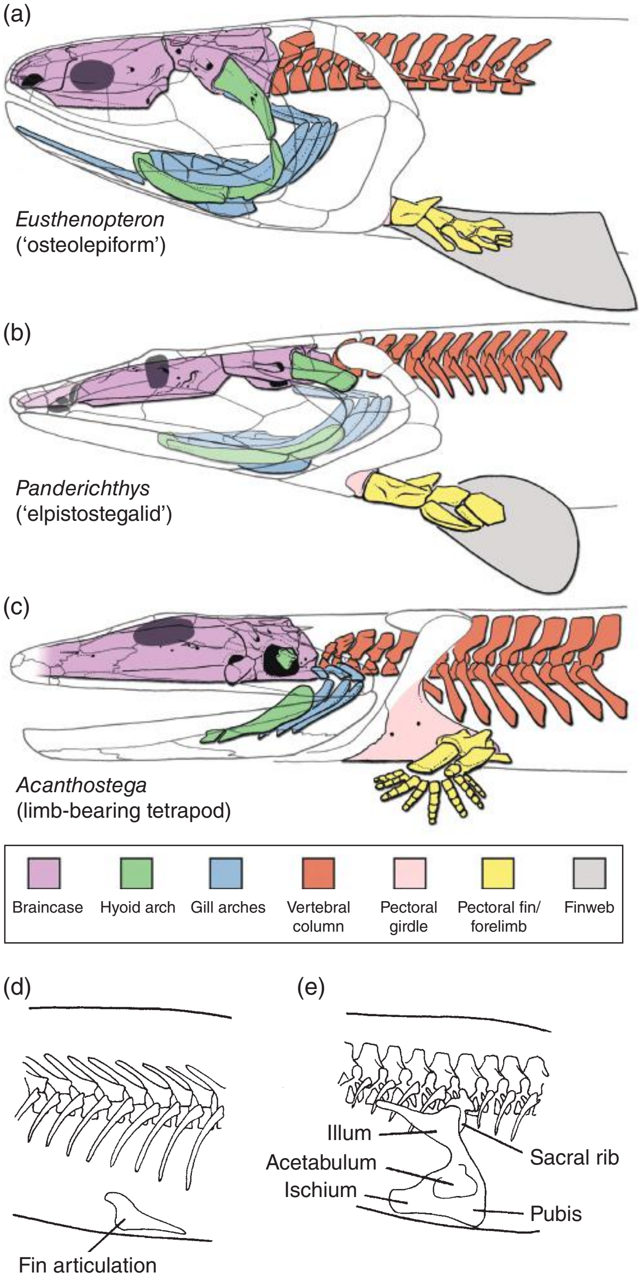
Colour plate 2.1 Macroevolution of tetrapods and the origins of dinosaurs. (a) The relative fates of therapsids (derived synapsids) and archosauromorphs (archosaurs and close relatives) through the Triassic and the early part of the Jurassic, showing a long-term diminution of mean body size (indicated by femur lengths) of therapsids and increase in mean body size of archosauromorphs. Model fitting indicates these trends were random (Brownian motion model). (b) Changing evolutionary rates of Avemetatarsalia (dinosaurs and immediate relatives) and Crurotarsi (crocodile-line archosaurs) through the Middle Triassic to Early Jurassic, showing parallel changes in disparity (measured by sum of ranges) in the Triassic, and decline in crurotarsan rates through the end-Triassic mass extinction. (c,d) Changing relative morphospace occupied by Dinosauria and Crurotarsi in the Late Triassic and Early Jurassic, suggesting a lack of impact of early dinosaurian evolution on crurotarsan morphospace in the Late Triassic, and a modest response by Dinosauria following substantial extinction of Crurotarsi through the end-Triassic mass extinction. Source: (a) Adapted from Sookias *et al.* (2012). (b) Adapted from Brusatte *et al.* (2008).



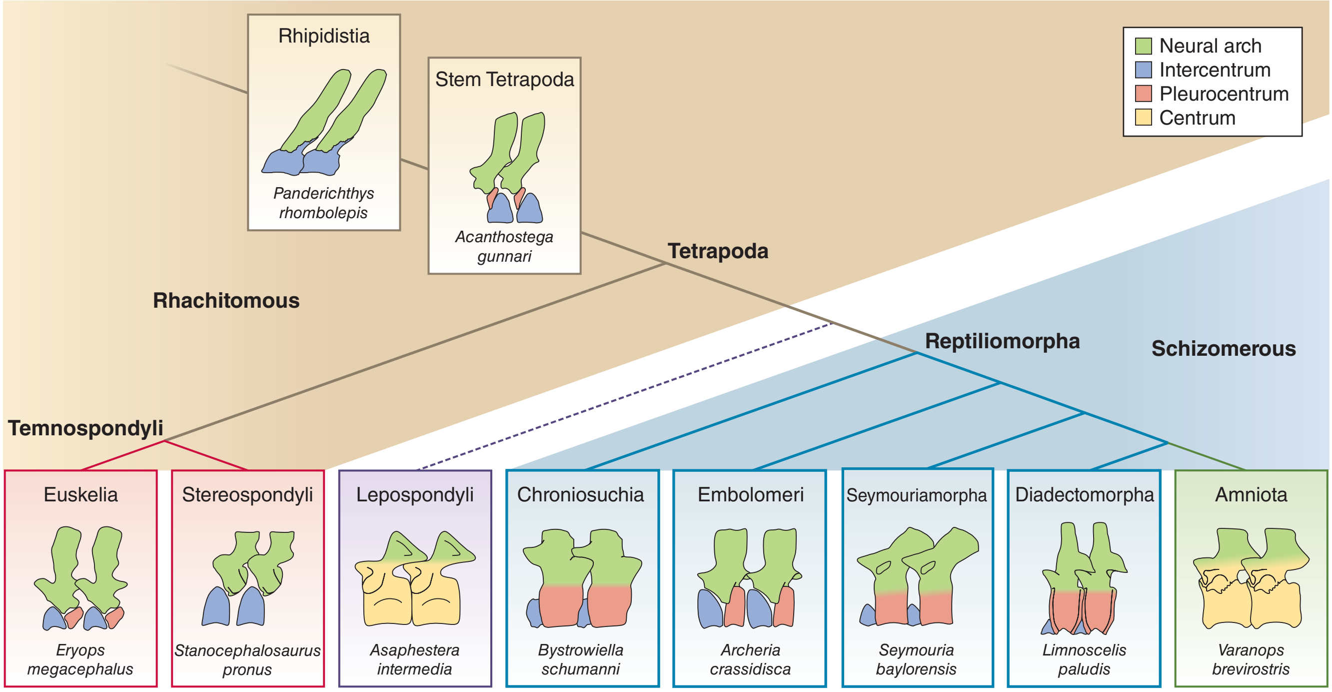
Colour plate 3.1 Internal anatomy of the head region of the Silurian galeaspid *Shuyu zhejiangensis*. (a) Virtual endocast, reconstructed from micro-CT scans; (b) reconstruction of external morphology; (c) evolution of the nasohypophyseal complex in craniates, shown in oblique view (left) and midline section (right). The disassociation of the nasohypophyseal complex, an evolutionary prerequisite for the origin of jaws, happened at least in the common ancestor of galeaspids, osteostracans and gnathostomes (arrow). The condition of osteostracans probably converged with that of lampreys. Abbreviations: ac.v, anterior cerebral vein; ade, adenohypophysis; br, branchial duct or slit; eso, oesophagus; et.r, ethmoid rod; hy.d, hypophyseal duct; hy.o, hypophyseal opening; m, mouth; na, nasal sac; nc, neural cord; no, nostril; nt, notochord; olf.b, olfactory bulb; olf.t, olfactory tract; orb, orbit; pha, pharynx; pi, pineal organ; ter, terminal nerve;vc, lateral head vein or dorsal jugular vein; II, V_0, V_1, cranial nerves II, V (superficial ophthalmic; profundus). Source: Gai *et al.* (2011). Reproduced with permission from Nature Publishing Group.



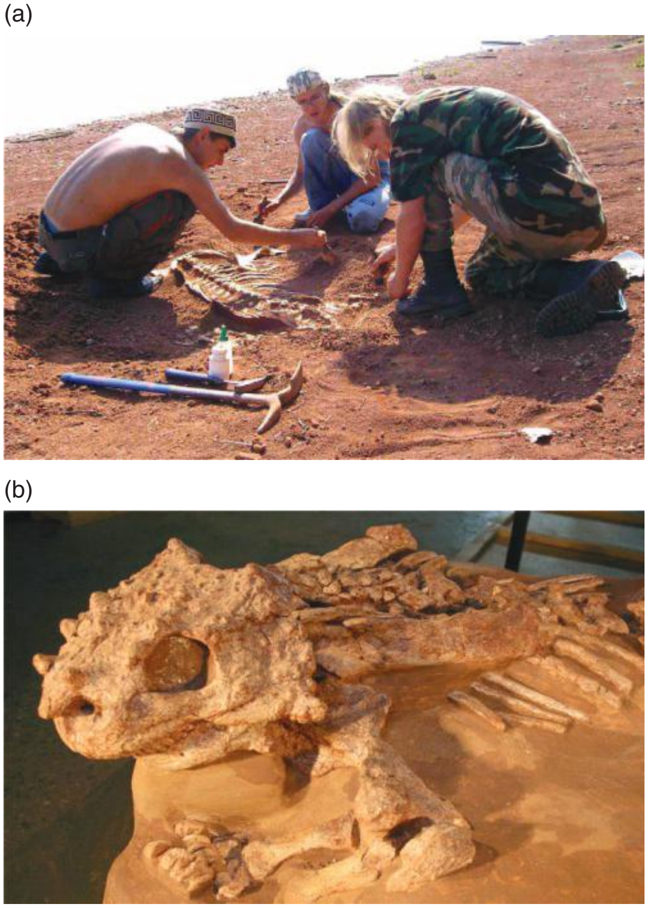
Colour plate 3.2 Anatomy and biomechanical model of the armoured skull and thoracic region of *Dunkleosteus terrelli*. (a) Anatomy of *Dunkleosteus terrelli*. (b) Drawing of (a) showing the four rotational joints (open circles) forming the four-bar linkage that mediates skull and mandibular rotation. The lines of action of four muscles are shown, including two jaw openers (epaxialis and coracomandibularis) and two jaw closers (cranial depressor and two alternate reconstructions of the adductor mandibulae). (c) Four-bar linkage motion during opening driven by EP and CM muscles. (d) Vector diagrams of the biomechanics of feeding, showing jaw opening (left) and jaw closing (right). During jaw opening, the muscle input force vectors (epaxialis vector 1- EPv1) and coracomandibularis vector 1 (CMv1) cause cranial elevation (EPv2) and lower jaw depression (EPv3–4 via the linkage). Jaw closing mechanics are driven by force vectors of the cranial depressor (CDv1) and the adductor mandibulae, reconstructed in two configurations (AM1v1, AM2v1). Bite force is exerted by both lever and linkage force vectors if a prey item is caught between the anterior fangs (BF1 and BF2) or between the rear dental blades (BF3 and BF4). Scale, 20 cm. Specimen no. CM6090. Cleveland Museum of Natural History, Cleveland. Source: Anderson and Westneat (2009). Reproduced with permission from The Paleontological Society.



Colour plate 4.1 The transition from tristichopterid fish (a) and (d), through panderichthyid (b), to basal tetrapod (c) and (e): (a–c) the separation of the skull from the shoulder girdle; (d) and (e) the enlargement of the pelvic girdle and its firm attachment to the vertebral column via the ilium and sacral rib. Source: (a–c) M. Coates, University of Chicago, IL, USA. Reproduced with permission. (d,e) Adapted from various sources.

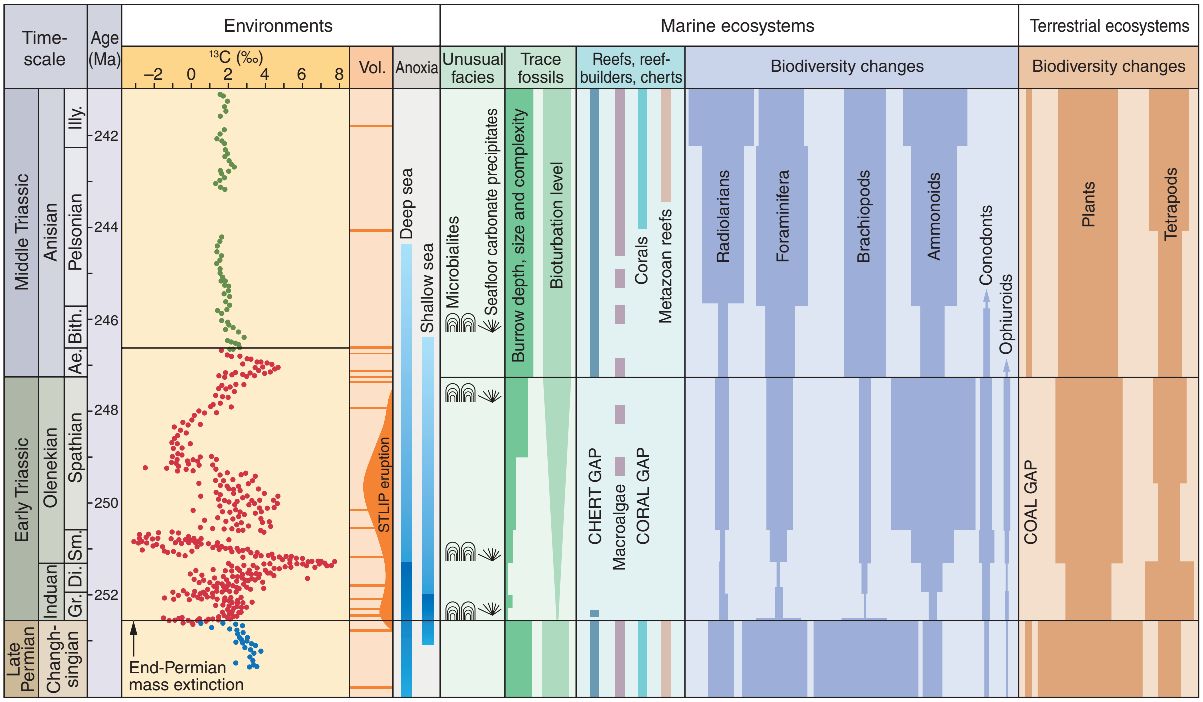


Colour plate 4.2 Evolution of the basic vertebral structure of tetrapods, showing the classic rhachitomous form to the left (intercentrum dominant) and schizomerous to the right (pleurocentrum dominant). These occur broadly in the Amphibia (Batrachomorpha) and Reptiliomorpha respectively, characterizing modern lissamphibians and amniotes respectively. New work (Pierce *et al*., 2013) has cast doubt on some aspects of this classic model, in demonstrating that the stem tetrapods *Acanthostega* and *Ichthyostega* have a different pattern, in which the intercentrum dominates (like the rhachitomous model), but that the intercentrum is associated, through the pleurocentrum, with the neural arch in front, not behind. Source: By Smokeybjb (Own work) [CC-BY-SA-3.0 (http://creativecommons.org/licenses/by-sa/3.0) or GFDL (http://www.gnu.org/copyleft/fdl.html)], via Wikimedia Commons. Adapted with the *Acanthostega* vertebrae modified.

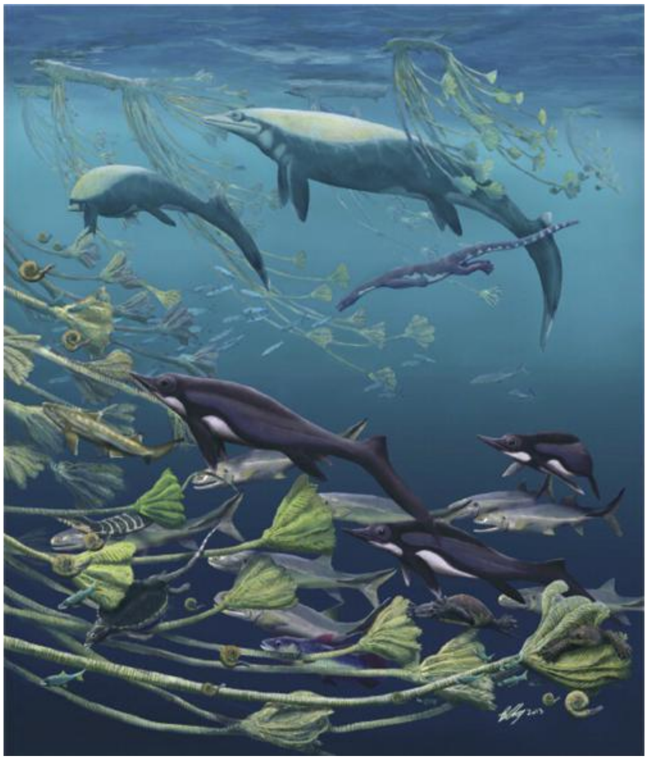


Colour plate 5.1 The Late Permian sediments and fossils of the Kotel'nich section. (a) Expedition of the Vyatka Palaeontological Museum: from left to right, Maxim Kovalyov, Alexey Toropov, and Il'ya Shumov remove sediment from a complete pareiasaur specimen near Boroviki, with the Vyatka River at top left. (b) Skeleton of *Deltavjatia vjatkensis* seen from the front, as preserved. Source: A. Yu Khlyupin, Vyatka Paleontological Museum, Kotel'nich, Russia. Reproduced with permission.

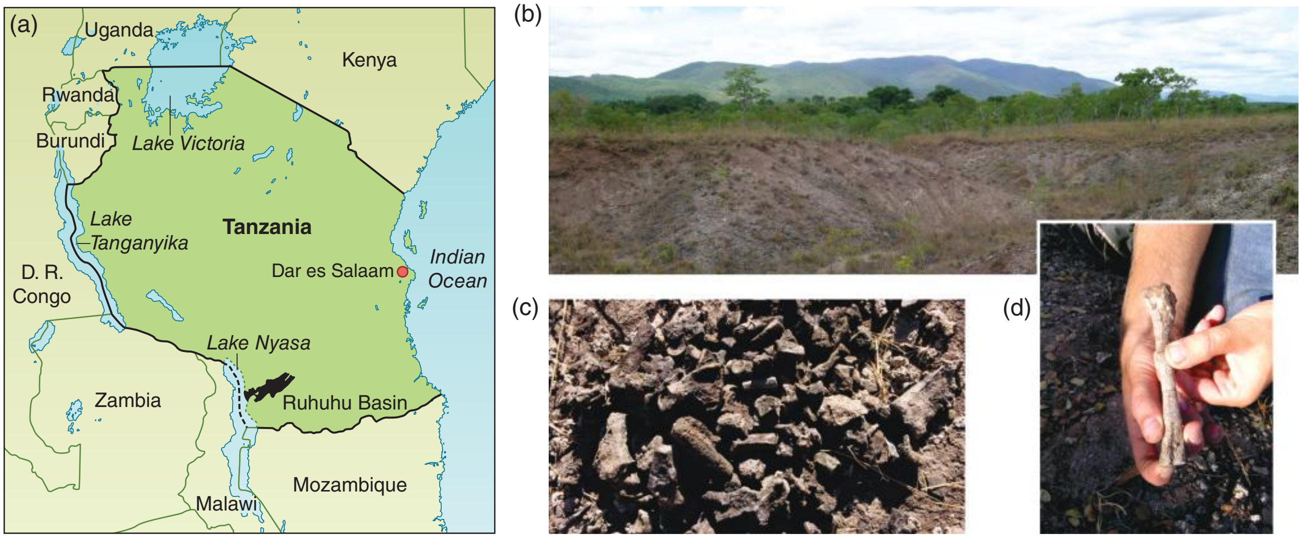
Colour plate 5.2 The odd couple: two species in an Early Triassic burrow form the Karoo. The therapsid *Thrinaxodon* (lower) was apparently there first, and an injured temnospondyl, *Broomistega*, entered later, and then both died together. This is an upper side 3D rendering of CT scans of the specimen. Source: Fernandez *et al.* (2013). Reproduced with permission.



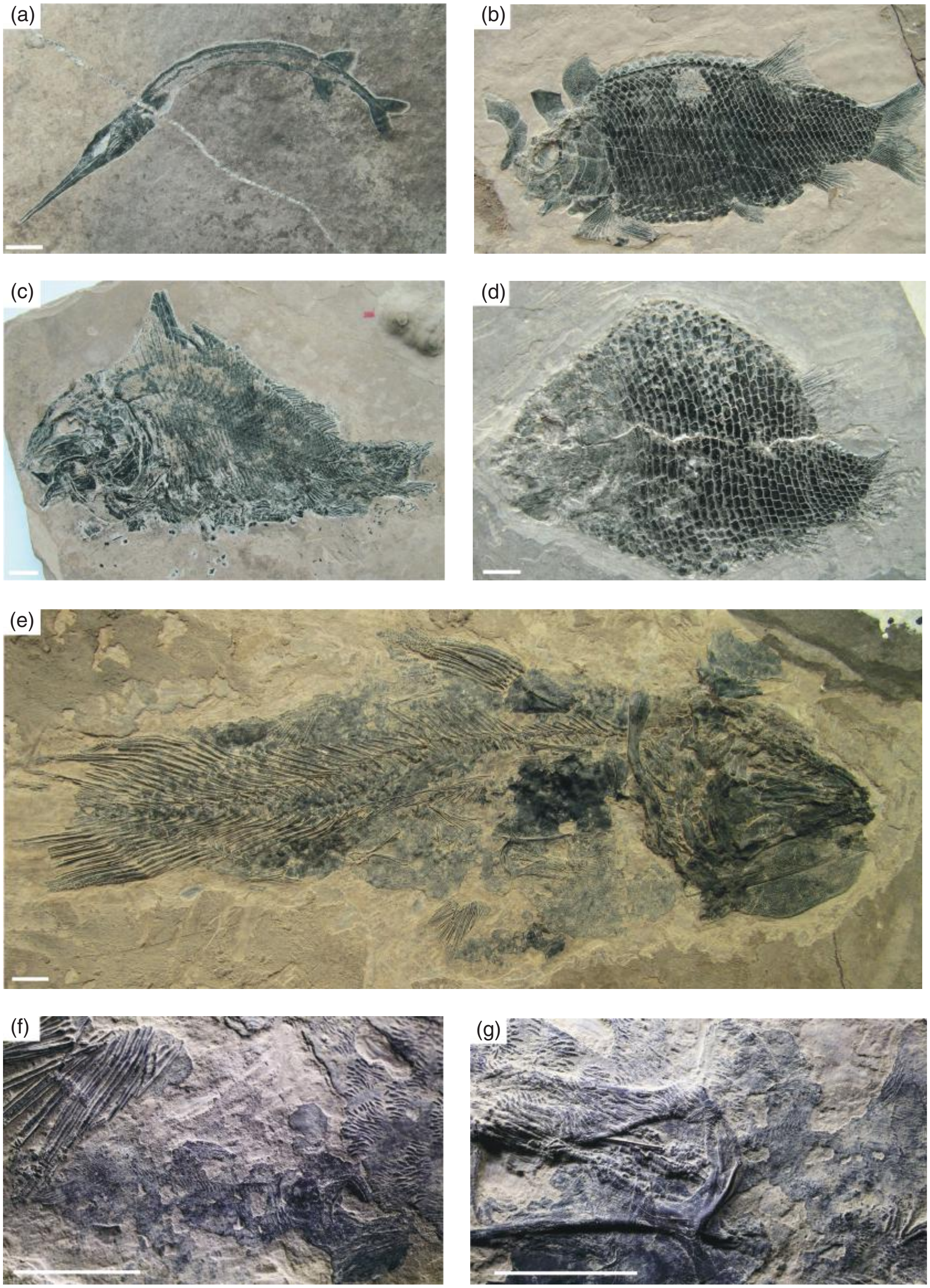
Colour plate 6.1 The recovery of life in the sea and on land during the Early and Middle Triassic, showing environmental changes and biodiversity variations. Carbon isotope fluctuations, Siberian Traps large igneous province (STLIP) eruption, anoxia ranges, trace fossil data, and reef, reef builder, chert and coal gap data from many sources. Abbreviations: Ae, Aegean; Bith, Bithynian; Di, Dienerian; Gr, Griesbachian; Illy, Illyrian; Sm, Smithian; Vol, volcanism. Source: Chen and Benton (2012). Reproduced with permission from Nature Publishing Group.



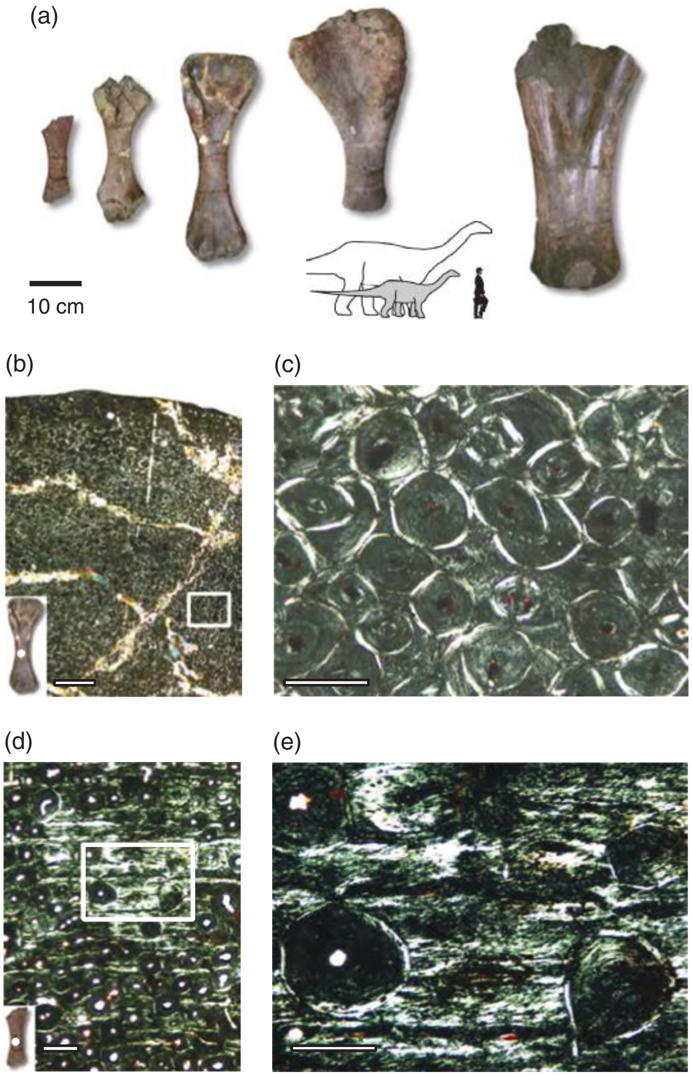
Colour plate 6.2 Among the floating lily fields of Guanling, original artwork by Brian Choo (http://gogosardina.deviantart.com/). The giant pseudopelagic crinoids *Traumatocrinus hsui* form massive curtains hanging below floating logs. From the top, the ichthyosaurs *Shastasaurus/ Guanlingsaurus liangae* and *Qianichthyosaurus zhoui* swim past the thalattosaurs *Xinpusaurus bamaolinensis* and *Miodentosaurus brevis*. Foraging among the giant sea-lillies are smaller armoured reptiles, the turtle-like placodont *Psephochelys polyosteoderma* (left foreground) and the early genuine turtle *Odontochelys semitestacea* (right foreground). Flitting around them are coiled ammonoids (*Trachyceras multituberculatus*) and a variety of fishes, including large predators (hybodont shark, *Guizhoucoelacanthus guanlingensis, Birgeria sp*.), the slender shoaling *Pholidopleurus xiaowaensis,* pursued by *Miodentosaurus* in the background, and the diminutive *Peltopleurus brachycephalus.* Source: B. Choo, Institute for Vertebrate Paleontology and Paleoanthropology, Beijing, China, and Flinders University, Australia.



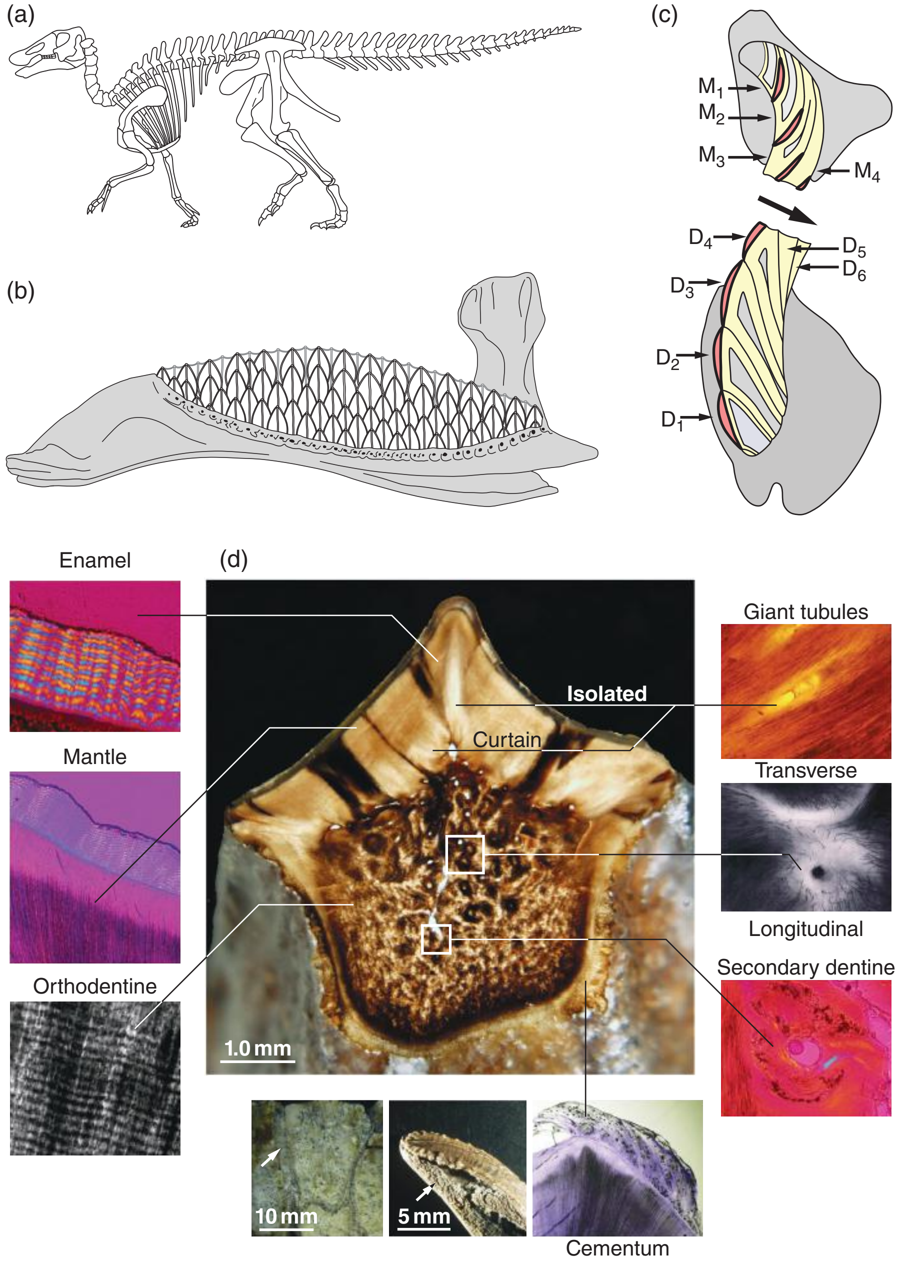
Colour plate 6.3 The Manda dinosauromorphs. (a) Map showing the location of the Manda beds in the Ruhuhu Basin in Tanzania. (b) Field photograph of the Manda beds. (c,d) Field photographs of surface-collected bones, (c) and a long bone of the dinosauromorph *Asilisaurus* (d). Source: M. Langer, University of São Paulo, São Paulo, Brazil (map and composition) and R. Smith, Iziko Museum of Natural History, Cape Town, South Africa (photographs). Reproduced with permission.



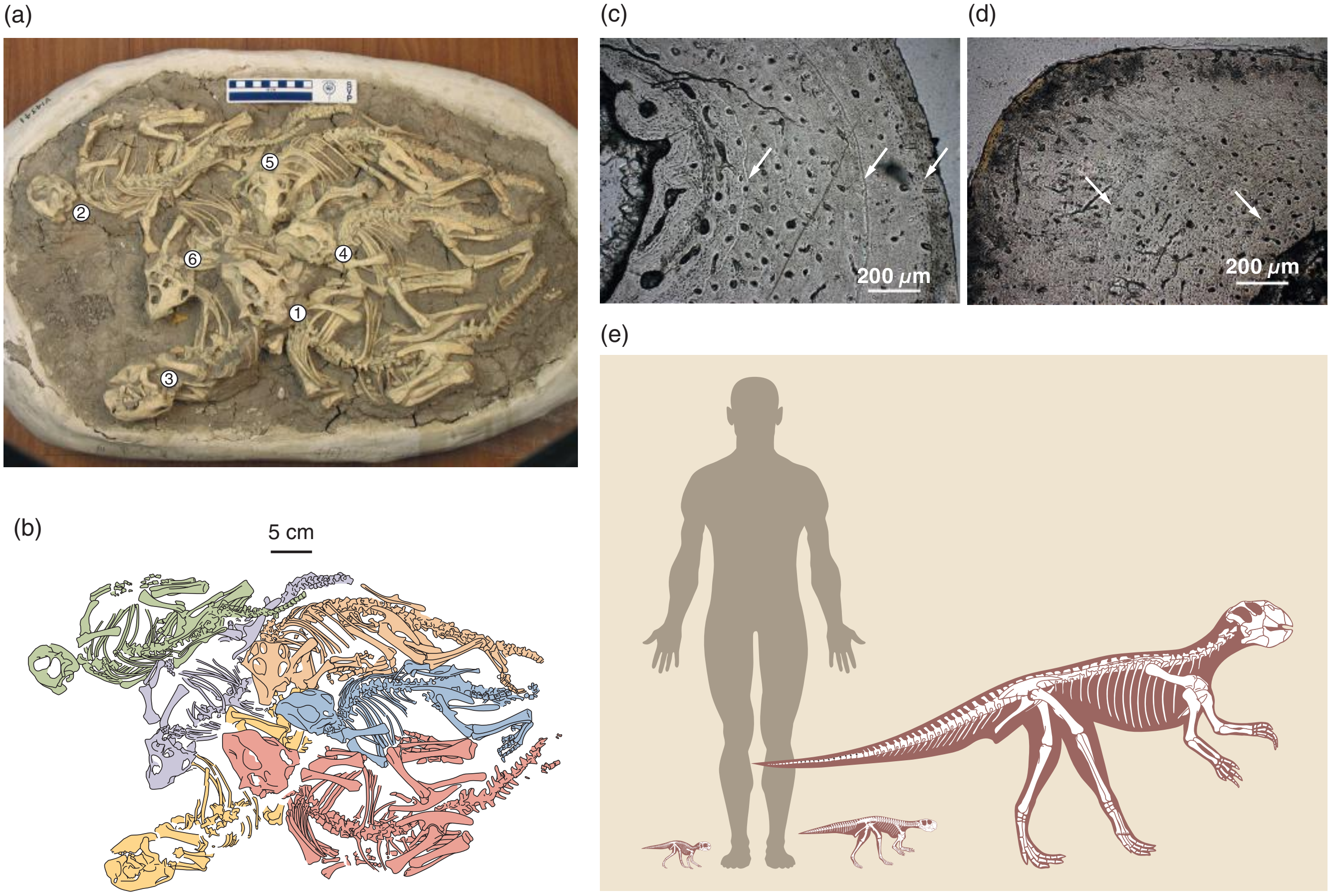
Colour plate 7.1 Some actinopterygians from Luoping: (a) the saurichthyid *Sinosaurichthys minuta*; (b) the perleidiform *Luopingichthys bergi*; (c) the neopterygian (basal halecomorph) *Luoxiongichthys hyperdorsalis*; (d) the neopterygian (basal ginglymodian) *Kyphosichthys grandei*; (e–g) the coelacanth *Luopingcoelacanthus eurylacrimalis*, mother (e), and her embryo 1 (f) and embryo 2 (g). Scale bar is 10 mm. Source: W. Wen and S. Hu, China Geology Center, Chengdu, China. Reproduced with permission.



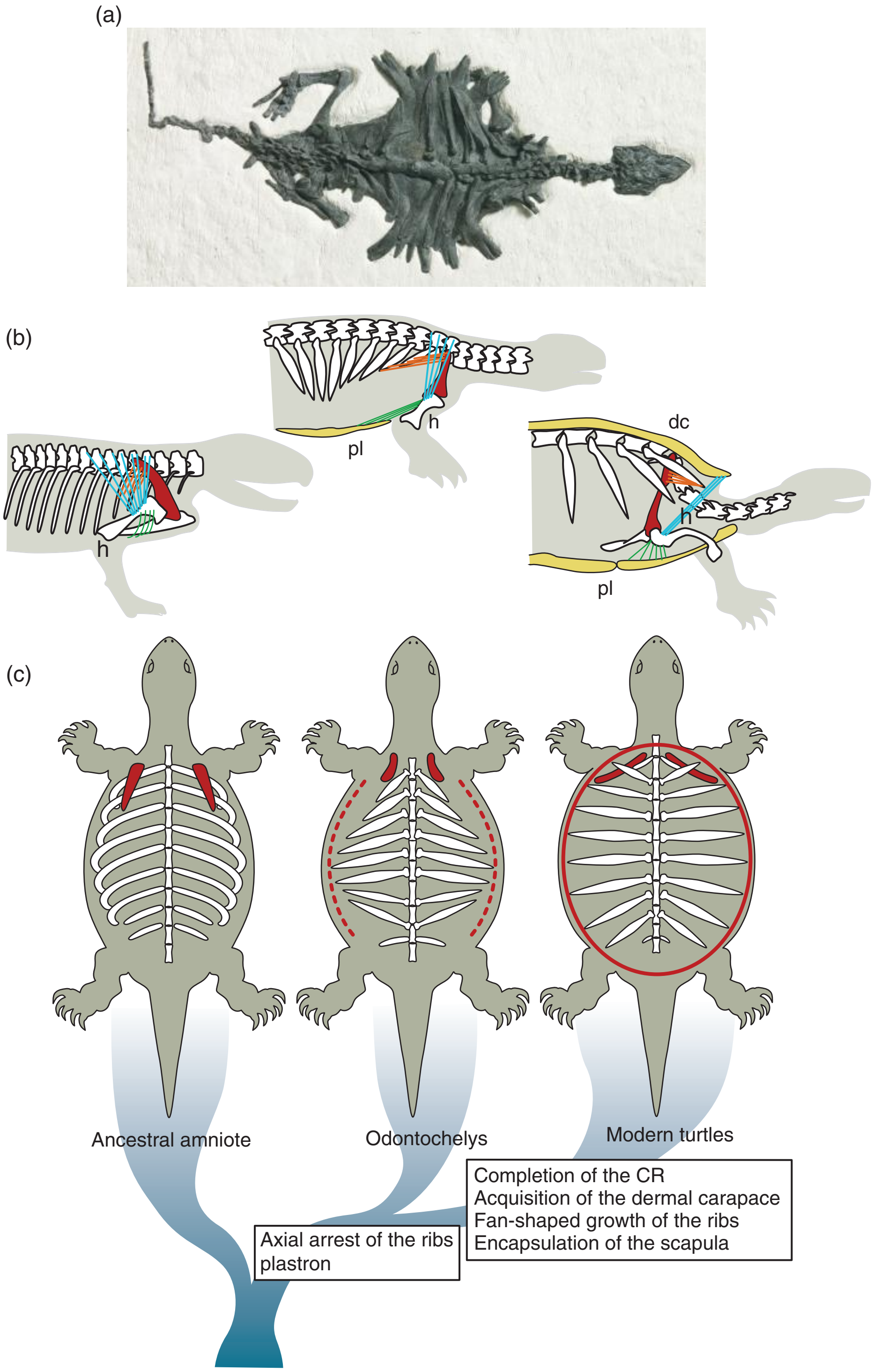
Colour plate 8.1 Relative growth and bone histology of the dwarf dinosaur *Magyarosaurus dacus* from the Late Cretaceous of Haţeg in southern Romania. (a) Photographs of sampled humeri, ranging from a juvenile (left; 45% maximum size) to the largest known specimen (second right), and an indeterminate, large titanosaur. Cartoon shows relative size of *Magyarosaurus* (grey), a close relative, and a human. (b,c) Overview of cross section (b) and close-up (c) from a subadult individual, showing the cortex dominated by secondary remodelling (the rounded structures with concentric laminae). (d,e) General view (d) and close-up (e) of largely interstitial laminar primary bone in outermost cortex of the smallest available specimen (45% maximum size), showing the vascular canals oriented circumferentially as in laminar fibrolamellar bone, but the bone matrix between the vascular canals consisting largely of parallel-fibred and lamellar bone, with only a minute fraction of fibrous (or woven) bone tissue. Source: Benton *et al*. (2010). Reproduced with permission from Elsevier.



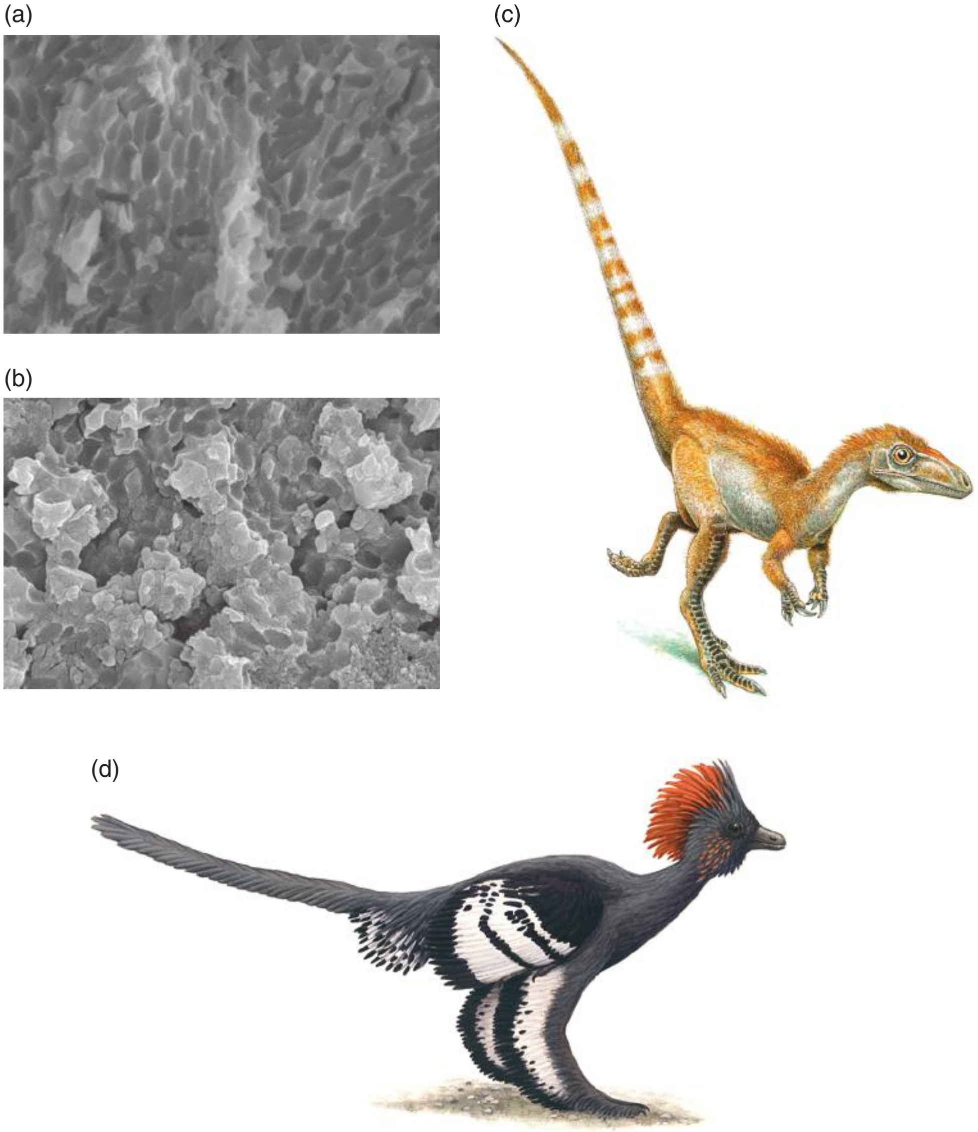
Colour plate 8.2 Hadrosaur grinding teeth: (a) Skeleton of the hadrosaurid *Edmontosaurus*; (b) hadrosaurid dental battery, viewed from inside, showing batteries of developing teeth; (c) the classic 'two-tissue model; in cross section, showing enamel (dark) and dentine (light), with dentary (D) and maxillary (M) teeth numbered in order from youngest to oldest, and the direction of tooth movement indicated by an arrow; (d) sections through Edmontosaurus teeth showing tissues such as enamel, orthodentine, and tubules. Source: Erickson *et al.* (2012). Reproduced with permission from the American Association for the Advancement of Science.



Colour plate 8.3 Juveniles of *Psittacosaurus lujiatunensis* from the Early Cretaceous of NE China. (a,b) Cluster of six individuals, photograph and drawing. (c,d) Histological thin sections from the fibula of a three-year old, showing three LAGs (white arrows; c), and a two-year-old, showing two LAGs (white arrows; d). (e) Growth in *Psittacosaurus*, from a one-year old hatchling (left), a three-year old juvenile, and a ten-year-old adult (right). Source: Zhao *et al.* (2013a). Reproduced with permission from Nature Publishing Group.

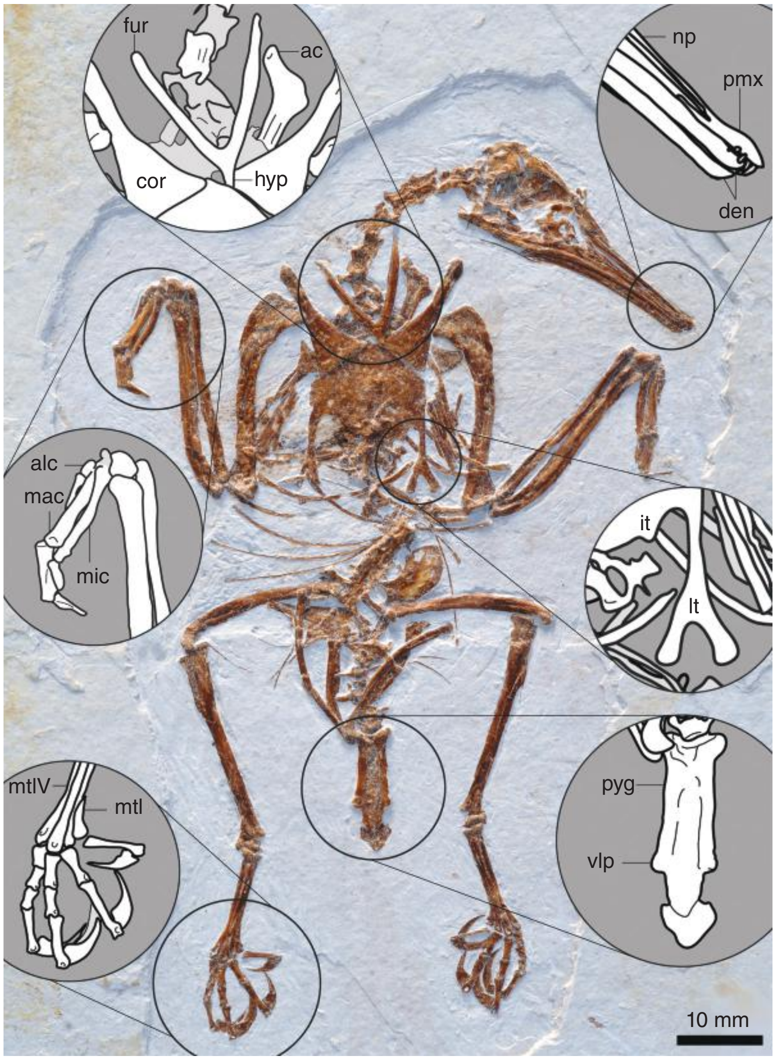


Colour plate 8.4 The oldest turtle, and evolution of the turtle body plan. (a) Skeleton of the type specimen of *Odontochelys semitestacea*, showing the rib-like plastron. (b) Evolution of the ribs, scapula, and carapace in an ancestral amniote (left), in *Odontochelys* (centre), and in a modern turtle (right), seen in lateral cross section (b) and in dorsal view (c). The scapula is red, and key shoulder muscles are indicated. In *Odontochelys*, the serratus anterior anlage would have connected the scapula and distal tips of anterior ribs antero-posteriorly. In *Odontochelys*, the carapacial ridge (CR; red broken line) may have developed only temporarily and incompletely in the embryo. In the modern turtle, the CR (red solid line) forms a complete circle, inducing the fan-shaped growth of the ribs. Abbreviations: dc, dermal carapace; h, humerus; pl, plastron. Source: (a) C. Li, Institute for Vertebrate Paleontology and Paleoanthropology, Beijing, China. (b) H. Nagashima, Meiji University, Meiji, Japan. Reproduced with permission.

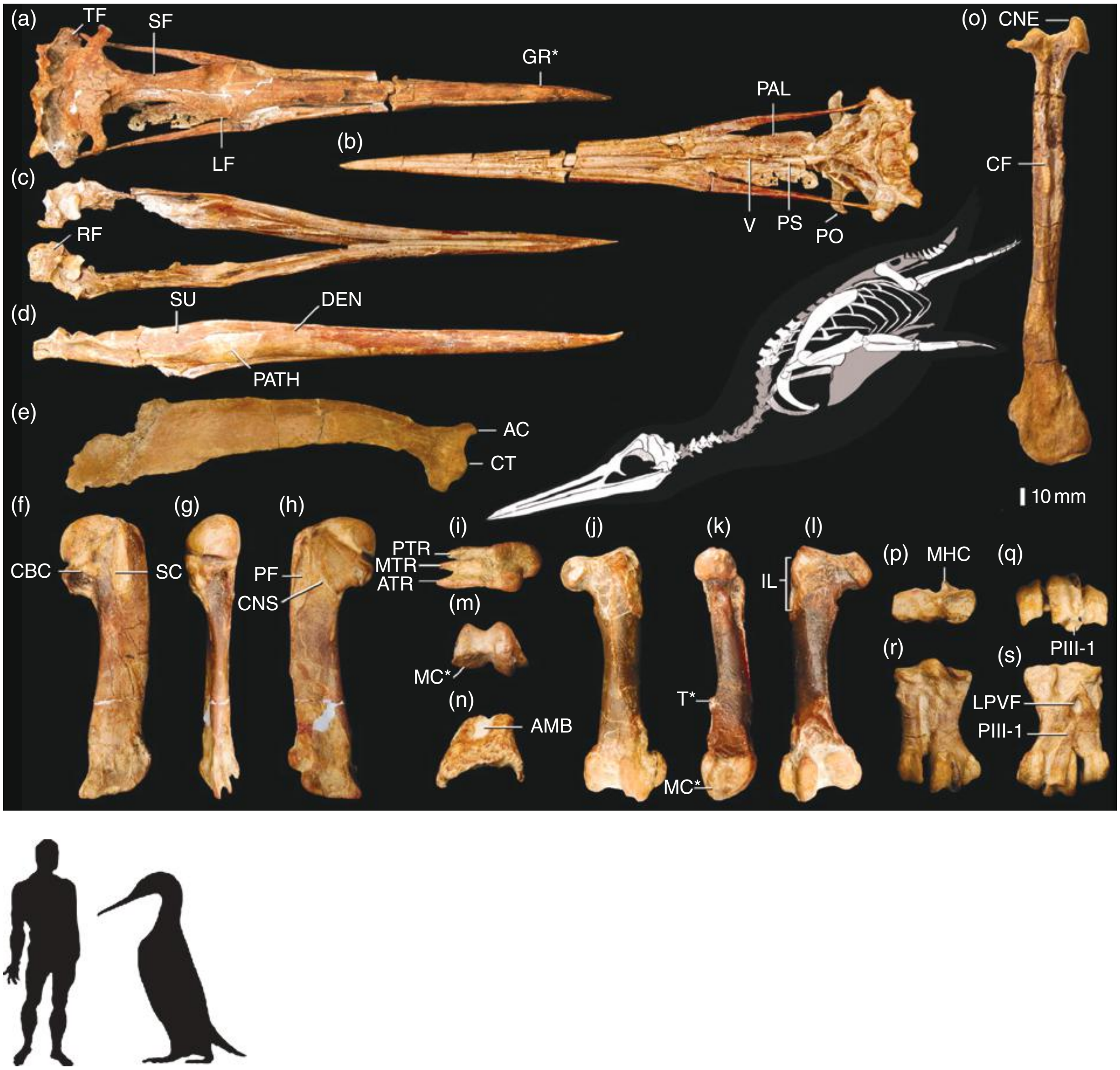


Colour plate 9.1 The colours of dinosaur feathers: (a,b) scanning electron microscope photographs of sausage-shaped eumelanosomes, indicating black, grey, or brown original colours (a), and of spherical phaeomelanosomes, indicating ginger colours (b); (c) reconstruction of *Sinosauropteryx*, showing the ginger and white striped tail; (d) reconstruction of *Anchiornis*, showing the black, grey, ginger, and white colour stripes and patches. Source: (a,b) Zhang *et al*. (2010). Reproduced with permission from Nature Publishing Group. (c) J. Robins (artist), Bath, UK. Reproduced with permission. (d) M. DiGiorgio, Madison, CT, USA. Reproduced with permission.

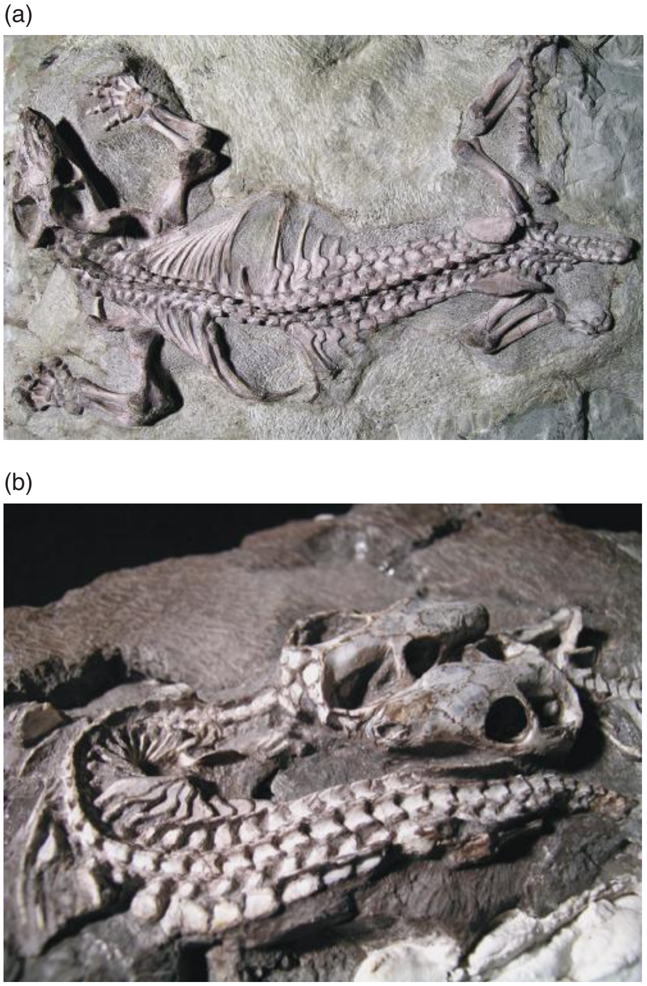
Colour plate 9.2 The derived dromaeosaurid *Microraptor gui* (IVPP V 13352), photographed under normal light. This shows the preserved feathers (white arrow) and the 'halo' around the specimen where they appear to be absent (black arrows). Scale bar is 50 mm. Source: Z. Zhonghe, Institute for Vertebrate Paleontology and Paleoanthropology, Beijing, China. Reproduced with permission.



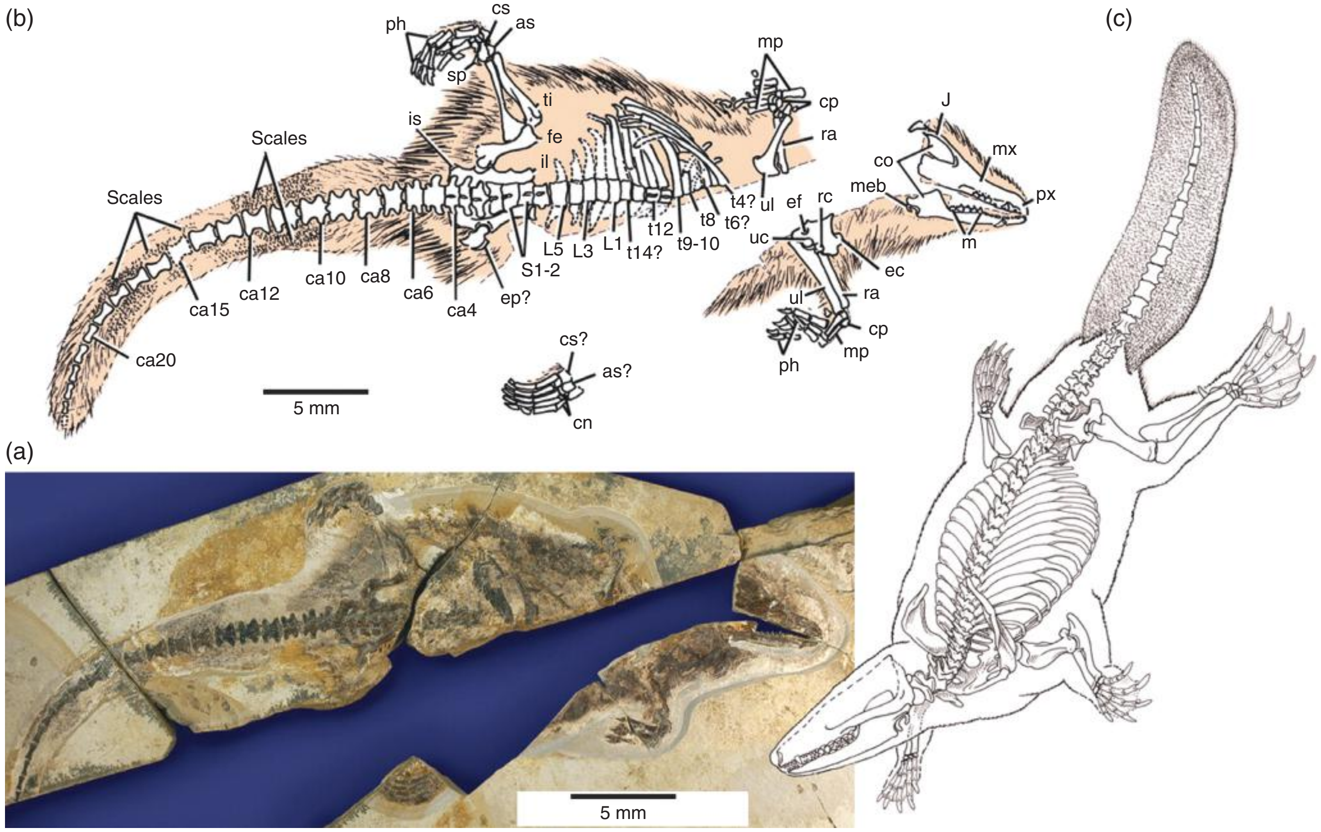
Colour plate 9.3 Key anatomical features of the enantiornithine *Rapaxavis* from the Jiufotang Formation (Early Cretaceous) of Liaoning, China (Dalian Museum of Natural History D2522; O'Connor *et al*., 2011). Enlarged areas highlight the unique characteristics of Enantiornithes; note the specialized dentition (rostrally restricted in this case), the Y-shaped furcula with long hypocleidium (broken during preparation in this case), the large unique pygostyle, the small intermediate trabeculae with large distal expansions on the lateral trabeculae, the minor metacarpal extending distally farther than the major metacarpal, the reduced hand (paralleling evolution in Ornithuromorpha), the reduced shaft of the metatarsal IV, and the distally elongate pedal phalanges and large curved claws indicating cursorial habits. Anatomical abbreviations: ac, acromion process of the scapula; alc, alular metacarpal; cor, coracoid; den, dentary; fur, furcula; it, intermediate trabecula (of the sternum); lt, lateral trabecula (of the sternum); mac, major metacarpal; mic, minor metacarpal; mtI, metatarsal I; mtIV, metatarsal IV; np, nasal (frontal) process of the premaxilla; pmx, premaxilla; pyg, pygostyle; vlp, ventrolateral processes. Source: J. O'Connor, Institute for Vertebrate Paleontology and Paleoanthropology, Beijing, China. Reproduced with permission.



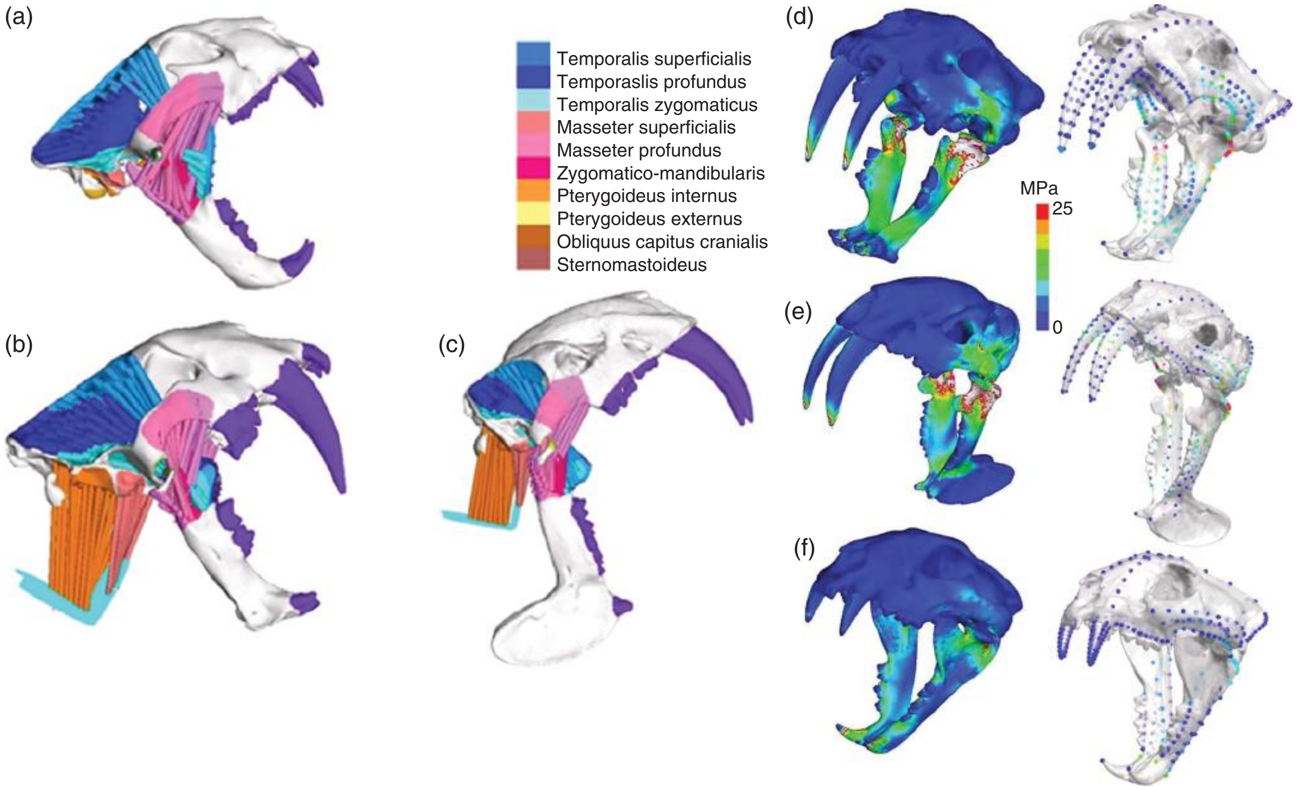
Colour plate 9.4 Reconstruction of *Inkayacu paracasensis* in oblique anterior view showing recovered elements in white on the reconstructed skeleton, and photographs of the holotype specimen: skull and mandible in (a and c) dorsal, (b) ventral, and (d) lateral views; scapula in (e) lateral view and humerus in (f) posterior, (g) ventral, (h) anterior, and (i) distal views; femur in (j) dorsal, (k) medial, (l) ventral, and (m) distal views; patella in (n) anterior view; tibiotarsus in (o) lateral view; and tarsometatarsus in (p) proximal, (q) distal, (r) anterior, and (s) plantar views. Anatomical abbreviations: AC, acromion; AMB, pathway of m. ambiens tendon; ATR, anterior trochlear process; CBC, m. coracobrachialis caudalis insertion; CF, fibular crest; CNE, cnemial crests; CNS, coracobrachialis nerve sulcus; CT, coracoid tuberosity; DEN, dentary; GR, groove on premaxilla; IL, m. iliofemoralis and iliotrochantericus insertions; LF, lacrimal facet; LPVF, lateral proximal vascular foramen; MHC, medial hypotarsal crest; MC, medial condyle; MTR, middle trochlear process; PIII-1, manual phalanx III-1; PAL, palatine; PATH, pathology; PF, pectoralis fossa; PO, postorbital process; PS, parasphenoid rostrum; PTR, posterior trochlear process; SC, m. supracoracoideus insertion; SF, salt gland fossa; SU, surangular; T, tab-like process; TF, temporal fossa; V, vomer. Asterisks demarcate autapomorphies referenced in the diagnosis. Below is a restoration of *Anthropornis* (right), a 1.7 m penguin from Seymour Island, Antarctica, compared to a 1.8 m human. Source: Clarke *et al.* (2010). Reproduced with permission from the American Association for the Advancement of Science.



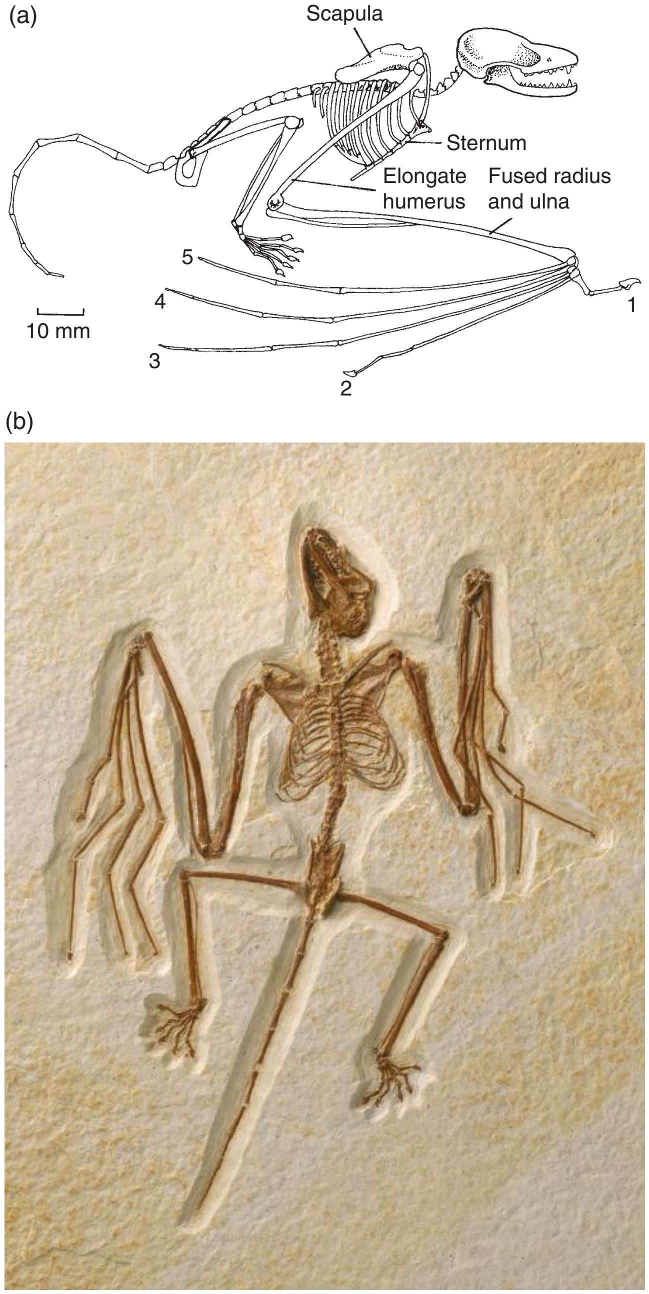
Colour plate 10.1 Early Triassic cynodonts: (a) *Galesaurus*, (b) two juveniles of *Thrinaxodon*.. Source: R. Smith, Iziko Museum of Natural History, Cape Town, South Africa. Reproduced with permission.



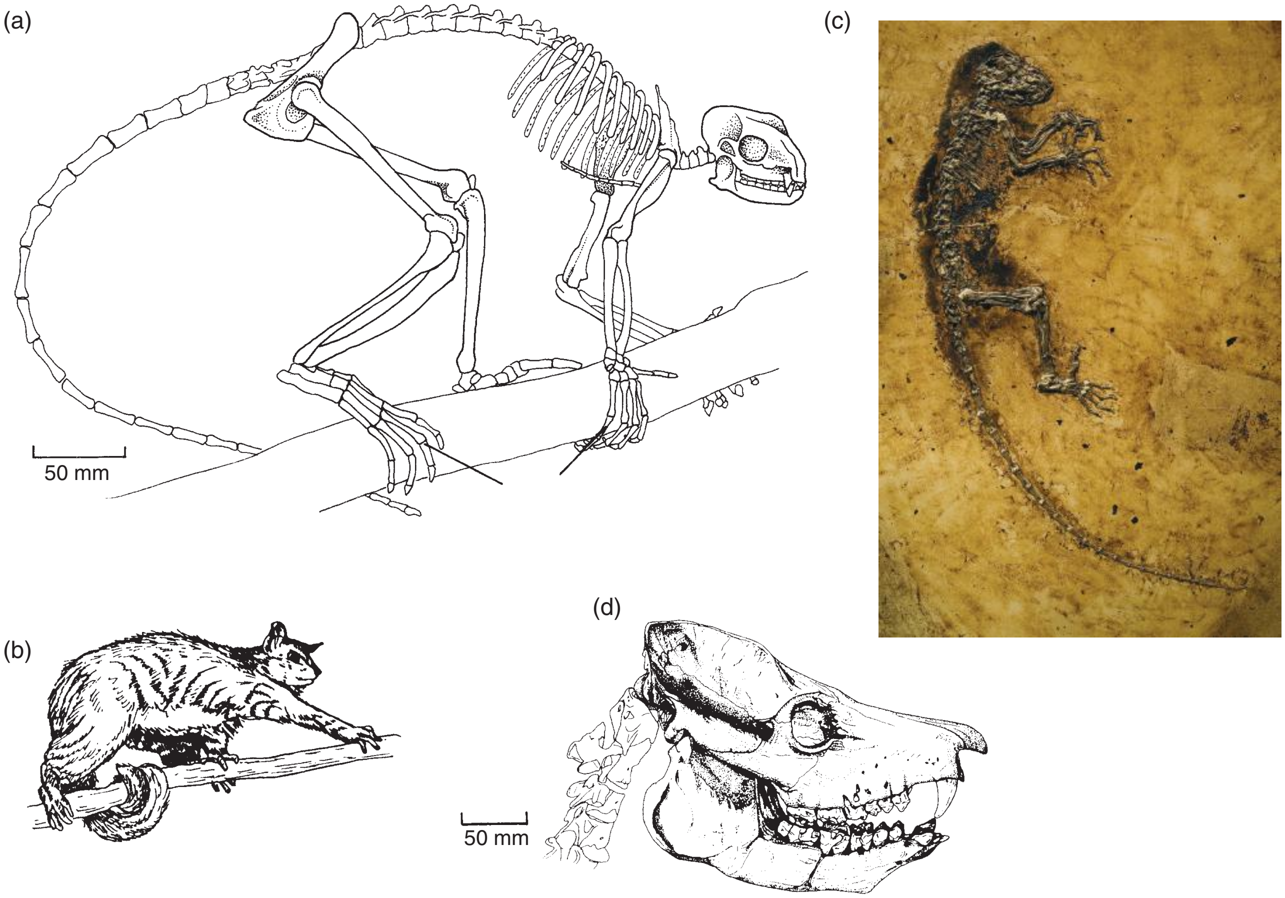
Colour plate 10.2 The first swimming mammal *Castorocauda*, showing the original specimen (a), an outline drawing of this specimen showing skeleton and surrounding hair (b), and a reconstruction as a swimmer and burrower (c). Abbreviations: as, astragalus; ca, caudal vertebrae; cn, ento-, meso-, and ecto-cuneiforms; co, coronoid process of dentary; cp, carpals; cs, calcaneus; ec, ectepicondyle and supinator shelf (humerus); ef, entepicondyle foramen; ep?, probable epipubis; is, ischium; J, jugal; L1-6, lumbar ribs 1 to 6; m, molars; meb, manubrium of malleus; mp, metacarpals; mx, maxilla; px, premaxilla; ra, radius; rc, radial condyle; S1-2, sacrals 1 and 2; sp, extratarsal ("poisonous") spur; t4-t14 (preserved ribs through thoracic 17); uc, ulnar condyle; ul, ulna. Source: Ji *et al.* (2006). Reproduced with permission from the American Association for the Advancement of Science.



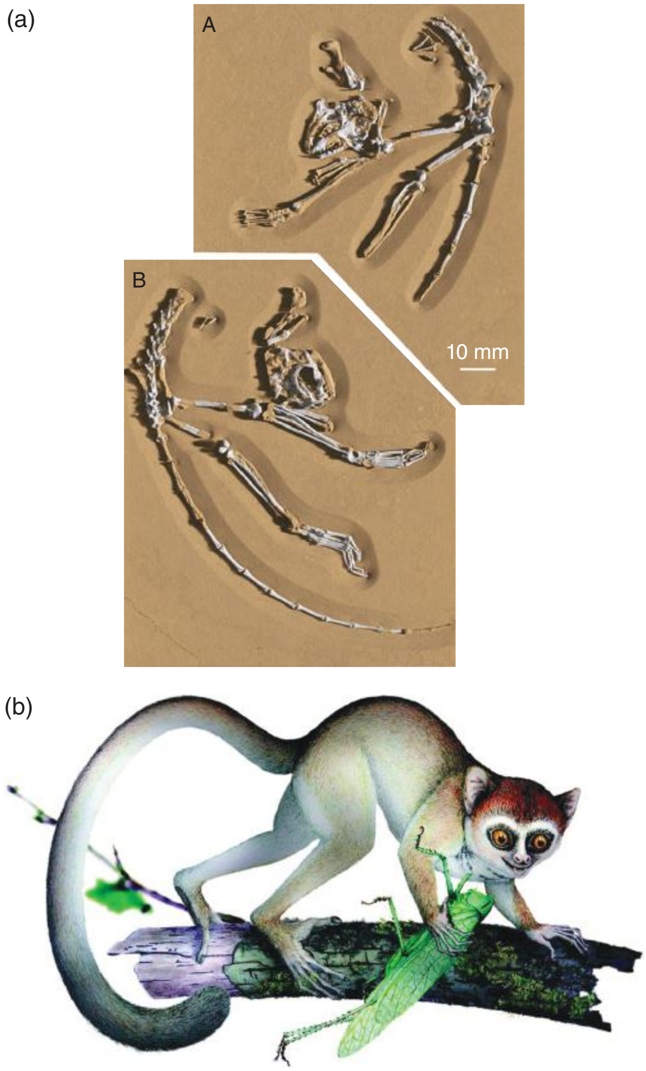
Colour plate 10.3 Jaw mechanics of the placental sabre-tooth *Smilodon*, the marsupial sabre-tooth *Thylacosmilus*, and the modern conical-toothed leopard, *Panthera*. (a–c) Jaw adductor muscles in *Panthera* (a), and reconstructed jaw adductor and head depressor muscles in *Smilodon* (b), and *Thylacosmilus* (c). (d–e) Stress distributions for bites powered by the jaw adductor muscles, showing the intensity of stresses by the hotness of the colour, in *Panthera* (d), *Thylacosmilus* (e), and *Smilodon* (f). Source: Wroe *et al*. (2013a). Reproduced with permission.



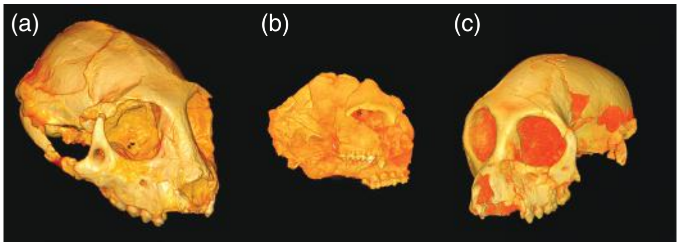
Colour plate 10.4 The oldest reasonably complete bat fossils, *Icaronycteris* (a) and *Onychonycteris* (b) from the Green River Formation (early Eocene) of Wyoming. Source: (a) Adapted from Jepsen (1970). (b) Simmons *et al*. (2008). Reproduced with permission from Nature Publishing Group.



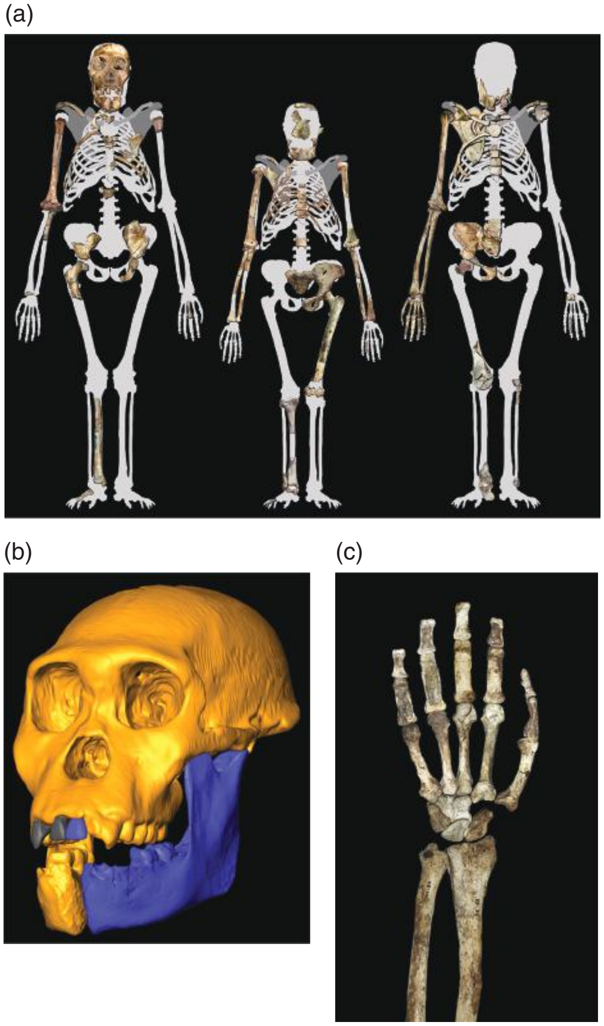
Colour plate 11.1 Fossil strepsirhine primates: (a b) the middle Eocene adapiform *Smilodectes*, skeleton and restoration of life appearance; (c) the type specimen of the adapiform *Darwinius*; (d) the Pleistocene giant lemur *Megaladapis*, lateral view of skull. Source: (a) Adapted from Simons (1964). (b) Adapted from Rose (2006). (c) © Jens L. Franzen, Philip D. Gingerich, Jörg Habersetzer1, Jørn H. Hurum, Wighart von Koenigswald, B. Holly Smith/CC-BY-SA-2.5/GFDL. (d) Adapted from Zapfe (1963).



Colour plate 11.2 The oldest haplorhine primate, the tarsiiform *Archicebus* from the early Eocene of Hubei, China: (a,b) dorsal and ventral views of the skeleton, showing the long tail, hindlimbs, partial trunk and forelimb, and skull, a composite image based on CT scans of the fossil, showing fossil bones (light grey) and restored elements based on impressions in the rock (dark grey); (b) life restoration. Source: (a,b) Adapted from Ni *et al.* (2013).



Colour plate 11.3 Crania of (a) the early Oligocene parapithecid anthropoid *Parapithecus grangeri*; (b) the late Eocene stem catarrhine *Catopithecus browni* (a substantially distorted skull); and (c) the early Oligocene stem catarrhine *Aegyptopithecus zeuxis*. Source: Seiffert (2012). Reproduced with permission from John Wiley & Sons.



Colour plate 11.4 Skeleton and skull of *Australopithecus sediba*: (a) the juvenile male, Malapa hominin 1 (MH1) left, Lucy (AL 288-1) centre, and the adult female, Malapa hominin 2 (MH2) right; (b) reconstruction of the MH1 skull; (c) hand and forearm. Source: L.R. Berger, University of the Witwatersrand, Johannesburg, South Africa. Reproduced with permission. (a,c) Image created by P. Schmid, Anthropological Institute, University of Zurich, Switzerland. (b) Reconstruction by K. Carlson, University of the Witwatersrand, Johannesburg, South Africa.

Colour plate 11.5 Diverse later Pleistocene Homo crania, in anterior view: (a) Guattari 1, Monte Circeo, Italy; (b) Skull 5, Simo de los Huesos, Atapuerca, Spain; (c) Cro-Magnon 1, Les Eyzies-de-Tayac, France; (d) Cast of Omo 1, Omo Kibish, Ethiopia. Source: Tattersall and Schwartz (2009). Reproduced with permission.