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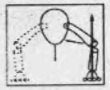


BIOMECHANICS AND BEHAVIOUR BOXES

Preface

Vertebrate palaeontology is always in the news: astonishing, ancient basal chordate and vertebrate fossils are announced from China; fossil hunters argue about which was the largest dinosaur of all, or the oldest dinosaur with feathers; an ancient fossil bird is announced that adds 100 million years to their history; ever-older specimens of human beings are unearthed in Africa.

When I wrote 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 summary of the latest of these exciting discoveries. The first edition was published in 1990. The second edition, substantially modified, appeared in 1997. It offered extensive coverage of the new discoveries of the early 1990s, as well as comprehensive cladistic coverage of the main vertebrate clades. Since 1990, the book has 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. I hope these wandering days are now over.

The first edition appeared in Spanish in 1995 (*Paleontologia y evolución de los vertebrados*, Edition Perfils, Lleida) and the second in Italian in 2000 (*Paleontologia dei Vertebrati*, Franco Lucisano Editore, Milano), and a German edition is in progress. 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—the origin of the vertebrates, dramatic new fish specimens unlike anything now living, the adaptations required for the move on to land, the relationships of the Palaeozoic and Mesozoic tetrapods, the origins and biology of the dinosaurs, the role of mass extinctions in vertebrate evolution, new Mesozoic birds, the earliest mammals, ecology and mammalian diversification, reconstructing the tree of life and reconciling morphological and molecular evidence, the origins and evolution of human beings.

I have four aims in writing this book. First, I want to present **a readable narrative of the history of the vertebrates** that is accessible to any interested person, whether having 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 pictures.

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, the jaws of bony fishes, 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. 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 short boxed thematic sections that are divided into three categories: tree of life controversies (deuterostome relationships, jawless fishes, sarcopterygians, basal tetrapods, amniotes, dinosaurs and the origin of birds, molecular information on mammalian phylogeny, hominin relationships), exceptional fossils or faunas (basal chordates from China, a rich fossil deposit of early tetrapods, dramatic new discoveries of Cretaceous birds, fossil mammals with hair, new basal humans from Chad) and palaeobiology of selected unusual ancient vertebrates (biology of a helmeted fish, jaw action and diet of dicynodonts, biology of a pack-hunting dinosaur, thermal physiology of the dinosaurs, hair in pterosaurs, horse-eating birds, the earliest whales).

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 full lists of 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).

I am indebted to many people. I thank Roger Jones and Clem Earle of Unwin Hyman who commissioned the first edition, and Ward Cooper of Chapman & Hall who steered the second edition through. The following people read parts of the first and second editions, or made other valuable contributions: Dick Aldridge, Peter Andrews, Chris Beard, Derek Briggs, Henri Cappetta, Bob Carroll, Luis Chiappe, Jenny Clack, Mike Coates, Liz Cook, Joel Cracraft, Eric Delson, David Dineley, 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, Liz Loeffler, John Maisey, Andrew Milner, Alec Panchen, Mike Parrish, †Colin Patterson, Mark Purnell, Jeremy Rayner, Robert Reisz, Bruce Rubidge, †Bob Savage, Pascal Tassy, Paul Sereno, Glen Storrs, Mike Taylor, Nigel Trewin, David Unwin, Cyril Walker, Peter Wellnhofer and Bernard Wood. For the third edition, I thank Phil Donoghue and Kevin Padian for their helpful advice on how to update the second edition, as well as Kenneth Angielczyk, David Archibald, David Berman, Jenny Clack, Mike Coates, Joel Cracraft, Phil Donoghue, Gareth Dyke, Andrzej Elzanowski, Susan Evans, David Gower, Lance Grande, Christine Janis, Philippe Janvier, Jürgen Kriwet, Adrian Lister, Luo Zhe-Xi, Sean Modesto, Kevin Padian, Kevin Peterson, Mark Purnell, Robert Reisz, Olivier Rieppel, Chris Stringer, Bernard Wood and Adam Yates who read individual chapters, and Bill Harrison and Hezy Shoshani, who volunteered valuable comments.

My special thanks go to three artists, Libby Mulqueeny (Belfast) who drew most of the diagrams for the book in a frenzy of work, John Sibbick (Bath) who prepared the spectacular 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 Blackwell Publishing for commissioning the revision, Rosie Hayden and Harry Langford for their careful work on the text, and Cee Pike for design work.

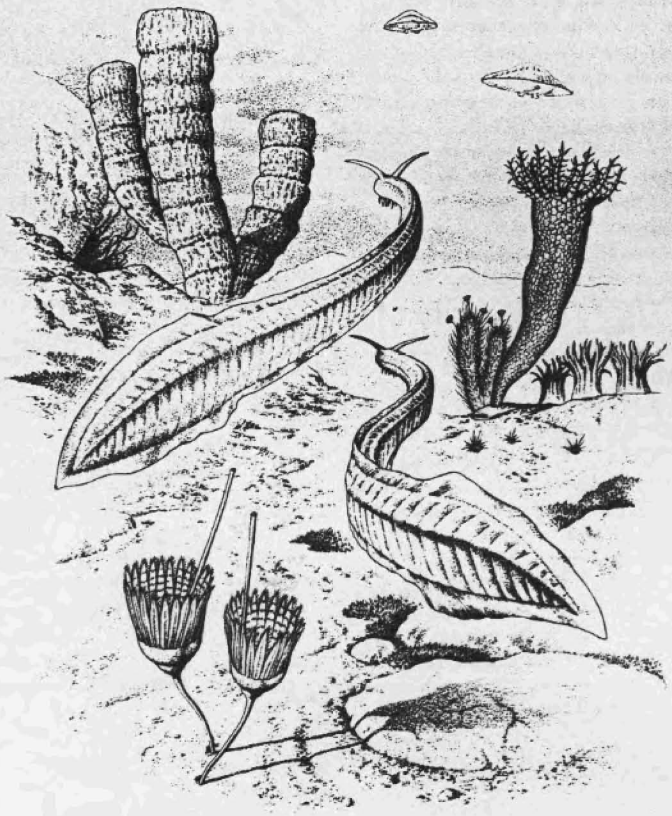
Michael J. Benton
March 2004

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/

There is a dedicated website for this book at http:// www.blackwellpublishing.com/benton where you can make web connections from, view the illustrations online, and find out more.

CHAPTER 1

Vertebrate Origin



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 extraordinary new fossil discoveries from China help us understand the ancestry of vertebrates?

INTRODUCTION

Vertebrates are all the animals with backbones, the fishes, amphibians, reptiles, birds, and mammals. These animals have attracted a great deal of study. The efforts of generations of vertebrate palaeontologists have been repaid by the discovery of countless spectacular fossils: the heavily armoured fishes of the Siluro-Devonian, seven- and eight-toed amphibians, 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 of this information that has accumulated over the past 200 years, the origin of the group is hotly debated.

One thing is clear from examination of living animals. The vertebrates are members of a larger group, termed the Phylum Chordata, and their closest living relatives are marine animals such as the sea squirts and amphioxus (see below). These creatures do not have bone, one of the characters of most vertebrates, 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. 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 focus on the origin of chordates.

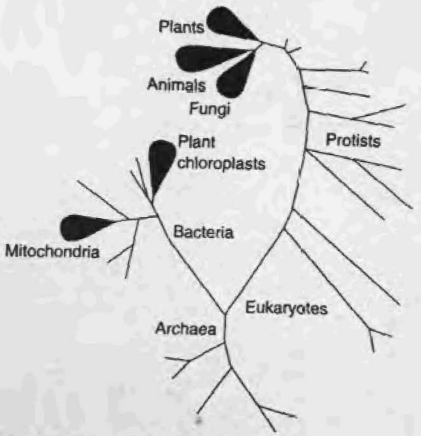


Fig. 1.1 The 'Universal Tree of Life', the commonly accepted view of the relationships of all organisms. Note the location of 'Animals', a minor twig in the tree, close to plants and Fungi. (Based on various sources.)

Looked at more widely, vertebrates are a minor twig on the 'Universal Tree of Life' (Figure 1.1). Molecular studies through the 1990s (e.g. Woese, 2000; Wolf *et al.*, 2002) showed that previous conceptions of the tree were wrong, and that the fundamental splits in the tree of life were all among Bacteria, separating the two major groups Bacteria and Archaea. The familiar plants, animals and fungi are part of Eukaryotes, the major group characterized by complex cells with a nucleus, relative late-comers in the broad scheme of things.

Modern studies (e.g. Nielsen *et al.*, 1996) confirm that a major clade within Metazoa, the animals, is Bilateria, supported by both morphological and molecular evidence (Eernisse and Peterson, in press). The Bilateria includes the bilaterally symmetrical organisms, comprising three clades: Lophotrochozoa (brachiopods, phoronids, annelids, molluscs and many minor groups), Ecdysozoa (arthropods, nematodes, priapulids and some minor groups) and Deuterostomia (echinoderms, hemichordates and chordates). The origin of vertebrates has long been a profound mystery, but now some clarity is emerging.

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

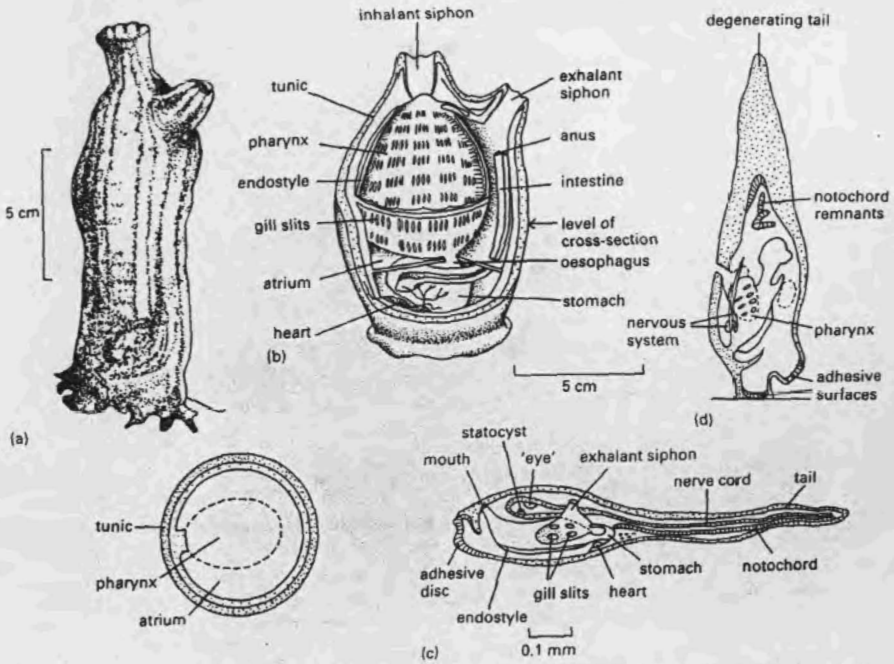


Fig. 1.2 The sea squirts: (a) *Ciona*, external view; (b) internal anatomy and cross-section of an adult; (c) swimming larva; (d) metamorphosing form. (Modified from Jefferies, 1986 and other sources.)

1.1 SEA SQUIRTS AND THE LANCELET

There are two basal groups of living chordates, the sea squirts and the cephalochordates (amphioxus). Amphioxus certainly looks superficially fish-like, but the adult sea squirts could hardly look like less likely 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 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 a gland known as the **endostyle**. During feeding, this gland continuously se-

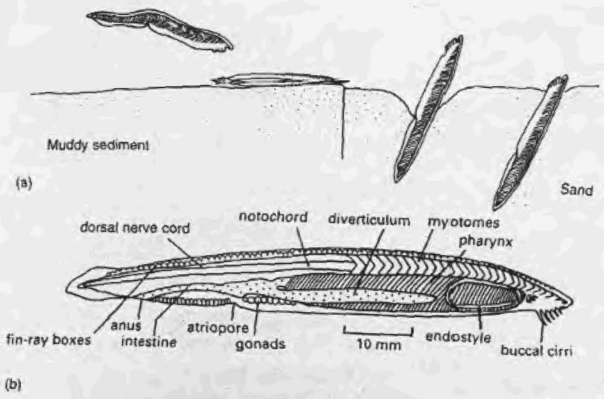


Fig. 1.3 Amphioxus, a cephalochordate: (a) modes of life, including swimming and burrowing into sand for protection; (b) internal anatomy. (Modified from Pough *et al.*, 2002 and other sources.)

cretes 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.

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 which includes a light sensor (an 'eye') and a tilt detector.

The larva then settles on a suitable surface. It upends on to 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 cigar-shaped animal which looks like a young lamprey or eel, yet lacking a head. 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 PHYLUM HEMICHORDATA: PTEROBRANCHS AND ACORN WORMS

Another unusual group of living marine deuterostomes may offer further clues about the origin of the chordates. These are the hemichordates, a **phylum** that includes 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 sea-bed 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 1.8 m. They

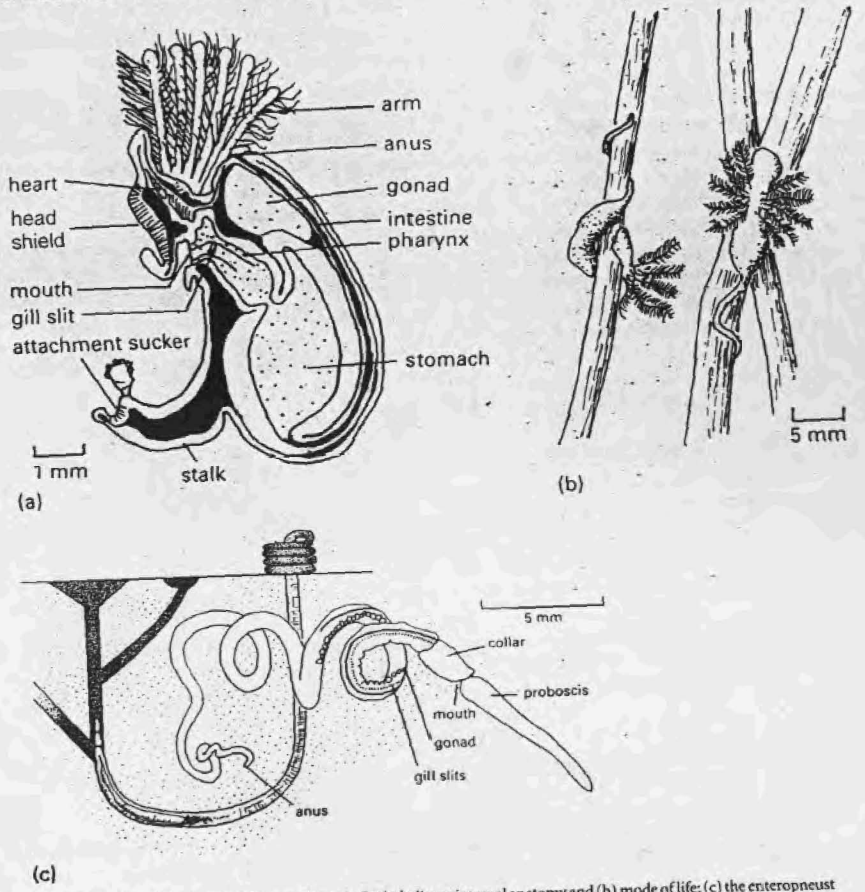


Fig. 1.4 Typical hemichordates: (a) the pterobranch *Cephalodiscus*, internal anatomy and (b) mode of life; (c) the enteropneust *Saccoglossus*, mode of life and external anatomy. (Modified from Jefferies, 1986.)

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 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, probably equivalent to the gill slits of *Cephalodiscus*, sea squirts, and amphioxus.

It was suggested that the Pterobranchia and Enteropneusta should be regarded as two separate, but closely-related, groups (Peterson, 1995), although more recent molecular work (Winchell *et al.*, 2002) concurs with morphological data (Smith *et al.*, in press) that Hemichordata is indeed a valid phylum, and more closely related to echinoderms than to chordates. 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.

1.3 DEUTEROSTOME RELATIONSHIPS

The relationships of chordates used to be rather problematic, but intensive analyses of morphological and molecular data have shown a clearer picture (Eernisse and Peterson, in press; Smith *et al.*, in press). The Phylum Chordata is part of a larger clade, the Deuterostomia, which in turn is part of a yet larger clade of all the bilaterally symmetrical animals, the Bilateria (see p. 2). But what exactly diagnoses the Deuterostomia? The clue comes from **embryology**, the study of the early phases of development in, and just out of, the egg.

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)), 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, in press). Nevertheless, this peculiarity of embryological development appears to solve the question of the broader relationships of chordates.

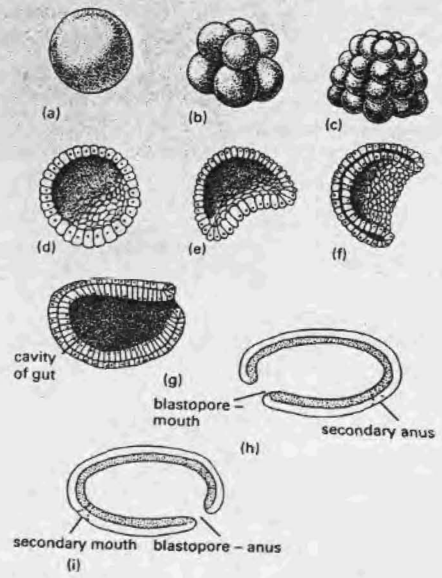


Fig. 1.5 Embryonic development: (a–g) sequence of cell division in amphioxus, from the single-cell stage (a), through the blastula stage (d), to the gastrula stage (g). (h) Fate of the blastophore in protostomes, and (i) in deuterostomes. [Figures (a–g), after Hildebrand and Goslow, 2001, copyright © 2001 John Wiley & Sons, New York; (h, i), after Jefferies, 1986.]

1.3.2 Relationships of the Deuterostomia

The deuterostomes are the phyla Chordata, Hemichordata and Echinodermata. Another minor phylum, the Chaetognatha, or arrow worms, was formerly included here, but they show more protostome than deuterostome characters. The closest major group of living relatives of the chordates and hemichordates are thus the echinoderms—sea urchins, star fish, sea lilies, and sea cucumbers.

Can the status of the Deuterostomia be confirmed? The assumption is that Deuterostomia is a **monophyletic** group, or a **clade**, in other words, a group that had a single common ancestor, and which includes all of the descendants of that ancestor (see p. 31). The monophyly of the Deuterostomia is confirmed by the fact that they possess unique characters that are not seen in other animals (Smith *et al.*, in press): a posterior blastopore that generally becomes the anus, gill slits (present only in precursors of the echinoderms) and other characters. There has been some dispute over the relationships of the taxa within Deuterostomia (see Box 1.1), although this is now largely resolved.

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 reckoned 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. Non-chordates, such as insects, worms, molluscs, jellyfish, and sea urchins, do not have tails. What of the fossil evidence?

1.4 CHORDATE ORIGINS

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 Formation of China, an Early Cambrian deposit (see Box 1.2). These new specimens, combined with studies of modern forms, give clues about the early evolution of chordates, but there are many disputes.

1.4.1 Diverse early chordates

There are four main categories of possible early chordates: possible urochordates, possible cephalochordates, vetulicolians, and carpoids. 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 taxa from Chengjiang, such as *Haikouichthys* and *Myllokunmingia* (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*, that 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 locality has also yielded a superficially amphioxus-like cephalochordate, *Cathaymyrus*, as well as the yunnanozoons, which have also been identified as cephalochordates, although others assign them to the Vetulicolia (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

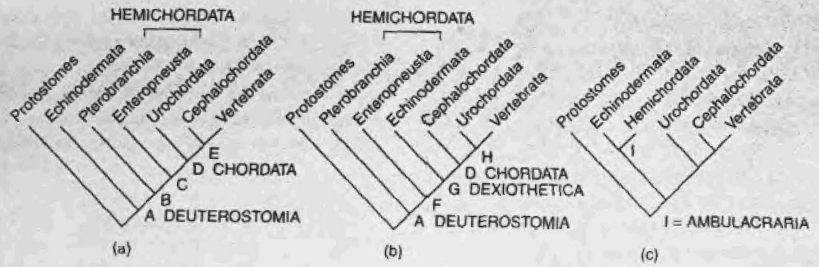
The Vetulicolia is a newly-named group, one of the most extraordinary findings from the Chengjiang

BOX 1.1 DEUTEROSTOME RELATIONSHIPS

Three substantially different schemes for deuterostome relationships have been proposed. The 'traditional' view (e.g. Maisey, 1986; Peterson, 1995; 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 (Peterson, 1995). Most authors regard amphioxus as the closest relative of the Vertebrata on the basis of 10–15 features that are not seen in tunicates.

The 'calcichordate' model (Jefferies, 1986, 1997; illustration (b)) places hemichordates basal to echinoderms and urochordates as sister group to vertebrates, based on evidence from embryology and fossils.

The third view (illustration (c)) is supported by morphological and molecular data and is now widely accepted (Smith *et al.*, in press). The first molecular studies in which the 18 S rRNA genes of echinoderms, hemichordates, and chordates were compared were inconclusive, but newer work (e.g. Bromham and Degnan, 1999; Cameron *et al.*, 2000; Peterson and Eernisse, 2001; Furlong and Holland, 2002; Winchell *et al.*, 2002) definitively pairs hemichordates with echinoderms, as the clade Ambulacraria, and places cephalochordates closer to chordates than urochordates. See Box 3.1 for phylogeny of Vertebrata.

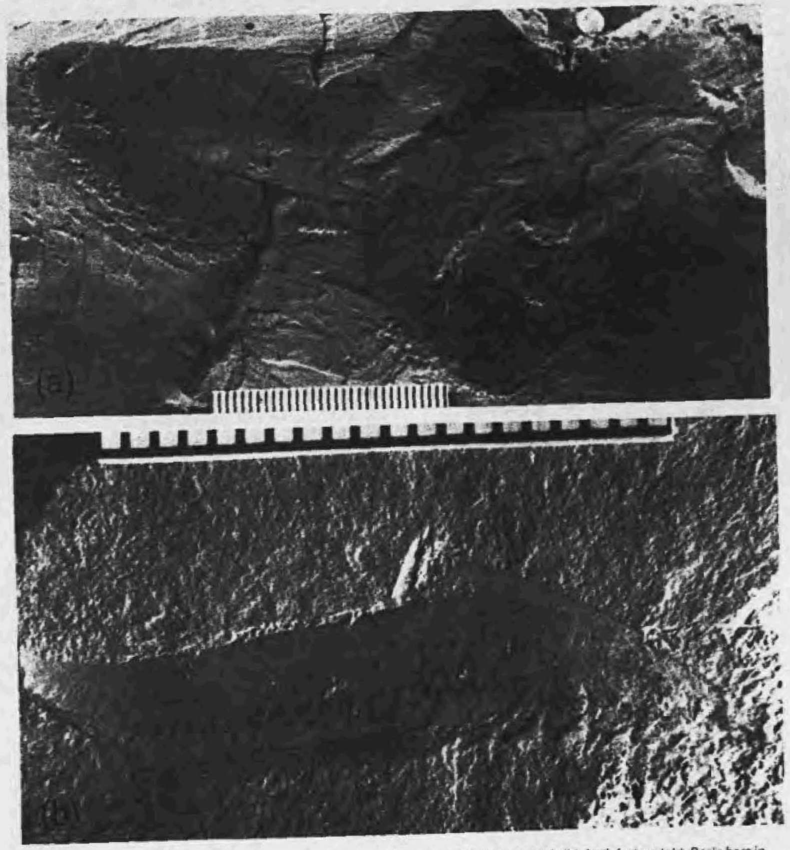


Cladograms showing the relationships of the main deuterostome groups: (a) the 'traditional' model, (b) the 'calcichordate' model, and (c) the molecular model. Synapomorphies: **A DEUTEROSTOMIA**, blastopore becomes anus during development, bipartite mesocoel, mesocoelomic ducts; **B**, stomochord, paired 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**, ciliated extensions of the mesocoel either absent or present as water vascular system (but not as lophophore), anus not anterior and dorsal; **G DEXIOTHETICA**, dexiothetism (rotation and partial loss of right side of precursor form), stone canal, calcite skeleton internalization of protostome; **H**, specialized olfactory areas in buccal cavity, hind-tail tripartite, dorsal longitudinal canal connected with notochord; **I AMBULACRARIA**, trimeric arrangement of the adult coelom, axial complex with hydropore, dipleureula larva with neotroch.

Formation, and still highly controversial. The group was named by Shu *et al.* (2001) on the basis of three genera, *Vetulicola*, *Xidazoon* and *Didazoon* (Figure 1.6(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 and a possible endostyle. Both parts of the body appear to be crossed by transverse bands of tissue. On the

BOX 1.2 THE CHENGJIANG FOSSIL SITE

The Chengjiang fossil site in 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. The fossils come from different levels through several hundred metres of mainly fine-grained sediments. 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.



Typical Chengjiang fossils, the vetulicolian *Xidazoon* (a), and the basal vertebrate *Myllokunmingia* (b), both facing right. Scale bars in millimetres. Compare with interpretive drawings in Figures 1.6 (b) and 3.1(a). (Courtesy of Shu Degan.)

continued

The Chengjiang site is rich, having produced more than 10,000 specimens, and the fauna consists of 90 or more 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 (Figure 1.7), as well as the first fishes (Shu, 2003). 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 sea-bed, 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://palaeo.gly.bris.ac.uk/Palaeofiles/Lagerstatten/chngjang/index.html and http://www.palaeos.com/Paleozoic/Cambrian/Chengjiang.html

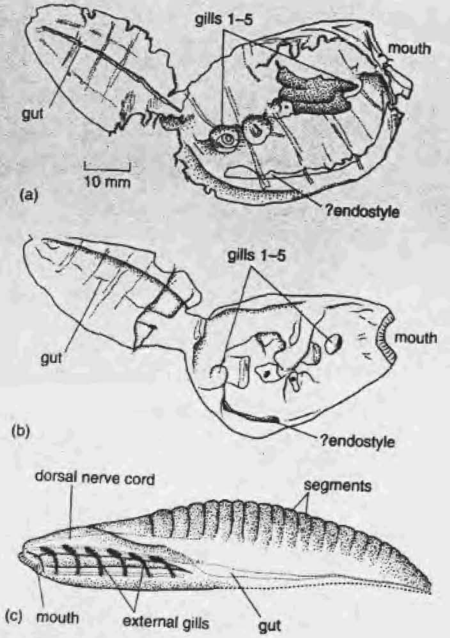


Fig. 1.6 Basal deuterostomes: (a, b) the vetulicolians *Didazoon* (a) and *Xidazoon* (b), showing how the body is divided into two sections that are joined by a flexible connection; (c) *Haikouella*. (Courtesy of Shu Degan.)

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 have been accorded three positions in the phylogenetic tree (Figure 1.7): as basal deuterostomes, as urochordates or as basal chordates. Evidence that vetulicolians are deuterostomes are the gill slits and the possible endostyle. They have been interpreted as basal deuterostomes by Shu *et al.* (2001) because they apparently lack an atrium, the internal chamber in 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. There are, however, some general resemblances to swimming tunicates in the bulbous streamlined body shape, the thin external tunic, and the regularly spaced transverse bands, which might be muscles that ran round the body in rings (Lacalli, 2002). The absence of a notochord in vetulicolians is not critical, since most adult tunicates also have lost this structure.

Additional invertebrate chordates from Chengjiang, the yunnanozoons *Yunnanozoon* and *Haikouella* (Figure 1.6(c)), have been interpreted by rival researchers both upwards and downwards in the scheme of things (Figure 1.7). 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.

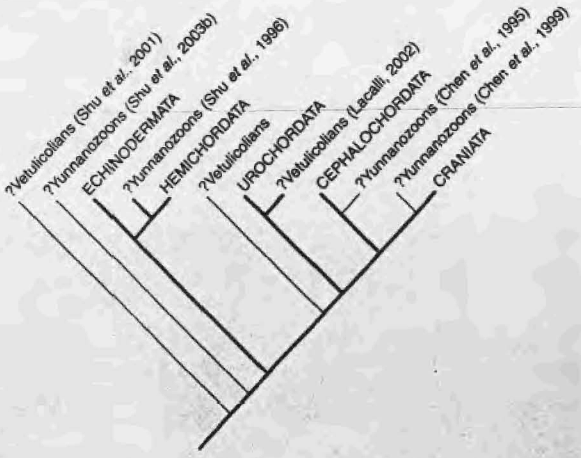


Fig. 1.7 Phylogenetic tree of the extant deuterostomes, with suggested locations of the major fossil groups.

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 (Figure 1.4(c)). Shu (2003) and Shu *et al.* (2003b) subsequently noted similarities between the yunnanozoons and the vetulicolians, and moved them down from the hemichordates to a basal position among deuterostomes (Figure 1.7): they could see no evidence of a notochord, a large brain, lateral eyes, or any of the other chordate features previously reported.

1.4.3 Carpoids

The fourth group of putative fossil chordates is much more diverse. The carpoids, sometimes called stylophorans or calcichordates, are a group of about 60 species of asymmetrical organisms that had a **calcitic** (calcium carbonate) outer skeleton of a particular kind in which the mineral is pierced by numerous small holes. They date from the Middle Cambrian to Middle Devonian (520–370 Myr). They consist of two parts (Figure 1.8), a compact body portion and a long segmented appendage. Most authors have interpreted the carpoids as aberrant echinoderms, but Jefferies (1986, 1997) argued strongly that they are a mix of basal echinoderms, cephalochordates, sea squirts, and vertebrates. There are four criticisms of Jefferies' (1986, 1997) 'calcichordate' hypothesis.

1 Morphological and molecular phylogenetic analyses agree on a tree of living forms (Box 1.1) that does not

Fig. 1.8 The carpoid *Mitrocystites mitra* from the Mid-Ordovician of Bohemia (Czech Republic), dorsal view, showing the calcite plates that compose the body and the flexible 'arm' folded over at the top. Scale, specimen is about 30 mm long. (Courtesy of Bernard Lefebvre.)

correspond to the requirements of the 'calcichordate' hypothesis.

2 Much of the 'calcichordate' hypothesis depends on interpretations of anatomical structures that are disputed. For example, Jefferies (1986, 1997) interprets the carpoid appendage as a tail, whereas his critics call it a locomotory stem or feeding arm. A major opening in the body is called a mouth by Jefferies, and an anus by others. He interprets a series of openings as pharyngeal gill slits, whereas others call them inhalant respiratory pores.

3 The theory also involves a number of major character losses. The calcite skeleton of the carpoids and echinoderms was apparently lost three times, on the lines to the cephalochordates, tunicates, and vertebrates. It is more **parsimonious** (economical) to assume that the calcite skeleton of echinoderms (and carpoids) evolved once and was not lost.

4 The carpoids have been determined as a monophyletic group (Ruta, 1999), sharing the flattened 'bag-like' shape, the appendage, and numerous details of the plates that cover the body, and the various openings. If the group is monophyletic, and that is debated, it cannot be distributed in different places all through the phylogeny of deuterostomes.

The postulated presence of gill slits in carpoids (Jefferies, 1986, 1997) is potentially interesting, as these could then be seen as a deuterostome character that was subsequently lost in the echinoderms. If then we are not descended from carpoids, where did the chordates come from?

1.4.4 Development and vertebrate origins

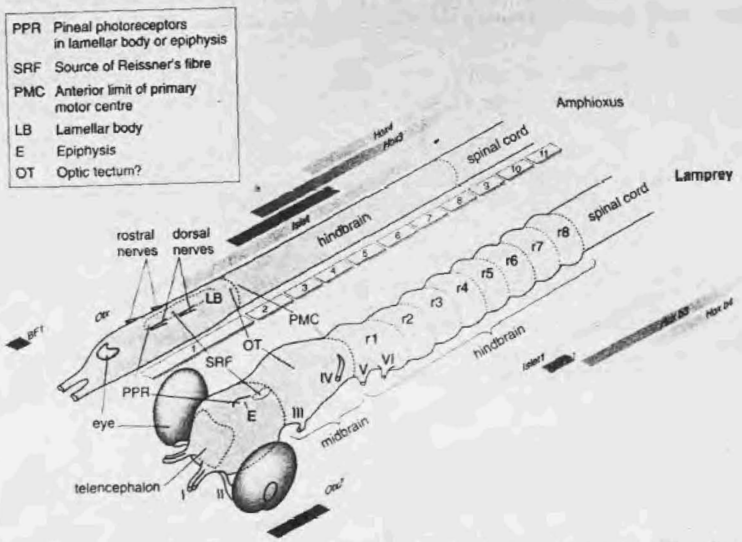
The **development** of living vertebrates and basal chordates indicates a great deal about their ancestry. Embryos may be sliced thinly on a microtome, rather like a mini salami-slicer, and three-dimensional reconstructions are made from tracings of the thin-sections by computerized methods. In addition, 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 1.3).

These recent studies shed light on an older theory for the origin of vertebrates, 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 (Figure 1.2(c)), adult amphioxus (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 reproductive abilities in an essentially juvenile body. According to his view, an ancient sea squirt

BOX 1.3 GENES AND BRAINS

New work on amphioxus has given clues about the origin of vertebrate characters, particularly the head. Amphioxus, the classic cephalochordate (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 basal 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 (Shimeld and Holland, 2000; Holland and Chen, 2001; Holland and Holland, 2001; Holland *et al.*, 2001). 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 genes, and the genes appear to express themselves in comparable parts of the body, hence pointing to potential homologies.



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. (Based on information from the cited papers, parts of which are copyright 2001, Holland and Chen; reprinted by permission of John Wiley & Sons Ltd.)

continued

There are many examples of such shared developmental genes. The expression patterns of amphioxus homologues of the genes called *Distal-less, Otx, Hox-1* and *Hox-3* have indicated that the amphioxus nerve cord, which has no obvious divisions except for a slight anterior swelling, has counterparts of the vertebrate forebrain and hindbrain. Expression of the genes *Pax-1, Pax-2/5/8* and *Brachyury* homologues has supported the 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.

Most importantly, amphioxus shares embryonic cells that are homologous with the **neural crest** of vertebrates. The neural crest was thought to be a unique developmental 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 genes *distal-less, snail, Pax-3/7* and *Msx* are expressed in migratory embryonic cells of amphioxus as well as in the neural crest of vertebrates, so the gene homologies point to morphological homologies, and indicate the evolutionary source of the neural crest.

Read more about amphioxus development at, http://academic.emporia.edu/sievertl/verstruc/ammodel.htm, and the neural crest at http://www.teaching-biomed.man.ac.uk/moran/Intro.htm and http://anatomy.med.unsw.edu.au/cbl/embryo/Notes/ncrest.htm, and the song 'It's a long way from amphioxus', sung to the tune of 'It's a long way to Tipperary', with audio performance, at http://www.flounder.com/amphioxus.htm.

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 1.9) shows all of the chordate characters so far described—notochord, dorsal nerve cord, pharyngeal 'gill' slits, postanal tail, myomeres, and so on. The special vertebrate characteristics 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.

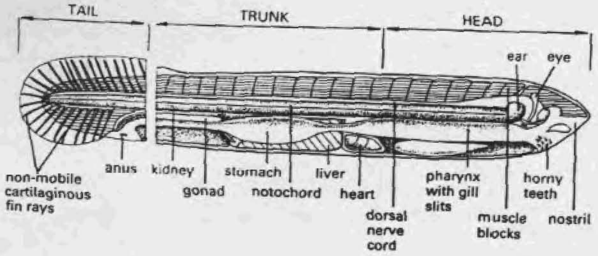


Fig. 1.9 The hypothetical 'basic' vertebrate body plan, shown in longitudinal section. (After Jefferies, 1986.)

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) and papers in Ahlberg (2001). Jefferies (1986) presents further detailed information on this topic, and makes an impassioned case for the role of carpoids in linking echinoderms and chordates. Peterson (1995) argues trenchantly against the 'calcichordate' hypothesis, and Holland and Chen (2001) give a good review of the origin of vertebrates. You can find out more about modern invertebrates, and in particular those classified as deuterostomes, in Barnes *et al.* (2001), Nielsen (2001) or Brusca and Brusca (2003). The embryology and anatomy of modern vertebrates is covered by many zoology texts, such as Romer and Parsons (1986), Kent and Miller (1997), Hildebrand and Goslow (2001), Kardong (2001), Liem *et al.* (2001) and Pough *et al.* (2002). Cracraft and Donoghue (in press) presents a review of current thinking on the relationships of the major clades of chordates.

CHAPTER 2

How to Study Fossil Vertebrates

KEY QUESTIONS IN THIS CHAPTER

1 How do you set about digging 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 scenes from fossilized bones and teeth?
4 How can you use clues from ancient bones and teeth to work out what happened between the death of the animal and burial in the rock?
5 How can palaeontologists work out how ancient animals used their limbs and jaws?
6 How are organisms classified, and how do fossils help us work out the shape of the tree of life?

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. They know that the bones are preserved in the rocks, and that teams of enthusiasts dig up the skeletons 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 the continents used to be distributed across the globe, and how the functions of extinct organisms may be inferred.

Vertebrate palaeontologists have to be familiar with a broad range of skills in geology and biology in order to work effectively. In this chapter, an outline is given of some aspects of field collecting, fossil preparation, and skeleton restoration. In addition, the geological topics of taphonomy, time, continental drift, and palaeoclimates are outlined, and the methods of phylogeny reconstruction and functional morphology are introduced.

2.1 DIGGING UP BONES

Everyone has seen dinosaur digs on television, even if they have never participated in one. It is usually assumed that the enthusiasts who dig up dinosaurs and later study them are paid handsomely by their respective benevolent governments. 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 rocks deposited in ancient lakes, rivers, or deserts. If their interest is 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 of 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

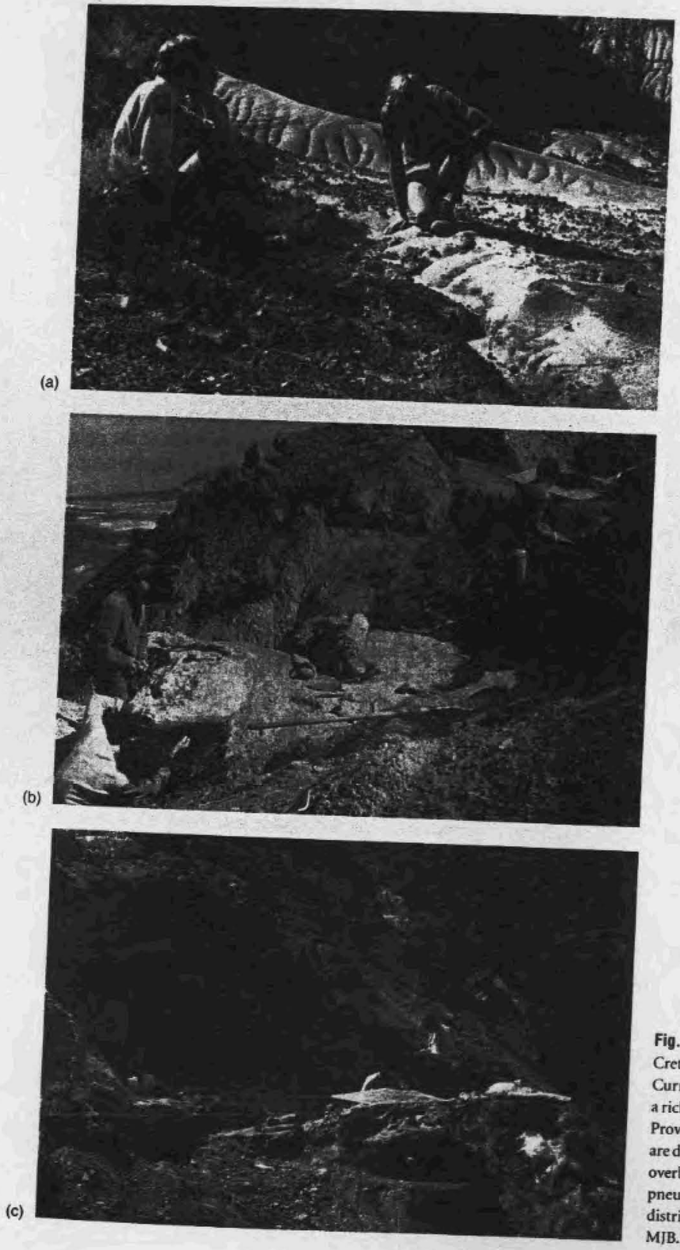


Fig. 2.1 Dinosaur digging in the Lower Cretaceous of Alberta, Canada: (a) Phil Currie (right) and a park ranger inspect a rich dinosaur bonebed at Dinosaur Provincial Park (all the irregular blocks are dinosaur bones); (b) digging away the overburden, and clearing the rock with pneumatic drills; (c) mapping the distribution of bones. (Photographs by MJB.)

switch to smaller power drills, hammers, and small 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 sack-cloth (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, often

Fig. 2.2 Excavating dinosaurs in the Lower 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. (Photographs by MJB.)

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.

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 in recent years. 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)). Airbrasive treatment may be applied, a system that blows fine abrasives in a focused blast of air at the specimen. 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.

The bones are generally strengthened by coatings of synthetic compounds that 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 that 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 small bones and teeth, microvertebrate remains, 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)).

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 at once by scientists in the institution that did the collecting, or they may be preserved 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 location of specimens from published descriptions of fossils and from various paper and electronic information services.

In studying a new fossil skeleton, the palaeontologist generally tries to reconstruct the animal as it was. This may be a difficult job. If there is a relatively complete and undamaged specimen, the palaeontologist may be able to test the fit of the bones directly. It is 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 different sized animals, and in difficult cases scale models may be made of missing bones. Extensive restoration is possible because vertebrate skeletons are bilaterally symmetrical, and because many bones, such as vertebrae and ribs, occur in repeating or gradually changing series.

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 this damage, and try to correct for it by restoring missing parts of bones and making careful measured drawings and models to remove the effects of distortion.

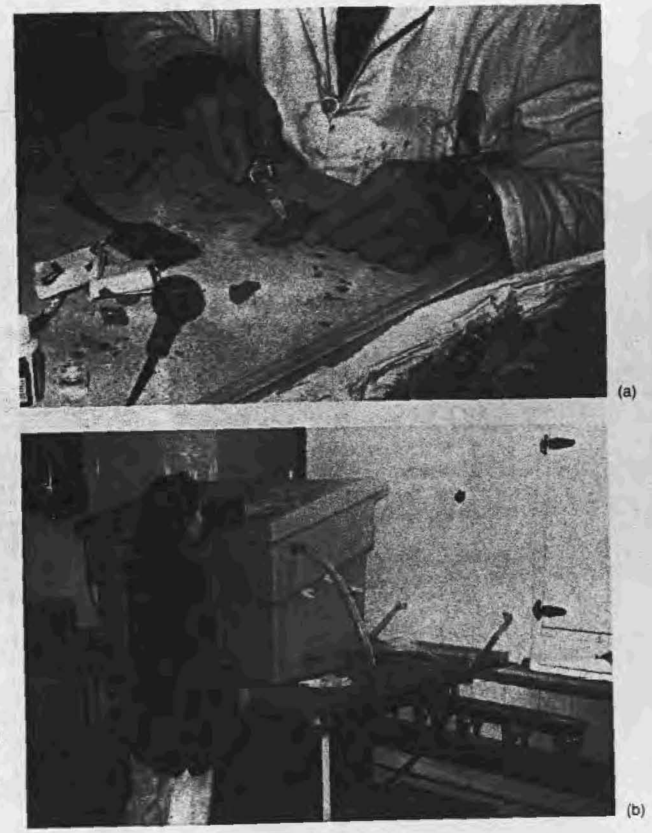


Fig. 2.3 Back in the laboratory: (a) preparation of dinosaur specimens at the Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada, using a dental drill to remove rock matrix from the bones; (b) Rachael Walker adjusts an automated sieving machine for processing sediment containing microvertebrate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

Fig. 2.4 Further techniques for studying fossil vertebrates: (a) casting some dinosaur vertebrae; (b) drawing the posterior view of a dinosaur braincase. (Photographs by MJB.)

Accurate reconstructions are the basis of further study in vertebrate palaeontology. The palaeontologist publishes 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 more artistic renditions 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, or as animations. The dinosaurs of *Walking with Dinosaurs* (see Box 2.1) looked so good because of the combined input of work by palaeontologists, artists, and animators.

2.2 GEOLOGY AND FOSSIL VERTEBRATES

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

2.2.1 Taphonomy

The mode of burial and preservation of fossils, their **taphonomy**, is important in their interpretation.

BOX 2.1 *WALKING WITH DINOSAURS*

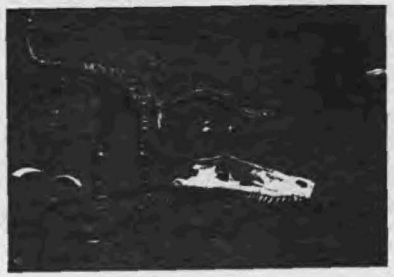
The BBC series, *Walking with Dinosaurs*, was the most successful science documentary series ever made: since 1997, it has been seen by over 200 million people in nearly every country in the world. The series of six programmes was conceived by Tim Haines a few years after he had seen Steven Spielberg's *Jurassic Park* (1993), in which a clever mix of computer animation and models gave the first glimpse of what might be possible. Older dinosaur films had used plasticene models or lizards with cardboard crests stuck on their backs. Haines reasoned that the new computer animation techniques would allow him to make films about dinosaurs that would be so lifelike that they were like wildlife documentaries.

There were six programmes: the Late Triassic of North America, the Late Jurassic dinosaurs of the Morrison Formation, the Late Jurassic marine reptiles of Europe, the Early Cretaceous of Australia, the Early Cretaceous pterosaurs of Brazil, and the latest Cretaceous of North America. In each programme there were six or seven featured organisms. Each of these was studied in depth by consultant palaeontologists and artists, and a carefully measured clay model (maquette) was made. This was the basis for the animation. The maquette was laser scanned, and turned into a 'stick model', which could be moved in the computer to simulate running, walking, jumping, and other actions. All aspects of locomotion and feeding were developed in consultation with relevant palaeontologists from all over the world.

The story board was planned in detail for each programme and, while the models were being developed, BBC film crews went round the world to film the background scenery. Places were chosen that had the right topography, climatic feel, and plants. Where dinosaurs splashed through water, or grabbed a branch, the action (splashing, movement of the branch) had to be filmed. Then the animated dinosaurs were married with the scenery in the studios of Framestore, the company that made the computer effects. This is hard to do, as shadowing and reflections had to be added, so the dinosaurs interacted with the backgrounds. If they run through a forest, they have to disappear behind trees and bushes.

The programmes were controversial. Some palaeontologists argued that the whole concept was improper as it mixed movements and behaviours for which there is strong fossil evidence with imagined colours and sounds. They were right, but boring. Most palaeontologists celebrated the accuracy and beauty of the work, and were glad that 200 million people had had the chance to see the results of their labours.

Find out more at http://www.bbc.co.uk/dinosaurs/ and my accounts of how palaeontologists worked with film producers to make the series, as well as a defence of the whole enterprise, at http://palaeo.gly.bris.ac.uk/dinosaur/walking.html.



The dinosaur *Coelophysis* from the first *Walking with Dinosaurs* programme about the Late Triassic of North America. In this image, the background is real—it is the modern Atacama Desert in Chile. The skull in the dirt is a plaster cast, and the dinosaur is a computer-generated image. (Courtesy of Tim Haines, image ©BBC 1999.)

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

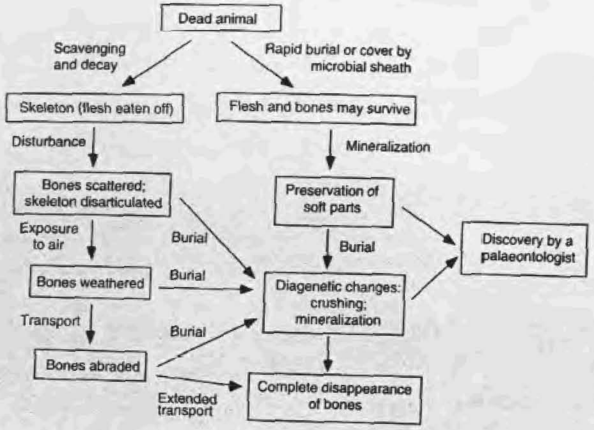


Fig. 2.5 Taphonomic processes affecting a fossil vertebrate, from death, through scavenging and decay, through transport and burial, to eventual discovery by a palaeontologist.

apatite. In rare cases, when decay is prevented, soft parts may be preserved.

Vertebrate bodies decay as they are valuable sources of food for other organisms. When large animals feed on the flesh of a dead vertebrate, the process is termed scavenging, and when microbes transform the tissues, the process is termed decay. In terrestrial settings, carcasses 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.

The style of decay by microbes 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 sea-floor, 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 pp. 9, 86, 269).

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 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 within sediment or rock.

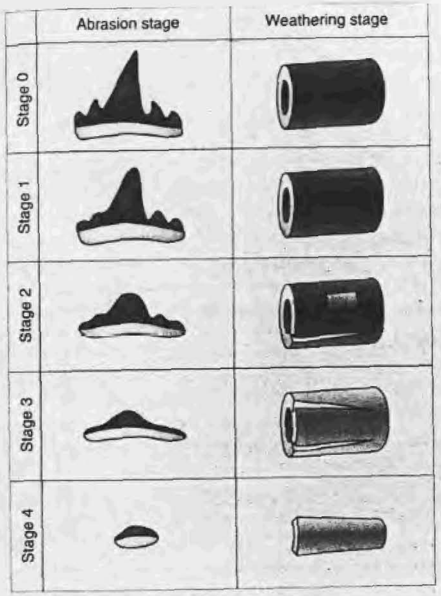


Fig. 2.6 Abrasion stages of a bone depend upon the amount of transport and physical battering. Sharp edges and processes are lost, the surface is polished, and the bone eventually becomes a bone pebble (Stage 4). Weathering progressively cracks the surface layers of bone off. (Courtesy of Liz Cook.)

2.2.2 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 had not always been the same was suggested in the 19th century, when some 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 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 uniformly welcomed 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-oceanic 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 termed **plate tectonics**. Molten rock, **magma**, circulates in great gyres beneath Earth's solid crust, moving upwards and leaking out through the mid-oceanic 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

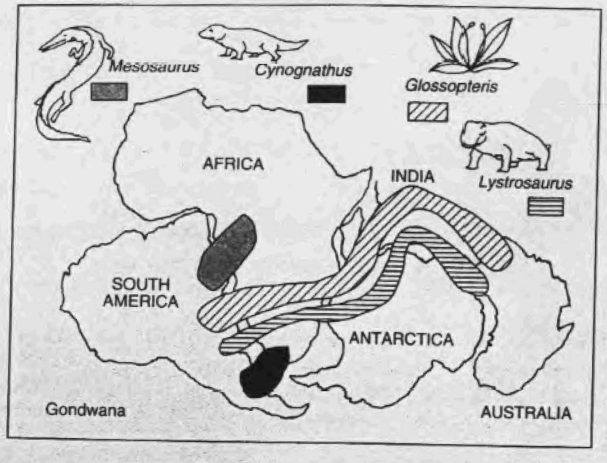


Fig. 2.7 Reconstruction of Gondwana as it was from the Late Carboniferous to the Late Triassic, based on the work of Alfred Wegener, showing how this arrangement of continents makes sense of the distributions of Permian reptiles such as *Mesosaurus*, Permian plants such as *Glossopteris*, and Triassic reptiles such as *Lystrosaurus* and *Cynognathus*.

BOX 2.2 GEOLOGICAL TIME

Earth is immensely ancient, and yet the history of 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, give a basis for the standard international geological time-scale.

Early in the twentieth century, numerical or **absolute dating** became possible 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.

Eon	Era	Period	Epoch	Date at beginning (Myr)
Phanerozoic	Cenozoic Era			
		Quaternary Period		
			Holocene Epoch	0.01
			Pleistocene Epoch	1.8
		Tertiary Period		
			Pliocene Epoch	5
			Miocene Epoch	24
			Oligocene Epoch	34
			Eocene Epoch	55
			Paleocene Epoch	65
	Mesozoic Era			
		Cretaceous Period		144
		Jurassic Period		200
		Triassic Period		251
	Palaeozoic Era			
		Permian Period		290
		Carboniferous Period		354
		Devonian Period		417
		Silurian Period		443
		Ordovician Period		495
		Cambrian Period		545
Precambrian				4560

The geological time-scale, showing the main divisions of geological time, and current numerical age dates, based on the Geological Society of America 1999 time-scale, with dates for the Triassic revised. Full version available at http://www.geosociety.org/science/timescale/timescl.htm

centre of the 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 critical 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 back through the Palaeozoic. Continental drift has affected animal and plant distributions: 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 pages 320–2).

2.2.3 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 moves. On land, there were at times abundant amphibians and reptiles, living 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 is derived from detailed study of the rocks and fossils at particular sites. 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. Ice scratches on rocks, and glacial **tills**, faceted and striated rocks and dust ground up by moving glaciers, show that conditions were cold.

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 Mesozoic, 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 both Arctic and Antarctic dinosaurs have been found. Increasingly through the Cenozoic, and today, climatic bands developed, and most plants and animals are much more restricted in the zones they can occupy.

2.3 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 an analysis. There are now a number of analytical techniques for studying functional morphology and palaeoecology.

2.3.1 Functional morphology

The first question that people ask about any fossil vertebrate is 'what did it do?' Just how did the heavily armoured Devonian fishes manage to swim? Why did some mammal-like reptiles have massively thick skull roofs? What did *Stegosaurus* use its back 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, 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 the ground, and to gather food and drink. A long neck has evolved in giraffes so they can feed higher in trees than any other living mammal (and reach the ground to drink). Tunas have more red muscle than most other fishes so they can swim faster and further.

The bones of a fossil skeleton can provide a great deal of information about function. The bones themselves show directly how much movement was possible at a particular joint, and this can be critical in trying to reconstruct how particular vertebrates could 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 two main approaches to the study of functional morphology (Figure 2.8). First is comparison with living animals. If the fossil form 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 fossil, whether it had a trunk or not, how it used its teeth, and how fast it could move.

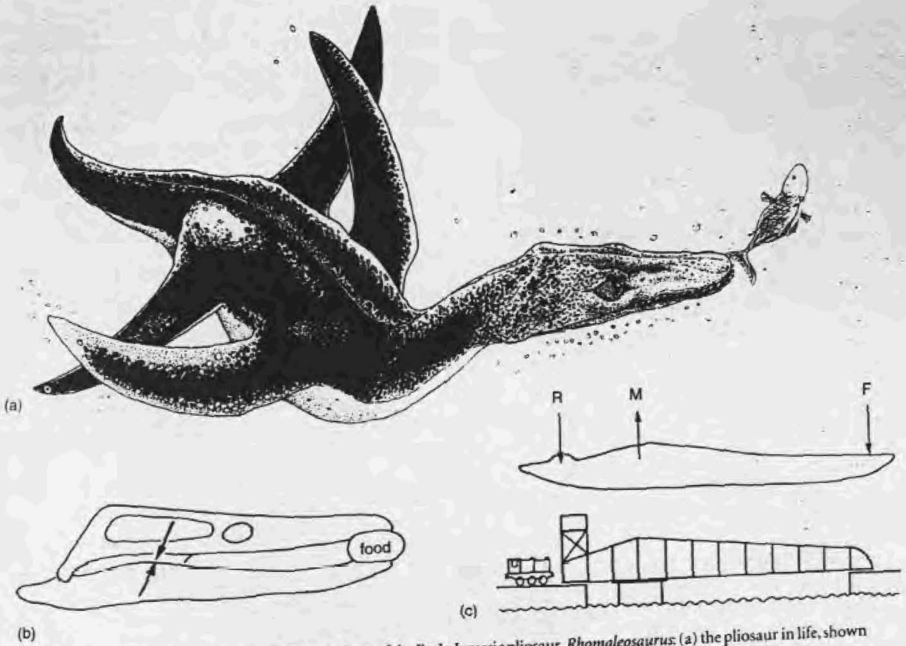


Fig. 2.8 Interpretations of the functional morphology of the Early Jurassic pliosaur, *Rhomaleosaurus*: (a) the pliosaur in life, shown chasing a fish; (b) the head in static equilibrium, gripping a piece of food at the front of the jaws; (c) the lower jaw modelled as an asymmetrical swing bridge, with major muscular forces (M), reactions from the food at the bite point (F), and reactions at the jaw joint (R). [Figure (a) courtesy of John Martin; (b, c) modified from Taylor, 1992.]

If there are no close living relatives, or if the living relatives are very different from the fossil species, then there may be problems. The **extant phylogenetic bracket** (EPB, Witmer, 1997) may help. The concept of the EPB is simple: even if a fossil form is distant from living forms, it will be bracketed in the phylogenetic tree by some living organisms. So, it would be wrong to interpret all dinosaurs in terms of their descendants, the birds, but, in the evolutionary scheme of things, 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 the Eocene elephant with modern elephants the EPB highlights one problem: it cannot be assumed that the Eocene elephants had all the characters of modern forms, as some characters may have been acquired between the Eocene and the present day.

In some cases, of course, the fossil form is entirely different from modern animals and has no obvious relatives that are close enough phylogenetically. An example is the group of giant marine reptiles called pliosaurs (see p. 245) 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 suggests that pliosaurs fed on other, smaller, marine reptiles, as well as fishes and **ammonites**, coiled swimming molluscs.

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 may be 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 in powerful twisting movements to tear off flesh (Taylor, 1992). These kinds of **biomechanical** studies are much enhanced by the application of simple mathematical models. The weakness of these kinds of functional studies is that they are not scientific, even though they may be quantifiable. Searching for plausible explanations may generally reveal the truth, but there is no hypothesis-testing. Ultimately, of course, when dealing with extinct organisms, it is hard to know how to devise directly testable hypotheses, because we will never know what a particular Devonian fish or pliosaur actually did.

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 plesiosaur vomit (? vomitite) are also known. There are even some specimens of plesiosaur bones bearing tooth marks that precisely match those of some pliosaurs.

2.3.2 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 work on modern ecology, the 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 some of the 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 show how the animal grew up. If several different 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 invention of new modes of life such as tree-climbing, flight, burrowing, or mollusc-eating.

2.4 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 5–10% 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 direction. There are two principal analytical techniques for establishing the relationships of vertebrates and their relatives, **cladistic** analysis of **morphological** data and **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 2.6).

2.4.1 Cladistics

Cladistic analysis of morphological characters is the main technique used for studies of the relationships of living and fossil vertebrates. The result of a cladistic analysis is a **cladogram**, such as those in Figure 1.7. 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* timescale, 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, and the shorter the linking lines, 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. When Jefferies (1986, 1997) and Peterson (1995) were trying to sort out relationships within the Deuterostomia (Figure 1.7), they looked for features that would support particular pairings of groups. Jefferies (1986, 1997), for example, argued that most of the calcichordates and the chordates shared a tail, a feature not seen in other groups. Peterson (1995), on the other hand, noted that hemichordates and chordates share gill slits, a unique character of these phyla.

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 as 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 cladist 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. In looking at theropod dinosaurs and basal birds, some specimens have feathers and others do not. Does one code a single character—feathers (present, absent)—or look into the anatomy in much more detail, and identify several kinds of feathers, from full flight feathers to wispy down 'hairs', and several detailed aspects of the anatomy of the feathers under the microscope? Character states are generally coded 0, 1, 2 . . . , and listed in a **data matrix**, a table of species/specimens versus characters. Well-established computer programs, such as PAUP, hennig86, NONA, MacClade, and others, are used to process the data matrices and extract patterns of relationships that are expressed as trees.

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 2.3). All members of the clade share at least one derived character.

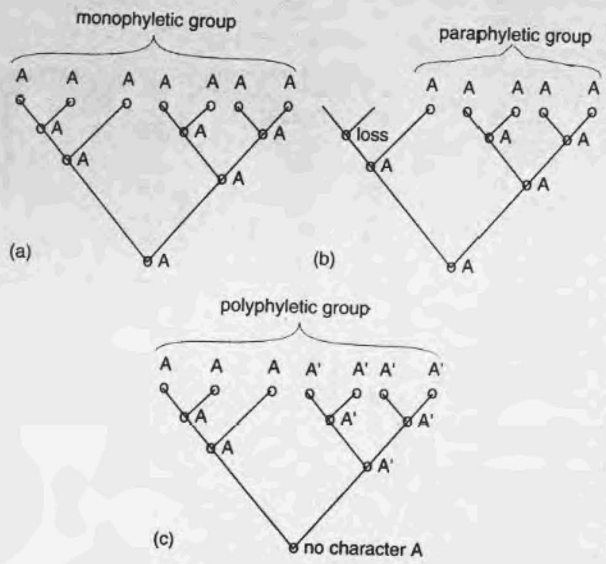


Fig. 2.9 Cladograms showing (a) a monophyletic group, (b) a paraphyletic group, and (c) a polyphyletic group, and the presence and absence of hypothetical characters A and A′ (character A′ is convergent on [very similar to] character A). In the monophyletic group (a), all species have character A, a synapomorphy of the clade. In the paraphyletic group (b), some species have lost the synapomorphy A by transformation (e.g. the keratinous scales of reptiles are 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.

BOX 2.3 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 intricate 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 geographical forms of the same basic kind. 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

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 Class 'Reptilia', which almost certainly arose from a single ancestor, but which excludes some descendants, the birds and the mammals. 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 reptiles lay a shelled egg (as do birds and basal mammals), but the upper bounds of the group 'Reptilia' are defined only by the absence of characters such as feathers and hair.

The other kind of non-monophyletic groups are **polyphyletic**, those that arose from several ancestors, and that are characterized by a convergent feature (Figure 2.9(c)). Two examples of polyphyletic groups of vertebrates are the 'Natantia', the classic grouping of fishes and whales together, because they look similar in shape and they swim in the sea, and 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, 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 broadly similar ways 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 structure shows that they arose independently, even though they perform similar functions. Homologies, then, are synapomorphies, the clues that indicate common ancestry.

2.4.2 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. 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.

There are several techniques for converting comparisons of molecules into phylogenies, and these may be applied to a broad range of molecules. Currently, most work focuses on comparisons of sequences of the **nucleic acids**, and many phylogenies (e.g. Box 1.1(c)) are now based on the different RNA molecules. 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. There are three distance methods 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** (steady rate of molecular change).

2 Neighbour joining (NJ) techniques pair off apparently similar species, and then make links between evermore 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 criticized, 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 phylogenetically informative characters). Cladistics is a phylogenetic method, of course.

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. There are two techniques 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, most likely to have produced the observed data. The method requires the input of a model of evolution 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.

Molecular phylogenies have been calculated since the 1960s, but the field has expanded rapidly only since the late 1980s, with the invention of the polymerase chain reaction (PCR) technique for cloning small samples of nucleic acids to analysable quantities. In addition, there have been advances in the speed and efficiency of tree-finding programs and desktop computers, which may now be used to analyse data matrices that would have been considered far too large at one time. 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 broad-scale approaches to reconstructing the tree of life, and they may be continually cross-compared.

2.5 THE QUALITY OF THE FOSSIL RECORD

Key questions in palaeontology concern the quality of the fossil record. Is the sample of known fossils enough to justify detailed studies of the history of life? Do palaeontologists know only 1% of all the species that ever lived, or 10%, or 70%? Life originated 3500 million years ago, and countless millions of species have come and gone since then. Today there may be 10–30 million species on Earth, and no-one can begin to estimate how many have become extinct in the past.

The history of life may be represented in many ways. 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

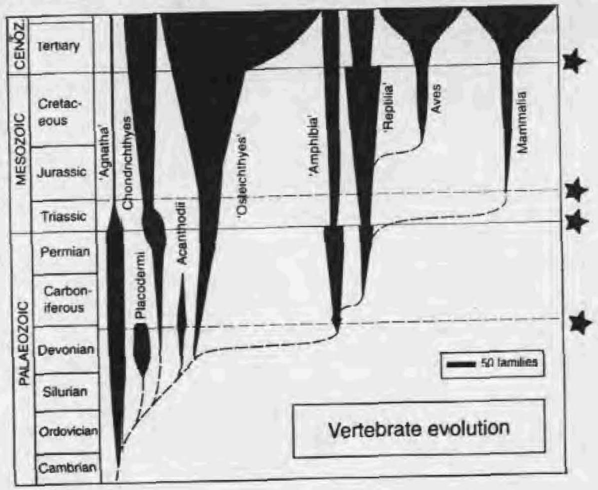


Fig. 2.10 The pattern of evolution of the vertebrates, showing the relative diversity of the major groups through time and mass extinction events (marked with stars). This is a 'spindle diagram', in which the vertical axis represents time, and the horizontal axis represents the diversity of the group. 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 (1993a). Dashed lines indicate hypothesized relationships. 'Agnatha' includes conodonts (see Chapter 3).

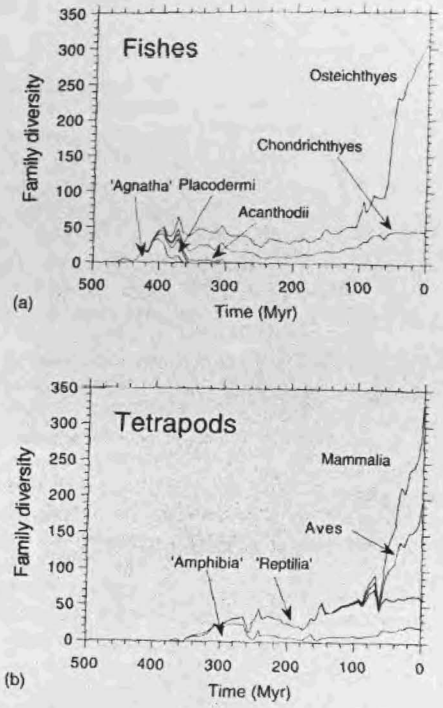


Fig. 2.11 The diversification of fishes (a) and tetrapods (b), based on the numbers of families of each group through time (data from chapters in Benton, 1993a). Mass extinction events are highlighted.

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 do these diagrams in any way approximate to the truth? Could it be that there are so many gaps in the fossil record that they are entirely misleading? This critical point was tested by Norell and Novacek (1992). They reasoned that if they compared independent evidence for the history of life, they might find whether our knowledge of the fossil record is hopelessly inadequate, or whether independent data sets tell the same story. Norell and Novacek compared geological evidence about the order of appearance of different groups of vertebrates in the rocks 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 (Benton and Simms, 1995). 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.*, 2000c).

Another observation confirms that palaeontological knowledge is not completely inadequate: dramatically unexpected fossils are hardly ever found. If the known fossil record were very incomplete, many dramatic new finds would be made, dinosaur fossils in the Permian or Tertiary, human fossils in the Miocene, shark fossils in the Precambrian. This does not happen. New finds are expected. For example, in 1985, the oldest monotreme mammal fossil came to light in the Lower Cretaceous of Australia (Archer *et al.*, 1985). This fossil extended the known range of monotremes backwards in time by more than 100 million years, but it merely filled a gap that was predicted from the cladogram. New finds improve our knowledge, but they rarely revolutionize it. Fossil discoveries since 1967 have plugged many gaps, and the quality of matching between fossil dates and phylogenies has improved by 5% (Benton and Storrs, 1994). Perhaps palaeontologists can rest easy, and freely integrate their information about the life of the past with their studies of modern organisms.

2.6 FURTHER READING

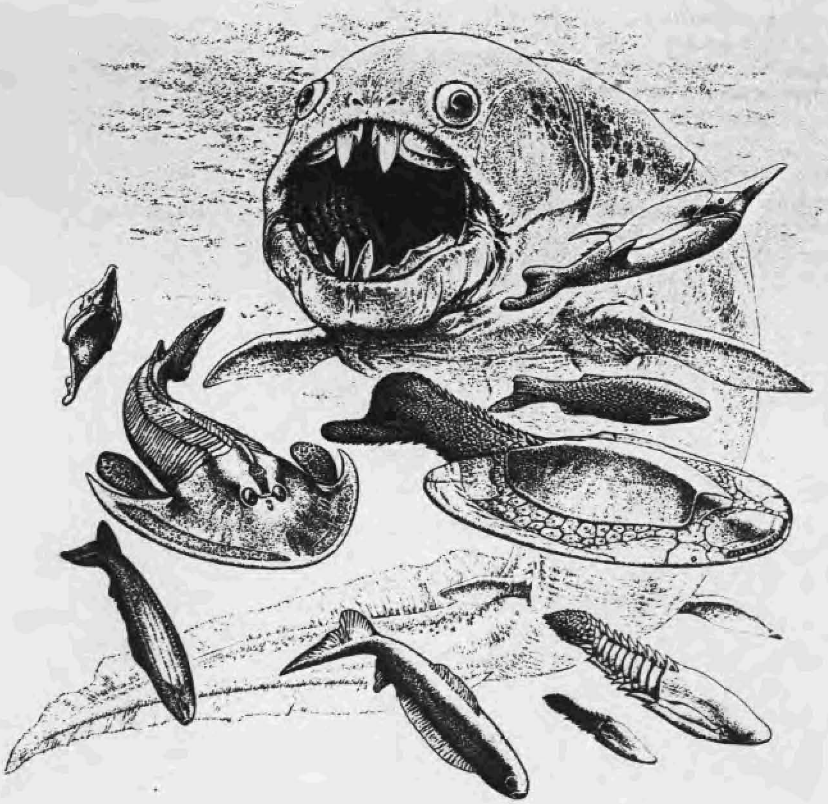
There are many useful books that cover basic palaeontological, geological, and palaeobiological principles. Briggs and Crowther (2001) is an excellent compendium of short articles on all aspects of palaeobiology, and Benton and Harper (1997) is a useful short introduction to all aspects of palaeontology. You can read more about excavating dinosaurs in an illustrated account by Benton (1989b), whereas Buffetaut (1987) and Colbert (1968) are highly readable accounts about the history of vertebrate palaeontology, expecially 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 Briggs (1991) and Lyman (1994) are good introductions to taphonomy, and you can read more about Earth history in Stanley (1998). The methods of cladistics are presented by Kitching *et al.* (1998), and Page and Holmes (1998) give a good overview 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, as do a number of authors in Donovan and Paul (1998). Meyer and Zardoya (2003) review molecular contributions to the phylogeny of vertebrates.

Useful web sites include: http://www.nhm.ac.uk/hosted_sites/paleonet/, the Paleonet web pages, which have links to societies, information pages, journals, jobs, and more; http://www.vertpaleo.org/, the premier international society for vertebrate palaeontologists; http://www.ucmp.berkeley.edu/diapsids/dinolinks.html, many links to sites detailing how dinosaurs are excavated and exhibited; http://www.nationalgeographic.com/, palaeontological work sponsored by the Society; http://www.amnh.org/exhibitions/expeditions/index.html, current expeditions of the American Museum of Natural History; http://www.paulsereno.org/, current expeditions by Paul Sereno; http://www.dallasdino.org/exhibits/paleontology_lab.asp, an example of one of many museum palaeontology laboratory web sites; http://www.scotese.com/, the Paleomap Project web site.

CHAPTER 3

Early Palaeozoic Fishes



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?

INTRODUCTION

The earliest remains of fishes from the Cambrian do not show much of their overall shape or anatomy, and very little can be deduced about their modes of life. Most of them are identified as vertebrates solely on the appearance and microstructure of their hard tissues. Fish fossils from the Ordovician (495–443 Myr) onwards, however, are often preserved complete, and with a great deal of fine anatomical detail. It is possible to identify nine or ten major fish lineages in the Ordovician, Silurian and Devonian. Although some of these fishes would look familiar to us, most of them were very different from modern forms.

The key episodes of early fish evolution seem to have taken place during the Ordovician and Silurian (443–417 Myr), when all the major groups appeared, but specimens become abundant only in the Devonian (417–354 Myr). During this time, the early dominance of the seas and freshwaters by heavily armoured forms gave way to the modern sharks and bony fishes and, secondly, the fishes gave rise to the land vertebrates, the tetrapods. Of course, terms such as 'fishes', osteichthyans and sarcopterygians all refer to paraphyletic groups because they exclude tetrapods.

3.1 CAMBRIAN VERTEBRATES

Until recently, the oldest putative vertebrates were isolated fragments of **dermal** armour from the Upper Cambrian of North America, and possibly also the superficially amphioxus-like *Pikaia* from the Mid-Cambrian Burgess Shale of Canada. New discoveries from the Chengjiang locality in China (see Box 1.2), the source also of many exceptionally preserved basal deuterostomes, have extended the range of vertebrates back to the Early Cambrian (Shu, 2003).

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.

Another vertebrate from Chengjiang, *Haikouichthys*, now known from over 500 specimens (Shu *et al.*, 1999, 2003a), 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, which may have been made from cartilage in life. The back 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 Hou *et al.* (2002) that in fact *Myllokunmingia* and *Haikouichthys* are a single species. A new taxon, *Zhongjianichthys*, has been added (Shu, 2003b), 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 no-

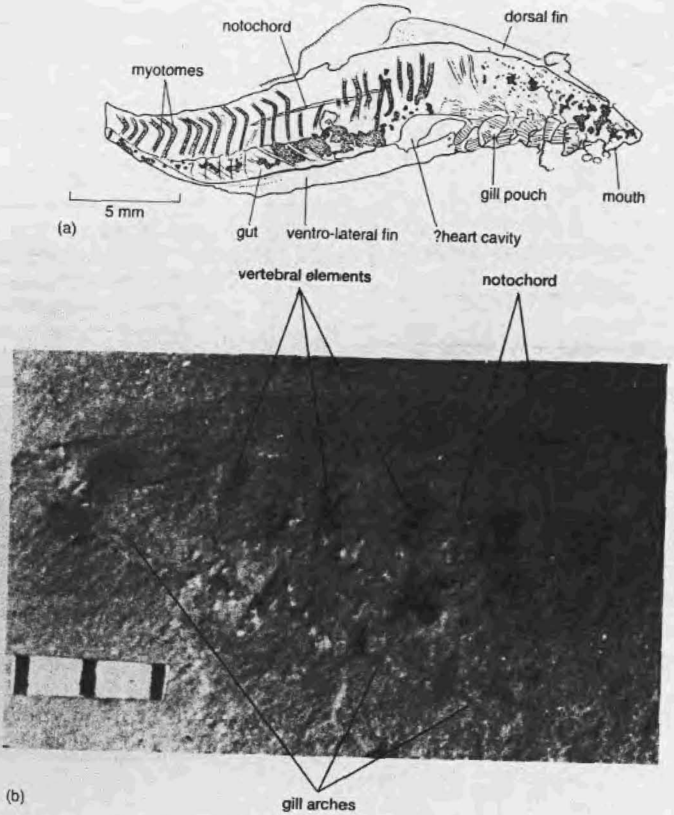


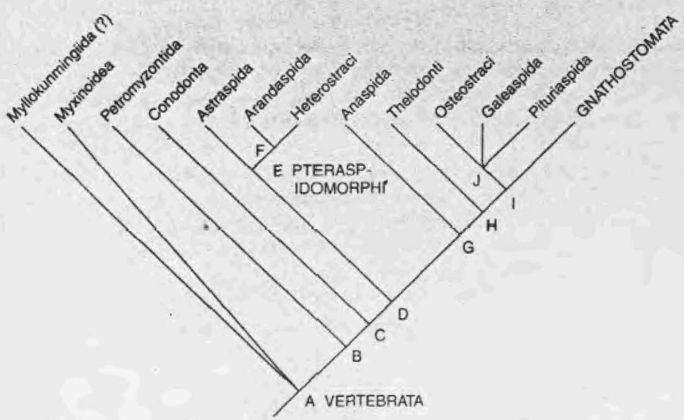
Fig. 3.1 The Lower Cambrian vertebrates *Myllokunmingia* (a) and *Haikouichthys* (b) from the Early Cambrian Chengjiang locality in China. In (b), showing the anterior half of the animal, the key chordate feature of a notochord is indicated, as well as the key vertebrate character of possible cartilaginous vertebrae surrounding it. (Courtesy of Shu Degan.)

tably *Anatolepis* from Wyoming and Greenland (Figure 3.2), both assumed to have come from jawless fishes. These tiny 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, nor 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). These specimens show that bone evolved some time after the origin of the vertebrates, and that the apatitic tissues of vertebrates may be complex.

BOX 3.1 BASAL VERTEBRATE RELATIONSHIPS

The relationships of the basal 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, however, broke up Cyclostomata, and distributed the various clades of jawless fishes between the two living groups, either as close relatives of the hagfishes or of the lampreys (reviewed, Janvier, 1984; Maisey, 1986; Forey and Janvier, 1993). A recent comprehensive cladistic analysis (Donoghue *et al.*, 2000; illustration) confirms that myxinoids (hagfishes) are the basal vertebrates. Next in the cladogram come petromyzontids (lampreys), and then conodonts. The pteraspidomorphs (astraspids, 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.

There is, however, a major discrepancy between this result and current molecular phylogenies. Analyses based on rRNA (Mallatt and Sullivan, 1998), nuclear DNA (Kuraku *et al.*, 1999), and on a variety of genes (Furlong and Holland, 2002; Takezaki *et al.*, 2003) strongly support Cyclostomata as quite distinct from Gnathostomata. Future work will focus on resolving this discrepancy in results: is Cyclostomata valid, and hence the morphological characters must be wrongly coded, or are they right and the molecular results somehow misleading, perhaps because of convergence in the genes?



Cladograms 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 Figure 3.12 for phylogeny of Gnathostomata. Selected synapomorphies from Donoghue *et al.* (2000): **A VERTEBRATA**, neural crest, brain, optic tectum in the brain, unpaired fin ray supports closely set, paired olfactory capsules, at least one set of semicircular canals; **B**, extrinsic eye musculature, two or more semicircular canals, sensory line-system with neuromasts, electroreceptive cells, gills symmetrical, open blood system, arcualia, braincase with lateral walls, sexual dimorphism; **C**, calcified dermal skeleton; **D**, cerebellum, vertical semicircular canals forming loops well separate from the utricle, trunk dermal skeleton; **E PTERASPIDOMORPHI**, oak-leaf-shaped tubercles; **F**, cancellar layer in exoskeleton, large unpaired dorsal and ventral dermal plates on head; **G**, 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 Petromyzontida]; **I**, large lateral head vein, neurocranium entirely closed dorsally and covering the brain, occiput enclosing cranial nerves IX and X, perichondral bone, globular calcified cartilage; **J**, gill openings and mouth ventral, massive endoskeletal head shield covering the gills dorsally.

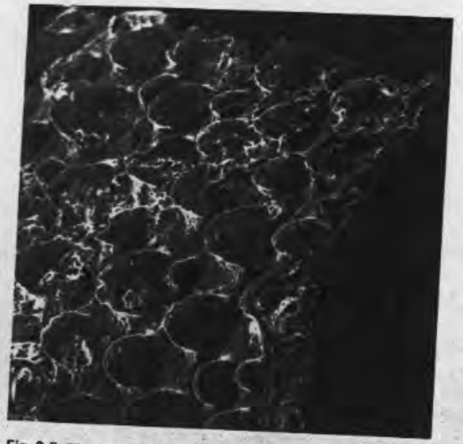


Fig. 3.2 The armour of *Anatolepis*, one of the first vertebrates with bone, from the Upper Cambrian of Crook County, Wyoming, USA. The scale-like tubercles are composed of dentine around a pulp cavity. Photograph ×200. (Courtsesy of J.E. Repetski.)

3.2 VERTEBRATE HARD TISSUES

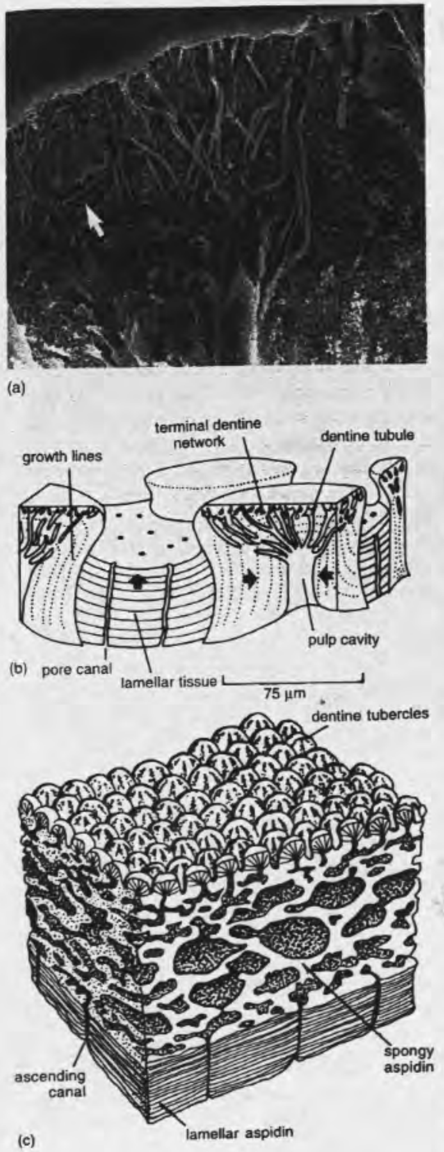
Bone is a key feature of vertebrates. There are different kinds of bone, and other bone-like hard tissues, and it is important for palaeontologists to understand these, especially when they are trying to classify isolated phosphatic scales and teeth. Bone is made from mineral and protein components. In fine detail, 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 which 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 internal skeleton that we have 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, 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.

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 found in our teeth. It is largely inert crystalline apatite with some structural proteins, but with no collagen or blood vessels in the structure.

The first vertebrates had bone that developed from different parts of the early embryo, some from deep sources, the **endodermal** bone, and some from more superficial sources associated with the skin layer, the **dermal** bone. Endodermal bone is seen in *Anatolepis* and thelodonts. Dermal bone is seen possibly in *Anatolepis* (Figure 3.2), which had scales made from dentine, containing dentine tubules (Figure 3.3(a)), but with no sign of enamel (Smith *et al.*, 1996), whereas the first conodonts had enamel and dentine. These astonishing observations show that the dermal plates of early vertebrates had more in common with our teeth than with true bone. 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 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**, which is a flexible material consisting mainly of collagen. The cartilage of these earliest vertebrates though was not composed of collagen (Donoghue and Sansom, 2002), as is the case also in lampreys and hagfishes. Cartilage makes up most of your nose and ears, and the cartilaginous fishes, sharks and rays, retain an internal skeleton made entirely from that material. At some point, possibly as the endoskeleton came into contact with the exoskeleton (induction), bone began to appear in internal skeletons, particularly in the head region, usually first surrounding, and then invading, cartilaginous structures. **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 appeared in later jawed fishes, and it forms 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 turn into 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.

3.3 THE JAWLESS FISHES

The earliest fishes are sometimes included in the paraphyletic group 'Agnatha' (literally, 'no jaw'), and they

Fig. 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 Upper 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. (Courtesy of Paul Smith.)

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 Myxinoidea (hagfishes), the Conodonta, the Ordovician Arandaspida and Astraspida, the heavily armoured Heterostraci, the Anaspida, the poorly armoured Thelodonti, and the armoured Osteostraci, Galeaspida and Pituriaspida. The armoured jawless fishes from the Early Palaeozoic are sometimes grouped loosely as **'ostracoderms'**, a term with no phylogenetic meaning.

3.3.1 Living jawless fishes

Two living groups of jawless fishes, the lampreys (Petromyzontida) and the hagfishes (Myxinoidea), lie close to the base of the Vertebrata, and they may share more primitive features with their Cambrian forebears than the other Palaeozoic fishes. 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.

The 30 or so species of lampreys 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 teeth that permit firm attachment to the prey. There is a fleshy protusible '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 marine hagfishes (Figure 3.4(c)) look superficially like lampreys, but they live in burrows in soft sediments, feeding on invertebrates and decaying carcasses on the sea-bed. 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 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 tying a knot in the tail, passing it forwards towards the head, and bracing against the side of their prey.

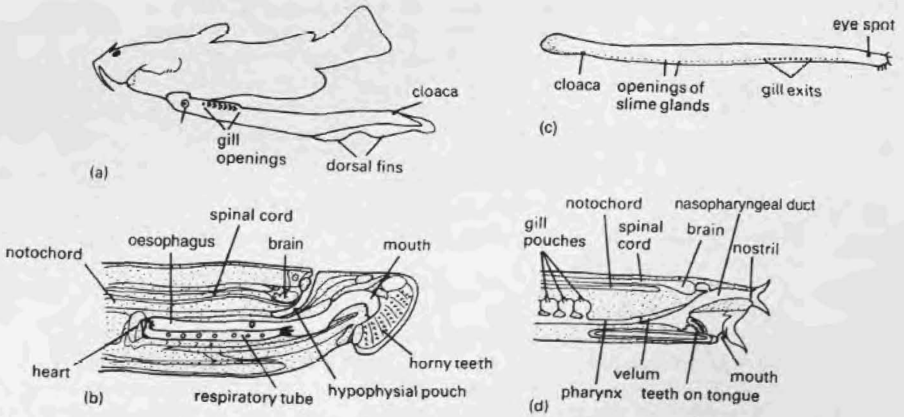


Fig. 3.4 Living jawless fishes: (a) lamprey, feeding by attachment to a bony fish, and (b) longitudinal section of anterior end of body; (c) Pacific hagfish, external lateral view of body, and (d) longitudinal section of anterior end of body. (Modified from Young, 1981, and other sources.)

3.3.2 Conodonta

One of the longest-lived groups of 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 when the first complete conodont, *Clydagnathus*, was reported from the Lower 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.*, 1998, 2000), as well as different conodont taxa from the Upper Ordovician of South Africa and the Lower 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

Fig. 3.5 The conodont animal *Clydagnathus* from the Lower 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. (Courtesy of Dick Aldridge.)

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 occasionally had 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 its food into its mouth, and perhaps prevent any live prey from escaping.

The body region of the Edinburgh conodont animals shows a clear midline structure (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 (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 (Figure 3.5(a)). Overall, the conodont animal looked very like a small lamprey (Figure 3.6(b)).

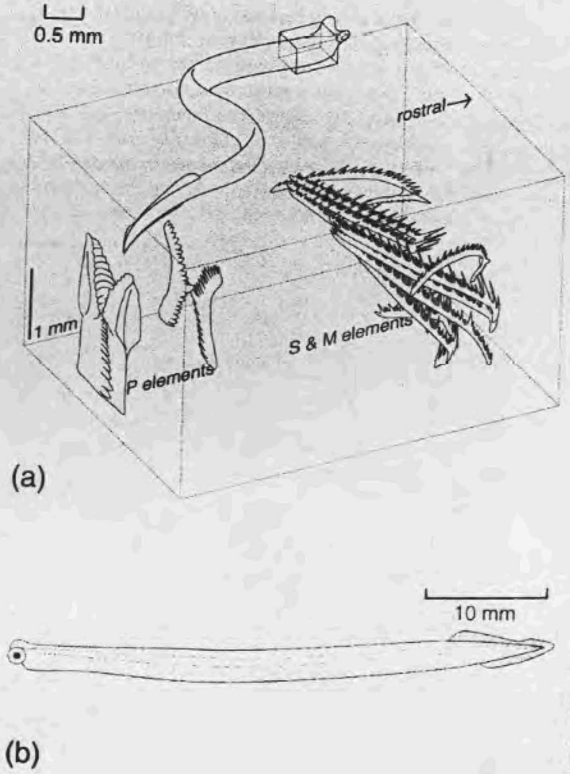


Fig. 3.6 The conodont animal: (a) a complete conodont apparatus of the type possessed by *Clydagnathus*, showing different tooth elements (P, S, and M types), and location of the apparatus; (b) restoration of *Clydagnathus* in life, showing the eyes and the eel-like body. (Courtesy of Mark Purnell.)

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 more derived than the extant lampreys and hagfishes (see Box 3.1). Chordate synapomorphies are the notochord, 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). Conodonts are more derived than living lampreys and hagfishes, as they share the presence of bone-like calcified tissue with other vertebrates, and there are at least two types: dentine and enamel-like tissue.

3.3.3 Ordovician jawless fishes

After the Cambrian radiation of basal vertebrates, with and without skeletons, and 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 Upper Ordovician (Sansom *et al.*, 2001).

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 (Gagnier, 1993) 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 (except hagfishes) — 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.

3.3.4 Heterostraci

The heterostracans, a large group of some 300 species, radiated extensively in the Silurian and Early Devonian. Their head shields vary tremendously in shape among different species, and they are distinguished from the astraspids and arandaspids by having a single exhalant opening on each side into which the gills open. Heterostracans all have in common a broad ornamented plate on top, one or more plates on either side of this, and a large element covering the underside (Halstead, 1973; Blieck, 1984). Heterostracans are grouped in a clade with Astraspida and Arandaspida, the Pteraspidomorphi, as all share the synapomorphy of aspidin on their dermal armour plates (Donoghue *et al.*, 2000; see Box 3.1).

There were four main groups of heterostracans, the cyathaspids, amphiaspids, pteraspids and psammosteids. The cyathaspids, 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

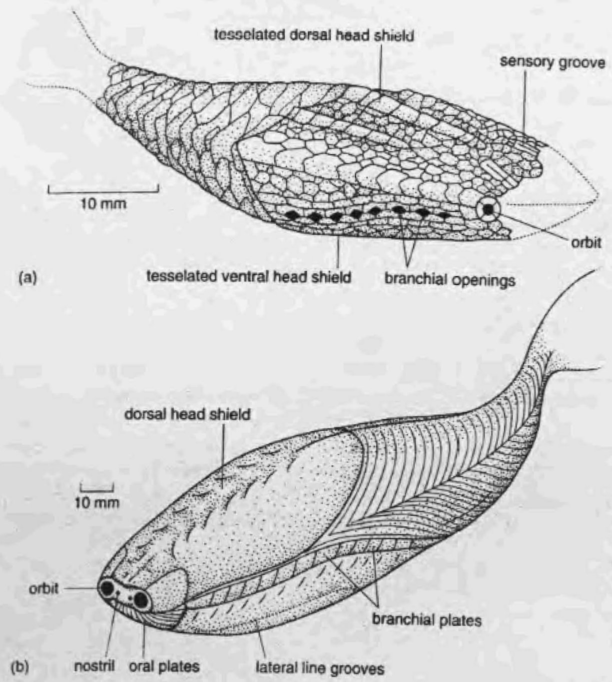


Fig. 3.7 Ordovician jawless fishes: reconstructions of (a) *Astraspis* from the Ordovician of North America, in dorsal view, and (b) *Sacabambaspis*, from the Ordovician of Bolivia, in side view. [Figure (a) after Sansom *et al.*, 1997; (b) after Gagnier, 1993 and Sansom *et al.*, 2001.]

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 fins or paddles, so heterostracans must have swum by moving their tails from side to side, a rather clumsy mode of locomotion because of the weight of the armour and the inability to adjust the direction of movement.

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 the 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. 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 flat (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 an 'exploded' pteraspid—all the major plates are the same, but they have moved apart.

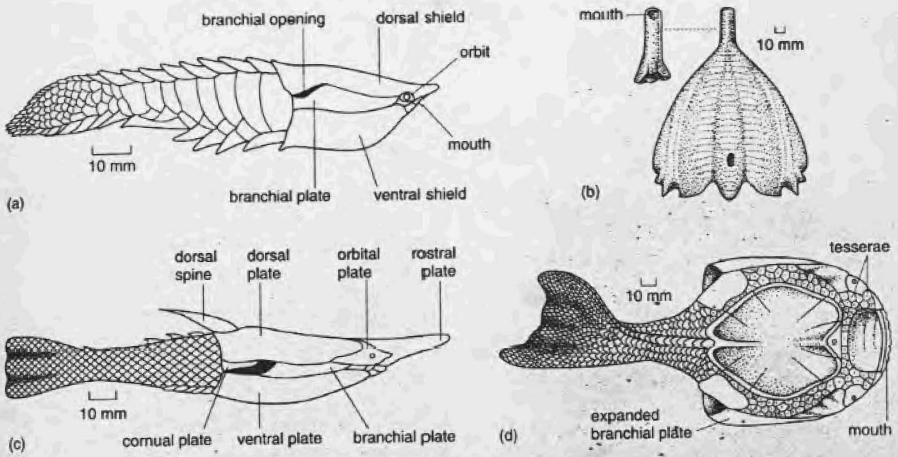


Fig. 3.8 Heterostracans: (a) *Anglaspis*; (b) *Eglonaspis*, dorsal view of head shield and underside of mouth tube; (c) *Errivaspis*; (d) *Drepanaspis*. (After Moy-Thomas and Miles 1971.)

Feeding in heterostracans has been controversial: did they snap up largish prey items, or did they plough through the sea-bed 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 sea-bed, taking in small prey items floating or swimming in the water.

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 are successive outgroups to osteostracans, galeaspids and higher forms (see Box 3.1). Anaspids are known from the Silurian and Devonian (Blom *et al.*, 2002). *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 (Märss and Ritchie, 1998; Donoghue and Smith, 2001). *Phlebolepis* (Figure 3.9 (b, c); Ritchie, 1968) is 70 mm long, with a slightly flattened body, a broad snout, an eye at each side and a wide mouth. There are lateral flaps, a dorsal and ventral 'fin' near the back, and a long lower 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.

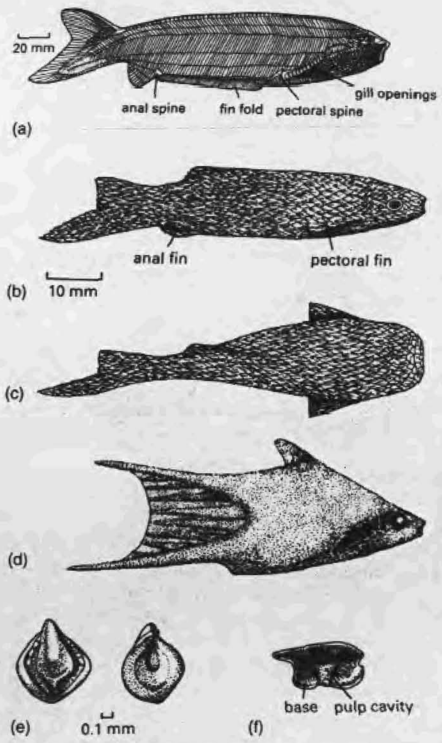


Fig. 3.9 Anaspids (a) and thelodonts (b–f): (a) the anaspid *Pharyngolepis*; (b, c) whole-body restoration of *Phlebolepis*, in (b) lateral and (c) dorsal views; (d) whole-body restoration of the fork-tailed thelodont *Furcacauda*; (e) scales of *Logania* in dorsal (left) and ventral (right) views; and (f) scales of *Thelodus* in cross-section. [Figures (a, e, f) after Moy-Thomas and Miles, 1971; (b, c) after Ritchie, 1968; (d) courtesy of Mark Wilson.]

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 rising to a point above. The exact shape of the scales and the arrangement of the spines and nodules are used to identify thelodont species based on isolated specimens. In cross-section (Figure 3.9(f)), the scale is seen to be made from 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 basal vertebrates.

3.3.6 Osteostraci and relatives

Three clades of jawless fishes are united by the possession of a massive head shield that covered the gills dorsally and ventrally-opening gills (see Box 3.1), i.e. the Osteostraci, Galeaspida and Pituriaspida.

The Osteostraci, including some 300 species, arose in the Ordovician, and radiated in the Late Silurian and Early Devonian (Janvier, 1996). 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(a)). Behind the head plate is a pair of pectoral fins covered with small scales, and these could presumably have been used in swimming (see Box 3.2). *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 which form a dorsal ridge and a dorsal fin.

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

The galeaspids are remarkable fossils from the Silurian and Devonian of China and Vietnam (Janvier, 1984, 1996). Many have broad head shields, but others show the development of an impressive array of processes (Figure 3.10(c)): 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 lack paired fins. 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. Some galeaspids have up to 45 gill pouches, the largest number in any vertebrate.

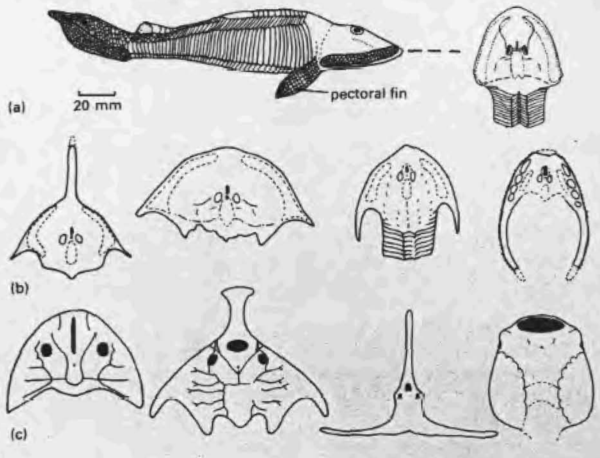


Fig. 3.10 Osteostracans (a, b) and galeaspids (c): (a) *Hemicyclaspis* in lateral view, and dorsal view of head shield; (b) osteostracan head shield diversity; from left to right, *Boreaspis*, *Benneviaspis*, *Thyestes*, and *Sclerodus*; (c) galeaspid head shield diversity; from left to right, *Eugaleaspis*, *Sanchaspis*, *Lungmenshanaspis*, and *Hanyanaspis*. [Figure (a) after Moy-Thomas and Miles, 1971; (b) based on Gregory, 1951; (c) after Janvier, 1984.]

The pituriaspids are represented by two incompletely preserved species from the Early Devonian of Australia. They share a heavy, bony head shield with osteostracans and galeaspids, and they have unusual, large openings immediately below the eyes.

3.4 ORIGIN OF JAWS AND GNATHOSTOME RELATIONSHIPS

The Gnathostomata, the jawed vertebrates (all fishes and tetrapods other than 'agnathans'), are marked by the possession of jaws, a feature that opened an enormous number of adaptive pathways that were closed to jawless forms in terms of diets and food-handling techniques. Jaws allowed gnathostomes to adopt a wide range of predatory modes of life for the first time: only jaws can grip a prey item firmly, and allow it to be manipulated, cut cleanly, and ground up. They also allow efficient suction feeding. How did jaws evolve?

3.4.1 Jaws

The classic theory for the origin of jaws is that they formed from modified anterior gill arches (Figure 3.11(a)). In jawless fishes, the gill slits are separated by bony or cartilaginous arches. A hypothetical ancestral basal 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.

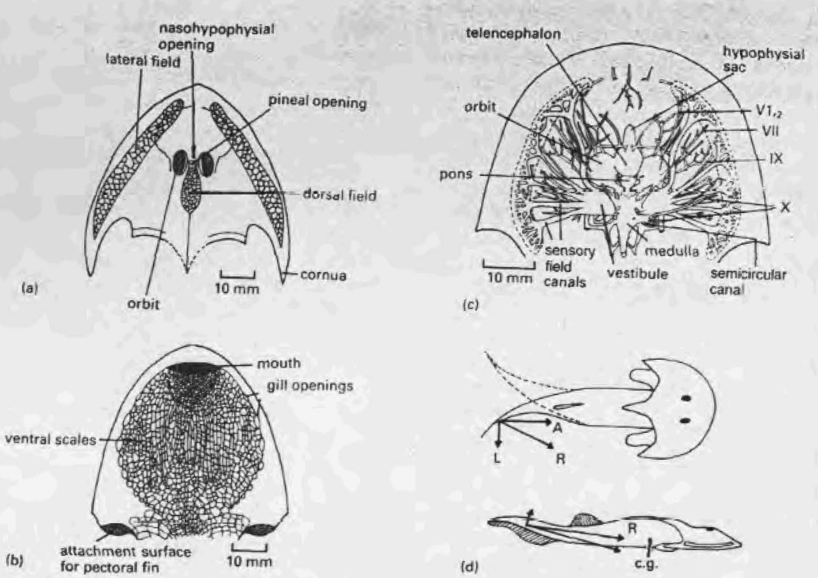
BOX 3.2 BIOLOGY OF THE CEPHALASPIDS

Certain of the cephalaspid osteostracans, such as *Hemicyclaspis* (Figure 3.10(a)) and *Cephalaspis*, are extremely well preserved, and it has been possible to extract a great deal of anatomical and biological information from the specimens.

The upper surface of the head shield (illustration (a)) shows two oval openings for the eyes, the orbits and a narrow keyhole-like slit in front of them in the midline, the **nasohypophysial 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.

There are three specialized areas on the head shield marked by small scales set in slight depressions, the dorsal field in the midline behind the orbits, and the two lateral fields (illustration (a)). They might have had an additional sensory function. These areas are connected to the auditory region of the brain by large canals in the bone that may have transmitted nerves or contained fluid. The fields may have functioned in detecting movements in the water nearby, either by physical disturbance of the water, or by weak electrical fields.

The curved notches on either side at the back of the head shield are occupied by the pectoral fins (illustration (a)), and pointed cornua run back on either side. The underside of the cephalaspid head shield (illustration (b)) 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.



Cephalaspid anatomy and function: (a) head shield of *Cephalaspis* in dorsal view, showing sensory fields; (b) head shield of *Hemicyclaspis* in ventral view; (c) internal structure of the head shield of *Kiaeraspis*, showing the brain and related sense organs and nerves; (d) locomotion of *Escuminaspis* in dorsal (left) and lateral (right) views. Abbreviations in (d): A, anterior component of force produced by tail; L, lateral component; R, resultant of A and L; c.g., centre of gravity. [Figures (a–c) after Zittel, 1932; (d) after Belles-Isles, 1987.]

The most notable features of the cephalaspid head shield are to be seen inside. The bony parts enclosed much of the brain and sensory organs, as well as parts of the blood circulatory system and digestive system. The brain and its associated cranial nerves, the major nerves that serve the various parts of the head region, have been reconstructed by the Swedish palaeontologist Erik Stensiö (1927) with a fair degree of confidence because of the extensive bony envelope (Illustration (c)). The large orbits and inner ear regions are quite clear. Even the semicircular canals of the inner ear, the organs of balance, can be seen. The brain stem itself is located in the midline, and it was made from the three main portions seen in primitive living fishes, 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 **hypophysial 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 identified by comparison with living vertebrates. The five broad canals running from the lateral sensory fields to the vestibule of the inner ear show clearly (illustration (c)).

An analysis of the locomotion of cephalaspids (Belles-Isles, 1987) has shown that they were capable of sustained swimming, short bursts of fast locomotion, and fairly delicate manoeuvring, rather like sharks that live on or just above the sea-bed. The shape of the head in side view is an aerofoil, so that forwards movement would have tended to produce lift. When the tail beat from side to side, it produced a resultant force that drove the fish forwards and slightly downwards (illustration (d)). The downwards component was produced by the presence of the long upper lobe on the tail, but it was counteracted by lift at the head end, and possibly also by the pectoral fins.

Cephalaspid fossils have been found in freshwater sediments from streams, lakes, and deltas, and in marine sediments. They may have foraged for detrital matter on the bottoms of lakes, moving by pulling their bodies along with the muscular pectoral fins. They could apparently also swim for long distances, however, in search of new feeding grounds, or rapidly to escape predators.

Anatomical evidence, however, suggests that the gill-arch theory may not be so simple in reality. 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. Mallatt (1999) has argued 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.

Developmental studies suggest that the classic theory is probably incorrect (Kuratani *et al.*, 2001). 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 that happens during development, and this implies that it is wrong to expect to see precursors of jaws in the adults of jawless vertebrates.

Developmental genetic studies of mice (Depew *et al.*, 2002) show that the first branchial arch has mandibular and maxillary bulges, precursors of the Meckel's cartilage and the palatoquadrate respectively. The homeobox genes *Dlx5* and *Dlx6* code for identity and anteroposterior orientation of the upper and lower jaws. Gnathostomes show **nested** *Dlx* gene action: they possess three pairs of *Dlx* homeobox genes that come into play sequentially. Lampreys show *Dlx* expression in their branchial arches, but the action is not nested, so indicating perhaps the condition in pre-gnathostomes.

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 Upper Carboniferous of North America (Figure 3.11(b)), there is a double attachment with links fore and aft, the **amphistylic** condition.

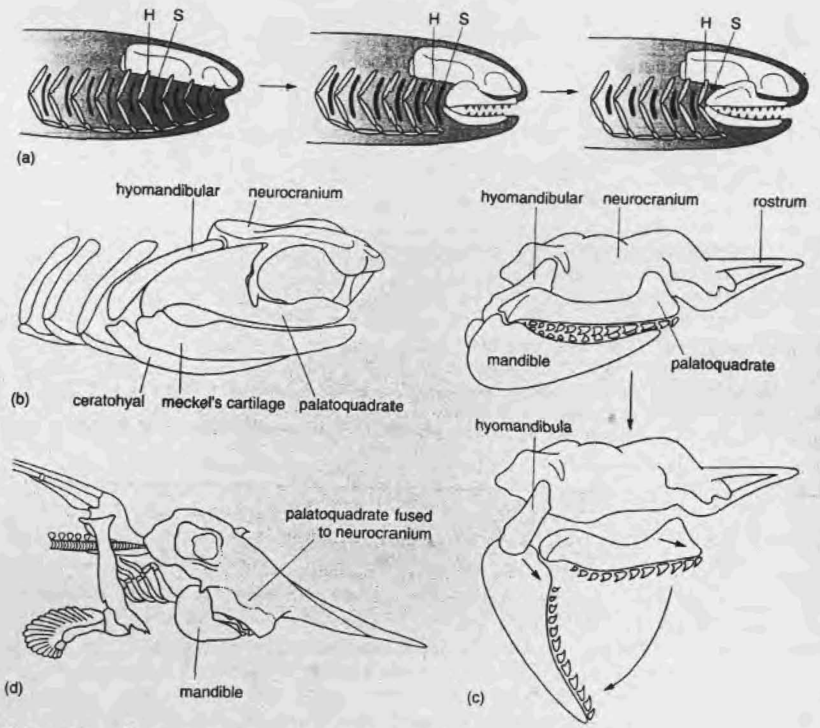


Fig. 3.11 The evolution of jaws and jaw suspension: (a) the 'classic' theory for the evolution of jaws from the anterior two or three gill arches of a jawless form (left) to the fully equipped gnathostome (right); gill openings in black; H, hyomandibular; S, spiracular gill opening; (b) braincase, jaws, and gill supports of the Carboniferous shark *Cobelodus*, to show the amphistylic system of jaw attachment to the neurocranium; (c) 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; (d) head of a chimaerid chondrichthyan, to show the autostylic, or fused, system of jaw attachment. [Figure (a) based on Romer, 1933; (b) after Zangerl and Williams, 1975; (c) based on Wilga *et al.*, 2000 and other sources; (d) based on various sources.]

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 3.11(c)). 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 3.11(d)) and lungfishes, as well as the tetrapods.

Living gnathostomes are grouped in the clades Chondrichthyes and Osteichthyes (bony fishes and tetrapods), and two extinct clades are the Acanthodii of the Ordovician to Permian, and the Placodermi of the Silurian and Devonian. Placoderms are generally ranked as the basal gnathostomes, then chondrichthyans, and acanthodians and osteichthyans are paired by a number of synapomorphies (Figure 3.12).

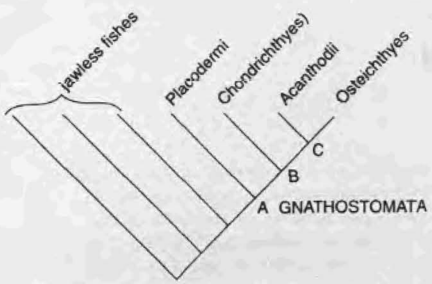


Fig. 3.12 Cladogram showing the relationships of the main groups of jawed fishes, based on Maisey (1986), Janvier (1996), Donoghue *et al.* (2000), Coates and Sequeira (2001a), and Goujet (2001). See Box 3.1 for context of Gnathostomata; see Box 3.6 for phylogeny of Sarcopterygii. Synapomorphies: A **GNATHOSTOMATA**, 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**, 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; **C**, ventral cranial fissure, glossopharyngeal nerve foramen exits dorsally posterior to otic capsule, palatobasal process, interhyal, lateral line passes through scales, paired fin radials barely extend beyond level of body wall.

3.5 PLACODERMI: ARMOUR-PLATED MONSTERS

The osteostracans and heterostracans (see above) were not the only heavily armoured fishes in Silurian and Devonian seas. The placoderms, found largely in the Devonian, bore similar bony carapaces over the regions of their heads and shoulders, but in all cases these bony shells were mobile. There was a special neck joint that allowed the anterior portion of the head shield to be lifted. Placoderms were the first vertebrates to have paired pelvic fins.

The Placodermi includes six clades (Denison, 1978; Goujet and Young, 1995), listed in phylogenetic sequence from most basal to most derived (Goujet, 2001; Smith and Johanson, 2003): Acanthothoraci, Rhenanida, Antiarchi, Petalichthyida, Ptyctodontida and Arthrodira. The arthrodires form the largest group, and they will be described in most detail.

3.5.1 Arthrodira

The arthrodires, nearly 200 genera, make up more than half of all known placoderms, and new taxa are still being found (see Box 3.3). The Mid-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.

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 lower jaw plates join weakly in the middle (Figure 3.13(c)), and their dorsal margin is worn to a sharp edge against a series of eight small plates in the upper jaw. These are not teeth, but they wear into equally effective sharp beak-like plates that would have been capable of an effective cutting, puncturing and crushing action. True teeth have been claimed in the arthrodires (Smith and Johanson, 2003), an unexpected discovery, suggesting a separate origin of teeth in this clade and in the other gnathostomes, although this has been disputed (Young, 2003). Arthrodire teeth are located inside the mouth, behind the main shearing bone plates at the edges of the jaws.

BOX 3.3 THE ARTHRODIRES FROM GOGO

The Gogo locality in Western Australia, of Late Devonian age, has produced some of the most spectacular fossil fishes in the world, including 20 species of arthrodires. The specimens are preserved uncrushed and in three dimensions. Fossils were first collected on the lands of the Gogo cattle station in the 1940s, but their true quality was not realized at first, because a great deal of detail was lost when they were cleaned using chisels and needles. It was only in the 1960s, when palaeontologists prepared the fossil-bearing carbonate nodules using dilute acetic acid, that the astonishing quality of preservation became apparent (see photograph). Further expeditions in the 1980s and 1990s have greatly increased the collections of spectacular Gogo fossils (Long, 1988, 1995).

Some of the Gogo arthrodires belong to groups that were already familiar from other parts of the world, but many of them are quite extraordinary and new to science. Several, such as *Fallacosteus*, belong to a new family, the Camuropiscidae, small 0.3 m long fast-swimming shark-like predators. The camuropiscids have pointed bony projections at the front of their snouts, giving the head shield a torpedo-like shape. The eyes are large, and the tooth plates are designed for crushing. They may have hunted the fast-moving shrimps that teemed in the tropical Gogo waters. The plourdosteids, like *Compagopiscis* (see photograph), were short-snouted relatives.

Find out more at http://palaeo.gly.bris.ac.uk/Palaeofiles/Lagerstatten/Gogo/index.html and http://www.heritage.gov.au/cgi-bin/ahpi/record.pl?RNE101335

The short-snouted arthrodire *Compagopiscis* from the Late Devonian Gogo locality of Western Australia, showing near-perfect three-dimensional preservation. Head shield, 130 mm long. (Photograph by Kristine Brimmell, courtesy of John Long.)

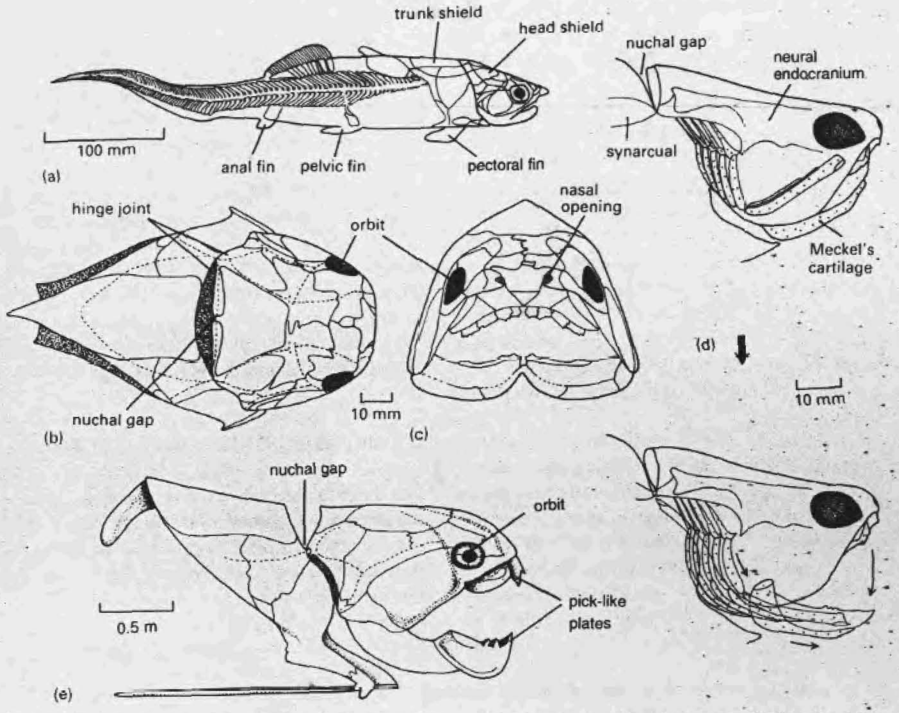


Fig. 3.13 The arthrodire placoderms *Coccosteus* from the Mid-Devonian of Scotland (a–d) and *Dunkleosteus* from the Upper Devonian of North America (e): (a) whole body in lateral view, (b) head shield in dorsal and (c) anterior views, and (d) jaw opening movements showing the position of the head and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

The jaws open (Figure 3.13(d)) by an upwards swing of the skull and dropping of the lower jaw (Miles, 1969). 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. With its vast jaws it could have crushed any other animal of its day.

3.5.2 Diverse placoderms

The acanthothoracids, the basal placoderms, 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.

The rhenanids have a body covering of small tesserae instead of the more typical large plates. *Gemuendina* from the Lower 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 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.

The antiarchs were a diverse group from the Mid- and 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 of all was the antiarch *Bothriolepis* (Figure 3.14(c)), known from more than 100 species found in Middle and Upper Devonian rocks of all parts of the world. *Bothriolepis* 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. One specimen shows possible 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.

The petalichthyids are another small group of bottom-dwelling forms. *Lunaspis* from the Lower 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.

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 Upper 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.

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 Upper Ordovician and Silurian (Sansom *et al.*, 2001). The first definitive remains containing prismatic calcified cartilage (see below) date from the Early Devonian. An early shark, *Cladoselache* from the Upper 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.

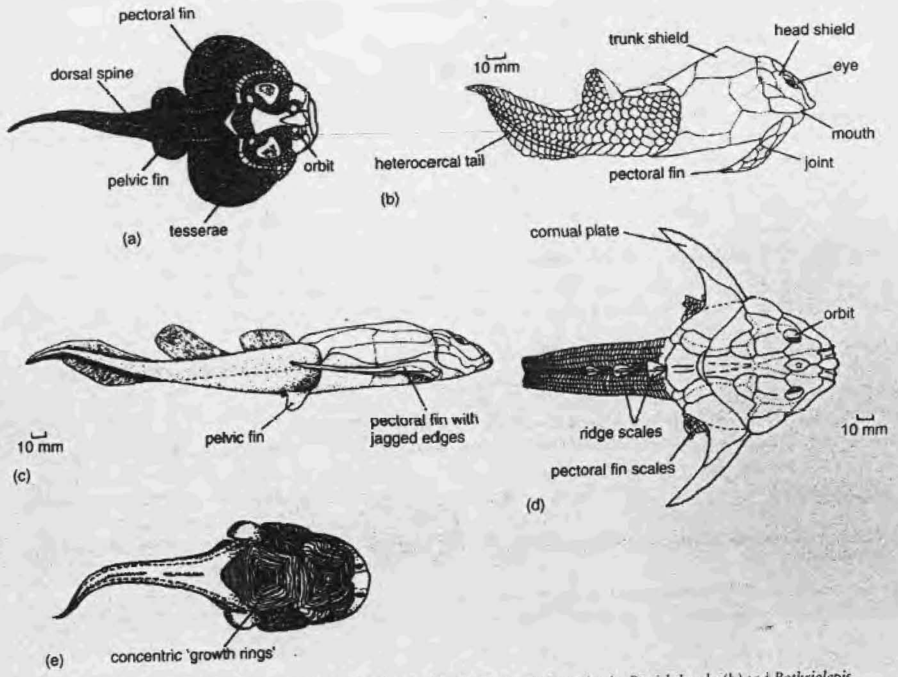


Fig. 3.14 Diverse placoderms: (a) the rhenanid *Gemuendina* in dorsal view; (b, c) the antiarchs *Pterichthyodes* (b) and *Bothriolepis* (c) in lateral view; (d) the petalichthyid *Lunaspis* in dorsal view; (e) the ptyctodont *Ctenurella* in lateral view. [Figures (a, c–e) after Moy-Thomas and Miles, 1971; (b) after Hemmings, 1978.]

Cladoselache is usually assigned to the order Cladoselachida, a group restricted to the Late Devonian. Other shark remains are known from rocks of this age (Zangerl, 1981), but none as well as *Cladoselache*. 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 ACANTHODII: THE 'SPINY SKINS'

The acanthodians (Denison, 1979) were generally small fishes, mostly less than 200 mm long, that include the oldest known gnathostomes. 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.

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 have been modified to long spines, and there may be as many

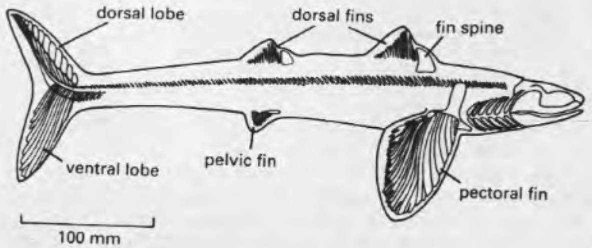


Fig. 3.15 *Cladoselache*, one of the first sharks. (After Zittel, 1932.)

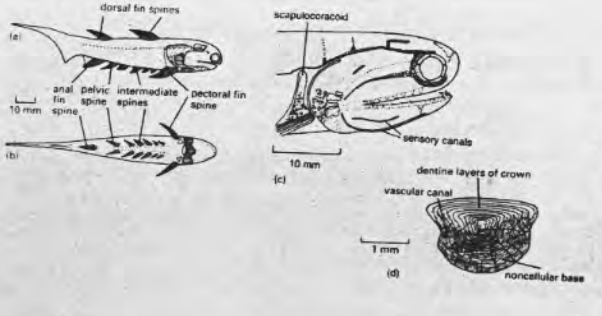


Fig. 3.16 Acanthodian diversity and anatomy: (a) *Climatius* in lateral view; (b) *Euthacanthus* in ventral view, showing the fin spines; (c) head region of *Ischnacanthus* in lateral view; (d) single scale of *Acanthodes*. (After Moy-Thomas and Miles, 1971.)

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. The shoulder girdle, or **scapulocoracoid**, is ossified in some forms, but is separate from the skull in later acanthodians (Figure 3.16(c)), thus allowing greater freedom of movement. Acanthodians have large eyes supported by a number of **sclerotic plates**, and there are lightly-scaled sensory canals set into the crania in many.

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.

Most acanthodians lack teeth. Toothless forms probably fed on small food particles which they may have filtered from the water. Only some of the later 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, and they may have fed at middle depths. 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.

3.8.1 Siluro-Devonian faunal provinces

It is possible to distinguish **faunal provinces** among early fishes. For example, there was a Scotto-Norwegian fauna of thelodonts in the Silurian that differed in many respects from the Acadian–Anglo-Welsh fauna (Figure 3.17(a)). In other words, Silurian fish fossils from Wales and southern England are more like those from the eastern parts of North America and Greenland (Acadia) than those from the central parts of Scotland or from Norway.

The extraordinary distributions of thelodont faunas make sense when Silurian geography is considered (Figure 3.17(a)). Scotland, Norway, Greenland and Canada formed a single land mass, located largely south of the equator. A separate Canadian Arctic–Russian thelodont fauna straddles the northern boundaries, and the Acadian–Anglo-Welsh fauna is typical of the southern region. The rest of Europe was separated from this continent by the Iapetus Ocean, and it was also located largely south of the equator. The Scotto-Norwegian thelodont fauna is restricted to the western end of this land mass. Siberia, with the Angaran thelodont fauna, was another land mass. Thelodonts do not appear to have reached the southern continents, Gondwana, at this time.

The Silurian thelodont 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, the *Turinia* fauna, occurs nearly worldwide (Figure 3.17(b)). One barrier was lost when the North American–Greenland–Scotland continent fused fully to the rest of Europe with the closure of the Iapetus Ocean. Thelodonts were able to spread worldwide, and they reached Australia and other parts of Gondwana. Only Siberia remained isolated to some extent, and the separate Angaran thelodont fauna survived there, although *Turinia* invaded southern regions.

Some other fish groups, such as the armoured jawless fishes and placoderms, do not show such uniform global distributions in the Devonian. Indeed, most 'ostracoderms', except conodonts, thelodonts and pituriaspids, were absent from Gondwana after the Ordovician. They divide into distinctive faunas in Euramerica, Siberia, eastern Siberia (Tuva), South China and eastern Gondwana (Australia and Antarctica) (Young, 1993). The galeaspids, for example, are found only in Vietnam and South China, whereas the camuropiscid arthrodires and others are restricted to Australia.

3.8.2 Siluro-Devonian environments

Silurian and Devonian seas and freshwaters were warm, and fish fossil localities are clustered in the equatorial and tropical belt (Figure 3.17). Important environmental changes took place on land during the Silurian and Devonian, and these affected vertebrate evolution. The first land plants appeared in the Mid- to Late Silurian. They were small and reed-like, and probably grew around ponds and lakes with their tuberous roots partly in the water. Early Devonian terrestrial rocks very rarely contain fossils of land plants or animals, but by Mid- and Late Devonian times, large horsetails and scale trees (lycopods) became quite common.

The first land animals were scorpions, millepedes and spider-like arthropods, all of which could live in water and on land. They first appear 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.

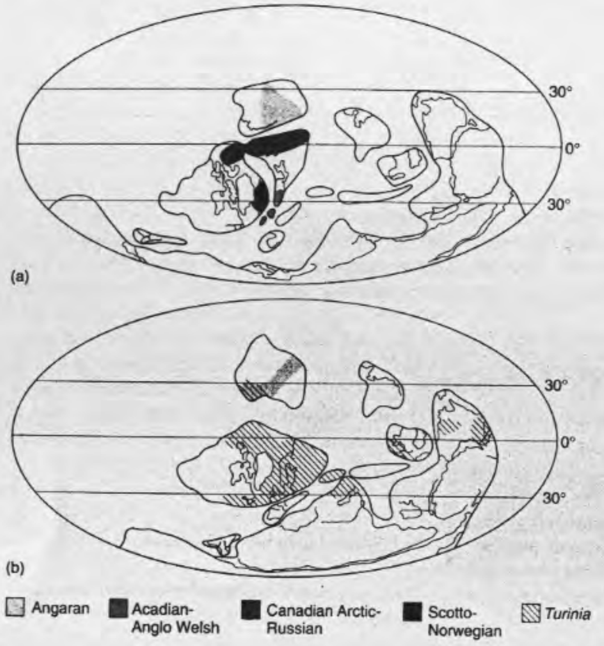


Fig. 3.17 Thelodont faunal provinces and palaeogeography in the Silurian (a) and Devonian (b). Continental outlines for those times are shown with heavy lines, and modern continental margins are shown with fine lines. The five thelodont provinces are indicated by shading. (After Halstead, 1985.)

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 3.4), were termed the Old Red Sandstone. This continent was a large tropical land mass, 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.

3.9 OSTEICHTHYES: THE BONY FISHES

The bony fishes are divided into two clades, the Actinopterygii and Sarcopterygii, both of which appeared in the latest Silurian, and radiated through the Devonian. These 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, and a new fossil fish from China sheds some light on the phylogeny of the group (see Box 3.5).

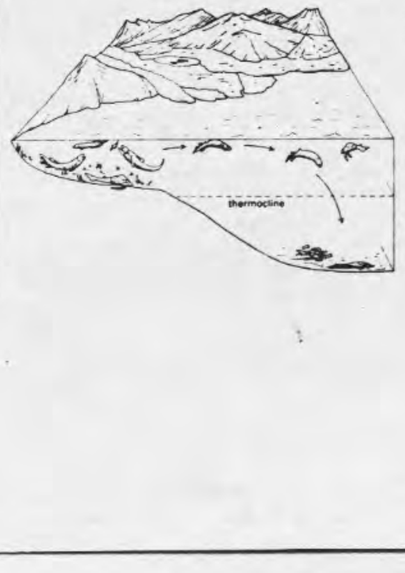
BOX 3.4 OLD RED SANDSTONE FISHES OF SCOTLAND

Some of the most prolific collections of Devonian jawless fishes, placoderms, acanthodians and lobefinned fishes, have come from the Old Red Sandstone 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 90,000 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). In places, annual varves, generally less than 1 mm thick, may be detected.

Fossil fishes occur in the Scottish Old Red Sandstone both as scattered fragments and in great concentrations within 'fish beds'. Mortality horizons, single layers containing high concentrations of fish carcasses, seem to have formed during deoxygenation events that may have occurred every 10 years or so when the lake was deepest. Repeated mortality events of this kind occurred over thousands of years, and built up major fish beds in several places. These could have either followed an algal bloom, when decaying algae removed oxygen from the water, or a severe storm that stirred up deep anoxic waters to the surface. Other likely causes of fish kills in the Old Red Sandstone lakes include 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 Old Red Sandstone 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* (Figure 3.20) and *Osteolepis* (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* (Figure 3.13) and the bony fish *Cheirolepis* (Figure 3.19) that have been found with remains of acanthodians and of *Dipterus* in their stomachs. The heavier placoderms such as *Pterichthyodes* (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 seems to have been 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.



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. (After Trewin, 1985, courtesy of Blackwell Science Ltd.)

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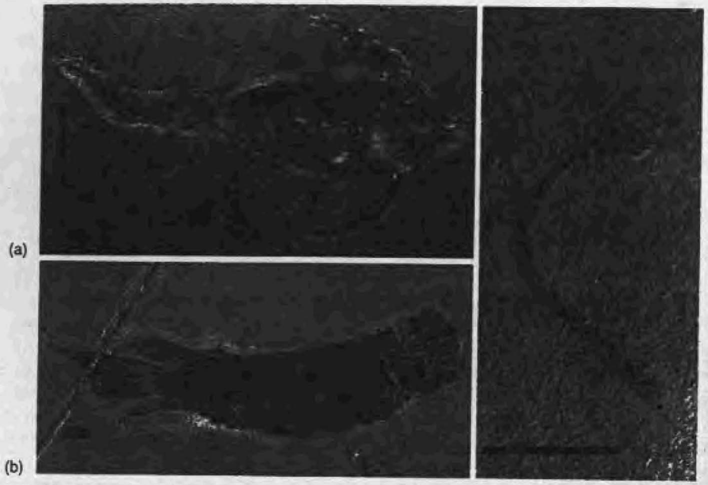


II Typical Old Red Sandstone fishes from Achanarras Quarry, Caithness: (a) juvenile *Pterichthyodes*; (b) *Dipterus*, showing slight separation of head elements on fossilization; (c) *Palaeospondylus*, a possible larval lungfish. Scales: 20 mm in (a) and (b); 10 mm in (c). (Courtesy of Nigel Trewin.)

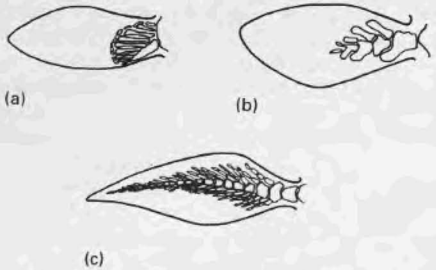


Fig. 3.18 The fins of (a) an actinopterygian, *Amia*, to show the simple basal skeleton, (b) the lobefin *Fusthenopteron*, an osteolepiform, and (c) the lobefin *Neoceratodus*, a lungfish, to show the more complex skeleton that supports a muscular lobe in the middle of the fin. (Modified from Zittel, 1932.)

3.9.1 Devonian actinopterygians

The oldest actinopterygians, represented by scales, are Late Silurian in age, but the group began to diversify only in the Late Devonian. An early form is *Cheirolepis* from the Mid-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

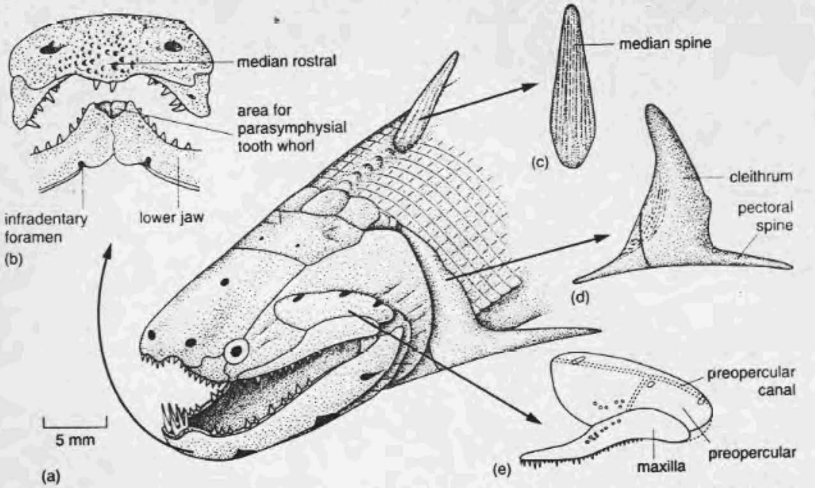
BOX 3.5 *PSAROLEPIS* AND THE ORIGIN OF BONY FISHES

Until recently, the actinopterygian and sarcopterygian fishes seemed to be quite distinct clades. Now, a fossil from the Upper Silurian and Lower Devonian of China and Vietnam has provided a probable missing link. *Psarolepis* (Zhu *et al.*, 1999) is known from many specimens from several localities. When it was first described, it was assigned to the sarcopterygians because the skull and jaws looked like those of primitive lungfishes and other Devonian forms. The cheek bones and the shoulder girdle, however, seem to share features of both osteichthyan groups.

In the skull (see illustration), *Psarolepis* shows a mix of actinopterygian and sarcopterygian features. In the lower jaw, for example, there are three large infradentary foramina and evidence of a parasymphysial tooth whorl, a set of long, hooked teeth that pointed up and forwards. Both features are typical of porolepiforms and other sarcopterygians. The teeth are also sarcopterygian in showing multiple infoldings and in bearing cosmine. In the cheek region, *Psarolepis* has actinopterygian features: it does not have the squamosal elements seen in sarcopterygians, and the canal running along the preopercular bone has a ventral extension towards the maxilla. The three large openings in the preopercular bone, near the canal, however, are more sarcopterygian-like.

There are also some characters that have never been seen before in the bony fishes: *Psarolepis* has a huge pectoral spine extending back from the shoulder girdle, and there is a median spine presumably located in the midline behind the head (see illustration). A pectoral spine like this is known in some placoderms and in acanthodians, and the median spine is known in sharks and acanthodians, but neither has been seen in other osteichthyans.

Zhu *et al.* (1999) were unable to locate *Psarolepis* in the cladogram with certainty—they thought it was either the basalmost sarcopterygian (see Box 3.6) or the basalmost osteichthyan. The second interpretation has been confirmed as more likely by Zhu and Schultze (2001), because *Psarolepis* lacks the closed pineal opening and large quadratojugal of other osteichthyans, and it has a posterior pectoral process and paired pectoral spines, which are absent in other bony fishes. Long (2001) points out many similarities between *Psarolepis* and the Onychodontida, and places both as basal sarcopterygians.



Reconstruction of *Psarolepis* from the Lower Devonian of China: (a) head and anterior part of the fish; (b) anterior view of the skull and lower jaws; (c) median fin spine; (d) shoulder girdle with pectoral spine; (e) cheek plate with maxilla and preopercular, sculpture omitted. (Courtesy of Zhu Min.)

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 it is covered by palatal bones that also bear 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, and possibly even in transfixing its prey before capture (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 shorter teeth 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.

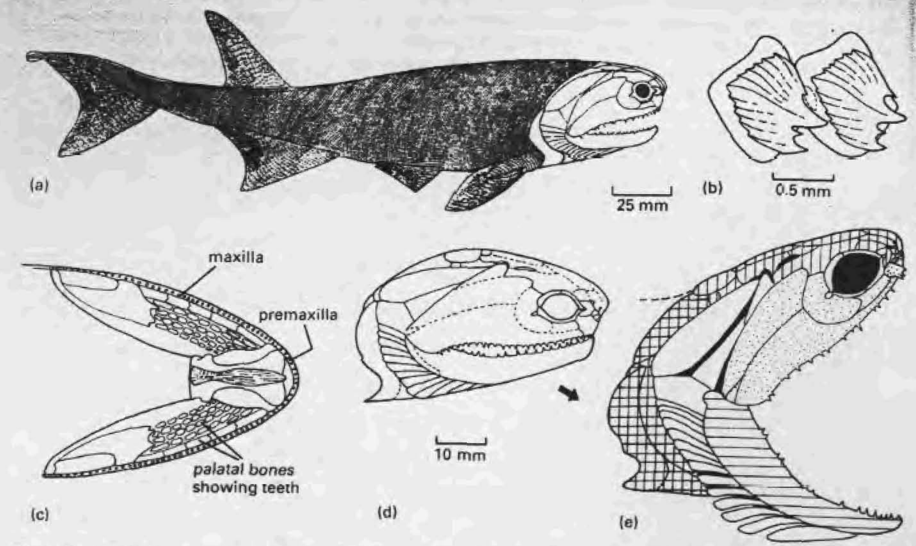


Fig. 3.19 The Mid-Devonian bony fish *Cheirolepis*: (a) reconstruction of the body in lateral view; (b) two trunk scales; (c) ventral view of the palate showing the teeth; (d, e) opening and closing of the jaws, showing the five major mobile units, as described in the text. (After Pearson and Westoll,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

Devonian actinopterygians such as *Cheirolepis* are known from all parts of the world, but only a dozen 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 Dipnoi: the lungfishes

The Sarcopterygii were a more significant group in the Devonian than the Actinopterygii, although sarcopterygian fishes have since become much rarer (the clade Sarcopterygii of course includes all tetrapods). Sarcopterygians share muscular lobed paired fins with bony skeletons (Figure 3.19), as well as several skull features not seen in other vertebrates. There are two living sarcopterygian groups, the lungfishes (Dipnoi) and coelacanths (Actinistia), as well as numerous extinct clades, all of which arose in the Devonian. Relationships among the living and extinct sarcopterygian groups have been highly controversial (see Box 3.6).

The lungfishes (Thomson, 1969; Bemis *et al.*, 1986) were particularly diverse in the Devonian, but they have dwindled in importance ever since, leaving only three genera still living. *Dipterus* from the Mid-Devonian of Scotland (Figure 3.20) has a long body, as in the osteolepiforms, 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.

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.

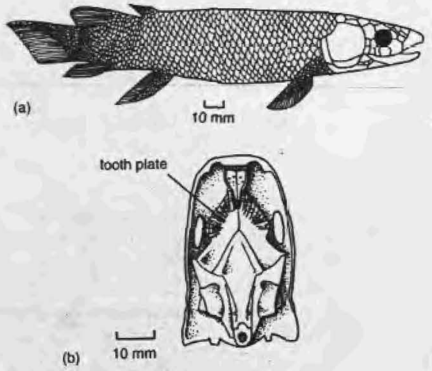


Fig. 3.20 The Devonian lungfish *Dipterus*, (a) in lateral view, and (b) ventral view of the palate, showing the tooth plates. (After Moy-Thomas and Miles, 1971.)

Several lineages of lungfishes radiated 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.

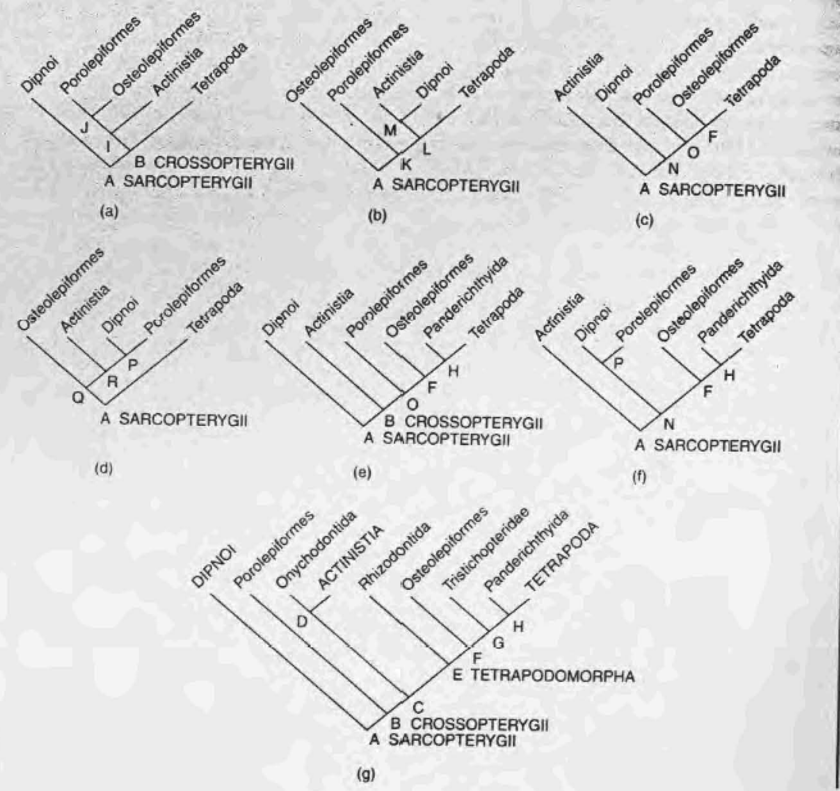
The three genera of living lungfishes (Figure 3.21) have reduced the bony parts of their skeletons. The braincase and parts of the backbone remain cartilaginous, and the outer skull bones are reduced in number and weight. The Australian lungfish *Neoceratodus* is deep-bodied and has broad pectoral and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

The modern lungfishes, as their name suggests, have lungs as well as gills. They 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

BOX 3.6 SARCOPTERYGIAN RELATIONSHIPS

The relationships of the sarcopterygian groups to each other have been controversial, and this interest has been heightened by the assumption that the tetrapods, the land vertebrates, arose within the Sarcopterygii. The problems concern the relationships of the lungfishes, coelacanths, and the diverse Devonian groups (= 'Rhipidistia') to each other, and the identification of one of these as the sister group of the Tetrapoda.

The 'classic' view (e.g. Romer, 1966) has been that the Rhipidistia and Actinistia together form the Crossopterygii. This is treated as the sister group of the Tetrapoda, with the Dipnoi as outgroup (cladogram (a)). This consensus view was given a jolt by Rosen *et al.*'s (1981) suggestion that the lungfishes are the sister group of the tetrapods. In a revised version of this hypothesis (cladogram (b)), Forey *et al.* (1991) argued that lungfishes and coelacanths pair off, and that these two are the sister group of Tetrapoda. The 'Crossopterygii' and 'Rhipidistia' are split into their constituent parts, Osteolepiformes, Porolepiformes and Actinistia, as outgroups.



Panchen and Smithson (1988) presented a third view (cladogram (c)) in which the 'Crossopterygii' and 'Rhipidistia' are also split up, but the Osteolepiformes are regarded as the sister group of the Tetrapoda. In further analyses, Chang (1991) suggested that the Sarcopterygii as a whole are sister group of the tetrapods (cladogram (d)). Schultze (1994) accepted the traditional sequence of outgroups (cladogram (e)), with osteolepiforms as sister group of tetrapods, then porolepiforms as next outgroup, as in Panchen and Smithson's (1988) proposal, but he then considered that the coelacanths were closer to that clade than the lungfishes. Finally, Cloutier and Ahlberg (1996) found a similar cladogram, except that lungfishes and porolepiforms are paired, as Chang (1991) had also suggested (cladogram (f)). Hence, the majority verdict seems to be that some of the 'rhipidistians' are the closest relatives of tetrapods.

In a reanalysis (cladogram (g)), Zhu and Schultze (2001) find that the upper part of the tree is relatively stable, but they move Porolepiformes to lie above Dipnoi and below Actinistia, and split the Tristichopteridae (*Eusthenopteron* and relatives) from the remainder of Osteolepiformes. The onychodonts are placed as a sister group of coelacanths.

Molecular evidence has been equivocal. Meyer and Wilson (1990) found that lungfishes are more closely allied to tetrapods than are coelacanths, according to an analysis of 12S rRNA sequences, a view that would fit Panchen and Smithson's (1988) phylogeny (cladogram (c)). In a revised analysis, based on the 28S rRNA gene, Zardoya and Meyer (1996) found that the coelacanth and the lungfishes form a clade, separate from tetrapods, hence matching the cladograms of Forey *et al.* (1991) and Chang (1991) (cladograms (b, d)). In the end, however, Zardoya and Meyer (2001a) were unable to discriminate relationships among lungfishes, the coelacanth and tetrapods for a variety of reasons. Lungfishes show significantly higher rates of evolution of the 28S rRNA gene sequences than coelacanths, other fishes and tetrapods, and this makes it hard to discriminate their correct position in the tree. In addition, the mitochondrial tRNA and nuclear rRNA sequences seem to give erroneous results overall because long branches pair with each other, as do short branches. Brinkmann *et al.* (2004) confirmed the close relationship of lungfish to tetrapods, based on nuclear genes.

Cladograms showing four competing theories for the relationships of the sarcopterygian fishes and tetrapods, according to (a) Romer (1966) and other 'classic' sources; (b) Forey *et al.* (1991); (c) Panchen and Smithson (1988); (d) Chang (1991); (e) Schultze (1994); (f) Cloutier and Ahlberg (1996); (g) Zhu and Schultze (2001). See Figure 3.12 for context of Sarcopterygii; see Box 4.1 for relationships of basal tetrapods and Figure 7.7 for relationships of Actinopterygii. Synapomorphies (selected, from Cloutier and Ahlberg (1996) and Zhu and Schultze (2001): **A 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; **B CROSSOPTERYGII (*sensu lato*)**, 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; **C**, entepicondylar foramen in humerus; **D**, more than two supraorbitals, branchiostegal rays absent; **E TETRAPODOMORPHA**, single external naris, posterior naris absent, two supraorbitals, palatal opening ('choana'), vomers articulate with each other, narrow parasphenoid, proximal articular surface of humerus convex, deltoid and supinator processes on humerus; **F OSTEOLEPIDIDA**, one branchiostegal ray per side, vomer has a posterior process, supraneural processes on only a few anterior vertebrae or absent; **G**, anterior palatal fenestra present, well ossified ribs; **H**, flattened head and dorsally-placed orbits, snout elongate, paired frontals, spiracle large and open posteriorly, preopercular canal reduced, fang pair on anterior end of dentary, scapular blade large, dorsal and anal fins absent, labyrinthodont plicidentine in teeth; **I CROSSOPTERYGII (*sensu stricto*)**, fleshy lobed pectoral and pelvic fins with asymmetrical arrangement of bones; **J RHIPIDISTIA**, many narrow submandibular bones, four infradentaries, three coronoids; **K**, many supraorbital bones, reduction of dorsal elements of gill arches; **L**, short hyomandibular free from palate, pectoral and pelvic fins equal in size; **M**, short cheek region, biting possible between teeth on palate, upright jaw suspension, short dentary, angular bone dominant, ball-and-socket joint between paired fins and girdles; **N**, preopercular does not contact maxilla; **O**, many narrow submandibular bones, four infradentaries, three coronoids, plicidentine; **P**, three or more tectals, posterior branched radial complex associated with posterior dorsal fin, same structure of the cosmine, leaf-shaped pectoral fins, predominant palatal bite; **Q SARCOPTERYGII (*sensu stricto*)**, cosmine (specialized scale tissue), intracranial joint, anocleithrum in shoulder girdle; **R**, double-headed hyomandibular, intracranial joint, three extrascapulars.

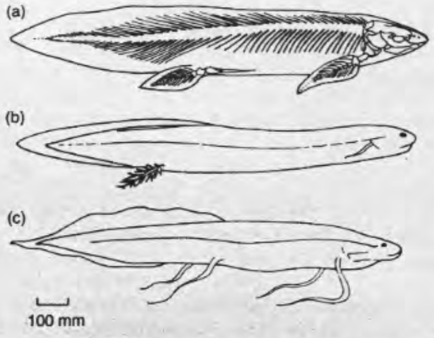


Fig. 3.21 The living lungfishes *Neoceratodus* from Australia (a), *Lepidosiren* from South America (b), and *Protopterus* from Africa (c). (Based on various sources.)

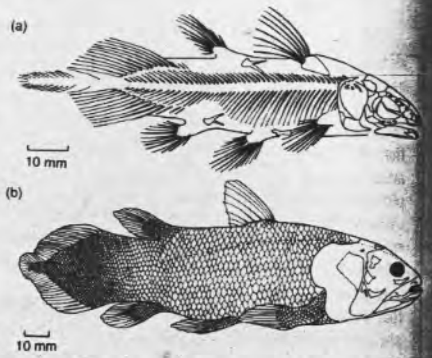


Fig. 3.22 Coelacanths, fossil (a) and living (b): (a) the Triassic *Osteopleurus* from North America; (b) the living *Latimeria* from the modern seas of the Indian Ocean. (After Andrews, 1973.)

season. When the monsoonal rains fall, the lungfishes come to life again, and creep out of their cocoons. Large fossilized burrows in Devonian and Triassic rocks suggest that early lungfishes also aestivated.

3.9.3 Actinistia: the coelacanths

The coelacanths arose in the Mid-Devonian, and are represented by fossils up to the Late Cretaceous, when it was thought they had died out. Typical coelacanths, such as *Osteopleurus* 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 osteolepiforms.

The coelacanths are particularly well known as **living fossils**. In 1938, an unusual large lobefinned 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, 1988, 1998) is 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. Since 1938, about 200 specimens of *Latimeria* have been fished up from the deep oceans off the coast of the Comoro Islands, and Sulawesi in Indonesia, where it feeds on fishes. *Latimeria* 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 primitive to all bony fishes.

3.9.4 Diverse Devonian sarcopterygians

At one time, the Devonian sarcopterygians that were not lungfishes were grouped together as 'Rhipidistia'. This assemblage, including the Porolepiformes, Onychodontida, Rhizodontida, Osteolepiformes, Tristichopteridae and Panderichthyida, is paraphyletic (see Box 3.6).

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 osteolepiforms. 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.

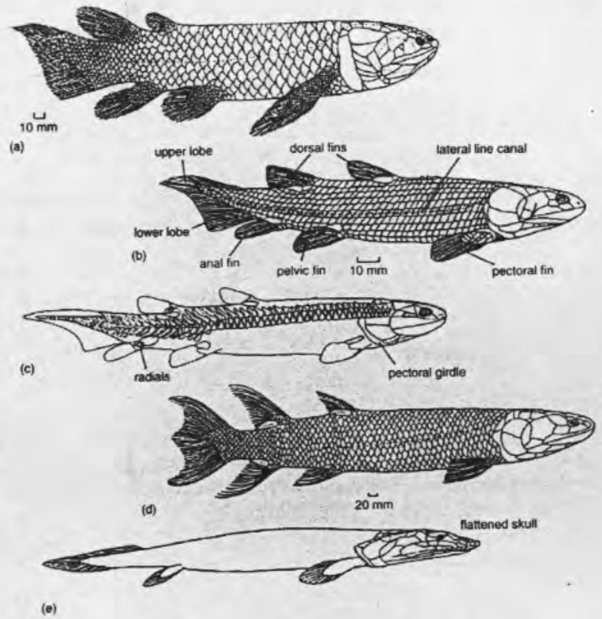


Fig. 3.23 Diversity of Devonian sarcopterygians: (a) lateral view of the porolepiform *Holoptychius*, (b, c) lateral views of the osteolepiform *Osteolepis*, with and without scales, (d) lateral view of the tristichopterid *Eusthenopteron*, (e) lateral view of the panderichthyid *Panderichthys*. [Figure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

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. They have not been known in detail up to now, but new specimens from Gogo (see Box 3.2) show many features in common with *Psarolepis* (see Box 3.5), and hint that the Onychodontida might turn out to be basal sarcopterygians (Long, 2001).

The rhizodontids from the Early Carboniferous were large hunters. One massive rhizodont jaw from Scotland suggests that its owner must have reached a length of 6–7 m (Jeffery, 2003). This was probably a fearsome hunter of some of the early tetrapods (see Chapter 4).

The osteolepiforms had their heyday in the Devonian, although certain forms survived through the Carboniferous and into the Early Permian. *Osteolepis* from the Mid-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 osteolepiforms were larger.

Eusthenopteron from the Upper Devonian of Canada (Figures 3.23(d) and 3.24) has generally been called an osteolepiform, although it seems likely that it, and its relatives, collectively the Tristichopteridae, are a closer sister group to the tetrapods (see Box 3.6). *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 teeth are large and fang-like, and they have complex, or labyrinthine, internal patterns of infolding (Figure 3.25(e)), the so-called labyrintho-

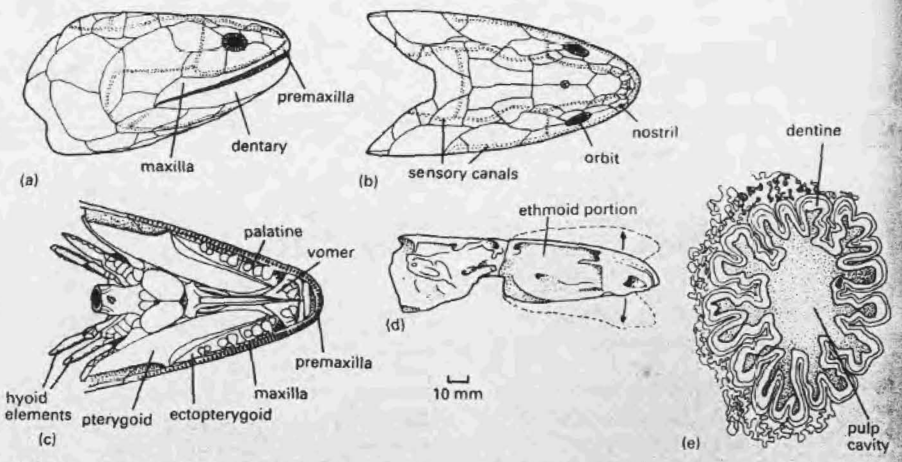


Fig. 3.24 The skull of the tristichopterid *Eusthenopteron* in (a) lateral, (b) dorsal, and (c) ventral views; (d) lateral view of the braincase, showing the postulated range of movement about the middle joint; (e) cross-section of a tooth to show the labyrinthine infolding of the enamel (tooth diameter,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

dont type of tooth, found also in early tetrapods. The skull is highly kinetic, being jointed in order to allow the mouth to open wide. 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 panderichthyids, or elpistostegids, of which *Panderichthys* from the Upper Devonian of Latvia (Figure 3.23(e)) is the best known, are rather stout fishes with long snouts. The skull is flattened, and the eyes are located partly on top of the head. Panderichthyids have only the paired pectoral and pelvic fins, as well as a tail fin, and they lack the midline fins seen above and below the body in their relatives (Vorobyeva and Schultze, 1991).

3.10 EARLY FISH EVOLUTION AND MASS EXTINCTION

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*. The Ordovician once seemed to be almost barren of fish fossils, 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 (Figure 3.25), 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 six important groups of bony fishes, including their derivatives, the tetrapods.

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 Mid-Devonian.

During the Late Devonian, a time span of 15 Myr (377–362 Myr ago), further groups disappeared, most of the 'agnathans', including many conodont families, and placoderms, as well as most remaining acanthodians and some bony fishes. Other groups that survived into the Carboniferous seem to have been heavily depleted. Of the 70 families of fishes currently recognized as present in the Late Devonian (Benton, 1993a), 51 died out during the next 15 Myr, a total extinction rate of 73%, which is high by any standards. The extinctions seem to have been spread through the Late Devonian, but only 17 families (24%) survived into the Carboniferous. A multiphase Late Devonian extinction event also has been recognized among marine invertebrates such as corals, brachiopods and ammonoids, as well as phytoplankton. The Devonian fish faunas were replaced in the Carboniferous by new groups (see Chapter 7).

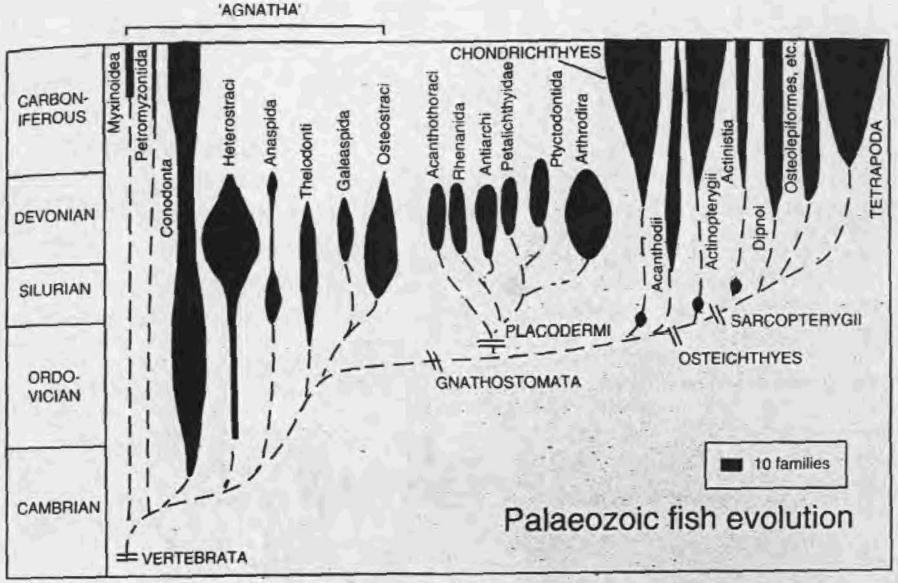


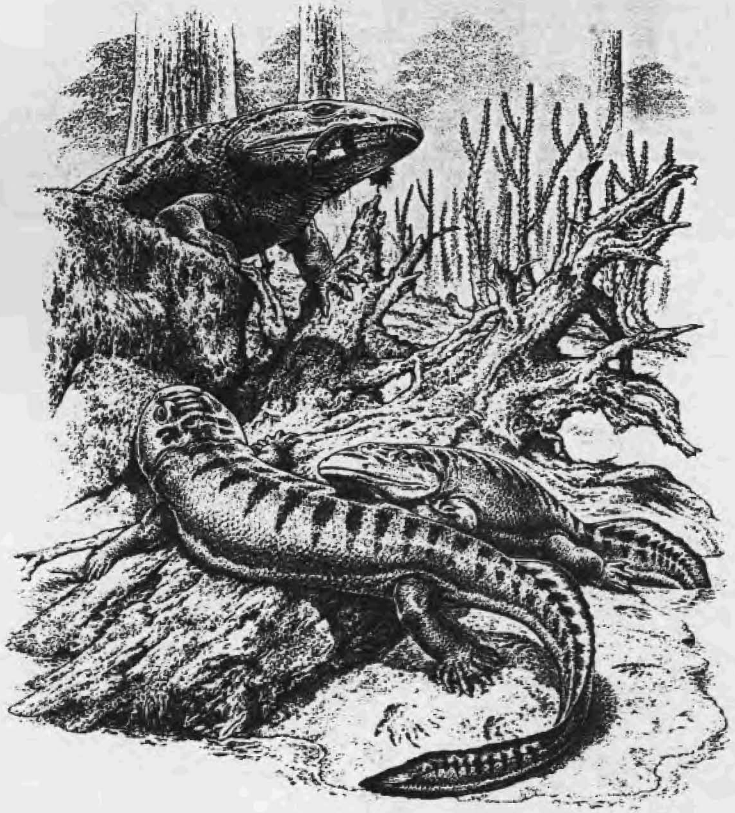
Fig. 3.25 The evolution of early and mid-Palaeozoic fishes. The pattern of relationships (indicated with dashed lines) is based on cladograms described above, and the 'balloon' shapes indicate the span in time of known fossils (vertical axis) and their relative diversity (horizontal axis).

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. Long (1995) is a well-illustrated, popular history of fishes. Aldridge *et al.* (1993) and Donoghue *et al.* (1998, 2000) are excellent overviews of current knowledge about the conodonts and the phylogeny of early vertebrates. Forey (1998) gives a full account of coelacanths and the living *Latimeria*, and the full story of its discovery is told by Weinberg (1999). Bemis *et al.* (1986) contains a number of papers about living and fossil lungfishes. There are good reviews of the relationships of sarcopterygians in Schultze and Trueb (1991), Ahlberg (2001) and Clack (2002c)

CHAPTER 4

The Early Tetrapods and Amphibians



KEY QUESTIONS IN THIS CHAPTER

1 What were the key challenges facing vertebrates when they moved on to the land?

2 Were the first tetrapods adapted to life on land or were they still swimmers?

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 What do sites of exceptional preservation tell us about early tadpoles?

6 How did the basal tetrapods evolve towards modern amphibians and reptiles?

INTRODUCTION

Vertebrates made a significant evolutionary move in the Devonian when the first **tetrapods** stepped on to the land. Dramatic new discoveries have filled in many details of the transition from fish to tetrapod. The basal tetrapods then radiated extensively during the Carboniferous and Early Permian, some as small semi-aquatic forms, but many as larger forms that fed on fishes and other tetrapods, and that could, in some cases, live fully terrestrial lives.

The basal tetrapods are often termed 'amphibians' in common with the living forms, frogs, salamanders and newts. The name amphibian ('both life') refers to the fact that the modern forms—frogs, newts and salamanders—live both in the water and on land, and it is assumed that many of the fossil forms 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, which arose in the Triassic and radiated thereafter.

In this chapter, the major anatomical and physiological changes that were necessary when a lobefin fish became a tetrapod are reviewed, and the evolution and biology of the extinct and living forms are described.

4.1 PROBLEMS OF LIFE ON LAND

The first tetrapods faced major problems in moving from the water on to the land. Air breathing was in fact not the key hurdle to cross, 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. One classic theory (e.g. Romer 1966) was that fishes moved on to land in order to escape from drying pools. The Devonian was supposedly a time of seasonal droughts, and the freshwater fishes probably found themselves often in stagnant and dwindling pools. The conclusion of this viewpoint is that terrestrial locomotion evolved as a means of staying in the water! This suggestion has been criticized as there is limited evidence for droughts, and because the theory would explain only moderate terrestrial adaptations, not the much-modified tetrapod limb for example. A simpler hypothesis is that vertebrates moved on to land 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 some group of organisms would exploit them sooner or later.

4.1.1 Support

A fish is buoyed up by the water and its body weight may be effectively zero. On land, however, the body is usually held up by 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.

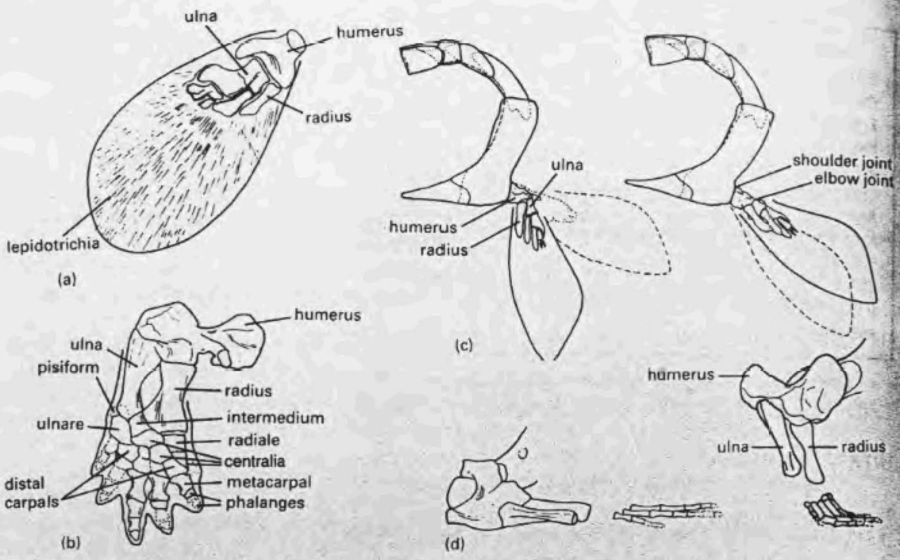


Fig. 4.1 The origin of tetrapod limbs and land locomotion: (a) pectoral fin of the tristichopterid fish *Eusthenopteron* showing interpreted identities of the bones; (b) equivalent forelimb of the basal tetrapod *Eryops*; (c) possible movements of the forelimb of *Eusthenopteron*; (d) step cycle of the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

4.1.2 Locomotion

Tetrapods move in a very different way from fishes in water. 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.

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 limb 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**) and 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 limbs point backwards and a little sideways, and the limb skeleton could swing back and forwards through only 20–25° (Andrews and Westoll, 1970a). 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; Shubin *et al.*, 2004). 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)) 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 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(b)).

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(c)), it eventually became grossly enlarged and firmly attached to the vertebral column in terrestrial tetrapods (Figure 4.2(d)). 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.

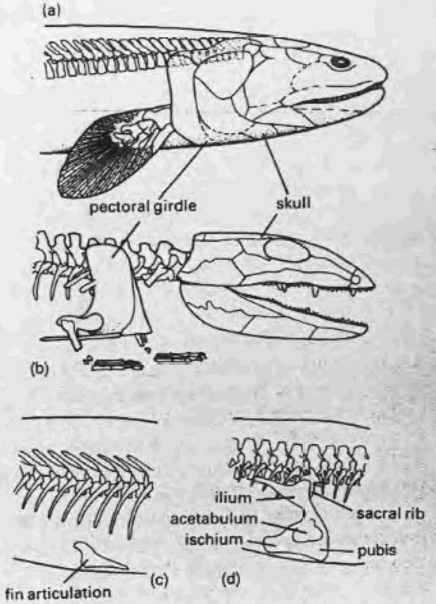


Fig. 4.2 The transition from tristichopterid fish (a, c) to basal tetrapod (b, d): (a) and (b) the separation of the skull from the shoulder girdle; (c) and (d) the enlargement of the pelvic girdle and its firm attachment to the vertebral column via the ilium and sacral rib. [Figures (a, c, d), after Stahl, 1974; (b) after Godfrey, 1989.]

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 p. 72), 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 — millepedes, 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 osteolepiforms 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. Perhaps the early tetrapods breathed partly, or mainly, by buccal pumping — this is suggested by their broad mouths and short, straight ribs.

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 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 p. 51).

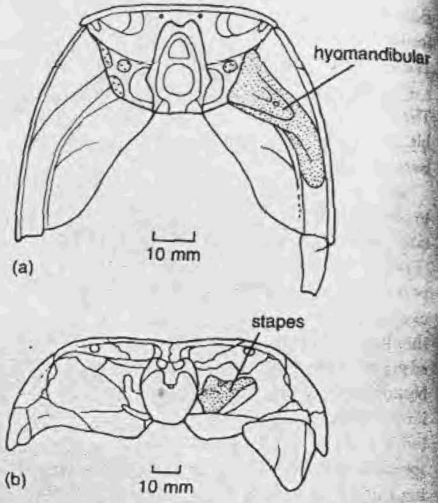


Fig. 4.3 Posterior views of the skulls of the sarcopterygian *Eusthenopteron* (a) and the tetrapod *Greererpeton* (b) to show the changing function of the fish hyomandibular, which acted largely as a supporting element, to the tetrapod stapes, which functions in transmitting sound vibrations in air from the tympanum to the brain. (Modified from Smithson, 1982, by permission of Academic Press Ltd, London.)

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 nostrils, and the early tetrapods risked desiccation. The earliest tetrapods probably remained close to fresh water, which they could drink in order to avoid this problem. Certain forms evolved semipermeable skin coverings that would have cut down water loss.

4.1.5 Reproduction

Living amphibians betray their ancestry in their mode of reproduction. Even highly terrestrial forms have to lay their eggs in water where the young hatch out as aquatic larvae, tadpoles. After some time in the water, breathing through gills, the tadpoles metamorphose into the adult form. Fossil tadpoles 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).

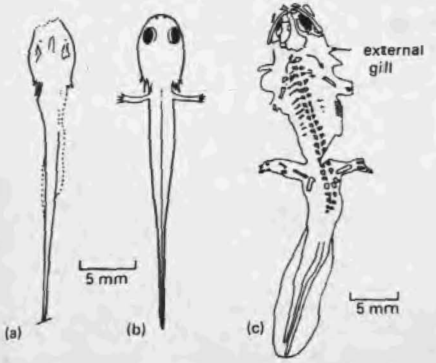


Fig. 4.4 Fossil 'tadpoles' of Carboniferous and Permian tetrapods; drawings of fossils from (a) France and (c) North America; (b) reconstruction of an intermediate stage. [Figures (a, b) after Boy, 1974; (c) after Milner, 1982.]

4.2 DEVONIAN TETRAPODS

Knowledge about Devonian tetrapods has increased dramatically since 1990. The oldest potential tetrapod remains are tantalizing: some ill-defined footprints from Australia, and isolated bones and footprints from different parts of the Old Red Sandstone continent. Some Late Devonian taxa, *Metaxygnathus* from Australia, *Elginerpeton* from Scotland and *Obruchevichthys* from the Baltic area, are close to the evolutionary transition from sarcopterygian fishes to basal tetrapods. In addition, unequivocal latest Devonian tetrapods have been reported from Russia (*Tulerpeton*), Latvia (*Ventastega*), China (*Sinerpeton*) and North America (*Hynerpeton*, *Densignathus*).

The most completely known Devonian tetrapods are *Acanthostega* and *Ichthyostega* from the latest Devonian of Greenland. Initially, attention focused on *Ichthyostega*, which had been described from nearly complete skeletal remains (Jarvik 1996). Since then, new specimens of *Acanthostega* have added greatly to knowledge of that animal (Coates and Clack, 1990, 1991; Clack, 1994, 1998a, 2002a, 2003a; Coates, 1996; Ahlberg and Clack, 1998). Discovering the relationships of these basal forms has been difficult (see Box 4.1).

4.2.1 Anatomy

The latest Devonian tetrapods all measure 0.5–1.2 m long, and they were carnivorous, presumably feeding on fishes. *Acanthostega* and *Ichthyostega* retain a fish body outline with a streamlined head, deep vertebrae and a tail fin (Figure 4.5(c, d)). Both forms 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.

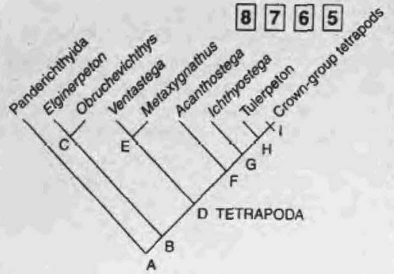
The skull of *Ichthyostega* looks generally like that of the sarcopterygians *Eusthenopteron* and *Panderichthys* in side view (Figures 4.5(a, b, d)), and it retains the buried lateral line canals. *Acanthostega*, however, has lost certain elements at the back that covered the gill and throat region, and the pectoral girdle is now separate. In dorsal view, it can be seen that *Acanthostega* (Figures 4.5(c), 4.6(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 sarcopterygian.

The pectoral girdle of *Acanthostega* (Figure 4.6(c)) is simplified in some respects when compared with that of a sarcopterygian. 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 4.6(d)) is a single plate, showing regions that correspond to the typical paired elements seen in

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. Panderichthyids seem to be the closest sarcopterygian relatives of tetrapods, sharing various features of the head and body that are not seen in osteolepiforms. The Tetrapoda, literally those vertebrates with 'four feet', certainly include *Ichthyostega* and *Ventastega* as basal forms. Their sister group, the elginerpetontids, may be the earliest tetrapods (Ahlberg and Milner, 1994) if their jaw and forelimb characters are confirmed.

There is disagreement about the relationships of the remaining Devonian tetrapods. In most analyses (e.g. Ahlberg and Milner, 1994; Coates, 1996; Laurin, 1998; Ruta *et al.*, 2003a, b), *Acanthostega* is seen as more basal than *Ichthyostega*, as shown here (see cladogram), whereas Ahlberg and Clack (1998) reversed the order. A further dispute concerns the location of the major split between the ancestors of modern amphibians and of amniotes. Coates (1996) located the split in the Late Devonian, placing *Tulerpeton* on the line to amniotes, a view that is not robust (Laurin, 1998). This simplifies our understanding of digital reduction: in Coates' (1996) scheme, reduction to five digits had to happen twice, once on the line to amphibians and once on the reptiliomorph line. In the scheme here, all the Devonian tetrapods are on the stem to later forms, and digital reduction happened once, between *Tulerpeton* and later tetrapods (Ruta *et al.*, 2003a, b). Here, it is assumed that all Devonian tetrapods fall along the line to a single clade of more derived tetrapods, following Ahlberg and Clack (1998) and Ruta *et al.* (2003a, b).



Cladogram showing postulated relationships of the basal tetrapods, based on Ahlberg and Clack (1998) and Ruta *et al.* (2003a, b), with some information from Ahlberg and Milner (1994) and Coates (1996). See Box 3.6 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**, flattened head with elongate snout, orbits on top of skull, external naris marginal, frontal bone present, body flattened, dorsal fin absent, enlarged ribs, humerus with anterior keel; **B**, 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; **C 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; **D TETRAPODA**, 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; **E**, coronoid fangs in tooth row; **F**, 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; **G**, 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; **H**, open lateral line system on most or all dermal bones, elongate scapula and distinct cleithrum, six or fewer digits, tail fin absent; **I**, five or fewer digits.

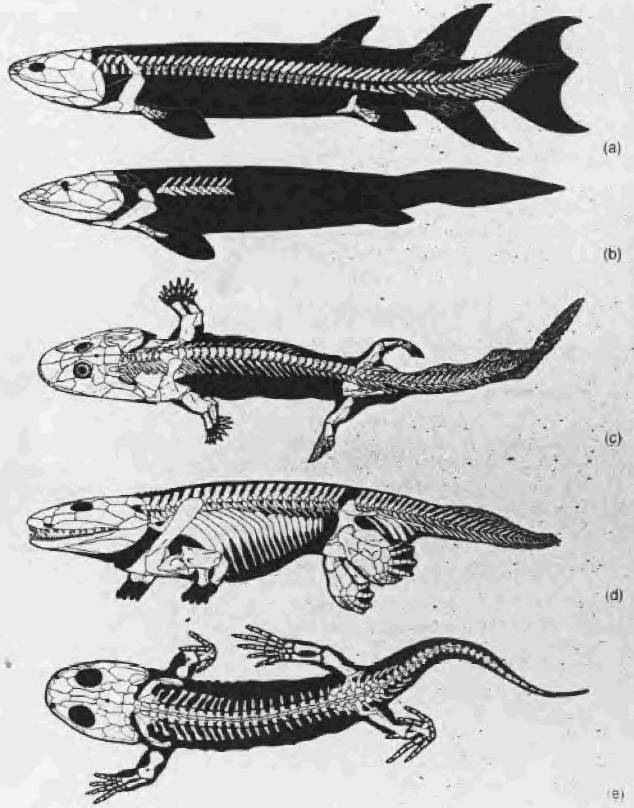


Fig. 4.5 Silhouette diagrams of tetrapod outgroups (a, b) and tetrapods (c–e): (a) *Eusthenopteron*; (b) *Panderichthys*; (c) *Acanthostega*; (d) *Ichthyostega*; (e) *Balanerpeton*. (Courtesy of Mike Coates.)

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 later tetrapods in most features, but recent work has shown that they are startlingly different in others. The arm of *Acanthostega*, for example (Figure 4.6(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 4.6(f)), and found that it had eight toes. *Ichthyostega* has seven toes,

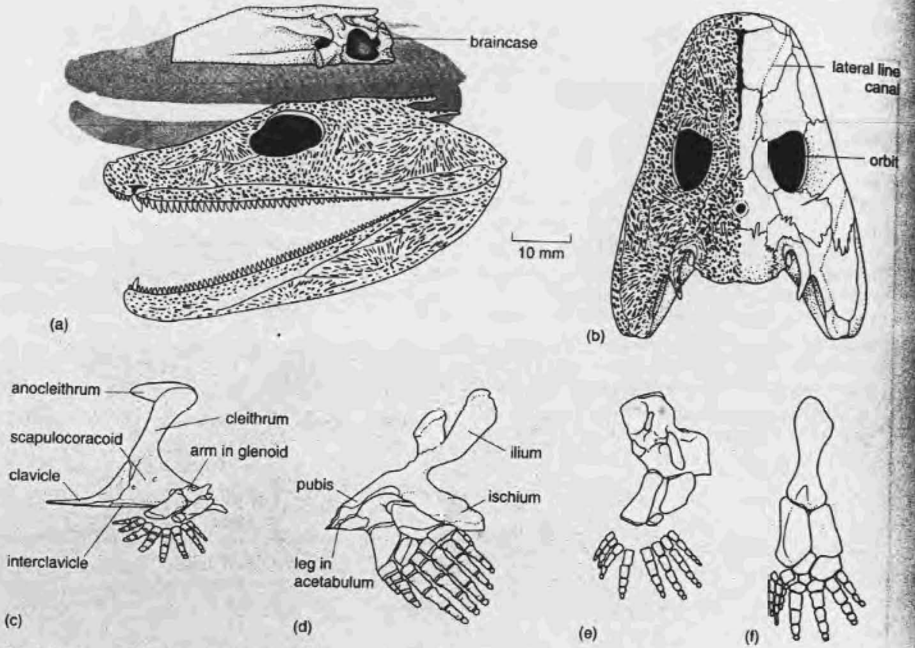


Fig. 4.6 The anatomy of *Acanthostega*: (a, b) skull in lateral view, with braincase (a) and dorsal view (b); (c) shoulder girdle and arm in lateral view; (d) pelvic girdle and leg in lateral view; (e) arm and hand in anterior view; (f) leg and foot of *Ichthyostega* in anterior view. [Figures (a, b), courtesy of Jenny Clack; (c–f), courtesy of Mike Coates.]

and *Tulerpeton* has six. Again, the remainder of 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 (see Box 4.2).

4.2.2 Modes of life

The Late Devonian tetrapods were clearly still aquatic, as is shown by the retention of a tail fin, a lateral line system and internal gills. The vertebral column was flexible, as in a fish, and *Ichthyostega* and *Acanthostega* 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 4.5 and 4.6(c, d)). These animals

BOX 4.2 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 (Shubin *et al.*, 1997; Coates *et al.*, 2002; Cohn *et al.*, 2002). At an early phase, the limb is represented simply by a limb bud, a small lateral outgrowth from the body wall. Limb growth is controlled by the *Hox* 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. Early in fish evolution, five of the 13 *Hox* genes, numbered 9–13, were co-opted to control limb bud development. Manipulation of embryos during three phases of development has shown how this works. In phase I, the stylopod in the limb bud sprouts, and this is associated with expression of the genes *HoxD*-9 and *HoxD*-10. 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 *HoxD*-9 to *HoxD*-13. 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 *HoxD*-10 to *HoxD*-13. Phases I and II have been observed in teleost fish development, but phase III appears to be unique to tetrapods.

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 an osteolepiform (see illustration (a)), the developmental axis presumably ran through the main bony elements, and additional bones, radials, developed in front of the axis (preaxial side). In tetrapods (see illustration (b)), 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, *HoxD*-9 is expressed in all five zones, *HoxD*-10 in the posterior four zones, down to *HoxD*-13 only in the posterior of the five. In the autopod, on the other hand, *HoxD*-13 is present in all zones, but *HoxD*-10 to *HoxD*-12 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 fore and aft. Since then, digital reduction has commonly occurred, down to four (frogs), three (many dinosaurs), two (cows and sheep), or one (horses) fingers and toes. In rare cases where there is a sixth digit (some large dogs, pandas) it is an outgrowth of the wrist or ankle bones.

Read more at http://www.press.uchicago.edu/books/gee/shubin2.html (the antero-posterior zonation of the limb bud and *Hox* gene mapping).

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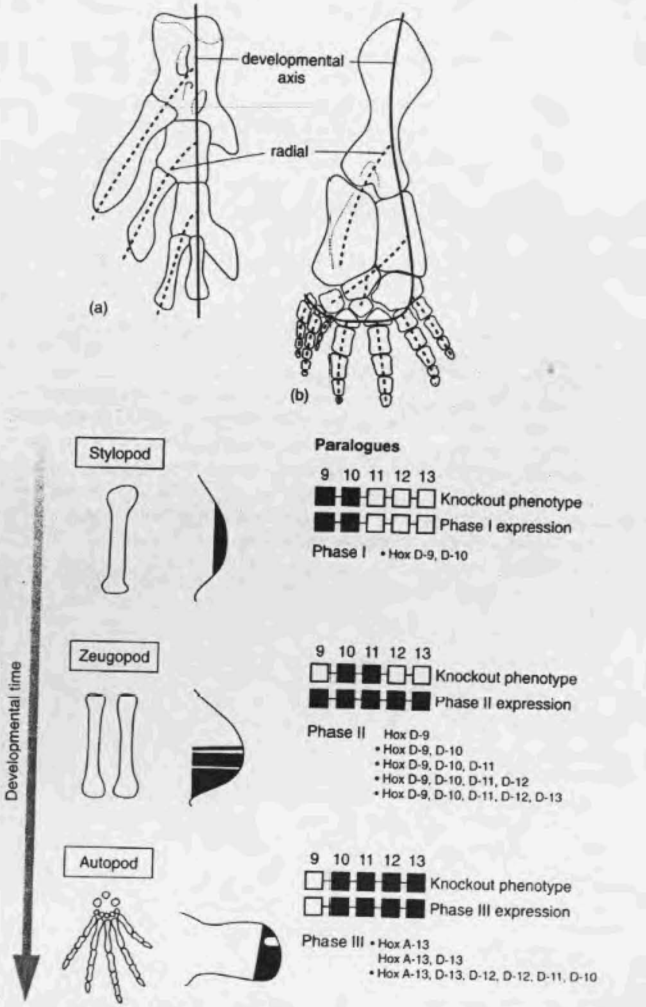


Tetrapod limb development. Developmental interpretation of the forelimbs of *Eusthenopteron* (a) and *Acanthostega* (b). The developmental axis (solid line) branches radial elements (dashed lines) in a preaxial (anterior) direction in both forms, and the digits of tetrapods condense in a postaxial direction. (c) The sequence of growth of a tetrapod limb bud, 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 *D*-9 to *D*-13. [(a, b) Modified from Coates and Clack, 1990; (c) based on information in Shubin *et al.*, 1997.]

could also probably waddle about on land, but the weight of the large skull and heavy ribcage of *Ichthyostega* probably meant that it had to rest its belly and head on the ground from time to time.

Acanthostega and *Ichthyostega* were found in sediments deposited by meandering rivers that flowed through forests of lycopods and low-growing ferns. The climate was monsoonal. Coates (1996) argues that *Acanthostega* lived most of the time in stagnant, vegetation-choked backwaters, emerging in damp conditions, but staying underwater in the dry season and gulping air at the surface. It walked largely underwater, stepping over vegetation, and kicking itself 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 perhaps largely aquatic. Coates and Clack (1995) argue 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). Perhaps fully terrestrial tetrapods emerged only 25 Myr later.

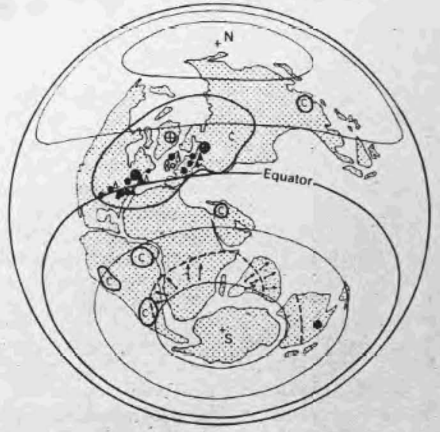


Fig. 4.7 Map of the world in Carboniferous times, showing the north (N) and south (S) poles, and the postulated continental positions. Coal forests are marked C, and the main amphibian localities are shown with symbols as follows: Late Devonian (⊖), Early Carboniferous (●), Late Carboniferous (○) for temnospondyls and anthracosaurs, and Early Carboniferous (▲) and Late Carboniferous (△) for 'lepospondyls' (mainly microsaurs). The dashed line over South America, southern Africa and India shows the known edge of Carboniferous glacial deposits, and the arrows show directions of glacier movement. (Modified from Pough *et al.*, 2002.)

4.3 THE CARBONIFEROUS WORLD

The main phases of early tetrapod evolution took place in the Carboniferous period (354–290 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 4.7). 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 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 millepedes (some up to 1.8 m long).

These new habitats opened up great possibilities for the early tetrapods, and they diversified extensively. Some forms continued to exploit freshwater fishes by becoming secondarily aquatic, whereas others became adapted to feed on the insects and millepedes. Early Carboniferous tetrapods were poorly known until recent 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.

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). Fossils were first found there in the 1830s, and include abundant plants and rare eurypterids, i.e. large aquatic arthropods. 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.

In 1984, Stan Wood, a professional collector, found tetrapod remains in a dry-stone wall that had been built from rocks taken out of an old quarry at East Kirkton. 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, millepedes), fishes (sharks, acanthodians, actinopterygians, a rhizodontid) and tetrapods (see illustration). The tetrapods include a broad-skulled temnospondyl, *Balanerpeton* (Figure 4.5(e)), and the baphetid *Eucritta*, both of which may have fed on arthropods, a limbless aistopod, and some anthracosaurs, *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.

Reconstructed scene at East Kirkton, Scotland, 340 million years ago, during the Early Carboniferous. The reptiliomorph *Westlothiana* sits on a rock contemplating the active volcanos in the distance, and the steaming hot springs closer by. Fragments of a dead millepede 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. (Courtesy of Mike Coates.)

Read more about the East Kirkton site and its tetrapod fossils at http://www.mwfossils.pwp.blueyonder.co.uk/Ekirk.htm and http://www.bbc.co.uk/worldservice/sci_tech/highlights/001219_blacklagoon.shtml

4.4 DIVERSITY OF CARBONIFEROUS TETRAPODS

The tetrapods radiated into about 40 families in the Carboniferous. Classically (e.g. Romer, 1966), the basal tetrapods were divided into three main groups, the Labyrinthodontia, characterized by the labyrinthodont tooth structure (shared with derived sarcopterygians, Figure 3.24e), large body size, and compound vertebrae; the Lepospondyli, characterized by small size, simple tooth structure, and fused spool-like vertebrae; and the Lissamphibia, the modern groups such as frogs and salamanders. It is clear, however, that the 'Labyrinthodontia' at least is not a monophyletic group, based on modern cladistic analyses (*see* Box 4.5).

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—whether they are basal forms, basal 'temnospondyls' or basal 'anthracosaurs'.

The colosteids, such as *Greererpeton* from the Lower 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 4.8). The skull is very different from that of anthracosaurs: the eyes are placed further forward, the skull and lower jaw are lower and flatter, and there is no otic notch. The lateral line canals are also well developed, suggesting an aquatic lifestyle.

Crassigyrinus from the Lower Carboniferous of Scotland (Clack, 1998b), was quite different (Figure 4.9(a–c)). It has a large skull 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 ear drum, 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 in the mouth. *Crassigyrinus* has minute forelimbs, a long narrow body and probably a flattened tail bearing a broad fin.

New finds from the earliest Carboniferous have revealed the existence of a further distinct clade, the Family Whatcheeriidae. *Whatcheeria* from Iowa, USA (Lombard and Bolt, 1995) and *Pederpes* from Scotland (Clack, 2002b) were both about 1 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 primitive and derived 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 4.9(c)), as in later tetrapods such as *Greererpeton* and *Proterogyrinus*, but the hand might still retain a tiny sixth finger. Functionally, though, these

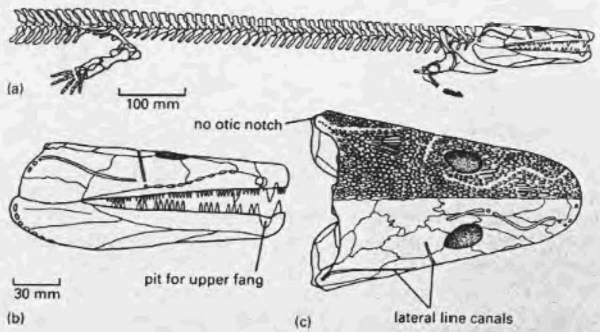


Fig. 4.8 The colosteid *Greererpeton*: (a) whole-body restoration; (b, c) skull in lateral and dorsal views, showing the sculpturing of the skull bones on the left side of the dorsal view (c) only. [Figure (a) after Godfrey, 1989; (b, c) after Smithson, 1982.]

were the first tetrapods adapted more to walking than swimming.

The baphetids, or loxommatids, are known from various Carboniferous localities (Beaumont, 1977; Clack, 2003b). *Megalocephalus* from the Early Carboniferous (Figure 4.10(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' set into the bones of 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**, the skeleton behind the head region, of any baphetids.

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 4.10(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. During this time, 170 genera in 40 families have been recorded. *Balanerpeton* from the Lower Carboniferous of Scotland (Figure 4.5(e)) and *Dendrerpeton* (Figure 4.11) from the Upper Carboniferous of Nova Scotia, Canada (Holmes *et al.*, 1998) have broader skulls than most anthracosaurs, and they have a rounded front margin, which is typical of temnospondyls. The palate of *Dendrerpeton* (Figure 4.11(b)) shows several characteristic temnospondyl features; a broad open space in the middle, the interpterygoid vacuity, which is very small in anthracosaurs, 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 strong, and there is a slender sound-conducting stapes, all of which suggest that *Dendrerpeton* was a largely terrestrial animal.

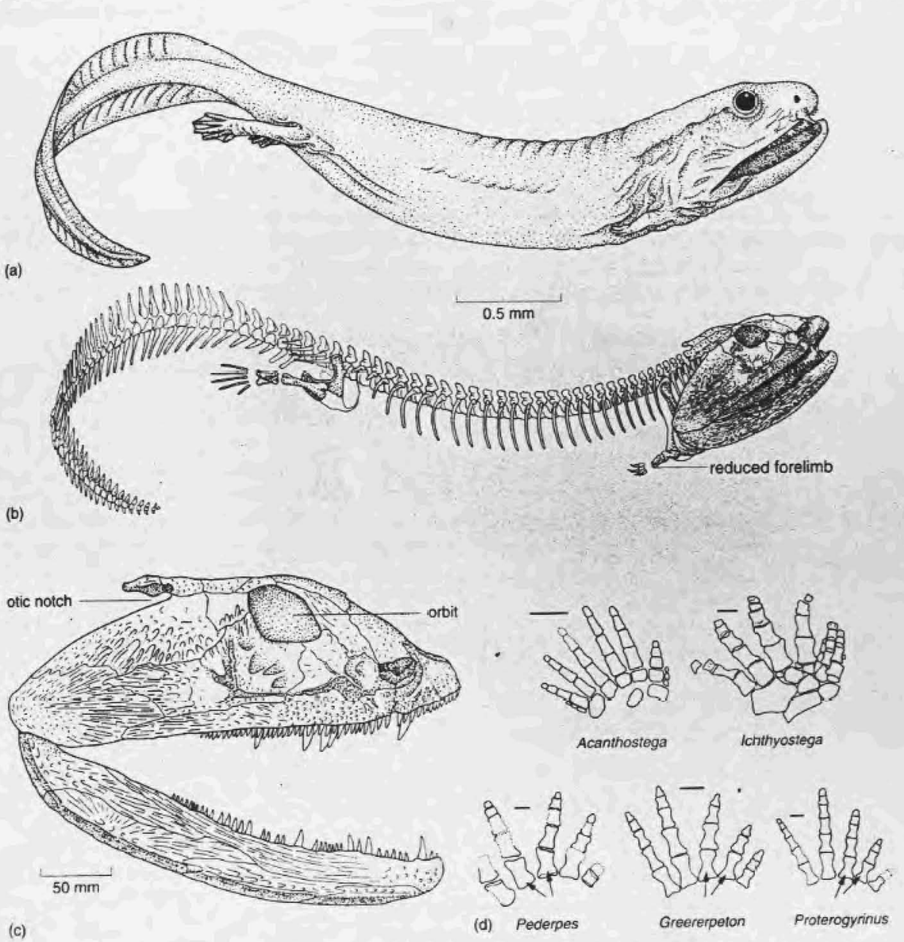


Fig. 4.9 Early Carboniferous tetrapods: (a–c) *Crassigyrinus*, whole-body restoration (a), skeleton (b) and skull and lower jaw in side view (c); (d) feet of various early tetrapods, including *Pederpes*. [Figures (a, b) courtesy of Mike Coates; (c, d) courtesy of Jenny Clack.]

4.4.3 Lepospondyli

The lepospondyls are generally small tetrapods that may form a clade (Carroll *et al.*, 1998), although this has been disputed. The microsaurs, the largest group of lepospondyls, from the Carboniferous and Early Permian animals (Carroll and Gaskill, 1978), were mainly terrestrial in habits. Recent cladistic analyses (e.g. Laurin, 1998; Anderson, 2001; Ruta *et al.*, 2003) show that the Microsauria is not monophyletic, with *Microbrachis* and some other close relatives falling in a clade that includes nectrideans and aïstopods. *Tudi-*

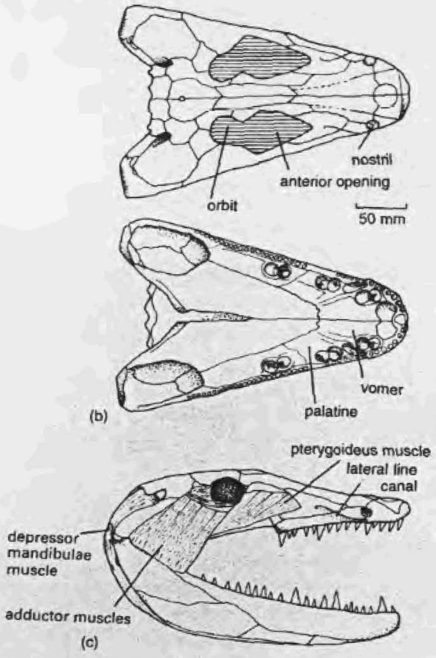


Fig. 4.10 The baphetid (loxommatid) *Megalocephalus*: (a, b) skull in dorsal and ventral views; (c) skull in lateral view, with a tentative reconstruction restoration of the main jaw muscles. [After Beaumont, 1977.]

tanus, an early form from the Upper Carboniferous of Ohio, USA (Figure 4.12(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 millepedes. Other microsaurs, such as *Microbrachis* (Figure 4.12(c)) from the Upper Carboniferous of the Czech Republic (see Box 4.4), 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 (A. C. Milner, 1980) were an aquatic group, known from the Late Carboniferous and Permian. Many, such as *Sauropleura* from the Upper Carboniferous of Europe and North America (Figure 4.13(a)), are newt-like in appearance, with very long flattened tails that were presumably used in swimming. The caudal vertebrae of these forms (Figure 4.13(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 Upper Carboniferous and Lower Permian of midwestern USA (Figure 4.13(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 of the squamosal and tabular bones, which normally form relatively small parts of the back corners of the tetrapod skull. Juveniles have almost no horns 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 4.13(f)). The function of the nectridean horns is more of a problem. Biomechanical studies (Cruickshank and Skews, 1980) on models of the head of *Diplocaulus* 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 Lower 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 4.14(a)). *Aornerpeton* has a light skull (Figure 4.14(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 4.14(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.

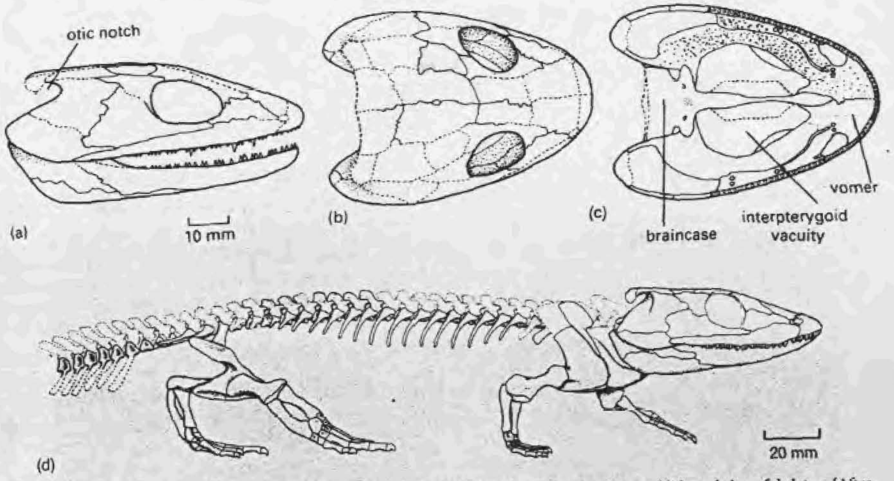


Fig. 4.11 The early temnospondyl *Dendrerpeton*: skull in (a) lateral, (b) dorsal and (c) ventral views; (d) lateral view of skeleton. (After Holmes *et al.*, 1998.)

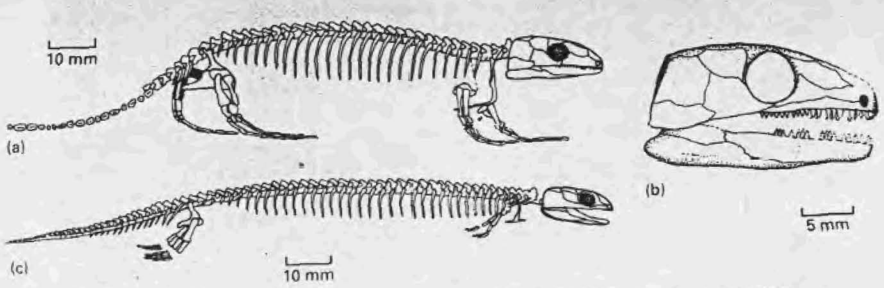
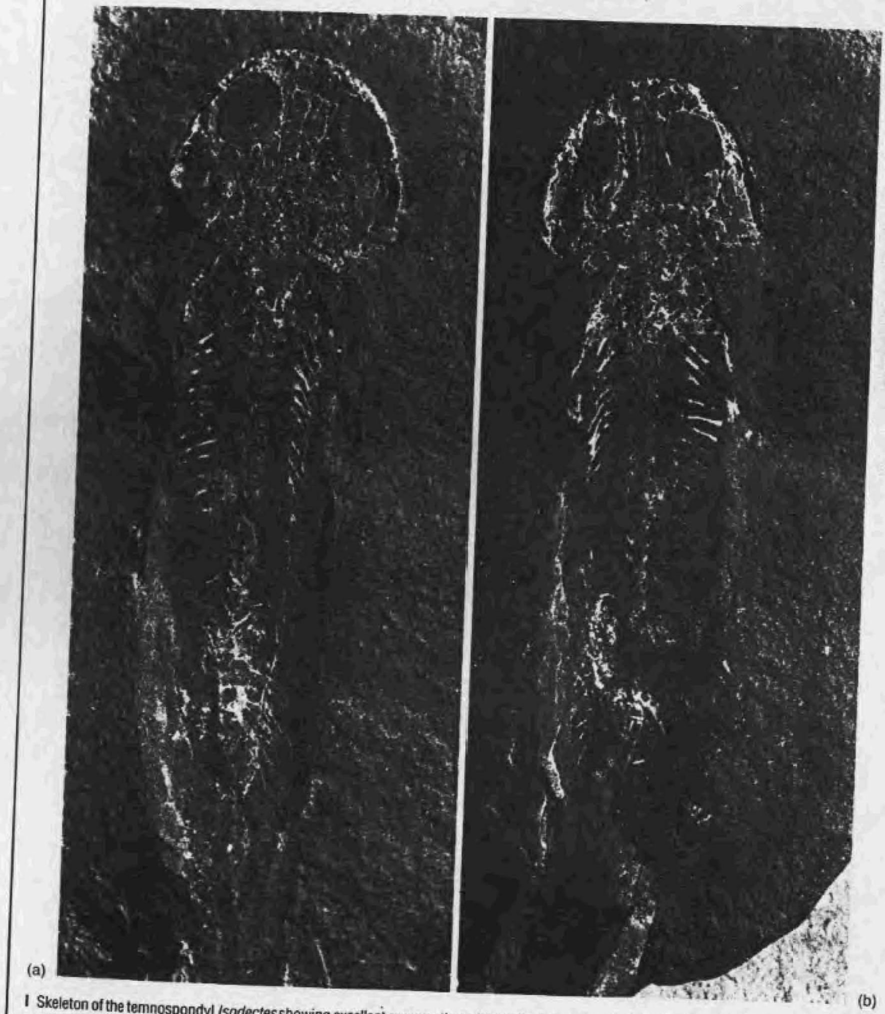


Fig. 4.12 Two microsaurs: (a, b) the terrestrial *Tuditanus*; and (c) the aquatic *Microbrachis*. (After Carroll and Gaskill, 1978.)

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 are 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.

BOX 4.4 THE NÝŘANY TETRAPOD COMMUNITIES

One of the most diverse faunas of Late Carboniferous tetrapods is from Nýřany, a small mining town in the Czech Republic. Fossil tetrapods were first reported from coal mines in this area in the 1870s (A. R. Milner, 1980), and since then many hundreds of specimens have been collected and studied.



I Skeleton of the temnospondyl *Isodectes* showing excellent preservation of the delicate bones, and of the body outline: (a) dorsal slab; (b) ventral slab of the same specimen. (The original specimen is 48 mm long and from the Upper Carboniferous of the USA; courtesy of Andrew Milner.)

The fossil tetrapods nearly all came from a 300-m-thick sequence of coalified shales and mudstones near the base of the Nýřany Gaskohle Series (Westphalian D, Late Carboniferous in age, c. 300 Myr ago). These sediments were laid down in an enclosed lake under gentle conditions, and they contain remains of plants such as *Calamites*, a giant horsetail that grew in up to 1 m of water. There are also rare fossils of small sharks, acanthodians and actinopterygians, as well as water-living arthropods and terrestrial millepedes. At the time of deposition of these beds, the lake was small and poorly aerated, and the sediments represent a fairly rapid accumulation.

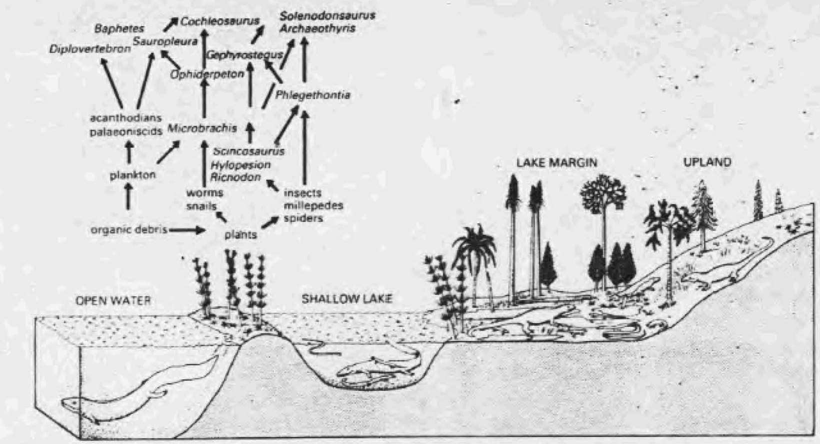
The fossil tetrapods are generally very well preserved, and they occasionally show traces of soft parts here, and in similar localities elsewhere (see illustration I). The cadavers seem to have sunk to the bottom rapidly, with relatively little decomposition and no scavenging. It may be that the animals swam a little too deep in the lake, and encountered anoxic bottom waters that suffocated them.

A census of most of the 700 or so Nýřany tetrapod specimens currently housed in museums around the world (A. R. Milner, 1980) shows that there were 20 species of basal tetrapods, with representatives of most major groups, and four species of amniotes. These fall into three main ecological associations (see illustration II).

1 Open-water/lacustrine assocation: three very rare forms from Nýřany, an eogyrinid anthracosaur and two baphetids presumably fished in the open water.

2 Terrestrial/marginal association: representatives of 13 species lived on or close to the shores of the lake. These include primitive temnospondyls, anthracosaurs, an aïstopod, four microsaurs and three primitive amniotes.

3 Shallow-water/swamp-lake association: the remaining seven tetrapods from Nýřany all appear to have been partially aquatic, and to have swum rapidly about in shallow parts of the lake where plants grew in the water and where the bottom was covered with plant debris. They include two temnospondyls, a branchiosaur, two nectrideans, a microsaur and an aistopod. Most of these presumably fed on small fishes or small tetrapods.



II A Late Carboniferous tetrapod community, based on the Nýřany locality, Czech Republic. Four main habitats are indicated, with representative vegetation and tetrapods, from left to right: open water (eogyrinid, *Baphetes*); shallow lake (*Ophiderpeton*, *Sauropleura*, *Microbrachis*, *Scincosaurus*); lake margin (*Gephyrostegus*, *Amphibamus*, *Aornerpeton*, *Ricnodon*, etc.); possibly upland (*Scincosaurus*). The food web on the left shows what eats what (the arrows run from the base of the food chains — the plants — through various invertebrates and fishes to the predatory tetrapods, and terminating at the top of the diagram with the 'top' carnivores that feed on other tetrapods). (Based on A.R. Milner, 1980 and other sources.)

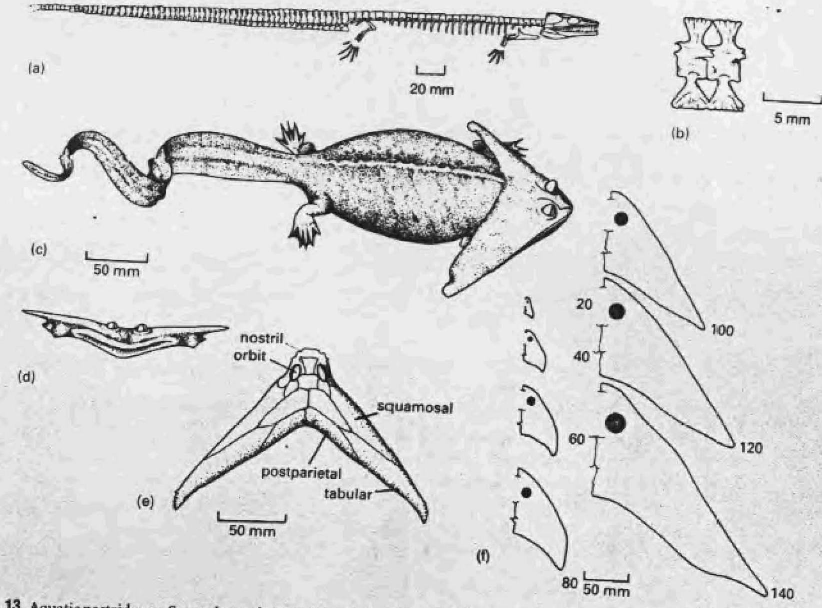


Fig. 4.13 Aquatic nectrideans, *Sauropleura*, skeleton (a) and caudal vertebrae in lateral view (b), and *Diplocaulus* (c–f): (c) life restoration; (d) anterior view of head; (e) dorsal view of skull; (f) sequence of growth stages, from juvenile (top left) to adult (bottom right), showing the growth of the projecting 'horns'. The numbers 20, 40, 60, etc., are measurements, in millimetres, of total body lengths. [Figures (a, b) after A.C. Milner, 1980; (c–e) after Cruickshank and Skews, 1980; (f) after Olson, 1951.]

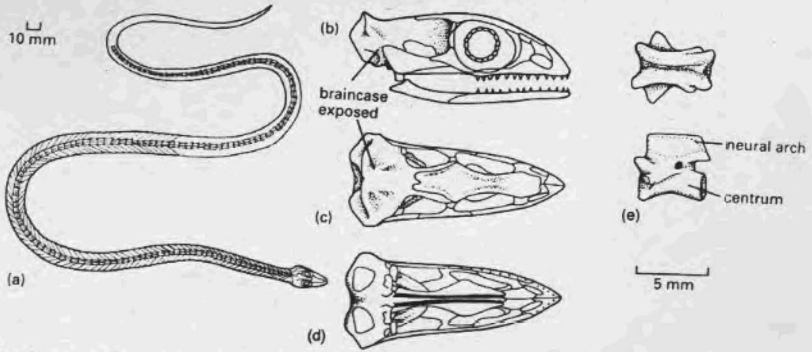


Fig. 4.14 The aïstopod *Aornerpeton*: (a) reconstructed skeleton; (b–d) skull in lateral, dorsal and ventral views; (e) trunk vertebra in dorsal (left) and lateral (right) views. (After Gregory, 1948, courtesy of the American Journal of Science.)

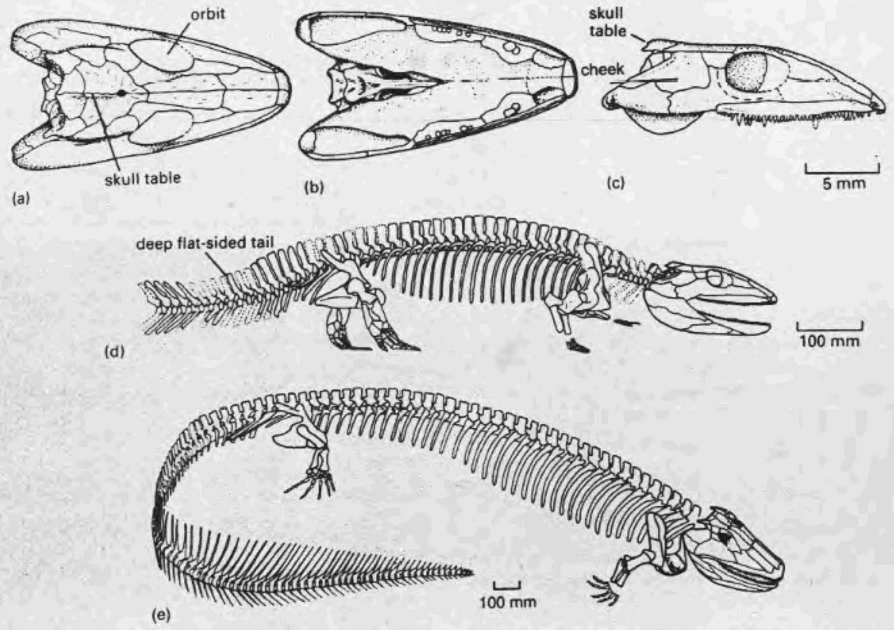


Fig. 4.15 The early anthracosaur *Proterogyrinus*: (a–c) skull in lateral, dorsal and ventral views; (d) restoration of the skeleton; (e) the anthracosaur *Pholiderpeton*. [Figures (a–d) after Holmes, 1984; (e) after Panchen, 1972.]

4.4.4 'Anthracosauria'

The anthracosaurs, a paraphyletic group that arose in the Early Carboniferous, and survived into the Early Triassic, include a number of moderate-sized fish-eaters. Some were apparently terrestrial, whereas others became secondarily adapted to life in the water.

Proterogyrinus from the Lower Carboniferous of West Virginia, USA (Holmes, 1984) and Scotland is about 1 m long and has an elongate skull (Figure 4.15(a–d)). The skull table, the square area at the back of the skull (Figure 4.15(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 anthracosaurs, such as *Pholiderpeton* from the Upper 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 4.15(e)).

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

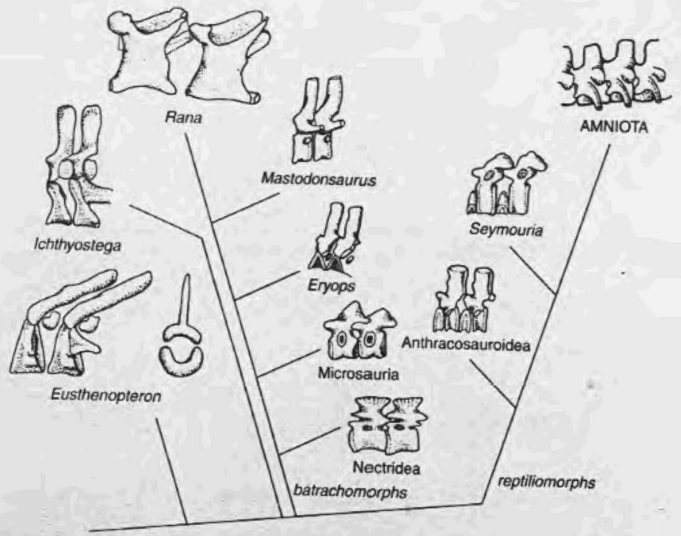


Fig. 4.16 Divergent evolution of the vertebrae in batrachomorphs, in which the intercentrum comes to dominate, and in lepospondyls and reptiliomorphs, where the pleurocentrum dominates. Examples of vertebrae from key taxa are shown around a simplified phylogenetic tree. (Based on various sources.)

a **neural arch** above (Figure 4.16). Then, in the early evolution of tetrapods, the pleurocentrum became the main element of the vertebra in reptiliomorphs and amniotes, and the intercentrum became the main element in temnospondyls and lissamphibians.

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 lies in front of the smaller pleurocentrum, composed of two short elements, one on each side. In 'anthracosaurs', the intercentrum and pleurocentrum 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. In temnospondyls, on the other hand, the intercentrum expands and the pleurocentrum reduces to a small wedge.

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 pleucrocentrum 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.

4.5 TEMNOSPONDYLS AND REPTILIOMORPHS AFTER THE CARBONIFEROUS

Several of the major Carboniferous lineages of tetrapods survived into the Permian (290–251 Myr ago) and beyond. These include groups such as the Anthracosauria, Aïstopoda, Nectridea and Microsauria, most of which died out by the end of the Early Permian, as well as the Temnospondyli, which lasted much longer, and two groups that were typically Permian, the Seymouriamorpha and the Diadectomorpha. These last three groups will be described now.

4.5.1 Temnospondyli: Permian to Cretaceous history

The temnospondyls radiated extensively after the Carboniferous, splitting into some 30 lineages (Yates and Warren, 2000). 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 Lower Permian of North America (Figure 4.17(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 4.17(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 Upper Carboniferous and Lower Permian of central Europe in particular. These small animals, 50–100 mm long, show larval characters (Figure 4.17(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 (1972) has concluded that, while some may be larvae (cf. Figure 4.4), most are in fact paedomorphic adults, sexually mature animals with juvenile bodies (see p. 12). The anatomy of the *Branchiosaurus* skull in particular (Figure 4.17(d)) shows so many synapomorphies with the dissorophids (Figure 4.17(b)) that Milner (1982) has interpreted the branchiosaurs as a paedomorphic sister group.

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; Shishkin *et al.*, 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 4.17(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 4.17(g)) was common in the Lower 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. The plagiosaurs, such as *Plagioscutum* (Figure 4.17(h)), had remarkably short, broad skulls and reduced limbs, and they were highly aquatic. Until 1980, it was thought that the last temnospondyls died out at the end of the Triassic, but two families, the Chigutisauridae and Brachyopidae, survived much later. An Early Jurassic chigutisaurid was reported from Australia in 1983, then a Mid-Jurassic brachyopid from China in 1985, then 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, but the temnospondyls were distinctly rare after the Triassic.

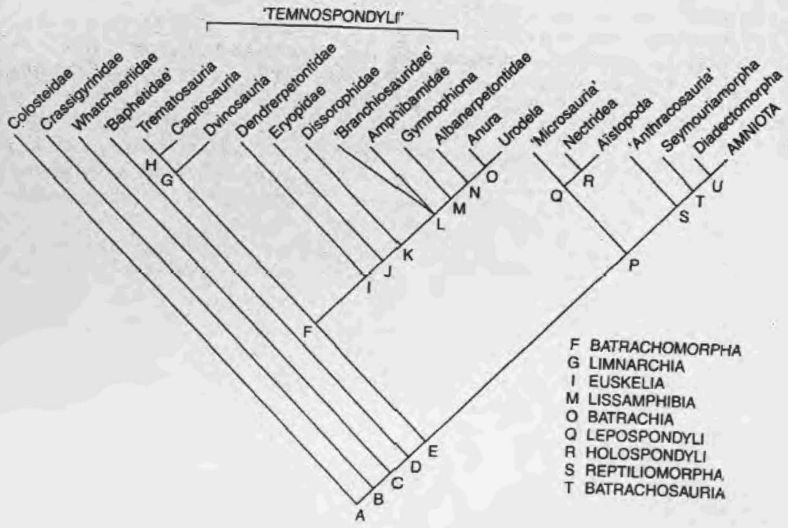
4.5.2 Seymouriamorpha

The seymouriamorphs are a small group of terrestrial and aquatic reptiliomorphs. *Seymouria* from the Early

BOX 4.5 RELATIONSHIPS OF THE BASAL TETRAPODS

The first cladistic analyses of basal tetrapods (e.g. Panchen and Smithson, 1988) showed that the classic division into Labyrinthodontia *for the larger ones, and* Lepospondyli for the smaller ones, did not work. The trees all showed that some or all of the Late Devonian tetrapods were outgroups to a major tetrapod clade that split two ways, with one line leading ultimately to the lissamphibians (frogs, salamanders, caecilians) and the other to amniotes ('reptiles', birds, mammals).

Controversial issues since 1988 have concerned the content of each of those lines. Panchen and Smithson (1988), Milner (1993), Ahlberg and Milner (1994) and others found that temnospondyls, microsaurs and nectrideans are closer to lissamphibians than to amniotes, and that anthracosaurs, seymouriamorphs and diadectomorphs are basal outgroups of Amniota. Laurin (1998) and Anderson (2001), *on the other hand, reinstated* Lepospondyli as a valid clade, and proposed they were a sister group to Lissamphibia, and moved the temnospondyls, anthracosaurs and seymouriamorphs to the stem, lying below the split between the amniote and the lissamphibian line.



A thorough new analysis (Ruta *et al.*, 2003a, b) confirms aspects of both views (see cladogram). Temnospondyls lie on the line to lissamphibians, as discovered by Panchen and Smithson (1988), and the Lepospondyli is indeed a valid clade and lies on the amniote line, as argued by Laurin (1998) and Anderson (2001). *But the lissamphibians return to the temnospondyl side,* and are not grouped with the lepospondyls, as Laurin (1998) and others have argued.

From the base, there are some stem-group taxa (Crassigyrinidae, Whatcheeriidae, Baphetidae), and then a major *split* into a batrachomorph clade, or the 'true' amphibians, and a reptiliomorph clade, or 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.*

The other line consists of lepospondyls (microsaurs, nectrideans and aïstopods) and reptiliomorphs. The Reptiliomorpha are characterized by changes in the snout region and in the foot. The paraphyletic 'anthracosaurs', the seymouriamorphs and the diadectomorphs form successively closer outgroups to the Amniota (= reptiles + birds + mammals).

For more information, go to http://tolweb.org/tree?group=Terrestrial_Vertebrates&contgroup=Sarcopterygii, where a series of pages take you through an alternative cladogram of basal tetrapods, based on the work of Laurin (1998). Do not be confused *by his rather heterodox use of group names* such as 'Amphibia, 'Anthracosauria' and 'Tetrapoda'.

Cladogram showing the relationships of the major groups of basal tetrapods, based on Ruta *et al.* (2003a), with divisions of 'Temnospondyli' from Yates and Warren (2000). *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**, five or fewer digits; **B**, orbits neither round nor elliptical, tabular does not contact squamosal, large scapular blade; **C**, anterior palatal vacuity absent, humerus shorter than the length of two and a half mid-trunk vertebrae; **D**, occipital condyles present, notochord excluded from braincase in adult, ectepicondylar foramen in humerus absent; **E**, lateral line system on skull roof absent, mandibular canal absent, *ventral humeral ridge absent;* **F**, *exposure of posterior* coronoid in lateral view, entepicondylar foramen absent; **G BATRACHOMORPHA**, parasymphysial plate absent, radius approximately as long as ulna, no more than four digits in hand; **H LIMNARCHIA**, ectopterygoid tooth row, maxilla sutures with vomer, denticles on vomers absent, interclavicle elongated; **I**, double occipital condyles with no contribution from basioccipital, denticle field on all three coronoids absent, tooth row on posterior coronoid; **J EUSKELIA**, postparietals wide, large *plate-like septomaxilla, short posterior skull table, intertemporal* absent, basicranial articulation fused and immobile, fewer than 23 presacral vertebrae, entepicondylar foramen absent; **K**, maxilla enters orbit margin, narrow interorbital bar, longest trunk ribs poorly ossified short rods, slender and elongate humerus; **L**, skull table very short, ectopterygoid reduced or absent, palatine poorly ossified, palatine without fangs, reduced interclavicle; **M LISSAMPHIBIA**, pedicellate teeth, teeth bicuspid or multicuspid, supratemporal absent, tabular absent, pineal foramen absent, two *coronoids absent;* **N**, *postorbital absent,* postfrontal absent, coronoids absent, splenials absent, surangular absent; **O BATRACHIA**, jugal absent, ossified opercular bone in oval window of middle ear, fewer than 20 presacral vertebrae, pubis unossified; **P**, premaxillae less than two-thirds of skull width, parietal-tabular contact, vomers elongate and strip-like, tarsus with L-shaped proximal element; **Q LEPOSPONDYLI**, supratemporal absent, stapedial foramen absent, vertebrae consist of cylindrical pleurocentra only, neural arches and centra fuse *indistinguishably early in ontogeny, atlantal intercentrum* absent; **R 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; **S REPTILIOMORPHA**, premaxillae less than half of skull width, vomers taper forwards, phalangeal formula of foot 2.3.4.5.4–5; **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**, postparietal and tabular entirely in occiput, supraoccipital present, first coronoid absent, sacrum with two vertebrae.

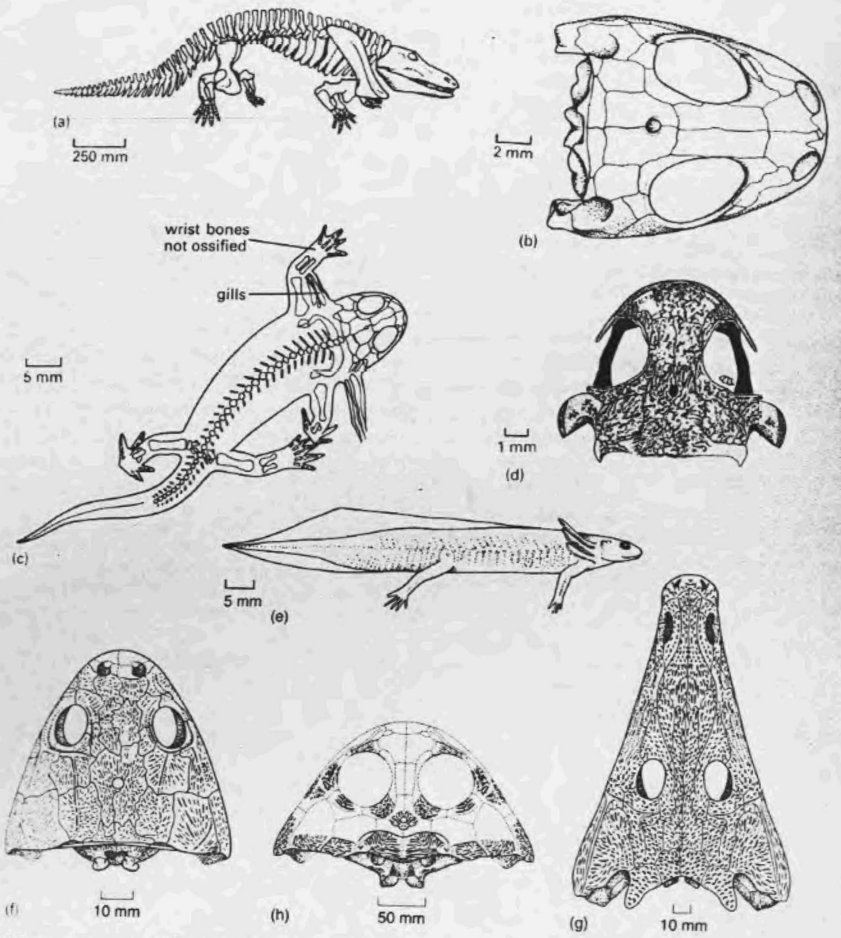


Fig. 4.17 Diverse temnospondyls from the Permian (a–e) and Triassic (f–h): (a) *Eryops*; (b) dorsal view of skull of *Doleserpeton*; (c, d) the neotenous branchiosaurid *Apateon*, showing tadpole-like characters, such as gills and poorly ossified bones: (c) reconstructed skeleton; (d) skull in dorsal view; (e) reconstructed branchiosaur; (f) the dvinosaur *Tupilakosaurus*; (g) the capitosaur *Benthosuchus*; (h) the plagiosaur *Plagioscutum*. [Figure (a) after Gregory, 1951; (b) after Bolt, 1977; (c, d) based on Boy, 1972; (e) based on A. R. Milner, 1981; (f–h) courtesy of Mikhail Shishkin.]

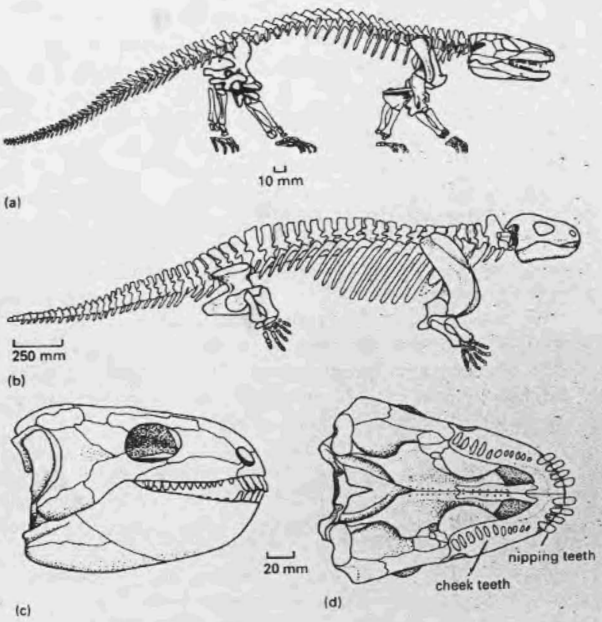


Fig. 4.18 Advanced reptiliomorphs: (a) *Seymouria* skeleton; (b–d) *Diadectes*: (b) skeleton; (c) skull in lateral and (d) ventral views, showing the herbivorous adaptations of the dentition. [Figure (a) after White, 1939; (b) altered from Romer, 1944; (c, d) after Carroll, 1969b.]

Permian (Figure 4.18(a)) was a 600-mm-long active terrestrial animal that lived in fair abundance in the southern midwestern USA and Germany (Berman *et al.*, 2000b). It had powerful limbs, and the body was held higher off the ground than in most tetrapods so far considered. Aquatic seymouriamorphs from the Upper Permian of Russia, the kotlassiids, had broad skulls and fed on fishes. The discosauriscids, another seymouriamorph group, were small, 400 mm long, terrestrial forms, known from the Upper Carboniferous to Upper Permian of Europe and Asia.

4.5.3 Diadectomorpha

The diadectomorphs, Late Carboniferous and Early Permian terrestrial forms, are reptiliomorphs, very close to the origin of the amniotes (see Box 4.5). *Diadectes* from the western USA and Germany (Figure 4.18(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.

4.6 EVOLUTION OF MODERN AMPHIBIANS

Modern amphibians, the Lissamphibia, are diverse, being represented by more than 4000 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 Mid-Jurassic to the Miocene of Europe, and most widely represented by *Albanerpeton* from North America (Gardner, 2001; McGowan, 2002). *Celtedens*, an early form, about 70 mm long, from the Upper Jurassic and Late Cretaceous of Europe (Figure 4.19(a,b)), looks just like a salamander, and it is no wonder that the albanerpetontids 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 4.19(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 vertebrae of the neck are most unusual (Figure 4.19(b))—there are effectively only two of them, the atlas and axis, and these fuse directly with the first vertebra of the trunk. The reduction of the cervical vertebrae to almost nothing in albanerpetontids presumably stiffened the neck, and it may have been an adaptation for burrowing.

4.6.2 Anura (Salientia)

Frogs and toads are so distinctive in their anatomy that they are immediately recognizable. The skeleton (Figure 4.19(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 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 lined with small gripping teeth for processing insects or other prey.

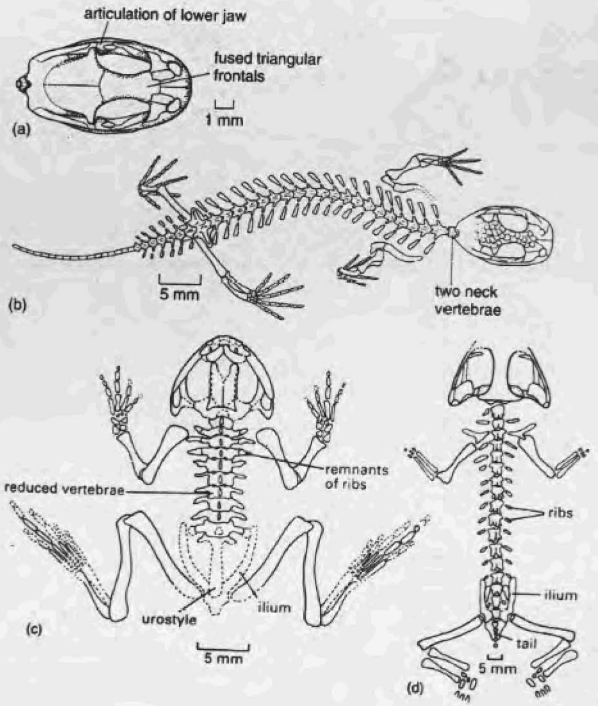


Fig. 4.19 Albanerpetontids (a, b) and early frogs (c, d): (a, b) skull and skeleton of the Cretaceous *Celtedens*; (c) the Jurassic *Vieraella*, showing most of the adaptations of modern frogs; (d) the first frog *Triadobatrachus*. [Figures (a, b) courtesy of Jerry McGowan; (c, d) after Estes and Reig, 1973, by permission of the editor, copyright © 1973 by the Curators of the University of Missouri.]

The specialized characters of the frog skeleton can be detected even in one of the earliest forms, *Vieraella* from the Lower Jurassic of South America (Figure 4.19(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 23 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; Sanchiz, 1998). *Triadobatrachus* from the Lower Triassic of Madagascar (Figure 4.19(d)) is the oldest known frog: it has a reduced number of vertebrae, reduced ribs, elongate ilia, and a frog-like skull.

4.6.3 Urodela (Caudata)

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. The fossil record of salamanders, like that of frogs, is patchy (Estes, 1981), but modern families are now known from the Mid-Jurassic onwards (Gao and Shubin, 2003). One of the oldest well-preserved salamanders, *Karaurus* from the Upper Jurassic of Kazakhstan (Figure 4.20(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 4.20(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. The teeth of salamanders bear two cusps (Figure 4.20(c)).

4.6.4 Gymnophiona

The Gymnophiona, or caecilians, are strange little amphibians that look like earthworms (Figure 4.20(d)). They have lost their legs, hence an alternative name, apodans (literally 'no feet'), and they live by burrowing in leaf litter or soil, or swimming in ponds, in tropical parts of the world. The skull is solidly built, and can be used for burrowing by battering the soil with the snout (Figure 4.20(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 and Walsh, 1993). *Eocaecilia* (Figure 4.20(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 orders

Most biologists regard the three modern groups as members of a clade Lissamphibia (e.g. Bolt, 1977; Milner, 1988, 1993; Ruta *et al.*, 2003). All of them share teeth that are both bicuspid (two-cusped) and **pedicellate** (Figure 4.20(c)), in other words, the base and crown are separated by a zone of fibrous tissue. The ancestry of the Lissamphibia, according to this analysis, is placed among the temnospondyls (see Box 4.5). The amphibamid *Doleserpeton* (Figure 4.17(b)) has pedicellate teeth (Bolt, 1977), and other temnospondyls, such as the branchiosaurs and dissorophids, show other lissamphibian features. An alternative view has been to seek the origins of the lissamphibians among the lepospondyls, and even to see each of the three modern

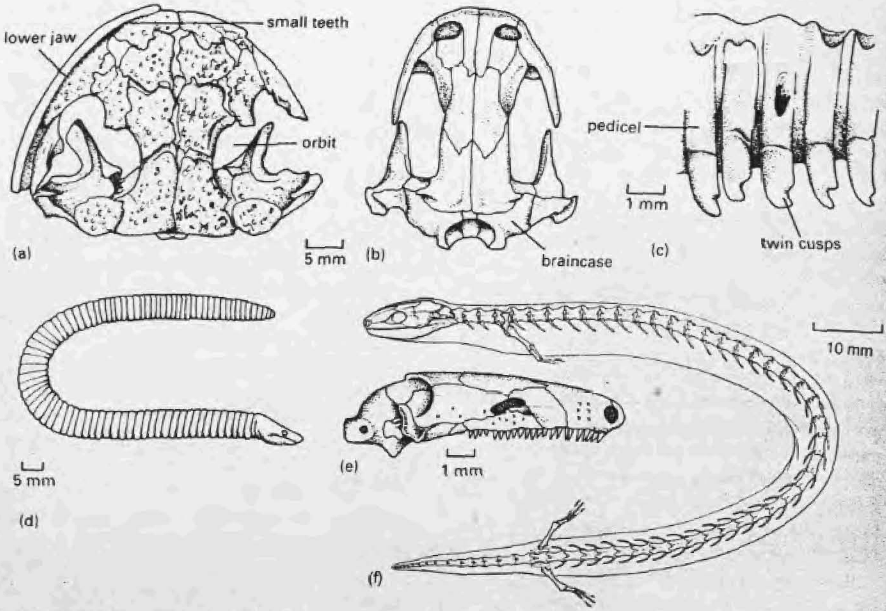


Fig. 4.20 Salamanders and caecilians: (a) dorsal view of the skull of the Jurassic salamander, *Karaurus*; (b) similar view of a modern salamander skull; (c) pedicellate teeth of the salamander *Amphiuma*; (d) a typical modern caecilian; (e) skull of the modern caecilian *Grandisonia*; (f) reconstructed skeleton of the oldest caecilian, *Eocaecilia*. [Figure (a) after Ivakhnenko, 1978; (b, c), altered from Romer and Parsons, 1986; (d, e) modified from Pough *et al.*, 2002; (f) courtesy of Farish Jenkins, Jr.]

orders as having a separate origin among the lepospondyls (e.g. Carroll, 1987, 1998; Laurin, 1998; Anderson, 2001). Lepospondyls and lissamphibians do indeed share many features, but probably largely as a result of miniaturization and loss of elements.

Relationships within Lissamphibia have been equally controversial. Generally, frogs and salamanders are paired as sister groups, together termed the Batrachia, with gymnophionans as an outgroup (see Box 4.5). Hitherto, the albanerpetontids had been regarded as rather odd salamanders, but new studies (Gardner, 2001; McGowan, 2002) show they are probably an outgroup to the Batrachia, but the gymnophionans remain as a basal outgroup within Lissamphibia. Molecular results so far are limited. Feller and Hedges (1998) compared the DNA sequences of four mitochondrial genes, and found a sister-group relationship of salamanders and caecilians, with frogs as the outgroup. This contradicts the more usual pairing of frogs and salamanders. A study based on the complete mitochrondrial genome of a representative of each group (Zardoya and Meyer, 2001b), however, confirms the traditional Batrachia (frogs + salamanders) grouping.

The pattern of evolution of the basal tetrapods (Figure 4.21) shows a major radiation in the Early Carboniferous, with new reptiliomorph and temnospondyl groups appearing in the Late Carboniferous and Early Permian. The temnospondyls continued radiating in the Triassic and dwindled through the Jurassic, whereas the reptiliomorphs had by then long made the transition fully to being amniotes. The modern amphibian groups probably arose in the Triassic, but scattered fossils are known only in the Jurassic and Cretaceous, before a major expansion in the Cenozoic.

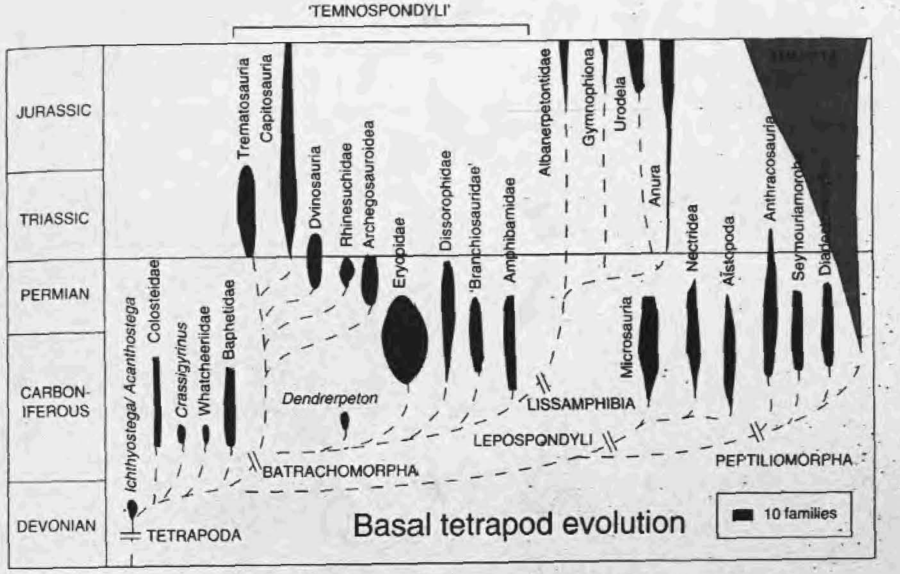


Fig. 4.21 Evolutionary tree showing the major basal tetrapod groups, their known fossil records (vertical scales), postulated relationships (dashed lines; based on cladogram in Box 4.5), and relative diversity (width of 'balloon').

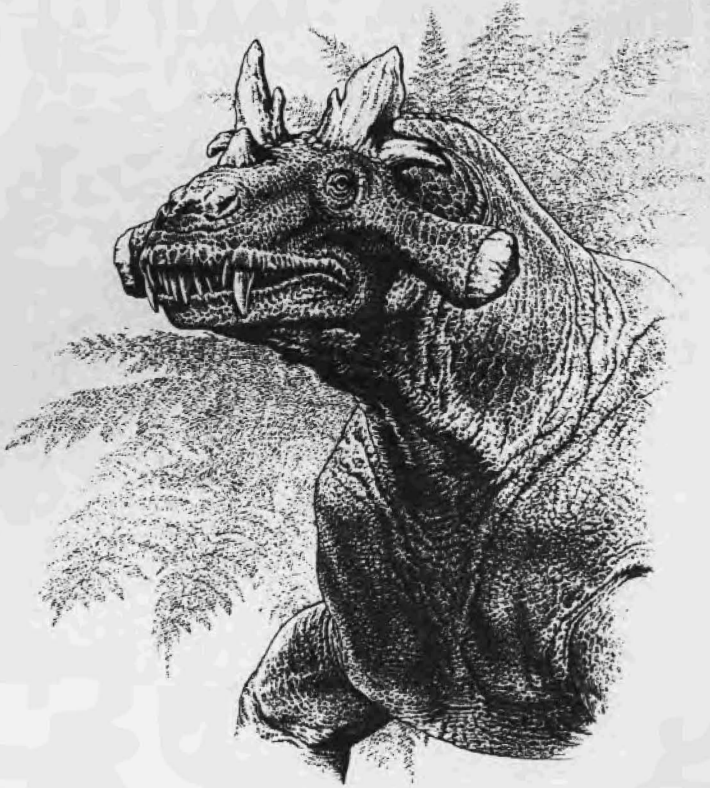
4.7 FURTHER READING

The biology of amphibians is outlined by Duellman and Trueb (1994). Heatwole and Carroll (2000) provide a detailed overview of basal tetrapods and fossil amphibians. Zimmer (1999) and Clack (2002c) 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.

These web sites offer fascinating glimpses of the excitement of current work on basal tetrapods: http://tolweb.org/tree?group=Terrestrial_Vertebrates&contgroup=Sarcopterygii, the 'Tree of Life' pages about basal tetrapods, and with links on many of the important Palaeozoic taxa. http://www.palantir.fsnet.co.uk/ and http://hometown.aol.com/darwinpage/tetrapods.htm offer overviews of recent work on basal tetrapods by Jenny Clack and her team; and http://www.carlzimmer.com/water_1.html presents excerpts from Zimmer (1999). Full three-dimensional details of the anatomy of the living coelacanth *Latimeria* are at http://digimorph.org/specimens/Latimeria_chalumnae/whole/.

CHAPTER 5

The Evolution of Early Amniotes



KEY QUESTIONS IN THIS CHAPTER

1 How did tetrapods complete their adaptation to life on land?
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 dominant Permian synapsids?
6 Are turtles diapsids or anapsids, and why do the fossils and molecules offer opposing evidence?
7 How did the tetrapods fare in the end-Permian mass extinction, when as many as 96% of species were wiped out?

INTRODUCTION

During the Late Carboniferous, the temnospondyls and anthracosaurs dominated most terrestrial landscapes, especially the damp forests. Small lizard-sized tetrapods were also in existence, creeping in and out of the vegetation in drier areas, in search of insects and worms. They laid eggs that did not have to hatch in water. These were the first **amniotes**, and they included the ancestors of all subsequent major tetrapod groups (i.e. reptiles, birds and mammals) that were to dominate Earth from Permian times onwards. These early amniotes are generally called *reptiles*, although the traditional 'Class Reptilia' is paraphyletic as it excludes the birds and mammals, descendants of these early forms.

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 dominated during the better-known ages of the dinosaurs and of the mammals.

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

The oldest amniotes are *Hylonomus* and *Paleothyris* from the mid-Carboniferous (310 and 300 Myr ago, respectively) of Nova Scotia (Carroll, 1964, 1969a). 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. The outer covering is perforated by two large orbits and two nostrils. The array of bones in the skull of *Paleothyris* is similar to that of advanced reptiliomorphs (cf. Figure 4.18), 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.

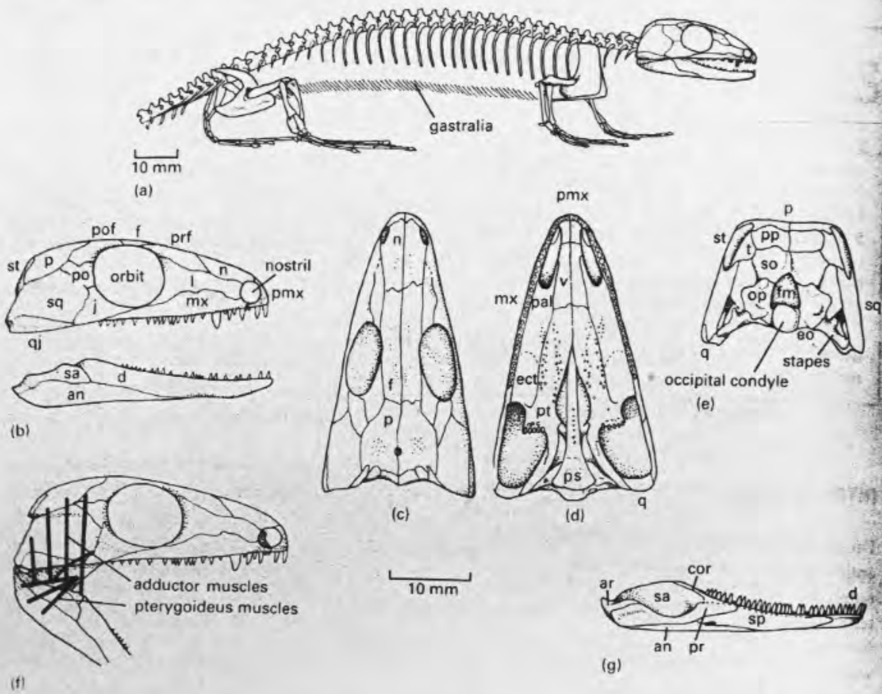


Fig. 5.1 The earliest amniote, *Paleothyris*: (a) skeleton in side view; (b–e) skull in lateral (b), dorsal (c), ventral (d), and occipital (e) views; (f) restoration of the main jaw closing muscles; (g) lower jaw. Abbreviations: an, angular; ar, articular; cor, coronoid; d, dentary; ect, ectopterygoid; 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, supratemporal; t, tabular; v, vomer. [Figure (a) after Carroll and Baird, 1972; (b–g) after Carroll, 1969a.]

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.

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 **proatlas** and atlas arch 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 27 in *Paleothyris*, making a total of about 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 4.6(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

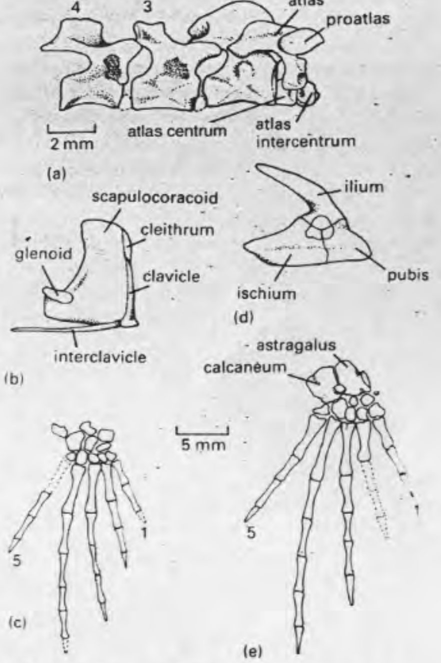


Fig. 5.2 Vertebrae and limbs of the earliest amniotes (a–c, e) *Paleothyris* and (d) *Hylonomus*: (a) cervical vertebrae 1–4; (b) pectoral girdle; (c) hand; (d) pelvic girdle; (e) foot. (After Carroll, 1969a.)

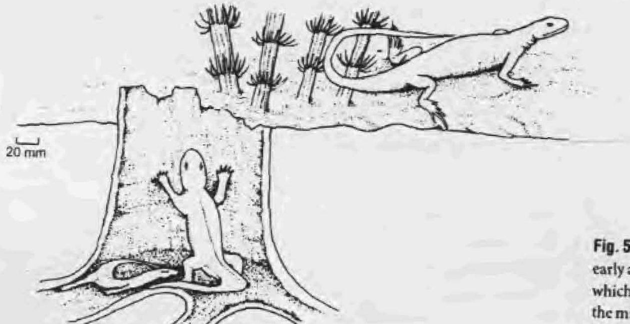


Fig. 5.3 The mode of preservation of the early amniotes *Hylonomus* and *Paleothyris*, which were trapped in hollow tree stumps in the mid-Carboniferous of Nova Scotia. (After Carroll, 1970, and other sources.)

long T-shaped element beneath. The arm is short (Figure 5.1(a)), and the hand (Figure 5.2(c)) long and slender. It shows all the wrist bones seen in *Eryops* (Figure 4.1b), and the phalangeal formula of the hand is 2,3,4,5,3—a typical value for anthracosaurs 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 4.6(d)). The hindlimb and foot are longer than the forelimb and hand. The ankle bones have changed in one respect from those of *Acanthostega* (Figure 4.6(f)), apart from becoming more slender. The tibiale, intermedium and a centrale of basal tetrapods have fused into a larger element termed the **astragalus**. The fibulare is also larger, and is termed the calcaneum. The phalangeal formula of the foot is 2,3,4,5,3.

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 (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 millepedes. 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 (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 is explicable because of the unique conditions of preservation: both *Hylonomus* and *Paleothyris* have been found in fossilized tree trunks.

Hylonomus comes from mudstones, sandstones and coals, deposited in shallow freshwater lakes and rivers of the Cumberland Group of Joggins, Nova Scotia (Carroll, 1970). In the 1840s geologists discovered abundant upright tree stumps of the lycopod (club moss) tree *Sigillaria*. 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 hundreds of basal tetrapods (six species of microsaurs, one temnospondyl, and one anthracosaur) 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*, up to 30 m tall. Occasionally, 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 millepedes, 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 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. During the Permian, 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 set apart 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, the 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.

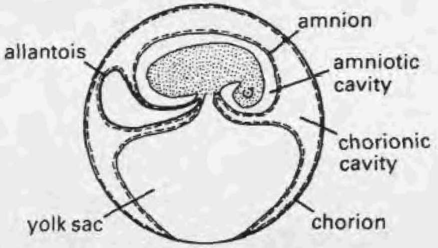


Fig. 5.4 The cleidoic egg, showing the semipermeable shell and the extraembryonic membranes.

The egg of amniotes, called the **amniotic or cleidoic** (literally 'closed') egg (Figure 5.4(a)), 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 intricate features of the cleidoic egg of all living amniotes develop in the same way, 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

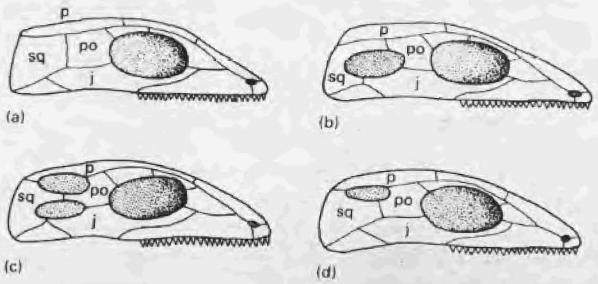


Fig. 5.5 The four main patterns of temporal fenestrae in amniote skulls: (a) anapsid; (b) synapsid; (c) diapsid; (d) euryapsid. Abbreviations: j, jugal; p, parietal; po, postorbital, sq, squamosal.

mammals (see p. 114), 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)).

(a) **Anapsid**: amniotes with no temporal fenestrae. Might include early forms such as *Hylonomus* and *Paleothyris*, as well as several lineages in the Permian and Triassic, and the turtles. The clade Anapsida includes turtles, and most of the Carboniferous to Triassic anapsid amniotes, but several anapsid forms, such as *Hylonomus* and *Paleothyris*, are excluded, and others exhibit temporal fenestrae.

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

(c) **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.

(d) **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 fenestra.

Whereas, at one time, it was thought that each of these four skull types indicated an independent and distinct line of evolution, the euryapsid type seems clearly to be a modified diapsid pattern.

The fundamental split in amniote evolution (see Box 5.1) took place in the Mid-Carboniferous, into two great clades, the Synapsida, leading eventually to mammals, and the Sauropsida (= monophyletic Reptilia), including Anapsida and Diapsida, which led to turtles, lizards, snakes, crocodilians and birds.

5.3 THE PERMIAN WORLD

During the Permian, the continents moved into even closer contact than in the Carboniferous (Figure 4.7), and the supercontinent Pangaea (literally 'whole world') came fully into being. 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, and disappeared in the Early Permian as Gondwana drifted north. 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 Late Permian, however, rich deposits of fossil tetrapods are known, from South Africa and Russia in particular.

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 disappeared as the previously dominant club mosses and horsetails died out. They 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 Permian must be related, in part at least, to these major climatic and floral changes.

5.4 THE EARLY EVOLUTION OF ANAPSIDS AND DIAPSIDS

The 'protorothyridids' and araeoscelids were the first anapsids and diapsids, respectively, in the Late Carboniferous, but both clades expanded during the Permian. Most of these animals were of small or medium size, but the pareiasaurs were an unusual and important group of Late Permian herbivores that achieved considerable size. The relationships of these disparate anapsid and diapsid groups have been controversial (see Box 5.1).

BOX 5.1 RELATIONSHIPS OF EARLY AMNIOTES

Amniotes fall into three main groups: the synapsids, the diapsids, and the anapsids (see p. 112). The Anapsida and Diapsida are broadly sister groups, forming the clade Sauropsida, and Synapsida is the outgroup. It has taken some time, however, to make sense of the relationships within each of these three major groups, and of the early anapsids in particular.

At first, attempts were made to group Protorothyrididae and Captorhinidae together (e.g. Romer, 1966; Carroll, 1987), but these two families share only primitive characters. Indeed, the family 'Protorothyrididae', containing the oldest amniotes, *Hylonomus* and *Paleothyris* (see pp. 107–11), turns out to be a polyphyletic assortment of small anapsids, some such as *Paleothyris* lying close to the diapsid line, and others occupying a variety of basal positions in the cladogram. Gauthier *et al.* (1988a) discovered that most of the Permian anapsid groups formed a clade they termed 'Parareptilia', a view generally confirmed subsequently. Lee (1995) and Laurin and Reisz (1995) found that the parareptiles were outgroups of Testudines, the turtles, and together they form a larger clade Anapsida. But what are the closest relatives of turtles among the Permian anapsids, pareaisaurs (Lee, 1995) or procolophonids (Laurin and Reisz, 1995)? The former view is accepted here (see cladogram). More distant outgroups of turtles are bolosaurids, millerettids and mesosaurids (Modesto, 1999; Berman *et al.*, 2000a).

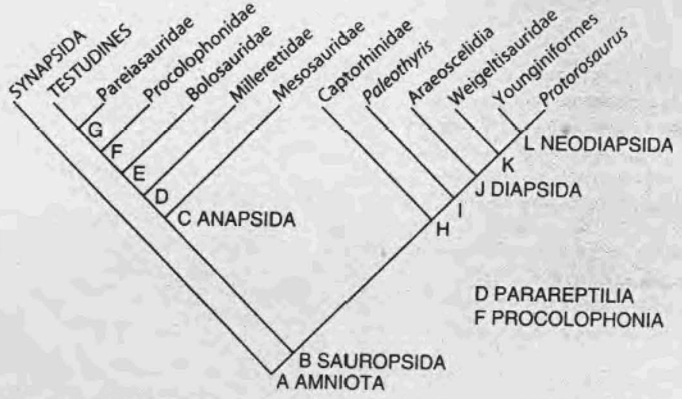
The relationships of the diapsids seem a little clearer. Captorhinids and *Paleothyris* appear to be outgroups of Diapsida. The weigeltisaurids are primitive in many respects and form an outgroup to the Younginiformes and *Protorosaurus* (Benton, 1985; Laurin, 1991). The diapsids of the Late Permian include two lineages that rose to importance later, one, the Archosauromorpha, leading to the dinosaurs, crocodilians and birds, and the other, the Lepidosauromorpha, to the lizards and snakes (see p. 150).

Molecular evidence could completely change this picture. Nearly all molecular analyses so far (e.g. Zardoya and Meyer, 1998; Hedges and Poling, 1999; Kumazawa and Nishida, 1999; Rest *et al.*, 2003) have placed turtles firmly within Diapsida, and associated closely with the archosaurs (i.e. crocodilians and birds). If this is the case, then Anapsida, as indicated here, would either be reduced to the extinct outgroups only, or indeed they might be dragged with turtles to lie within Diapsida. In this case, the diapsid skull arrangement would be the basal form from which the anapsid evolved. It has also been argued (deBraga and

continued

Rieppel, 1997) that morphological evidence supports the placement of turtles among the diapsids, although this time in the lepidosauromorph clade. Morphological support for this arrangement is, however, weak (Wilkinson *et al.*, 1997). Rieppel (2000b) has found very little morphological support for the molecular pairing of turtles and archosaurs. Lee *et al.* (in press) argue that both data sets are suspect: the morphological data contain a great deal of homoplasy and secondary signals push turtles artificially close to lepidosauromorphs, whereas high rates of molecular evolution in squamates push them too low in the tree, hence artificially pairing turtles and archosaurs. This clash of molecular and morphological data has yet to be resolved and explained: only one result can be correct and one data set then is giving a misleading and false signal.

Read more about basal amniote phylogeny at http://tolweb.org/tree?group=Amniota&contgroup=Terrestrial_vertebrates



Cladogram showing the postulated relationships of the major groups of amniotes, based on Laurin and Reisz (1995), Lee (1995) and Modesto (1999). See Box 4.5 for context of Amniota; see Box 5.3 for relationships of Synapsida and Figure 6.6 for relationships of Neodiapsida. Synapomorphies: **A AMNIOTA**, frontal contacts orbit, rounded occipital condyle, three ossifications in scapulocoracoid, astragalus; **B SAUROPSIDA**, 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 ANAPSIDA**, caniniform maxillary tooth absent, caudal haemal arches attached to anterior centrum, supraglenoid foramen absent, femoral shaft long and slender; **D PARAREPTILIA/E**, 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; **F PROCOLOPHONIA**, enlarged quadratojugal, pineal foramen near fronto-parietal 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**, massive horizontal paroccipital process fused to squamosal, fused basioccipital and basisphenoid, palate raised above margin of maxilla, 22 or fewer presacral vertebrae, long straight lateral processes on caudal vertebrae, dorsal buttress over acetabulum, reduced phalangeal formula of hand, astragalus and calcaneum fused, short slender fifth digit in foot, reduced phalangeal formula of foot, heavy dorsal dermal armour; **H**, postorbital does not reach supratemporal, supratemporal small, caniniform maxillary tooth, quadrate anterior process is short; **I**, tabular separate from opisthotic, ventral keel on anterior vertebral centra, carpus and tarsus long and slender, metatarsals and metacarpals overlap; **J 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; **K**, lacrimal reduced, caniniform maxillary teeth absent, quadratojugal reduced; **L NEODIAPSIDA**, anterior process of squamosal narrow, trunk ribs mostly single-headed, ends of humerus robust.

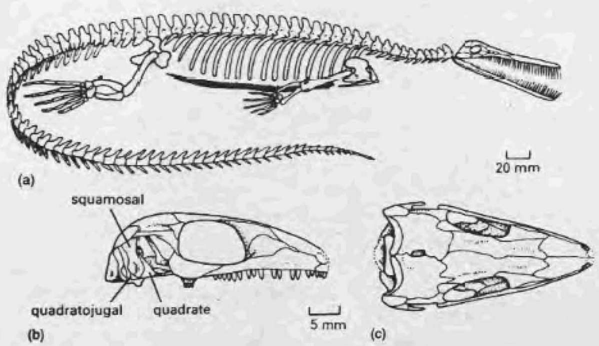


Fig. 5.6 Small Permian anapsids: (a) the mesosaur *Mesosaurus*; (b, c) the millerettid *Millerosaurus* skull in lateral and dorsal views. (After Carroll, 1987.)

5.4.1 'Protorothyrididae'

The basal anapsids include animals such as *Hylonomus* and *Paleothyris* (Figures 5.1–5.3) and six other genera from the Upper Carboniferous and Lower Permian of North America and Czechoslovakia that have been assigned to the Protorothyrididae (Carroll and Baird, 1972; Clark and Carroll, 1973). The 'protorothyridids' were agile insectivores, rather like modern lizards in their ecology. It was once thought that the protorothyridids were a highly conservative family, a group that had evolved little during its 30 Myr history. Cladistic studies indicate, however, that the family is paraphyletic, defined only by primitive characters, and the various protorothyridid genera are in fact basal members of all three major amniote lineages (Laurin and Reisz, 1995).

5.4.2 Mesosauridae

Mesosaurs (Modesto, 1999) are the first-known fully aquatic amniotes, represented by abundant small skeletons, up to 1 m long, from the Lower Permian of South America and South Africa, areas that were in contact at the time. They were used by Alfred Wegener as key evidence for the existence of Gondwana (see p. 25). The body (Figure 5.6(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.

5.4.3 Millerettidae

The millerettids from the Upper Permian of South Africa show some superficially lizard-like features in the skull (Figure 5.6(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.

5.4.4 Bolosauridae

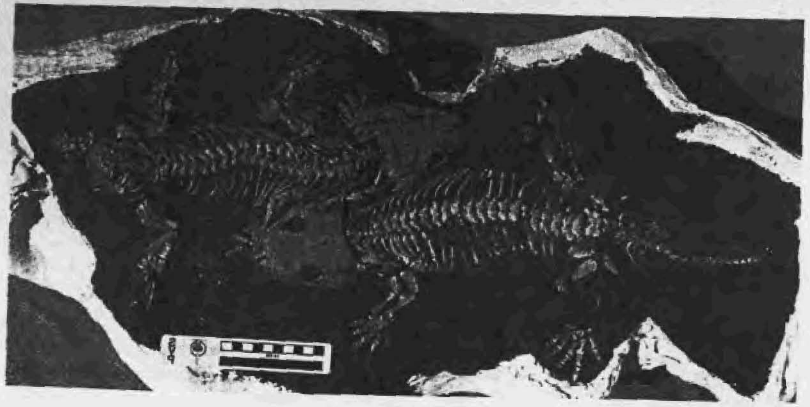
The bolosaurids are a somewhat enigmatic group of five or six genera that were known only from the Lower Permian of North America and the Upper Permian of Russia until the recent (Berman *et al.*, 2000a) discovery of Early Permian *Eudibamus* from the Bromacker locality (see Box 5.2) in Germany. This slender reptile, some 250 mm long, was bipedal, the first bipedal tetrapod ever. Its hindlimbs are twice as long as the forelimbs, and its feet are long, so that it probably ran up on its toes when

BOX 5.2 THE BROMACKER LOCALITY

Rich new tetrapod localities are not often discovered in Europe because so much collecting has already been done over the past two centuries. But a chance discovery in the 1980s by Thomas Martens, a palaeontologist at the Museum der Natur Gotha, has revealed a rich assemblage of basal tetrapods and amniotes. Martens, working in what was then East Germany, had little contact at first with the west, but then made connections with palaeontologists in North America after the Berlin wall came down (see illustration (a)).

The fossils come from the Tambach Formation, a sequence of conglomerates, sandstones and mudstones 200–400 m thick, deposited in a small, internally drained basin. The sediments were deposited on an alluvial plain with minor stream channels, and the climate showed seasonal wet–dry cycles of a savanna type climate. This upland type of setting is unusual, and none of the fishes and aquatic tetrapods that are typical elsewhere have been found here. The fauna identified so far (Berman *et al.*, 2000a, b) consists of *Tambachia*, a trematopid temnospondyl, adult *Seymouria*, a *Diadectes*-like reptiliomorph (see p. 101), the bolosaurid diapsid *Eudibamus* (Figure 5.9), a captorhinomorph reptile, *Thuringothyris*, and the sphenacodont *Dimetrodon*. Yet to be described are a small dissorophid, a caseid and a varanopid. The dominance by large herbivores and the absence of aquatic species suggest that the Bromacker assemblage may represent one of the first terrestrial vertebrate ecosystems.

Many of the fossils are nearly complete with very little abrasion, and they are probably preserved at or very close to their site of death (see illustration (b)). But, because of the friable nature of the shales and fine sandstones in which they are preserved, preparation of the delicate fossils can take a long time.



Read more at the 'official' home pages:
http://www.erin.utoronto.ca/~w3reisz/germany.htm, http://www.carnegiemuseums.org/cmnh/research/eudibamus/ and http://www.epilog.de/Dokumente/Show/Ausstellung/Prehistoric/Gotha_Ursaurier.htm.
These give more information, and illustrations of the site and some of the fossils.

The Bromacker locality, Germany: (a) American and German palaeontologists work through the red-brown shales at the Bromacker locality; (b) a pair of skeletons of *Seymouria*. (Courtesy of Robert Reisz and David Berman.)

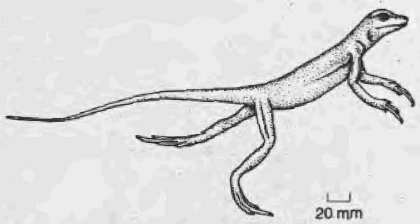


Fig. 5.7 The bolosaurid *Eudibamus* running at speed. (Courtesy of Diane Scott and David Berman.)

moving at high speed (Figure 5.7). The tail is as long as the body, and was probably used for balancing. Bolosaurids have bulbous teeth that **occlude**—that is, they meet on distinct facets—indicating a diet perhaps of tough plants. Despite their unusually advanced locomotion, bolosaurids were never more than a rare group, and did not outlive the Permian.

5.4.5 Procolophonidae

The procolophonids arose in the Late Permian and lived for about 50 Myr to the end of the Triassic, becoming rather diverse in the Triassic (Spencer and Benton, 2000; Sues *et al.*, 2000). *Procolophon* from the Lower Triassic of South Africa and Antarctica (Carroll and Lindsay, 1985; deBraga, 2003) is 300–400 mm long and has a stocky body and a relatively large broad skull (Figure 5.8(a–c)). 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 meet during occlusion. They suggest a diet of fibrous plant material, and possibly arthropods with tough cuticles. The broad paddle-like feet suggest that procolophonids might have been burrowers (deBraga, 2003).

5.4.6 Pareiasauridae

The pareiasaurs (Lee, 2000) are restricted in time to the Late Permian. Most are large, typically 2–3 m long and heavily built. The Russian *Scutosaurus* (Figure 5.8(d–f)) 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 incized 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. In recent debates, pareiasaurs and procolophonids have been proposed as a sister group of the turtles (see Box 5.1).

5.4.7 Captorhinidae

The captorhinids are known from the Lower Permian of North America primarily, with late survivors in the Upper Permian of Africa and Eurasia. *Captorhinus* (Figure 5.9(a–c)) is a small animal, about 400 mm long, but with a relatively large heart-shaped head (Heaton and Reisz, 1986; Holmes, 2003). 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

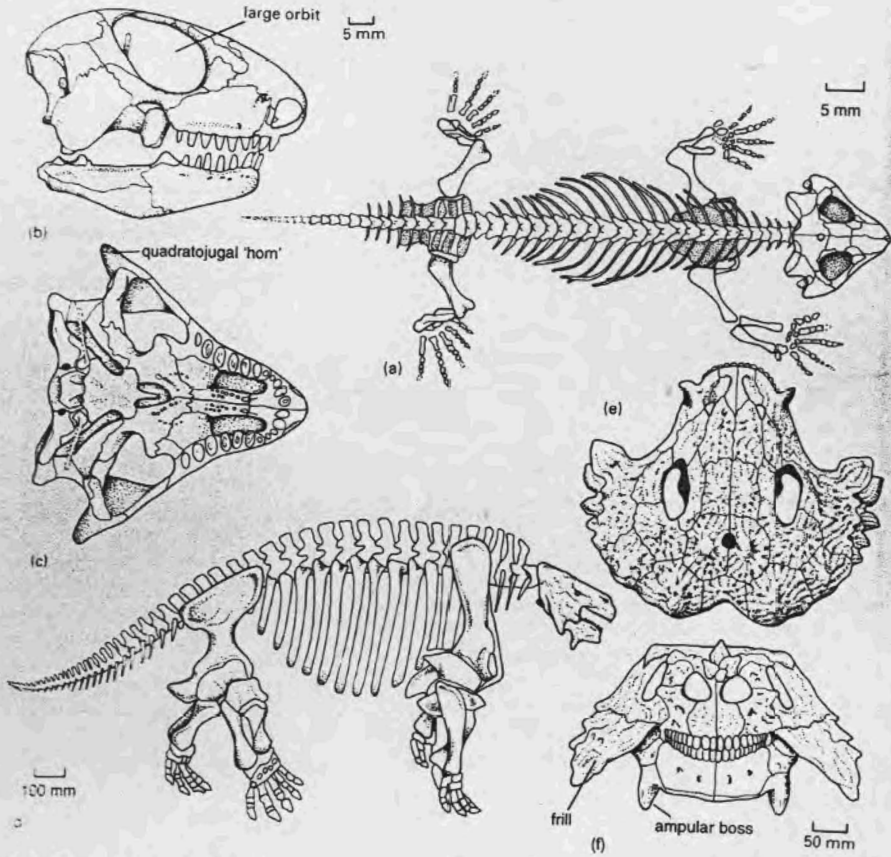


Fig. 5.8 Early anapsids: (a–c) the procolophonid *Procolophon*, skeleton and skull in lateral and ventral views; (d–f) the pareiasaur *Scutosaurus*, skeleton and skull in lateral and ventral views. [Figures (a–c) after Carroll and Lindsay, 1985; (d–f) after Kuhn, 1969.]

the dentition. The peg-like teeth are often present in multiple rows (Figure 5.9(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 gum tissue which produces teeth, that lay medially. 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 interpreted as an adaptation for piercing or grinding tough plant material or hard-shelled invertebrates.

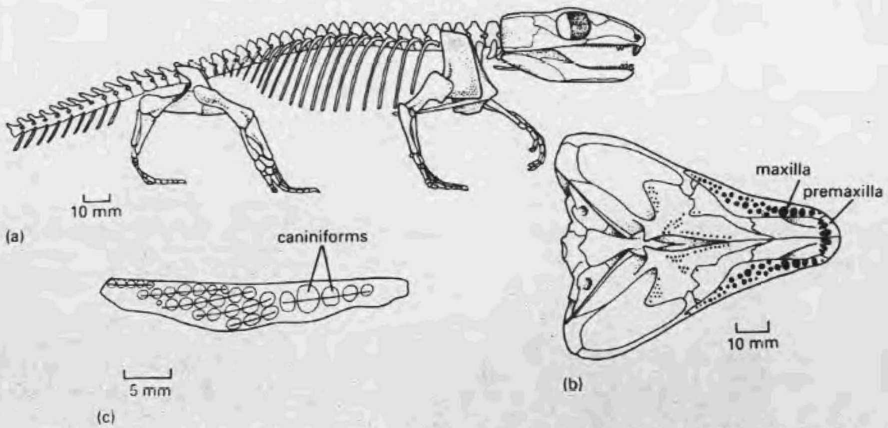


Fig. 5.9 The captorhinid *Captorhinus*: (a) skeleton in walking posture; (b) ventral view of the palate; (c) ventral view of the maxilla, showing the multiple rows of teeth. [Figure (a) after Heaton and Reisz, 1986; (b, c) after Ricqlès and Bolt, 1983.]

5.4.8 Araeoscelidia

Diapsids are rare in the Carboniferous, being known from only two taxa from the Upper 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 5.10(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 5.10(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 5.10(d)).

5.4.9 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 5.11(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 5.11(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 5.11(c)), a slender long-necked animal from the Upper Permian of Germany, the first representative of the Archosauromorpha (see p. 138). *Youngina* (Figure 5.11(d)), only 350–400 mm long, was probably an active lizard-like insectivore and carnivore (Gow, 1975). The skull is similar to that of *Petrolacosaurus* (cf. Figure 5.10), 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.

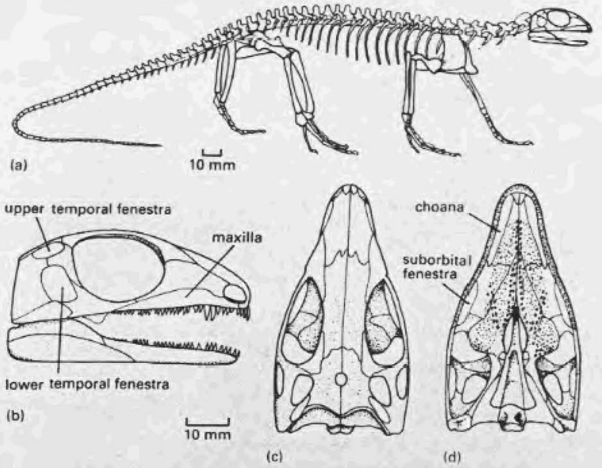


Fig. 5.10 The first diapsid, *Petrolacosaurus*: (a) skeleton; (b–d) skull in lateral, dorsal, and ventral views. (After Reisz, 1981.)

5.5 BASAL SYNAPSID EVOLUTION

The synapsids split from the sauropsids (anapsids + diapsids) in the Mid-Carboniferous, and they expanded in diversity enormously during the Permian, becoming the dominant land animals. The clade is generally divided into two groups. The 'pelycosaurs' (Romer and Price, 1940; Reisz, 1986) are a paraphyletic group of six families of basal synapsids that were particularly important in the Early Permian. These were succeeded in the Late Permian by the Therapsida, a diverse clade of small to large plant- and flesh-eaters (see Box 5.3).

5.5.1 Carboniferous and early Permian synapsids

The Ophiacodontidae, a group of six or seven genera, arose in the Mid-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 5.12(a)). Its relative *Ophiacodon*, from the Upper Carboniferous and Lower 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 5.12(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 eothyrid *Eothyris*, a small animal from the Lower Permian of Texas (Figure 5.13(a)), 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 mid-Permian of North America and Europe, include small and large forms. *Cotylorhynchus* from Texas and Oklahoma (Figure 5.13(b–d)), is the largest pelycosaur, 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 5.13(b, d)): 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.

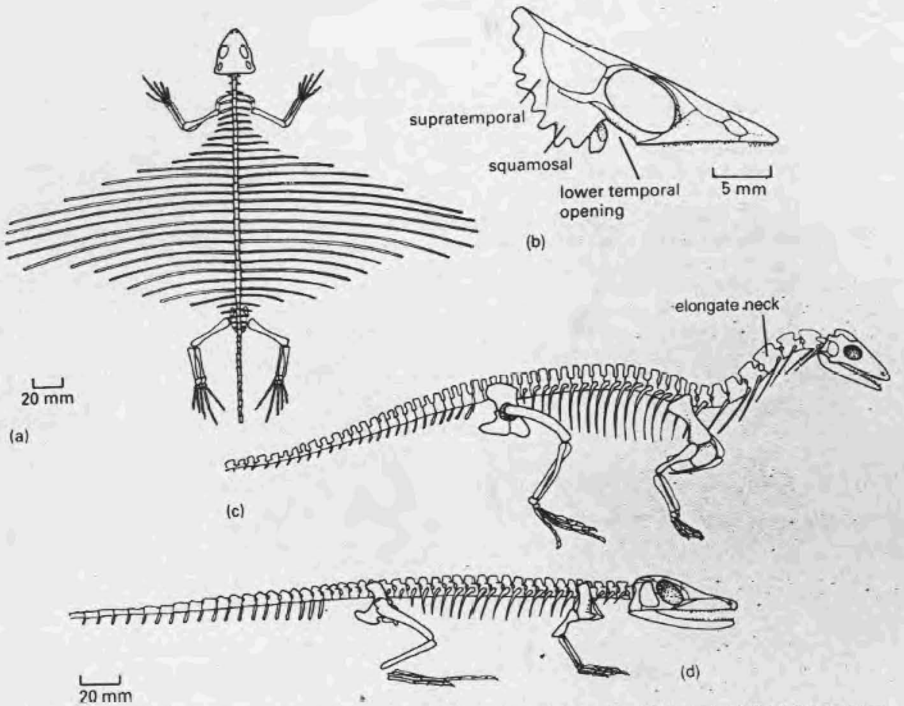


Fig. 5.11 Late Permian diapsids: (a, b) *Coelurosauravus*, restored skeleton in dorsal view, and lateral view of the skull; (c) *Protorosaurus*; (d) *Youngina*. [Figure (a) after Carroll, 1978; (b) after Evans and Haubold, 1987; (c) after Seeley, 1888; (d) after Gow, 1975; (a, d) courtesy of the Bernard Price Institute.]

The varanopids, six or seven genera of small carnivores known until recently only from the Lower Permian of North America, survived into the Upper Permian in Russia and South Africa (Modesto *et al.*, 2001). The limbs are long and the skeleton lightly built, so that they are interpreted as active and agile in their habits. *Varanops* (Figure 5.13(e, f)) has a long low skull, with the dentition extending unusually far back to lie below the temporal fenestra.

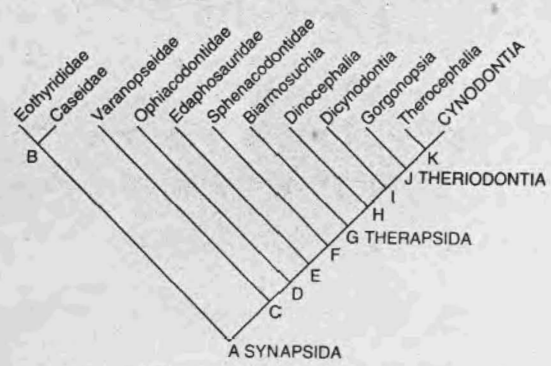
5.5.2 The sail-backed synapsids

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 Lower Permian of New Mexico and Texas (Figure 5.14), were herbivores. They have enormously elongated neural spines of the cervical and dorsal vertebrae that were

BOX 5.3 RELATIONSHIPS OF THE SYNAPSID GROUPS

Synapsida traditionally have been divided into 'pelycosaurs', a paraphyletic group, and therapsids, a well-characterized clade (see cladogram). Both groups together were formerly sometimes called 'mammal-like reptiles'. The pelycosaurs appear to form a sequence of outgroups to Therapsida, with the sphenacodontids being the most derived (Reisz, 1986). The Biarmosuchia, perhaps a paraphyletic group, are the most basal therapsids. The dinocephalians, dicynodonts and gorgonopsians follow next (Hopson and Barghusen, 1986; Sidor and Hopson, 1998). Some have suggested the dinocephalians and dicynodonts should be paired as Anomodontia (King, 1988), but the dinocephalians may in fact be paraphyletic (Sidor and Hopson, 1998). The dicynodont branch is probably more extensive, i.e. the Anomodontia proper, consisting of basal taxa such as the venyukovioids from Russia and relatives from South Africa (Modesto and Rybczynski, 2000). The therocephalians are a sister group of the cynodonts, which properly include the mammals.

For more detail on the phylogeny of basal synapsids, go to http://tolweb.org/tree?group=Synapsida&contgroup=Amniota#TOC2



Cladogram showing the postulated relationships of the main groups of synapsids, according to Hopson and Barghusen (1986), Reisz (1986) and Sidor and Hopson (1998). 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**, pointed snout formed by anteriorly tilted premaxilla, external nostril elongated, maxilla enters ventral margin of orbit; **C**, frontal forms at least one-third of dorsal margin of orbit, narrow long supratemporal located in a groove formed by parietal and squamosal; **D**, dorsal process of stapes articulates in a socket on the paroccipital process, cheek margin concave; **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.

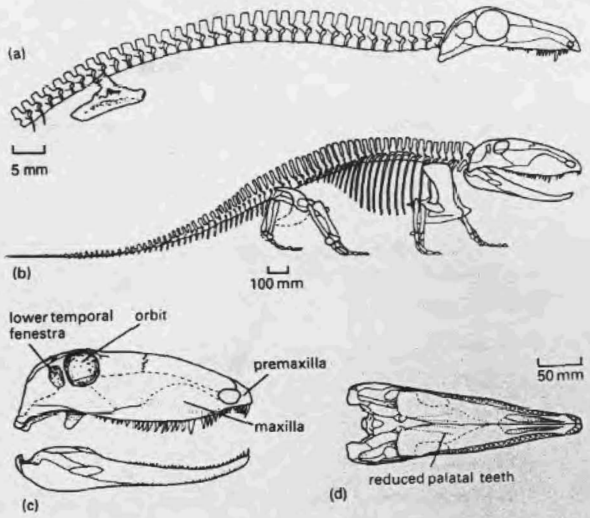


Fig. 5.12 The ophiacodonts (a) *Archaeothyris* and (b–d) *Ophiacodon*: (a) partial skull and skeleton in lateral view; (b) skeleton; (c, d) skull in lateral and ventral views. (Modified from Romer and Price, 1940, and Reisz, 1986.)

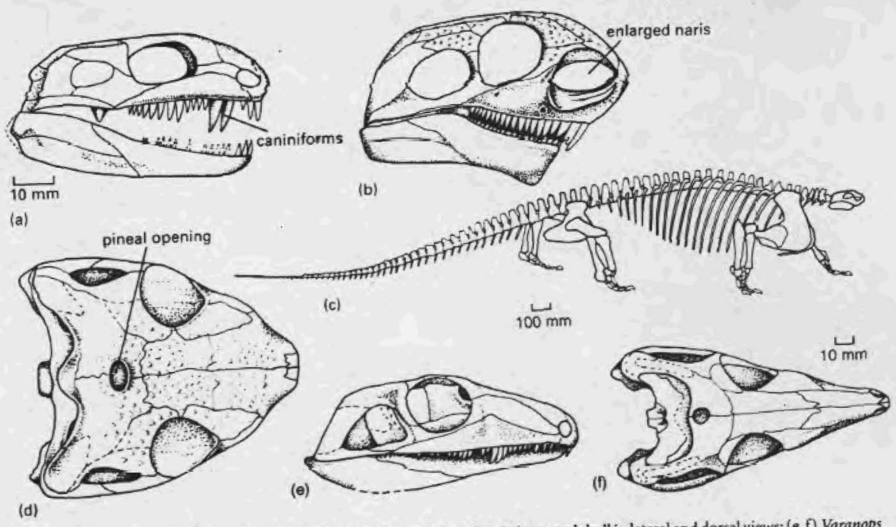


Fig. 5.13 Three early pelycosaurs: (a) *Eothyris* skull; (b–d) *Cotylorhynchus* skeleton and skull in lateral and dorsal views; (e, f) *Varanops* skull in lateral and dorsal views. (After Romer and Price, 1940.)

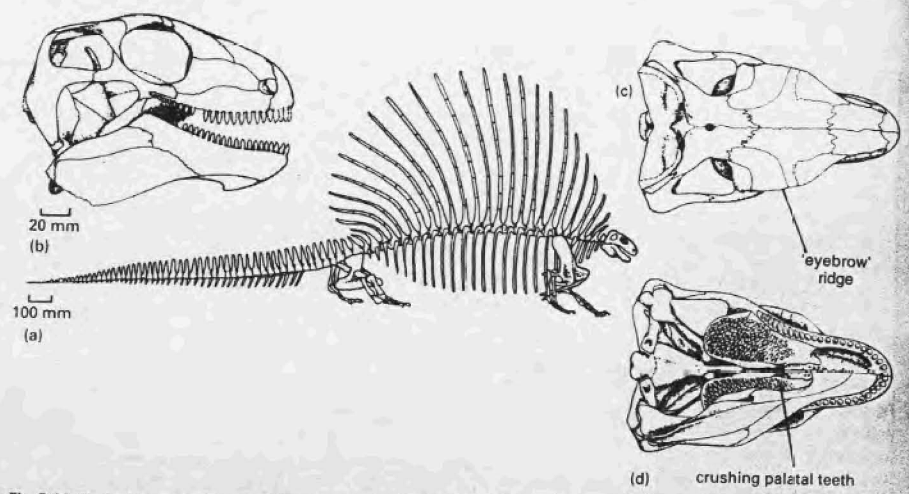


Fig. 5.14 The herbivorous pelycosaur *Edaphosaurus*: (a) skeleton; (b–d) skull in lateral, dorsal, and ventral views. [Figure (a) after Romer and Price, 1940; (b–d) courtesy of Sean Modesto.]

probably covered by skin, hence the popular term 'sail backs'. 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 5.14(d)) that are large and form a broad crushing surface, and occlude against a similar battery on the lower jaw.

The sphenacodontids (Reisz, 1986) were medium-to large-sized carnivores from the Upper Carboniferous and Lower Permian of North America and Europe. *Dimetrodon* from the Lower 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 5.15). The powerful jaw muscles of *Dimetrodon* have been reconstructed (Figure 5.15(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.

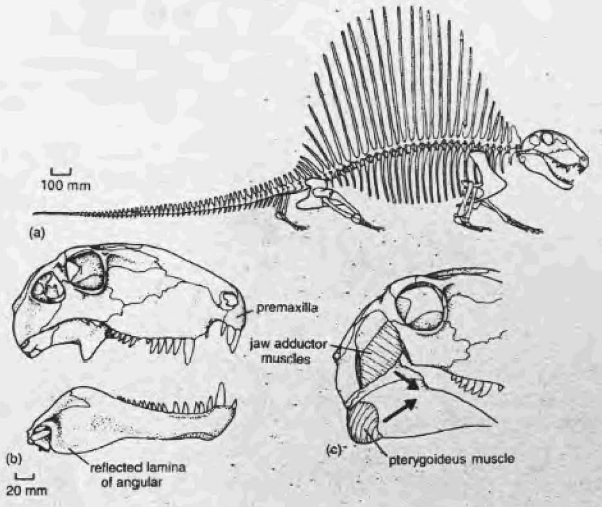


Fig. 5.15 The carnivorous pelycosaur *Dimetrodon*: (a) skeleton; (b) skull in lateral view; (c) major jaw muscles reconstructed, in lateral view. (After Romer and Price, 1940.)

5.5.3 Biarmosuchia: the basal therapsids

Derived characters of therapsids, in comparison with the 'pelycosaurs', include an enlarged temporal fenestra, loss of the supratemporal bone, a deeply notched reflected lamina on the angular bone (Figure 5.16(c)), a forwards position of the jaw joint, reduction of the palatal teeth, as well as modifications of the shoulder and pelvic girdles and of the hindlimb (Kemp, 1982; Hopson and Barghusen, 1986; Sidor and Hopson, 1998; see Box 5.3).

A synapsid from the Early Permian of Texas, USA, *Tetraceratops* (Figure 5.16(a, b)), may be the oldest-known therapsid (Laurin and Reisz, 1996). In many features, it seems to be intermediate between sphenacodontid pelycosaurs and later therapsids, but it shows an enlarged temporal fenestra and some reduction in the palatal teeth. Further early therapsids come from the Late Permian of Russia (Battail and Surkov, 2000). *Biarmosuchus* (Figure 5.16(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 pelycosaurs, is now exposed on the side of the skull.

5.5.4 Dinocephalia

The dinocephalians include 40 genera of synapsids known only from the Upper Permian of Russia and South Africa, which fall into both carnivorous and herbivorous lineages (Kemp, 1982; King, 1988; Battail and Surkov, 2000). A carnivorous form, *Titanophoneus* from the Upper Permian of Russia (Figure 5.16(e)), is 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 Tapinocephalidae includes a range of herbivorous forms, some quite bizarre in appearance. *Moschops* from South Africa (Figure 5.16(f)) is a large animal about 5 m long with a massive ribcage and heavy limbs, but tiny feet. The hindlimbs were held close under the

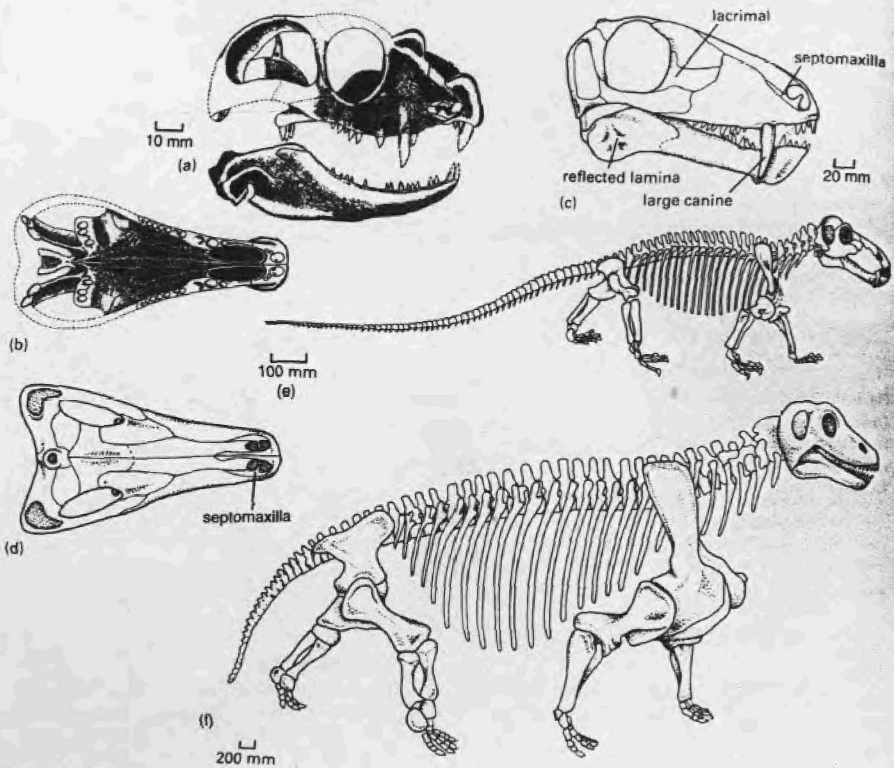


Fig. 5.16 Early therapsids: (a, b) skull of *Tetraceratops* in lateral and ventral views; (c, d) skull of *Biarmosuchus* in lateral and dorsal views; (e) carnivorous dinocephalian *Titanophoneus*; (f) herbivorous dinocephalian *Moschops*. |Figures (a, b) modified from Laurin and Reisz, 1996; (c, d) after Sigogneau and Chudinov, 1972; (e, f) after King, 1988.|

body in a derived 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 pelycosaurs (cf. Figures 5.13(c) and 5.14(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 5.17). 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.

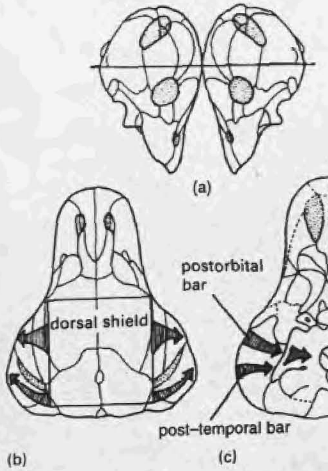


Fig. 5.17 Head-butting behaviour in *Moschops*: (a) lateral view of the skulls of two butting individuals showing the line of transmission of the impact through the occipital condyle; (b, c) dorsal and ventral views of the skull showing the broad thickened dorsal shield, and transmission of forces from it through the postorbital and post-temporal bars to the occipital condyle. (After Barghusen, 1975.)

5.5.5 Dicynodontia

The dicynodonts, a group of over 70 genera, were dominant herbivores in the Late Permian (Kemp, 1982, King, 1988; Angielczyk, 2001), and nearly all 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 5.18(a)). Dimensions ranged from rat- to hippo-sized. Dicynodonts were hit hard by the end-Permian mass extinction (see p. 133), but several new dicynodont lines 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 5.18(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 biology has been studied in some detail (see Box 5.4).

5.5.6 Gorgonopsia

The dominant carnivores in the Late Permian were the gorgonopsians (Figure 5.19(a, b)), a group of some 35

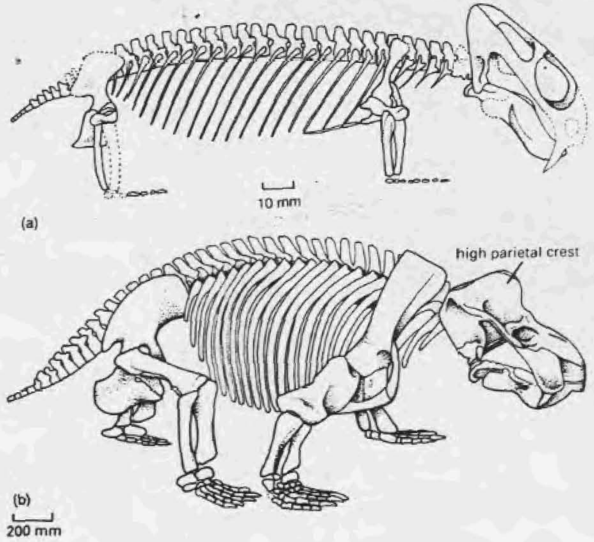


Fig. 5.18 Skeletons of dicynodonts: (a) *Robertia* from the Upper Permian; (b) *Kannemeyeria* from the Middle Triassic. (After King, 1988.)

BOX 5.4 DICYNODONT DIETS

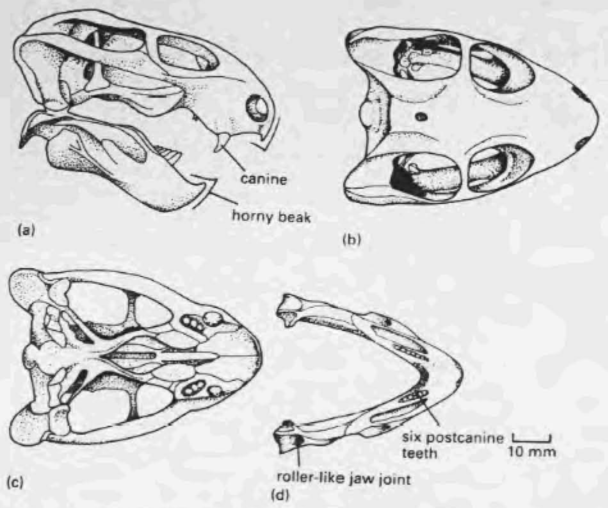
In the Late Permian, dicynodonts such as *Pristerodon* made up 80–90% of species in typical faunas (Benton, 1983a). Often, five or six dicynodont species of different sizes were present in a fauna, and they were preyed on by carnivorous dinocephalians or gorgonopsians. The huge success of these Late Permian dicynodonts may relate to their specialized jaw apparatus.

Pristerodon, a small dicynodont from the Upper 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.

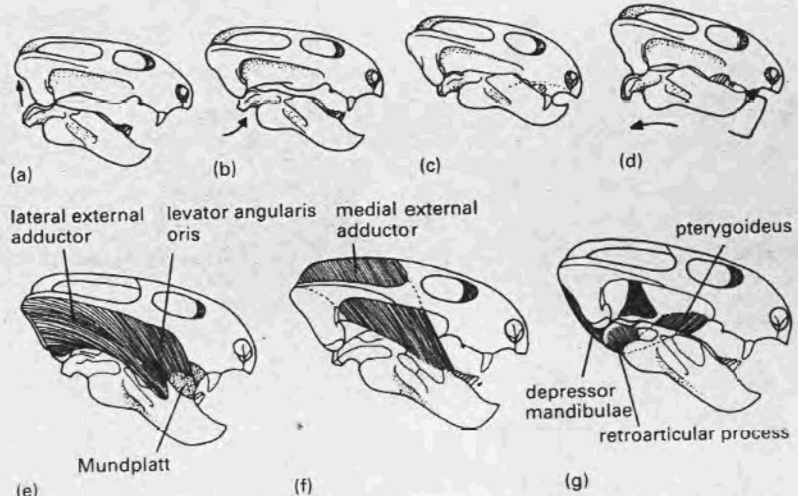
Pristerodon had a highly mobile jaw joint. The articulating surface of the articular is nearly twice as long as that of the quadrate, so that the lower jaw could slide some distance back and forwards during a jaw opening cycle. Crompton and Hotton (1967) reconstructed the jaw actions of *Pristerodon* 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 Mundplatt, 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.



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

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 swallowable chunks of flesh (Kemp, 1969). The gorgonopsians are reminiscent of sabre-toothed cats, which arose much later on and had similar enlarged canines and vast gapes (see p. 349). 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.

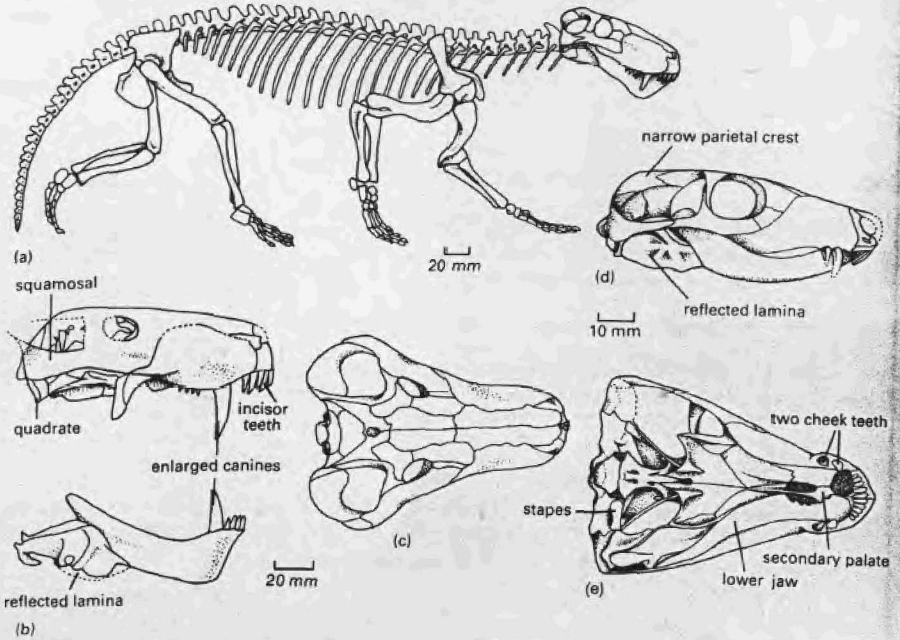


Fig. 5.19 The gorgonopsians (a) *Lycaenops*, (b) *Arctognathus*, and (c) *Leontocephalus*; (d, e) the therocephalian *Theriognathus*. [Figure (a) after Broom, 1932; (b, c) after Kemp, 1969; (d, e) after Brink, 1956, courtesy of the Bernard Price Institute.]

5.5.7 Suborder Therocephalia

The therocephalians, another group of carnivorous therapsids, survived from the Late Permian into the Triassic. 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 Upper Permian of South Africa (see Box 5.5), has a skull 75 mm long (Figure 5.19(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 5.19(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 Lower Triassic of South Africa (Figure 5.20(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.

5.5.8 Cynodontia

The cynodonts, as a clade, include the mammals (see

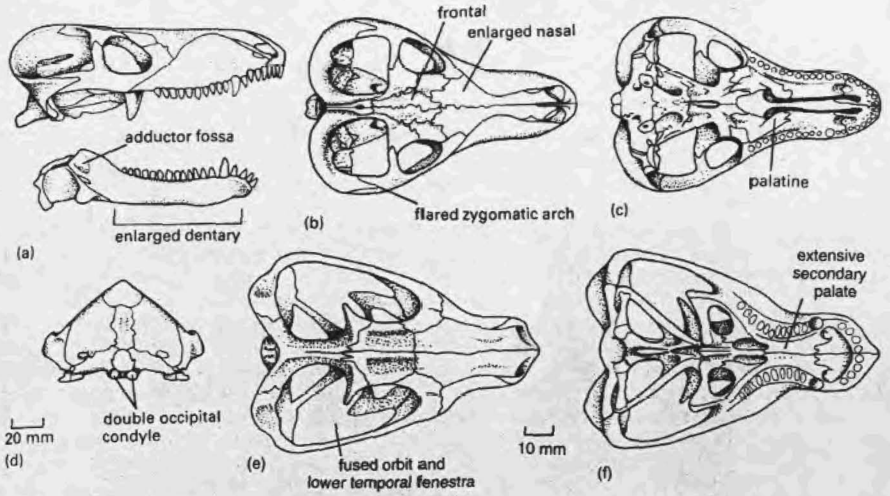


Fig. 5.20 The early cynodont *Procynosuchus*, skull in (a) lateral, (b) dorsal, (c) ventral, and (d) occipital views; (e, f) the herbivorous therocephalian *Bauria*, skull in dorsal and ventral views. [Figures (a–d) after Kemp, 1979; (e, f) modified from Carroll, 1987.]

BOX 5.5 THERAPSIDS OF THE KAROO

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. The Karoo basin covers a huge area, some 600,000 km^2, more than half of South Africa, and the sequences of Permian to Jurassic sediments total 12 km in thickness (Smith, 1995). 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 Upper Permian and Lower 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 anapsids (*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 dicynodont skeletons in coiled burrows (see illustration). The animals evidently constructed deep burrows near to river channels, perhaps to escape the midday sun, and occasionally the hapless animals were trapped by an unexpected flash flood.

continued

For everything on the fossils of the Karoo, the locations and the specimens, go to http://www.museums.org.za/sam/resource/palaeo/cluver/index.html, an online reference, and http://www.wits.ac.za/science/palaeontology/bpihome.html, home page of the Bernard Price Institute for Palaeontological Research.

Dicynodont burrows from the Late Permian, Karoo basin, South Africa: (a) part of a corkscrew-shaped living burrow (matchbox is 50 mm long); (b) skeleton of a curled-up dicynodont, overwhelmed by a flash flood (skeleton is 200 mm long). (Courtesy of Roger Smith.)

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.

Procynosuchus from the uppermost Permian of southern Africa (Kemp, 1979) has a long-snouted skull with an expanded temporal region (Figure 5.20(a–d)). *Procynosuchus* shows a large number of features that are generally mammalian in character (Kemp, 1982; 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 5.20(d)); and the beginnings of a secondary palate composed largely of the maxillae and palatines (Figure 5.20(c)), rather than the vomers and maxillae, as in therocephalians. The size of *Procynosuchus*, and the nature of its teeth, suggest that it ate insects or small tetrapods.

5.6 MASS EXTINCTION

The greatest mass extinction of all time took place at the end of the Permian (Benton, 2003), and the tetrapods were involved. Of the 48 families that were present in the last 5 Myr of the Permian, the Tatarian Stage, 36 died out (a loss of 75%). These include ten families of basal tetrapods (mainly anthracosaurs), captorhinids, millerettids and pareiasaurs, as well as the younginids, and 17 families of therapsids, including the gorgonopsians, the last dinocephalians, most of the dicynodonts, and many families of small insect-eaters (Figure 5.21). Only 12 families of tetrapods survived (Benton, 1993a). It is hard to estimate the levels of loss at generic or specific level, because of patchiness of the fossil record. Modesto *et al.* (2003) have shown, for example, that when a cladogram is drawn, several lineages can be shown to have survived the extinction horizon, even though fossils are yet to be found.

This dramatic loss of tetrapod families represents the largest mass extinction in their history. The families that died out include a broad range of ecological types, from small to large, from carnivores to herbivores, and the event affected tetrapods worldwide. At the same time, more than 50% of marine invertebrate families died out, the highest rate of extinction in the history of the seas. Losses of 50–75% of families on land and in the sea equate to losses of 80–96% of species, according to different calculations.

Estimates for the timing of the end-Permian event have tightened up considerably. Whereas in 1990 many geologists estimated a duration of 5–10 Myr, more precise radiometric dating (Bowring *et al.*, 1998) shows that the Permo-Triassic boundary is dated at 251 Myr ago, and the mass extinction was rapid, taking less than 500,000 years. Studies of continental sequences in the Karoo (see Box 5.5) show a stepwise loss of tetrapod genera through a short span of the sedimentary sections (Smith and Ward, 2001).

Catastrophists have attempted to explain the end-Permian mass extinction by the impact of an asteroid, the favoured explanation for the KT event (see pp. 248–55), but there is limited evidence for this at the end of the Permian. There were, however, massive eruptions of basalt lava in Siberia. Over the course of perhaps 500,000 years, some 3 million km^3 of lava were erupted over a vast area. The eruption released huge volumes of gases such as CO_2 and SO_2 into the atmosphere, and this probably caused catastrophic temperature changes and oxygen depletion (Wignall, 2001). The oxygen depletion, associated with greenhouse heating of the atmosphere and oceans, combined to kill off most plants on land and much of the plankton. With the plants gone, soils and organic matter were washed into the sea. Heating may have reached such a level that gas hydrates, huge volumes of methane frozen in ice deep around the continental margins, were unfrozen and released. These would have burst to the surface of the oceans, expanding massively in volume and further driving the greenhouse heating effect.

Whatever the cause, the mass extinction was profound. It 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. Where there had once been

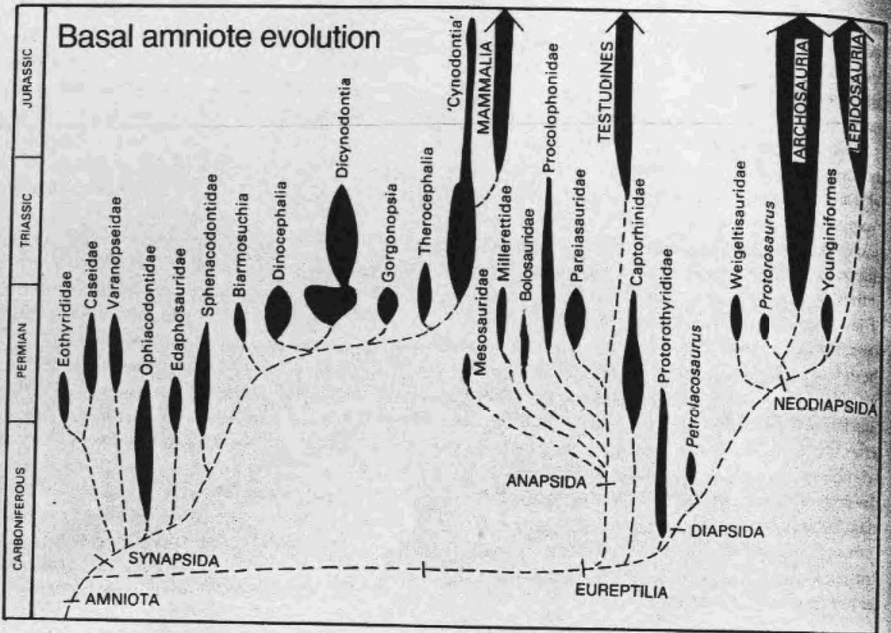


Fig. 5.21 Phylogeny of the early amniotes, showing the known fossil record (vertical scale), relative abundance (horizontal dimension of 'balloons'), and postulated relationships (dashed lines).

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 dinocephalians, 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 95% of the post-extinction faunas, is a sure indication that a major crisis has happened. Other survivors included two or three 'temnospondyl' lines (see p. 97), some procolophonids, some basal archosaurs and lepidosauromorphs (see Chapter 6), and some therocephalians and cynodonts.

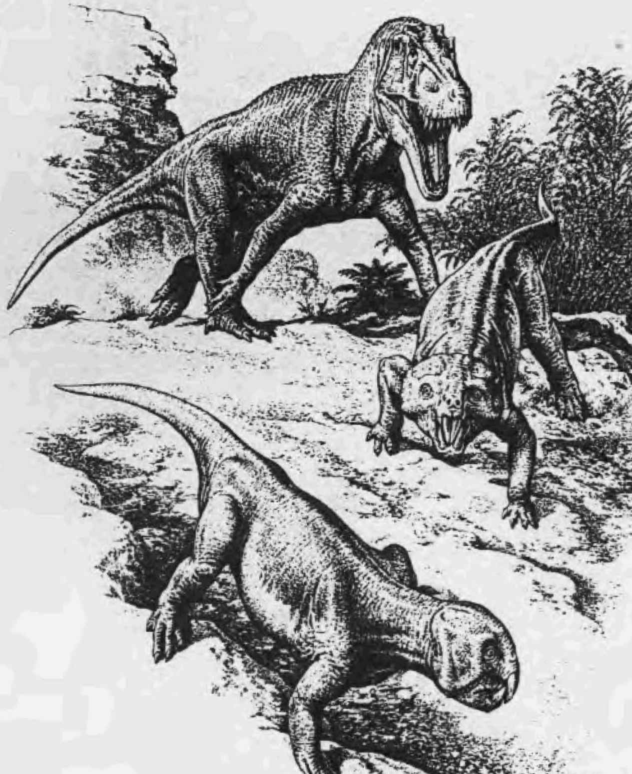
5.7 FURTHER READING

You can read more about the phylogeny of early amniotes in Sumida and Martin (1997). Two older accounts of Permo-Triassic synapsids are Kemp (1982) and Hopson and Barghusen (1986), and a more recent survey is given by Rubidge and Sidor (2001). An overview of the stratigraphy and faunas from the Permo-Triassic of Russia is given in Benton *et al.* (2000b). Benton (2003) gives an account of the current understanding of the end-Permian extinction event.

Learn more about the first reptile *Hylonomus*, Nova Scotia's provincial fossil, at http://www.gov.ns.ca/legislature/HOUSE_OF_ASSEMBLY/Symbols/fossil.htm, procolophonids at http://www.ucmp.berkeley.edu/anapsids/procolophonoidea.html and pareiasaurs at http://www.ucmp.berkeley.edu/anapsids/pareiasauria.html. You can find more information about the end-Permian mass extinction at http://palaeo.gly.bris.ac.uk/Palaeofiles/Permian/front.html and http://www.bbc.co.uk/science/horizon/2002/dayearthdied.shtml.

CHAPTER 6

Tetrapods of the Triassic



KEY QUESTIONS IN THIS CHAPTER

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

INTRODUCTION

Some of the key episodes in tetrapod evolution occurred during the Triassic period (251–200 Myr ago), marking the transition from faunas of Palaeozoic-style tetrapods to modern forms. The Triassic began with restricted faunas, of lower diversity than those of the Late Permian, depleted by the great mass extinction. On land, the synapsids re-radiated during the Triassic, but they had already lost a number of their key adaptive zones to two new groups—the archosaurs and the rhynchosaurs. In the seas, several lines of fish-eating reptiles emerged, the nothosaurs, placodonts and ichthyosaurs. Synapsid dominance in the Permian had been destroyed and replaced by diapsid dominance throughout the Mesozoic.

The Late Triassic was a key episode in the evolution of tetrapods. Not only did the dinosaurs appear, but a number of other major groups also arose: the crocodilians, the pterosaurs, the turtles and the mammals (see Chapters 8 and 10).

6.1 THE TRIASSIC SCENE

The Triassic world was similar in many ways to that of the Permian. All continents remained united as the supercontinent Pangaea (Figure 6.1), although the North Atlantic Ocean began to open at the very end of the period, with rifting in eastern North America, southern Europe and North Africa. Nevertheless, there is strong evidence that tetrapods could disperse widely because faunas of continental tetrapods were similar worldwide. For example, the first faunas of the earliest Triassic were dominated by the dicynodont *Lystrosaurus*, and included other elements such as small therocephalians and cynodonts, the early archosaur *Proterosuchus* (see below), prolacertiforms and procolophonids. These animals were found first in the Karoo Basin of South Africa (see p. 131), but similar faunas were later found in Antarctica, India, South America, China and Russia, evidence for a global supercontinent at the time (see p. 25).

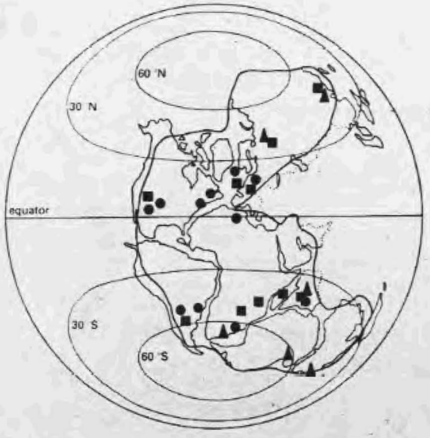


Fig. 6.1 Map of the Triassic world, showing the arrangement of the present continents (light line) and the Triassic coastline (heavy line). Fossil reptile localities are indicated with symbols: ▲, Early Triassic; ■, Middle Triassic; ●, Late Triassic. (Modified from Tucker and Benton, 1982.)

Triassic climates were warm, with much less variation from the poles to the equator than exists today. There is no evidence for polar ice-caps, and the north and south poles both lay over oceans at the time. During the Triassic, there was apparently a broad climatic shift, at least in terms of the reptile-bearing rock formations, from warm and moist to hot and dry (Tucker and Benton, 1982). This may have been caused partly by a northwards drift of southern reptile-bearing sites into the tropical climatic belt.

The 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 they 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 pp. 159–61).

6.2 EVOLUTION OF THE ARCHOSAUROMORPHS

The archosauromorph branch of the diapsids (see p. 113) includes several groups, the trilophosaurids, rhynchosaurs, prolacertiforms and archosaurs. The first two are known only from the Triassic, but the prolacertiforms had arisen in the mid-Permian, and the archosaurs by the Early Triassic. The most important of the archosauromorph groups is the Archosauria, and their evolution in the Triassic was critical for the later history of vertebrate life on land: here were laid the foundations of the radiation of the dinosaurs, pterosaurs and crocodiles, and ultimately of the birds. These later stages of archosaur evolution are described in Chapters 8 and 9.

6.2.1 Basal archosaurs

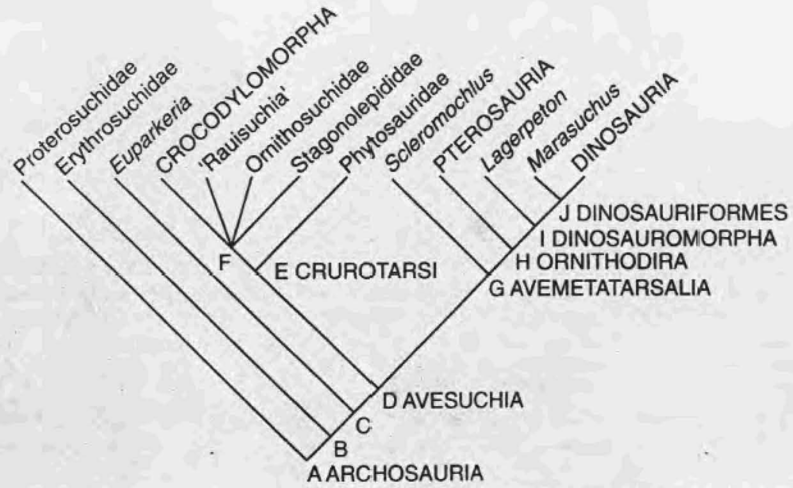
During the Triassic the archosaurs radiated into several groups. There were some short-lived forms in the Early Triassic, before a major split in the archosaur clade took place. One line led to the crocodilians, and the other to the pterosaurs, dinosaurs and birds (see Box 6.1). The Triassic archosaurs that do not belong to any of these terminal clades were previously called 'thecodontians', a paraphyletic group.

BOX 6.1 ARCHOSAUR DIVERSIFICATION

The archosaurs underwent a major phase of evolutionary diversification at the end of the Early Triassic. They branched into two major groups, one of which led to the crocodilians and the other to the dinosaurs and birds. The precise compositions of these two lineages were hard to resolve (Gauthier, 1986; Benton and Clark, 1988; Sereno, 1991; Gower and Wilkinson, 1996; Benton, 1999a), as there were a large number of convergences, particularly in modifications of the limbs and changes in posture (see Box 6.2). The current view (Gower and Wilkinson, 1996) is that the crocodilian lineage, the Crurotarsi, includes most of the Late Triassic archosaurs, whereas the dinosaur lineage, the Ornithodira (see p. 153), includes dinosaurs, pterosaurs and a number of basal forms (see cladogram). Note that I use the term 'Archosauria' to refer to the whole clade, the normal usage, whereas some authors (e.g. Gauthier, 1986) have suggested restricting the term to the clade termed Avesuchia here.

In the cladogram, the key contentious issues have been the placement of *Euparkeria* and of the ornithosuchids and the relationships of rauisuchians. On the basis of the structure of the ankle, *Euparkeria* was assigned by Gauthier (1986) to the dinosaur lineage, but these characters are outweighed by features of the derived archosaurs that are absent in *Euparkeria* (Benton and Clark, 1988; Sereno, 1991; Gower and Weber, 1998).

The Ornithosuchidae (see p. 141) were also placed on the dinosaur line by Gauthier (1986) and Benton and Clark (1988) as they apparently share features of the limbs with ornithodirans. All subsequent analyses (e.g. Sereno, 1991; Parrish, 1993; Benton, 1999a), however, have shown that they are part of the Crurotarsi. Relationships within Crurotarsi are still uncertain. Phytosaurs appear to be the basal branch (Sereno, 1991), although only just (Benton, 1999a), but the relationships among ornithosuchids, stagonolepidids, rauisuchians and crocodylomorphs have so far defied analysis (Benton, 1999a).



Cladogram showing the relationships of the Triassic archosaurs, based on the work of Gauthier (1986), Benton and Clark (1988), Sereno (1991), Parrish (1993), Sereno *et al.* (1993), Gower and Wilkinson (1996) and Benton (1999a). See Figure 6.6 for context of Archosauria; see Box 8.5 for relationships of Dinosauria and Box 8.8 for more detail on crocodylomorph and pterosaur relationships. Synapomorphies: **A ARCHOSAURIA**, antorbital fenestra in snout wall between nostril and orbit, laterally flattened teeth with serrations, ossified laterosphenoid in braincase, lateral mandibular fenestra in posterior lower jaw bones, **B**, antorbital fossa surrounding the fenestra, pubis and ilium elongated, anterior process on iliac blade, fourth trochanter on femur, canal between astragalus and calcaneum absent, distal tarsals 1 and 2 not ossified, metatarsal 3 longer than 4; **C**, parietal foramen absent, sigmoid (S-shaped) curvature of shaft of femur, osteoderms (bony plates) running along the back; **D AVESUCHIA**, loss of palatal teeth, calcaneal tuber oriented more than 45° posterolaterally, continuous articular surfaces for fibula and distal tarsal 4 on calcaneum; **E CRUROTARSI**, 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 shaft broader than tall, calcaneal tuber distal end rounded, hemicylindrical calcaneal condyle, osteoderm sculpture; **F**, pubic acetabular margin posterior portion recessed, calcaneal tuber distal end with dorsoventrally aligned median depression; **G 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; **H ORNITHODIRA**, presacral centrum 8 longer than presacral centrum 18, deltopectoral crest on humerus subrectangular, fibula tapering and calcaneum reduced in size, astragalar posterior groove and calcaneal tuber rudimentary or absent; **I 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; **J 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.

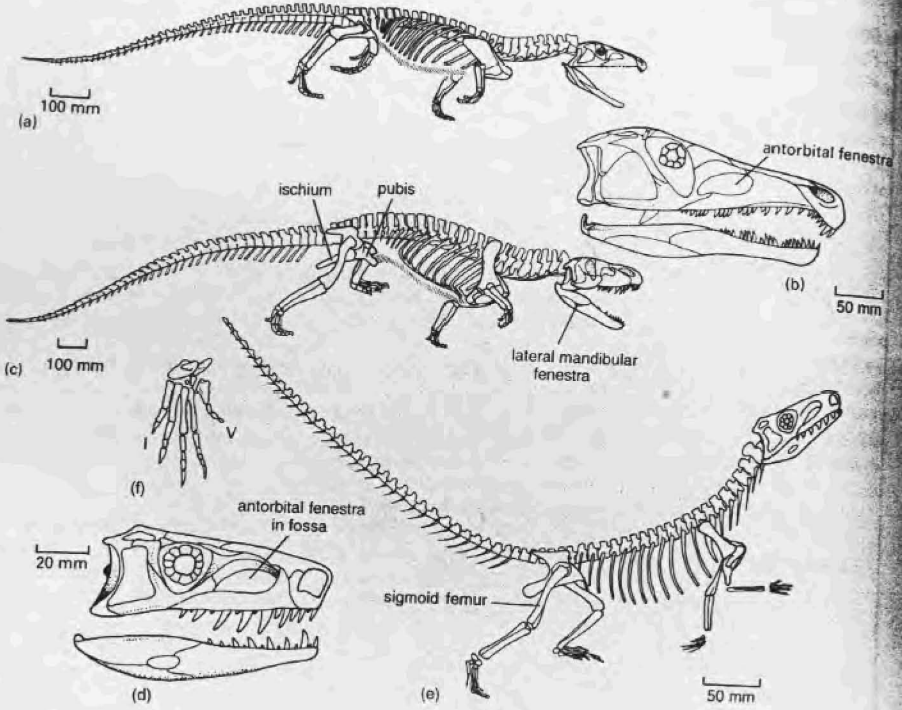


Fig. 6.2 Early Triassic archosaurs: (a, b) the proterosuchid *Proterosuchus*, skeleton in running posture and skull; (c) the erythrosuchid *Vjushkovia*, skeleton in running posture; (d–f) the agile *Euparkeria*, skull in lateral view, skeleton and foot. [Figures (a, c) based on Greg Paul *in* Parrish 1986; (b) after Cruickshank, 1972; (d–f) after Ewer, 1965.]

The Early Triassic archosaurs took over the carnivorous niches formerly occupied by the gorgonopsids and titanosuchids that had died out at the end of the Permian. *Proterosuchus* (Figure 6.2(a, b)) from South Africa (Cruickshank, 1972) shows four archosaurian 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.

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 Mid-Triassic, further basal archosaur lineages flourished for a short while. The erythrosuchids, such as *Vjushkovia* from Russia (Figure 6.2(c)), 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 pelvis, with an elongate pubis and ischium, a knob-like muscle attachment on the femur, termed the **fourth trochanter**, and metatarsal 3 longer than 4 (Gower, 2003).

A small archosaur from the early part of the Mid-Triassic of South Africa heralds the beginning of the first major radiation of the archosaurs. *Euparkeria* (Ewer, 1965), only 0.5 m or so in length (Figure 6.2(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 **osteoderms**, or bony dermal plates down the middle of the back, that place it close to the common ancestry of crocodilians and birds (Gower and Weber, 1998; Box 6.1).

6.2.2 Crurotarsi: Late Triassic archosaur diversity

The crurotarsans, members of the 'crocodilian line' of archosaur evolution, are characterized by an ankle joint that allows rotation between the astragalus and calcaneum (Sereno, 1991). The basal crurotarsans, the phytosaurs, are known mainly from the Upper Triassic of Germany (Hungerbühler, 2002) and North America. *Parasuchus* from India (Chatterjee, 1978) is 2.5 m long and exhibits crocodilian-like adaptations to fish-eating (Figure 6.3(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 prolacertiforms 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 Upper Triassic of Scotland and South America. They include forms such as *Ornithosuchus* (Walker, 1964), which ranged in length from 0.5 to 3.0 m (Figure 6.3(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 has the crurotarsan ankle, as well as numerous other characters of that clade (see Box 6.1).

The aetosaurs (Stagonolepididae) were the first herbivorous archosaurs, and they radiated nearly worldwide in the Late Triassic (Harris *et al.*, 2003). *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 6.3(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 Late Triassic carnivores, some quadrupedal and some possibly bipedal, referred to the Prestosuchidae, Rauisuchidae, Poposauridae and Chatterjeeidae. Relationships among these forms are unclear: Rauischia may be a clade, or it may be a paraphyletic group that includes ever-closer outgroups to Crocodylomorpha (Benton and Clark, 1988; Gower, 2002). The poposaurid *Postosuchus* (Figure 6.3(f)), a 2- to 5-m-long carnivore from Texas, USA (Long and Murry, 1995), was a top predator, with a high skull and deep jaws lined with long recurved teeth. The skull was narrow from side to side, and in many ways it is superficially similar to the skull of a carnivorous theropod dinosaur (see p. 155).

Saurosuchus, a rauisuchid from Argentina (Bonaparte, 1981), is one of the largest rauisuchians, reaching 6 or 7 m in length (Figure 6.3(g)). The skull (Figure 6.3(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

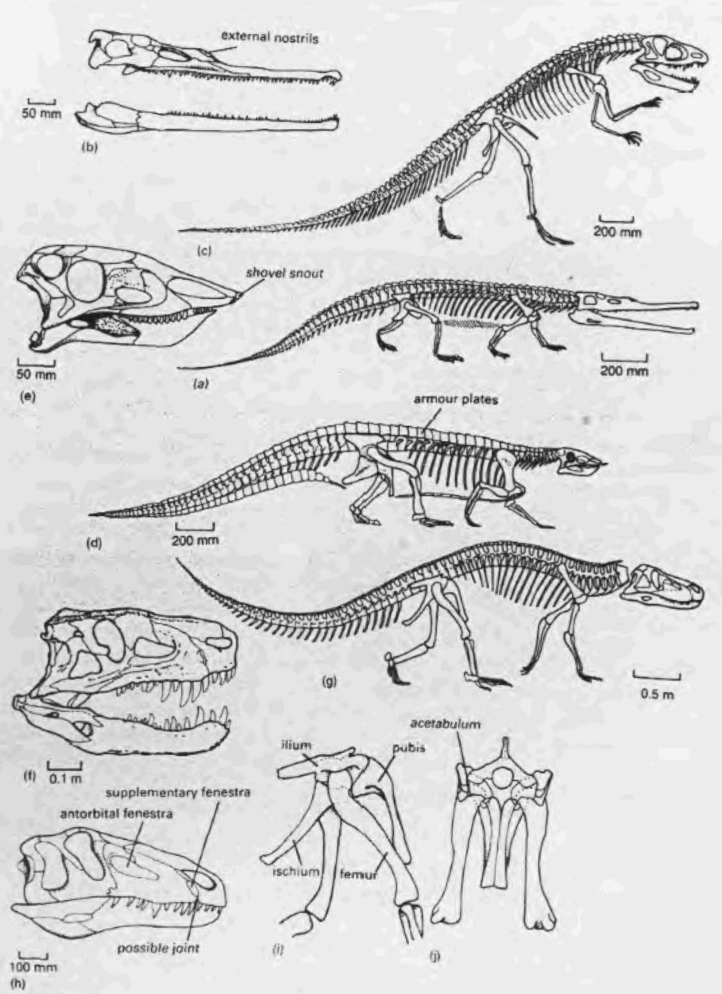


Fig. 6.3 Crurotarsal archosaurs: (a, b) the phytosaur *Parasuchus*, skeleton and skull in lateral view; (c) the ornithosuchid *Ornithosuchus*, skeleton in lateral view; (d, e) the aetosaur *Stagonolepis*: skeleton in lateral view, showing part of the armour, but most armour missing to show skeleton and skull in lateral view: (f) the rauisuchian *Postosuchus*, skull in lateral view; (g–j) the prestosuchid *Saurosuchus*, skeleton in walking pose (g), skull in lateral view (h), pelvic girdle and hind limbs in lateral (i) and anterior (j) views to show the 'pillar erect' gait. [Figures (a, b) after Chatterjee, 1978; (c) after Walker, 1964; (d, e) after Walker, 1961; (f) modified from Long and Murry, 1995; (g,h) after Bonaparte, 1981.]

(see Box 6.2) in which the femur remained vertical, the pillar-erect posture (Figure 6.3(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 skeletons of *Saurosuchus* were found in association with a rich fauna of aetosaurs, rhynchosaurs, small and large synapsids (dicynodonts and cynodonts) and some rare temnospondyls and small dinosaurs (see p. 155). *Saurosuchus* probably fed on all of these animals, but the rhynchosaur *Hyperodapedon* in particular, as it was extremely abundant in the

BOX 6.2 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 archosaurs such as *Proterosuchus* were sprawlers. **Sprawling** is the standard reptilian posture, in which the limbs are directed sideways and the body is held only a little way off the ground. Some later archosaurs, 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, possibly several times, in different Late Triassic archosaur groups: ornithosuchids, rauisuchians, early crocodylomorphs, pterosaurs and dinosauromorphs. The erect posture also arose independently during the Triassic in the cynodonts (see p. 292), 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.

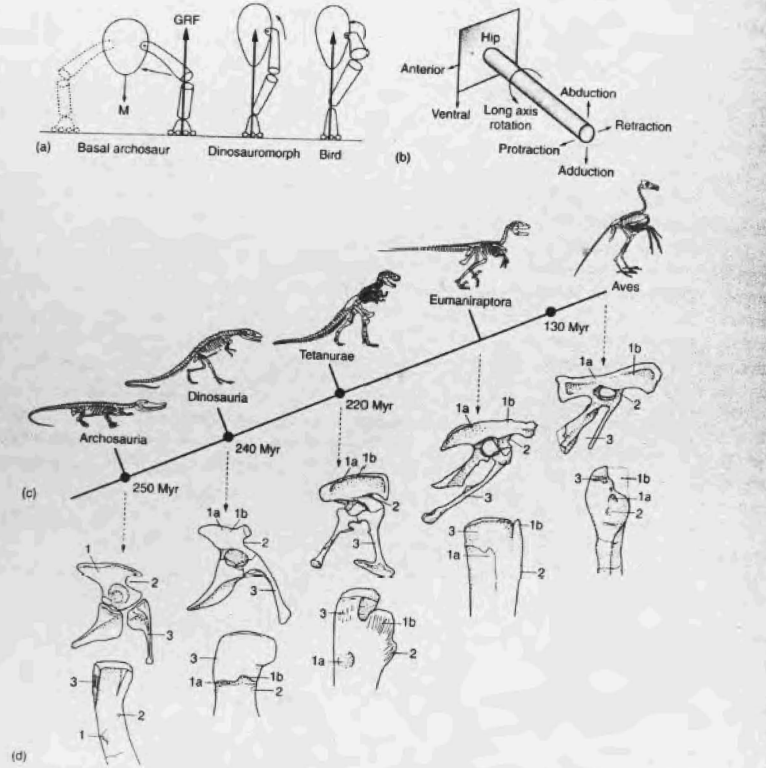
In the switch from sprawling to an erect posture (illustration (a, b)), muscle forces changed and these can be seen in a comparison of living crocodilians and birds, and in the fossils (Hutchinson and Gatesy, 2000). When a sprawler is standing still, its body is liable to collapse. This forces the knee 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 basal* 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** (forwards movement) 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

continued

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.



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 skeletons 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). (Based on information in Hutchinson and Gatesy, 2000.)

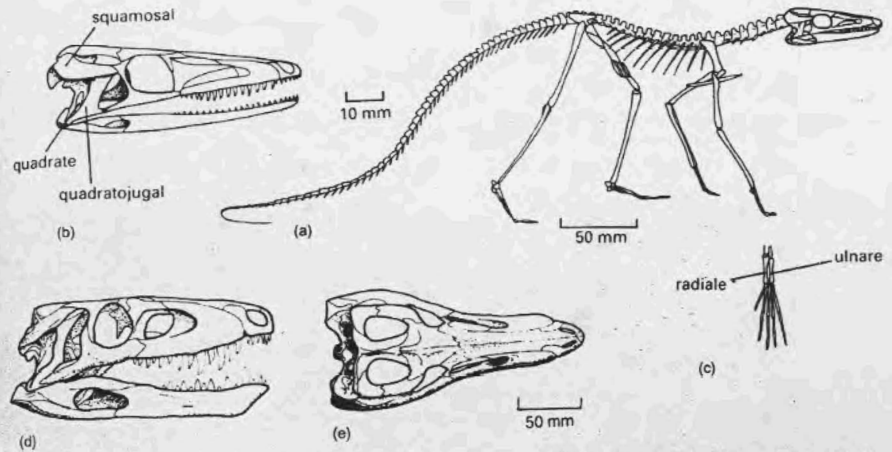


Fig. 6.4 Basal crocodylomorphs: (a–c) the saltoposuchid *Saltoposuchus*, skeleton and skull in lateral view, hand in anterior view; (d, e) the sphenosuchid *Sphenosuchus*, skull in lateral and dorsal views. [Figures (a–c), after Crush, 1984; (d, e) modified from Walker, 1990.]

Ischigualasto fauna and was large enough to make a succulent meal.

6.2.3 Crocodylomorpha: origin of the crocodilians

True crocodilians arose in the Early Jurassic (see pp. 232–7), but there were a number of close relatives in the Late Triassic. Some of the Late Triassic crocodylomorphs seem most uncrocodilian at first sight. An example is the saltoposuchid *Saltoposuchus* (Crush, 1984) from South Wales, a lightly built, delicate animal 0.5 m long (Figure 6.4(a–c)). It has a long skull with slender pointed teeth and long hindlimbs that suggest it was a biped. It probably fed on small reptiles, insects and other invertebrates.

How can this fully terrestrial insectivorous biped be a close relative of the crocodilians? *Saltoposuchus* 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 6.4(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). In addition there are a number of crocodylomorph specializations in the skull (Figure 6.4(b)): the quadrate and quadratojugal are displaced inwards towards the braincase and the cheek region is overhung by the squamosal.

Another crocodylomorph family of the Late Triassic and Early Jurassic, the Sphenosuchidae, were rather more crocodile-like in appearance. *Sphenosuchus* from the Lower Jurassic of South Africa (Walker, 1990) was a slightly heavier animal than *Saltoposuchus*, 1.4 m long, a fast runner and probably usually quadrupedal. Its skull (Figure 6.4(d, e)) is crododilian in many regards: the forwards sloping quadrate and quadratojugal, as in *Saltoposuchus*, 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 squamosal, whereas in later crocodilians it slopes further forward and also meets the laterosphenoid, a midline element, typical of archosaurs, that lies in front of the basipterygoid and prootic. The saltoposuchids and sphenosuchids were grouped as a clade Sphenosuchia in some recent cladistic analyses, but Clark and Sues (2002) suggest that 'sphenosuchians' are paraphyletic with respect to later crocodylomorphs.

6.2.4 Other archosauromorphs of the Triassic

The archosaurs were the main group of archosauromorph diapsids to rise to prominence in the Triassic, but there were three other groups. *Trilophosaurus* from the Upper Triassic of Texas (Gregory, 1945) 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 (see Box 6.3). Early forms (Dilkes, 1998) were small, but Late Triassic rhynchosaurs such as *Hyperodapedon* (Benton, 1983b; Langer *et al.*, 2000) 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 6.7(e)). The back of the skull is broader than the total length, and this vast width seems to have provided space for strong jawclosing 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.

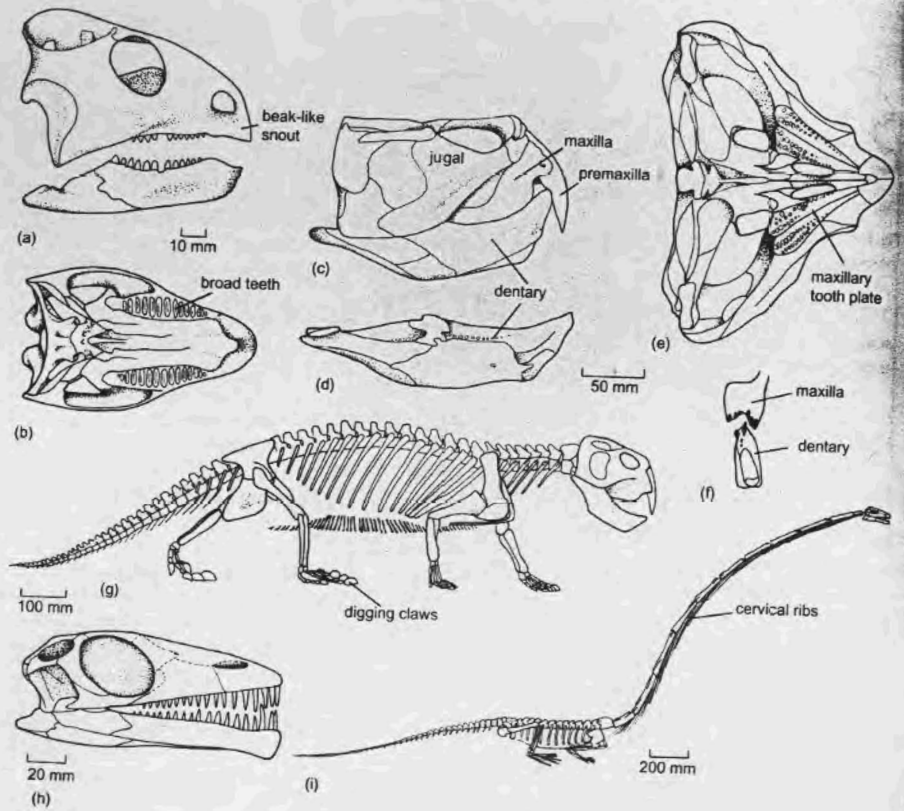


Fig. 6.5 Archosauromorphs of the Triassic: (a, b) the trilophosaurid *Trilophosaurus*, skull in lateral and ventral views; (c–g) the rhynchosaur *Hyperodapedon*: (c) skull in lateral view, (d) lower jaw in medial view, (e) skull in ventral view, (f) vertical cross-section through the tooth-bearing bones of the skull (maxilla) and lower jaw (dentary) to show the precise fit, (g) skeleton; (h, i) the prolacertiform *Tanystropheus*: (h) skull, (i) skeleton of a large species, showing the enormously elongated neck. [Figures (a, b) after Gregory, 1945; (c–g) after Benton, 1983b; (h, i) after Wild, 1973.]

The fourth group of archosauromorphs, the prolacertiforms, had appeared first in the mid-Permian, represented by *Protorosaurus* (see p. 119), and they radiated in the Triassic. Most of the Triassic forms probably looked like lizards, but by the Mid-Triassic, one of the most unusual reptilian lineages had arisen within this clade. Prolacertiforms are characterized by long necks, but that of *Tanystropheus* from Central Europe (Wild, 1973) 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) reconstructs *Tanystropheus* as a coastal swimmer that fed on small fishes that it caught by darting its head about.

The trilophosaurids, rhynchosaurs and prolacertiforms all died out in the Late Triassic, the rhynchosaurs and many of the prolacertiforms well before the end of the period, about 220 Myr ago, and the others right at the end of the period. These three groups and the archosaurs belong to the Archosauromorpha, one of the main divisions of the Diapsida (Benton, 1985; Evans, 1988; Laurin, 1991; Dilkes, 1998). The prolacertiforms and archosaurs are sister groups (Figure 6.6), sharing many characters, such as a long snout and narrow skull, long nasal bones, backwardly curved teeth and long thin cervical ribs. Dilkes (1998) found that the prolacertiforms split into two clades, *Prolacerta*, lying close to archosaurs in the cladogram, and the remaining prolacertiforms closer to the base of Archosauromorpha.

The phylogenetic scheme shown here (Figure 6.6) is very different from older views (e.g. Romer, 1966). Rhynchosaurs and prolacertiforms were regarded as true lepidosaurs, relatives of the modern lizards, and they were thus placed on the other major diapsid branch, the Lepidosauromorpha. *Tanystropheus*, for example, shares various features with the lizards, such as its incomplete lower temporal bar (Figure 6.5(h)) and specialized teeth and vertebrae (Wild, 1973). These must be convergences, however, as they are far outweighed by the evidence for archosauromorph affinity.

6.3 IN TRIASSIC SEAS

There were four main groups of reptiles in Triassic seas (McGowan and Motani, 2003; Rieppel, 2000c), the placodonts, pachypleurosaurs, nothosaurs and ichthyosaurs, all of which have the euryapsid skull pattern (see p. 112), with one (upper) temporal fenestra. Each has very different aquatic adaptations and they represent a major radiation of marine predators, probably from independent sources among the early diapsids.

BOX 6.3 THE ELGIN REPTILES

Late Triassic reptile communities are important because they document a major transition from faunas dominated by synapsids, basal archosaurs and rhynchosaurs to the new dinosaur-dominated faunas. An example is from the Lossiemouth Sandstone Formation (Carnian, c. 225 Myr ago) from Elgin in north-east Scotland, a fauna of eight reptile genera (Benton and Walker, 1985). The fossil bones were found in a fine-grained whitish-buff sandstone that was evidently deposited in sand dunes by the wind, rather than in water, because it shows dune bedding and the sand grains are well-rounded.

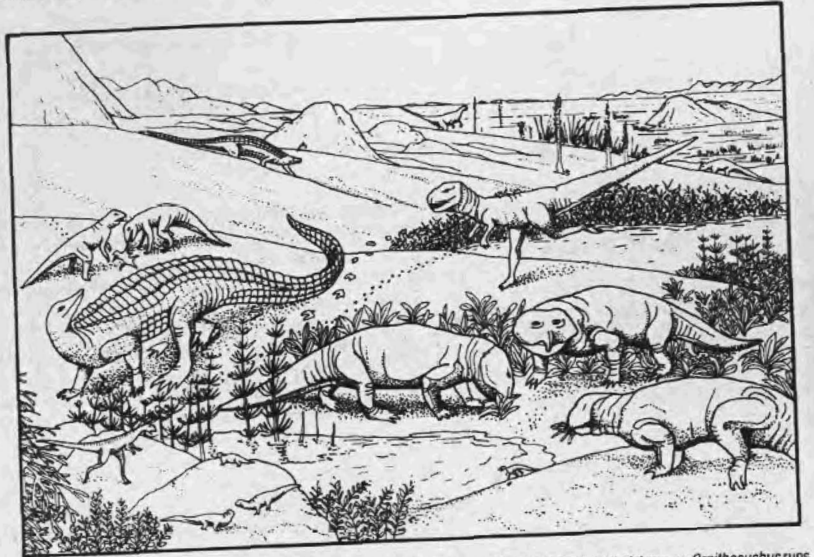
Initially, the Elgin reptiles were studied as they were found, without any preparation. Then a number of specimens were cleaned up by removing the rock with chisels, but this was not successful because the rock is hard and the bone is soft. Alick Walker pioneered a casting technique in the 1950s and 1960s in which the soft and incomplete bone was removed by the use of acid, leaving near-perfect natural moulds in the rock. Casts were taken in flexible rubber and plastic compounds; these show exquisite detail of the bone surface (illustration I) and they are easier to work with than bone as they are not fragile. The details of the anatomy of *Stagonolepis*, *Ornithosuchus*, *Hyperodapedon* and *Scleromochlus* described by Walker (1961, 1964) and Benton (1983b, 1999a) have been obtained largely by these techniques.

The dominant animals in the Elgin fauna (illustration II) are the rhynchosaur *Hyperodapedon* (Figure 6.5(c–g)) and the aetosaur *Stagonolepis* (Figure 6.3(d, e)), both medium-sized herbivores that fed on tough vegetation which they may have dug up with their snouts and powerful feet. The main predator was the crurotarsan archosaur *Ornithosuchus* (Figure 6.3(c)), large specimens of which could have attacked either of the herbivores.

Three small reptiles, the procolophonid *Leptopleuron*, the sphenodontian (see pp. 237–8) *Brachyrhinodon* and the ornithodiran archosaur *Scleromochlus* (Figure 6.8), were each about 150–200 mm long and represented 5–25% of the total fauna. *Leptopleuron* may be seen as a 'reptilian rodent' with its broad grinding back teeth and chisel-like front teeth. *Brachyrhinodon* has sharper teeth, probably for chopping small plants. *Scleromochlus* has long slender legs and it may have been able to leap around in the moving sands on the edges of the well-watered feeding grounds. These small animals were probably preyed on by young *Ornithosuchus*, by the very rare archosaur *Erpetosuchus* and the possible dinosaur *Saltopus*.

I Close-up views of specimens of *Hyperodapedon* from the Upper Triassic of Elgin, north-east Scotland, to show the quality of preservation of surface detail: (a) premaxillary beak (left) and maxilla (right), showing striation on the premaxilla and blood vessel openings in the maxilla; photograph of PVC cast (×1.3); (b) the lacrimal (tear) duct leading from the eye socket (top) into the nasal cavity (below); photograph of natural rock mould (×3.0).

Read more at http://www.morayfirth-partnership.org/mfptreasure/infozone/56.htm, a very brief account of the Elgin reptiles, and http://aleph0.clarku.edu/huxley/guide6.html, a quirky guide to Thomas Henry Huxley, the great Victorian anatomist, and his early work on the Elgin reptiles.



II The Late Triassic Elgin fauna: three *Hyperodapedon* feed on low waterside plants at the lower right; behind them, an *Ornithosuchus* runs towards an armoured *Stagonolepis* (middle left); behind it, two *Erpetosuchus* feed on a carcase, and in the lower left, a tiny dinosaur, *Saltopus*, runs towards a tiny *Brachyrhinodon* and two *Leptopleuron*. The plants are based on similar localities elsewhere, because no plants have ever been found at Elgin. (Based on a drawing by Jenny Middleton; in Benton and Walker, 1985.)

6.3.1 Placodontia

The placodonts were also most abundant in the Mid-Triassic of central Europe, some Mediterranean areas and southern China, and disappeared during the Late Triassic. *Placodus* (Figure 6.7(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 6.7(b, c)) shows all of the remarkable features of this group (Rieppel, 2000a). The teeth consist of three spatulate incisors on each pre-

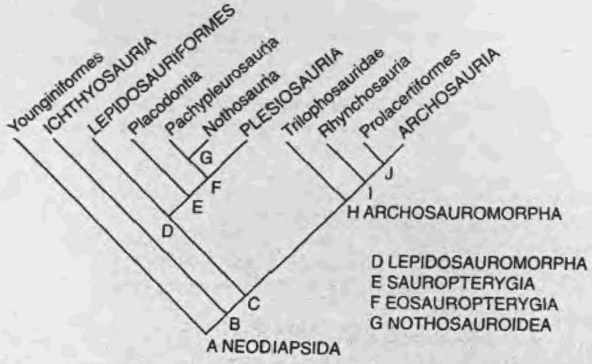


Fig. 6.6 Cladogram showing the postulated relationships of the major diapsid groups, based on the work of Benton (1985), Laurin (1991), Dilkes (1998) and Rieppel (1998). See Box 5.1 for context of Neodiapsida; see Box 6.1 for phylogeny of Archosauria. Synapomorphies: **A NEODIAPSIDA**, anterior process of squamosal narrow, trunk ribs mostly single-headed, ends of humerus robust; **B**, 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; **C**, tabular absent, squamosal mainly restricted to top of skull, quadrate deeply emarginated posteriorly, stapes slender, cleithrum absent, lateral centrale in hand small or absent, fifth distal tarsal absent, fifth metatarsal hooked; **D LEPIDOSAUROMORPHA**, supratemporal absent, teeth absent on transverse pterygoid flanges, dorsal intercentra absent, thyroid fenestra in pelvic girdle; **E 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; **F EOSAUROPTERYGIA**, 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; **G NOTHOSAUROIDEA**, quadratojugal without anterior process, occiput plate-like, clavicles broad medially, coracoid strongly waisted; **H 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; **I**, ectopterygoid expanded posteriorly, upturned retroarticular process, second sacral rib bifurcates and posterior process truncated sharply, anterior apron of pubis; **J**, long snout and narrow skull, nasals longer than frontals, recurved teeth, extensive participation of parasphenoid/basisphenoid in lateral wall of braincase, long thin tapering cervical ribs with two or three heads and an anterior process.

maxilla, 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 adductors 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.

6.3.2 Pachypleurosauria and nothosauria

The pachypleurosaurs are elongate animals with small heads, long necks and tails and paddle-like limbs

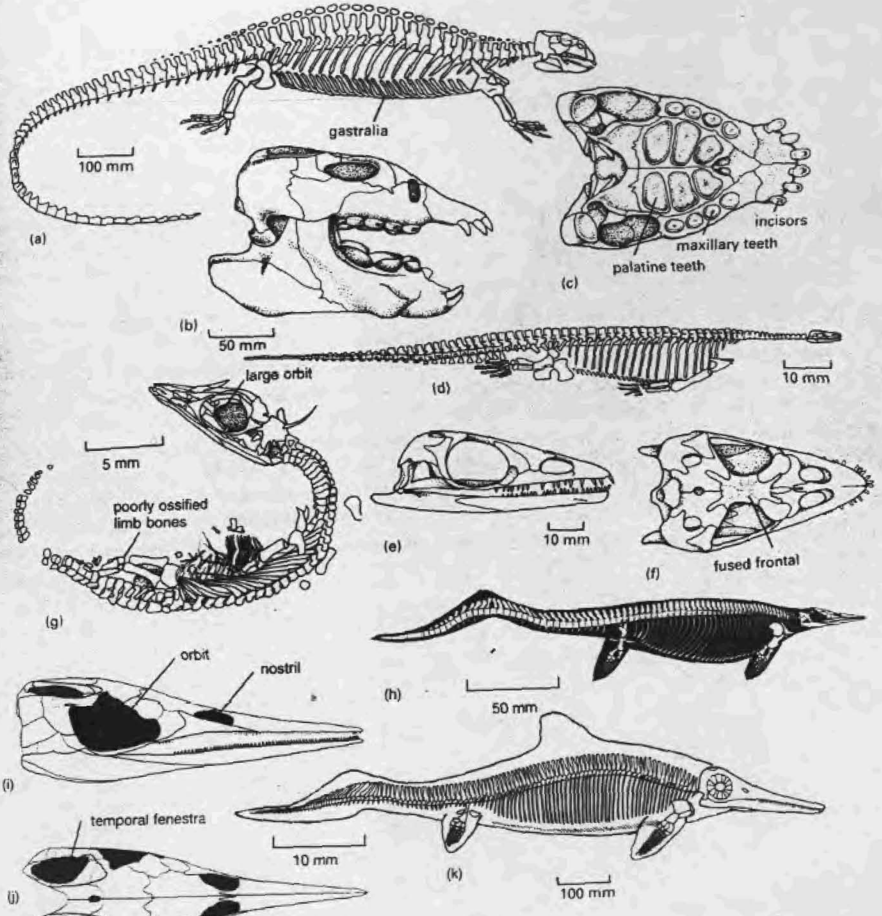


Fig. 6.7 The marine reptiles of the Triassic: (a–c) the placodont *Placodus*: (a) skeleton in walking pose; (b, c) skull in lateral and ventral views; (d–f) the pachypleurosaur *Pachypleurosaurus*: (d) skeleton; (e, f) skull in lateral and dorsal views; (g) putative embryo pachypleurosaur; (h–j) the ichthyosaur *Utatsusaurus*, skeleton and skull in lateral and dorsal views; (k) the ichthyosaur *Mixosaurus*. [Figures (a) after Peyer, 1950; (b, c) after Peyer and Kuhn-Schnyder, 1955; (d–f) after Carroll and Gaskill, 1985; (g) after Sander, 1988; (h–j) courtesy of Ryosuke Motani; (k) after Kuhn-Schnyder 1963.]

(Figure 6.7(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; Rieppel, 1995). These 0.2–1 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 6.7(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.

Among the abundant remains of pachypleurosaurs from Switzerland, Sander (1988) found a specimen of a young animal, less than 50 mm in length (Figure 6.7(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. Perhaps this juvenile had just been born, or it may even be an embryo.

The larger nothosaurs (Rieppel, 1998), 1–4 m long, had elongate heads and large temporal fenestrae, but were otherwise similar to pachypleurosaurs in their adaptations. They appear to be closely related to plesiosaurs, a group that first appeared in the Mid-Triassic, and radiated dramatically in the Jurassic and Cretaceous (see pp. 245–6).

6.3.3 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 (Motani *et al.*, 1998), a 3-m-long basal form (Figure 6.7(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 6.7(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 Mid- and Upper Triassic of central Europe, Nevada, Spitsbergen and the Far East (Massare and Callaway, 1990; McGowan and Motani, 2003). *Mixosaurus* (Figure 6.7(k)) has derived paddles with short limb bones and an excess number of phalanges. Some Late Triassic ichthyosaurs reached lengths of 15 m. They had long bullet-shaped heads, teeth only at the front of the snout, a vast rib cage and tremendously elongated limbs. The later ichthyosaurs (see pp. 246–7) were important in Jurassic and Cretaceous seas, but never reached this huge size.

6.3.4 Relationships of the Triassic marine reptiles

The placodonts, pachypleurosaurs, nothosaurs and ichthyosaurs were formerly (e.g. Romer, 1966) combined in the group Euryapsida, whose ancestry was seen as rather mysterious. Since then, many authors have argued that all these marine groups are modified diapsids of one kind or another (Carroll, 1987; Massare and Calloway, 1990), and more particularly neodiapsids, with sauropterygians at least lying on the lepidosauromorph line (Rieppel, 1993, 1995, 1998). The position of the ichthyosaurs is uncertain, either as close relatives of the lepidosauromorphs too, or as an outgroup to Lepidosauromorpha + Archosauromorpha (Motani *et al.*, 1998).

Equally, it is clear that the marine groups fall into at least two clades, the Ichthyosauria and the Sauropterygia, which consists of placodonts, pachypleurosaurs, nothosaurs and plesiosaurs (Storrs, 1991; Rieppel, 1993, 1995, 1998). In earlier analyses, placodonts fell between pachypleurosaurs and nothosaurs, but Rieppel (1998) finds a monophyletic Nothosauroidea, consisting of pachypleurosaurs and nothosaurs, as is shown here (Figure 6.6).

6.4 THE ORIGIN OF THE DINOSAURS

The major radiation of archosaurs in the Mid- to Late Triassic, marked by the split of the Crurotarsi and the Ornithodira (see pp. 138–45), provided a starting point for the radiation of the dinosaurs. The oldest dinosaurs date from the earliest Late Triassic (mid-Carnian), although their sister group, *Marasuchus*, is latest Mid-Triassic in age, which implies an origin of dinosaurs at least by that time. The dinosaurs radiated dramatically during the last 20 Myr of the Triassic, the Norian Stage, 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 an extinction event. An understanding of the origin of the dinosaurs must start with a study of the earliest ornithodirans.

6.4.1 Ornithodira: dinosaurs and relatives

The closest major outgroup of the dinosaurs may be 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 pp. 224–9). Pterosaurs and dinosauromorphs together are termed the Ornithodira.

A small reptile from the Upper Triassic of Elgin, *Scleromochlus* (Figure 6.8(a, b)), appears to be an outgroup to Ornithodira, the basal member of the dinosaur branch of archosaurian evolution, termed the Avemetatarsalia (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 ornithodirans. *Scleromochlus* has sometimes been allied with Pterosauria (Sereno, 1991), but it appears more firmly located in the phylogeny at the base of Avemetatarsalia (Benton, 1999a). 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 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 Mid-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), characterized 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 6.8(c, d)) was a lightly built flesh-eater, some 1.3 m long, that 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 (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

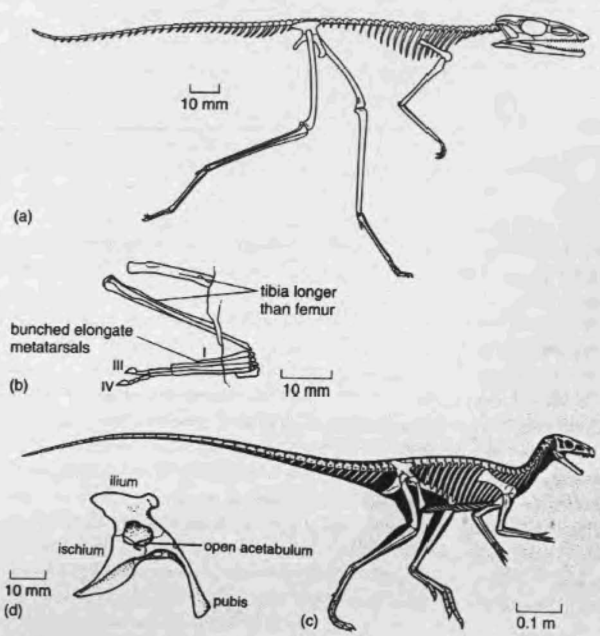


Fig. 6.8 Basal avemetatarsalians: (a, b) *Scleromochlus*: (a) skeleton in lateral view, (b) anterior view of the foot; (c, d) the basal dinosauromorph *Marasuchus*: (c) skeleton in lateral view, (d) pelvis in lateral view. [Figures (a, b) based on Benton (1999a); (c, d) courtesy of Carol Abraczinskas and Paul Sereno.]

for grappling with prey and for passing food to its mouth.

6.4.2 The oldest dinosaurs

Older accounts frequently state that dinosaurs arose early in the Triassic and evidence in the form of skeletons and footprints is often quoted. The supposed skeletal remains of dinosaurs from before the Late Triassic turn out, though, to belong to prolacertiforms, rauisuchians and other non-dinosaurian groups (Wild, 1973; Benton, 1986a, 1994). Dinosaur footprints, generally showing three toes and no heels, because of their digitigrade posture and the reduction of toes 1 and 5, had also been recorded from the Lower and Mid-Triassic of various parts of the world, but critical re-examination (Thulborn, 1990; King and Benton, 1996) shows that they have been wrongly identified.

The oldest true dinosaurs are known from the early part of the Late Triassic (the Carnian Stage, 230–220 Myr ago) from various parts of the world. The best specimens come from the Ischigualasto Formation of Argentina, source also of the rauisuchid *Saurosuchus* (see p. 141). The Ischigualasto dinosaurs, *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) is a lightweight animal 1 m long (Figure 6.9(a)), 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.

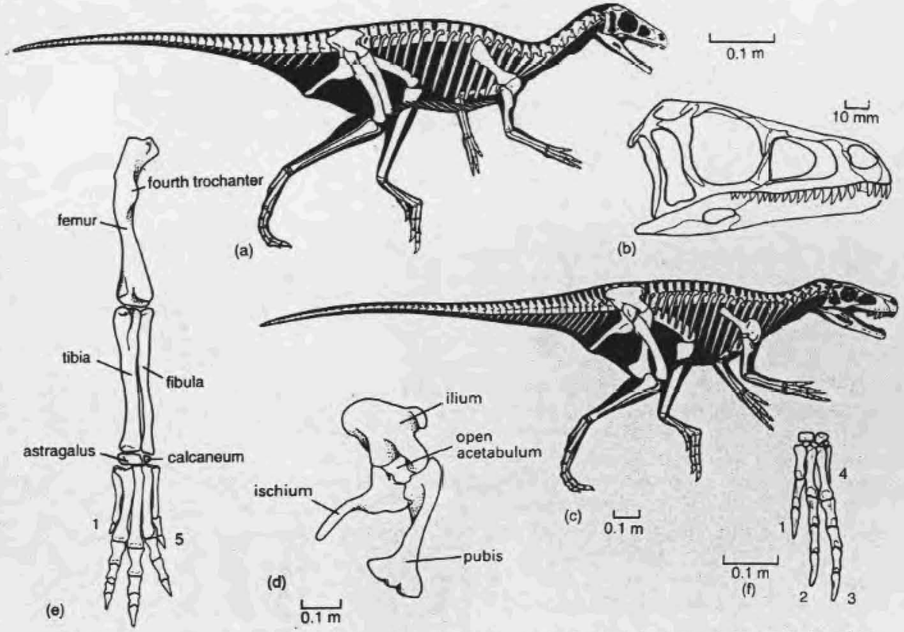


Fig. 6.9 The first dinosaurs: (a, b) *Eoraptor*, skeleton and skull in lateral view; (c–f) *Herrerasaurus*, skeleton in lateral view (c), pelvic girdle showing dinosaurian lay-out of the bones and open acetabulum (d), hindlimb, showing large fourth trochanter on femur and long digitigrade foot (e), hand, showing reduced digits 4 and 5 (f). [Figures (a–c, f) courtesy of Carol Abraczinskas and Paul Sereno; (d, e) after Galton 1977.]

Herrerasaurus (Sereno and Novas, 1992) is a larger, more heavily built animal 3 m long (Figure 6.9(c–f)). It shows a number synapomorphies of the Dinosauria, features that are not seen in *Marasuchus* or the pterosaurs: the acetabulum is fully open (Figure 6.9(d)) and the head of the femur is bent inwards (Figure 6.9(e)). *Herrerasaurus* has a short arm and a strong hand (Figure 6.9(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.*, 1993) as basal theropods, although they may turn out either to be basal saurischians or even basal dinosaurs (Langer *et al.*, 1999; see Box 8.5).

At one time, most palaeontologists regarded the dinosaurs as a diverse assemblage of archosaurs that arose from several ancestors—a polyphyletic group. Cladistic analyses (e.g. Gauthier, 1986; Benton and Clark, 1988; Sereno, 1991) have indicated, however, that the Dinosauria is a monophyletic group, characterized by many features (see Box 6.1). Other Carnian dinosaurs include basal ornithischians and basal sauropodomorphs (Langer *et al.*, 1999), but they, *Eoraptor* and *Herrerasaurus*, were only rare elements in their faunas (1–3% 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?

6.4.3 Radiation of the dinosaurs—competition or mass extinction?

There are currently two ways of viewing the radiation of the dinosaurs in the Late Triassic. Either they radiated opportunistically after a mass extinction event, or they competed over a longer time-span with the synapsids, rhynchosaurs and basal archosaurs, and eventually prevailed.

Until recently, most authors (e.g. Bakker, 1972; Charig, 1984) favoured the competitive model for four reasons. First, as mentioned above, many considered that the dinosaurs were a polyphyletic assemblage and hence that dinosaurs arose several times as a result of similar competitive pressures. Second, the origin of the dinosaurs was seen as a drawn-out affair that started early in the Mid-Triassic and involved extensive and long-term competition (Figure 6.10). The dinosaur ancestors were regarded as superior animals, with advanced locomotory adaptations (erect gait) or physiological advances (warm-bloodedness, or cold-bloodedness: both cases have been argued!) that progressively competed with, and caused the extinction of, all of the synapsids and basal archosaurs. Third, the appearance of the dinosaurs has often been regarded as a great leap forward in evolutionary terms.

A fourth reason why many palaeontologists accepted the competitive model for the radiation of the dinosaurs was more general. It had commonly been assumed that the evolution of life is in some way progressive, that more recent plants and animals are inevitably better than those that went before. So, modern mammals might be said to be better competitors than archaic mammals, archaic mammals might be better than dinosaurs and dinosaurs might be better than their forerunners. This assumption of progress has never been demonstrated (Benton, 1987), and indeed the major changes in world floras and faunas might equally well be associated with expansions into new ecospace, involving no direct competition with pre-existing forms at all.

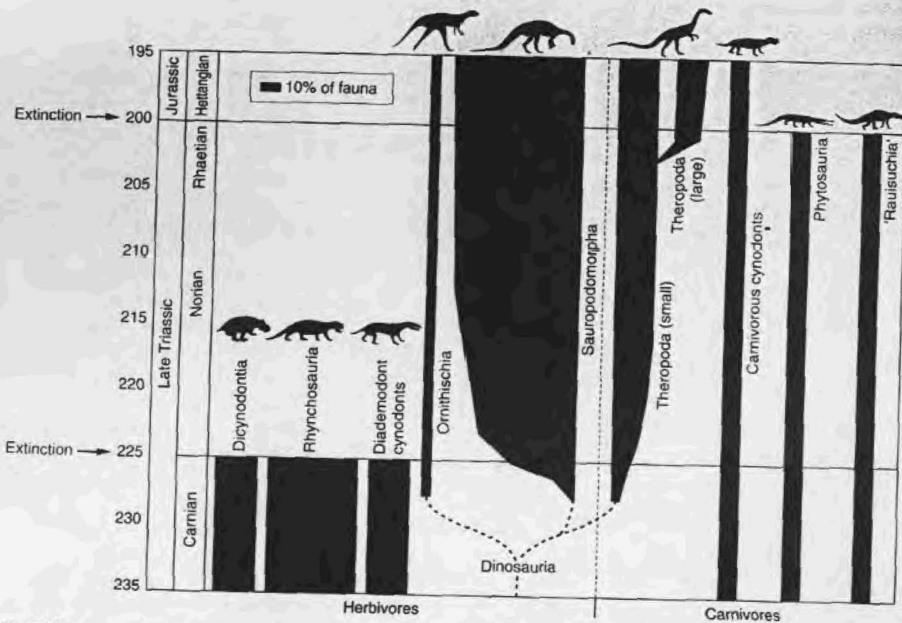


Fig. 6.10 The expansion of the dinosaurs in two phases: (1) sauropodomorphs expanded in abundance and diversity at the beginning of the Norian, after the extinction of dominant herbivore groups (rhynchosaurs, dicynodonts, chiniquodontid cynodonts); (2) theropods diversified, with the appearance of large species, after the extinction of phytosaurs and 'rauisuchians' at the end of the Triassic. The end-Carnian and end-Triassic extinction events are indicated.

Several lines of evidence (Benton 1983a, 1986a, 1994) suggest that the dinosaurs radiated after ecospace had been cleared during the end-Carnian extinction event (Figure 6.10) and that the dinosaurs did not establish their pre-eminence after a long period of competition with precursor groups.

1 The fossil record does not show a gradual take-over, but two rapid expansions after extinction events. The first dinosaurs in the Carnian were rare (1–3% of individuals). An extinction event at the end of the Carnian saw the disappearance of all dominant herbivore groups—the dicynodonts, herbivorous cynodonts and rhynchosaurs. Herbivorous dinosaurs then radiated seemingly rapidly in the early Norian, rising to 50–90% of individuals. Dinosaurs diversified further in the Early Jurassic after a second mass extinction at the very end of the Triassic when the remaining basal archosaurs and other groups died out.

2 The first dinosaurs had the key characters that assured their later success, but they did not take over at once (Sereno, 1999). During the Carnian, all three major dinosaurian lineages were present, but theropods and sauropodomorphs did not radiate for some 5–10 Myr after their origin, and ornithischians 20–25 Myr later, in the Early Jurassic.

3 The 'superior adaptations' of dinosaurs were probably not so profound as was once thought. Many other archosaurs also evolved erect gait in the Late Triassic, and yet they died out (e.g. aetosaurs, rauisuchians, ornithosuchids and some early crocodylomorphs).

4 There were other extinctions at the end of the Carnian. The *Dicroidium* flora of the southern hemisphere gave way to a worldwide conifer flora about this time (see p. 138). 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.

5 The idea that simple competition can drive the replacement of one major group by another is an oversimplification. Competition between families or orders of animals is very different from the ecological observation of competition within or between species. In palaeontological examples such as this, competition has often been assumed to have been the mechanism, but the evidence has generally been shown to be weak (Benton, 1987).

This kind of macroevolutionary debate is hard to set out in clearly testable form. Many palaeontologists would prefer not to investigate such questions, regarding them as story-telling of the worst sort. Intelligent people are bound to ask questions about major events, whether mass extinctions or evolutionary replacements; it would be unsatisfactory simply to say 'we do not know, and never will'. And, as the quality of our understanding of the fossil record improves (more fossils, better dating, better geographical coverage), it is possible to home in on events and dissect them in increasing detail.

6.5 FURTHER READING

Research on Triassic vertebrates, including aspects of faunal change and the origin of the dinosaurs, is presented in volumes of collected papers, such as Padian (1986) and Fraser and Sues (1994). Tetrapods of the Russian Permo-Triassic are summarized in Benton *et al.* (2000b). Sereno (1991) and Benton (1999a) present comprehensive cladistic overviews of archosaur phylogeny, and Sereno (1999) gives a broad picture of dinosaur phylogeny.

Useful web pages include http://rainbow.ldeo.columbia.edu/courses/v1001/9.html on the Triassic and its fossil tetrapods, http://www.museums.org.za/sam/resource/palaeo/cluver/ on the Permo-Triassic in the Karoo, South Africa and http://tolweb.org/tree?group=Diapsida&contgroup=Amniota on diapsid phylogeny. You can see a detailed three-dimensional dissection of the skull of the 'rauisuchian' *Saurosuchus* at http://digimorph.org/specimens/Saurosuchus_galilei/.

CHAPTER 7

The Evolution of Fishes after the Devonian

KEY QUESTIONS IN THIS CHAPTER

1 How did modern fish groups evolve after the Devonian?
2 What were 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 Where do the modern 'living fossil' fishes, such as bichirs, sturgeons, paddlefishes, gars and bowfins, fit into the phylogeny of fossil forms?
7 Where did the teleosts originate from?
8 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, placoderms and acanthodians (see Chapter 3), two main groups filled the seas. The Chondrichthyes (sharks and rays) diversified at different points and achieved high diversity at times. The 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 so on, are bony fishes that form part of a vast radiation that began over 150 Myr ago. Several primitive fish lineages that were important in the Silurian and Devonian—the agnathans and lungfishes, as well as the coelacanths (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 (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 Gaudin (1991), de Carvalho (1996) and Coates and Sequeira (2001a) are followed.

7.1.1 Symmorida

The symmoridans, possibly a clade or possibly paraphyletic (Coates and Sequeira, 2001a), include some unusual early shark families. The symmoriids such as *Denaea* (Figure 7.1(a)) have 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.

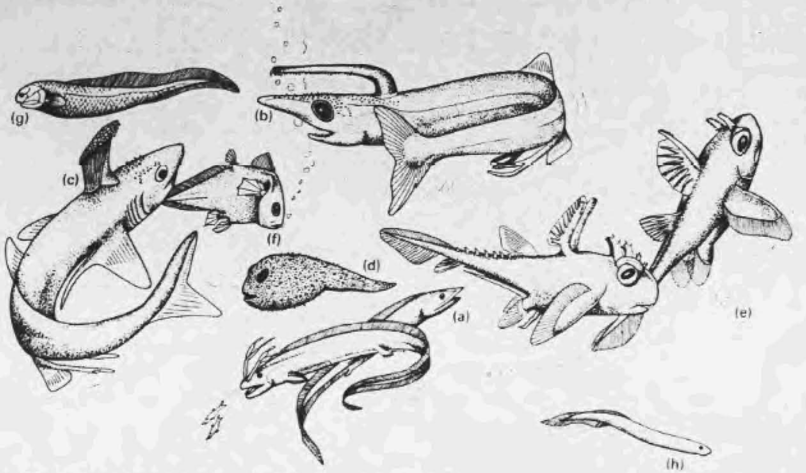
The most striking symmoridans are the falcatids and stethacanthids, two families of Carboniferous spined sharks (see Box 7.1). *Falcatus* (Lund, 1985), a small shark up to 145 mm long (Figure 7.1(b)), looks like a dogfish except that a long shelf-like spine extends from roots deep in the muscles of the 'shoulder' region to run over the head, 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). It 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

BOX 7.1 THE AGE OF SHARKS

Recent studies of Lower Carboniferous rocks in central Scotland (Wood, 1982; Coates and Sequeira, 1998, 2001b) and Montana, USA (Lund, 1985, 1989; Janvier and Lund, 1985) have revealed a wealth of new fossils, often beautifully preserved. The Montana fauna, from the Bear Gulch Limestone (Namurian, c. 325 Myr ago), is particularly striking—a world of sharks (see illustration I)! *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*; 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, a professional collector, in 1981 (Wood, 1982), and it has yielded superb specimens of *Akmonistion* (see illustration II) and other sharks like those from the Bear Gulch Limestone, as well as numerous palaeoniscoid bony fishes, acanthodians and a coelacanth.



I The world of (a–e) sharks and chimaeras and (f–h) other fishes, in the mid-Carboniferous Bear Gulch Limestone of Montana, USA: (a) the chondrenchelyiform *Harpagofutator*; (b) the symmoridan *Falcatus*; (c) the symmoridan *Stethacanthus*; (d) the holocephalan *Delphyodontos*; (e) the holocephalan *Echinochimaera*; (f) the coelacanth *Allenypterus*; (g) the actinopterygian *Paratarassius*; (h) the lamprey *Hardistiella*. (After Janvier and Lund, 1985.)

Read more about the Bear Gulch fishes and their setting at http://www.sju.edu/research/bear_gulch and the Bearsden *Akmonistion* at http://www.hunterian.gla.ac.uk/news/archive/shark/shark.shtml and http://www.hunterian.gla.ac.uk/museum/earth/bear.html.

II A specimen of *Akmonistion*, a close relative of *Stethacanthus*, from the Mid-Carboniferous of Bearsden, Glasgow, Scotland, showing the remarkable shoulder spine. The specimen is 0.5 m long. (Courtesy of Stan Wood.)

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 (Zangerl, 1981). 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. In edestids uniquely, the older small teeth are retained in the whorl. The tooth whorl fits between the two lower jaws (Figure 7.1(e)) and operates against similar sharp teeth in the upper jaw. The rest of the eugeneodontid skeleton is poorly known, except in *Fadenia* from the Lower 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.

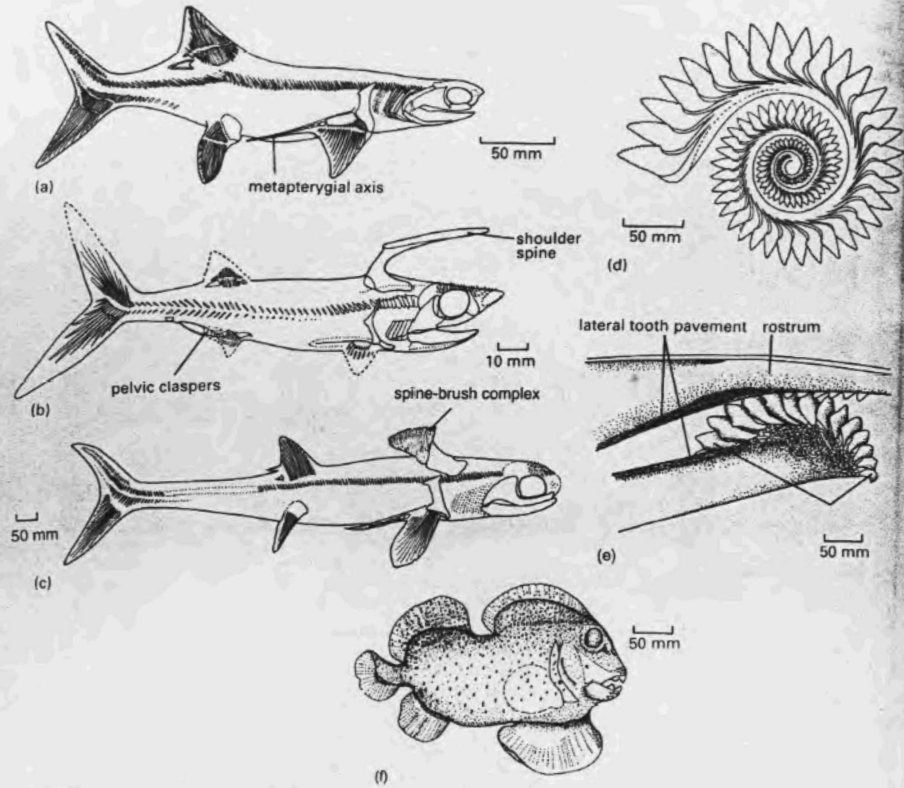


Fig. 7.1 Early sharks: (a–c) symmoridans, (d, e) eugeneodontiforms and (f) petalodontiform: (a) *Denaea*; (b) male *Falcatus* with spine and claspers; (c) *Stethacanthus*; (d) tooth whorl of *Helicoprion*; (e) tooth whorl of *Sarcoprion* in place at the tip of the lower jaw and acting against a tooth pavement in the snout (rostrum); (f) *Belantsea*. [Figure (a) after Schaeffer and Williams, 1977; (b) after Lund, 1985; (c) modified from Zangerl, 1981; (d, e) after Moy-Thomas and Miles, 1971; (f) after Lund, 1989.]

7.1.3 Xenacanthiformes, ctenacanthiformes and hybodontiformes

The xenacanths (Hampe, 2003), 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 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. 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.

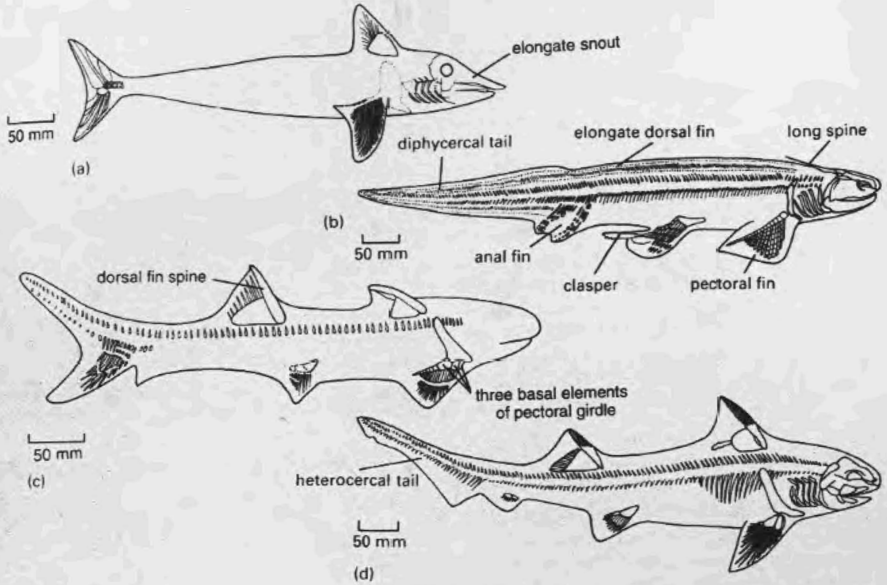


Fig. 7.2 Derived Palaeozoic and Mesozoic sharks: (a) eugeneodontiform, (b) xenacanth, (c) ctenacanth and (d) hybodont: (a) *Fadenia*; (b) *Xenacanthus*; (c) *Ctenacanthus*; (d) *Hybodus*. [Figure (a) after Dick, 1981; (b–d) after Schaeffer and Williams, 1977.]

The ctenacanths, an ill-defined group, include many forms dating from the Devonian to the Triassic. They showed a close approach in their fin spines to modern sharks: there are two dorsal fin spines, the fin spines 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 of preservation problems.

The hybodonts may have arisen as early as the Devonian and certainly by the Carboniferous, but their main diversification apparently 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 pages 164–9). Typical hybodonts, such as *Hybodus* (Figure 7.2(d)), were probably sluggish swimmers, but capable of short fast bursts of speed 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 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 some 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 Subterbranchialia: Holocephali

The chondrichthyans so far described are known largely from the Carboniferous and Permian periods, but another clade that originated in the Devonian and radiated in the Carboniferous, the subterbranchialians, still survives today. The Subclass Subterbranchialia includes two extinct groups from the Carboniferous, the orders Iniopterygiformes and Chondrenchelyiformes, as well as the extant Superorder Holocephali, the chimaeras or ratfishes (Stahl, 1999).

The iniopterygiforms *Sibyrhynchus* and *Iniopteryx* from the Upper Carboniferous of midwestern USA (Figure 7.3(a, b)) have large heads, very long pectoral fins and rounded tail fins (Zangerl and Case, 1973). 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 Lower Carboniferous of Scotland (Figure 7.3(c)) 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 p. 54). The pelvic fin is small and males have claspers.

Typical chimaeras of modern form appeared in the Jurassic, although there are some tantalizing relatives from the Carboniferous. An example is *Helodus* (Figure 7.3(d)), known from freshwater sediments of Europe, which has the fins and jaws of a chimaeroid, but has a number of small teeth and a heterocercal tail. Later 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, also evolved from Palaeozoic ancestors. Modern sharks, the neoselachians, diversified in the later Mesozoic and Cenozoic seas.

7.2.1 Neolselachii: 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 42 families. 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 (Cuny and Benton, 1999). The neoselachians are characterized by numerous derived characters (de Carvalho, 1996; Shirai, 1996), such as the possession of calcified centra. Many other derived characters relate to a more adaptable feeding system and capabilities of faster swimming than in precursor shark groups.

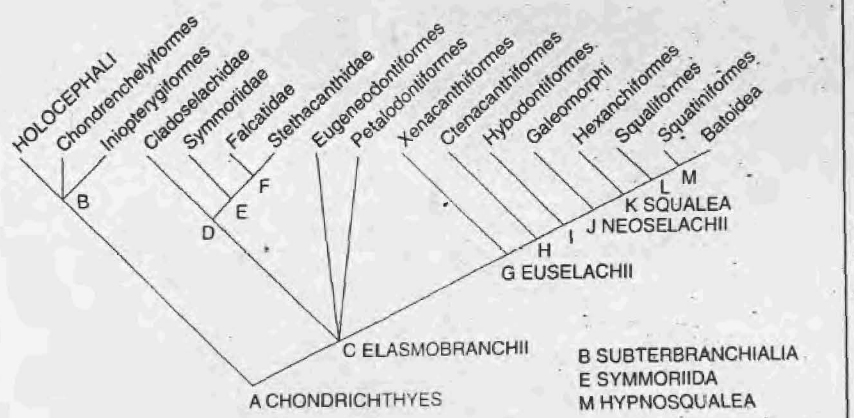
The jaws of neoselachians open more widely than in earlier forms because of greater mobility about the jaw joint and a highly kinetic palatoquadrate and hyomandibular (see p. 54, Figure 3.11(c)). This allows most neoselachian sharks to have a wide gape, as the palatoquadrate moves forwards relative to the braincase and the hyomandibular rotates as the lower jaw opens (Wilga *et al.*, 2000). 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

BOX 7.2 CHONDRICHTHYAN RELATIONSHIPS

Living chondrichthyans are readily classified as either sharks and rays (elasmobranchs) or chimaeras (holocephalans), and most fossil taxa can be assigned to one or other branch of chondrichthyan evolution. There has been a great deal of debate about the placement of major taxa, whether for example the holocephalans are part of the elasmobranch clade, with symmoridans and cladoselachids as their outgroups, or whether there was a clear division between the clades Elasmobranchii and Subterbranchialia (Gaudin, 1991), the view accepted here (see cladogram).

The hybodonts, ctenacanths and xenacanths form successive outgroups to the Neoselachii, but below that, the classification of elasmobranchs is uncertain and one possible solution, based on the work of Gaudin (1991) and Coates and Sequeira (2001a), is shown here. The relationships of the extant neoselachians are debated, but the pattern indicated here is supported by several analyses (de Carvalho, 1996; Shirai, 1996).

Molecular analyses of chondrichthyan phylogeny so far do not support the morphological tree. Douady and Douzery (2003) find that Galeomorphii are paraphyletic to other sharks and that batoids are not a part of Squalea and Hypnosqualea, but are a basal group to all the sharks, quite separate, as was the traditional, pre-cladistic view. Winchill *et al.* (2004) confirm the molecular evidence against Hypnosqualea, but they find some evidence for monophyly of Galeomorphii.



Cladogram showing postulated relationships of cartilaginous fishes, based on Gaudin (1991), de Carvalho (1996), Shirai (1996) and Coates and Sequeira (2001a). 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 SUBTERBRANCHIALIA**, pelvic metapterygium that spans the entire fin base; **C ELASMOBRANCHII**, hypochordal (lower) lobe of caudal fin large; **D**, hyomandibular crescentic; **E SYMMORIIDA**, posterior dorsal fin with delta-shaped cartilage; **F**, dorsal spine concave forwards and with large opening behind; **G EUSELACHII**, braincase with elongated otic region, anal fin, tribasal pectoral fin (metapterygium, mesopterygium, propterygium); **H**, two dorsal fin spines, fin spines with pectinate ornament, deeply inserted fin spines; **I**, palatoquadrates fused at the symphysis, calcified ribs, pelvic metapterygium articulates with all or all but first radials; **J NEOSELACHII**, extrabranchial cartilages on hyomandibular (epihyal) only, right and left coracoids fused; **K 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; **M HYPNOSQUALEA**, anterior expansion of pectoral fin.

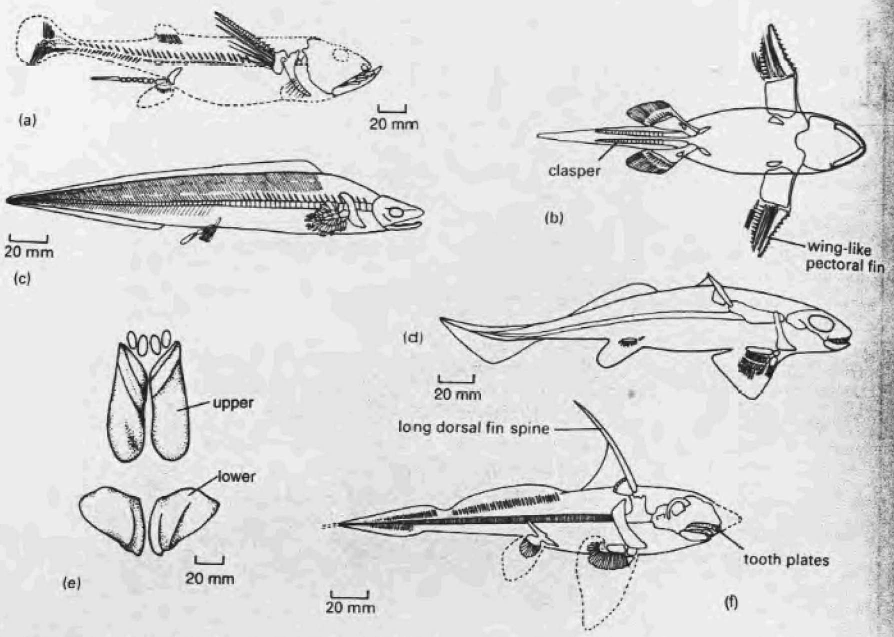


Fig. 7.3 Early subterbranchialians (chimaeras and relatives) from (a–e) the Carboniferous and (f) the Jurassic: (a) the iniopterygian *Sibyrhynchus*; (b) the iniopterygian *Iniopteryx* in ventral view; (c) the chondrenchelyiform *Chondrenchelys*; (d) the holocephalan *Helodus*; (e) upper and lower dentition of the holocephalan *Deltoptychius*; (f) the holocephalan *Ischyodus*. [Figures (a, b) after Zangerl and Case, 1973; (c, d) after Moy-Thomas and Miles, 1971; (e) after Patterson, 1965; (f) after Schaeffer and Williams, 1977.]

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 the primitive 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

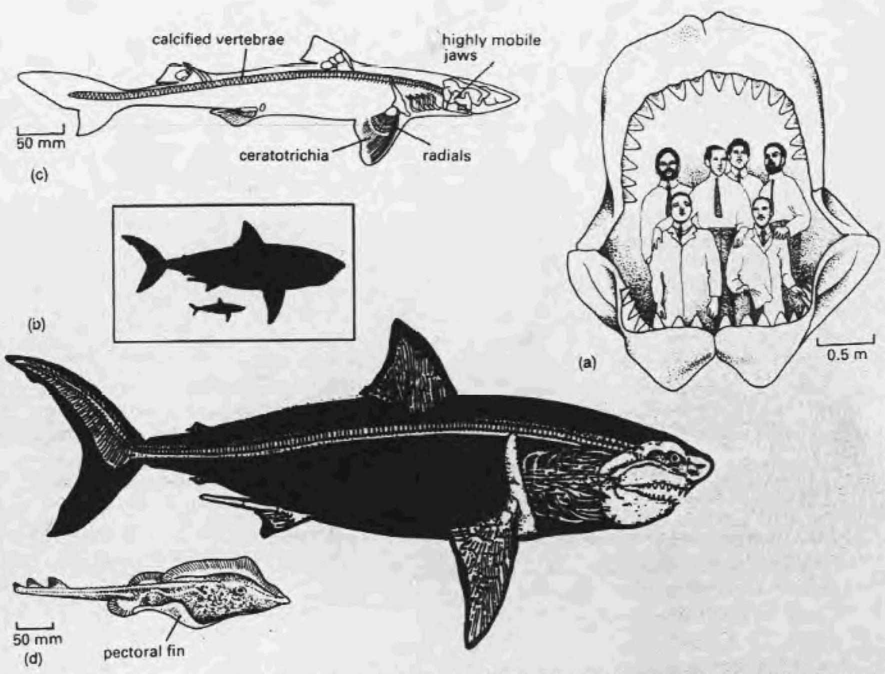


Fig. 7.4 Modern sharks and rays: (a) the jaws of the giant Tertiary galeomorph shark *Carcharocles*, reconstructed from isolated teeth and probably too large; (b) restoration of the giant fossil *Carcharocles* and compararison of its size with the living great white shark *Carcharodon* (in box); (c) the modern squalomorph shark *Squalus*; (d) the modern ray *Raja*. [Figure (a) based on Pough *et al.*, 2002; (b) courtesy of Mike Gottfried; (c) after Schaeffer and Williams, 1977; (d) after Young, 1981.]

by flexible collagenous rods called ceratotrichia or actinotrichia (Figure 7.4(c)).

The modern neoselachians fall into five main clades (de Carvalho, 1996; Shirai, 1996; see Box 7.2).

1 The galeomorphs, the largest group of some 250 species, are divided into the orders Heterodontiformes (the bullhead sharks, 8 species), Orectolobiformes (the carpet sharks, including the whale shark, 30 species), Lamniformes (the mackerel sharks, including the great white shark, 15 species) and Carchariniformes (the requiem and hammerhead sharks, 200 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 feed on krill, small floating crustaceans that they strain from the water. An even larger fossil shark has been reported. *Carcharocles*, a relative of the living great white shark, is known only from triangular teeth up to 168 mm long 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 *et al.*, 1996), however, has suggested that

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 two recent studies of lamniform sharks. Shimada (1997) documents predatory behaviour by the ginsu shark *Cretoxyrhina* from the Upper Cretaceous Niobrara Chalk of Kansas. In one specimen, a complete 5-m-long *Cretoxyrhina* skeleton is closely associated with bones of the large teleost *Xiphactinus* (see Figure 7.9(f)), and other sharks contain smaller teleost fishes in their stomach areas. Vertebrae of mosasaurs (see p. 243) show series of bite marks and some even have *Cretoxyrhina* teeth embedded in the bone. *Xiphactinus* and mosasaurs were themselves active predators, so *Cretoxyrhina* was evidently the top predator, or 'superpredator', in Niobrara Chalk seas, something like the great white shark today. There are three lines of evidence that *Cretoxyrhina* was attacking live prey: (1) some bitten bones show evidence of healing (Martin and Rothschild, 1989); (2) whole large fishes in the stomach area were presumably attacked and swallowed; (3) the tooth shape is the 'tearing type', with long slender cusps and gaps between teeth.

While *Cretoxyrhina* 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 sea-bed. 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.

Read more at http://www.elasmo-research.org/education/evolution/cretoxyrhina.htm, http://www.elasmo-research.org/education/evolution/squalicorax.htm, http://www.oceansofkansas.com/sharks.html and http://www.oceansofkansas.com/bite.html.

Shark attack in the Late Cretaceous: (a) right metatarsal of a young hadrosaur showing an embedded *Squalicorax* tooth; (b) a rib of the mosasaur *Platecarpus* showing scratch marks produced by *Squalicorax*. (Photographs by Jon Haney; courtesy of David Schwimmer.)

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) *Carcharodon*. Nonetheless, this was a terrifying giant marine predator (Figure 7.4(b)).

2 The hexanchiforms, the frilled and cow sharks, are a small group 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 The squaliforms, three families containing over 70 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 The squatiniforms are a small group containing one family, known from the Late Jurassic to the present day. These sharks, represented today by 13 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 (Shirai, 1996).

5 The batoids include more than 500 species of skates and rays. They are specialized mainly for life on the sea-floor, 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. Most of the earlier shark groups had died out in the Carboniferous and Permian, but the xenacanths and ctenacanths survived well into the Triassic. There is no evidence that the new shark groups were competitively replacing their forebears: indeed, an observer in the Late Triassic might have had some trouble finding any chondrichthyan fishes other than hybodonts. It is odd also that the dramatic radiation of neoselachians corresponded with the radiations of other marine predators, the ichthyosaurs and plesiosaurs (see Chapter 8), some of which at least must have competed for the same food.

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, perhaps originating from Triassic ctenacanths, 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 p. 243), 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 pp. 66–7). The clade was traditionally subdivided into three, the chondrosteans, holosteans and teleosts, which form a rough time sequence of origins and radiations. The terms 'chondrostean' and 'holostean', however, refer to paraphyletic groups that include successive outgroups of the teleosts, and they are used here only in that grade-group sense. The bony fishes underwent three major phases of radiation:

1 basal actinopterygian ('chondrostean') radiation, Carboniferous–Triassic;

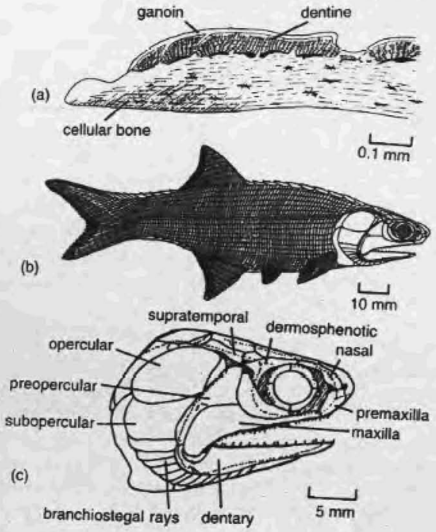


Fig. 7.5 Characters of *Mimia*, a basal actinopterygian from the Late Devonian: (a) cross-section of a scale, showing ganoin, a tissue that characterizes actinopterygians; (b) and (c), body and skull in lateral view. (Modified from Gardiner, 1984.)

2 basal neopterygian ('holostean') radiation, Triassic–Jurassic;
3 teleost radiation, Jurassic–present.

7.3.1 The first actinopterygians

Basal actinopterygians are characterized by specialized ganoid scales, which are thick bony elements composed of spongy bone on the inside, covered with dentine, and then ganoin on the outside, a layered shiny enameloid material (Figure 7.5(a)). Actinopterygian (and sarcopterygian) scales also have a characteristic rhomboid shape and peg-and-socket articulations that lock them together (Figure 3.19(b)). Scales of this type have been found in the Upper Silurian of China and Europe and the Lower Devonian of Canada and Australia.

The first complete specimens of actinopterygians are known from the Devonian, fishes such as the cheirolepidid *Cheirolepis* (Figure 3.19), a heavily built fish covered with tiny bony scales. Also from the Upper Devonian, *Mimia* from Australia (Figure 7.5(b, c)) is more derived than *Cheirolepis* in several features (Gardiner, 1984; Gardiner and Schaeffer, 1989). Its 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 *Mimia* (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 midline braincase element in the palate, the **parasphenoid** and on many other small bones in the palate. 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)). 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 pages 68–73). 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 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 basal actinopterygians form a series of outgroups to the derived neopterygians, a group that includes the majority of post-Palaeozoic actinopterygians. At one time, virtually all the Carboniferous to Triassic actinopterygians were called 'palaeoniscids', a wastebasket term. The most basal actinopterygians included *Cheirolepis* and *Mimia*, and these were followed by numerous non-neopterygians, traditionally lumped together as 'chondrosteans', known especially from the Carboniferous, Permian and Triassic. One basal group, the guildayichthyids, known from two genera from the Bear Gulch Limestone (see Box 7.1), were small deep-bodied forms (Lund, 2000).

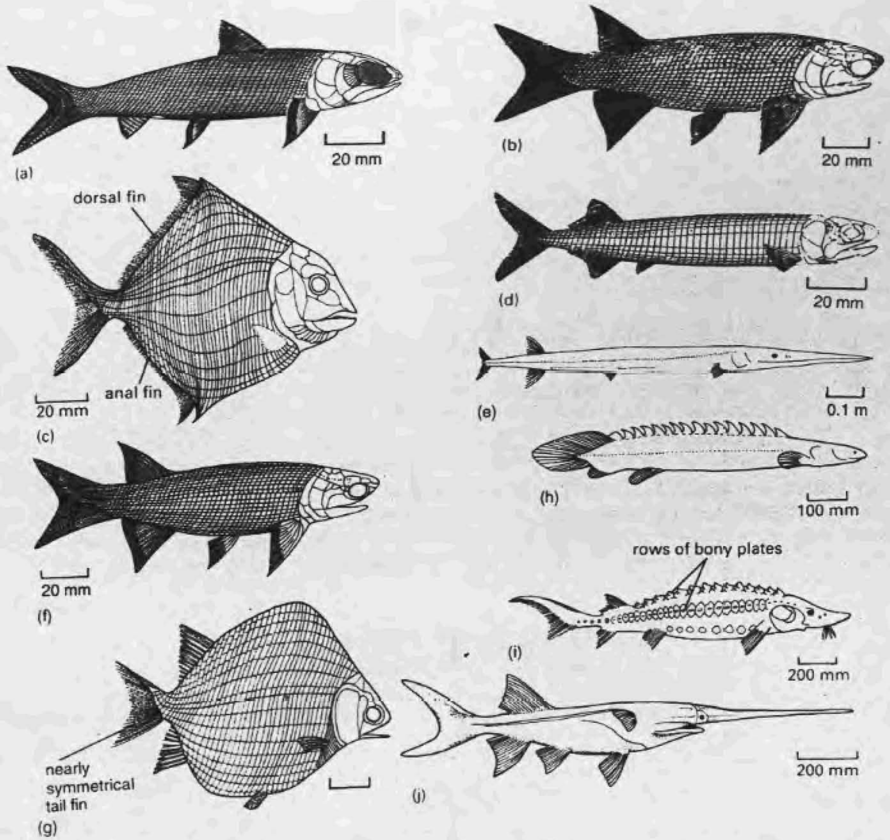


Fig. 7.6 Basal actinopterygians from the Carboniferous (c), Permian, Triassic (a, b, d–g) and extant (h–j): (a) the ptycholepid *Ptycholepis*; (b) the redfieldiid *Redfieldius*; (c) the amphicentrid *Amphicentrum*; (d) the pholidopleuriform *Pholidopleurus*; (e) the saurichthyid *Saurichthys*; (f) the perleidiform *Perleidus*; (g) the perleidiform *Cleithrolepis*; (h) the bichir *Polypterus*; (i) the sturgeon *Acipenser*; (j) the paddlefish *Polyodon*. [Figure (a) after Schaeffer *et al.*, 1975; (b) after Schaeffer and McDonald, 1978; (c, h, i) after Nicholson and Lydekker, 1889; (d) after Bürgin, 1992; (e) after Rieppel, 1985; (f, g) after Lehman, 1966; (j) after Stahl, 1974.]

The stegotrachelids, such as *Moythomasia* from the Upper Devonian of Europe and Australia (Gardiner, 1984), show some additional derived features of the skull. The ptycholepids, such as *Ptycholepis* from the Triassic and Lower Jurassic of North America and Europe (Figure 7.6(a)), have a reduced dermosphenotic element that no longer contacts the nasal and numer-

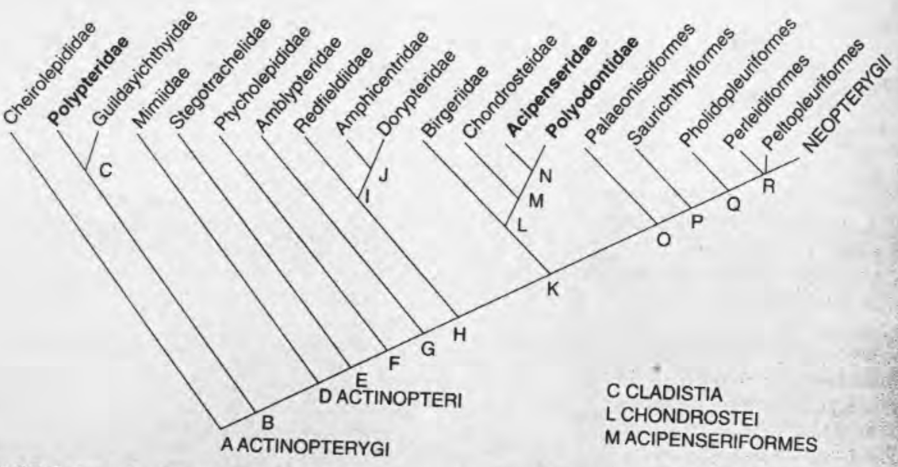


Fig. 7.7 Cladogram showing relationships of the basal ray-finned bony fishes (Actinopterygii), based on the work of Gardiner and Schaeffer (1989), Grande and Bemis (1996) and Lund (2000). Extant families are indicated in bold. See Box 3.6 for context of Actinopterygii and Box 7.6 for neopterygian relationships. 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 CLADISTIA**, round body form, postrostrals median and paired, maxilla posterior end narrow, maxilla mandibular fossa absent, median gular absent, lateral gular extended, clavicles rudimentary, postspiraculars present, caudal outline rounded, caudal fin rays webbed; **D ACTINOPTERI**, accessory vomerine tooth plate, branching rays in all fins; **E**, intertemporal bone meets nasal bone, supra-angular element in mandible; **F**, prismatic ganoin in teeth and scales, suborbital bone, antopercular bone; **G**, dermopterotic element; **H**, reduction in number of branchiostegal rays; **I**, snout blunt and rounded, preopercular reduced, suborbitals absent, marginal teeth reduced or absent, crushing tooth plates, body deep and laterally compressed; **J**, marginal teeth peg-like or absent, crushing tooth plates present, two sets of radials in median fins, body deep and laterally compressed; **K**, keystone-shaped dermosphenotic, series of supraorbital bones; **L CHONDROSTEI**, operculum reduced, elongate posterior extension of the parasphenoid, body scalation reduced to tiny elements or absent; **M 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; **N**, operculum absent, fewer than four branchiostegal rays, endocranium with extensive rostrum, dorsal and ventral rostral bones, ventral process of post-temporal bone; **O**, numerous irregular supraorbital bones between nasal and dermosphenotic; **P**, cerebellar corpus undivided, arches over fourth ventricle and produces a median anteriorly-directed portion; **Q**, premaxilla and antorbital bones present, hyomandibular nearly vertical; **R**, premaxilla with rudimentary nasal process, equal number of radials in dorsal and anal fins, upper caudal fin elongated beyond end of body.

ous suborbital bones behind the eye socket. The amblypterids, from the Carboniferous and Permian, have a dermopterotic element that abuts or overlaps the dermosphenotic.

A number of Carboniferous, Permian and Triassic families appear to form a clade (Figure 7.7), characterized by reduced numbers of branchiostegal rays in the gill region: some forms have only one, instead of the more typical 12–13. The redfieldiids, such as *Redfieldius* from the Upper Triassic and Lower Jurassic of North America (Figure 7.6(b)), are characterized by modifications to the snout and orbit region. These fishes are known worldwide in the Triassic and especially in the freshwater lakes of the Newark Supergroup (Upper Triassic to Lower 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 possible members of this clade, such as the Permian dorypterids, were also deep-bodied, and had elongate dorsal fins.

Further basal actinopterygian clades radiated in the Carboniferous to Jurassic interval. The palaeonisciforms existed throughout this time. They show additional supraorbitals and a keystone-shaped dermosphenotic, characters shared with more derived actinopterygians. The birgeriids are known from the Triassic and Early Jurassic and they were large, up to 2 m long and equipped with massive jaws and teeth. The pholidopleuriforms, such as *Pholidopleurus* from the Mid-Triassic of Switzerland (Figure 7.6(d)), were slender fishes with large rectangular flank scales (Bürgin, 1992). The saurichthyiforms such as *Saurichthys* (Figure 7.6(e)) were elongate fishes, up to 1 m long, with the dorsal and anal fins set well back and close to the tail (Rieppel, 1985). The jaws are narrow and long, and it is likely that *Saurichthys* was an ambush predator adapted for rapid bursts of swimming when it leapt at its prey. The perleidiforms, also best known from the Triassic, include mainly small fishes, some such as *Perleidus* (Figure 7.6(f)) with slender bodies, and others such as *Cleithrolepis* (Figure 7.6(g)) with deep bodies. These fishes, as well as contemporary peltopleuriforms and pholidopleuriforms, had nearly symmetrical tail fins, although the internal skeleton, the backbone, still bent upwards in the primitive heterocercal style. The perleiforms and some of the other Triassic relatives, such as the peltopleuriforms, appear to fall on the evolutionary line to more advanced actinopterygians, as suggested by some modifications to the jaws and the increasing symmetry of the tail (Figure 7.7).

Remnants of the basal actinopterygian radiation have survived to the present, but with only eight genera in three families. The bichirs, Polypteridae, are heavily armoured fishes (Figure 7.6(h)) that live in the streams and lakes of tropical Africa. Their dorsal fin runs the whole length of the body and is divided into finlets, each with a spine at the front. The 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(i)). The paddlefishes, Polyodontidae (Grande *et al.*, 2002), 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(j)). Sturgeons and paddlefishes appear to be related and to form a clade including the Jurassic chondrosteids, which may be termed Chondrostei in a restricted sense (Figure 7.7).

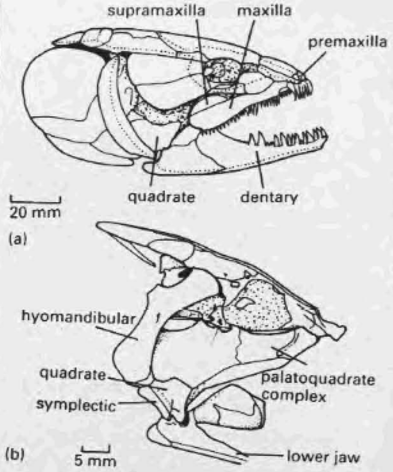
The phylogeny of this series of mainly Carboniferous to Triassic fishes has proved hard to establish, but cladistic analyses, concentrating on skull and fin characters (Gardiner and Schaeffer, 1989; Grande and Bemis, 1996), have produced a cladogram (Figure 7.7) that consists of a series of outgroups to the Neopterygii. The modern basal actinopterygians, the bichir and the sturgeons and paddlefish, are located at different positions in the cladogram, the bichir (Polypteridae) low in the sequence and the sturgeons (Acipenseridae) and paddlefish (Polyodontidae) in the middle. These relationships have been confirmed by a study of mitochondrial DNA sequences (Inoue *et al.*, 2003), although the morphological tree is unstable and further character evidence is required.

7.3.3 The basal neopterygian radiation

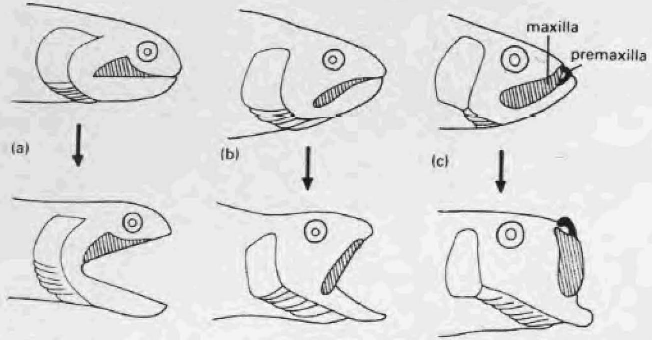
A major new actinopterygian clade, Neopterygii, arose in the Late Permian and radiated through the Mesozoic and Cenozoic. Neopterygians are characterized by major modifications to the feeding apparatus (see Box 7.4), braincase and tail. In the tail, the terminal portion of the backbone is reduced and the tail-fin rays are symmetrical above and below, more fully than even in the perleidiforms. The scales covering the body became thinner and flexible in many lines and changed from a rhomboid to a circular, or cycloid, shape. There are four main groups of neopterygians, the gars, the semionotids and other extinct forms,

BOX 7.4 JAWS AND FEEDING IN BONY FISHES

Amia illustrates an intermediate kind of jaw apparatus between that of the palaeonisciforms and the teleosts. The skull of *Amia* (illustration I(a)) shows how the jaws are relatively shorter than in the basal actinopterygians (cf. Figure 3.19(d, e)). The maxilla is highly 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 (illustration I(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.



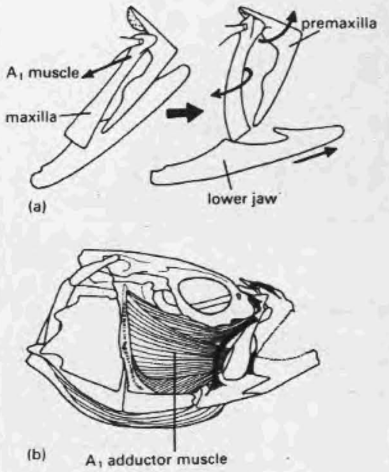
I The jaws of non-teleost neopterygians: (a) skull of *Amia* showing the major jaw elements; (b) detailed view of the jaw joint elements in the early neopterygian *Watsonulus*, reconstructed with the outer skull elements removed. [Figure (a) after Patterson, 1973; (b) after Olsen, 1984.]



II Sketches of the heads of (a) a basal actinopterygian ('chondrostean'), (b) a basal neopterygian ('holostean') or early teleost and (c) a herring (typical teleost) showing the jaws closed (top) and open (bottom). (After Alexander, 1975, courtesy of Cambridge University Press.)

The heads of bony fishes of 'chondrostean', 'holostean' and teleost grades show three rather different sets of jaw opening adaptations (illustration II). Palaeonisciforms 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). This protrusion is most marked in higher teleosts, where the sudden opening of the mouth produces a marked 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.

Advanced teleosts, the Neoteleostei (see pp. 182–4), show a further modification of the jaw apparatus (Alexander, 1967). 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 (illustration III(a)). The maxilla is attached to the lower jaw and to the suspensorium. As the mouth opens, an anterior adductor muscle (illustration III(b)) 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.



III The jaw action and musculature of acanthomorph teleosts: (a) 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; (b) jaw musculature of *Epinephelus*, showing the muscles and bones indicated in (a). [Figure (a) after Alexander, 1975, courtesy of Cambridge University Press; (b) after Schaeffer and Rosen, 1961.]

the bowfins and the teleosts (Gardiner *et al.*, 1996).

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 Lower Tertiary of North and South America, Europe, Africa and India, but their distribution has since shrunk.

Further basal neopterygians arose in the Late Permian and Triassic and radiated in the Jurassic in particular, but only one lineage has survived to the present. The Semionotidae include 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. Semionotids occur in great diversity in some areas, such as the Newark Group (Upper Triassic and Lower Jurassic) lakes of the eastern seaboard of North America, where they appear to have formed species flocks (see Box 7.5). The dapediids, possible relatives of the semionotids, were deep-bodied fishes of the Triassic and Jurassic.

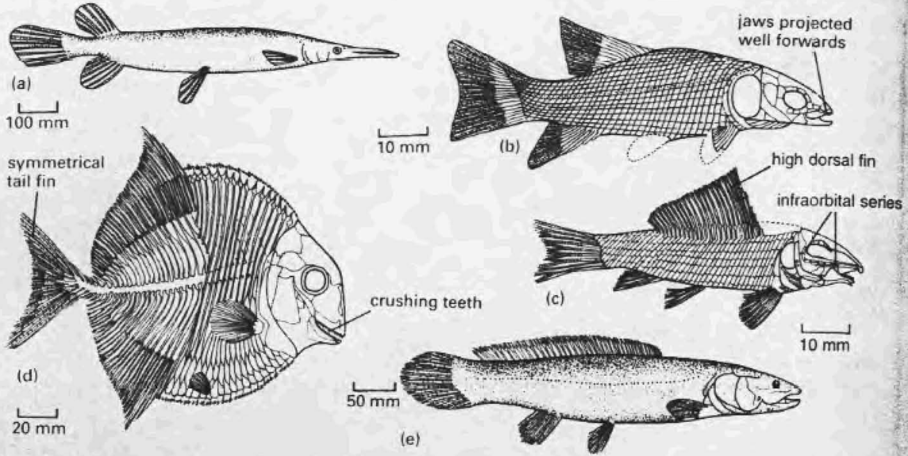


Fig. 7.8 The diversity of basal neopterygians, dating from the Triassic (b), Jurassic (c, d) and recent (a, e): (a) the gar *Lepisosteus*; (b) the semionotid *Semionotus*; (c) the macrosemiid *Macrosemius*; (d) the pycnodont *Proscinetes*; (e) the bowfin *Amia*. [Figures (a, e) after Goode and Bean, 1895; (b) after Schaeffer and Dunkle, 1950; (c) after Bartram, 1977; (d) after Woodward, 1916.]

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 pycnodontiforms, also from the Triassic to Cretaceous, are mostly deep-bodied forms with long dorsal and anal fins and a symmetrical (homocercal) tail fin. *Proscinetes* (Figure 7.8(d)) 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).

The Halecomorphi, a group of basal neopterygians that arose in the Triassic and survives today, is most closely related to the teleosts, and together the two form the Division Halecostomi (see Box 7.6). The halecomorphs are characterized by a specialized jaw joint involving an additional ventral element, the **symplectic**, as well as the quadrate (see Box 7.4, illustration I(b)). The earliest halecomorphs, the parasemionotids of the Triassic, were small fishes with large eyes and neopterygian jaw patterns. The modern bowfin, *Amia* (Figure 7.8(e) and Box 7.4, illustration I(a)), lives in fresh waters 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 m. Amiids were formerly diverse and have shown slow evolution (Grande and Bemis, 1998).

7.4 RADIATION OF THE TELEOSTS

The teleosts are an extremely diverse group of fishes, with well over 23,000 living species that are classified in 40 orders (Nelson, 1994). This enormous diversity is clearly impossible to survey in detail and only the main groups can be mentioned. The teleosts are characterized by modifications to the tail that give it 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

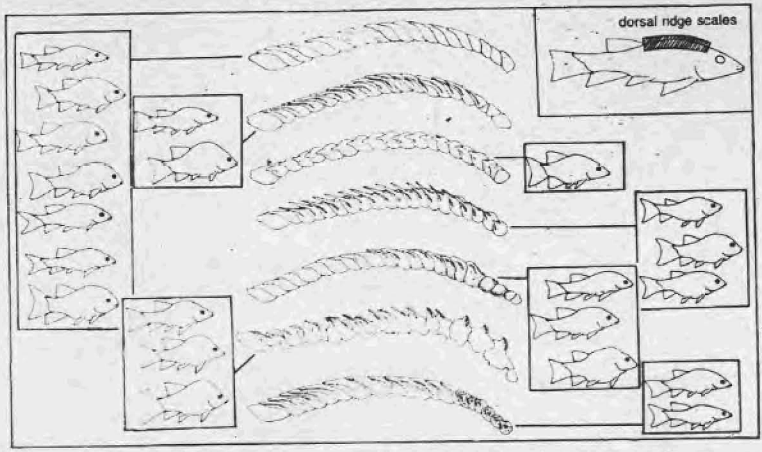
BOX 7.5 SEMIONOTID SPECIES FLOCKS

During the Late Triassic and Early to Mid-Jurassic, a time span of 45 Myr, there were 20 or more large lakes on the eastern seaboard of North America along a great rift valley that was formed by the initial phases of opening of the North Atlantic. The sediments deposited in these lakes, the Newark Supergroup, record in detail the histories of filling and drying of the lakes, and in places annual varves have allowed geologists to reconstruct the histories and time-scales in astonishing detail.

The lake cycles in the Newark Basin, like those in the Old Red Sandstone of northern Scotland (see pages 63–4), include dark mudstones laid down during anoxic phases and that are especially rich in fish fossils. Semionotids are particularly abundant, and excavations of a single lake cycle of the Towaco Formation of the Newark Basin in New Jersey, representing a single cycle of lake formation, deepening, shallowing and evaporation, lasting perhaps 21,000–23,500 years, showed their true diversity. The excavation yielded 2000 specimens belonging to 21 species (McCune, 1996), which are distinguished on the basis of body shape and the nature of the scales that run along the midline of the back (see illustration).

This is only a small sample of the total diversity of semionotids in the Newark Supergroup and many hundreds or thousands of species must have existed in the lakes, and during the repeated lake cycles. Whole faunas were wiped out by catastrophic drying episodes and replaced by new species flocks that evolved rapidly when the lakes became re-established. Modern parallels exist today in central African lakes where the cichlid teleosts have achieved great diversity by rapid speciation.

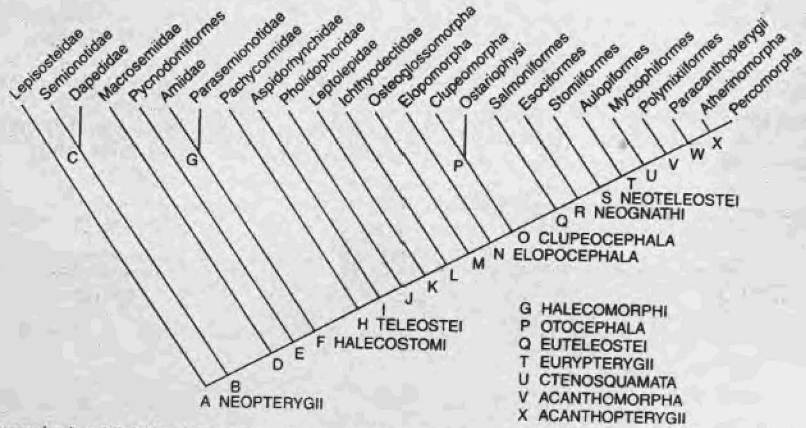
Read more at http://www.monmouth.com/~bcornet/blufhead.htm.



A semionotid species flock from the Towaco Lake cycle of the Newark Basin, New Jersey. In a short interval of time, 21 species coexisted in these lakes and they are distinguished by body shape and by the patterns of dorsal scales. Seven species groups have been identified, each with a different type of dorsal scale sequence. (Modified from McCune, 1996.)

BOX 7.6 RELATIONSHIPS OF NEOPTERYGII

The Neopterygii are a vast and diverse group and there is still much confusion over their relationships. Most studies (e.g. Patterson and Rosen, 1977; Lauder and Liem, 1983; Gardiner *et al.*, 1996; Johnson and Patterson, 1996), however, agree on the main points (see cladogram). The basal neopterygians, formerly termed 'holosteans', form a series of outgroups to the Teleostei. In previous versions, all subsequent taxa formed a series of outgroups, but new work (Johnson and Patterson, 1996) shows that Clupeomorpha and Ostariophysi pair as the clade Otocephala.



Cladogram showing relationships of the derived ray-finned bony fishes (Neopterygii), based on the work of Patterson and Rosen (1977), Lauder and Liem (1983), Gardiner *et al.* (1996) and Johnson and Patterson (1996). See Figure 7.7 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, quadratojugal forms brace for quadrate, symplectic present, upper pharyngeal dentition consolidated, fin rays equal in number to their supports in the dorsal and anal fins, 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**, 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; **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.

In an alternative view, Arratia (1997, 2001) argues that the clade Teleostei should be restricted to node J, as she has evidence that the Pachycormidae, Aspidorhynchidae, Pycnodontiformes and Dapedidae form a clade that is a sister group to a more restricted Teleostei. She also reverses the order of Elopomorpha and Osteoglossomorpha, but confirms the clade Otocephala.

Molecular data on relationships of the major neopterygian groups was limited until a flurry of publications appeared in 2003. Gardiner *et al.* (1996) noted that, among basal neopterygians, mitochondrial and nuclear DNA support a pairing of *Amia* and *Lepisosteus* as a resurrection of a clade 'Holostei', separate from teleosts, a result confirmed by Inoue *et al.* (2003) on the basis of mitochondrial DNA sequencing. New molecular studies of higher teleosts have mainly used mitochondrial DNA. Inoue *et al.* (2003) confirmed the lower part of the cladogram, including the clade Otocephala. Ishiguro *et al.* (2003) also found the Otocephala clade, as well as an Esociformes–Salmoniformes clade. Chen *et al.* (2003) and Miya *et al.* (2003) found the broad pattern in the upper part of the morphological tree (see cladogram), except that Polymixiiformes and Paracanthopterygii are paired as a side clade.

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 these living teleost groups (see Box 7.6).

7.4.1 Basal teleosts

The most primitive 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 7.9(a)), was a monstrous scaleless filter-feeder up to 10 m in length (Martill, 1988). *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 7.9(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. The aspidorhynchids, such as *Aspidorhynchus* (Figure 7.9(c)), were smaller and had long pointed snouts.

The pholidophorids of the Late Triassic and Early Jurassic, such as *Oreochima* (Figure 7.9(d)), 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 (Patterson and Rosen, 1977). The leptolepids of the Jurassic and Cretaceous (Arratia, 1997), such as *Varasichthys* (Figure 7.9(e)) 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).

Another important extinct group, the ichthyodectids of the Jurassic and Cretaceous(Figure 7.9(f, g)), 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*, 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.

7.4.2 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 (Li and Wilson, 1996). Living forms include *Osteoglossum* from South America (Figure 7.10(a)), which has posteriorly placed elongate dorsal and anal fins, and the elephant-snout fish *Mormyrus* from Africa (Figure 7.10(b)), which has electric organs in the tail region. Osteoglossiforms are characterized by features of the feeding system (Figure 7.10(c)) that have shifted the

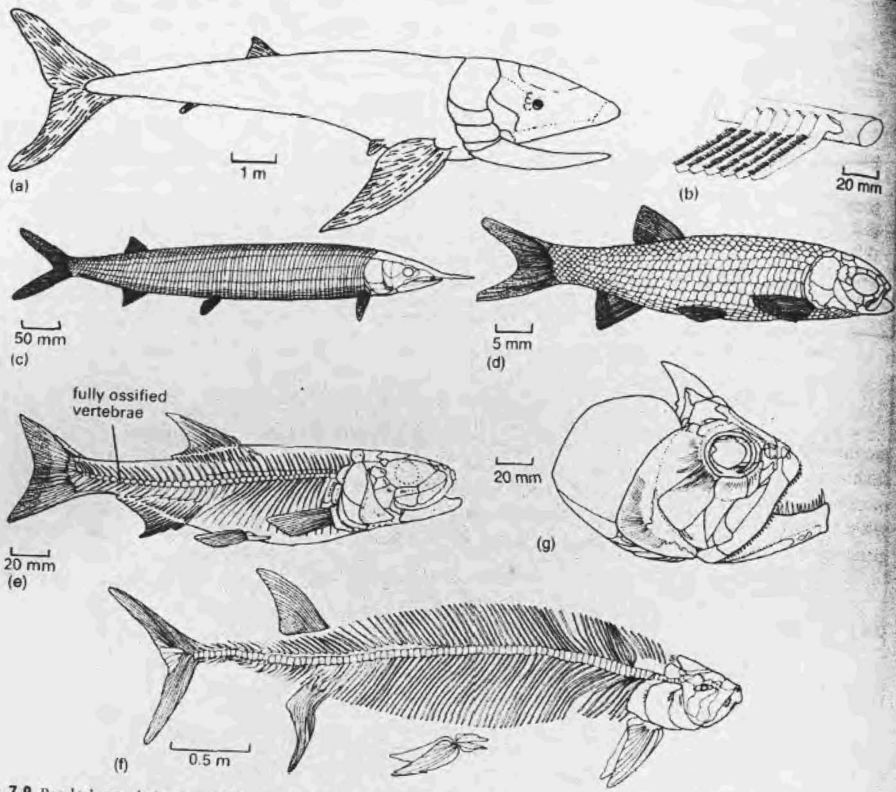


Fig. 7.9 Basal teleosts, dating from the Jurassic (a–e) and Cretaceous (f, g): (a) the giant pachycormid *Leedsichthys*; (b) gill rakers on the gill arches of *Leedsichthys*, probably used for filter-feeding; (c) the aspidorhynchid *Aspidorhynchus*; (d) the pholidophorid *Oreochima*; (e) the leptolepid *Varasichthys*; (f) the ichthyodectid *Xiphactinus*; (g) skull of the ichthyodectid *Cladocyclus*. [Figures (a, b) after Martill, 1988; (c) after Nicholson and Lydekker, 1889; (d) after Schaeffer, 1972; (e) after Arratia, 1997; (f) after Osborn, 1904; (g) modified from Patterson and Rosen, 1977.]

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').

7.4.3 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). The tarpon, *Megalops* (Figure 7.10(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 7.10(e)). All elopomorphs are characterized by a specialized marine larval stage, the leptocephalus (Figure 7.10(f)) that is thin and leaf-shaped. The leptocephalus larvae can passively migrate long distances before they metamorphose.

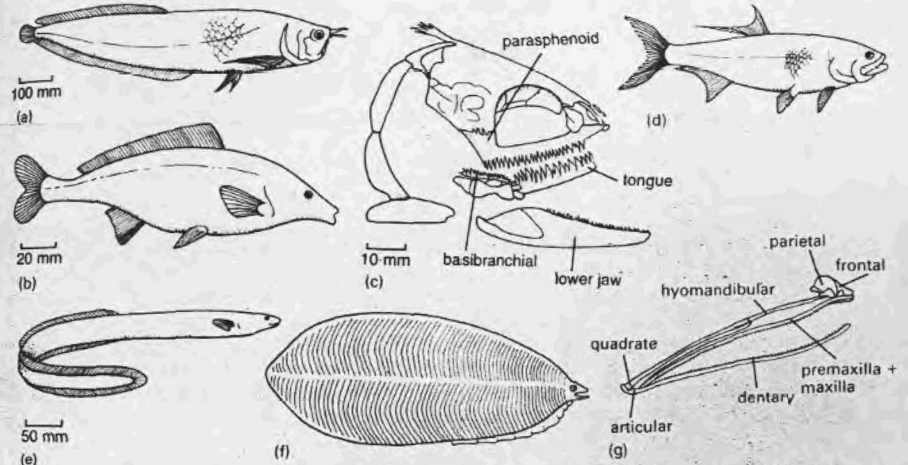


Fig. 7.10 The osteoglossomorph (a–c) and elopomorph (d–g) teleosts; all extant: (a) *Osteoglossum*; (b) the elephant fish *Mormyrus*; (c) internal jaw system of *Hiodon*, showing toothed tongue and palate elements (lateral jaw bones removed); (d) the tarpon *Megalops*; (e) the eel *Anguilla*; (f) the leptocephalus larva of an elopomorph; (g) the skull of the saccopharyngoid eel *Eurypharynx*. [Figures (a, b, d–f) after Greenwood *et al.*, 1966; (c) after Lauder and Liem, 1983; (g) after Gregory, 1933.]

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 7.10(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.

7.4.4 Otocephala: herrings and carp

The otocephalans are a new group (Johnson and Patterson, 1996) that includes the Clupeomorpha and Ostariophysi, previously seen as distinct and successive outgroups to Euteleostei, but paired on the basis of morphological and molecular evidence (see Box 7.6).

The clupeomorphs contain 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 7.11(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 7.11(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 'weight' of the fish to the pressure that acts at whatever depth it finds itself. In

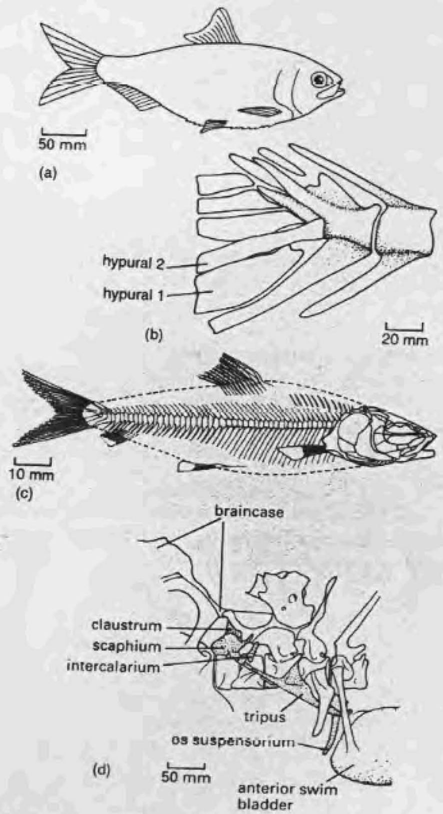


Fig. 7.11 The otocephalan teleosts, clupeomorphs (a–c) and ostariophysan (d): (a) the herring *Clupea*; (b) the tail of a clupeomorph, showing the hypural elements; (c) the Cretaceous clupeomorph *Ornategulum*; (d) the Weberian ossicles, which transmit vibrations from the swimbladder to the inner ear in ostariophysan fishes (ossicles are shaded and named). [Figure (a) after Greenwood *et al.*, 1966; (b) based on Lauder and Liem, 1983; (c) after Forey, 1973; (d) after Fink and Fink, 1981.]

clupeomorphs, the swimbladder has a unique extension into the braincase and is also concerned with hearing.

Clupeomorphs assigned to the Ellimmichthyiformes arose in the Early Cretaceous and are not known past the early Oligocene. *Ornategulum* from the Late Cretaceous (Figure 7.11(c)), a possible early clupeomorph, was a small fish. Abundant herring-like fishes, *Knightia*, have also been found in the Eocene Green River Formation (see Box 7.7), often preserved in huge masses, suggesting that they lived in vast shoals, like modern herring-like fishes.

The Ostariophysi contains carp, goldfish, minnows, catfish and indeed most freshwater fishes (Fink and Fink, 1996). They are characterized by several features, including a specialized hearing system composed of modified cervical vertebrae, ribs and neural arches, called the Weberian ossicles (Figure 7.11(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 17,000 species in 375 families. These may be divided into three main subgroupings, the salmoniforms, the esociforms and the neoteleosts (Lauder and Liem, 1983; Johnson and Patterson, 1996).

The Salmoniformes, the smelts, salmon and trout, possibly includes the early form, the tiny *Gaudryella* from the mid-Cretaceous (Figure 7.12(a)). True salmon appeared only later. The Esociformes is a small group containing 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 15,000 species of advanced teleosts, fall in the clade Neoteleostei. The Neoteleostei are characterized 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

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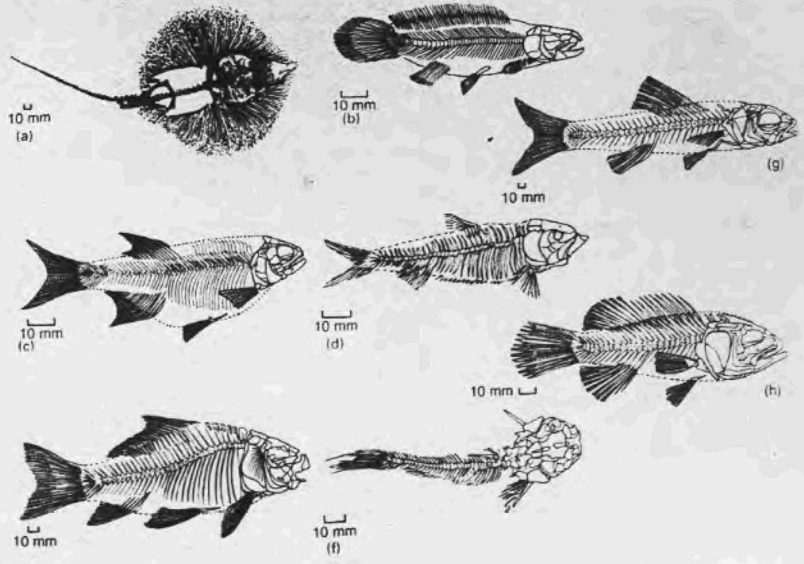
BOX 7.7 THE GREEN RIVER FISHES OF WYOMING

The Green River Formation of Wyoming, Utah and Colorado preserves some of the most spectacular fish fossils, with over 1 million specimens collected so far. The deposits range in age from late Palaeocene to late Eocene (57–38 Myr ago). Many of the specimens are found in finely layered buff-coloured limestones that were laid down in three large inland lakes, Lake Gosiute, Lake Uinta and Fossil Lake (Grande, 2001). Lake Gosiute and Lake Uinta are interpreted as playa lakes, ephemeral salt-water bodies in a generally hot arid setting, whereas Fossil Lake seems to have been a more stable body of fresh water. Many of the fish may have been killed by annual anoxic events, as in the Old Red Sandstone lakes (see Box 3.4).

The fish faunas (Grande, 2001) consist mainly of teleosts, such as the small herring *Knightia*, catfishes, suckers, perch, as well as the gar *Lepisosteus*, the bowfin *Amia*, the paddlefish *Crossopholis* and a stingray *Heliobatis* (see illustration). Grande (2001) records 27 species of bony fishes from the three main Green River lakes. Their distribution generally differs from lake to lake. For example, the gar *Lepisosteus* is very common at some localities (25–50% of all specimens), but extremely rare at others. Only *Knightia* is common or extremely common (5–50% or more of all specimens) at most localities. Other taxa are present in only one lake (e.g. suckers and catfishes from Lake Gosiute; hiodontids, paddlefish and stingrays from Fossil Lake). The fishes are associated with rich fossil remains of plants, insects, molluscs, turtles, crocodiles and other lake creatures.

Read more and see colour photographs of the spectacular Green River fossils at http://www.ucmp.berkeley.edu/tertiary/eoc/greenriver.html, http://www.fossilnews.com/2000/grnrv/grnrv.html and http://www.aqd.nps.gov/grd/parks/fobu/.



Typical fishes of the Eocene Green River Formation of Wyoming: (a) the ray *Heliobatis*; (b) the bowfin *Amia*; and teleosts (c–h): (c) the hiodontid *Eohiodon*; (d) the clupeomorph *Knightia*; (e) the catostomid *Amyzon*; (f) the ictalurid *Astephus*; (g) the percopsid *Amphiplaga*; (h) the asineopsid *Asineops*. (Based on Grande, 2001.)

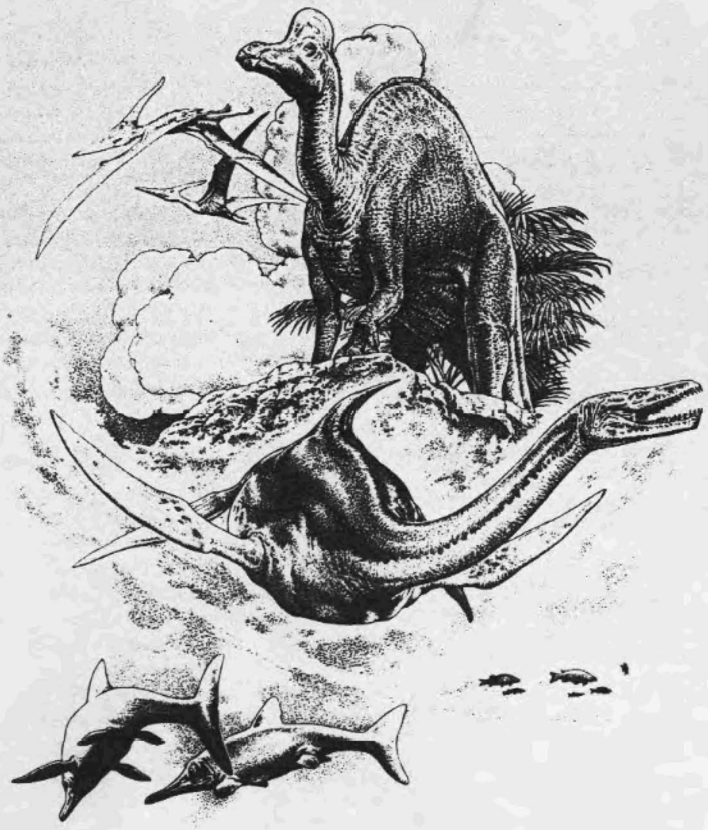
7.6 FURTHER READING

Fully illustrated accounts of fossil fishes are given by Long (1995) and Maisey (1996). The diversity of living fishes is covered by Nelson (1994), and Kocher and Stepien (1997) present papers on the molecular systematics of fishes. Detailed reviews of the sharks and their relatives from the Palaeozoic and post-Palaeozoic are given by Zangerl (1981) and Cappetta (1987) respectively, and of holocephalans by Stahl (1999). The latest overviews of the phylogeny of many chondrichthyan and osteichthyan groups are given in Stiassny *et al.* (1996), and Arratia and Schultze (1999) is a good collection of papers on Mesozoic fishes.

Broad introductions to Chondrichthyes and Actinopterygii may be found at http://www.ucmp.berkeley.edu/vertebrates/basalfish/chondrofr.html and http://www.ucmp.berkeley.edu/vertebrates/actinopterygii/actinofr.html and detailed cladograms at http://www.geocities.com/kajejenson/chondrichthyes.html and http://tolweb.org/tree?group=Actinopterygii&contgroup=Gnathostomata. 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 and everything you ever wanted to know about sharks at http://www.elasmo.com/. Read about an excavation of new *Leedsichthys* specimens in 2002 at http://www.nerc.ac.uk/publications/planetearth/pe-autumn02.shtml.

CHAPTER 8

The Age of Dinosaurs



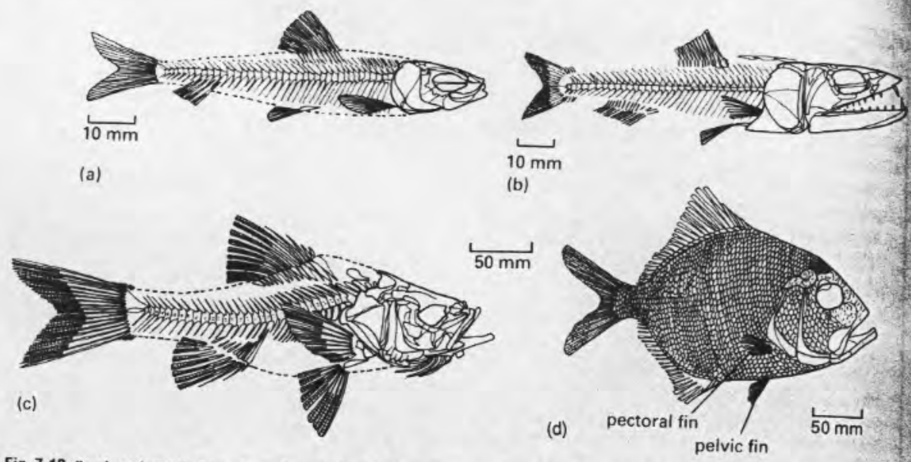


Fig. 7.12 Basal euteleosts (a, b) and acanthomorphs (c, d) from the Cretaceous (a, c) and recent (b, d): (a) the salmoniform *Gaudryella*; (b) the aulopiform *Eurypholis*; (c) the paracanthopterygian *Mcconichthys*; (d) the acanthomorph *Berycopsis*. [Figure (a) after Patterson, 1970; (b) after Goody, 1969; (c) after Grande, 1988; (d) after Patterson, 1964.]

neoteleosts include the stomiiforms and the aulopiforms (Figure 7.11(b)), mostly deep-sea fishes dating from the Cretaceous. Another basal neoteleostean group, the myctophiforms or lantern fishes, possess photophores, light-producing structures that show up when they descend into deep waters. These also are found in many stomiiforms.

The remaining neoteleosts are termed the spiny teleosts, or acanthomorphs, because they bear stiff fin spines. These may be moved by muscles at the base, and they have a defensive function because they can be erected if the fish is threatened, effectively stopping it from being swallowed! 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 the swimming thrust 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 Box 7.4).

Within the Acanthomorpha, the paracanthopterygians include some 250 genera of cod, haddock, anglerfishes and clingfishes, and date back to the Late Cretaceous (Figure 7.12(c)). The acanthopterygians contain 12,000 species that fall into two major groups, the atherinomorphs (1300 species) and the percomorphs. The atherinomorphs (killifishes, flying fishes, guppies) date from the Eocene to the present. The percomorphs (Johnson and Patterson, 1996) include a tremendous range of forms, from seahorses to flatfishes and from tunas to porcupine fishes. The group as a whole is known from the Late Cretaceous, with well preserved representatives in some Eocene fish beds (see Box 7.7), but most families have a very limited fossil record, often confined to the past 20 Myr or so. The polymixiiforms (Figure 7.12(d)) have deep bodies and the pelvic fin is below the pectoral fin.

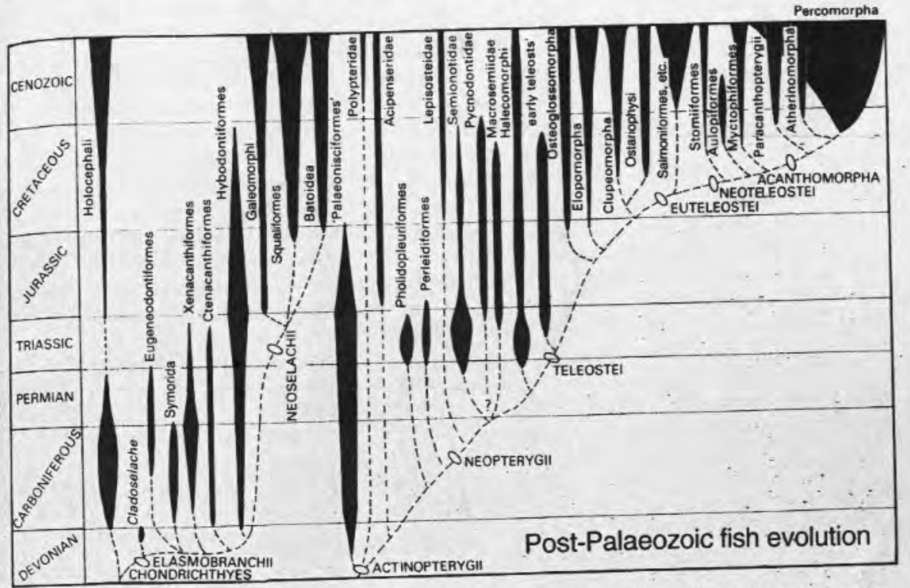


Fig. 7.13 Phylogenetic tree showing the radiations of the cartilaginous fishes (left) and the bony fishes (right). Postulated relationships, based on cladograms in Figure 7.7 and Box 7.6, are shown by dashed lines, the known fossil record by solid shading in the vertical dimension (time-scale on the left) and relative abundance by the width of the 'balloons'.

7.5 POST-DEVONIAN EVOLUTION OF FISHES

The evolution of modern fishes (Figure 7.13) shows roughly parallel patterns between the chondrichthyans and the actinopterygians. The 'palaeonisciform' radiation is matched by the Carboniferous–Permian shark groups. The semionotids and others of the Triassic and Early Jurassic had their heyday at the same time as the hybodonts, and the greatest radiations of all, of teleosts and neoselachians, seem to go in parallel. The radiation of modern sharks began rather earlier, in the Early Jurassic, than did that of the teleosts.

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 and again at the end of the Triassic, several groups of chondrichthyans and actinopterygians disappeared, and the end-Cretaceous event marked the end of hybodont sharks and numerous basal neopterygian groups. Detailed calculations of extinction rates for sharks (Kriwet and Benton, in press) show that seven out of 39 families (18%) became extinct, corresponding to 34% loss of genera and 45% loss of species. These extinction rates are entirely comparable with other groups that were also affected by the KT 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.

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?
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 ichthyosaurs die out 65 Myr ago?

INTRODUCTION

The most famous fossil vertebrates, the dinosaurs (literally 'terrible lizards') arose in the Late Triassic, about 230 Myr ago (see pp. 153–7), and dominated terrestrial faunas for the next 165 Myr until their extinction at the end of the Cretaceous (65 Myr ago). The earliest dinosaurs were moderate-sized bipedal carnivores, but large quadrupedal herbivores had come on the scene by the end of the Triassic. During the Jurassic and Cretaceous, the dinosaurs diversified into a great panoply of carnivores large and small, massive herbivores, small fast-moving specialized plant-eaters and forms 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, also arose. Other land animals included the more familiar 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 considered in this chapter.

8.1 BIOLOGY OF *PLATEOSAURUS*

The oldest-known dinosaurs are dated as Carnian (Late Triassic, 230–220 Myr ago) and they include forms such as *Eoraptor* and *Herrerasaurus* from Argentina (see p. 154) and *Coelophysis* from North America. One of the most abundant Late Triassic dinosaurs was *Plateosaurus*. The first specimens were found in southwestern 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. 215 Myr ago). The best locality was 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 could have adopted either a bipedal or a quadrupedal posture. 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 advanced 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), however, as those of rauisuchians, phytosaurs and theropod dinosaurs that were scavenging on plateosaur carcasses and had shed their teeth when biting on bones, a common enough phenomenon among sharks and crocodilians today. The teeth of *Plateosaurus* have serrated edges, but these 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)), an adaptation seen in herbivorous synapsids (see p. 121) and other dinosaurs (see p. 206) 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 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 swallowed pebbles. This is shown by finds of gizzard stones, or **gastroliths**, inside the upper rib cage of plateosaur skeletons. 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 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

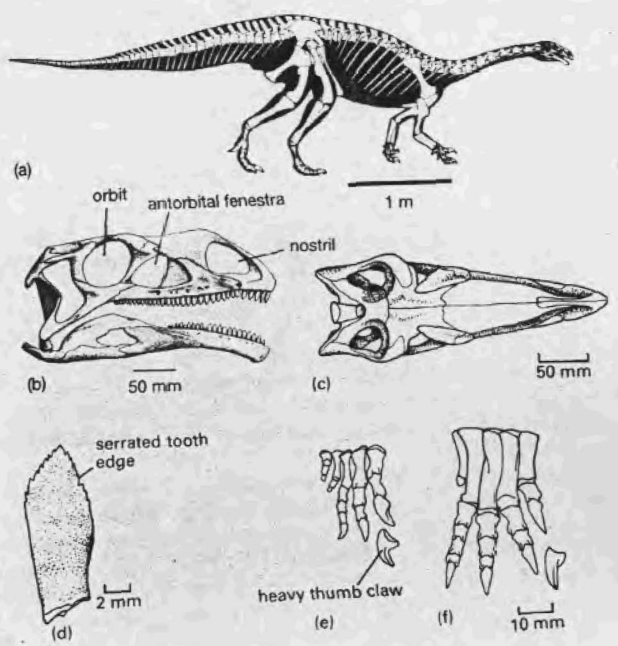


Fig. 8.1 The plant-eating dinosaur *Plateosaurus* from the Upper Triassic of Germany: (a) skeleton in lateral view; (b, c) skull in lateral and dorsal views; (d) tooth; (e) hand in anterior view, with lateral view of heavy thumb claw; (f) foot in anterior view, with lateral view of heavy claw on digit 1. [Figures (a–c) courtesy of Adam Yates; (d–f) after Galton, 1985.]

(Figure 8.2). Jurassic climates were moister than in the Triassic (see p. 137) and warm conditions prevailed right to the polar regions (Hallam, 1985). Ferns and conifers of subtropical varieties have been found as far north as 60° palaeolatitude, and rich floras are known from Greenland and Antarctica.

Cretaceous climates were probably similarly warm, although there have been suggestions, yet to be confirmed, that ice-caps existed at both poles during part of the Cretaceous. The floras show similar patterns to the Jurassic. Polar regions had warm-temperate climates and the boundary between the subtropical and temperate floras was 15° closer to the poles than it is today. Thus most of the USA, Europe as far north as Denmark and most of South America and Africa enjoyed tropical climates. Dinosaurs and other fossil reptiles are known from all climatic zones, from the equator to the poles.

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 dominance (Crane *et al.*, 1995). The earliest angiosperms included magnolia, beech, fig, willow, palm and other familiar flowering shrubs and trees.

8.3 THE DIVERSITY OF SAURISCHIAN DINOSAURS

Dinosaurs have traditionally been divided into two groups, the Saurischia and the Ornithischia, on the basis of their radically different pelvic regions. Indeed, the hindlimbs play a large part in characterizing Dinosauria and clades within Dinosauria. The saurischian dinosaurs, carnivorous theropods and herbivorous sauropodomorphs such as *Plateosaurus* and its descendants, will be reviewed here. The ornithischians are considered later (see pp. 205–19).

8.3.1 Dinosaur hips and hindlimbs

Saurischian and ornithischian dinosaurs have long been 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 6.2, 6.3, 6.4, 6.8 and 6.9). 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)).

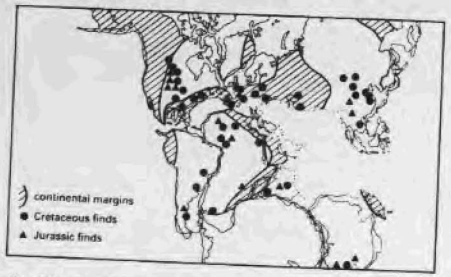


Fig. 8.2 Map of the Jurassic—Cretaceous world, showing the distribution of land and sea at the time (ancient coastlines shown with heavy lines, and shallow seas cross-hatched) and localities of major dinosaur finds in the Jurassic and Cretaceous. [Map based on the Late Jurassic (150 Myr ago), from several sources.]

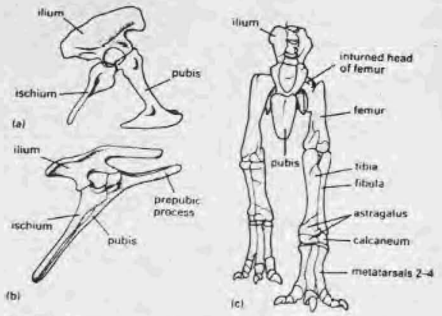


Fig. 8.3 Dinosaurian pelvic girdles: (a) the typical saurischian pelvic girdle, in lateral view, in *Tyrannosaurus*; (b) the typical ornithischian pelvic girdle, in lateral view, in *Thescelosaurus*; (c) anterior view of the hindlimbs of *Tyrannosaurus* to show the fully upright posture. [Figures (a, c) after Osborn, 1916; (b) after Romer, 1956, courtesy of the University of Chicago Press.]

Many dinosaurian characters of the hindlimbs are related to the acquisition of upright posture (see p. 143). 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 articulatory surface from the top of the femur to a distinct ball on its inside. The reorientation of the limbs from a partial sideways sprawl has 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 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.

8.3.2 The basal theropods

The theropods include all the flesh-eating dinosaurs and they ranged in size from small turkey-like forms to the 6-tonne giants of the Cretaceous. The herrerasaurids from the Carnian of South America (see p. 154) are often regarded as the first theropods, although others regard them as generalized basal saurischians or basal dinosaurs. There have been dozens of studies of theropod phylogeny (e.g. Gauthier, 1986; Holtz, 1994; Sereno, 1999), all of which agree on the broad outlines, but differ in details. I use the most thorough recent analyses: Rauhut (2003) for the outline of major theropod groups, and Clark *et al.* (2002) and Maryańska *et al.* (2002) for maniraptorans and basal birds (see Box 8.5).

The first unequivocal theropods, the coelophysoids, consist of some five or six Late Triassic and Early Jurassic genera. *Coelophysis* from the Upper 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 the primitive two. It shows the coelophysoid character of an ischium that is two-thirds or less of the length of the pubis.

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 on the basis of variations in body proportions, and one adult specimen gives evidence for cannibalism: it has a smaller specimen inside its rib cage. 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 disturbed by water currents before they were buried.

The ceratosaurs were close relatives of the coelophysoids. Many ceratosaurs have crests and horns, perhaps developed most in the males, and these could have had a function in sexual display. *Dilophosaurus* (Welles, 1984) has two flat-sided crests over the skull roof (Figure 8.4(b)), whereas *Ceratosaurus* has a pair of 'horns' on the nasal bones (Figure 8.4(c)). These two genera come from the Jurassic of North America and they reached lengths of 5–7 m. Ceratosaur snout shapes vary from long and slender in *Dilophosaurus* to shorter and higher in *Ceratosaurus*. One unusual ceratosaur group were the abelisaurids, known primarily from the mid- to upper Cretaceous of South America, many of which had extremely short skulls. In some forms, such as *Carnotaurus* (Figure 8.4(d)), the frontal and parietal bones were hugely expanded into two triangular 'horns' over the eyes.

The remaining theropods, the tetanurans, are characterized 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 is a marked keel on the underside of the centra of the anterior dorsal vertebrae.

The basal tetanurans were all large predators and they fall in a clade called the Carnosauria (Rauhut, 2003), characterized by the shape of the maxilla, **opisthocoelous** cervical centra (the posterior face of the vertebral centrum bulges backwards) and a very

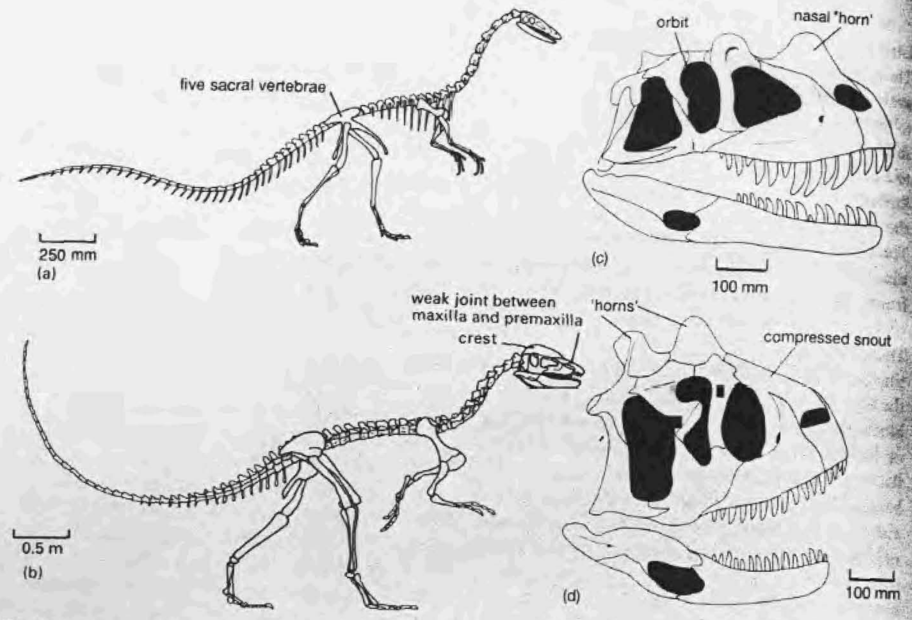


Fig. 8.4 Basal theropods: (a) a coelophysoid and (b–d) ceratosaurs, of Triassic (a), Jurassic (b, c) and Cretaceous (d) age: (a) *Coelophysis*; (b) *Dilophosaurus*; (c) *Ceratosaurus* skull; (d) *Carnotaurus* skull. [Figure (a) after Colbert, 1989; (b) after Welles, 1984; (c, d) courtesy of Oliver Rauhut.]

stout first metacarpal. Carnosaurs include the megalosaurids, essentially *Megalosaurus* from the Mid-Jurassic of Europe. *Megalosaurus* was the first dinosaur to be named, in 1824. Its relative, *Magnosaurus* from the Upper Jurassic of Europe (Figure 8.5(a)), was half the size of *Allosaurus* from the Upper Jurassic of North America (Figure 8.5(b)), which was 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.

Further carnosaurs are best known from Africa. The spinosaurids, first reported from Egypt in 1915, are represented all over North Africa by their characteristic broad teeth. New finds, of *Baryonyx* from England (Charig and Milner, 1997) and *Suchomimus* from Niger (Sereno *et al.*, 1998), show the characteristics of the clade — they have long spines on their backs, 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? The carcharodontosaurids, such as the giant *Carcharodontosaurus* from Morocco, had a skull 1.6 m long (Figure 8.5(d)) and was one of the largest predatory dinosaurs (Sereno *et al.*, 1996). The new discoveries of dinosaurs in Africa and in Madagascar are shedding light on continental movements through the Cretaceous (see Box 8.1).

8.3.3 Coelurosauria

The remaining theropods form the major clade Coelurosauria (Rauhut, 2003) as they share a large number of derived characters with each other and with the birds (see Box 8.5), most notably an enlarged maxillary fenestra and no serrations on the premaxillary teeth. The basal coelurosaurs are the coelurids, such as *Compsognathus* from the Upper Jurassic of Germany, one of the smallest dinosaurs at 0.7–1.4 m long. Its close relative from China, *Sinosauropteryx*, apparently has feathers: did feathers appear long before the origin of birds (see Box 8.2)?

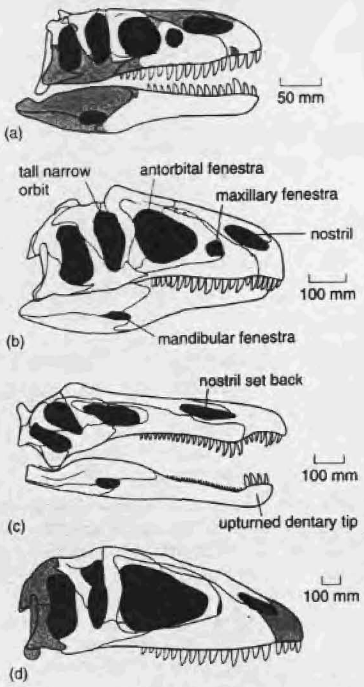


Fig. 8.5 Carnosaur skulls from the Jurassic (a, b) and Cretaceous (c, d): (a) *Magnasaurus*; (b) *Allosaurus*; (c) *Suchomimus*; (d) *Carcharodontosaurus*. Unknown areas are shaded. (Courtesy of Oliver Rauhut.)

The tyrannosaurids, such as *Tyrannosaurus*, arguably the largest terrestrial carnivore of all time at 14 m long, radiated in North America and central Asia during the Late Cretaceous (Holtz, 1994; Brochu, 2003a). *Tyrannosaurus* has a large head (Figure 8.6(a)) with an extra joint in the lower jaw between the dentary and the elements at the back. This allowed *Tyrannosaurus* to increase its gape for biting large prey. It is debated whether tyrannosaurids were active hunters or scavengers. But they could certainly bite! Bones from the pelvis of a *Triceratops* 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). Tyrannosaur stomach contents show that they digested bones with acid, as modern crocodiles do, and a 1-m-long tyrannosaur coprolite full of *Triceratops* bones (Chin *et al.*, 1998) and another with bones and putative muscle tissue of perhaps a pachycephalosaurid (Chin *et al.*, 2003) offer further intimate evidence of their feeding activities.

Tyrannosaurids 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. They may have been used to help *Tyrannosaurus* get up from a lying position, by providing a push while the head was thrown back and the legs straightened. These dinosaurs 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 these dinosaurs a stronger metatarsus than in other theropods in which the three bones were not tightly bunched, but not so 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

BOX 8.1 AFRICAN DINOSAURS AND CONTINENTAL MOVEMENTS

Africa became an island during the Cretaceous: how did this affect the dinosaurs? Following fragmentation of the supercontinent Pangaea, 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. A major marine transgression about 95 Myr ago then flooded most of North Africa and the Sahara, forming a seaway that extended from Algeria southwards across the Sahara, separating the north-western portion of Africa from the rest of the continent.

Late Jurassic dinosaurs from Africa are best known from Tendaguru in Tanzania. The Tendaguru fauna is very like that of the Morrison Formation in the mid-central USA, even sharing genera such as the theropod *Ceratosaurus*, the sauropods *Barosaurus* and *Brachiosaurus* and the ornithopod *Dryosaurus*. Dinosaurs from the middle of the Cretaceous of North Africa show similarities with those from South America and with Euramerica (Sereno *et al.*, 1996, 1998). For example, the spinosaurid theropod *Suchomimus* from Niger (see Figure 8.5(c)) is virtually indistinguishable from *Baryonyx* from England and *Irritator* from Brazil. Likewise, the carcharodontosaurid *Carcharodontosaurus* from Morocco (see Figure 8.5(d)) is similar to *Giganotosaurus* from Argentina and *Acrocanthosaurus* from North America.

Late Cretaceous dinosaurs are rare in Africa, because much of the continent was under the sea at this time and terrestrial rocks of that age are poorly exposed. New discoveries from Madagascar (Sampson *et al.*, 1998) indicate that the Late Cretaceous dinosaurs from Madagascar, India and South America retained close resemblances to one another, whereas those of Africa were somewhat different as Africa had become essentially an island by this time. The dinosaurs from the Upper Cretaceous of Madagascar include the abelisauroid theropods *Majungatholus* and *Masiakasaurus*, both of which had close relatives in South America (see Figure 8.4(d)). Sauropods include the titanosaurid *Rapetosaurus* (Curry Rogers and Forster, 2001). The abelisauroid dinosaurs, together with members of other groups (e.g., mammals and crocodiles), suggest close faunal links between South America and India-Madagascar, perhaps indicating a dispersal route via Antarctica (Sampson *et al.*, 1997, 2001). This idea remains to be tested by future discoveries, particularly from the Upper Cretaceous of Africa.

Read more about Scott Sampson and his work on Madagascar at http://www.vertpaleo.org/education/SpeakerOfTheYear.html and at http://www.umnh.utah.edu/museum/departments/paleontology/paleostaff_scottsampson-currentproj.html, as well as a review of the new discoveries at http://www.timeforkids.com/TFK/magazines/story/0,6277,97951,00.html.

The Madagascan abelisaurid theropod *Majungatholus*, reconstructed skull (a) and restored head (b) in lateral view. (Courtesy of Scott Sampson and artist Bill Parsons.)

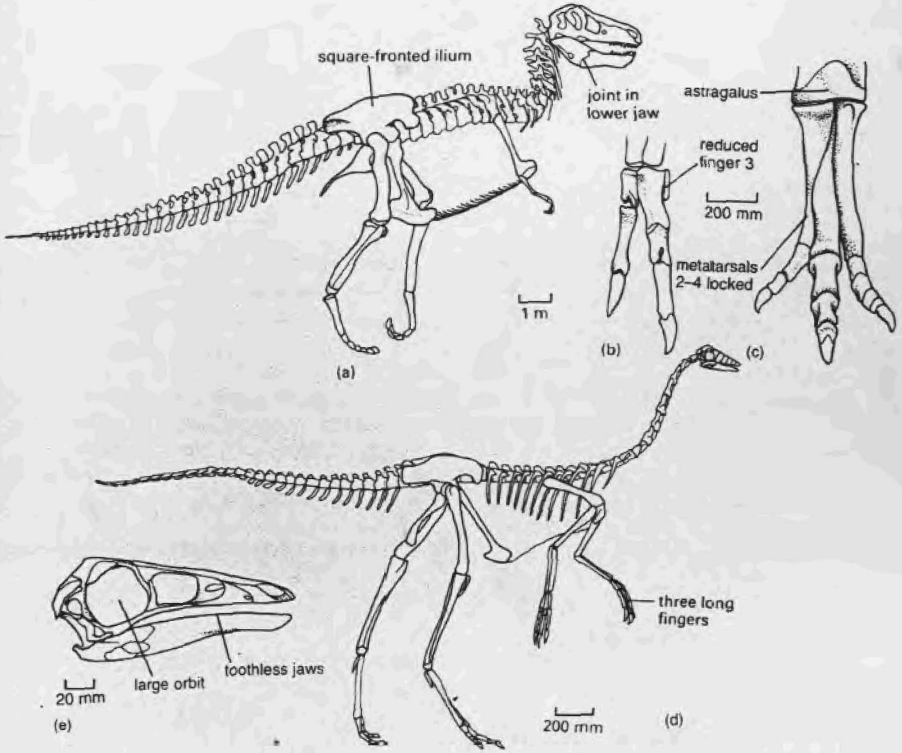


Fig. 8.6 Coelurosaurian theropods: (a–c) tyrannosaurids and (d, e) ornithomimids, all from the Cretaceous: (a) skeleton of *Tyrannosaurus*; (b) hand of *Tarbosaurus*; (c) foot of *Albertosaurus*; (d) skeleton of *Struthiomimus*; (e) skull of *Dromiceiomimus*. [Figure (a) after Newman, 1970; (b, c) after Norman, 1986a; (d, e) after Russell, 1972.]

mass to leg muscles, which is clearly impossible. With its leg muscle volume, *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 speeds of 72 km h^{-1} that have been suggested.

The ornithomimids of the Late Jurassic to Late Cretaceous (Russell, 1972) were highly specialized theropods with a slender ostrich-like body and long arms and legs (Figure 8.6(d)). The hands have three powerful fingers that may have been used for grasping prey 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 (Figure 8.6(e)) and the ornithomimid diet may have included small prey animals such as lizards or mammals, or even plants. Well preserved specimens (Norell *et al.*, 2001) show that the toothless jaws were covered by a keratinous beak that bore vertical ridges inside the jaws, similar to those in ducks, used perhaps in the same way for straining small animals, or even plant material, from pond water.

8.3.4 Maniraptora

The most derived theropods, the Maniraptora (see Box 8.5), include the alvarezsaurids, therizinosaurids, troodontids, dromaeosaurids and birds. The contents of this clade are, however, somewhat controversial: Gauthier (1986) identified the dromaeosaurids and troodontids as close relatives of birds and forming the clade Maniraptora. Alvarezsaurids were until recently, however, classed as birds, whereas therizinosaurids were often hard to place. Oviraptorosaurs, still regarded as dinosaurian maniraptorans by many (e.g. Clark *et al.*, 2002), have been assigned to birds by Maryańska *et al.* (2002) and they will be treated in Chapter 9.

The alvarezsaurids are a small group of five genera, known from the Upper Cretaceous of Mongolia, Argentina and the USA (Sereno, 2001; Chiappe *et al.*, 2002). The best known alvarezsaurid 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 8.7(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 8.7(b)) with a short humerus, ulna and radius, a massive fused wrist consisting mainly of metacarpal I 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, but the arms seem to be ridiculously short for such an activity: *Mononykus* would have toppled over if it bent down to use its arms on the ground, and they certainly could not have reached the mouth.

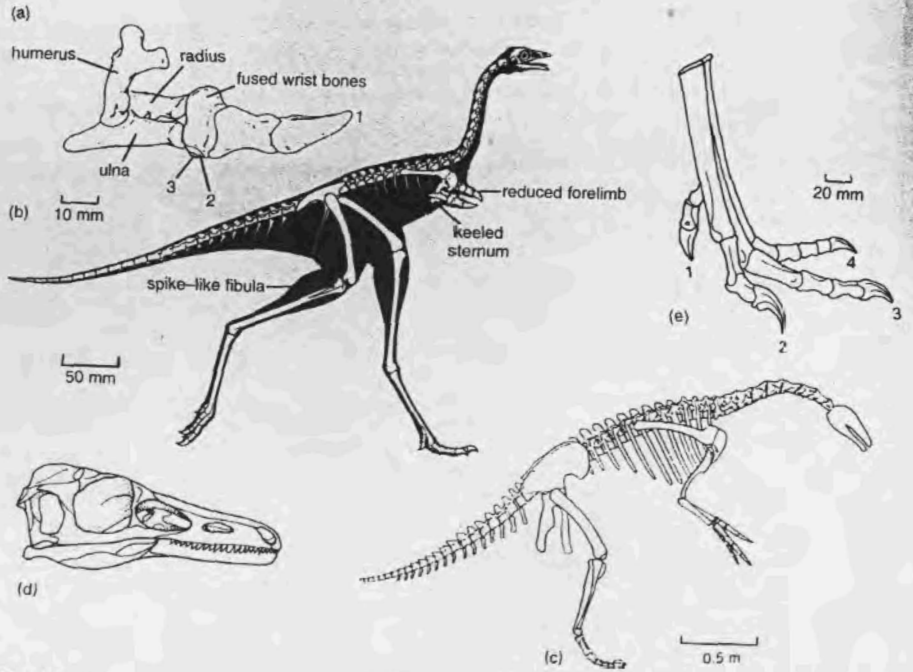


Fig. 8.7 Basal maniraptorans, all from the Cretaceous: (a, b) the alvarezsaurid *Mononykus*, reconstructed skeleton and arm in lateral view; (c) the therizinosaurid *Alxasaurus*; (d, e) the troodontids *Saurornithoides* (d) and *Troodon* (e), skull in lateral view and foot. [Figures (a, b) modified from Perle *et al.* (1993), used with permission from *Nature* © 1993, Macmillan Magazines Ltd; (c) modified from Russell and Dong, 1993; (d) after Russell, 1969; (e) after Sternberg, 1932.]

The therizinosaurids, such as *Alxasaurus* (Figure 8.7(c)) from Mongolia and China, were the most bizarre theropods of all. Their affinities were for a long time problematic, having been identified as turtles, theropods, or something between saurischians and ornithischians. They were large animals, 4–5 m long, 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 and equipped with apparently rather feeble peg-like teeth and a toothless beak at the front. Russell and Dong (1993) suggested that the therizinosaurids were foliage-eaters, rather like certain mammals, the chalicotheres and giant ground sloths (see pp. 317, 348). *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 troodontids from the Upper Cretaceous of North America and Mongolia, such as *Saurornithoides*, had long slender skulls (Figure 8.7(d)) with the orbits facing partly forwards so that they may 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 8.7(e)) has three functional toes, of which number 3 is the longest, a bird-like structure designed for fast running.

The dromaeosaurids, a family of six or seven genera from the Cretaceous of North America, Mongolia and China, have also been identified elsewhere on the basis of isolated teeth. The best known dromaeosaurid is *Deinonychus* from the Lower Cretaceous of North America (Ostrom, 1969), a small animal about 3 m long, 1 m tall and weighing 60–75 kg (Figure 8.8). The skull is incompletely known. 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 invested 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, three functional toes and a small backwardly-pointing first toe. The astragulus 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 elongate toe 2, which is armed with a vast sickle-shaped claw up to 120 mm long that 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

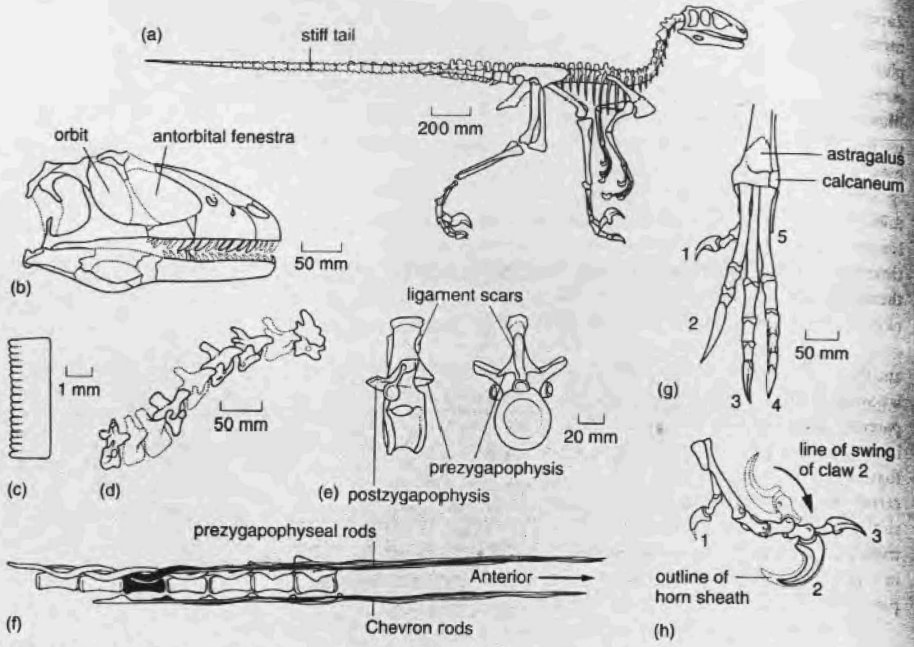


Fig. 8.8 The Early Cretaceous dromaeosaurid *Deinonychus*: (a) skeleton in running pose; (b) lateral view of the skull; (c) posterior edge of a maxillary tooth, showing the serration; (d) reconstructed neck, showing the curvature; (e) a dorsal vertebra in lateral and posterior views; (f) outline of a series of caudal vertebrae, with one vertebra and its elongate prezygapophyseal rods (above) and chevron rods (below), shaded black; (g) left foot in anterior view; (h) left foot in lateral view, showing the swing of the scythe claw. (After Ostrom, 1969.)

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 up to 1 m long. The most likely prey for *Deinonychus* seems to be *Tenontosaurus*, a fairly abundant relative of *Hypsilophodon* (see pp. 206–7), that 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 tiny dromaeosaurid *Microraptor* from the Lower Cretaceous of China (Xu *et al.*, 2003) is so well preserved that it shows feathers. There are rows of 'flight feathers' (see Box 8.2) behind the arm bones, but also attached along the hindlimb. *Microraptor* could not fly – 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.

8.3.5 Sauropodomorpha

The Sauropodomorpha, the second major saurischian clade, arose in the Late Triassic and the early forms of

BOX 8.2 DINOSAURS WITH FEATHERS

Professor Chen Pei-ji of the Nanjing Institute of Geology and Palaeontology created a sensation at a conference in October 1996 when he announced that he had found a dinosaur with feathers. He showed pictures of a small theropod, preserved complete, with tufts of hair-like structures all along its back and tail. The dinosaur was named *Sinosauropteryx* and it was shown to be a close relative of *Compsognathus*, a coelurid, by Chen *et al.* (1998). If these truly were feathers of some kind, then all coelurosaurs (see Box 8.5) must have had feathers too, and that includes *Tyrannosaurus rex*!

The discovery was controversial. Was not the specimen just a bird, somewhere in the cladogram above *Archaeopteryx*? Surely the so-called feathers were not feathers at all, just shreds of skin or scales? The specimens came from the Yixian Formation, now dated as Early Cretaceous (125–120 Myr ago), near Beipiao, Liaoning Province, China. The sites around Beipiao had already produced spectacular specimens of early birds (see Box 9.3) and many other fossil groups, all showing soft-tissue preservation. After 1996, new discoveries of dinosaurs with feathers from these sites came thick and fast: two maniraptorans, *Protarchaeopteryx* and *Caudipteryx* (Ji *et al.*, 1998), the therizinosauroid *Beipiaosaurus* (Xu *et al.*, 1999a), the dromaeosaurids *Sinornithosaurus* (Xu *et al.*, 1999b) and *Microraptor* (Xu *et al.*, 2003). Schweitzer (2001) also reports fibrous feather-like structures in the alvarezsaurid *Shuvuuia* from Mongolia. If the fossils are correctly interpreted, there is no question then that all coelurosaurs, from the Mid-Jurassic onwards, were feathered (Padian *et al.*, 2001a). But what kinds of feathers, and does this mean they could all fly?

It is unlikely that the dinosaurs with feathers could fly. The kind of feather most people visualize is a flight feather from the wing, a quill (illustration (a)), with a central hollow shaft, the **rachis**, 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 right 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:

- 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

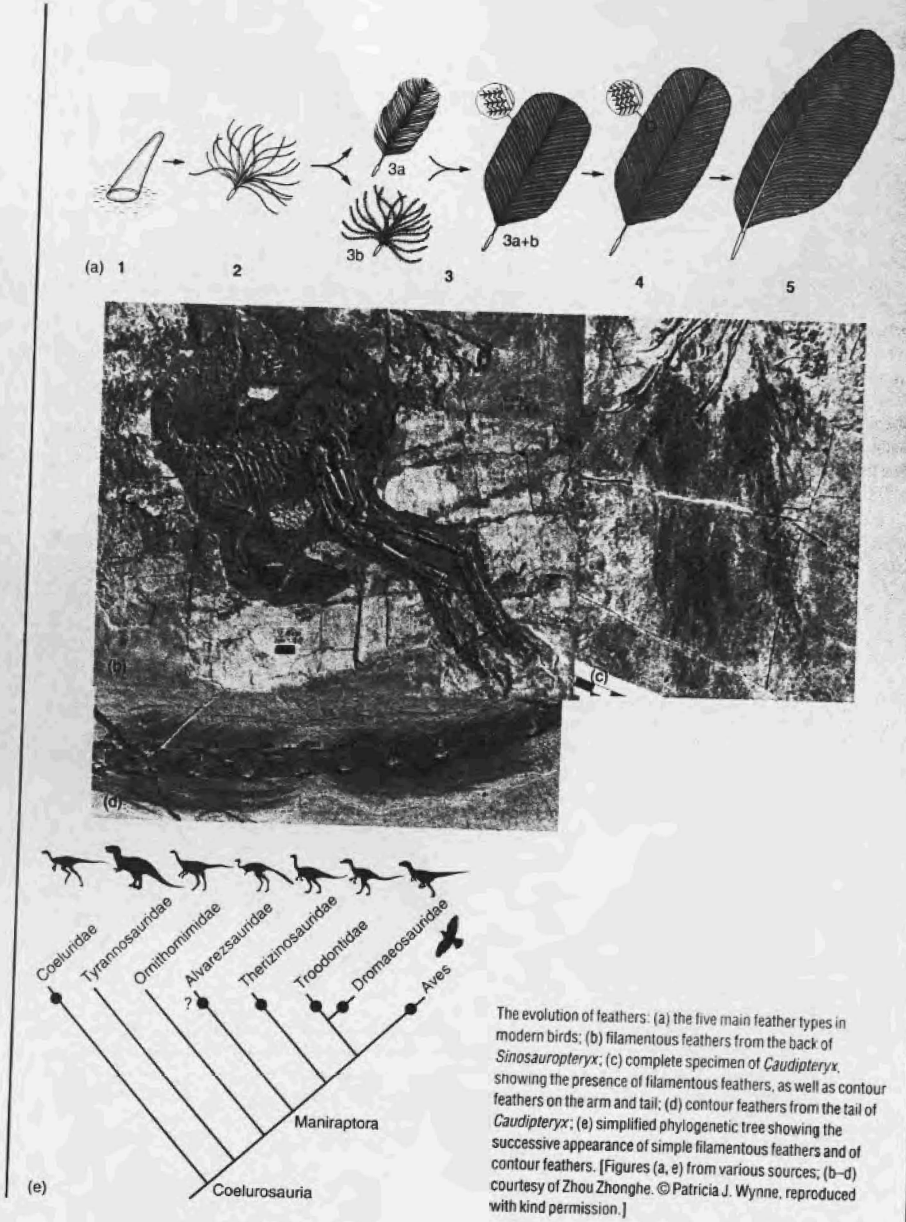
These five feather types (illustration (a)) form a sequence that matches a developmental theory for the origin of feathers (Prum and Brush, 2002): reptilian scale → bristle → down feather → simple contour feather or down feather with barbs, but no barbules → contour feather with barbs and barbules → contour feather in which barbules interlock and produce a closed vane → flight feather with asymmetrical vanes.

Sinosauropteryx, the most basal of the feathered dinosaurs known so far, has tufts of simple filaments (illustration (b)). Along the back, the fibres are 8–13 mm long and there are about ten fibres per millimetre. Towards the end of the tail, the fibres may be up to 40 mm long. The therizinossauroid *Beipiaosaurus* has similar filaments, 50–70 mm long, associated with the bones of the forearm and leg. These are not the same as any modern feathers – they do not branch from the base as down feathers do, nor are they bristles. On the other hand, they occur on the skin surface, they consist of filaments and preliminary geochemical studies suggest they are made from the protein beta keratin, as are the feathers of modern birds (Schweitzer, 2001), whereas mammalian hair and finger nails are made from alpha keratin.

More derived maniraptorans show some advances. *Protarchaeopteryx* has two kinds of feathers: (1) contour feathers on the tail that are up to 160 mm long and have a rachis and two asymmetrical vanes made from numerous lateral barbs, and (2) fluffy feathers over the body and upper legs that comprise filaments about 30 mm long that are gathered at the base. *Caudipteryx* (illustrations (c, d)) has both of these feather types, as well as some 14 contour feathers attached along the second hand digit.

These new discoveries from China confirm that birds are maniraptoran theropods (see Chapter 9) and that feathers evolved in the earliest coelurosaurs, if not earlier (illustration (e)). The first feathers, in coelurids 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

continued



The evolution of feathers: (a) the five main feather types in modern birds; (b) filamentous feathers from the back of *Sinosauropteryx*; (c) complete specimen of *Caudipteryx*, showing the presence of filamentous feathers, as well as contour feathers on the arm and tail; (d) contour feathers from the tail of *Caudipteryx*; (e) simplified phylogenetic tree showing the successive appearance of simple filamentous feathers and of contour feathers. [Figures (a, e) from various sources; (b–d) courtesy of Zhou Zhonghe. © Patricia J. Wynne, reproduced with kind permission.]

function in insulation, and possibly also in display if they were brightly coloured. Contour feathers appeared first along the sides of the tail, and then behind the arm, in the maniraptorans. Their function in such non-flying dinosaurs is mysterious, unless they also formed part of a display structure. Only in the first bird, *Archaeopteryx*, did contour feathers take over a major role in flight.

Read more about the discoveries and see colour images of the fossils at http://www.peabody.yale.edu/exhibits/cfd/CFDintro.html and http://www.nhm.ac.uk/museum/tempexhib/dinobirds/, and of imaginative life restorations at http://www.austmus.gov.au/chinese_dinosaurs/feathered_dinosaurs/photo_gallery.htm.

the Late Triassic and Early Jurassic were termed prosauropods. There has been some debate about whether the prosauropods form a distinct clade, but most evidence suggests that they do not and are outgroups of the Sauropoda (see Box 8.5).

Thecodontosaurus, a basal sauropodomorph from the Upper 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 (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 pp. 188–9) as well as animals such as *Riojasaurus* from Argentina and *Melanorosaurus* from South Africa, which were obligatory quadrupeds up to 10 m long.

The sauropods appeared first in the Upper Triassic of South Africa (Yates and Kitching, 2003) and radiated in the Early Jurassic with forms such as *Vulcanodon* from Zimbabwe. The 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

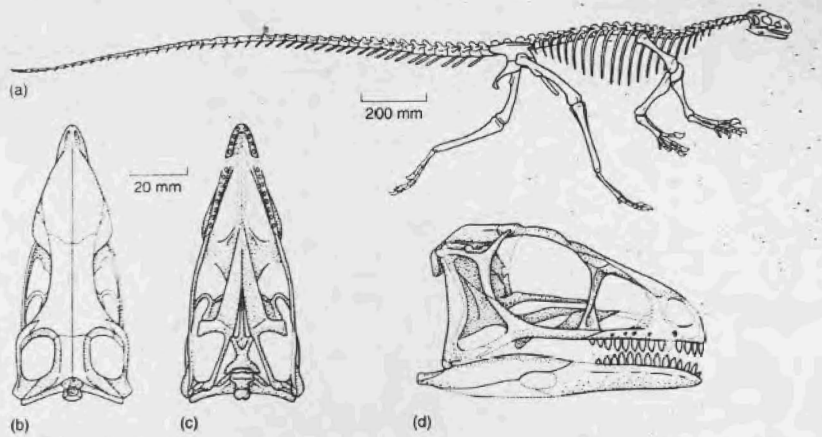


Fig. 8.9 The basal sauropodomorph *Thecodontosaurus*, from the Late Triassic: skeleton in lateral view; (b–d) skull in ventral, dorsal and lateral views. [Figure (a) modified from Benton *et al.* (2000a); (b–d) courtesy of Adam Yates.]

their massive weight. The euhelopodids from the Middle Jurassic of China, such as *Shunosaurus* (Figure 8.10(a)), are generally regarded as basal sauropods (Upchurch, 1998), although they have been assigned a position close to titanosaurids by Wilson (2002). The skull of *Shunosaurus* is less open than that of other macronarians and the jaws were designed for slicing tough vegetation. The omeisaurids, such as *Mamenchisaurus* from the Upper Jurassic of China, with an immensely long neck, appear to be close relatives of the euhelopodids.

The remaining sauropods, the neosauropods, include *Cetiosaurus* (Figure 8.10(b)) from the Middle Jurassic of England, although its precise relationships are unclear. In *Cetiosaurus*, the external mandibular fenestra in the lower jaw has been lost and the lower temporal fenestra lies completely beneath the orbit. The neck has become elongate by lengthening of the cervical vertebrae and increasing their number to 12 or more. There are five or six sacral vertebrae and 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, 1998). The cetiosaurids are close to the ancestry of the classic giant sauropods of the Late Jurassic, which split into two major lineages, the diplodocids and the macronarians (Upchurch, 1998; Wilson, 2002; see Box 8.5).

The diplodocids, such as *Diplodocus* (Figure 8.10(c)) from the Upper Jurassic of North America, 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 crop vegetation. Neosauropod characters in the skull are: the nostrils and nasal bones have moved well back and the skull roof is shortened, the lower temporal fenestra lies largely beneath the orbit, the teeth point forwards and they are restricted to the anterior part of the jaws. There has long been a debate about the function of the long neck of *Diplodocus* (see Box 8.3). 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 only the astragalus, all other elements having been lost or are present only as cartilaginous masses. 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.

Through their evolution, the sauropodomorphs increased the pneumaticity of their vertebral column (Wedel, 2003). In early forms, the presacral column was extensively pneumatized. The sacrum was also pneumatized in neosauropods, and the proximal vertebrae of the tail also became pneumatized independently in diplodocids and titanosaurians. The pneumatization is shown by a complex of cavities in the sides of sauropod vertebrae, supported by a latticework of narrow bone struts (Figure 8.10(d)). As in modern birds, air sacs existed in various parts of the body and they were presumably connected to the lungs. Air sacs have two functions:

1 to reduce weight, by replacing bone and other body tissues with cavities;

2 to enhance respiratory efficiency; birds, and presumably dinosaurs, breathe in a single direction, with the air entering the lungs, passing to the air sacs and then out, hence avoiding the 'dead space' of uncirculated air in mammals, which breathe in a tidal way ('in–out').

Weight reduction was clearly important in sauropods, and this and the efficient respiration system may have permitted them to function at large size and with long necks.

The Macronaria include the camarasaurids, brachiosaurids and titanosaurids. 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. *Brachiosaurus* from the Upper Jurassic of North America and 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 80 tonnes. *Brachiosaurus* is a dinosaurian giraffe, designed to reach high into trees, and the body shape differs from other sauropods in having longer forelimbs than hind and a shorter tail. 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 *Brachiosaurus* had powerful muscles and ligaments to lift its crane-like neck up and down.

The titanosaurids are best represented in the Upper Cretaceous of South America, but occurred elsewhere

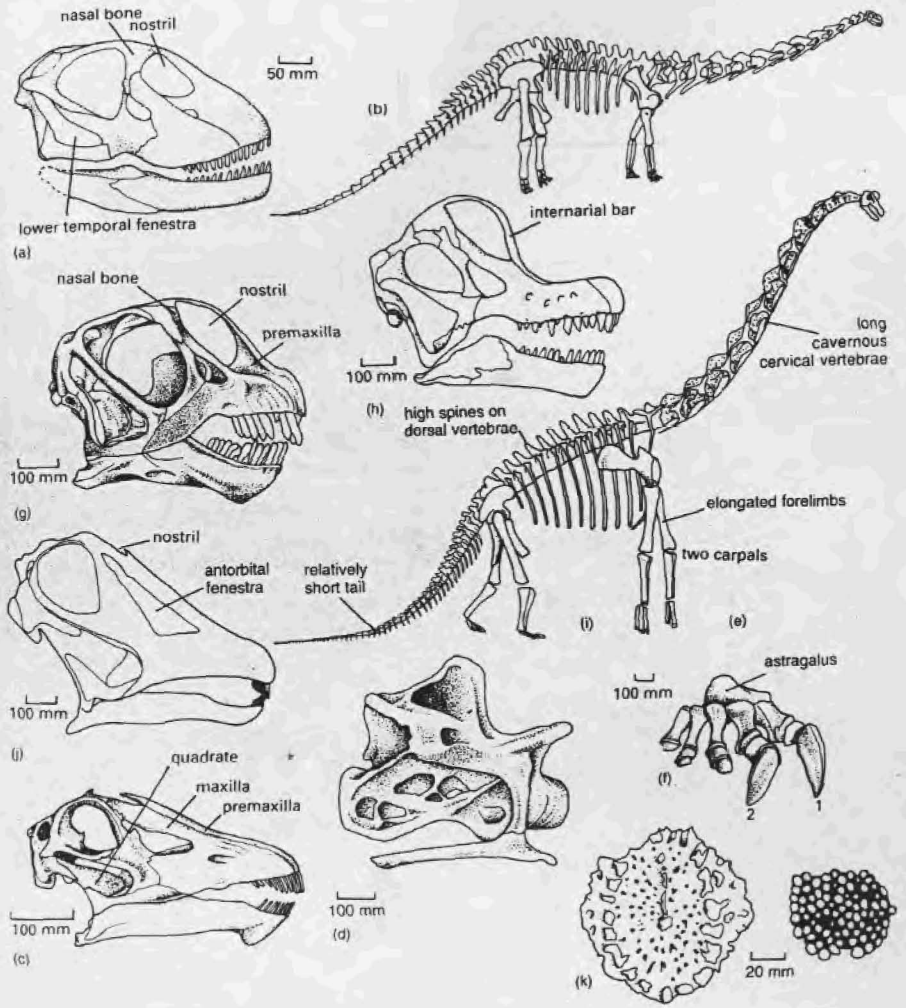


Fig. 8.10 Sauropods, all Jurassic in age, except (j, k) are Cretaceous: (a) skull of the euhelopodid *Shunosaurus*; (b) the cetiosaurid *Cetiosaurus*; (c) skull of the diplodocid *Diplodocus*; (d) cervical vertebra of *Diplodocus*; (e, f) hand and foot of *Diplodocus*; (g) skull of the camarasaurid *Camarasaurus*; (h, i) skull and skeleton of the brachiosaurid *Brachiosaurus*; (j) skull of the titanosaurid *Antarctosaurus*; (k) armour plate and armour pattern of the titanosaurid *Saltasaurus*. [Figure (a) after Dong and Tang, 1984; (b) after Crowther and Martin, 1976; (c, d) after Hatcher 1901; (e, f) after Coombs, 1975; (g–i) after Lapparent and Lavocat, 1955; (j, k) after Bonaparte, 1978.]

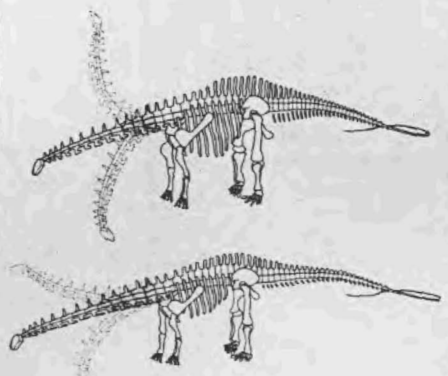
BOX 8.3 THE NECKS OF SAUROPODS

Sauropods all had long necks and in some, such as *Diplodocus*, the neck at 6 m was as long as the body and tail together. Did these sauropods operate like reptilian giraffes, reaching high with their necks into the tops of trees? Indeed, could *Diplodocus* perhaps have reared up and balanced on a tripod formed from its hind legs and tail to reach up 10 m or more?

This view has been disputed by Crowther and Martin (1976) who showed that the neck of *Cetiosaurus*, for example, had to be held at a level below the shoulders (see Figure 8.10(b). Close study of the necks of the diplodocids *Diplodocus* and *Apatosaurus* has confirmed this conservative viewpoint. Stevens and Parrish (1999) measured the angles of movement between cervical vertebrae all along the necks of those two dinosaurs and entered the figures into their DinoMorph software. Summing all the horizontal and vertical measures showed that both dinosaurs had a narrow envelope of neck movement. The envelope can be thought of as a huge cone, expanding from the root of the neck: at most *Diplodocus* and *Apatosaurus* could swing their heads 4 m to either side. *Diplodocus* could raise its head to shoulder level, about 4 m above the ground, but *Apatosaurus* had a more flexible neck and could raise its head to 6 m. Oddly, both dinosaurs could bend their necks down to a level some 1.5 m below ground level. But they were not burrowers! The downward neck bend may have been used for snatching plants from ponds and rivers.

Stevens and Parrish (1999) have shown that neither of these sauropods could have swung its neck above the horizontal—the arrangement of zygapophyses would have prevented it—but they might have been able to rear up on their hind legs to extend their reach. Other sauropods such as *Brachiosaurus* (see Figure 8.10(i)) did have more vertically placed necks and could have fed higher in trees.

Explore the DinoMorph software at http://www.cs.uoregon.edu/~kent/dinoMorph.html and view an animated *Apatosaurus* at http://www.nationalgeographic.com/dinorama/sauro.html.



The feeding envelopes of *Apatosaurus* (top) and *Diplodocus* (bottom) as shown in the DinoMorph software. (Courtesy of Kent Stevens.)

throughout the Cretaceous (Wilson & Upchurch, 2003). The skull (Figure 8.10(j)) was superficially like that of *Diplodocus* and the body was covered with an armour of roughly hexagonal bony plates (Figure 8.10(k)). New analyses (Curry Rogers and Forster, 2001; Wilson, 2002) suggest that *Nemegtosaurus* and *Quaesitosaurus* from the Upper Cretaceous of Mongolia, formerly classed as relatives of *Diplodocus*, are titanosaurids, although Upchurch (1999) makes a strong case that they are diplodocids.

Brachiosaurus was huge, but other sauropods might have been larger, although most are incomplete. The titanosaurid *Argentinosaurus* might have weighed 50–100 tonnes in life, close to the theoretical maximum size that any land animal could achieve without rendering itself unable to walk. As body size increases, the cross-sectional area of the legs increases in proportion: small animals have slender legs, whereas large animals have legs like tree trunks. At body weights of more than 100–150 tonnes, the cross-sectional areas of the legs would become so large that all four limbs would meet as a solid mass under the body.

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 (Figure 8.3(b)) as well as over 30 other derived characters of the skull and skeleton (Sereno, 1986, 1999).

The ornithischians arose during the Carnian (Late Triassic, 230–220 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 8.5).

8.4.1 *Pisanosaurus*—the first possible ornithischian

Pisanosaurus from the Carnian of Argentina is known from only its jaws, neck and a few limb elements (Bonaparte, 1976). The cheek teeth (Figure 8.11(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 sug-

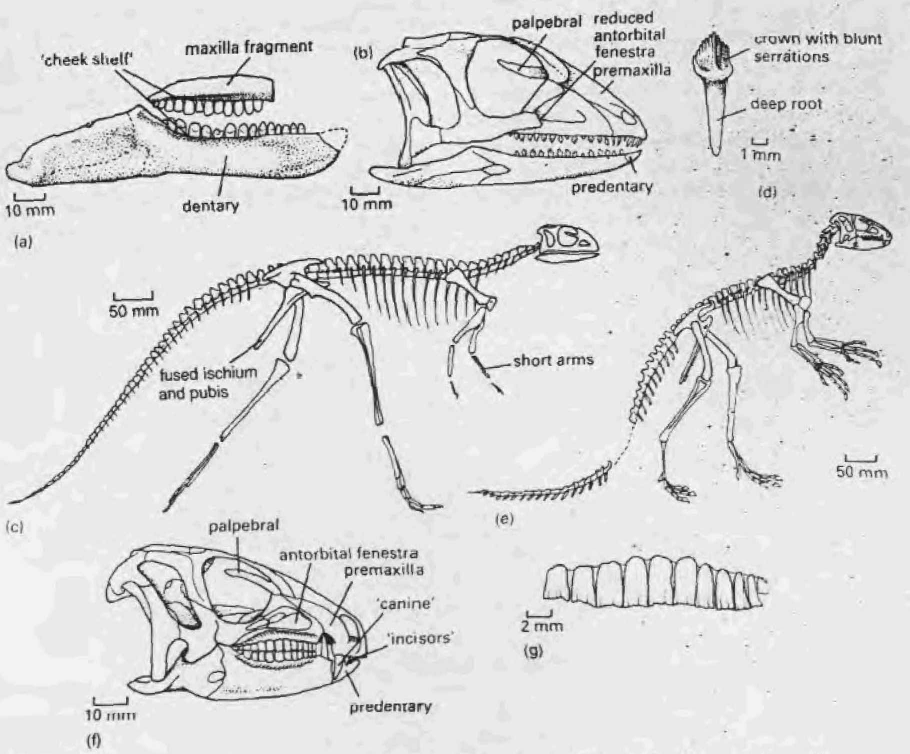


Fig. 8.11 Early ornithischians: (a) *Pisanosaurus*, maxilla fragment and partial lower jaw in lateral view; (b–d) the fabrosaurid *Lesothosaurus*, skeleton, skull and tooth; (e–g) the heterodontosaurid *Heterodontosaurus*, skeleton, skull in lateral view, maxillary tooth row. [Figure (a) after Bonaparte, 1976; (b–d) after Galton, 1978; (e) after Santa Luca, 1980; (f, g) after Charig and Crompton, 1974.]

gests 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. If *Pisanosaurus* is an ornithischian, it is followed by a long gap in their fossil record: the next ornithischians appear only some 20 Myr later.

8.4.2 Fabrosauridae

Small ornithischians, often called fabrosaurids, have been reported from the Lower Jurassic of several parts of the world (Galton, 1978; Knoll, 2002), but only *Lesothosaurus* from southern Africa is reasonably complete. It is a lightly built animal 0.9 m long, with long hindlimbs and short arms (Figure 8.11(c)). It has the typical ornithischian pelvis, an ilium with a narrow anterior process and fusion of the ischia and pubes at their tips. The skull (Figure 8.11(b)) shows even more ornithischian characters. 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 8.11(d)) 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.

8.4.3 Basal ornithopods

The ornithopods were the largest and most successful ornithischian group, comprising more than 100 species and achieving great abundance in Cretaceous faunas. There are four main groups, the heterodontosaurids, hypsilophodontids, 'iguanodontids' and hadrosaurids.

The heterodontosaurids lived at the same time as the fabrosaurs. *Heterodontosaurus*, from southern Africa (Charig and Crompton, 1974; Santa Luca, 1980), just over 1 m long, is similar to *Lesothosaurus* in many ways. The bodily proportions (Figure 8.11(e)) differ only in the slightly longer arms and the shorter body. The skull (Figure 8.11(f)) 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 features that group it with later ornithopods: 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 pp. 121, 189), the cheek teeth wear against the opposite teeth of the lower jaw forming a straight line at the crest of the teeth (Figure 8.11(g)), and the outer surfaces of the lower teeth fit inside the upper teeth and wear them from the inside. Unlike *Lesothosaurus*, *Heterodontosaurus* was capable of a small amount of sideways chewing by rotation of the lower jaw about its long axis (see Box 8.4).

The hypsilophodontids, typified by *Hypsilophodon* from the Lower Cretaceous of England (Galton, 1974), but known from the Late Jurassic to the Late Cretaceous, ranged in length from 3 to 5 m or so. The bodily proportions (Figure 8.12(a)) and the skull (Figure 8.12(b,c)) are similar to those of *Heterodontosaurus*, except that the skull lacks tusks and is narrower in the midline. The ventral view (Figure 8.12(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 8.12(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, as in *Deinonychus* (Figure 8.8(a)). The limb proportions of *Hypsilophodon* are similar to those of a fast-moving gazelle, especially the very long shin and foot.

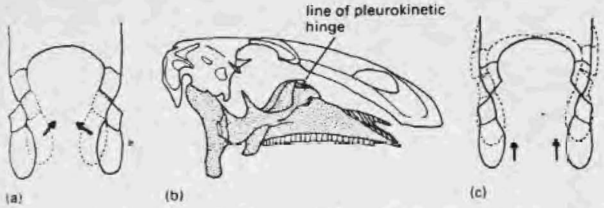
BOX 8.4 CHEEKS AND CHEWING IN ORNITHOPODS

Ornithopod dinosaurs were unique among reptiles in that they could chew their food. Chewing, in which the back teeth move sideways and back and forwards, is normally thought to be a special feature of mammals. We chew our food before swallowing in order to aid digestion: reptiles and birds just gulp their food down. Ornithopods hit on two solutions to the problem, and both of these are different from the mammalian technique (see pp. 292–6).

Heterodontosaurus had a rotating lower jaw. The articular–quadrate joint at the back and a special ball and socket joint at the front between the dentary and predentary, allowed rotation as the jaws opened and closed. This mode of jaw rotation provided one solution to the problem of creating an efficient shearing scissor-like cutting movement between the cheek teeth (see illustration (a)).

All later ornithopods adopted the other option, of rotating the maxilla, in order to achieve lateral shearing, and this adaptation is said to lie at the root of the great success of the ornithopods in the Cretaceous (Norman and Weishampel, 1985). The hypsilophodontids, 'iguanodontids' and hadrosaurids have essentially fixed lower jaws that simply moved up and down without distortion during chewing, while the side of the skull (maxilla, lacrimal, jugal, quadratojugal, quadrate) as well as attached palatal elements (ectopterygoid, palatine, pterygoid) flap in and out. This specialized **pleurokinetic hinge** (illustration (b)) produces the same lateral shearing effect (illustration (c)) as did the rotating mandible of the heterodontosaurids.

Most ornithopods had single rows of teeth on the crests of their jaws. As in all reptiles, teeth were replaced continuously as they became worn out and replacement teeth lined up below the currently functioning teeth on the inside of the jaws. This pattern was taken to an extreme in hadrosaurids, which had a dental battery in which five or six rows of teeth below the jaw line could also be in use (see Figure 8.14(a–c)). Ceratopsians could probably also slice their plant food effectively between powerful shearing jaws, but the other herbivorous dinosaurs lacked chewing adaptations. Perhaps this ability explains the vast success of ornithopods in the Cretaceous after the heyday of the sauropods had passed.



Ornithopod jaw mechanics: the lower jaws of *Heterodontosaurus* (a) slide outwards as they close, hence producing a kind of 'chewing', whereas later ornithopods have a pleurokinetic hinge, which allows the cheek portion of the skull and the maxillary teeth, shown stippled in (b), to move outwards as the jaws close (c). (Modified from Norman and Weishampel, 1985.)

Galton (1974) made a detailed restoration of the muscles of the hindlimbs of *Hypsilophodon* (Figure 8.12(e)), based on muscle scars and processes on the bones and comparison with dissections of modern birds and alligators (see Box 6.2). 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.

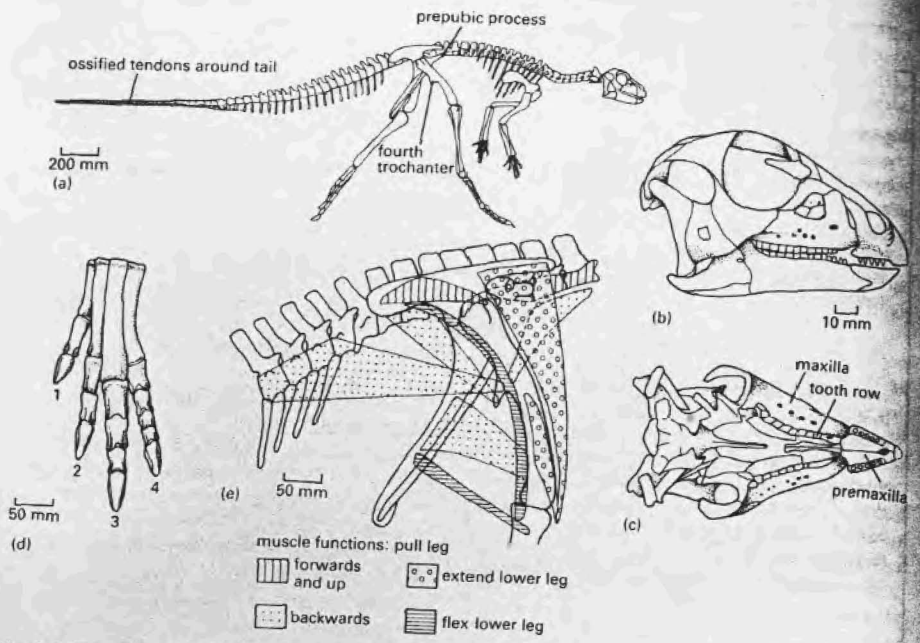


Fig. 8.12 The ornithopod *Hypsilophodon*: (a) skeleton in running pose; (b, c) skull in lateral and ventral views; (d) foot in anterior view; (e) restoration of the muscles of the pelvis and hindlimb, coded according to their functions. (After Galton 1974.)

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.

The 'iguanodontids' are a paraphyletic group representing stages of the acquisition of advanced hadrosaurian characters (Sereno, 1986). *Iguanodon* from the Lower Cretaceous of Europe (Norman, 1980, 1986b) has a horse-like skull (Figure 8.13(a)). In the skeleton (Figure 8.13(b)), the prepubic process is expanded, the postpubic process is very short and there is a complex lattice of ossified tendons over the neural spines of all vertebrae of the trunk and tail. The most remarkable modifications are seen in the hand (Figure 8.13(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) and in defence or display (thumb spike). *Iguanodon* could walk on all fours, or equally well on its hindlegs alone with the tail and the backbone extended horizontally. Another 'iguanodontid', *Ouranosaurus* from the Lower Cretaceous of North Africa, has spines on its back, perhaps supporting a sail for thermoregulation. The snout (Figure 8.13(d)) is elongate and rather flattened.

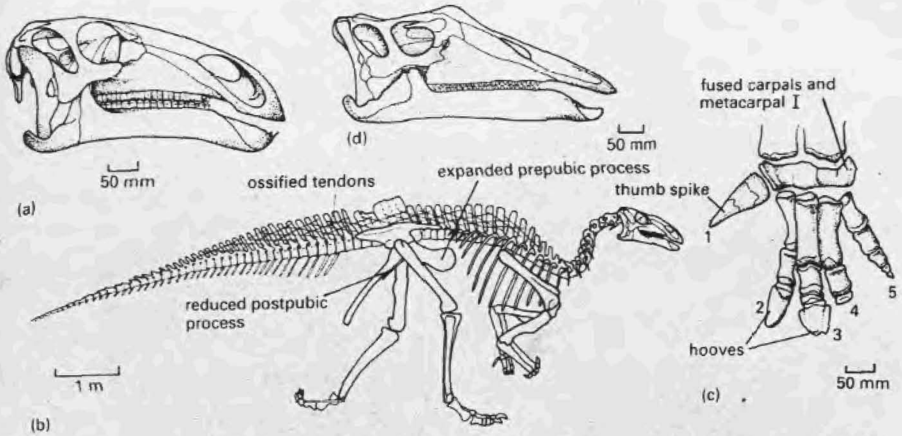


Fig. 8.13 Ornithopod anatomy: (a) skull of *Iguanodon*; (b) skeleton of *Iguanodon* in running pose; (c) hand of *Iguanodon* in anterior view; (d) skull of *Ouranosaurus*. [Figures (a, b) after Norman, 1986b; (c) after Norman, 1980; (d) after Norman, 1984.]

8.4.4 Hadrosauridae: the duckbills

The most diverse, and most successful, ornithopod clade were the hadrosaurs or 'duck-billed' dinosaurs of the Late Cretaceous. They are especially well-known from North America (Ostrom, 1961), 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 8.14(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 pushed 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 8.14(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 8.14(d)) as sloping downwards and outwards. As the lower jaw closes, the cheek region of the skull moves outwards on the pleurokinetic hinge (see Box 8.4) and the plant food is ground with a strong sideways shearing movement. In addition, the jaws move back and forwards a little, giving a further 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 (Weishampel, 1984) 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, which suggests that the hadrosaurs were terrestrial browsers that stripped trees of their foliage by stretching up on their hindlegs.

Hadrosaurs were once said to have spent most of their time swimming in lakes, a view perhaps derived

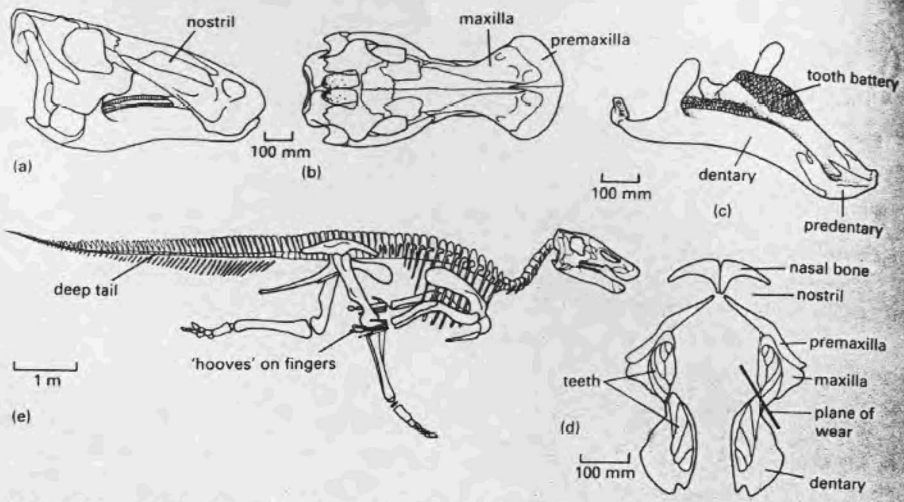


Fig. 8.14 Hadrosaur anatomy: (a, b) skull of *Edmontosaurus* in lateral and dorsal views; (c) lower jaw of *Kritosaurus* seen at an angle to show the dental batteries; (d) cross-section through the snout of a hadrosaur to show patterns of tooth replacement; (e) skeleton of *Anatosaurus* in running pose. [Figures (a, b) after Norman, 1984, courtesy of the Zoological Society of London; (c, d) after Ostrom, 1961; (e) after Galton, 1970a.]

from their duck bills. They could doubtless have swum, but the skeleton (Figure 8.14(e)) is particularly adapted (Galton, 1970a) for efficient running with the body held horizontally as in other bipedal dinosaurs. The hands bear small hooves on the fingers, so they could also be used in slower locomotion.

Hadrosaurs all have essentially the same skeletons and skulls (Figure 8.14), 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, and in others a long 'tube', spike, or forwards-directed rod (Figure 8.15(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 8.15(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.

What was the function of hadrosaur crests? Probably they were used as visual species and sexual signalling devices (Hopson, 1975; Weishampel, 1997), just as modern birds use colourful and often elaborate patterns of feathers to recognize potential mates and to signal their position in dominance hierarchies. Males and females of the same species had rather different crests (Figure 8.15(c)) and the crest was undeveloped in juveniles. Further, 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.

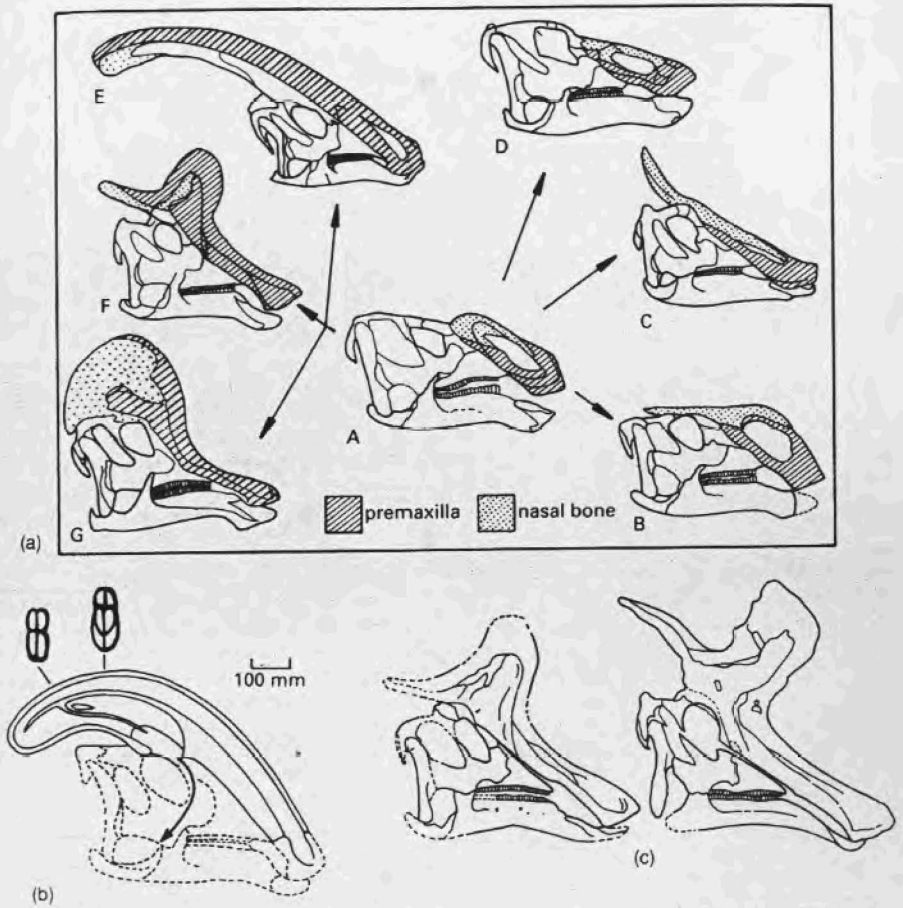


Fig. 8.15 Hadrosaur skulls and crests: (a) several lines of hadrosaurian evolution from a crestless form (A, *Kritosaurus*) to crested genera (B, *Brachylophosaurus*; C, *Saurolophus*; D, *Edmontosaurus*; E, *Parasaurolophus*; F, *Lambeosaurus*; G, *Corythosaurus*); (b) internal structure of the crest 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). (Modified from Hopson, 1975.)

8.4.5 Pachycephalosauria: the bone-heads

The pachycephalosaurs, a small clade of mainly Late Cretaceous herbivores from North America and central Asia (Maryańska and Osmólska, 1974), are characterized by their unusually thick skull roofs (Figure 8.16(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 ele-

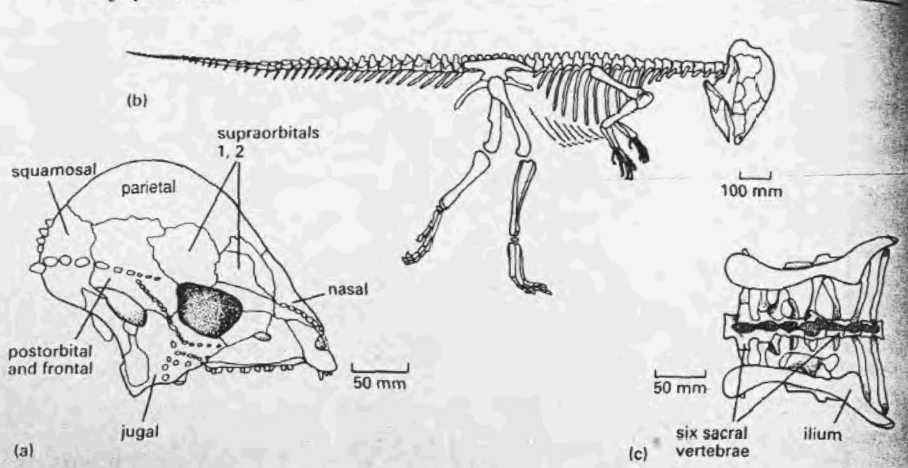


Fig. 8.16 The pachycephalosaurs: (a) skull of *Prenocephale*; (b) skeleton of *Stegoceras* in butting position; (c) pelvis of *Homalocephale* in dorsal view. [Figures (a, c) after Maryańska and Osmólska, 1974; (b) modified from Galton, 1970b.]

ments as well as two supplementary supraorbital elements. Several of the skull bones are further ornamented by lines of bony knobs.

The pachycephalosaurs may have used their thickened heads in butting contests when seeking mates (Galton, 1970b), as is seen today among wild sheep and goats. The pachycephalosaur, a biped, adopted a horizontal-backbone posture during the charge (Figure 8.16(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 p. 126). Confirming evidence for this theory is that the presumed males have thicker skulls than females.

Pachycephalosaurs are also characterized by an unusually broad pelvis (Figure 8.16(c)) with gently curved iliac blades that contact the ribs of up to eight sacral vertebrae. This firm attachment of the pelvis may relate to the need to dissipate the forces of head-butting. Pachycephalosaurs appear to be allied to the horned ceratopsians, forming with them a clade Marginocephalia (see Box 8.5), 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).

8.4.6 Ceratopsia: the horn-faced dinosaurs

The Ceratopsia (literally 'horned faces') comprise a relatively large group of about 25 genera known mainly from the Upper Cretaceous of North America (Ostrom, 1966). All are characterized by a triangular skull when viewed from above (Figure 8.17(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 Lower Cretaceous of eastern Asia (Figure 8.17(a)), were bipeds that had body forms very similar to ornithopods, but the skull is clearly ceratopsian. *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 8.17(b)). It also shows the second major ceratopsian characteristic, a bony frill formed from the parietals and squamosals (Figure 8.17(c)). The frill probably served as the origin of part 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 8.17(d)). Vertebrae of the neck and

BOX 8.5 RELATIONSHIPS OF THE DINOSAURS

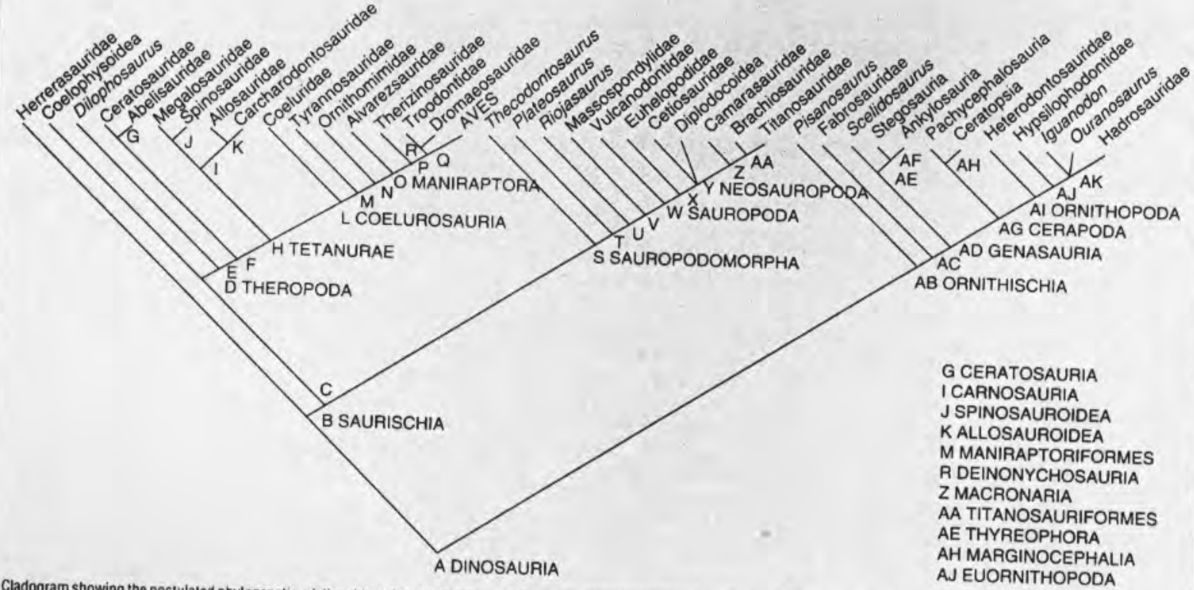
The Dinosauria (see cladogram) consist of two main clades (Gauthier, 1986; Benton, 1990a; Sereno, 1999), the Saurischia and Ornithischia. The Saurischia fall into two main clades, the Theropoda and Sauropodomorpha. Within Theropoda, the main outlines are widely agreed, with the coelophysoids and ceratosaurs near the base, then various larger flesh-eating groups (e.g. megalosaurids, allosaurids, spinosaurids), then tyrannosaurids and maniraptorans (troodontids, dromaeosaurids, birds). Much of the detail is controversial.

We use here the most thorough recent analyses of theropod relationships: Rauhut (2003), for the outline of major theropod groups, and Clark *et al.* (2002) and Maryańska *et al.* (2002) for maniraptorans and basal birds. Sereno (1999) regards herrerasaurids as basal theropods, whereas they are indicated as basal saurischians here (Langer *et al.*, 1999). Earlier authors (e.g. Gauthier, 1986; Holtz, 1994; Sereno, 1999) recognized a broad-based ceratosaur clade, whereas Rauhut (2003) finds that coelophysoids and ceratosaurs are successive outgroups. Holtz (1994) identified a major theropod clade, termed the Arctometatarsalia, that included tyrannosaurids, ornithomimids and troodontids. This is not accepted here (Rauhut, 2003). Among Maniraptora (Gauthier, 1986), major changes have been the move down the tree of the alvarezsaurids (Chiappe *et al.*, 2002), formerly regarded as fully-fledged birds, and the move of oviraptorosaurs into Aves (Maryańska *et al.*, 2002). Sereno (2001) pairs alvarezsaurids with ornithomimids, but we retain them simply as an outgroup on the main stem to birds.

The Sauropodomorpha includes the Triassic and Jurassic Prosauropoda, possibly a clade, or more probably a sequence of outgroups to Sauropoda (Yates, 2003b). Within Sauropoda (Upchurch, 1998; Curry Rogers and Forster, 2001; Wilson, 2002), the Early and Middle Jurassic vulcanodontids and euhelopodids are outgroups to six major families of giant sauropods, mainly Late Jurassic to Cretaceous in age.

The Ornithischia (Sereno, 1986, 1999) have a possible primitive member, *Pisanosaurus*, and two main clades, the Cerapoda and the armoured Thyreophora, jointly the Genasauria. The Early Jurassic fabrosaurid *Lesothosaurus* is an outgroup to the Genasauria. 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. The Thyreophora consists essentially of the Stegosauria and the Ankylosauria, with *Scelidosaurus* and *Scutellosaurus*, Early Jurassic forms, as basal representatives.

continued



Cladogram showing the postulated phylogenetic relationships of the main groups of dinosaurs. Synapomorphies from Rauhut (2003) and Clark *et al.* (2002) on theropods, Yates (2003b) on basal saurischians and basal sauropodomorphs, Upchurch (1998), Curry Rogers and Forster (2001) and Wilson (2002) on sauropods and Sereno (1986, 1999) on ornithischians. Synapomorphies: **A DINOSAURIA**, exposed quadrate head in lateral aspect, ectopterygoid lies dorsal to pterygoid, elongate deltopectoral crest on the humerus, brevis shelf on ventral surface of postacetabular part of ilium, extensively perforated acetabulum, tibia with a posterolateral flange, ascending astragalar flange on anterior face of tibia; **B SAURISCHIA**, lacrimal exposed on the dorsal skull roof, cervicals 3–6 longer than the axis, accessory articulations between vertebrae (hyposphene–hypantrum), hand more than 45% of humerus + radius, first phalanx of thumb longer than metacarpal I, hand digits 1 and 2 reduced to two and one phalanges respectively, prominent supraacetabular–preacetabular buttress on the ilium; **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**, tooth row ends at anterior rim of the orbit, pleurocoels in cervicals developed as foramina that invade the vertebral body; **F**, 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 the tibia on the calcaneum; **G CERATOSAURIA**, external nares face anterolaterally, upper temporal fenestrae almost meet in front, quadrate foramen absent, neural spines of mid-caudals rod-like and vertical; **H 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; **I CARNOSAURIA**, ascending process of maxilla offset from anterior rim of maxilla, cervical centra strongly opisthocoelous, metacarpal I very stout and about as broad as long; **J SPINOSAUROIDEA**, premaxilla in front of naris elongate and rounded snout, enlarged fang-like teeth in the dentary; **K ALLOSAUROIDEA**, antorbital fossa extends on to the nasals, distal ends of paroccipital processes entirely below the foramen magnum; **L COELUROSAURIA**, maxillary antorbital fenestra more than 40% the length of the external antorbital fenestra, no serrations on premaxillary teeth, feathers; **M MANIRAPTORIFORMES**, upper temporal fenestrae confluent over the parietals and parietals form a sagittal crest, fewer than 41 caudals, medial side of metacarpal II straight and without proximal expansion, femoral head separated from the greater trochanter by a cleft, lesser trochanter as high as or higher than greater trochanter; **N**, jugal antorbital fossa absent or a slight depression, lacrimal fenestra absent, more than five sacral vertebrae; **O MANIRAPTORA**, fewer than 35 caudals, coracoid longer than high, internal tuberosity on humerus rectangular, semilunate carpal, obturator process of ischium distally placed, distal end of tibia broadly rectangular and more than three times wider than long, fibular shaft narrows to a thin splint, metatarsal V reduced and rod-like, contour feathers; **P**, ossified ventral rib segments, sternum with lateral process, glenoid facet on scapula faces ventrolaterally; **Q**, hyposphene wide, ten or fewer caudals with transverse processes, fewer than 11 caudals with well developed neural spines, anterior caudals box-like, acromion process of scapula low, coracoid subrectangular in outline, shaft of metacarpal III bowed laterally, anterior process of ilium longer than posterior; **R DEINONYCHOSAURIA**, premaxillary teeth with serrated carinae, digit IV of the foot much longer than II and only slightly shorter than III; **S 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; **T**, five premaxillary teeth, hand claw II is less than 75% the size of claw I in all dimensions; **U**, short hand, femur straight in anterior view, femoral head not offset; **V**, short lacrimal and triangular antorbital fenestra, jugal excluded from margin of antorbital fenestra, four premaxillary teeth, digit I is longest in the hand, phalanges in digits II and III shortened; **W 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; **X**, fourth trochanter reduced to a low rounded ridge; **Y NEOSAUROPODA**, upper temporal fenestrae separated by broad bone bar, external mandibular fenestra closed, marginal tooth denticles absent, two or fewer carpal bones; **Z 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; **AA TITANOSAURIFORMES**, mid-cervical centra elongate, dorsal ribs with pneumatic cavities, metacarpal I distal condyle undivided and perpendicular to shaft, iliac preacetabular process semicircular; **AB ORNITHISCHIA**, cheek teeth with low subtriangular crowns, muscular cheeks [?or at V]; **AC**, reduced antorbital opening, palpebral bone, toothless and roughened tip of snout, predentary bone, jaw joint set below level of upper tooth row, at least five sacral vertebrae, ossified tendons above the sacral region, pelvis with pubis directed backwards, small prepubic process on pubis, long thin anterior process on ilium; **AD GENASAURIA**, muscular cheeks, spout-shaped front to mandibles, reduction in size of mandibular foramen; **AE THYREOPHORA**, transversely broad postorbital provess of jugal, parallel rows of keeled scutes on the back and sides; **AF**, additional bones in margins of orbit, posterior process of ilium reduced and anterior part enlarged, fourth trochanter on femur reduced, short and stocky metacarpals and metatarsals, loss of phalanx in digit 4 of foot; **AG CERAPODA**, gap between teeth of the premaxilla and maxilla, five or fewer premaxillary teeth, finger-like lesser trochanter on femur; **AH MARGINOCEPHALIA**, narrow shelf formed from parietal and squamosal bones that extends over the back of the skull, reduced contribution of premaxilla to palate, short pubis; **AI ORNITHOPODA**, elongation of lateral process of premaxilla to contact lacrimal and/ or prefrontal, premaxillary tooth row offset ventrally compared with maxillary tooth row, crescentic paroccipital process, jaw joint set well below level of tooth rows; **AJ EUORNITHOPODA**, absence of prominent boss in cheek region, high angle between prepubic process and body of pubis; **AK**, external naris enlarged, antorbital fenestra reduced, back of skull narrow, close-packed teeth, premaxillary teeth absent, maxillary teeth with relatively high crowns and prominent ridge on outside, wrist bones fused, spiked thumb, digits 1–4 of hand reduced, digit 5 of foot absent, ossified tendons extend from base of neck to middle of tail.

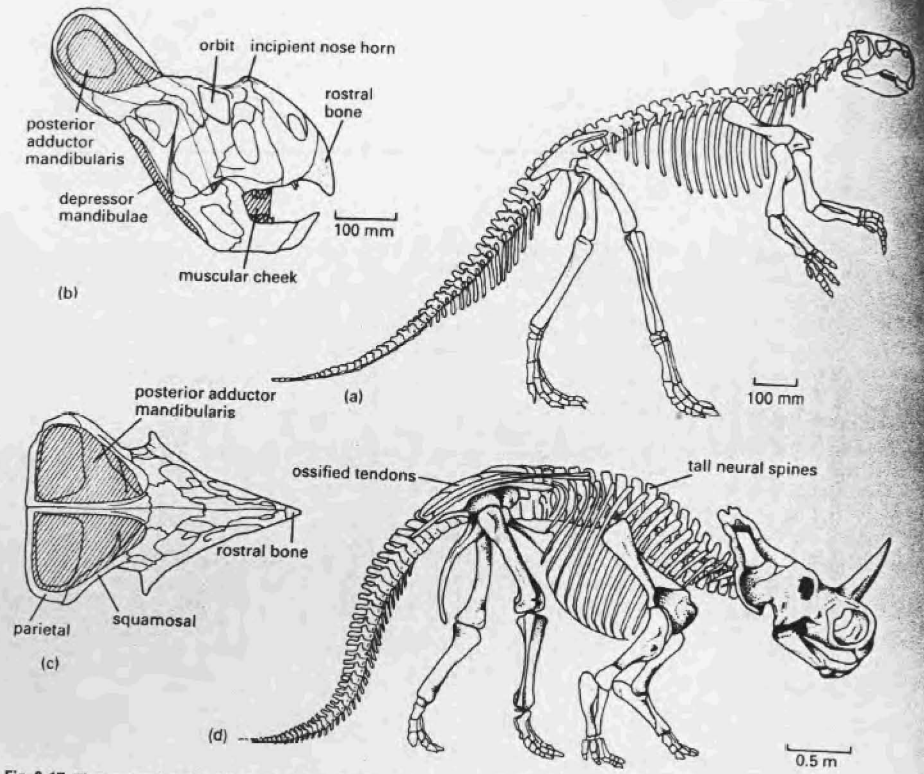


Fig. 8.17 The ceratopsians: (a) skeleton of *Psittacosaurus*; (b, c) skull of *Protoceratops* in lateral and dorsal views, with the cheek and major muscles restored; (d) skeleton of *Centrosaurus*. [Figure (a) after Zittel, 1932; (b, c) modified from Ostrom, 1966; (d) after Brown, 1917.]

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 8.17(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 *Torosaurus* had a skull 2.6 m long in which the frill is longer than the rest of the skull, 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.

8.4.7 Stegosauria: the plated dinosaurs

The thyreophorans, the truly armoured ornithischians, are characterized by a transversely broad postorbital process of the jugal and by parallel rows of keeled scutes on the back surface of the body. The clade Thyreophora (see Box 8.5) includes some basal forms from the Early Jurassic, such as *Scelidosaurus* from England (and reported also from North America and China) and *Scutellosaurus* from Arizona, USA (Colbert, 1981), and the more familiar larger groups Stegosauria and Ankylosauria that radiated in the Middle Jurassic. *Scutellosaurus* (Figure 8.18(a)) is a modest-sized biped, with a skeleton similar to that of *Lesothosaurus* (Figure 8.11(c)), but it has numerous rows of keeled scutes (Figure 8.18(b)) over the back and in regular rows on the flanks.

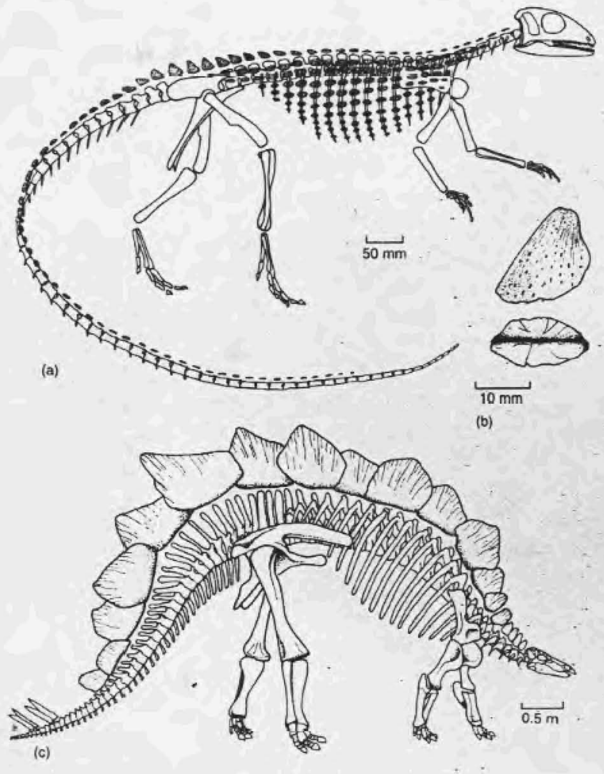


Fig. 8.18 A basal thyreophoran (a, b) and a stegosaur (c): (a, b) skeleton of *Scutellosaurus* and an armour plate in lateral and dorsal views; (c) *Stegosaurus*. [Figures (a, b) after Colbert, 1981; (c) after Zittel, 1932.]

Typical stegosaurs, such as *Stegosaurus* from the Upper Jurassic of North America (Figure 8.18(c)), have low, almost tubular skulls. 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 was hard to determine as 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 and they must have been covered by skin. Postulated functions for the plates include: (1) armour, (2) sexual display structures, (3) deterrent display structures and (4) thermoregulatory devices. Farlow *et al.* (1976) noted that the arrangement of the

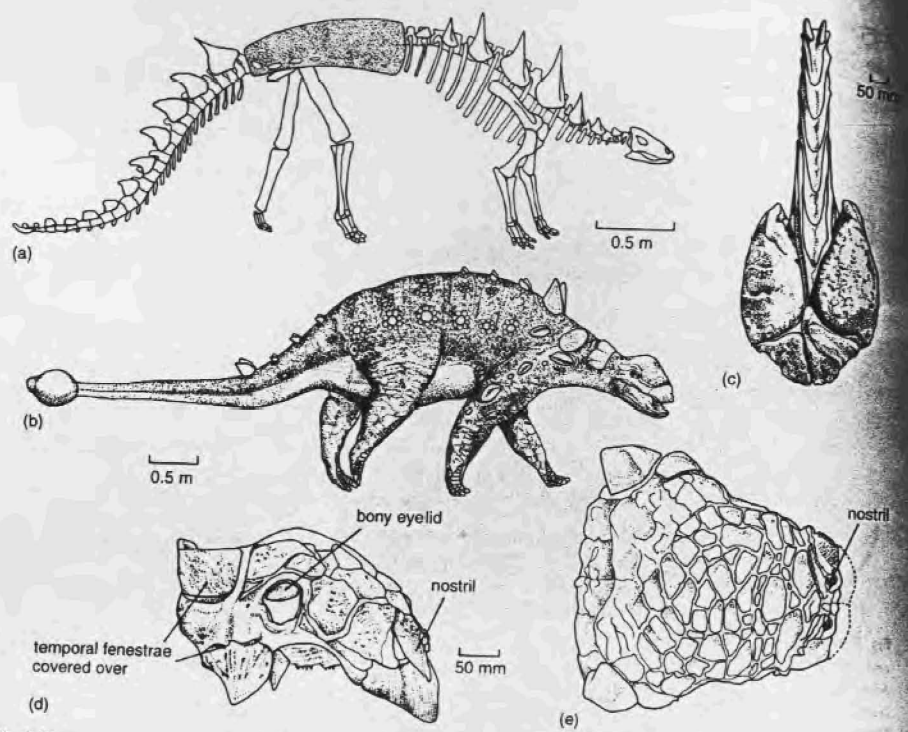


Fig. 8.19 The ankylosaurs: (a) *Polacanthus*; (b) *Euoplocephalus* body restoration; (c) *Ankylosaurus* tail club; (d, e) *Euoplocephalus* skull in lateral and dorsal views. [Figure (a) after Blows, 1987; (b) after Carpenter, 1982; (c–e) after Coombs, 1978.]

plates fitted engineering design models for heat-dissipation structures. As with the sails of the pelycosaurs (see p. 121), *Stegosaurus* could have modified its body temperature by adjusting the blood flow to the fins and its orientation to the wind. An overheated animal could cool down rapidly by pumping high volumes of blood over the plates and standing broadside on to the prevailing wind.

8.4.8 Ankylosauria: armour-covered dinosaurs

Like the stegosaurs, the ankylosaurs (Coombs, 1978) arose in the Mid-Jurassic, but they are not well known until the Early Cretaceous. *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 8.19(a)). The ankylosaurids such as *Euoplocephalus* and *Ankylosaurus* (Figure 8.19(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 8.19(c)). A blow from this club would readily disable *Tyrannosaurus* or any other contemporary predator.

The ankylosaur skull (Figure 8.19(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 they are heavily overgrown.

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. Ostrom, 1969; Galton, 1970a, b), 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. Additional lines of evidence have been brought to bear, and the debate continues.

8.5.1 The evidence

Palaeoclimatology and distribution

Finds of dinosaurs within the Cretaceous polar regions (Figure 8.20) have been thought to indicate endothermy, because a typical reptile could not survive in cold polar conditions. Polar dinosaurs were found first in Alaska in the 1960s, and further collecting has revealed a restricted fauna dominated by hadrosaurs, with rarer ceratopsians and isolated remains of a troodontid and a tyrannosaurid (Clemens and Nelms, 1993). Several localities in the Lower Cretaceous of Victoria, south Australia, a region that was located well within the Antarctic Circle at the time, have yielded dinosaur finds (Rich *et al.*, 1988): hypsilophodontids, an allosaurid, crocodilians, pterosaurs, turtles, amphibians and fishes. There is geological evidence for winter freezing in South Australia, and that would be expected —even in the absence of a permanent ice-cap, polar regions receive very little sunlight in winter.

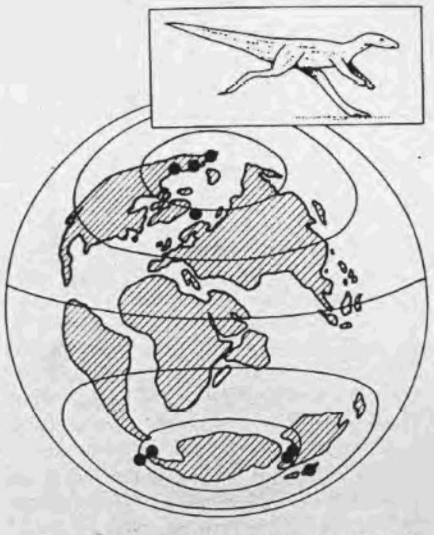


Fig. 8.20 Distribution of dinosaurs in polar regions during the Cretaceous, mapped on a Late Cretaceous palaeogeographical reconstruction. A hypsilophodontid, typical of discoveries from the polar regions of Australia, is shown at the top. (Based on several sources.)

Did the Alaskan and South Australian dinosaurs live in the ice and snow? Seebacher (2003) has shown that ectothermic dinosaurs of all body sizes could have maintained body temperatures of 30°C or above, up to latitude 55–55°, even in the winter. North and south of that latitude, winter body temperatures of ectothermic dinosaurs would fall below 30°C. The dinosaurs of Alaska and Australia probably migrated away to avoid the months of darkness and absence of plant food, so polar dinosaurs do not prove endothermy.

Predator–prey ratios

Herbivores (whether endothermic or ectothermic) can support about 5% of their biomass of endothermic predators, and for ectothermic (reptile) carnivores this predator–prey ratio is apparently nearer 30–50%. Bakker (1972) showed that predator–prey ratios for fossil populations dropped from 50 to 60% in the Early

Permian to 10% in the Late Permian, and to 2–3% in Late Triassic, Jurassic and Cretaceous dinosaur faunas. He interpreted this as strong evidence for dinosaur endothermy. There are many practical problems in calculating such ratios, and the ratios for large ectothermic predators closely approach those for endothermic predators. The ratios seem to vary with the size of the animals involved rather than simply with their thermoregulatory state.

Erect gait and high speeds

Dinosaurs had an erect stance and advanced gait compared with most of their predecessors (see Box 6.2). Among living animals, only endotherms (birds, mammals) have erect gait, and Bakker (1972) suggested that this, and the supposed ability of dinosaurs to achieve fast speeds, indicated endothermy. There is, however, no demonstrated causal link between endothermy and erect gait and the data on dinosaur running speeds are also equivocal. Estimates of speeds, based on fossilized trackways and limb dimensions, range from 6 to 60 km h^{-1} (1.5–7 m s^{-1}: Alexander, 1976; Thulborn, 1990). But only small bipedal dinosaurs could achieve the higher speeds of 35–60 km h^{-1}, and 40 km h^{-1} may be a more likely maximum. Larger dinosaurs were probably restricted to walking or slow trotting gaits and speeds of 10–20 km h^{-1}.

Haemodynamics

The long-necked sauropods must have had problems in pumping blood up their necks to supply the brain and face. It has been suggested that these dinosaurs probably had to have a powerful four-chambered heart, a feature seen only in living birds and mammals, and that dinosaurs were thus endothermic. This correlation is uncertain, however, not least because crocodilians have a four-chambered heart.

Bone histology

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.

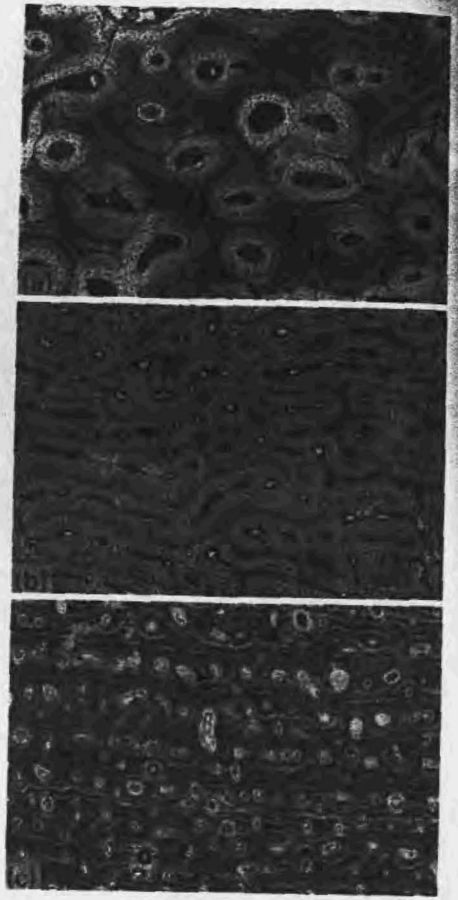


Fig. 8.21 Dinosaur bone at high magnification: (a) Haversian bone tissue, showing secondary remodelling; (b) fibrolamellar bone; (c) lamellar-zonal bone, showing growth rings running vertically. (Courtesy of Robin Reid.)

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 now found 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 Box 8.6).

Modern reptiles have lamellar-zonal bone, which grows slowly and often intermittently, producing growth rings, or lines of arrested growth, 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), so a mixed thermoregulatory regime is suggested with a combination of fast and episodic growth rates.

High growth rates

Modern reptiles typically grow slowly, whereas endotherms can grow fast—an ostrich or a whale reaches adult size in five to ten years. Studies of dinosaurian bone show that dinosaurs were fast growers (Padian *et al.*, 2001b), reaching adult size in only a few years (see Box 8.6). Even the large sauropods grew at rates more equivalent to whales than to crocodilians (Erickson *et al.*, 2001), reaching adult size in 10–15 years, rather than 100. Such fast growth in dinosaurs has been assumed to imply endothermy, but inertial homeothermy (see below) cannot be ruled out (Seebacher, 2003).

Feathers

When Bakker (1972, 1986) suggested that some dinosaurs might have had feathers, he was ridiculed. New finds from China, however, have shown that coelurosaurs had simple filament-like feathers and maniraptorans had true contour feathers (see Box 8.2). These theropods presumably evolved their first simple feathers for insulation and this implies a measure of endothermy.

Core and peripheral temperatures

Barrick and Showers (1994) tested for differences between core and peripheral body temperatures in *Tyrannosaurus*, a seemingly impossible task without a time machine, a large thermometer and a certain amount of foolhardiness! They measured oxygen isotopes in core bones (ribs and dorsal vertebrae) and peripheral bones (limbs and tail) to assess temperatures, on the assumption that the ratio of $^{18}O/^{16}O$ in the apatite would have been fixed at the time of bone formation. They found evidence that body temperatures were 4°C higher in the core elements than the peripheral and they argued that this proved constancy of body temperature, and hence endothermy. Critics have noted that the data could have been over-interpreted (Reid, 1997), and the implied constancy of body temperature could in fact be achieved by inertial homeothermy (see below). The idea has been extended by a comparison of the oxygen isotope ratios in the enamel of crocodilian and theropod teeth from four Late Cretaceous localities, ranging from equatorial to temperate zones (Fricke and Rogers, 2000): the crocodilians showed changes in the ratio of $^{18}O/^{16}O$ that match modern ectotherms, whereas the theropod figures were those of endotherms.

Noses

Birds and mammals have complex scrolls of thin bone within the nasal cavity, termed **turbinates**. These are covered with mucous membranes in life and their function is to conserve water by extracting it from respiratory air before it is exhaled. Modern ectotherms lack turbinates and so too did dinosaurs (Ruben, 1995), evidence perhaps against endothermy.

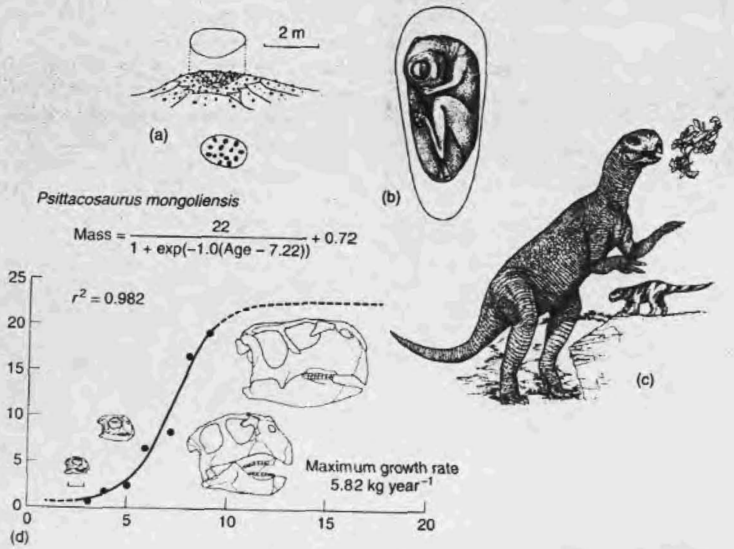
8.5.2 Endothermy and gigantothermy

Bakker (1972, 1986) was wrong to claim that all

BOX 8.6 BABY DINOSAURS

Dinosaurs laid eggs (Carpenter *et al.*, 1994; Horner, 2000), and most laid them in nest-like structures that were dug in the sand or earth (illustration (a)) and then covered over for incubation, as in present-day crocodilians. In many cases, the eggs are long and ellipsoid in shape and they were laid in concentric circles, upright and with the narrow end downwards. On hatching, the young left through the top of the eggs, leaving the lower halves intact within the sediment. Some finds indicate brooding; an adult *Oviraptor*, perhaps a bird in any case (see p. 275), seated on a nest of unhatched eggs (Norell *et al.*, 1995). But what happened after the babies hatched?

Among modern reptiles and birds, many are **precocial**, meaning they get up and run immediately. Others, are **altricial**, meaning that the young stay in the nest and have to be cared for. A strong case was made for altriciality in dinosaurs. Excavations of Late Cretaceous nests of the hadrosaur *Maiasaura* (Horner and Makela, 1979) revealed skeletons of 15 juveniles, each about 1 m long, around a nest mound that contained egg fragments. Perhaps they stayed together for some time after hatching. This view was criticized by Geist and Jones (1996) who reported precocial features in *Maiasaura*; the pelvic bones and limb bones are complete and well ossified, suggesting that the babies were ready to jump up and run off as soon as they hatched.



Dinosaur nests, eggs and juveniles: (a) nest mound of the hadrosaur *Maiasaura* from Upper Cretaceous sediments of Egg Mountain, Montana, in lateral view and plan view, and section showing the eggs in black; (b) reconstruction of an embryo of the theropod *Troodon* in a 170 mm long egg; (c) adult and juvenile *Psittacosaurus* reconstructed; (d) sequence of skulls of *Psittacosaurus* from hatchling to adult, showing changes in proportions with growth, overlain on a growth curve. [Figures (a) after Horner and Makela, 1979, copyright © 1979 Macmillan Magazines Ltd; (b) based on a reconstruction by Matt Smith; (c) based on a restoration by John Sibbick in Norman, 1986b; (d) after Coombs, 1982, and graph based on data from Erickson *et al.*, 2001, © 2001 Nature Publishing Group, reproduced with kind permission.]

Horner (2000) made a case for site fidelity, based on ten nests at different stratigraphic levels at the same site in Montana. Sander *et al.* (1998) report some 90,000 egg clutches at a single large site in the Upper Cretaceous of northern Spain, accumulated over a time span of some 10,000 years, again suggesting that the dinosaurs returned repeatedly to lay their eggs in the same area.

Some of the unhatched eggs from these sites have been dissected to reveal the tiny bones of embryonic dinosaurs (Horner and Weishampel, 1988). The troodontid embryo just before hatching (illustration (b)) would have been about 0.2 m long, and adults reached lengths of 2.5 m.

Juvenile dinosaurs have big heads, short necks and big feet, and the proportions change in a fairly regular way. One of the smallest baby dinosaurs, a young *Psittacosaurus* (Coombs, 1982), is about 0.24 m long, compared with an adult length of 2 m (illustration (c)). A sequence of juvenile to adult skulls (illustration (d)) shows how the proportions changed and the especially characteristic ceratopsian features—the beak, high snout, small orbit, large lower temporal fenestra—progressively developed.

A key question concerns growth rates. If large dinosaurs grew at the rates of many modern reptiles, they might have taken 100 years or more to reach sexual maturity. It seems that dinosaurs grew faster, based on counts of growth rings and comparisons of juvenile and adult specimens (Erickson *et al.*, 2001). Small theropods took only two to four years to reach maturity, medium-sized dinosaurs such as *Maiasaura* and *Psittacosaurus*, took five to ten years (illustration (d)), and sauropods such as *Apatosaurus* took 15 years. So, a 25-tonne *Apatosaurus* added some 14.5 kg per day to its body mass, comparable to the fast growth rates of modern whales (21 kg per day). The growth curves are **sigmoid** (S-shaped), with an **exponential** (accelerating) early phase, and then a slowing down.

Read more about dinosaur eggs and embryos at http://www.nationalgeographic.com/features/96/dinoeggs/, and about Jack Horner and his research at http://museum.montana.edu/ and http://www.prehistoricplanet.com/features/articles/jack_horner.htm.

dinosaurs were full-blown endotherms, but equally it is wrong to say that they were all ectotherms like modern lizards and crocodilians. There are two major groups of dinosaurs for which different physiologies may have applied: small and large forms.

Many small dinosaurs may indeed have been endotherms. Some, such as *Hypsilophodon*, are known to have had fibrolamellar bone, which has generally been interpreted as an indicator of sustained high growth rates (see Box 8.6). The feathered coelurosaurs must also have had some degree of endothermy, whether they maintained their body temperatures at the same high levels as birds today or, more probably, at a lower level.

Large dinosaurs were probably inertial homeotherms, or gigantotherms, animals that have constant body temperature by virtue of being large (Ruben, 1995; Reid, 1997). 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 body weight, the rate of heat loss (thermal conductance) becomes equivalent to that of mammals (Figure 8.22). 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 internal heat production.

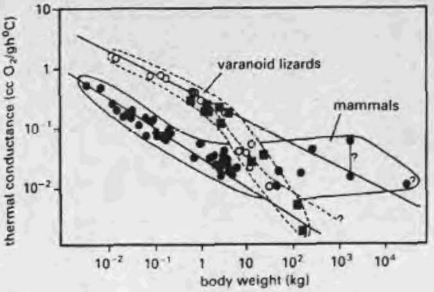


Fig. 8.22 The effect of body size on thermal biology of varanid lizards (○), other reptiles (■) and mammals (●); as body size increases, thermal conductance values converge. (After McNab and Auffenberg, 1976.)

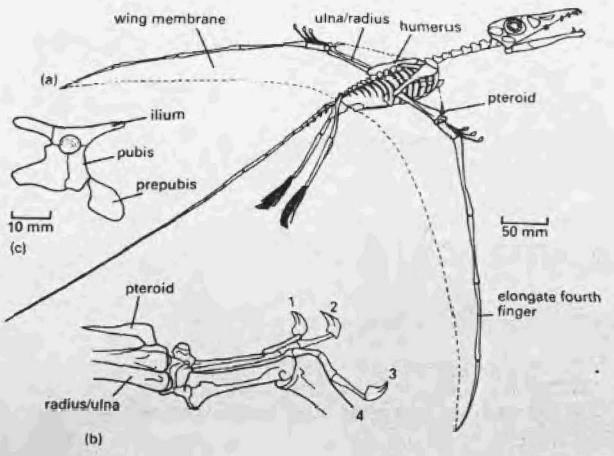


Fig. 8.23 The first pterosaur, the Late Triassic *Eudimorphodon*: (a) skeleton in flying pose; (b) hand region of the right wing; (c) pelvis in lateral view. (After Wild, 1978.)

8.6 PTEROSAURIA

The pterosaurs (literally 'winged reptiles'), known from just over 100 species, existed for 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 (Wild, 1978), show all the unique characters of the group (Figure 8.23(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 8.23(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 supported a small anterior flight membrane, which joined on to the short robust humerus (Figure 8.23(a)). The pelvis (Figure 8.23(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. The tail is stiffened with ossified tendons, as in some dinosaurs, and it may have been used as a rudder during flight.

The pterosaurs diversified in the Jurassic and Cretaceous (Wellnhofer, 1978, 1991; Buffetaut and Mazin, 2004). Basal lines are often grouped in the paraphyletic 'Rhamphorhynchoidea', but most diverse was the clade Pterodactyloidea, which arose in the Late Jurassic and radiated during the Cretaceous.

Much of the diversity of pterosaurs may be appreciated by an examination of a selection of skulls (Figure 8.24). 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 8.24(b, c, f)) were probably used for piercing and holding fish, whereas the shorter teeth of *Dimorphodon* (Figure 8.24(a)) may have been used for insect-eating. *Ctenochasma* and *Pterodaustro* (Figure 8.24(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 in trapping thousands of small organisms that could be licked off and swallowed. The jaws of *Dsungaripterus* and *Pteranodon* (Figure 8.24 (g, h)) are deep and hatchet-shaped and bear very few, or no, teeth. These forms also probably fished by beak trawling and swallowed their catch so rapidly that no teeth were needed.

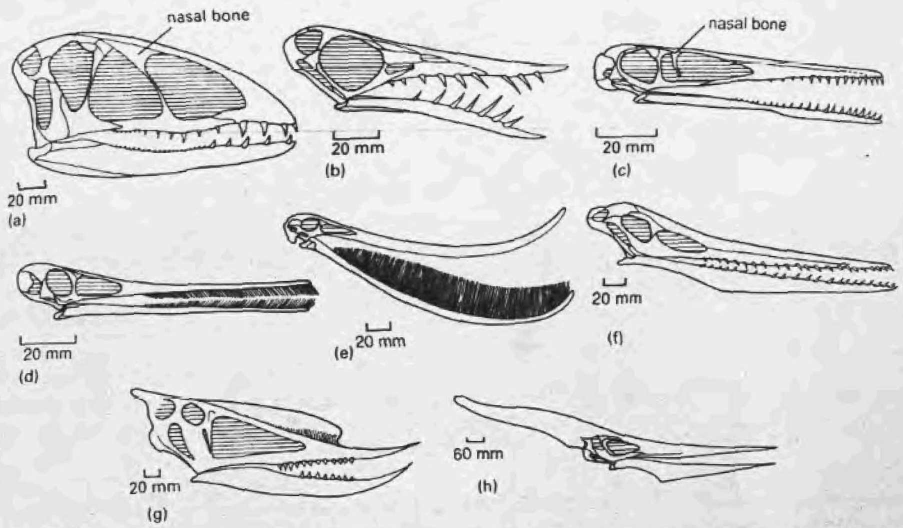


Fig. 8.24 Diversity of pterosaurs, shown by their skulls: (a) *Dimorphodon*; (b) *Rhamphorhynchus*; (c) *Pterodactylus*; (d) *Ctenochasma*; (e) *Pterodaustro*; (f) *Ornithocheirus*; (g) *Dsungaripterus*; (h) *Pteranodon*. (After Wellnhofer, 1978)

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 8.25(a)) and its length is doubled by the pointed crest at the back that may have functioned like a weathercock to keep the head facing forwards during flight. However, the crest is sexually dimorphic, so the aerodynamic function might have been less important than display. Each massive cervical vertebra (Figure 8.25(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 8.25(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 8.25(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 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 12 m (Figure 8.25(f)). *Quetzalcoatlus* was the largest known flying animal, three times the size of the largest bird, and more like a small aeroplane in size than any familiar living animal. *Quetzalcoatlus* and its relatives, the azhdarchids, are known from fragmentary remains from the uppermost Cretaceous of many parts of the world.

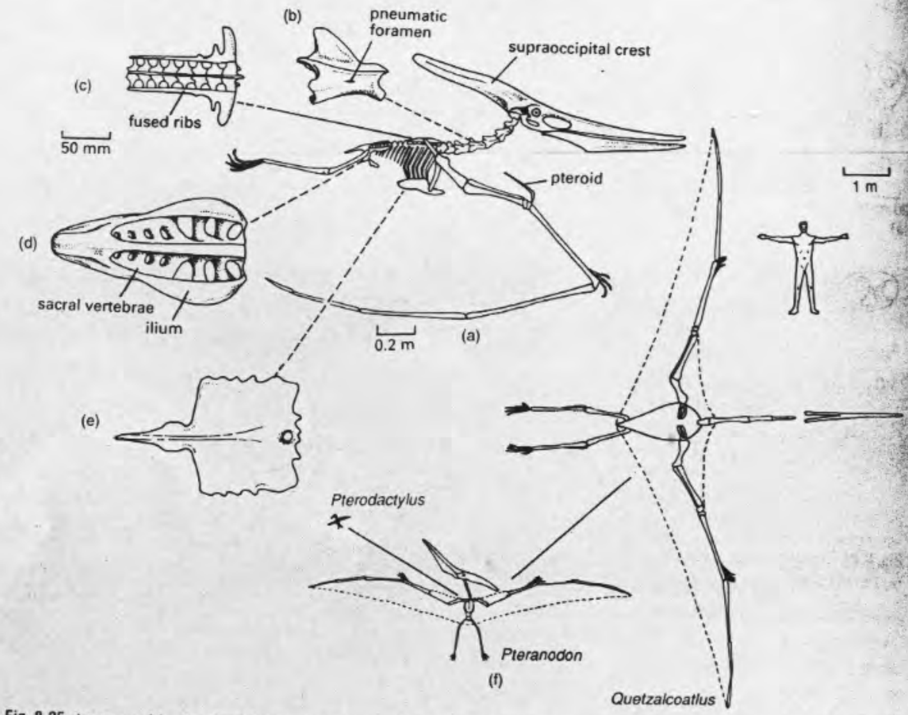


Fig. 8.25 Anatomy of the giant Late Cretaceous pterosaurs: (a–e) *Pteranodon*: (a) flying skeleton in lateral view, (b) cervical vertebra in lateral view, (c) notarium in dorsal view, (d) synsacrum in dorsal view, (e) sternum in ventral view, (f) *Quetzalcoatlus* shown in proportion to *Pterodactylus* and *Pteranodon*. [Figures (a–e) after Eaton, 1910; (f) modified from Langston, 1981.]

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 be 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; Padian and Rayner, 1993; Unwin and Bakhurina, 1994) counters these views and presents a picture of the pterosaurs as efficient flapping flyers like modern birds. 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 probably endothermic, as they appear to have had hair (see Box 8.7). Only endotherms have external insulation and endothermy gave the pterosaurs the high sustained metabolic rates necessary for flight.

The 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 8.25(a) and 8.26(a)). It has been argued that the pterosaur wing was a slender structure rather like that of a gull (Wellnhofer, 1978; Padian and Rayner, 1993), but it was broader as the flight membrane also attaches to the

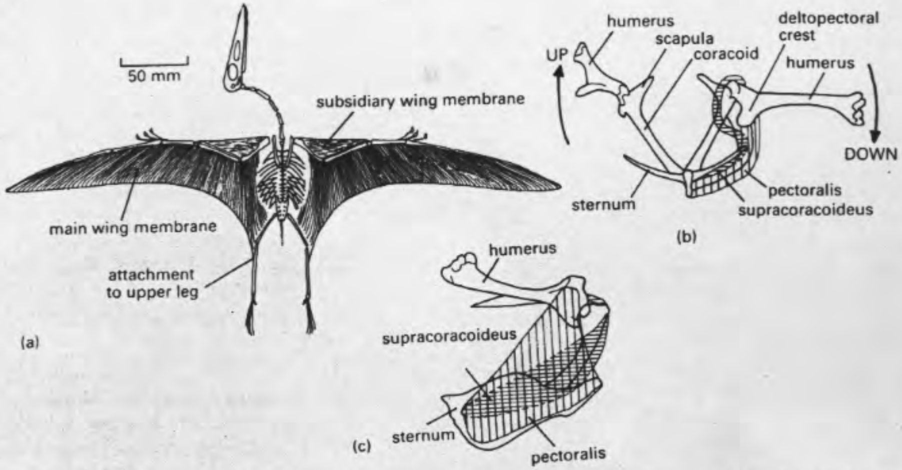


Fig. 8.26 Pterosaur wings and flight: (a) skeleton of *Pterodactylus* with the wing membranes preserved and showing partial attachment to the legs; (b, c) anterior and lateral views of the shoulder girdle and humerus of a pterosaur showing the humerus in the upstroke and downstroke positions and the main flight muscles (pectoralis, downstroke; supracoracoideus, upstroke). [Figure (a) after Wellnhofer, 1987; (b, c) after Padian, 1984.]

BOX 8.7 HAIRS AND FIBRES

Pterosaurs have been credited with a hair covering for more than a century (Wellnhofer, 1978), and hair has been reported in well-preserved specimens of *Dorygnathus*, *Anurognathus*, *Rhamphorhynchus* and *Pterodactylus* from the Upper Jurassic of Germany and in *Sordes* from the Upper Jurassic of Kazakhstan. The details of pterosaur 'hair' are currently disputed.

Studies of exceptionally preserved fossils (Martill and Unwin, 1989; Unwin and Bakhurina, 1994) show unexpected details of the pterosaur wing membrane. The membrane was about 1 mm thick and it was made from several layers of tissue (illustraion (a)), a thin outer epidermis over a dermis that probably contained capillaries. Beneath this lay a tissue containing (?) collagenous fibres, and on the lower surface a relatively thick layer of striated muscles.

Microscopic investigation of wing membranes from several species (Padian and Rayner, 1993; Unwin and Bakhurina, 1994) has shown that they are reinforced with parallel stiff fibres, termed actinofibrils, particularly in the distal region. The actinofibrils are clear in *Sordes* (Unwin and Bakhurina, 1994), in which each fibre can be seen to be made from bundles of smaller strands (illustrations (b, c)). *Sordes pilosus*, or 'hairy devil', is renowned for its supposedly thick pelt of hair. Most of the so-called 'hair', however, consists of displaced actinofibrils. Nonetheless, hairs have been detected in non-flight areas and Padian and Rayner (1993) confirm the distinction between actinofribrils and hairs in German specimens. 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).

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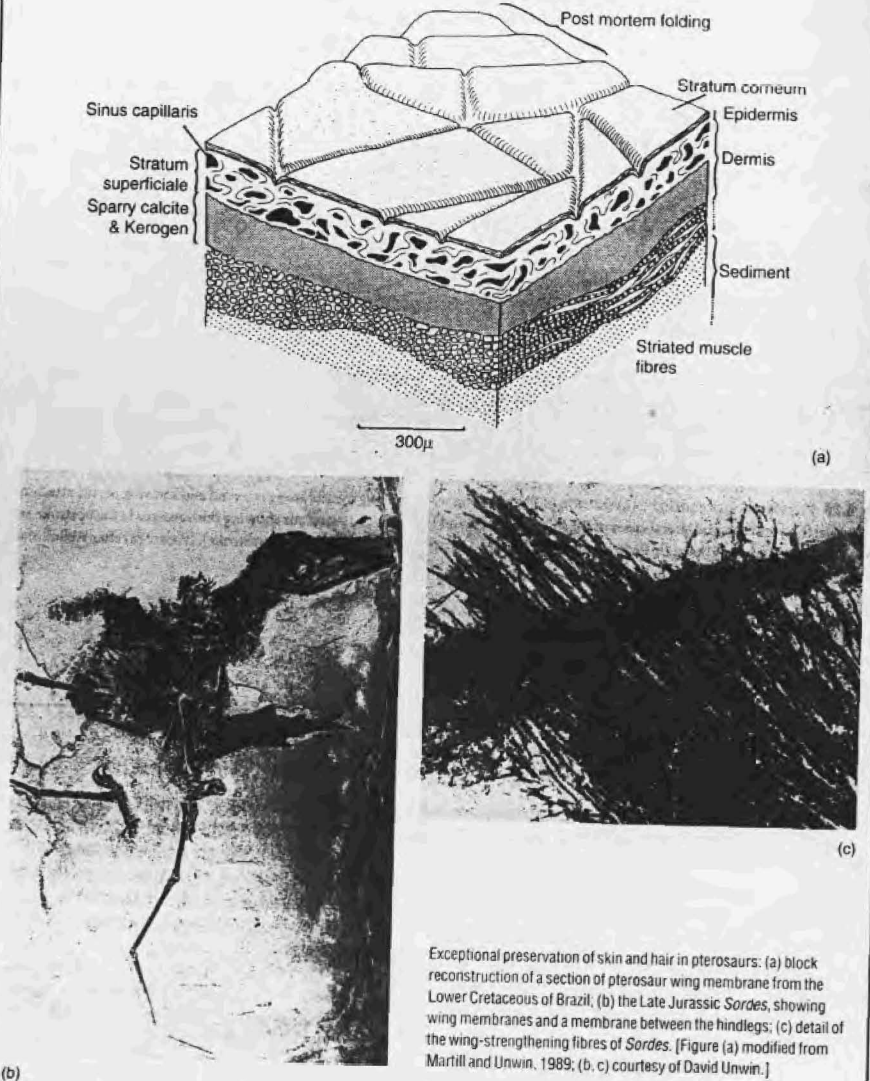


Exceptional preservation of skin and hair in pterosaurs: (a) block reconstruction of a section of pterosaur wing membrane from the Lower Cretaceous of Brazil; (b) the Late Jurassic *Sordes*, showing wing membranes and a membrane between the hindlegs; (c) detail of the wing-strengthening fibres of *Sordes*. [Figure (a) modified from Martill and Unwin, 1989; (b, c) courtesy of David Unwin.]

femur (Figure 8.26(a)) in well-preserved specimens (Wellnhofer, 1987; Unwin and Bakhurina, 1994).

The pterosaur power stroke was directed down and back and the recovery stroke up and forward, 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 by the **supracoracoideus muscle** (Figure 8.26(b, c)), which ran from the sternum, over a pulley arrangement at the shoulder joint, to the dorsal face of the humerus. When it contracted, the supracoracoideus muscle, although placed below the wing, actually pulled it up, just as in birds (Padian, 1984).

Pterosaurs flew relatively slowly because of their large wings, but efficiently, and they were highly manoeuvrable. Their wing designs were comparable to those of modern marine soarers such as frigate birds and albatrosses, and aerial predators such as gulls and falcons (Hazlehurst and Rayner, 1992). Pterosaurs probably took off from trees or cliffs, or jumped into the air after a short run to pick up speed. Even in the larger pterosaurs, the take-off speed was low, possibly 4 m s^{-1} in *Pteranodon*. 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 pterosaurs had good vision and balance areas in the brain, although overall their brains were relatively smaller than those of birds.

If there is relatively little controversy over the flying abilities of pterosaurs, there certainly is a debate over how well they could walk. Padian (1984) and Padian and Rayner (1993) argue that they could walk well on fully erect hindlimbs. Padian reconstructs the pelvic girdle of various pterosaurs as firmly fused beneath, and the limb motions just like those of a small bipedal dinosaur. The wings are held tucked horizontally beside the body during running. This view has been fairly conclusively disproved on the basis of three independent lines of evidence.

1 New, 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 (Wellnhofer, 1988a). 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 (Henderson and Unwin, 2004).

3 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 (Unwin, 1999).

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 TESTUDINES: THE TURTLES

The turtles and tortoises, Testudines or Chelonia, arose in the Late Triassic and later achieved a diversity of 25 families, of which 13 families and 295 species are extant (Mlynarski, 1976). It seems that early on they hit on a successful design, the 'shell', and stayed 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 8.27(a, f)). The plastron is a smaller unit (Figure 8.27(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 p. 110).

The shoulder girdle of modern turtles (Figure

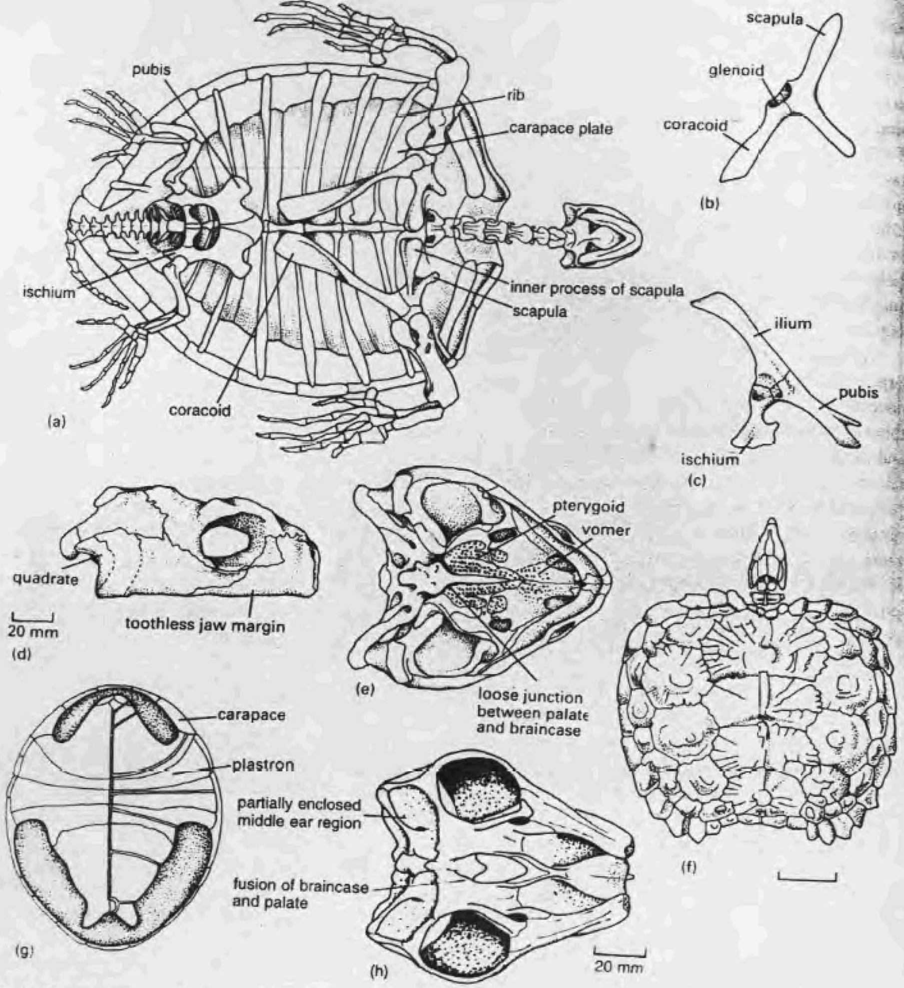


Fig. 8.27 Turtle anatomy: (a–c) *Chelone*, a modern turtle, skeleton in ventral view, pectoral and pelvic girdles; (d–f) *Proganochelys* from the Upper Triassic of Germany, skull in lateral and ventral views and carapace and skull in dorsal view; (g) *Proterochersis* from the Upper Triassic of Germany, reconstructed plastron showing the divisions between the bones (left) and between the horny covering scutes (right); (h) *Australochelys* from the Lower Jurassic of South Africa, skull in ventral view. [Figure (a) after Young, 1981; (b, c) after Carroll, 1987; (d, e) after Gaffney and Meeker, 1983; (f, g) after Zittel, 1932; (h) modified from Gaffney, 1994, used with permission from *Nature*, © 1994, Macmillan Magazines, Ltd.]

8.27(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 8.27(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 neck of turtles is long and flexible (Figure 8.27(a)), and the head is relatively small, but strongly constructed.

8.7.2 The first turtles

The origin of turtles was seen as rather mysterious until recently, but several studies have indicated that the pareiasaurs and procolophonids of the Permo-Triassic are close relatives (see pp. 113–4).

The first turtles, *Proganochelys* and *Proterochersis*, show the key features that are common to all modern forms (Gaffney and Meeker, 1983). The skull (Figure 8.27(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 8.27(d)), the skull shows two 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 8.27(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 8.27(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 8.27(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.

Somewhat more derived are the Australochelidae, from the Lower Jurassic of Africa (Gaffney, 1994) and the Upper Triassic of South America (Rougier *et al.*, 1995). Australochelids, such as *Australochelys* (Figure 8.27(h)) 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.

8.7.3 Pleurodires and cryptodires

The remaining turtles from the Jurassic to the present day form a clade, the Casichelydia (see Box 8.8), composed of two major groups, Pleurodira and Cryptodira (Gaffney and Meylan, 1988). These turtles 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 casichelydian turtles, unlike the proganochelyids and australochelids, can retract their heads under the carapace when they are threatened by danger, and the way in which they achieve this distinguishes the two groups today. The pleurodires pull the head in by making a sideways bend in the neck (Figure 8.28(a)), whereas the cryptodires make a vertical bend (Figure 8.28(b)). This distinction works for living turtles, but basal members of both groups cannot retract their necks. More appropriate synapomorphies of Pleurodira and Cryptodira (Gaffney and Meylan, 1988) are found in modifications to the lateral regions of the palate that are designed 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 8.28(c)), whereas in cryptodires, the trochlear process is formed further back by the otic capsule, the part of the braincase involved with hearing and balance (Figure 8.28(d)).

Proterochersis from the Upper Triassic of Germany (Figure 8.27(g)) is classified as the first pleurodire because its pelvis is fused to the carapace and plastron (Gaffney and Meylan, 1988). Living pleurodires, the snake necks and matamatas, are freshwater 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*.

The cryptodires date back to the Early Jurassic, but they radiated only after the Late Jurassic. They fall into six main clades, each characterized by features of the skull and shell (Młynarski, 1976; Gaffney and Meylan, 1988). *Kayentachelys* from the Lower Jurassic of Arizona, USA, is the oldest cryptodire. It shows the otic capsule trochlea characteristic of the clade, but still possesses pterygoid teeth, which are lost in later forms. The baenids (Figure 8.28(e)) from the Upper Jurassic to Eocene of North America and Europe have a narrow snout region. The meiolanids (Figure 8.28(f)), an odd group mainly from the Pleistocene of Australia, have broad skulls up to 500 mm wide and armoured with horns.

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 8.28(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 Upper Cretaceous of North America (Figure 8.28(j)) is 4 m long.

8.8 CROCODYLIA

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 220 Myr ago and their first representatives were small bipedal insectivores (see p. 145). Since the Triassic, most crocodilians have been semi-aquatic and some Jurassic forms were highly adapted to marine life. In the Tertiary, other groups became fully terrestrial and, in South

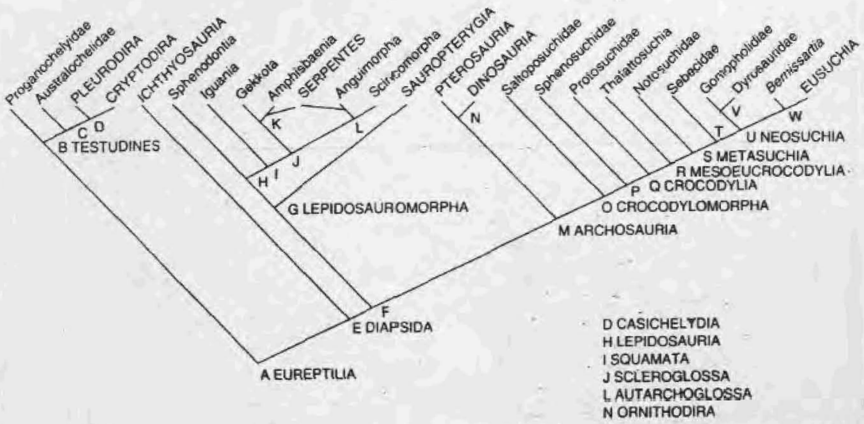
BOX 8.8 RELATIONSHIPS OF MESOZOIC REPTILES

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, Testudines, form a well-characterized clade that is part of the larger clade Anapsida (see Box 5.1). Within Testudines, the Late Triassic and Early Jurassic forms, Proganochelyidae and Australochelidae, are outgroups to the Casichelydia, consisting of Pleurodira and Cryptodira, all subsequent turtles (Gaffney and Meylan, 1988; Gaffney, 1994).

The Diapsida includes the Ichthyosauria, and then it divides into two major clades (Benton, 1985; Laurin, 1991; Dilkes, 1998; Rieppel, 1998), Lepidosauromorpha and Archosauromorpha, which diverged in the Permian, and both of which radiated in the Triassic (see Figure 6.6). Lepidosauromorphs may include the Sauropterygia, two groups of marine reptiles that probably independently lost the lower temporal fenestra (Rieppel, 1998). The main lepidosauromorph clade, the Lepidosauria, includes the sphenodontians and the squamates, five 'lizard' clades plus the snakes (Estes *et al.*, 1988; Caldwell, 1999; Lee and Scanlon, 2002). The relationships of snakes (Serpentes) are unclear, i.e. whether a sister group of Amphisbaenia or Anguimorpha (see Box 8.10).

The main archosauromorph clade of the Mesozoic and Cenozoic, the archosaurs, split in the Triassic into a line that led to crocodiles, and another, the Ornithodira, that led to pterosaurs, dinosaurs and birds (see Box 6.1). The Crocodylomorpha includes some basal forms, the Saltoposuchidae and Sphenosuchidae, from the Late Triassic and Early Jurassic, and the Crocodylia, which arose in the Early Jurassic. The Crocodylia (Benton and Clark, 1988; Clark and Norell, 1992) 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 to Mid-Cretaceous.



Cladogram showing the postulated phylogenetic relationships of the main groups of non-synapsid reptiles. Synapomorphies: **A EUREPTILIA**, 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; **B TESTUDINES**, lacrimal small or absent, 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 carapace and plastron; **C**, fusion of the braincase and palate, partial enclosure of the middle ear region laterally; **D CASICHELYDIA**, lacrimal foramen absent, vomer single, interpterygoid vacuity small or absent, middle ear region enclosed ventrally; **E 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; **F**, lacrimal reduced, caniniform maxillary teeth absent, quadratojugal reduced; **G LEPIDOSAUROMORPHA**, postparietal absent, prominent lateral conch on quadrate for support of tympanum, retroarticular process large and formed entirely from prearticular bone, interclavicle gracile with slender lateral processes, ossified sternum, ectepicondylar foramen in humerus, pelvic girdle fenestrate; **H 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; **I SQUAMATA**, high degree of skull kinesis, premaxillae fused, nasals reduced, squamosal reduced or absent, parietals fused, quadratojugal absent, lower temporal bar absent, posterior conch-like notch on quadrate, proatlas absent, ribs single-headed, gastralia absent; **J SCLEROGLOSSA**, vomer elongate, more than 26 presacral vertebrae; **K**, no contact between nasal and prefrontal; **L AUTARCHOGLOSSA**, no contact between jugal and squamosal; **M ARCHOSAURIA**, 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; **N ORNITHODIRA**, presacral centrum 8 longer than presacral centrum 18, deltopectoral crest on humerus subrectangular, fibula tapering and calcaneum reduced in size, astragalar posterior groove and calcaneal tuber rudimentary or absent; **O 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; **P**, antorbital fenestra small, parietals fused; **Q CROCODYLIA**, basisphenoid rostrum dorsoventrally expanded, basipterygoid processes reduced, lower portion of coracoid expanded and anterior margin concave, scapula very broad dorsally; **R 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; **S METASUCHIA**, pterygoid strongly sutured to quadrate, maxilla with single wave of enlarged teeth, anterior process of ilium nearly absent; **T**, quadratojugal narrows dorsally, single palpebral ossification, premaxillary teeth uniform in shape; **U NEOSUCHIA**, maxilla subvertical, antorbital fenestra absent, retroarticular process narrow, maxilla and dentary with two sinusoidal waves of teeth; **V**, rostrum nearly tubular, basioccipital with large pendulous tubera, retroarticular process posterodorsally curving and elongate, splenial involved extensively in symphysis; **W**, inset postorbital bar, biconvex first caudal vertebra, osteoderms in more than two longitudinal rows.

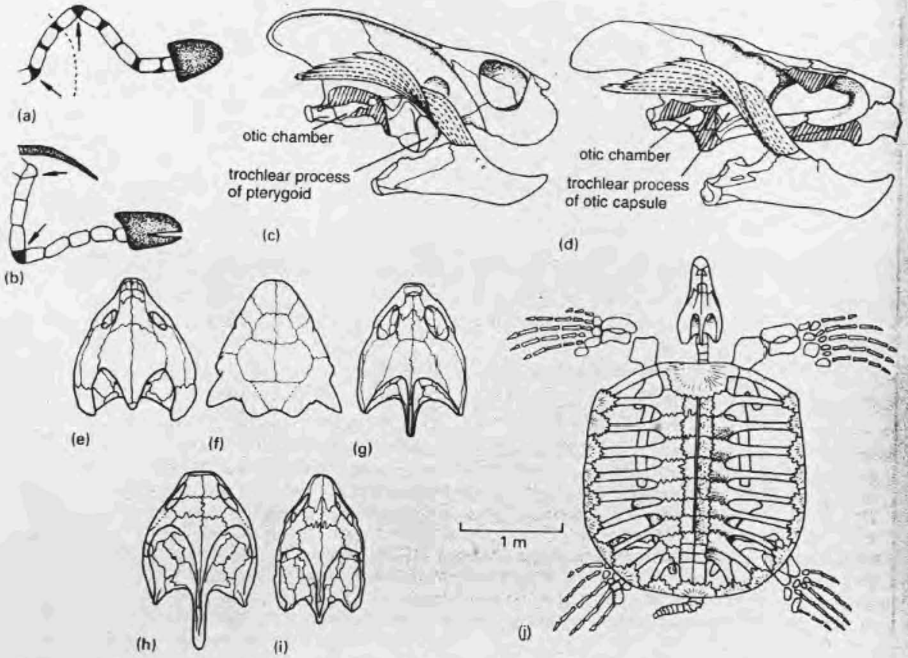


Fig. 8.28 Turtle classification and diversity: mode of neck folding in (a) a typical pleurodire in dorsal view and (b) a cryptodire in lateral view; course of main jaw adductor muscle mass in *Emydura*, a pleurodire (c) and *Chelydra*, a cryptodire (d); (e–i) the diversity of turtle skulls, all in dorsal 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. [Figures (a, b) after Mlynarski, 1976; (c–i) after Gaffney and Meylan, 1988; (j) after Zittel, 1932.]

America, disputed the top carnivore niches with birds and mammals. This extraordinary history is based around a conservative body design.

8.8.1 Crocodilian characteristics

Crocodilians have long snouts with the nostrils at the tip (Figure 8.29(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 maxillae and palatines and, in derived forms, the pterygoids also (Figure 8.29(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 typically 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 (Taylor, 1987).

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;
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.

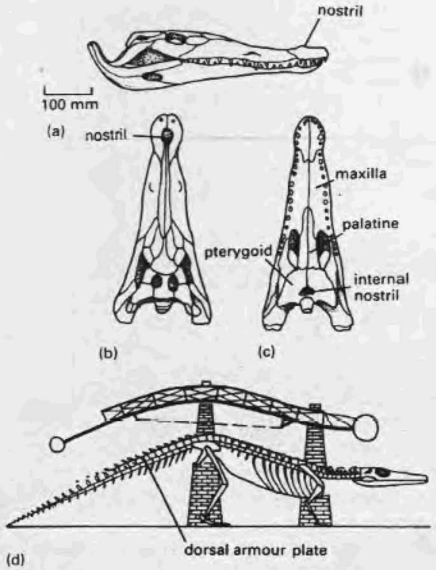


Fig. 8.29 Crocodilian anatomy: (a–c) skull of the modern African crocodile *Crocodylus* in (a) lateral, (b) dorsal and (c) ventral views; (d) mechanical analogy between the box-like girder structure of the crocodilian backbone and dorsal scutes and a box-girder bridge. [Figures (a–c) based on Iordansky, 1973; (d) after Frey, 1984.]

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 (Frey, 1984). 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 8.29(d)).

8.8.2 The first crocodilians

The first crocodilomorphs such as *Saltoposuchus* from the Late Triassic (see p. 145) were lightly built and probably bipedal. The sphenosuchid *Sphenosuchus* from the Early Jurassic (see pp. 145–6) 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 8.30(a)), but the hindlimbs are longer than the forelimbs, betraying their bipedal ancestry.

The protosuchids display a variety of crocodilian synapomorphies. The skull is ornamented with irregular pits in the bone surface (Figure 8.30(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 p. 205). 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 8.30(c)), a perforated acetabulum and reduced pubis (Figure 8.30(d)), elongate wrist elements and extensive armour covering. *Protosuchus* probably fed mainly on small terrestrial animals.

8.8.3 Jurassic–Cretaceous crocodilians

In the classification of the 150 or so genera of fossil crocodilians, most of those of the Jurassic and Cretaceous were classically placed in a group called the 'Mesosuchia', mainly aquatic forms that lack the specializations of the living groups, the Eusuchia. The 'Mesosuchia' is, however, a paraphyletic group containing a great diversity of forms (Buffetaut, 1982), and it is more correctly united with the Eusuchia in a clade Mesoeucrocodylia (Benton and Clark, 1988; see also Box 8.8).

The basal mesoeucrocodylians are the Thalattosuchia, a group of thoroughly marine-adapted croco-

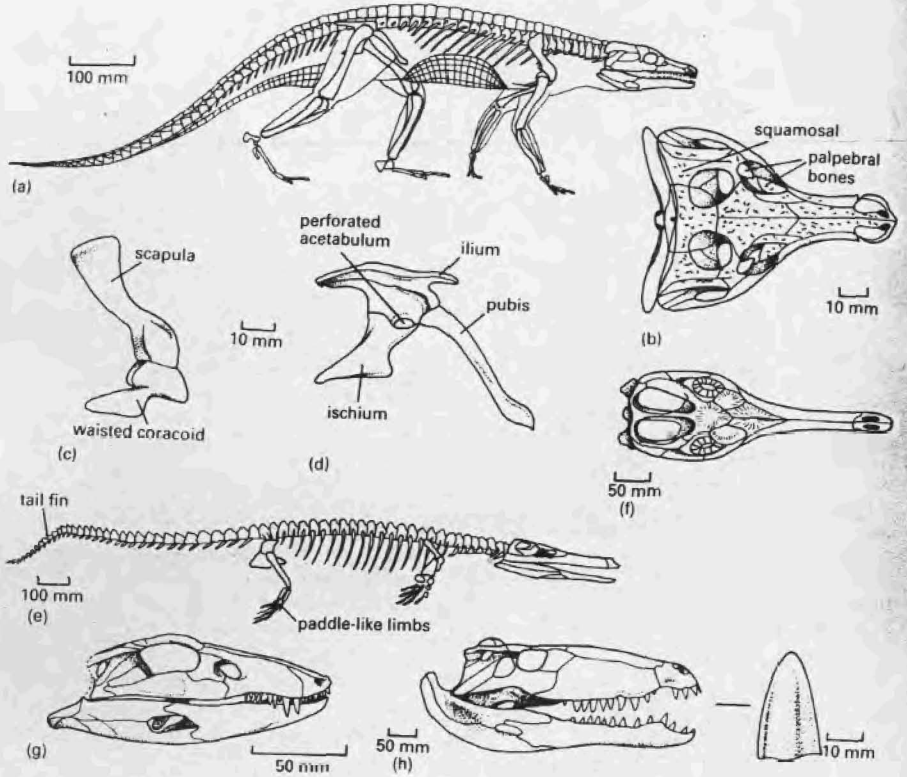


Fig. 8.30 Mesozoic crocodilians: (a–d) the Early Jurassic protosuchids *Protosuchus* (a, c, d) and *Orthosuchus* (b), (a) skeleton and armour plates, (b) skull in dorsal view, (c) shoulder girdle, (d) pelvic girdle; (e, f) the Late Jurassic metriorhynchid *Geosaurus*, skeleton and skull in dorsal view; (g) the Late Cretaceous notosuchid *Argentinosuchus*; (h) the Tertiary sebecid *Sebecus*, skull in lateral view and a characteristic flattened (ziphodont) tooth. [Figures (a, c, d) after Colbert and Mook, 1951; (b) after Nash, 1975; (e–h) after Steel, 1973.]

dilians that are best known from the Jurassic. The 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 Upper Jurassic of Europe (Figure 8.30(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.

The remaining crocodilians, the Metasuchia, show modifications in the palate, braincase and skull roof. The metasuchians include highly terrestrial forms. In South America and Africa, several lineages became tiny and almost mammal-like in habits. For example, the notosuchid *Argentinosuchus* (Figure 8.30(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. One notosuchid from the Lower Cretaceous of China, *Chimaerasuchus*, may even have been a herbivore. The Sebecidae, known from the Palaeocene to Miocene (60–10 Myr ago) of South America have large skulls (Figure 8.30(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 eventually replaced by mammalian carnivores in the later Tertiary.

More derived crocodilians, the neosuchians, include some long-snouted aquatic forms, such as the goniopholidids, abundant in freshwater and marine deposits from the Middle Jurassic to the end of the Cretaceous, the dyrosaurids from the Early Cretaceous to late Eocene (including some giant forms, see Box 8.9) and the Eusuchia. *Bernissartia* and *Hylaeochampsa* from the Lower Cretaceous of Europe (Clark and Norell, 1992) are similar to Eusuchia in many ways, 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 8.29(c)), and some other skull features.

Modern crocodilians are divided into three families, consisting of the crocodiles, alligators and gavials (Brochu, 2003b). The first two families are known from the Late Cretaceous and all through the Tertiary, 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.

8.9 LEPIDOSAURIA

Lepidosaurs today include 4470 species of lizards and 2920 species of snakes, as well as the tuatara, *Sphenodon* from New Zealand, an isolated member of the clade. This grouping is confirmed by molecular evidence (Hedges and Poling, 1999; Zardoya and Meyer, 2001c; Rest *et al.*, 2003). The first known lepidosaurs are sphenodontians, distant ancestors of the living tuatara, and the Lepidosauria radiated dramatically in the Mid-Jurassic, coincident with the oldest known lizards, and again in the Early Cretaceous, with the origin of snakes. Lepidosaurs form part of a larger clade Lepidosauromorpha, which traces its origin back to the Permian (see p. 113).

8.9.1 Sphenodontia: reptilian 'living fossils'

Sphenodon, the living tuatara (Figure 8.31(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 it is now regarded as the sister group of lizards and snakes (e.g. Benton, 1985; Evans, 1988). *Sphenodon* is said to be a 'living fossil' because it lacks the special features of lizards and snakes (for example, the lower temporal bar is complete and the skull is immobile) and because it is the single surviving member of a group known only much earlier in time.

The earliest sphenodontians are known from the Triassic when as many as eight or nine genera lived in Britain. These animals vary in body length from 150 to 350 mm and the skulls and teeth of different forms vary, suggesting a diet ranging from insectivory to herbivory. *Planocephalosaurus* (Fraser and Walkden, 1984) is about 150 mm long (Figure 8.31(d)), smaller than *Sphenodon*, and it has a blunt-snouted skull. The long

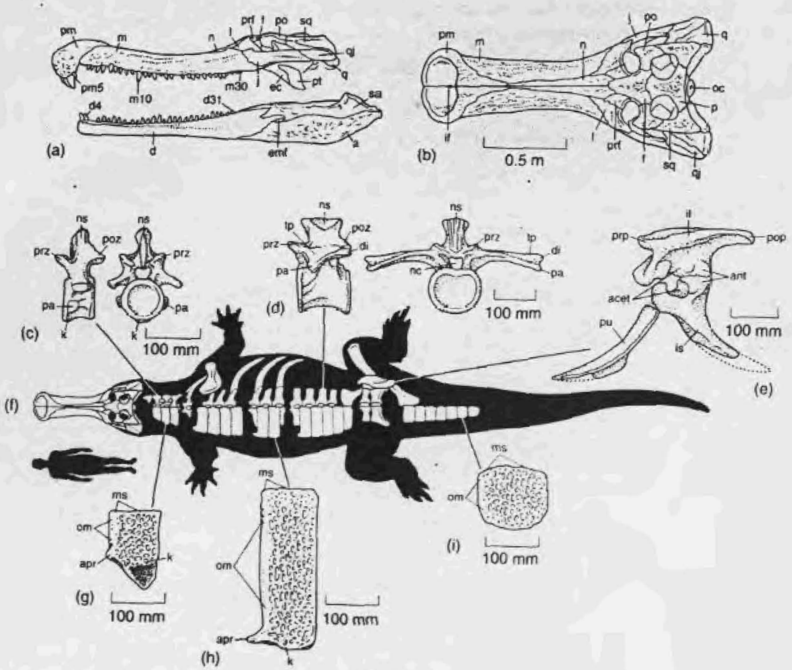
BOX 8.9 GIANT CROCODILE FROM AFRICA

Many crocodilians today are rather terrifying creatures, but the dyrosaurid *Sarcosuchus*, from the Lower Cretaceous of Niger, was a monster. Palaeontologists first found remains of *Sarcosuchus* in the Ténéré Desert of Niger in the 1960s, and the initial description was based on only a few bones and a partial skull. In 2000, Paul Sereno and his team found remains of five supercrocs, including skulls and partial skeletons of juveniles, as well as the complete skull of an adult.

The new specimens show that *Sarcosuchus* had a skull 1.6 m long, which corresponds to a maximum body length of 12 m and a body mass of some 8 tonnes (Sereno *et al.*, 2001). No complete specimens of *Sarcosuchus* are known, so the body length is estimated by extrapolating from a plot of skull length versus body length in living crocodilians.

The skull table of *Sarcosuchus* is broad, the snout narrow in the middle, but broader at the front. The terminal nares are huge. The premaxilla overhangs the rather shorter lower jaw and the teeth are numerous, but rather short. The broad snout, shortish teeth and huge body size of *Sarcosuchus* suggest that it was not solely a fish-eater. Its remains come from an ancient river system located a long way from the sea, so perhaps it preyed on the abundant dinosaurs that lived alongside.

Read more about *Sarcosuchus* at http://www.nationalgeographic.com/supercroc/ and http://www.sciencenews.org/20011027/fob1.asp and see (and hear) the beast at http://www.supercroc.com/.



Skull and skeleton of *Sarcosuchus*. (Courtesy of Carol Abraczinskas and Paul Sereno.)

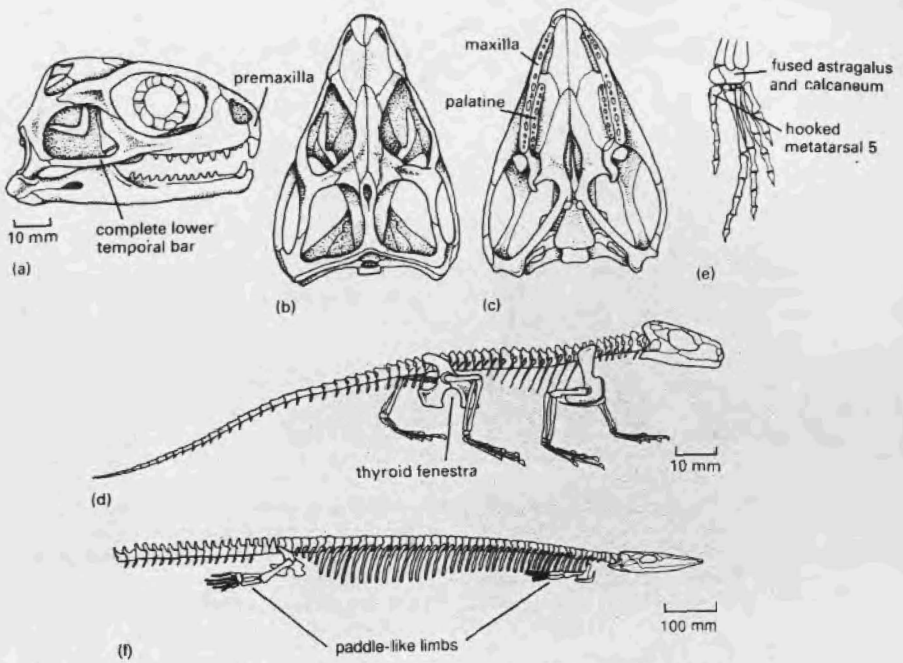


Fig. 8.31 The sphenodontians: (a–c) skull of the living *Sphenodon* in lateral, dorsal and ventral views; (d) skeleton of the Late Triassic sphenodontid *Planocephalosaurus*; (e) left foot and lower leg of the Jurassic sphenodontid *Homoeosaurus*; (f) skeleton of the Late Jurassic pleurosaur *Pleurosaurus*, with most of the tail omitted. [Figures (a–c) after Zittel, 1932; (d) after Fraser and Walkden, 1984; (e) based on Cocude-Michel, 1963; (f) after Carroll, 1987.]

slender limbs and body outline are very lizard-like, and indeed the Triassic sphenodontians 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 8.31(e)).

Later sphenodontians 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 Upper Jurassic of Germany (Figure 8.31(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 organ, with the short limbs restricted to steering. Pleurosaurs share with other sphenodontians a specialized pattern of tooth implantation in which the teeth are fused to the jaw bone, the **acrodont** condition (Figure 8.31(a)).

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 sphenodontians. Indeed, a number of poorly preserved skeletons of small

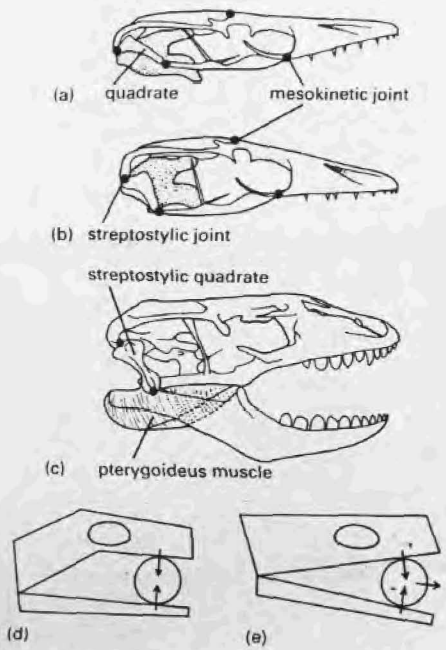


Fig. 8.32 Lizard jaw mechanics: (a, b) skull of *Varanus*, showing the skull flexed up (a) and (b) down; (c) lizard skull with the jaws open and the streptostylic quadrate swung back so that the pterygoideus jaw muscles have their maximum effect; (d, e) diagrammatic lizard skulls showing the advantages of kinesis in holding a food particle (left) that would otherwise be forced out by the bite in a non-mobile skull (right). [Figures (a, b) after Alexander, 1975, courtesy of the Cambridge University Press; (c) after Smith, 1980, copyright © 1980 Macmillan Magazines Ltd; (d, e) after Frazzetta, 1986.]

diapsid reptiles have been described as the first lizards (e.g. Estes, 1983), but these have all turned out to lack clearcut characters of the Squamata (Benton, 1985; Evans, 1988). Lizards and snakes form a clade, the Order Squamata (see Box 8.8), that is characterized by a number of synapomorphies, including a high degree of skull **kinesis**, or mobility.

The cranial kinesis of lizards consists of up to three separate hinging systems (Figure 8.32(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 (supratemporal + squamosal + paroccipital process) at the top, and the quadrate and pterygoid at the bottom, the **streptostylic joints**.

When the jaws open (Figure 8.32(a)), the snout tips up and the quadrate is nearly horizontal. When the jaws close (Figure 8.32(b)), the snout tips down and the quadrate becomes more vertical. This kinetic system has important adaptive advantages (Smith, 1980; Frazzetta, 1986). The pterygoideus muscle, which runs from the pterygoid to the outside of the lower jaw (Figure 8.32(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 8.32(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 8.32(e)).

The Squamata is divided into six clades, one of which is the snakes (Serpentes) and the other five of which (Iguania, Gekkota, Amphisbaenia, Scincomorpha, Anguimorpha) are generally called lizards. The lizard group, formerly termed Lacertilia (or Sauria), is clearly paraphyletic, as it excludes the snakes. The relationships among the six squamate clades are not certain (see Box 8.8), although cladistic evidence supports the view that Iguania are a sister group of the other five, which are collectively termed Scleroglossa, as they all share a keratinized tongue and other features (Estes *et al.*, 1988; Caldwell, 1999). Within Scleroglossa, Gekkota may be a sister group of Amphisbaenia. Anguimorpha and Scincomorpha form a crown clade, Autarchoglossa. Molecular evidence (Harris, 2003) gives some support to the morphological trees, but the scincomorphs are split into three subclades distributed around the tree. There is currently a heated debate about the placement of Serpentes: are the snakes the sister group of Amphisbaenia or members of Anguimorpha (see Box 8.10)?

The history of squamates (Evans, 2003) is patchy at first. Three of the six clades are recorded first in the

BOX 8.10 THE ORIGIN OF SNAKES

Since 1997, twenty or more papers have appeared that purport to tackle the question of snake origins. The issue is still unresolved: are the snakes closely related to amphisbaenians, or are they part of the anguimorph clade, close to the mosasaurs and aigialosaurs (mosasauroids)? If the former, their origin is from land-dwelling burrowers, if the latter, snakes were primitively marine.

Snakes are known to belong to Squamata and to have originated from among lizards. 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. 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.

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. The forelimb is absent, but there is a small pelvis and much reduced hindlimb. Caldwell and Lee (1997) determined that *Pachyrhachis* was a snake, basal to the living forms, and that snakes were anguimorphs close to the mosasauroids. Caldwell (1999) repeated this finding in a more detailed phylogenetic analysis of Squamata. 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 and Scanlon (2002) and Lee *et al.* (2004) reaffirm this view in detailed cladistic analyses of snakes and squamates respectively.

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.

Rieppel and Zaher (2000a, b) further 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 are closely related to 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. Zaher and Rieppel (2002) and Rieppel *et al.* (2003) redescribed *Pachyrhachis* and *Haasiophis* respectively and reaffirmed their earlier findings.

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 — mosasauroids or amphisbaenians? 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 emphasized, 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? Note that tentative molecular results (Harris, 2003) make snakes the sister group of (Anguimorpha + Iguania), so different from both fossil-based views.

Read more at http://news.bbc.co.uk/1/hi/sci/tech/680116.stm, http://www.karencarr.com/News/legs/legged_snake.htm and http://www.sciencedaily.com/releases/2000/03/000317051940.htm.

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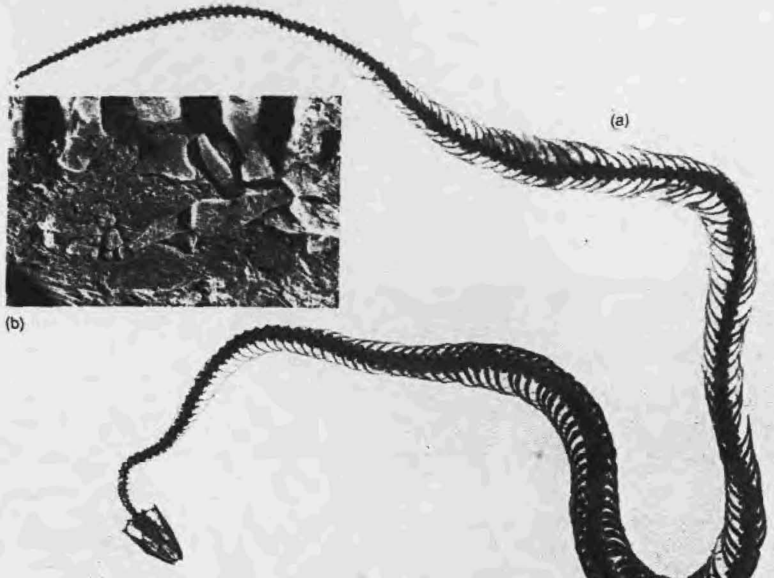


The snake with limbs *Haasiophis terrasanctus* from the mid-Cretaceous of Israel, an essentially complete specimen, shown as an X-ray (a), and showing the retention of tiny hindlimbs, seen in a normal, light photograph (b). (Courtesy of Olivier Rieppel.)

Mid-Jurassic of England, the Gekkota, Scincomorpha 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 are Cretaceous. The Mid-Jurassic scincomorphs (three species) and anguimorph (one species) are represented by jaws, skull bones and vertebrae, and the gekkotan by some vertebrae (Evans, 1998).

The Iguania includes the iguanas, agamids and tree-living chameleons today. The group arose in the Triassic or Jurassic, but the oldest unequivocal fossil is an unusual 30-cm-long lizard from the Mid-Cretaceous of Mexico, *Huehuecuetzpalli* (Reynoso, 1998). The genus *Euposaurus* from the Upper 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 sphenodontians.

The Gekkota are recorded first with confidence in the Early Cretaceous. The group today includes the tiny geckos that can cling to walls and ceilings. *Ardeosaurus*, a doubtful gekkotan from the Upper Jurassic of Germany (Mateer, 1982), reached a total length of only 120–140 mm. The skeleton (Figure 8.33(a)) is like that of most modern lizards, with a slender flexible body, long tail and short sprawling limbs. The skull (Figure 8.33(b)) shows a number of squamate derived characters: the parietals are fused and they meet the frontals on a broad transverse suture that can hinge up and down, the lacrimal and quadratojugal bones have been lost and the quadrate is streptostylic.

The Amphisbaenia are heavily modified for a life of

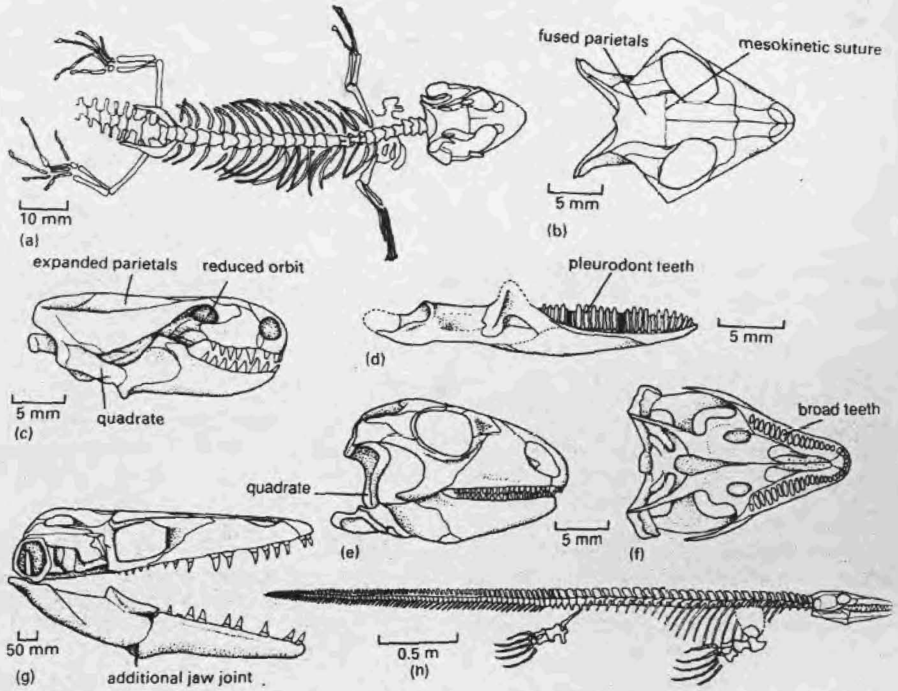


Fig. 8.33 Fossil lizards: (a, b) skeleton and skull of the Late Jurassic supposed gekkotan *Ardeosaurus* in dorsal view; (c) skull of the living amphisbaenid *Amphisbaena* in lateral view; (d) lower jaw of the Late Jurassic scincomorph *Paramacellodus* in internal view; (e, f) skull of the Late Cretaceous teiid *Polyglyphanodon* in lateral and ventral views; (g, h) the Late Cretaceous mosasaur *Platecarpus*, skull in lateral view and skeleton in swimming pose. [Figures (a, d–f) after Estes, 1983; (b) after Mateer, 1982; (c) after Romer, 1956, courtesy of the University of Chicago Press; (g, h) after Russell, 1967.]

burrowing, with their 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 8.33(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 fossil forms 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 Upper Cretaceous of Mongolia turns out (Kearney, 2003) to be a scincomorph.

The Scincomorpha, including today the skinks, European lacertids and others, has been traced back to the Middle Jurassic (Evans, 1998). One of the first genera, *Paramacellodus*, is known also from the Lower Cretaceous of southern England. *Paramacellodus* shows **pleurodont** dentition (Figure 8.33(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. Scincomorphs became especially diverse from the Late

Cretaceous onwards, when the herbivorous teiids, such as *Polyglyphanodon* (Figure 8.33(e, f)), arose in the Americas. The skull is strong and deep-sided, and the broad cheek teeth show that this lizard fed on tough vegetation.

The anguimorphs, the final lizard group, are also the most diverse. Modern anguimorphs are the monitor lizards (varanids), the anguids, mainly limbless forms, the gila monster, a venomous form, and others. Three families of Late Cretaceous varanoid anguimorphs became highly adapted to marine life (DeBraga and Carroll, 1993): the aigialosaurs, dolichosaurs and mosasaurs. The last group were the most spectacular, 20 genera of Late Cretaceous predators that ranged in length from 3 to 10 m (Russell, 1967). *Platecarpus*, a typical smaller form, has an elongate body, deep tail and paddle-like limbs (Figure 8.33(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 by some 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 the biting force.

8.9.3 Serpentes: the snakes

The sixth squamate group, the snakes (Serpentes or Ophidia), are believed to have arisen from 'lizard' ancestors, but the nature of those ancestors is a mystery (see Box 8.10). The main characters of snakes of course include limblessness (living boas still have a small remnant of a hindlimb), a greatly increased number of vertebrae (120–500), venom in certain advanced forms and a great increase in skull kinesis.

The snake skull (Figure 8.34(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 joint 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. These can be moved independently so that the prey is virtually stuffed down the throat and has no chance of 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 in the main fang.

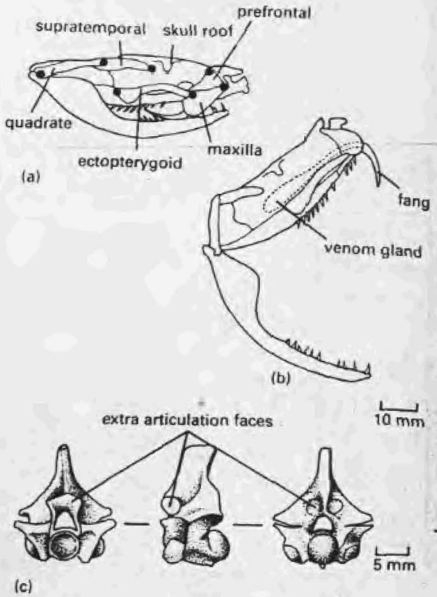


Fig. 8.34 Snake anatomy: (a, b) skull of a viperid snake in lateral view, showing the jaws closed and open; (c) mid-trunk vertebra of the living *Python* in posterior, lateral and anterior views. [Figures (a, b) after Alexander, 1975, courtesy of the Cambridge University Press; (c) after Rage, 1984.]

Snakes are known from the Early Cretaceous and they radiated greatly during the Tertiary (Rage, 1984) in line with the radiation of the mammals on which they preyed. These first snakes may have fed on insects and other small prey. Only later did some groups 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 as much as by crushing of the body, as is often assumed. The poisonous forms appeared first in the Late Eocene. Snakes range in length up to 6–7 m in a large python, but a huge vertebra from the Palaeocene of North Africa indicates a 9 m monster. Snake vertebrae have a complex shape (Figure 8.34(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 neoselachian sharks that preyed on them (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 pp. 224–9, 232–7), and mosasaurs (see p. 243) were important carnivores in the Late Cretaceous. Certain groups of birds also fed on marine fishes (Chapter 9), but the main reptilian predators were the ichthyosaurs and plesiosaurs, both of which groups had appeared in the Triassic (see pp. 149–53). After early finds in the 1820s and 1830s, they came to be known collectively as 'sea dragons'.

Plesiosaurs and ichthyosaurs were traditionally grouped as Euryapsida, a reptilian subclass that stood apart from the major terrestrial groups. Both ichthyosaurs and plesiosaurs are almost certainly modified diapsids, the ichthyosaurs falling low in the phylogeny, before the split of lepidosauromorphs and archosauromorphs, and the plesiosaurs lying on the lepidosauromorph branch (see p. 150 and Box 8.8). Both groups lost the lower temporal fenestra independently some time in their Permian ancestry. Sauropterygians (plesiosaurs, nothosaurs, placodonts) at least share some lepidosauromorph characters, such as a thyroid fenestra in the pelvis (Rieppel, 1993).

8.10.1 Plesiosauria

The first true plesiosaurs are known from the Late Triassic and they are believed to be closely related to the nothosaurs. Plesiosaurs were generally larger, ranging typically from 2 to 14 m in total body length. Plesiosaurs are divided into the long-necked plesiosauroids and the short-necked pliosauroids (O'Keefe, 2002).

The plesiosauroids include four families. The cryptoclidids from the Late Jurassic to the Late Cretaceous (Figure 8.35(a, b)) have long necks with 30 cervical vertebrae and a skull with a long snout, single (upper) temporal fenestrae, the euryapsid skull pattern and nostrils set back from the tip of the snout. The jaw joint is set below the level of the tooth row, which 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 cimoliasaurids are a small group of Late Jurassic long-necked plesiosauroids, whereas the polycotylids are short-necked Late Cretaceous forms, long classified with the pliosauroids. The elasmosaurids, such as *Muraenosaurus* from the Late Jurassic (Figure 8.35(c)), have very long necks and some Late Cretaceous forms boast as many as 76 cervical vertebrae.

The pliosauroids include the Jurassic rhomaeleosaurids (Figure 2.8) and the pliosaurids, such as the Late Jurassic *Liopleurodon* (Figure 8.35(d)), up to 12 m long, and with a long heavy skull and a relatively short neck. 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 (Taylor, 1992; see pp. 29–31), 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.

Plesiosaurs were highly adapted for submarine locomotion, with powerful paddle-like limbs and heavily reinforced limb girdles. Three swimming modes have been proposed (Figure 8.36(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. The first two styles are problematic (Taylor, 1986): in rowing, the back-

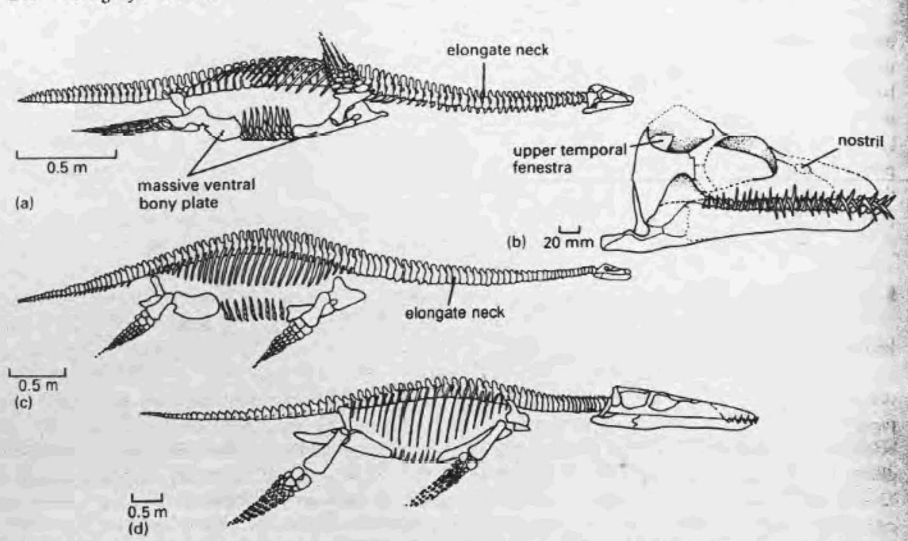


Fig. 8.35 The plesiosaurs: (a, b) the Middle Jurassic cryptoclidid *Cryptoclidus*, skeleton in swimming pose and skull in lateral view; (c) the Late Jurassic elasmosaur *Muraenosaurus*; (d) the Late Jurassic pliosaur *Liopleurodon*. [Figures (a, b) after Brown, 1981; (c, d) after Robinson, 1975.]

stroke creates a counterthrust that would slow the plesiosaur down; the flying stroke is much more efficient, but the skeleton of plesiosaurs does not allow the paddles to be lifted above shoulder level. So, Godfrey (1984) proposed the crescentic path, which has the benefits of the figure-of-eight, but allows for 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 8.36(d)), and that the limb girdles are too weak for strong vertical movements.

8.10.2 Ichthyopterygia

Ichthyosaurs arose in the Triassic (see pp. 152–3), diversified in the Early Jurassic and became much reduced in diversity in the Late Jurassic and Cretaceous, being represented then only by the Ophthalmosauria (Motani, 1999, 2000; McGowan and Motani, 2003). There is considerable variation in size, with lengths of 1–16 m, but the dolphin-like body shape, long snout and large eyes remain common features throughout (Figure 8.37(a)).

The body outline of ichthyosaurs (Figure 8.37(b)) is well known because of the exquisite preservation of specimens, especially in the Lower 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 Late Cretaceous ichthyosaur from Australia contains bones of a hatchling protostegid turtle and an enantiornithine bird (Kear *et al.*, 2003), an eclectic dietary selection.

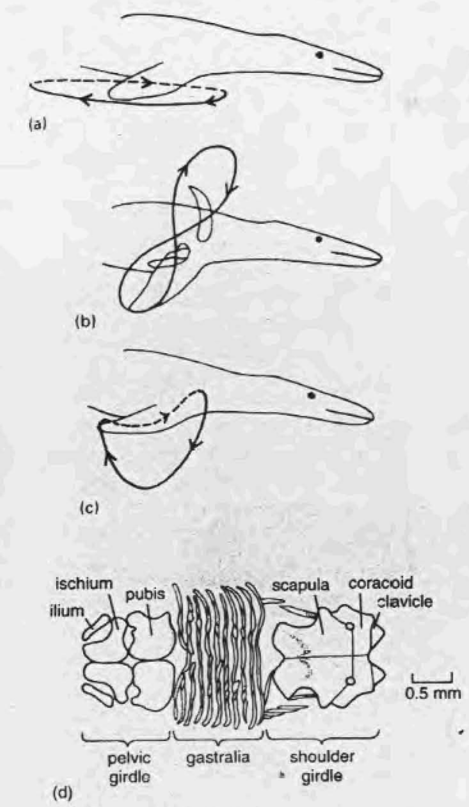


Fig. 8.36 Plesiosaur locomotion: (a–c) three hypotheses: (a) rowing underwater like a duck, (b) flying underwater like a penguin and (c) an intermediate style like a sealion; (d) ventral view of the heavy bony covering of the plesiosaur belly. [Figures (a–c) after Taylor, 1986, copyright © 1986 Macmillan Magazines Ltd; (d) after Robinson, 1975.]

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 and in whales (Motani, 2002). Based on comparisons with living forms, *Stenopterygius* probably cruised at about $1.5\,\mathrm{m\,s^{-1}}$ (or $5.4\,\mathrm{km\,h^{-1}}$) 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 weakness of the limb girdles of ichthyosaurs and their overall 'fishy' body shape suggest that they could not venture on to land. Marine turtles, penguins and probably plesiosaurs, 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 Lower 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 (Böttcher, 1990). Several specimens show the young apparently in the process of being born (Figure 8.38). 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 the death of the mother by gases of putrefaction.

8.11 DIVERSIFICATION OF JURASSIC-CRETACEOUS REPTILES

The diapsids diversified enormously during the Mesozoic, the dinosaurs, crocodilians and lizards on land, the pterosaurs in the air, and the ichthyosaurs and plesiosaurs in the sea. The great mass extinction at the end of the Cretaceous marked a major switch in tetrapod evolution from diapsid-dominated faunas to mammals.

The evolution of reptiles in the Mesozoic and Cenozoic (Figure 8.39) shows two main phases of expansion, the radiation of the dinosaurs, pterosaurs, crocodilians and the marine reptiles in the Late Triassic and Jurassic, and the radiation of the 'modern' groups (lizards, snakes, turtles, birds) from the Late Cretaceous onwards. Mass extinctions among tetrapods have been postulated in the Late Triassic (see pp. 156–7) and, of

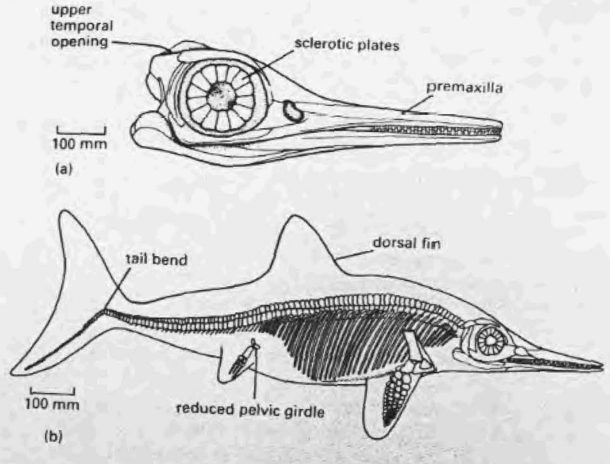


Fig. 8.37 The ichthyosaurs: (a) skull and (b) skeleton of the Early Jurassic *Ichthyosaurus*; the body outline is based on skin impressions preserved with some European material. (After Andrews, 1910.)

Fig. 8.38 Adult specimen of the ichthyosaur *Stenopterygius*, from the Lower Jurassic of Holzmaden, Baden-Württemberg, south-west 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. (Courtesy of Rupert Wild; specimen in the Museum für Naturkunde, Stuttgart.)

course, at the end of the Cretaceous. Others, at the end of the Jurassic and in the mid-Cretaceous, are probably artefacts of an incomplete fossil record (Fara and Benton, 2000).

8.12 THE KT EVENT

Often the only question people ask about the 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 65 Myr ago at the Cretaceous–Tertiary (KT) boundary have been proposed. It might seem odd that there is still so much debate: after all, the KT boundary is the most studied point in geological time. Despite all this study, however, many key questions remain about the timing of the event, the patterns of what died out and what survived, and the precise nature of the physical environmental crisis.

8.12.1 What died out?

Among terrestrial tetrapods, the dinosaurs and

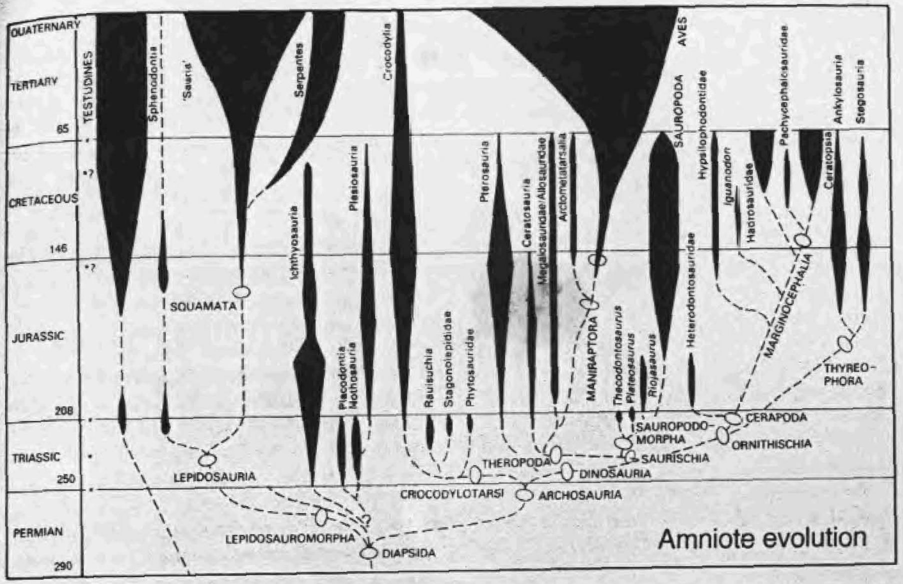


Fig. 8.39 Phylogenetic tree of the diapsid reptiles and turtles, showing postulated phylogenetic relationships of the main groups (dashed lines), known fossil record of each (vertical time dimension) and their relative abundance through time (horizontal axis). Mass extinctions, and possible mass extinctions, are noted with asterisks on the left.

pterosaurs disappeared, as well as several families of birds and marsupial mammals. In the sea, plesiosaurs, mosasaurs and some families of sharks and teleost fishes disappeared. 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. Many groups, such as diatoms, radiolaria, benthic foraminifera, brachiopods, gastropods, some fishes, amphibians, turtles, lizards and terrestrial plants, were apparently little affected (MacLeod *et al.*, 1997).

It is hard to separate the survivors and nonsurvivors into simple ecological categories. Most of the land animals that survived were small, except for certain crocodilians. Most of the marine forms that died out were free-swimming or surface forms (plankton, ammonites, belemnites), but of course many open-water fishes survived. Among forms that lived on the sea-bed, 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 and Raup (1995) looked at how marine bivalves fared across the KT boundary, and found that the only factor that promoted survival was the geographical range of genera. In other words, a species of bivalve could insure itself against the risk of a mass extinction by belonging to a genus that was distributed over several faunal provinces. Diet, body size, mode of reproduction, water depth inhabited, ability to burrow, latitudinal distribution (tropical versus temperate) and other factors made no difference whatever to survival chances. There is little evidence for selectivity during the KT extinction event, so that any explanation has to account for an essentially random set of disappearances.

8.12.2 How long did it take?

Some geologists assume that all major extinctions occurred essentially instantaneously, in as little as one week or one year. Others posit a 'sudden' event, but allow several thousands or tens of thousands of years. At the level of discrimination that is possible, there is no way of distinguishing such time spans because both appear to be the same in the geological record.

Radiometric dating of KT boundary volcanic rocks using the $^{40}Ar/^{39}Ar$ technique can give dates in Myr with uncertainties of as little as ±0.1 Myr. This technique works well when such igneous rocks are available, but the majority of fossil-bearing KT sequences are not associated with volcanics. Another technique is to measure 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 KT boundary lying in polarity band 29R (i.e. reversed), which lasted as little as 0.5 Myr. Magnetostratigraphic techniques can identify the likely age of particular geological formations, but the precision is still too poor for a decision on the exact duration of the KT event.

Classic sedimentology and stratigraphy, however, suggest that the KT event was effectively instantaneous, even though an exact age date cannot be assigned. Some two hundred KT boundary sections have been recorded from all over the world, in sediments deposited under the sea and on land, and they all show the same succession (Smit, 1999). The KT boundary is defined formally at the base of the boundary layer, and then follows an ejecta layer and a clay enriched in iridium.

Not only was the KT event rapid, but it happened in early June! Wolfe (1991) examined sediments in a lily pond less than 2 m deep that straddles the KT boundary. 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, for a period of less than 2 months. In all, the sequence of catastrophic events, he argues, lasted from 3 to 4 months.

8.12.3 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 KT boundary, whereas others were in long decline before the end of the Cretaceous.

The ichthyosaurs, for example, disappeared 30 Myr earlier than the KT 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 quality of the record. An apparently gradual pattern of extinction may arise if all the last fossils have not been collected. The first studies of ammonite distributions in the north of Spain suggested that the group had dwindled to very low diversities by the very end of the Cretaceous, but more intensive collecting (Ward, 1990) showed that several species survived right up to the boundary. What was a gradual pattern became catastrophic after more intensive collecting. 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.

What of the dinosaurs and other vertebrates? The stratigraphic ranges of vertebrates across the KT interval certainly indicate a mass extinction: one estimate (Benton, 1989a) showed that 28 out of 89 families of terrestrial tetrapods died out at that time, a percentage loss of 31%. Revised results calculated (Table 8.1) from chapters in Benton (1993a), indicate an overall loss of 64 out of 210 families of vertebrates, a drop of 30%. This is made up (Figure 8.40) 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 dinosaurs, pterosaurs and plesiosaurs (all 100%), with high rates also for birds and marsupials (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 placental mammals are all lower than 15%, and hence not different from normal, or 'background', extinction rates.

Table 8.1 Data on the rates of extinction of vertebrates at the KT 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. All data are taken from chapters in Benton (1993a).

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

These results confirm that reptiles as a whole, and dinosaurs in particular, suffered a devastating loss of diversity at the end of the Cretaceous. The figures are based on documentation at the level of the stratigraphic stage, and the last stage of the Cretaceous, the Maastrichtian, was probably 5–8 Myr long. It is hard to correlate precisely the ages of rocks from Asia to Europe to North America, so it is not clear whether all the dinosaurs, pterosaurs, plesiosaurs, mosasaurs and other groups died out right at the end of the Maastrichtian, or scattered through the whole time span.

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 more detailed work, Archibald and Bryant (1990) surveyed collections of 150,000 specimens, representing 111 species of fishes, amphibians, reptiles and mammals from latest Cretaceous and earliest Tertiary beds of north-east Montana. They found that 36–47% of commoner species died out across the KT boundary, but apparently over a long span of time.

On-the-ground collecting, however, shows no long-term decline. Sheehan *et al.* (1991) summarized 15,000 hours of fieldwork by scores of volunteers who marched across the Hell Creek Formation picking up anything that did not move. The thousands of bones collected were plotted against time and the majority of extinctions appeared to fall right at the KT boundary. Hurlbert and Archibald (1995) argued that Sheehan and colleagues had over-interpreted their data, whereas Sheehan and Fastovsky (1992) reinterpreted the Archibald–Bryant data base to show that, although freshwater fishes and tetrapods (amphibians, turtles, crocodiles) showed a species extinction rate of only 10%, 88% of the fully terrestrial species died out at the

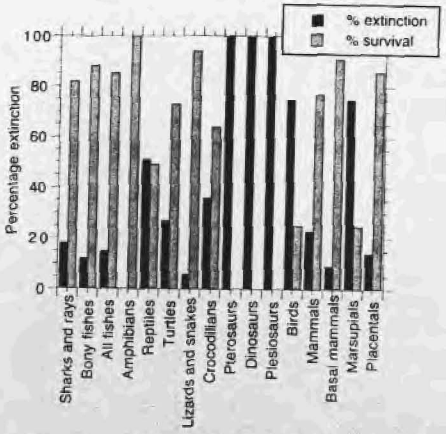


Fig. 8.40 The proportions of different vertebrate families that became extinct during the KT event, based on data from Benton (1993a), listed in Table 8.1. Note the 100% extinction of pterosaurs, dinosaurs and plesiosaurs, but 0% extinction of amphibians, and extinction rates of less than 20% for fishes, lizards and snakes, basal mammals and placental mammals.

KT boundary, hence making it a catastrophic event. Sheehan *et al.* (2000) went on to show that a long-held belief, that there were no dinosaurs in the last 3 m of the Hell Creek Formation, immediately below the KT boundary, was false: they found as many bones in that interval as in any other 3 m unit and concluded that dinosaur extinction was abrupt. This result was confirmed by Lillegraven and Eberle (1999) in the Lancian of Wyoming, who found no evidence for a decline among dinosaur species, but rather a geologically sudden disappareance. They note, however, that there is a zone of uncertain stratigraphy 8 m thick spanning the KT boundary, so cannot rule out the possibility of a decline over thousands, or tens of thousands, of years. Contrary to some previous statements, mammal fossils are rare in the dinosaur-bearing beds and mammals appear in some diversity and abundance only after the disappearance of the dinosaurs.

In Montana and Wyoming, then, several dinosaur families lasted right to the end of the Cretaceous: the tyrannosaurids, 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.

8.12.4 Theories of extinction

Over the years, more than a hundred hypotheses have been presented for the extinction of the dinosaurs (Benton, 1990b). A common view in the latter half of the nineteenth century and in the first three decades of the twentieth was that the dinosaurs simply 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 giantism (if not acromegaly), excessive spinosity and 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 interest in sex) 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 KT event.

1 The gradualist ecological succession model sees a decline caused by long-term climatic changes in which the subtropical lush dinosaurian habitats gave way to the strongly seasonal temperate conifer-dominated mammalian habitats. The evidence for this hypothesis is mainly palaeontological and stratigraphic.

2 The catastrophist vulcanological model explains the geochemical data in the boundary rocks by means of a major volcanic eruption that caused abrupt extinction.

3 The catastrophist extraterrestrial model explains the extinction as a result of the after-effects of a major extraterrestrial impact on the Earth from geochemical and astrophysical evidence.

A catastrophist would argue that the main extinction event lasted less than a year, or perhaps as much as a few hundred or thousand years, whereas a gradualist would argue for a longer-term decline lasting for 1 Myr or more.

The gradualist model sees declines in many groups of organisms (Archibald, 1996a; MacLeod *et al.*, 1997) caused by long-term climatic changes in which the subtropical lush dinosaurian habitats gave way to the strongly seasonal temperate conifer-dominated mammalian habitats. The gradualist scenario has been extended to cover all aspects of the KT events on land and in the sea, with evidence from the gradual declines of many groups through the Late Cretaceous. Climatic changes on land are linked to changes in sea level and in the area of warm shallow-water seas, and the impact and volcanism are either discounted or seen as the *coup de grâce*. This position is disputed by those who claim the extinctions were rapid and the apparent long-term declines are artefacts of incomplete collecting.

The second school of thought has focused on explaining the KT event by volcanic activity (Courtillot, 1999). The Deccan Traps in India represent a vast outpouring of lava that occurred over the 2–3 Myr spanning the KT 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. Petrologists and geochemists argue that the shocked quartz and iridium spike could not be produced by any known kind of volcano, that the geochemistry of the glassy spherules indicates a source from rocks lying below a postulated impact site and that they do not have a volcanic signature (see below).

The impact hypothesis was presented in 1980, when Luis Alvarez and colleagues published their view that the extinctions had been 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. There are four key pieces of evidence for the impact hypothesis.

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 KT boundary, that rate increased dramatically, giving an iridium spike (Figure 8.41).

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 sites 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 8.39) is found in many terrestrial KT boundary sections, indicating an abrupt shift in pollen ratios from angiosperm-dominated to fern-dominated. This indicates the aftermath of a catastrophic ash fall: 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.

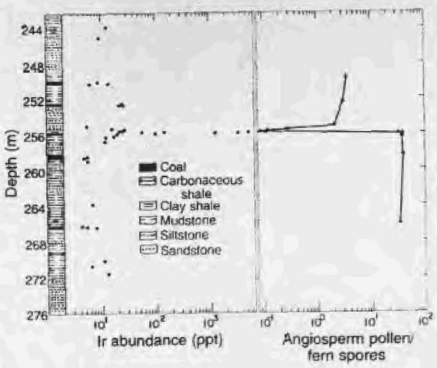


Fig. 8.41 A typical iridium spike (left) and fern spike (right) from a core taken through the KT boundary in freshwater coal swamp deposits in York Canyon, New Mexico, USA. Note that both the iridium abundances, measured in parts per trillion (ppt), and the ratios of angiosperm-pollen:fern-spores are plotted on logarithmic scales. (Courtesy of Carl Orth.)

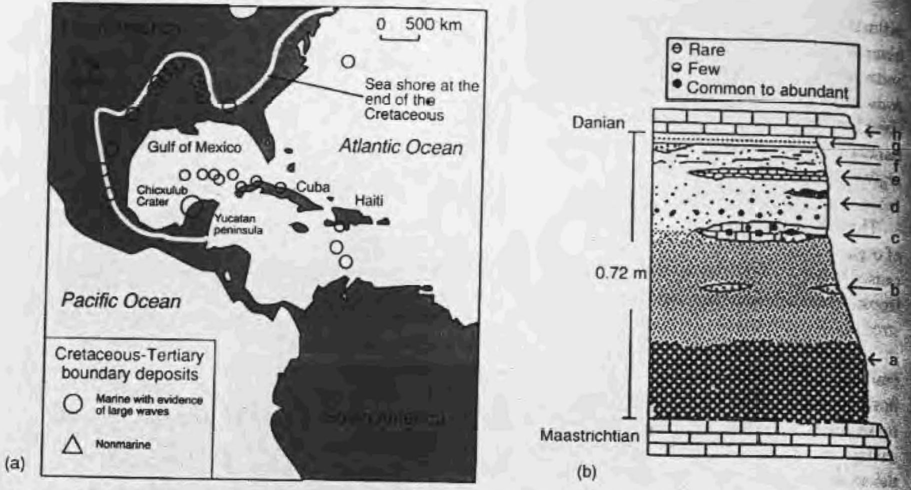


Fig. 8.42 Evidence for the impact site: (a) location of Chicxulub Crater, on the Yucatán Peninsula, Mexico, as well as the end-Cretaceous coastline of the proto-Caribbean Sea and sites indicating activity of tsunamis (tidal waves); (b) the KT boundary section at Beloc, showing the sequence of arrivals 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). [Figure (a) from various sources; (b) modified from Florentin *et al.*, 1991.]

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 8.42(a)), is 195 km in diameter, with inner rings at 130 km and 80 km, and is filled with Tertiary sediments (Morgan and Warner, 1999). A ring of coeval coastline deposits shows evidence for tsunami (massive tidal wave) activity, presumably set off by a vast impact into the proto-Caribbean (Smit, 1999). Further, the KT boundary clays ringing the site also yield abundant shocked quartz and glassy spherules that match geochemically the bedrock under the crater site. 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 KT boundary sections around the proto-Caribbean have allowed geologists to reconstruct what happened. The famous section at Beloc on Haiti (Figure 8.42(b)), a boundary clay that is 0.7 m thick (Florentin *et al.*, 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 indicating 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, consist of marls and clays with large limestone clasts and are 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.

Deposition finally reverted to normal limestone, as it had been before the impact. This three-phase pattern is seen in all other KT boundary layers throughout the world (Smit, 1999), although the tsunami layers are omitted 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.

There is little doubt that there was a major impact on Mexico 65 Myr ago. But much of the palaeontological data indicates longer-term extinction over 1–2 Myr. Key research questions are whether the long-term dying-off is a genuine pattern, or whether it is partly an artefact of incomplete fossil collecting, and, if the impact occurred, how it actually caused the extinction. Available killing models are either biologically unlikely, or too catastrophic: recall that a killing scenario must take account of the fact that 70–75% of families survived the KT event, many of them seemingly entirely unaffected. Whether the two models can be combined so that the long-term declines are explained by gradual changes in sea-level and climate and the final disappearances at the KT boundary were the result of impact-induced stresses is hard to tell.

8.13 FURTHER READING

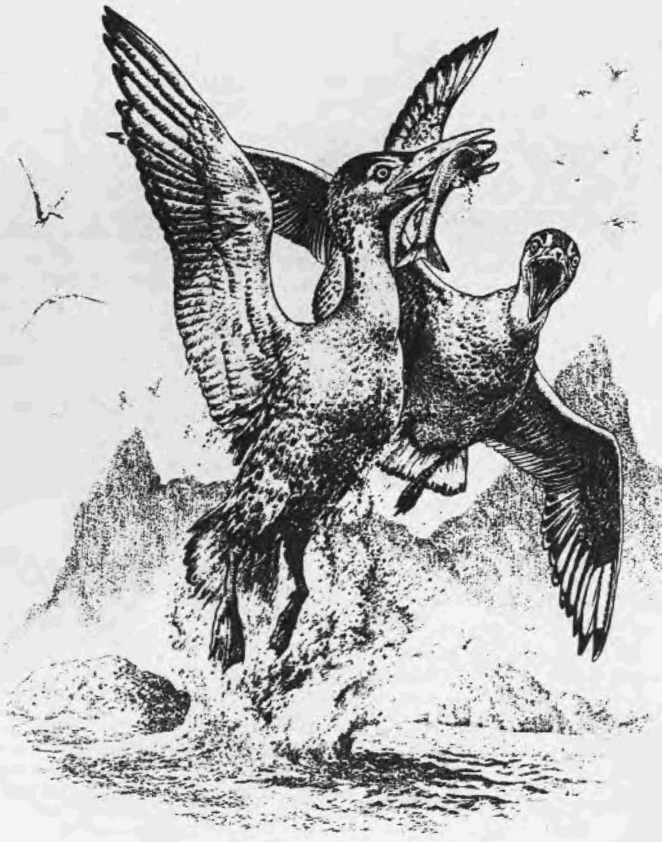
Farlow and Brett-Surman (1997) is the best single-volume text about dinosaurs for students, and Weishampel *et al.* (1990) is the 'bible' for dinosaur-lovers, with full documentation of all dinosaur groups, their anatomy, relationships and distributions. Currie and Padian (1997) is a comprehensive encyclopaedia of everything dinosaurian, and Fastovsky and Weishampel (1996) is the best of various textbooks. Colbert (1968) is the classic history of dinosaur collectors, and Cadbury (2001) investigates the rivalry between Mantell and Owen and the first dinosaur discoveries. Norman (1986a) is the best 'popular' dinosaur book, and Benton (1989b, 1997, 2000) are also aimed at adults. Particular dinosaur groups are covered by Currie *et al.* (2004) on theropods, Lockley *et al.* (1994) on sauropods, Dodson (1996) on the ceratopsians and Carpenter (2001) on the stegosaurs and ankylosaurs, and dinosaur eggs and babies by Carpenter *et al.* (1994).

Smaller Mesozoic animals are considered in Fraser and Sues (1994), pterosaurs by Wellnhofer (1991) and Buffetaut and Mazin (2003) 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 Zug *et al.* (2001) and Pough *et al.* (2003), and about lizards in Pianka (2003). There are many books on the KT extinction event, but Archibald (1996a), Alvarez (1997) and Courtillot (1999) expound the gradualist, impact and volcanic models respectively. Koeberl and MacLeod (2002) includes many papers about the KT, and other, mass extinctions.

There are more excellent web sites about dinosaurs than stars in the heavens, but three good ones are http://www.ucmp.berkeley.edu/diapsids/dinosaur.html and http://dino.lm.com/ and http://www.dinosaur.org/. All the latest dinosaur news stories from *New Scientist* are at http://www.newscientist.com/hottopics/dinosaurs/dinosaurs.jsp. Hear the sounds made with models of the hadrosaur *Parasaurolophus* at http://museums.state.nm.us/nmmnh/p3_staff_res_parasaur.html. Everything about pterosaurs may be found at http://www.pterosaur.org/, everything on modern crocodilians at http://www.flmnh.ufl.edu/natsci/herpetology/brittoncrocs/cnhc.html and the anatomy and classification of turtles at http://tolweb.org/tree?group=Testudines&contgroup=Amniota. 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 and pterosaurs are at http://digimorph.org/listbygroup.phtml?grp=dinosaur&sort=SpeciesName

CHAPTER 9

The Birds



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 Did the KT event hit birds hard?
6 What is the fossil and molecular evidence about the origin of modern birds?
6 What are the relationships of the major modern bird groups – and why has it proved so hard to work this out?
7 Did birds eat horses?

INTRODUCTION

Birds are a large group of highly successful flying vertebrates, with just over 9000 living species. The oldest bird, *Archaeopteryx* from the Late Jurassic, is known in detail on the basis of several well-preserved specimens, but there are some gaps in the later history of bird evolution. The bird fossil record is better than has often been assumed (Unwin, 1993): of 153 families of living birds, 134 have described fossil representatives and there are a further 77 extinct families.

Birds apparently remained rare during most of the Cretaceous, more than half their history, and the group went through several phases of expansion in the Cenozoic. Recent discoveries have turned up some remarkable extinct bird groups: Early Cretaceous specimens from China and Spain that fill a major gap between *Archaeopteryx* and the later birds, Late Cretaceous flightless birds, birds that ate horses and many more. Key problems remain in understanding bird phylogeny: ironically, we seem to understand more about the relationships among Cretaceous birds than among the living orders.

9.1 *ARCHAEOPTERYX*

Archaeopteryx has been justly famous since its 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, and 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: creationists attempt to argue that it is either a true bird with no hint of intermediate characters, and hence not part of an evolutionary transition series, or that it is a forgery. In both views they are mistaken.

9.1.1 Specimens and environment

Eight skeletons of *Archaeopteryx* are now known, as well as a single feather impression (Figure 9.1), all collected from the Upper Jurassic limestones of Solnhofen, Bavaria. The first specimen to be found, a single feather (Figure 9.1(a)), was collected in 1860, and the first skeleton with clear feather impressions, the London specimen (Figure 9.1(b)), was named *Archaeopteryx lithographica* in 1861. The most famous example, the Berlin specimen (Figure 9.1(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. Six more skeletons were collected in 1855 (recognized 1970), 1951, 1956, 1987, 1992 and 1997. The history and anatomy of these specimens are described by Elzanowski (2002) and several detailed monographs on their anatomy have been published (e.g. Wellnhofer, 1974, 1988b, 1993; Ostrom, 1976).

There has been some debate about the naming of these bird skeletons: do they all come from one species, or do they represent several species or even several genera? Certainly, the seven skeletons vary greatly in size: the Eichstätt specimen indicates an animal about 300 mm long, and the sixth (Solnhofen) specimen was 500 mm, or more, in length. Houck *et al.* (1990) suggested that the six specimens known at that time form a growth series of a single species, *Archaeopteryx lithographica*: for most individual measurements, the Eichstätt specimen is half the size of the Solnhofen example, but the other five skeletons fall neatly on a straight line between these two end-members. Wellnhofer (1993)

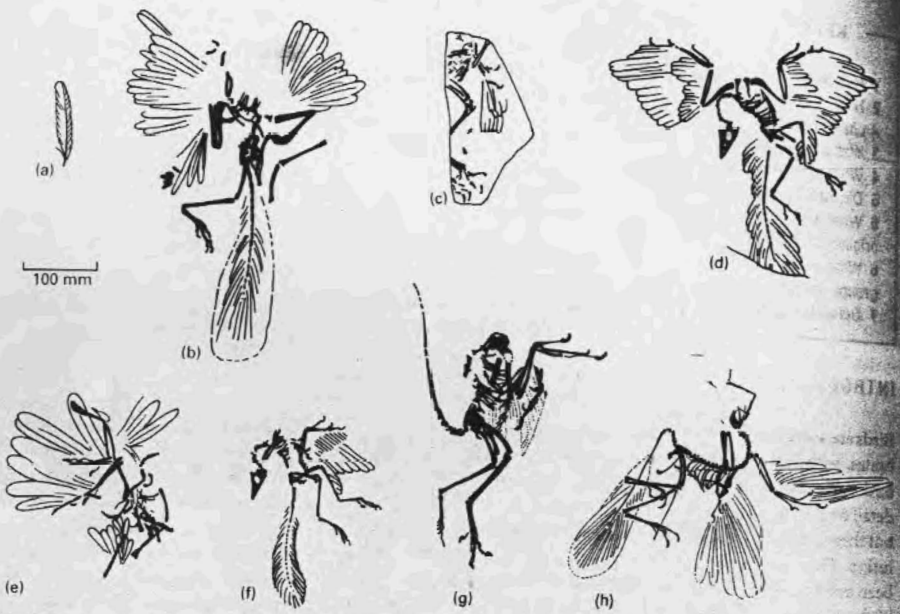


Fig. 9.1 Eight of the nine specimens of *Archaeopteryx*, all drawn to the same scale, with the bones shown in black and the feathers in rough outline. The commonly used specimen names and dates of discovery are as follows: (a) Berlin/München 1860; (b) London 1861; (c) Haarlem 1855 (1970); (d) Berlin 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. (After Wellnhofer, 1988b, 1993.)

subsequently made a case that the seventh (Munich) specimen is a distinctive small species, *Archaeopteryx bavarica*, because it was clearly an adult as it has an ossified sternum. It differs also in having longer tibia bones and longer legs than *A. lithographica*. Elzanowski (2001) assigned the sixth (Solnhofen) specimen to a 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. It is unclear whether these additional species and genera will be accepted and in the following I refer to all the Solnhofen bird specimens as *Archaeopteryx*.

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*) 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.

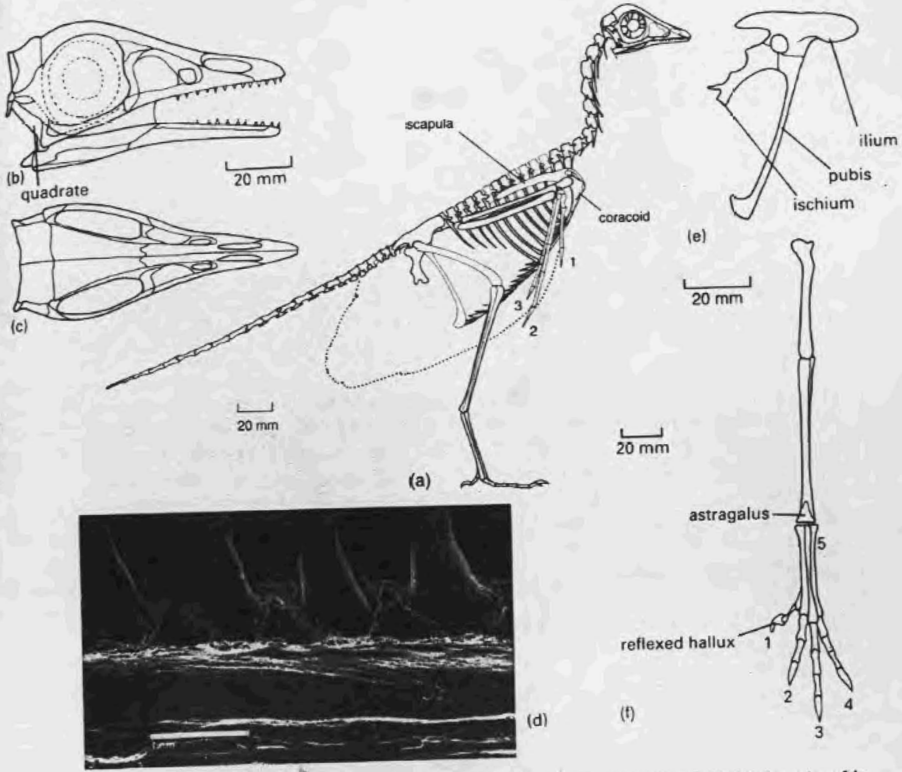


Fig. 9.2 The anatomy of *Archaeopteryx*: (a) skeleton in lateral view; (b, c) skull in lateral and dorsal views; (d) right lower jaw of the seventh specimen, showing slightly recurved teeth and interdental plates (scale bar, 1 mm); (e) pelvis in lateral view; (f) hindlimb in anterior view. [Figure (a) courtesy of Andrzej Elzanowski; (b, c, e) after Wellnhofer, 1974; (d) courtesy of Peter Wellnhofer; (f) after Wellnhofer, 1988b.]

9.1.2 Anatomy

Archaeopteryx is a medium-sized bird, 300–500 mm long from the tip of its snout to the end of its tail (Figure 9.2(a)), and it may have stood about 250 mm tall, about the size of a common magpie. The skull (Figure 9.2(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 pp. 239–40). 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, a feature of theropods and other archosaurs, and there is a constriction between the root and the crown of the tooth. The seventh (Munich) specimen shows that *Archaeopteryx* had interdental plates (Figure 9.2(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; Elzanowski and Wellnhofer, 1996). *Archaeopteryx* 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, like theropod dinosaurs, a short back and a long straight tail with 21–22 caudal vertebrae. 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. Until the discovery of the seventh (Munich) skeleton, an ossified sternum, typical of later birds, had not been identified in *Archaeopteryx*, but the new specimen shows a broad plate-like element linking the two coracoids in the midline (Wellnhofer, 1993). 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. The new specimens confirm the first view (Figure 9.2(e)). The hindlimb (Figure 9.2(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 appears to be an ascending process associated with the astragalus, the outer (5) toe is virtually lost and the inner (1) toe is short and lies at the rear of the foot, the **reflexed hallux** typical of many birds. The foot could be used for climbing tree trunks, based on comparisons of the toes and claws of *Archaeopteryx* with living birds, whereas the hindlimbs and pelvis are built for moving about on the ground (Elzanowski, 2002).

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 pp. 199–200) show considerable detail. There are short contour feathers over the lower neck, body, base of the tail and legs. The wings look surprisingly modern, with 11 or 12 primary flight feathers attached to the hand and at least 12 secondaries attached to the ulna. The bases of the quills of these flight feathers were covered with three rows of covert feathers, as in modern birds. The 16–17 pairs of tail feathers attach to the caudal vertebrae, one per vertebra, from the sixth caudal back.

9.1.3 Relationships

There have been endless debates about the relationships of *Archaeopteryx* over the years. It is generally accepted that *Archaeopteryx* is the oldest known bird; older records of supposed birds from earlier in the Jurassic, and most notably *Protoavis* from the Late Triassic (Chatterjee, 1991), have been rejected as inconclusive (Witmer, 2002). *Archaeopteryx* is a form with a mixture of characters intermediate between reptiles and birds, the classic example of a 'missing link'. Palaeontologists have disagreed strongly, however, on the closest reptilian relatives of birds, and this has led to three very different models of bird origins.

1 The mammal–bird hypothesis. Birds and mammals are endothermic, both groups have four-chambered hearts, advanced brains and insulating skin coverings (feathers and hair) made from the protein keratin. Gardiner (1982) enumerated these and further supposed shared characters to support his view that, among living animals, birds are not archosaurs, or even diapsids, but the closest living sister group to the mammals. In addition, some evidence from blood proteins shows a pairing of birds and mammals as sister groups. There is little morphological evidence for such a view, however, especially when fossil taxa are included in the analysis (Gauthier *et al.*, 1988b; Benton, 1990c), and current molecular evidence (e.g. Hedges and Poling, 1999; Zardoya and Meyer, 2001a) favours the traditional view.

2 The basal diapsid–bird hypothesis. A vocal minority argue the case that birds evolved in the Triassic from a diapsid or archosaur ancestor. Their choice of ancestor has varied considerably, from Late Triassic crocodilomorphs (see p. 145), a basal archosaur such as *Euparkeria* (see p. 141), the basal ornithodiran *Scleromochlus* (see p. 153), the long-limbed prolacertiform *Megalancosaurus* (Feduccia, 1999a), or the crested diapsid *Longisquama* (Jones *et al.*, 2000). The anatomical evidence for all these suggestions has been shown to be spurious, and the supporters of this view are characterized as presenting 'an argument of opposition rather than an argument of advocacy' (Witmer, 2002); in other words, they know they are against the dinosaur–bird hypothesis and so seek to pick holes in it, but they do not have an alternative phylogenetic view of their own.

3 The dinosaur–bird hypothesis. Ostrom (1976) catalogued dozens of similarities between the skull and skeleton of *Archaeopteryx* and those of derived theropod dinosaurs such as *Deinonychus*. Subsequent cladistic analyses (e.g. Gauthier, 1986; Holtz, 1994; Sereno, 1999, 2001; Chiappe, 2002b; Clark *et al.*, 2002) have fully supported this view and establish beyond all reasonable doubt that the birds are derived theropod dinosaurs, related closely to the dromaeosaurids or the deinonychosaurs (see Box 8.5).

The debate on bird origins has sometimes confused function and evolution. Proponents of the basal diapsid origin of birds are mainly supporters of the arboreal hypothesis, that flight originated from climbing ancestors ('trees down'), and they regard the dinosaur–bird hypothesis of relationships as necessitating a cursorial origin of flight ('ground up'; see section 9.2). There is, however, no such necessary linkage between the origin of flight and the origin of birds, and an argument for the arboreal functional hypothesis does not reject the bird–theropod phylogenetic hypothesis (Witmer, 2002). Logically, phylogeny must come first and phylogenies must be supported by character data.

The debate has been unnaturally prolonged by media attention. The origin of birds has been a topic of great public interest for the past twenty years, so much so that the leading proponents are frequently interviewed for newspaper articles and TV specials. The rules of journalism require that 'equal time' is given to representatives of each viewpoint. So the supporters of the basal diapsid origin of birds often have as much airtime as the supporters of birds as dinosaurs, even though the latter represent probably more than 99% of working vertebrate palaeontologists.

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.

9.2.1 The flight apparatus of modern birds

In the forelimbs of modern birds (Figure 9.3), the hand and wrist elements are greatly reduced, 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 9.1) 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 carpals are fused to the metacarpals to form a simple hinge joint. The humerus has clearly defined processes at each end for the attach-

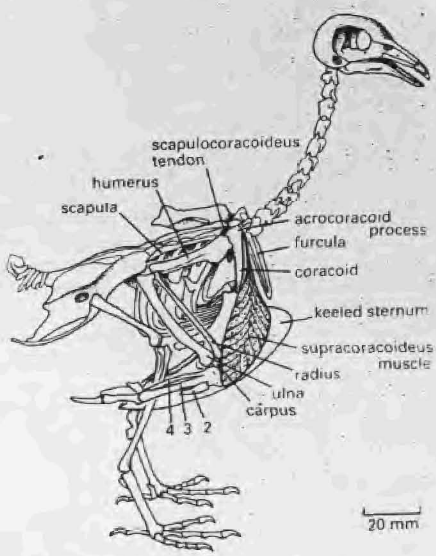


Fig. 9.3 The skeleton of a typical modern bird, the pigeon *Columba*, showing the wing and the supracoracoideus muscle that raises the wing by acting over the acrocoracoid process, a pulley-like system. (Based on Young, 1981, and other sources.)

ment of flight muscles, and at least one 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 humerus, a pulley-like arrangement seen also in pterosaurs (see p. 227). 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 small squarish element in *Archaeopteryx* (Figure 9.2(a)).

BOX 9.1 BIRD FINGERS: 1, 2, 3 OR 2, 3, 4?

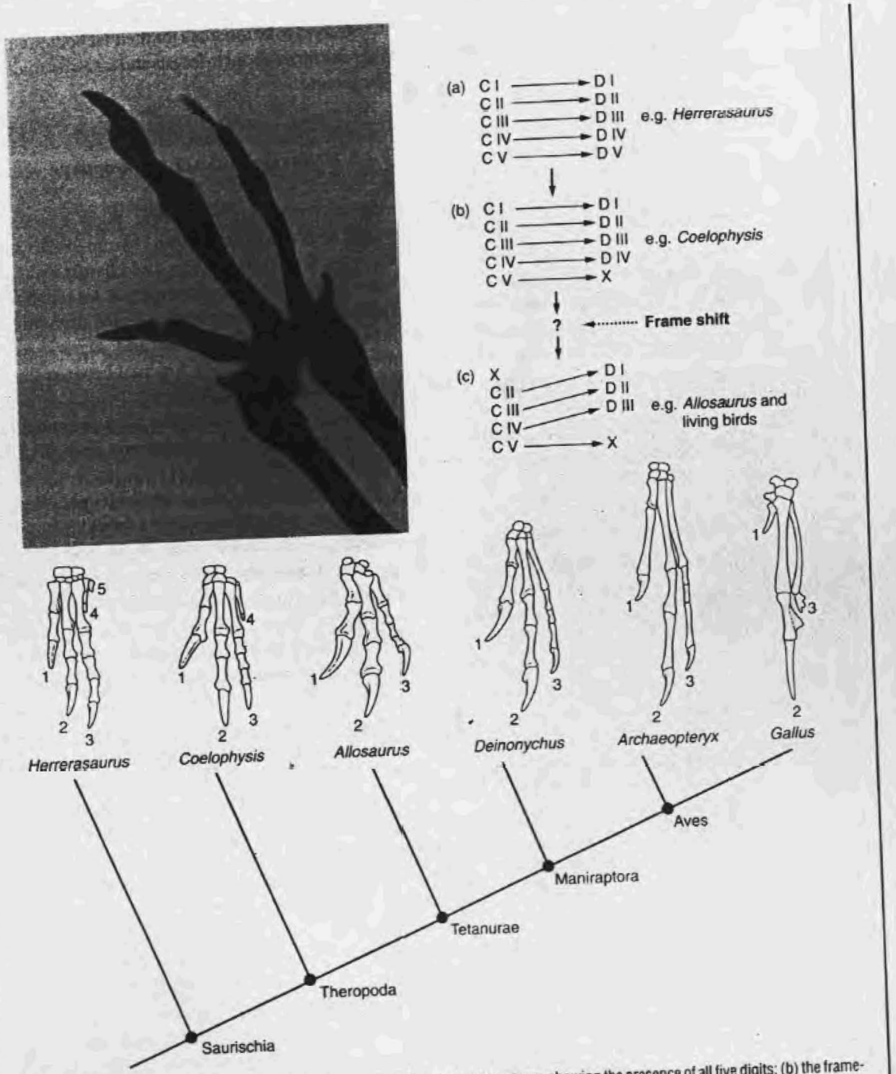
How do you number the fingers of a bird? This may seem a bizarre question – surely modern bird fingers are unimportant and does it really matter what they are called? All birds, from *Archaeopteryx* onwards, have three fingers. It is clear in the evolution of theropods, that digits four and five (equivalent 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?

There is no doubt about the embryological evidence (Burke and Feduccia, 1997): the fourth digit condenses first during early development of the hand and foot in all tetrapods (see Box 4.2), 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, the fifth digit appears in cartilaginous form early in development, but is lost before ossification. It was assumed that bird embryos never had a trace of the cartilaginous precursor of digit 1, but this has now been demonstrated (Larsson and Wagner, 2002). The three digits that ossify are then unequivocally numbers 2–4.

This observation has been hailed as clear evidence that birds did not evolve from theropod ancestors (Burke and Feduccia, 1997). Does this evidence overwhelm all the other apparent synapomorphies of theropods and birds (see Box 8.5), as suggested by Feduccia (1999b)? Wagner and Gauthier (1999) have argued that it does not. They 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 Box 4.2). They suggest that Burke and Feduccia (1997) 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. They 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 *Coelophysis* and *Allosaurus*). Functionally, those two fingers were reduced and lost, but embryologically this could only have been achieved by a developmental 'frameshift' (Wagner and Gauthier, 1999): 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.

The frameshift hypothesis has been criticized strongly (Feduccia, 1999b), but it has been confirmed in an unexpected way. Dahn and Fallon (2000) showed, in experiments on bird embryos, that there is no necessary linkage between the numbering of cartilaginous precursors and of digits. The identity of the developing digits is at first unspecified, despite their positions, and digits acquire their ossified characteristics upon interaction with gradients of bone morphogenetic proteins. The timing and pattern of ossification in the limbs are controlled by *Hox* genes (see Box 4.2), sometimes called **homeotic** genes, and hence the frameshift hypothesis is based on **homeotic** transformations, and the new experiments show that such shifts can occur.

Read more about this debate at http://www.devbio.com/article.php?ch=16&id=161.



Understanding evolution and development: (a) photograph of the hand of a bird embryo, showing the presence of all five digits; (b) the frameshift hypothesis, in which digits 2–4 are expressed in the adult before the shift and digits 1–3 after; (c) phylogeny of theropods, showing the reduction of hand digits seen in fossils, and the implied frameshift between *Archaeopteryx* and the modern bird *Gallus*. [Figure(a) © Alan Feduccia, reproduced with kind permission; (b) based on Wagner and Gauthier (1999); (c) based on various sources.].

9.2.2 Flight mechanics in modern 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 (Rayner, 1988). Wing loading is a measure of the relative 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 (Rayner, 1996). The aspect ratio of a wing is a measure of wing shape, defined as (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.

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 so small that they cannot fly in air.

3 **Thermal soarers** (low aspect ratio and low wing loading). These include larger owls, flycatchers, 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 *Archaeopteryx*

Archaeopteryx has asymmetric flight feathers and wings, so it was clearly a flyer. Ostrom (1976) argued, however, 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 small sternum, 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 deltoids.

3 *Archaeopteryx* has asymmetrical vanes on its feathers as in modern flying birds (flightless birds have 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.

By comparison with modern birds, *Archaeopteryx* probably 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.

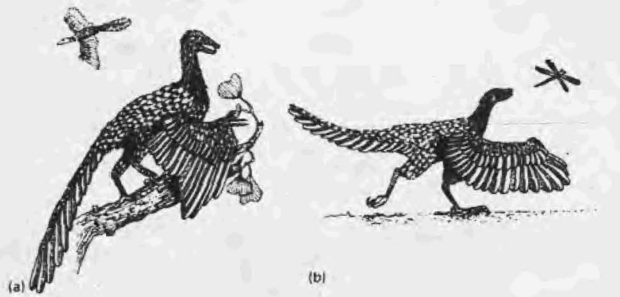


Fig. 9.4 Two models for the origins of flight: (a) *Archaeopteryx* as a tree-dweller that flew from branch to branch and (b) as a ground-dweller that leapt up to catch insects. (Based on drawings in Rayner, 1988.)

The origin of bird flight must be entirely speculative. Numerous ideas have been aired, but there are two main current models, the cursorial ('ground up') and arboreal ('trees down') (Figure 9.4).

The cursorial hypothesis has been developed from Ostrom's idea 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. It is not clear in this model, however, why flapping would have started in a running animal, whether for insect catching or for assisted leaping (Rayner, 1988).

The arboreal hypothesis is based on the older idea that *Archaeopteryx* could climb trees using the claws on its hands and feet. An ancestor initially leapt between branches and then evolved to be able to leap and parachute 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) and others have presented aerodynamic arguments that gliding flight is pre-adapted for the evolution of flapping flight.

This may, however, be an unhelpful dichotomy, maintained by the linkage of the cursorial and theropod origin models and the arboreal and non-theropod origin models (see Section 9.1.3). Perhaps more important is to accept a transition from a non-flying form to a glider and then to a bird such as *Archaeopteryx* that uses flapping flight (Rayner, 2001). Gliding can be from tree to tree, or over irregular ground. Rayner (2001) emphasizes that the transition from non-flight to gliding is far more straightforward than from non-flight to flapping, an assumption in many of the current cursorial models, whether the protobird is running along a flat surface (Burgers and Chiappe, 1999) or up an incline (Dial, 2003), and whether it is assisted by a favourable following wind or not.

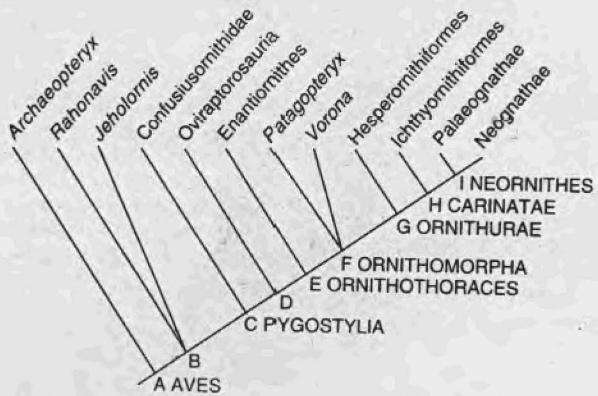
Elzanowski's (2002) 'climbing escape' model takes this a step further. The feathered protobirds presumably foraged on the ground. When threatened by a predator, the protobird could scramble or run up to a perch in a tree or on a rock for safety. It then glided down to the ground, spreading its wing feathers to enlarge the lift surface. Flapping then evolved to extend the length of the flight path to the ground.

9.3 CRETACEOUS BIRDS, WITH AND WITHOUT TEETH

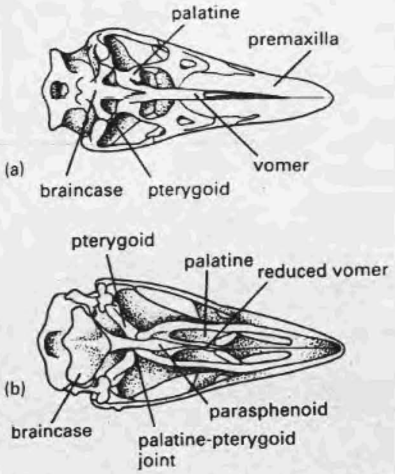
Until 1990, there was a long gap in the fossil record of birds between *Archaeopteryx*, dated at 150 Myr ago, and *Hesperornis* and *Ichthyornis* from the Upper Cretaceous of North America, dated at 90–65 Myr ago. This time span represents the first half of the history of birds. New discoveries from the Lower 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, and older materials, are arranged here according to the phylogenetic tree of Chiappe (2002b) (see Box 9.2).

BOX 9.2 RELATIONSHIPS OF THE BASAL BIRDS

Archaeopteryx is the basal bird, the sister group of *Rahonavis* and the Pygostylia (Chiappe, 2002b), which includes all other birds (see cladogram). The Pygostylia, consisting of the Confuciusornithidae and the Ornithothoraces, share the pygostyle (fused caudal vertebrae) and a backwards-pointing pubis. The oviraptorosaurs fit in the scheme next, controversially: they have a pygostyle and other generalized bird characters (Maryańska *et al.*, 2002), as well as other features of the skull, cervical vertebrae and pelvis seen only in more derived birds. The major Cretaceous bird group, the Enantiornithes, shares a number of typical avian characters with more derived forms, and two Late Cretaceous forms, *Patagopteryx* and *Vorona*, come next in the phylogeny.



I Cladogram showing the postulated relationships of the major groups of birds, based on Chiappe (2002b). For the location of birds among theropod dinosaurs, see Box 8.5, and for the phylogeny of Neognathae, see Box 9.4. Synapomorphies: **A AVES**, nostril moved back to lie partially above the antorbital fenestra, prominent acromion process on the scapula, papillae on ulna for flight feathers, pointed and low posterior process of the ilium, reversed hallux (first toe points back); **B**, procoelous synsacrum, shaft of ulna considerably thicker than shaft of radius, fibula does not reach proximal tarsals, tubercle on dorsal face of metatarsal III; **C PYGOSTYLIA**, absence of the hyposphene–hypantrum accessory articulation in the thoracic vertebrae, pygostyle, backwards-turned (retroverted) pubis at an angle of 45–65° below the vertebral column, wide and bulbous medial condyle of the tibiotarsus; **D**, fused premaxillae, lacrimal is curved and open posteriorly, jugal bar slender and rod-like, mobile quadrate–quadratojugal articulation, 13 cervical vertebrae, cervical ribs fused to centra, more than eight sacral vertebrae, ilia that are close together dorsally; **E ORNITHOTHORACES**, fewer than 13 thoracic vertebrae, strut-like coracoid, triosseal canal, alula; **F ORNITHOMORPHA**, loss of caudal prezygapophyses, metacarpals 2 and 3 partially or completely fused distally, complete fusion of metatarsals 2, 3 and 4; **G ORNITHURAE**, sharp pointed anterior process of quadrate, fewer than 11 thoracic vertebrae, procoracoid process, globe-shaped convex proximal head of humerus, small acetabulum, pubis runs back parallel to ischium and ilium, femur with prominent patellar groove; **H CARINATAE**, extensor process on alular metacarpal well developed, ungual phalanx of major digit (finger 2) absent; **I NEORNITHES**, teeth absent, quadrate articulates with prootic, gastralia (abdominal ribs) absent, pneumatic fossa and foramen in humerus.



II The (a) palaeognathous and (b) neognathous palates, from a cassowary and a bronze turkey respectively. (Modified from various sources.)

The more derived birds, the Ornithurae, include hesperornithiforms, ichthyornithiforms and Neornithes, the modern groups (Cracraft, 1988; Chiappe, 2002b). These are all characterized by a pointed orbital process of the quadrate (see Figure 9.8(c)), a shortened back and pelvic elements that run back almost in parallel (see Figure 9.8(a)). *Ichthyornis* shares features of the hand with modern birds. The modern birds, termed the Neornithes (illustration I), are distinguished from the extinct groups by further derived characters (Cracraft, 1988), 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.

The modern birds fall into two clades, the Palaeognathae, flightless ratites and tinamous, and the Neognathae, all other flying birds (Cracraft, 1988). 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.

Most of the Cretaceous birds reported since 1990 may be assigned to positions in a cladogram of early birds (see Box 9.2) as a result of intensive anatomical description of the spectacular new finds, especially the specimens from Spain, Argentina, Madagascar and China (summarized by Padian and Chiappe, 1998; Gauthier and Gall, 2001; Chiappe and Dyke, 2002; Chiappe and Witmer, 2002). Other Cretaceous birds, especially some less complete specimens from the Cretaceous of Europe, are less easy to place.

9.3.1 *Rahonavis* and *Jeholornis*

The most basal Cretaceous bird appears to be *Rahonavis* from the Upper Cretaceous of Madagascar (Forster *et al.*, 1998). Its avian status has been disputed, but it 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* (Figure 9.5(a)) was the size of a raven, it was a flyer and it had an enlarged claw on its second toe, perhaps used for killing prey by slashing, as in dromaeosaurids and troodontids (see pp. 197–8). *Rahonavis*, although living long after *Archaeopteryx*, retains the long bony tail and other primitive features that were lost in all other birds. It differs from *Archaeopteryx* in having a nostril that has moved back to lie partially above the antorbital fenestra, a prominent acromion process on the scapula, a pointed and low posterior process of the ilium and different leg proportions. Forster *et al.* (1998) believed *Rahonavis* was a close relative of *Archaeopteryx*, perhaps a member of the Family Archaeopterygidae, but the new cladistic analysis (Chiappe, 2002b) shows that the Madagascar bird differs in at least five characters.

Jeholornis (Zhou and Zhang, 2002) from the Lower Cretaceous Jehol Group of China (see Box 9.3) also appears low in the cladogram, close to *Rahonavis*. *Jeholornis* has a long bony tail, like *Archaeopteryx*, but shows advances in the structure of the hand. The unique

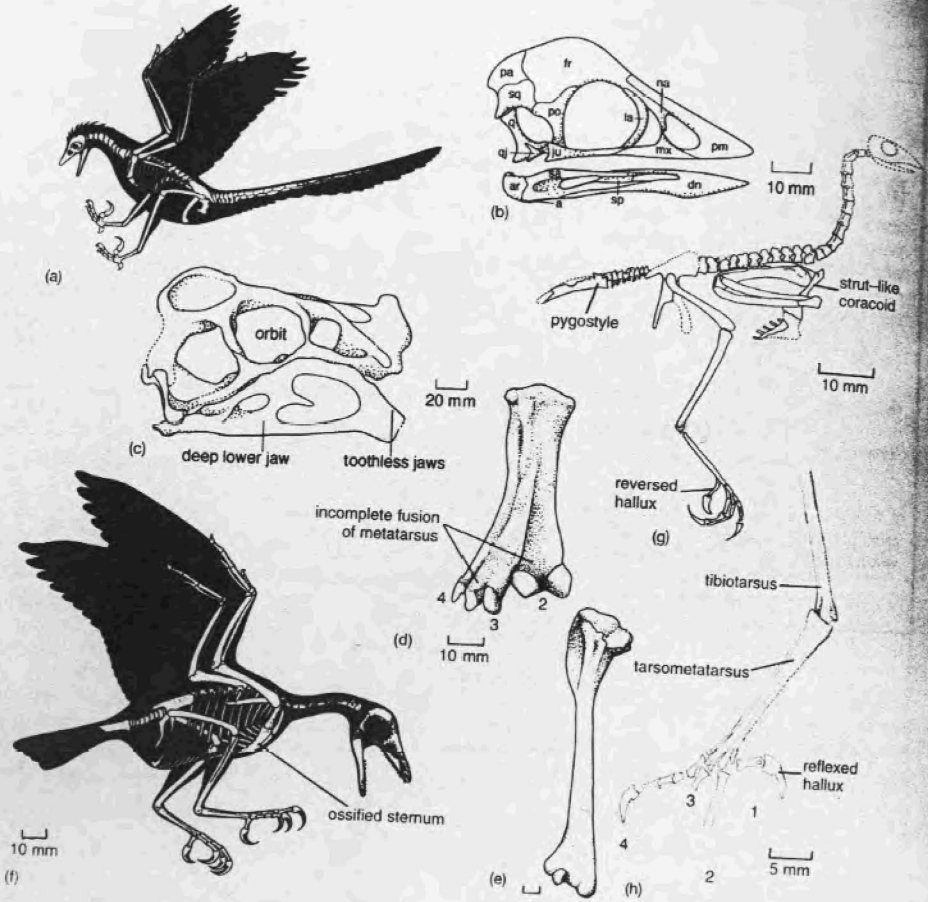


Fig. 9.5 Basal birds from the Cretaceous: (a) *Rahonavis* from the Upper Cretaceous of Madagascar; (b) skull of the confuciusornithid *Confuciusornis* from the Lower Cretaceous of China; (c) skull of the oviraptorosaur *Oviraptor* from the Upper Cretaceous of Mongolia; (d) tarsometatarsus of *Yungavolucris* from the Upper Cretaceous of Argentina; (e) humerus of an unidentified enantiornithine from the Upper Cretaceous of Argentina; (f) reconstructed skeleton of *Sinornis* from the Lower Cretaceous of China; (g) *Iberomesornis* from the Lower Cretaceous of Spain, reconstructed skeleton; (h) hindlimb of *Concornis* from the Lower Cretaceous of Spain. [Figure (a) courtesy of Cathy Forster; (b) courtesy of Zhou Zhonghe; (c) after Zittel, 1932; (d, e) modified from Chiappe and Walker, 2002; (f) courtesy of Paul Sereno; (g) modified from Sanz and Bonaparte, 1992; (h) modified from Sanz *et al.*, 1995.]

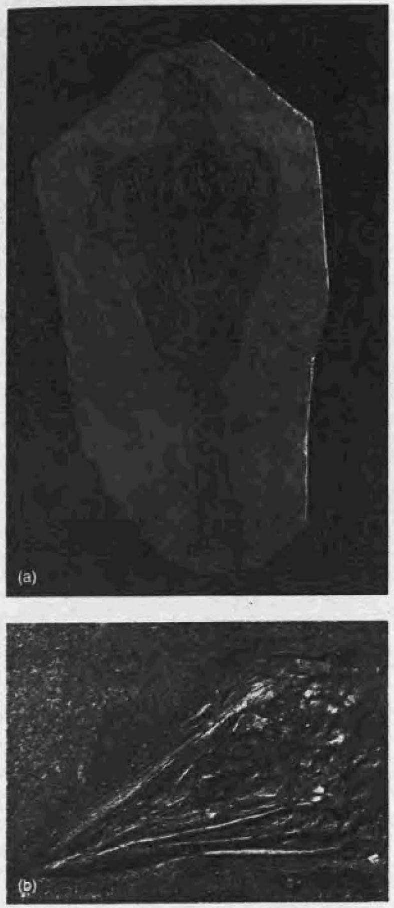
BOX 9.3 THE WONDERFUL BIRDS OF LIAONING

The first reports of spectacular bird fossils from Liaoning Province in north-east China came out 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 research began in the 1990s and so far some 15 genera of birds have been described, seven of which are enantiornithines (Zhou and Hou, 2002; Zhou *et al.*, 2003). The fossiliferous horizons are in the 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, 128–110 Myr ago).

The fine limestones, laid down by slow accumulation of sediments in ancient lakes, have produced rich floras and faunas. The flora is dominated by conifers, but many other groups, including angiosperms, are represented by leaves, flowers, fruits, stems and roots. Invertebrates include insects (mayflies, dragonflies, cockroaches, bugs, flies), spiders, ostracods, concostracans, crayfish, bivalves and gastropods. Other than birds, the vertebrates include bony fishes, frogs, salamanders (see p. 103), turtles, choristoderes, lizards, pterosaurs and dinosaurs, including the feathered theropods (see Box 8.2), and mammals (see pp. 305, 311).

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 *Compsognathus* from the Upper 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 confuciusornithid birds are also unique to eastern Asia. Are the Jehol biotas freaks, assemblages of unusual and bizarre plants and animals that do not represent the mainstream? Seemingly not. Most of the organisms are typical of Early Cretaceous localities elsewhere, and this is true of the majority of the birds.

The book of the touring exhibition of dino-birds from China (Milner, 2002) contains colour photographs of specimens and life restorations.



The Early Cretaceous bird *Confuciusornis*: (a) complete (?) male specimen, with long tail; (b) lateral view of the skull. (Courtesy of Zhou Zhonghe.)

continued

An early Palaeocene fauna from Tiupampa, Bolivia, includes 11 marsupials, mostly showing similarities to later uniquely South American groups (Muizon and Cifelli, 2000, 2001), as well as representatives of several placental groups, most of them showing relationships to North American forms (cimolestans, mioclaenids, pantodonts), but some (notoungulates) unique to South America.

10.5.2 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, the Ameridelphia, include three clades. The Didelphimorphia, essentially the opossums, are well known from the Upper Cretaceous in North America (e.g. *Alphadon*; Figure 10.13(c–e)) and 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 re-entered North America at the time of the Great American Interchange (see p. 320).

The Paucituberculata includes several families of insect-eaters, carnivores and herbivores, spanning the Cenozoic. The oldest paucituberculate from South America, the caroloameghinid *Roberthoffestetteria* (Figure 10.18(a, b)), was a small insectivore (Marshall and Muizon, 1988). The caenolestids, such as *Palaeothentes* from the late Oligocene and early Miocene, were also small insectivores or omnivores with an elongate lower incisor and blade-like cheek teeth (Figure 10.18(c)). The family survives today: *Caenolestes* is a small shrew-like animal that lives in the higher Andes. The kangaroo rat lookalike *Argyrolagus* (Figure 10.18(d)) 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.

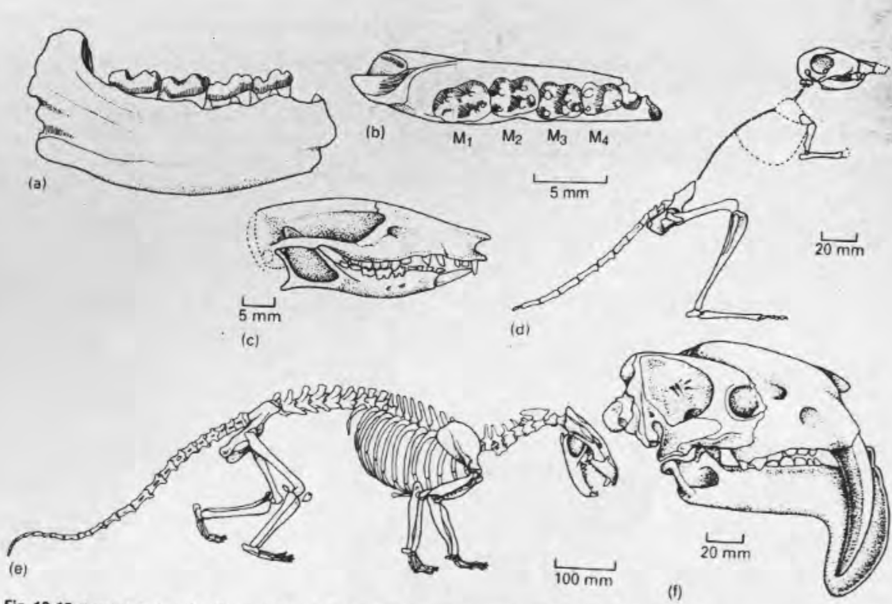


Fig. 10.18 South American fossil marsupials: (a, b) the Palaeocene caroloameghinid *Roberthoffstetteria*, lower jaw fragment in lateral and occlusal views; (c) the Oligocene to Early Miocene caenolestid *Palaeothentes*; (d) the Pliocene argyrolagid *Argyrolagus*; (e) the Early Miocene borhyaenid *Prothylacinus*; (f) the sabre-toothed Pliocene thylacosmilid *Thylacosmilus*. Abbreviations: M_1–M_4, molars. [Figures (a, b) after Marshall and Muizon, 1988; (c) after Marshall, 1980; (d) after Simpson, 1970; (e) after Sinclair, 1906; (f) after Riggs, 1934.]

The third clade, the Sparassodonta, consists of two groups of larger animals, both carnivorous. The borhyaenids, known from the Palaeocene (Muizon *et al.*, 1997) to the Pliocene, such as *Prothylacynus* (Figure 10.18(e)), have short limbs and rather dog-like skulls. Their later relatives, the late Miocene and Pliocene thylacosmilids, have skulls (Figure 10.18(f)) that are almost indistinguishable from 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 (see pp. 319–21).

10.5.3 Xenarthra: armadillos, sloths and ant-eaters

Some of the most characteristic mammals of South America are the Xenarthra, which include the armadillos, tree sloths and ant-eaters (Rose and Emry, 1993). This group has had a spectacular history, which is not evident from the living forms (Simpson, 1980). The name Xenarthra (literally 'extraneous joints') refers to supplementary articulations that are present in all forms between some of the trunk and tail vertebrae (Figure 10.19(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 10.19(c)). Thirdly, the teeth are much reduced: xenarthrans have few or no incisors and the ant-eaters have no teeth at all. The Xenarthra used to be classified with the pangolins (Pholidota), but the latter group now appears to be allied with the Carnivora (see p. 353).

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 10.19(a)), they all have a bony shield over their heads, a 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 10.19(b, c)), which reached very large sizes in the Pliocene and Pleistocene (Gillette and Ray, 1981). 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 p. 316). The skull is short and deep (Figure 10.19(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 10.19(e)) that was probably used to whack sabre-tooths. In calculating the energy of the blow, 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.

The sloths date back to the Oligocene and they had a broad radiation, even though only five species of tree sloths survive today. A Miocene sloth *Hapalops* (Figure 10.19(d)) is a small semi-arboreal animal that has only four or five cheek teeth in the jaws. Sloth evolution followed two 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 10.19(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

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