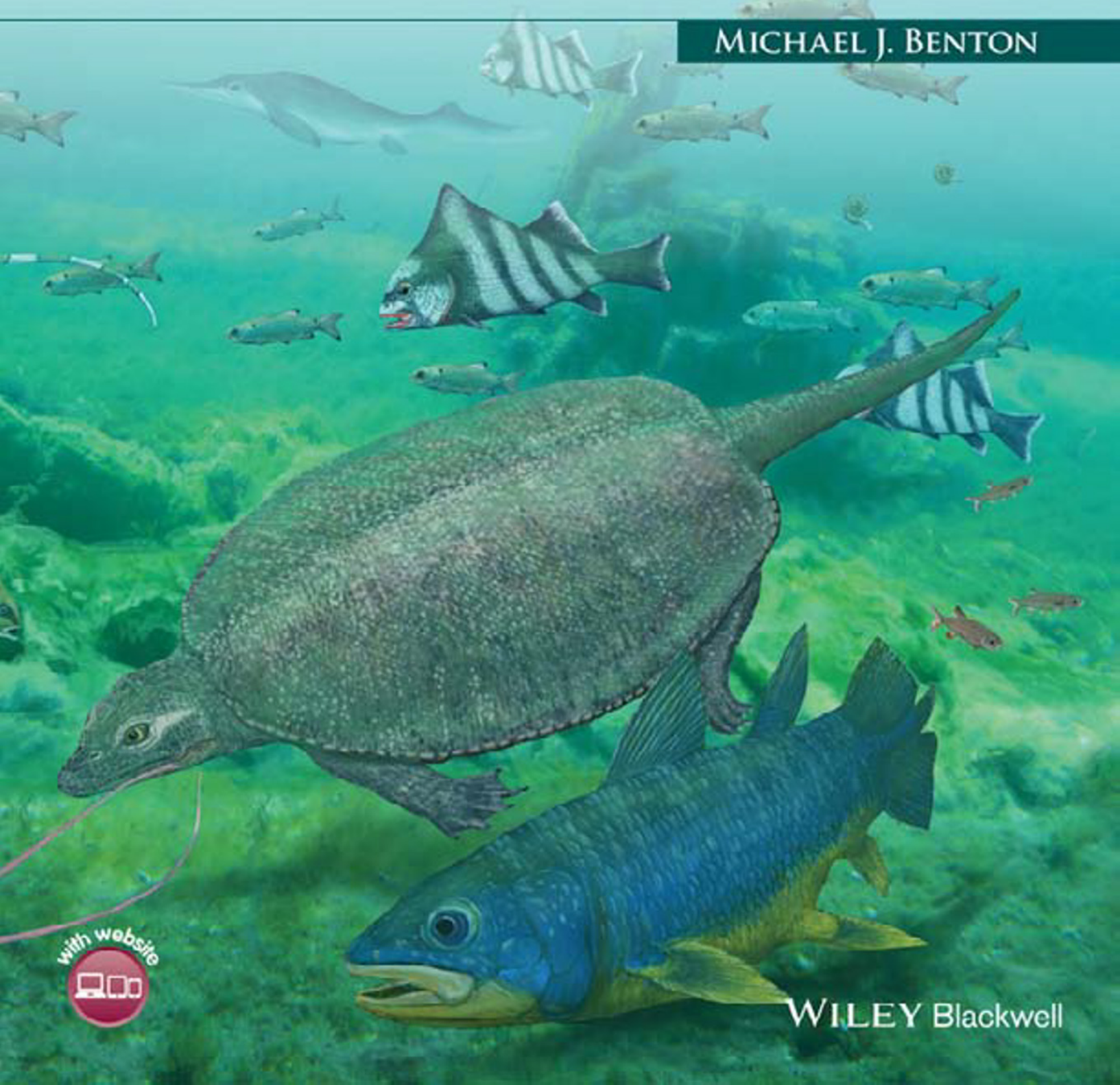# FOURTH EDITION

VERTEBRATE PALAEONTOLOGY

MICHAEL J. BENTON

with website

WILEY Blackwell

VERTEBRATE PALAEONTOLOGY

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

VERTEBRATE PALAEONTOLOGY

Fourth edition

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Chapter opening illustrations drawn by John Sibbick

WILEY Blackwell

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

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Preface

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

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

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

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

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

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

The third aim is to show **how palaeobiological information is obtained**. It is important to understand the methods and debates, and not simply to assume that all knowledge is fixed and immutable. Further, science is about testing hypotheses against evidence, not about who shouts loudest, and it is important to realize that even historical sciences such as palae-ontology, can work through hypothesis testing. Science is not all mathematics or chemistry! To do this, I summarize in Chapter 2

the methods used by vertebrate palaeontologists in collecting and preparing the fossils, in using them to learn about ancient environments, biomechanics and palaeobiology, and as evidence for discovering parts of the great evolutionary tree of life. Then, throughout the text, I present box features that are divided into three categories: tree of life controversies (deuterostome relationships, jawless fishes, osteichthyans, sarcopterygians, basal tetrapods, amniotes, dinosaurs and the origin of birds, molecular information on mammalian phylogeny, hominin relationships), exceptional fossils or faunas (new exceptionally preserved basal chordates from China, a rich fossil deposit of early tetrapods, exceptional fishes and marine reptiles from the Triassic of China, dramatic new discoveries of Cretaceous birds, fossil mammals with hair, new basal humans from Africa, the Flores 'hobbit') and palaeobiology of selected unusual ancient vertebrates (limb mechanics of the first tetrapods, jaw action and diet of dicynodonts, archosaur locomotion, hadrosaur chewing adaptations, locomotion of the largest pterosaurs, giant penguins, horse-eating birds, rodents as large as rhinos).

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

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

I am indebted to many people. I thank †Roger Jones and Clem Earle of Unwin Hyman who commissioned the first edition 25 years ago, Ward Cooper of Chapman & Hall who steered the second edition through, and Ian Francis and Delia Sandford who worked hard on the third edition. The following people read parts of the first, second, and third editions, or made other valuable contributions: Dick Aldridge, Peter Andrews, Kenneth Angielczyk, David Archibald, Chris Beard, David Berman,

†Deceased

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

Michael J. Benton

NOTE CONCERNING THE REFERENCES

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

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

List of Boxes

TREE OF LIFE BOXES

EXCEPTIONAL FAUNAS AND PALAEOGEOGRAPHY BOXES

BIOMECHANICS AND BEHAVIOUR BOXES

About the Companion Website

This book is accompanied by a companion website:

www.wiley.com/go/benton/vertebratepalaeontology

The website includes:

- PowerPoints of all figures from the book for downloading

CHAPTER 1
Vertebrates Originate
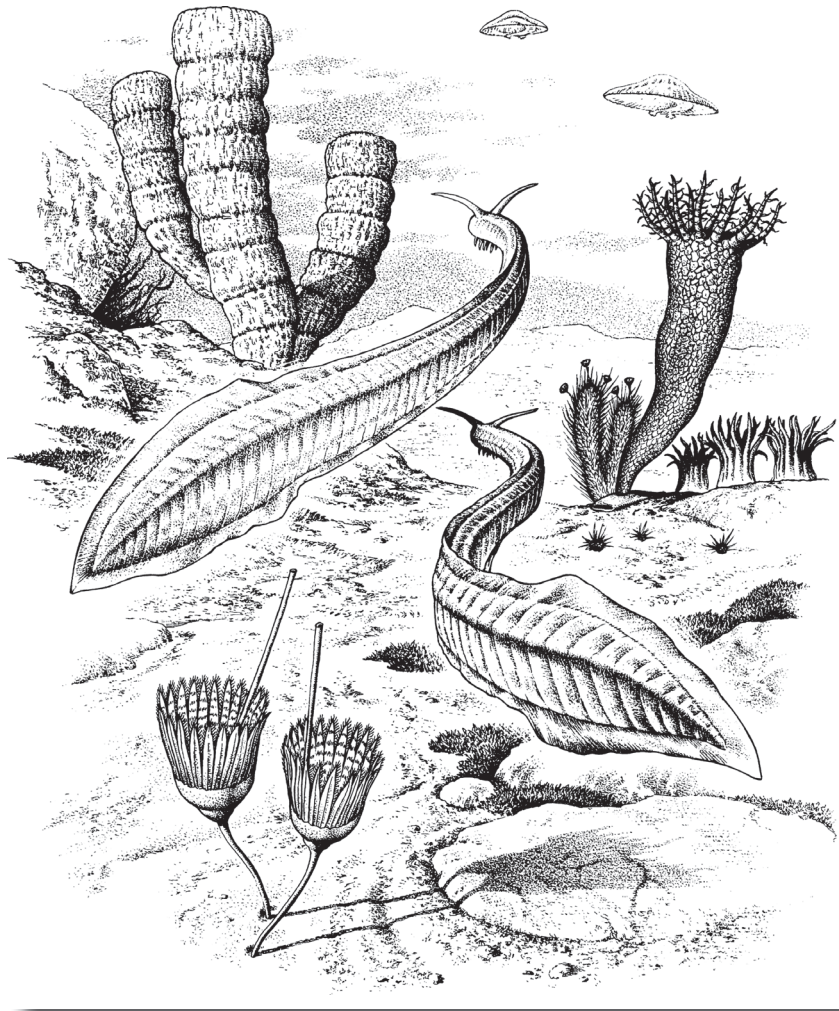
INTRODUCTION

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

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

Looked at more widely, vertebrates are a minor twig in the 'Tree of Life' (Figure 1.1). It is common to think of the major divisions of life as being animals, plants, protists, and simple organisms classed broadly as bacteria and viruses. However, molecular studies since the 1990s (e.g. Woese, 2000; Wolf *et al.*, 2002) have shown that the fundamental splits were between Bacteria, Archaea, and Eukaryota. The familiar plants, animals and fungi are members of Eukaryota, all diagnosed by complex cells with a membrane-bound nucleus and the primitive presence of mitochondria. Within Eukaryota are various protist groups, as well as plants, fungi, and animals, and of course vertebrates are animals. Among animals, it has always been assumed that chordates are closely related to hemichordates
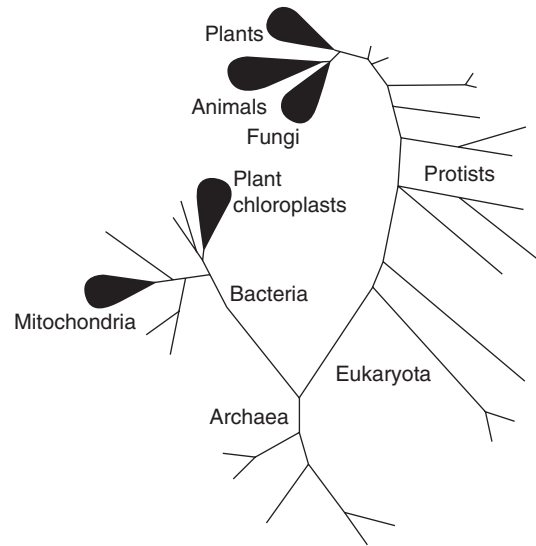
Figure 1.1 The 'Tree of Life', the commonly accepted view of the relationships of all organisms. Note the location of 'Animals', a minor twig in the tree, close to plants and Fungi. Source: Adapted from various sources.

(acorn worms and pterobranch worms) and echinoderms (starfish, sea lilies, and sea urchins), and this is now widely confirmed, based on morphological, developmental and molecular evidence.

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

1.1 SEA SQUIRTS AND THE LANCELET

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

1.1.1 Urochordata: sea squirts

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

The internal structure is fairly complex (Figure 1.2(b)). A large **pharynx** fills most of the internal space, and its walls are perforated by hundreds of gill slits, each of which bears a fringe of **cilia**, fine hair-like vibratile structures. Seawater is pumped through the inhalant siphon into the pharynx by beating movements of the cilia, and the water is then passed through a surrounding cavity, the **atrium**, and ejected through the exhalant siphon. The pharynx serves mainly to capture food particles
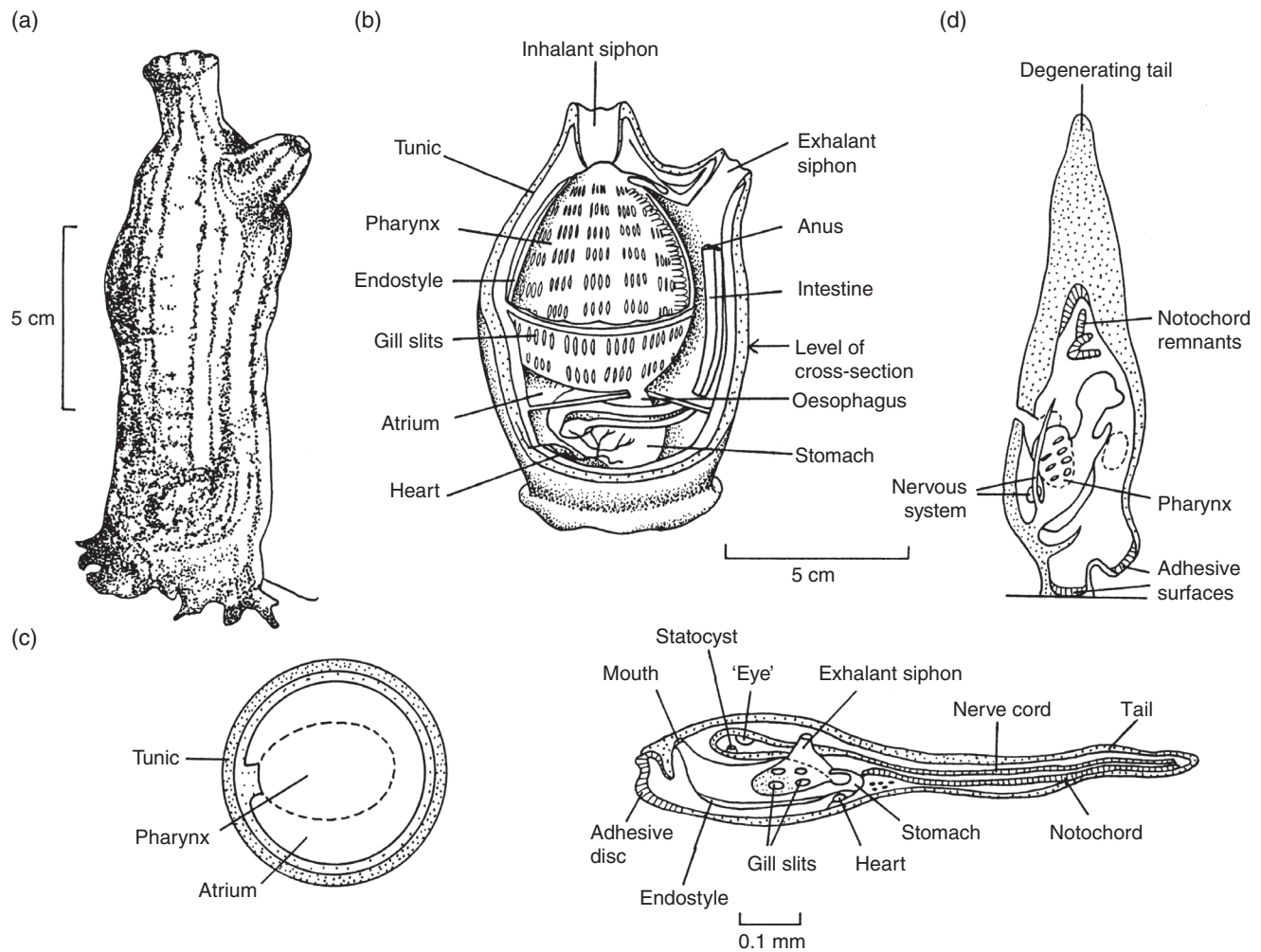
Figure 1.2 The sea squirts: (a) *Ciona*, external view; (b) internal anatomy and cross-section of an adult; (c) swimming larva; (d) metamorphosing form. Source: Adapted from Jefferies (1986) and other sources.

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

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

just above the notochord, and this expands at the front into a very simple brain that includes a light sensor (an 'eye') and a tilt detector.

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

1.1.2 Cephalochordata: amphioxus

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

(a)

Muddy sediment

Sand

(b)

Dorsal nerve cord

Notochord   Diverticulum   Myotomes

Pharynx

Fin-ray boxes   Anus   Atriopore

Intestine   Gonads

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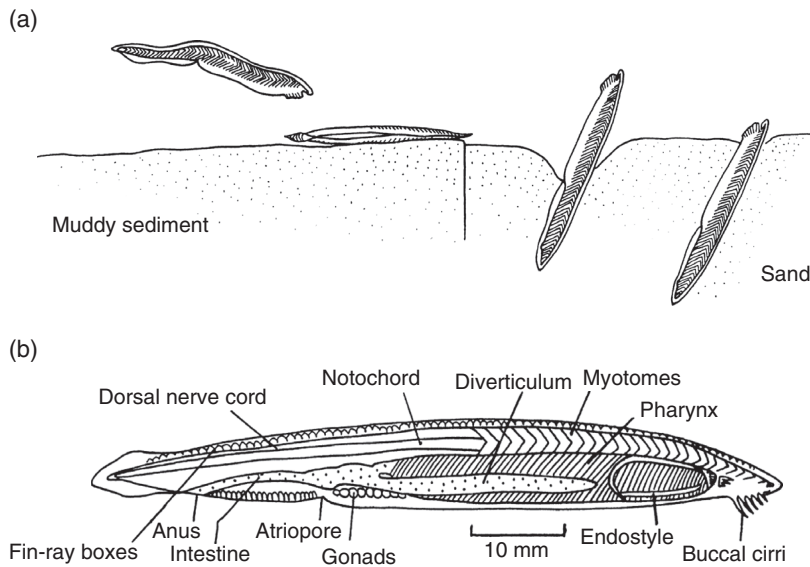
Figure 1.3 Amphioxus, a cephalochordate: (a) modes of life, including swimming and burrowing into sand for protection; (b) internal anatomy. Source: Adapted from Pough *et al.* (2012) and other sources.

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

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

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

1.2 AMBULACRARIA: ECHINODERMS AND HEMICHORDATES

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

Echinoderms today include such familiar animals as starfish and sea urchins, as well as ophiuroids (brittle stars), crinoids ('sea lilies') and holothurians ('sea cucumbers'). There are some 7000 species of living echinoderms and 13,000 extinct species. Echinoderms all share four key features: (1) a calcite skeleton made from many ossicles, each composed of many aligned small crystals in a somewhat spongy arrangement called stereom; (2) a water vascular system that functions in locomotion, respiration,

and feeding; (3) ossicles are linked by mutable collagen, ligaments that are normally rigid, but can be loosened; and (4) pentaradial (five-fold) symmetry. Most of these special features of echinoderms do not show close similarities to other deuterostomes, but the water vascular system may have evolved from simple tentacular systems, such as those of pterobranch hemichordates.

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

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

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

BOX 1.1   DEUTEROSTOME RELATIONSHIPS

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

The second view (illustration (b)) is supported by morphological and molecular data and is now widely accepted (Swalla and Smith, 2008; Edgecombe *et al.*, 2011). The first molecular studies, in which the 18S rRNA genes of echinoderms, hemichordates, and chordates were compared were inconclusive, but newer work (e.g. Eernisse and Peterson, 2004; Delsuc *et al.*, 2006; Swalla and Smith, 2008; Edgecombe *et al.*, 2011; Röttinger and Lowe, 2012; Cannon *et al.*, 2013) pairs hemichordates with echinoderms as the clade Ambulacraria, and within the clade Chordata places cephalochordates as the basal clade, and pairs Urochordata and Vertebrata, as clade Olfactores because of shared characters in the olfactory region. See Box 3.1 for phylogeny of Vertebrata.
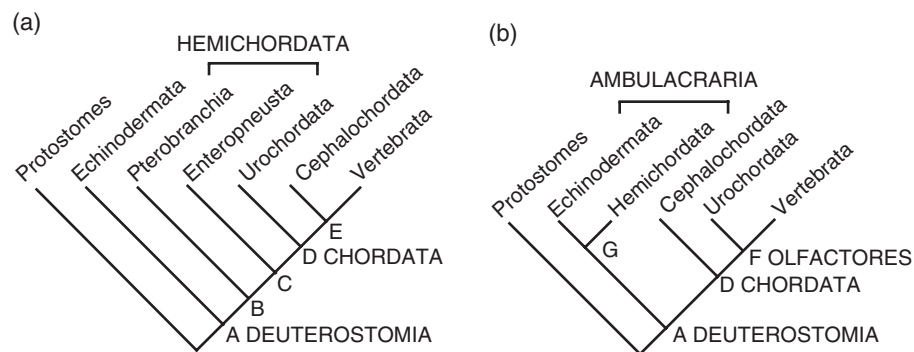
Cladograms showing the relationships of the main deuterostome groups: (a) the 'traditional' model, and (b) molecular model. Synapomorphies: **A DEUTEROSTOMIA**, blastopore becomes anus during development, bipartite mesocoel, mesocoelomic ducts; **B**, stomochord, paired gill slits; **C**, multiple pairs of gill slits, pharyngeal slits U-shaped, dorsal hollow nerve cord, preoral ciliary organ, mouth anterior and ventral and anus posterior and ventral or dorsal, multiciliated cells; **D CHORDATA**, notochord present and not attached to gut, dorsal hollow nerve cord with neural-plate stage in development, endostyle organ, a true tail used in swimming; **E**, digestive caecum, open capillary junctions, somites present, lateral-plate mesoderm, neural tube differentiated into grey and white matter, cerebral vesicle in brain; **F OLFACTORES**, specialized olfactory areas in buccal cavity, hind-tail tripartite, dorsal longitudinal canal connected with notochord; **G AMBULACRARIA**, trimeric arrangement of the adult coelom, axial complex with hydropore, dipleureula larva with neotroch.

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

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

shows a fibrous tube that might be a precursor of the pterobranch periderm, suggesting that pterobranchs arose from enteropneust-like ancestors.

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

(a)

(b)

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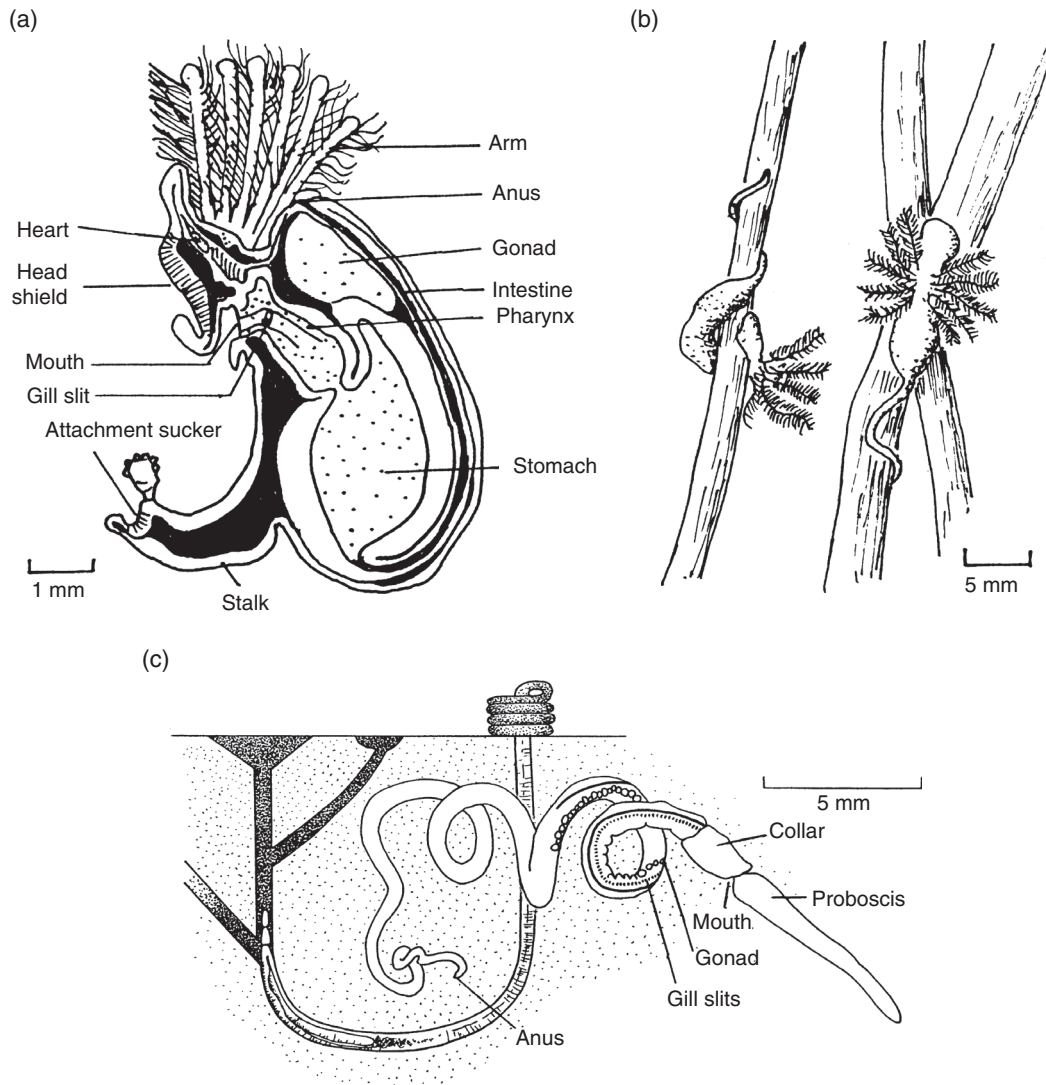
Figure 1.4 Typical hemichordates: (a) the pterobranch *Cephalodiscus*, internal anatomy and (b) mode of life; (c) the enteropneust *Saccoglossus*, mode of life and external anatomy. Source: Adapted from Jefferies (1986) and other sources.

1.3 DEUTEROSTOME RELATIONSHIPS

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

1.3.1 Embryology and the position of the anus

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

Embryologists noticed some time ago that animals fall into two large groups depending on the relative orientation of the mouth and anus. The classic story is that in most invertebrates (the **protostomes**), the blastopore becomes the mouth (Figure 1.5(h)),
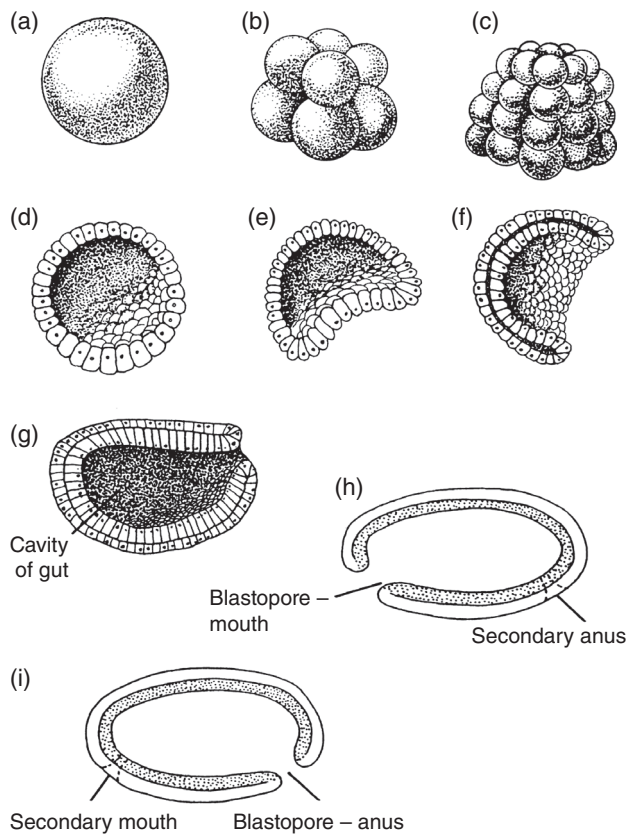
Figure 1.5 Embryonic development: (a–g) sequence of cell division in amphioxus, from the single-cell stage (a), through the blastula stage (d), to the gastrula stage (g). (h) Fate of the blastophore in protostomes, and (i) in deuterostomes. Source: Adapted from Jefferies (1986) and other sources.

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

1.3.2 Animal phylogenomics

Numerous zoologists have contributed over the years to disentangling the relationships of animals. All creatures from sponges and corals to crabs, clams, and birds, are animals, members of the clade Metazoa, diagnosed by a combination of feeding, being motile, lacking rigid cell walls, and passing through the blastula embryonic stage. These characteristics are not all exclusive, however. First, metazoans are distinguished from most plants and algae by being **heterotrophs**, meaning they feed on other organisms to acquire carbon, which is digested in an internal chamber

(gut), whereas plants and algae are able to fix carbon from the atmosphere or water. Fungi and many bacteria, however, are also heterotrophs. Secondly, metazoans are **motile**, meaning they use energy to move spontaneously and actively, at least at some stage in their lives (larval stages in 'fixed' forms such as sponges and corals can swim), although some bacteria and protists are also motile, moving by means of a flagellum. Thirdly, animals lack the rigid cell walls seen in plants, fungi, and algae, and fourthly most pass through the blastula embryonic stage (see Section 1.3.1).

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

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

The monophyly of Deuterostomia is confirmed both by morphology and by phylogenomics. All deuterostomes share the posterior blastopore that generally becomes the anus, as well as gill slits (present only in precursors of the echinoderms). Further, most molecular phylogenetic analyses indicate monophyly (e.g. Eernisse and Peterson, 2004; Swalla and Smith, 2008; Edgecombe *et al.*, 2011; Röttinger and Lowe, 2012; Cannon *et al.*, 2013), although this is queried in some studies (e.g. Delsuc *et al.*, 2006; Mallatt *et al.*, 2010). Some recent phylogenomic studies have suggested the addition of two further clades to Deuterostomia, the Xenoturbellida and the Acoelomorpha, simple worms with no through gut and a simple nervous system. However, these assignments are controversial (Edgecombe *et al.*, 2011; Röttinger and Lowe, 2012). Further, there has been some dispute over the interrelationships among these deuterostome taxa (see Box 1.1).
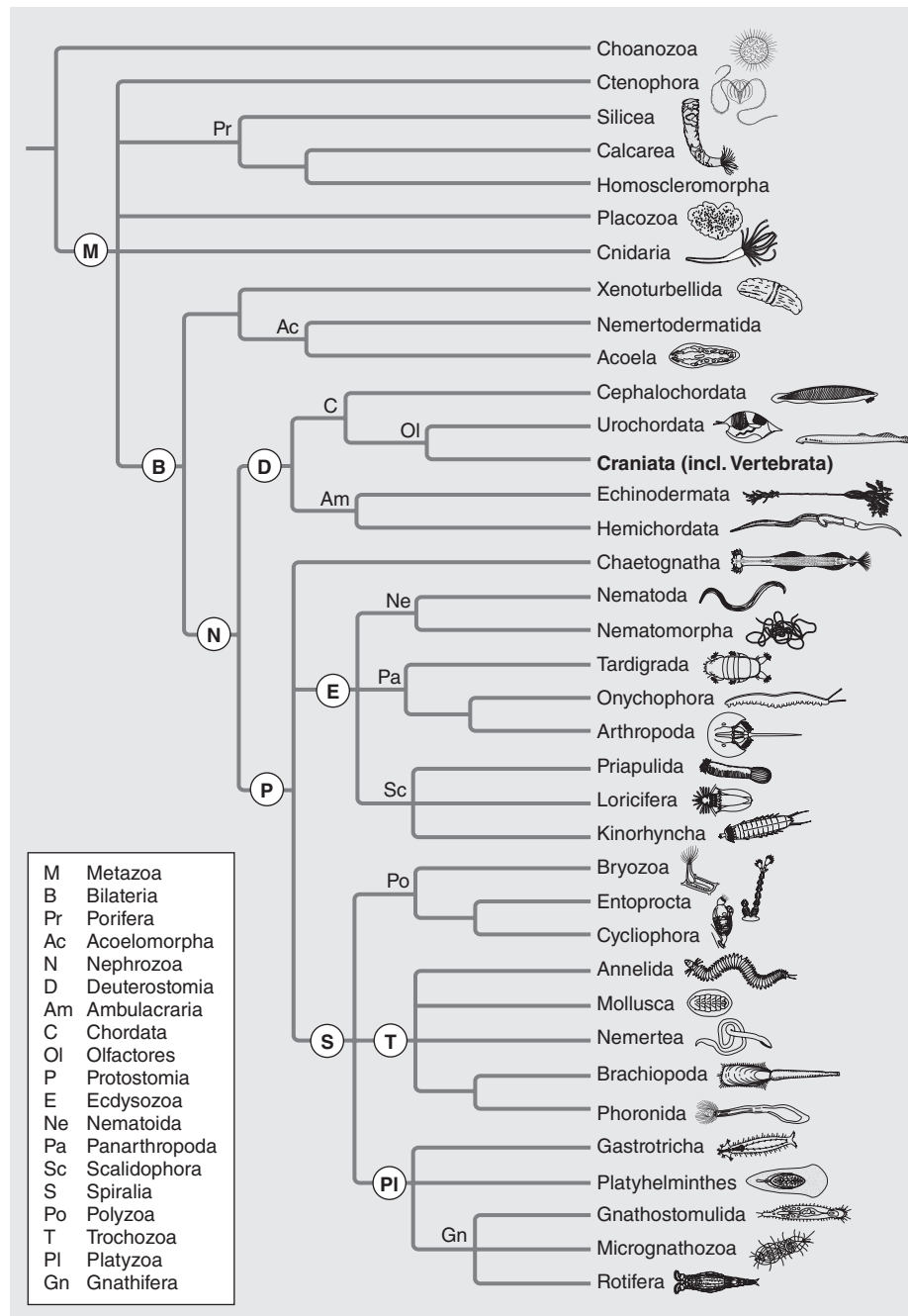
Figure 1.6 Relationships of the major phyla of animals, based on accumulated knowledge from anatomy and embryology, combined with current phylogenomic work. Source: G. Edgecombe, The Natural History Museum, London, UK. Reproduced with permission.

1.4 CHORDATE ORIGINS

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

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

BOX 1.2   THE CHENGJIANG BIOTA

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

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

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

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

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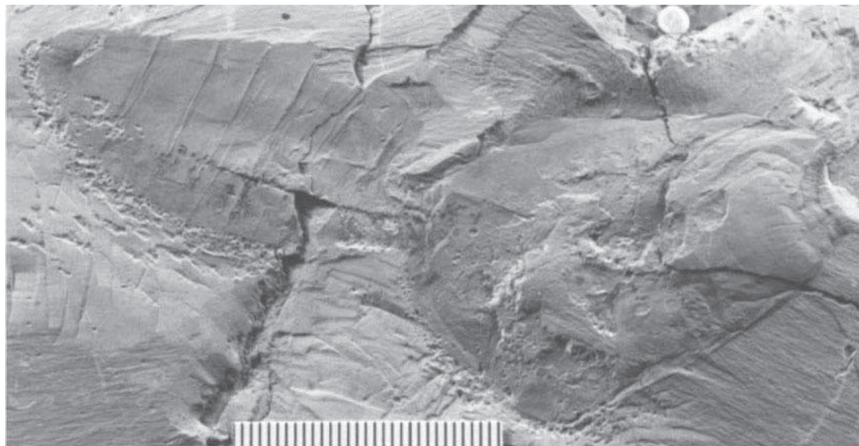
(b)
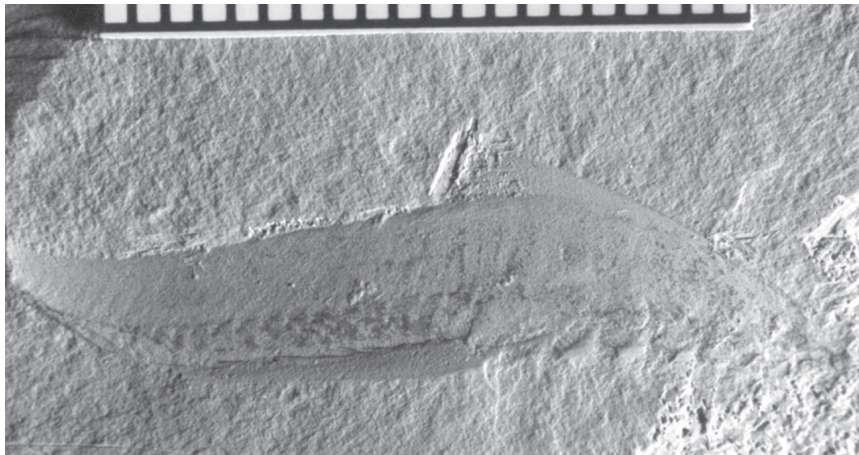
Typical Chengjiang fossils, the vetulicolian *Xidazoon* (a), facing left, and the basal vertebrate *Myllokunmingia* (b), facing right. Scale bars in millimetres. Compare with interpretive drawings in Figures 1.7 (b) and 3.1(a). Source: D. Shu, Northwest University, Xi'an, China. Reproduced with permission.

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

1.4.1 Diverse early chordates

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

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

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

1.4.2 Vetulicolians and yunnanozoons

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

The vetulicolians were regarded first as unusual arthropods, and then as deuterostomes. In their review and phylogenetic analysis, Aldridge *et al.* (2007) were unable to determine whether vetulicolians were arthropods, deuterostomes, or even kinorhynchs, a clade of segmented ecdysozoans close to priapulids. Most recent authors, however, assign vetulicolians to Deuterostomia, and they have been accorded three positions (Figure 1.8): as basal deuterostomes, as urochordates or as basal chordates (Gee, 2001). Evidence that vetulicolians are deuterostomes are the gill slits and a possible endostyle, although the latter identification has been questioned. They were interpreted as basal deuterostomes by Shu *et al.* (2001, 2010) because they apparently lack an atrium, the internal chamber in cephalochordates and tunicates into which the gill slits and anus open. In vetulicolians, the intestine terminates at the end of the body, and the gill slits presumably opened directly to the outside through openings in the external body wall. Vinther *et al.* (2011) confirmed this, based on new specimens from Greenland that show the lateral pouches that appear to be homologues of gill slits, a large sediment-filled atrium (in opposition to the interpretation by Shu *et al.* (2010)), which they regard as possibly a character of all deuterostomes and not just urochordates, and possible lateral flexure of the tail. Their terminal anus, if the gut is correctly interpreted, means that vetulicolians lack a postanal tail, and so they cannot be regarded as stem-group chordates. Ou *et al.* (2012) confirm this view with their observations of the lateral gill slits in new Chinese material. Others had earlier assigned vetulicolians to Urochordata because of the general resemblance in the bulbous streamlined body shape, as well as the thin external tunic, and the regularly spaced transverse
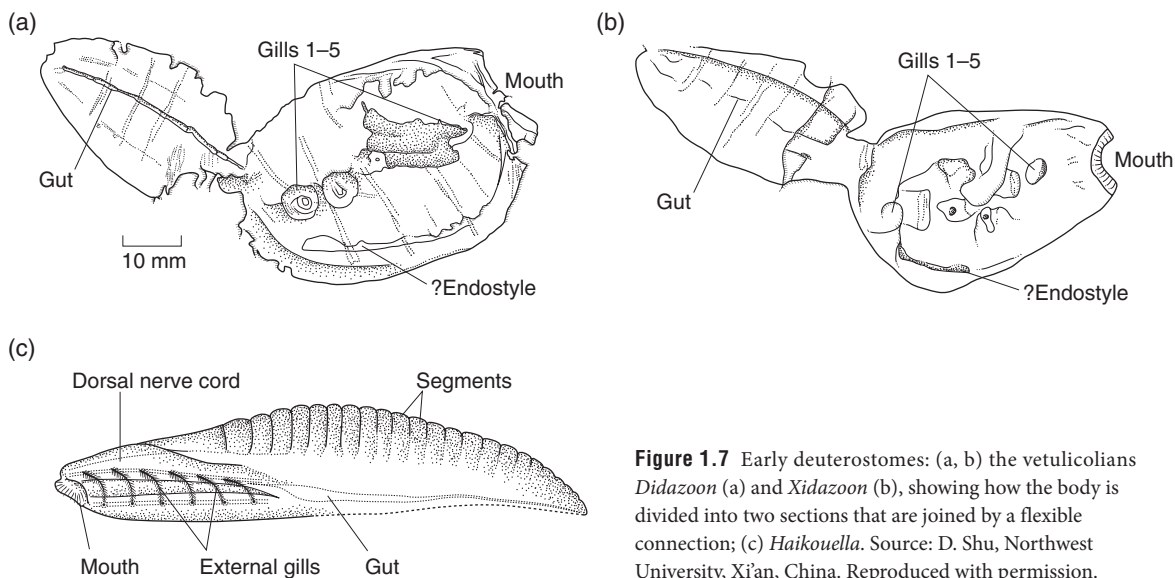
Figure 1.7 Early deuterostomes: (a, b) the vetulicolians *Didazoon* (a) and *Xidazoon* (b), showing how the body is divided into two sections that are joined by a flexible connection; (c) *Haikouella*. Source: D. Shu, Northwest University, Xi'an, China. Reproduced with permission.
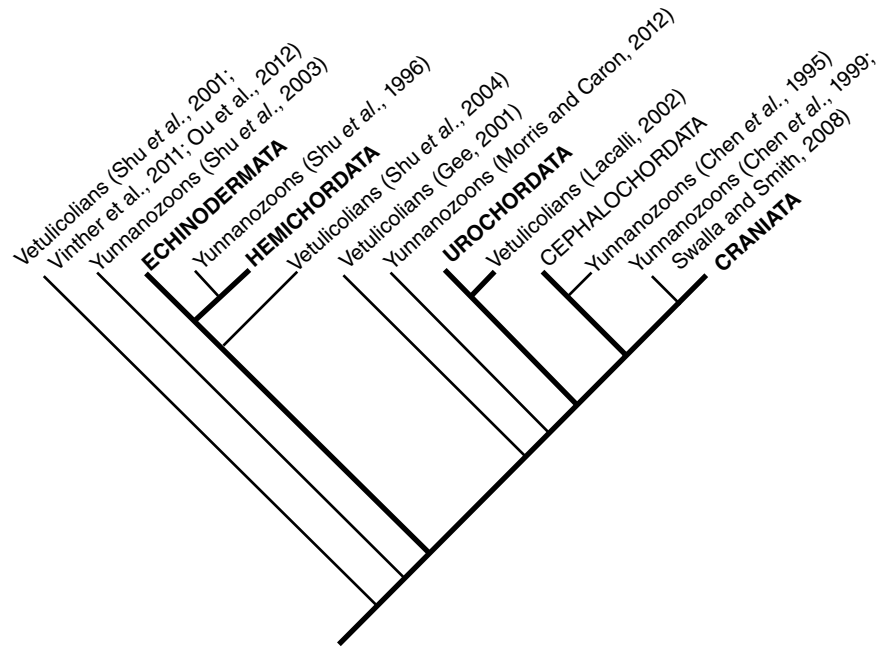
Figure 1.8 Phylogenetic tree of the extant deuterostomes, with suggested locations of the major fossil groups. Source: Adapted from various sources.

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

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

Haikouella and *Yunnanozoon* are 25–40 mm long, and preserved as flattened bluish-grey to black films on the rock. Chen *et al.* (1995) were able to see a notochord, a filter-feeding pharynx with an endostyle, segmented musculature, and branchial arches, all chordate characters. Chen *et al.* (1999) and Mallatt and Chen (2003) went further, identifying an enlarged, possibly three-part, brain and paired lateral eyes in *Haikouella*, hence indicating it might have had a distinctive, enlarged head, a key feature of vertebrates. Shu *et al.* (1996) argued, however, that there is no notochord, and that this tubular structure is actually the gut. In addition, they

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

suggested that the segmented musculature was wrongly identified. In contrast, they claimed to see key hemichordate features in *Yunnanozoon*, and especially that the body is divided into three parts from front to back, a proboscis, a collar, and a trunk that is divided into a branchial and a gut region, just as in the living acorn worm (see Figure 1.4(c)). Shu *et al.* (2003, 2010) subsequently noted similarities between the yunnanozoons and the vetulicolians, and moved them down from the hemichordates to a basal position among deuterostomes (Figure 1.8): they could see no evidence of a notochord, segmented muscles, a large brain, lateral eyes, or any of the other chordate features previously reported.

The final early chordate to consider is *Pikaia* from the Burgess Shale in Canada, named in 1911 as an annelid, but subsequently widely regarded as a basal chordate or even basal vertebrate (Figure 1.9). In a thorough redescription of 114 specimens, Conway Morris and Caron (2012) highlight its chordate characteristics: a laterally compressed, hydrodynamic body with about 100 myomeres, a thin dorsal fin, a small bilobed head with tentacles but no eyes, possible pharyngeal pores, a pharyngeal cavity, an almost terminal mouth, a probable terminal anus (and hence no postanal tail), a dorsal nerve cord, a possible notochord, and a blood vascular system. As with the yunnanozoons, however, determining the phylogenetic

position of *Pikaia* is problematic. It is a chordate because of the sigmoidal (S-curved) myomeres and the putative notochord. Some would classify it as a chordate, or even a vertebrate, on the basis of the head and putative sensory organs, but Conway Morris and Caron (2012) see it as allied with yunnanozoons, at the base of Chordata (see Figure 1.8). In a revision of the new morphological data, Mallatt and Holland (2013) cannot resolve the phylogenetic position of *Pikaia*, but find it located higher in the tree, either as sister group to Chordata or to Vertebrata.

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

BOX 1.3   ROTTING BIAS

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

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

The initial suite of characters that disappeared in the decaying amphioxus specimens were those diagnostic of Cephalochordata, and the myomeres and notochord are the most general chordate characters. Normal decay processes then favour preservation of primitive characters, and phylogenetic analysis of chordate fossils will position the fossils in a more basal position than is correct. These decay experiments strongly suggest that the fossil record of non-vertebrate chordates is affected by a systematic bias of stem-ward slippage down the cladogram, and that some Cambrian chordate fossils are placed too deep in the phylogeny. These experiments partly explain why palaeontologists have had such a hard time in finding the diagnostic characters that would help them to identify the true phylogenetic positions of vetulicolians, yunnanozoons, *Pikaia*, and early vertebrates such as *Haikouichthys* (see Chapter 3).
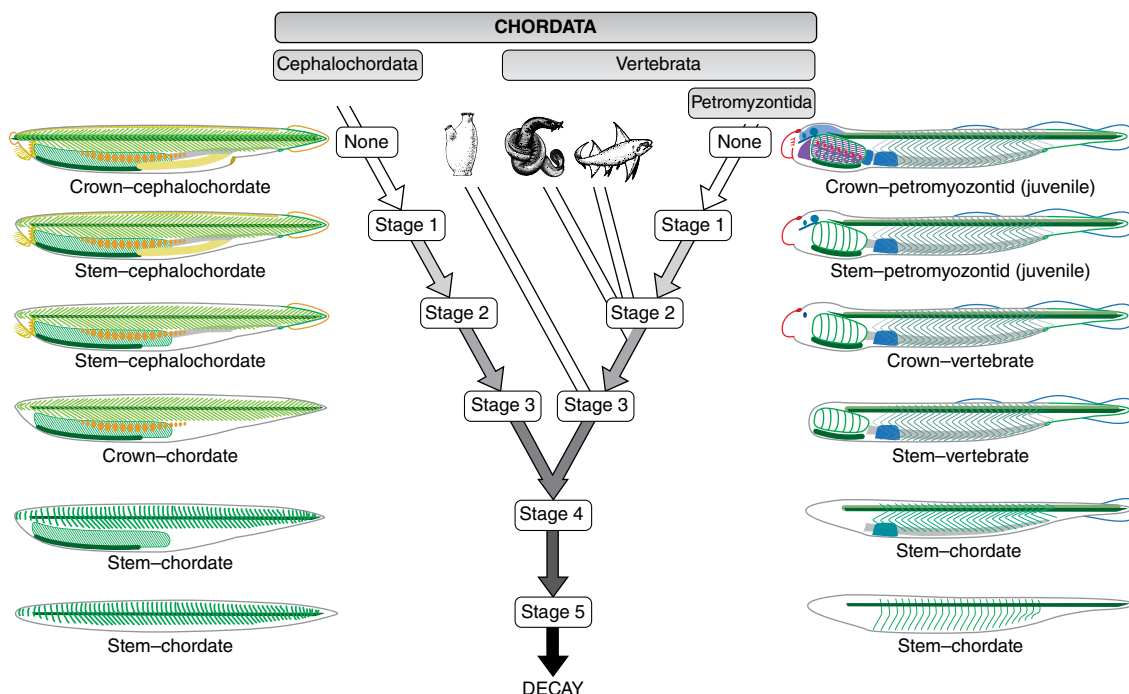
Morphological decay stages of amphioxus (left) and larval lamprey (right) and the phylogenetic position of each stage if interpreted as a fossil. Rectangles on branches of the phylogeny are morphological characters, their shade indicating the order of loss (white, early; dark, late). As each organism decays, its phylogenetic position moves down the tree; this is evidence for taphonomic bias in the identification of fossil chordates. Characters are colour coded according to the hierarchical level for which they are informative (green, chordate; yellow, cephalochordate; blue, vertebrate; purple, cyclostome and vertebrate; red, petromyzontid – see Colour plate 1.1). Source: Sansom *et al.* (2010). Reproduced with permission from Nature Publishing Group.

1.4.3 Development and vertebrate origins

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

shared genes, and recent work on amphioxus has been remarkably informative (see Box 1.4).

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

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BOX 1.4   GENES AND BRAINS

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

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

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

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

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

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

PPR Pineal photoreceptors
     in lamellar body or epiphysis
SRF Source of Reissner's fibre
PMC Anterior limit of primary
     motor centre
LB   Lamellar body
E   Epiphysis
OT   Optic tectum?
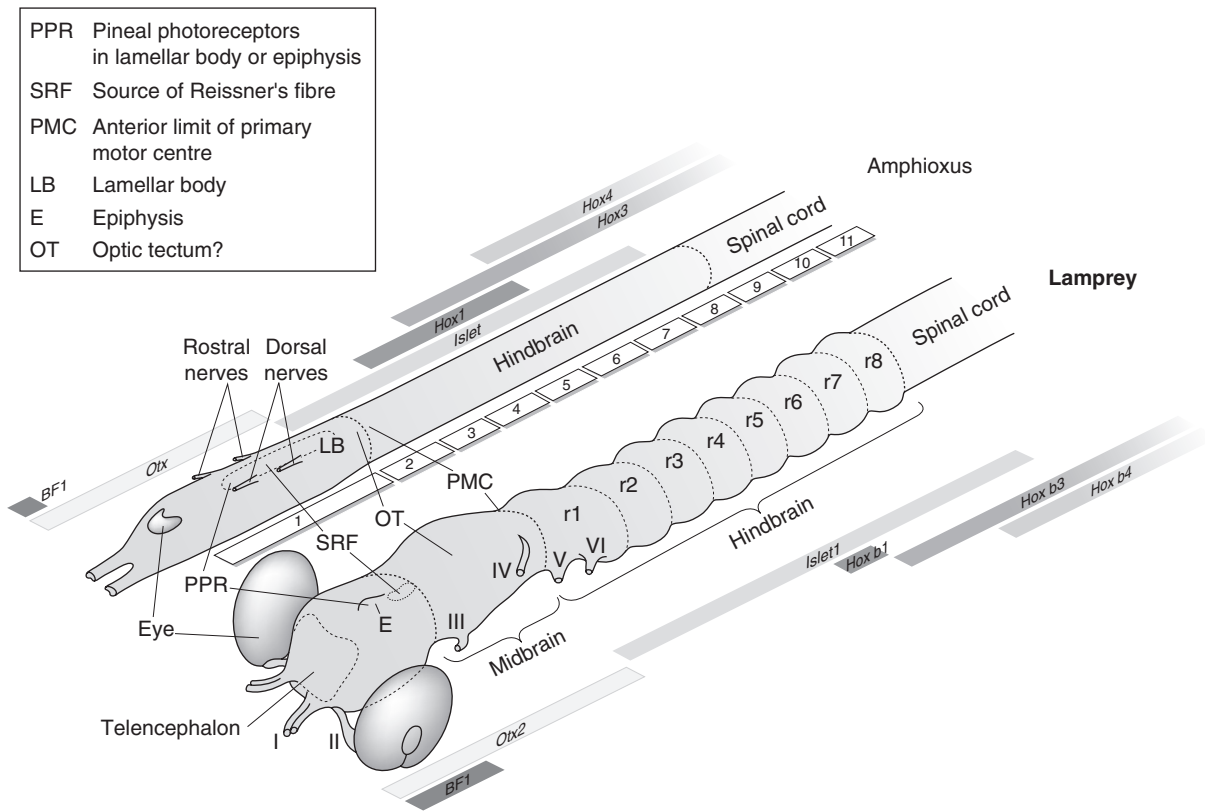
The front part of the developing nerve cords of amphioxus (left) and a vertebrate (right), viewed from above. In amphioxus, the cerebral vesicle, the brain region, is stippled and the numbered rectangles represent the muscular segmentation. Key features of the head and brain of the vertebrate are labelled, and possible homologies with amphioxus are indicated. The zones of expression of developmental genes are indicated to the side, confirming that amphioxus has morphological homologues of the three-part vertebrate brain (forebrain, midbrain, hindbrain), and a segmental structure to the hindbrain, which is composed of eight segments in each case. Source: Adapted from Holland and Chen (200) and Holland and Holland (1999).

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

1.5 VERTEBRATES AND THE HEAD

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

The basic vertebrate body plan (Figure 1.10) shows all of the chordate characters so far described – notochord, dorsal nerve cord, pharyngeal gill slits, postanal tail, myomeres, and

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

1.6 FURTHER READING

You can read more about the palaeontological, embryological, and molecular debates concerning the origins of chordates and vertebrates in Gee (1996). Jefferies (1986) provides the fullest
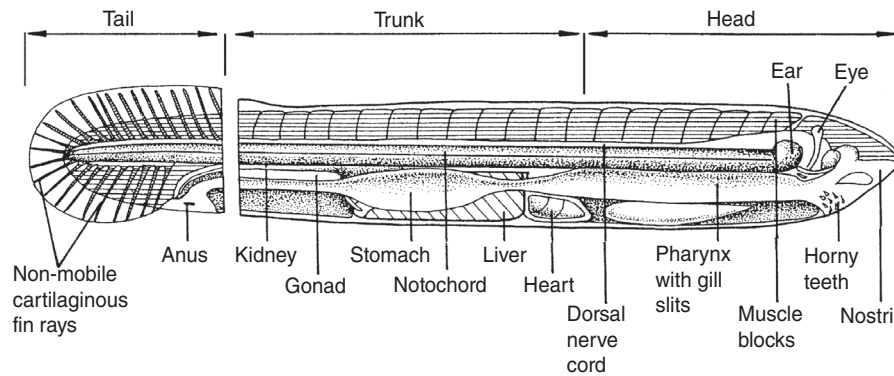
Figure 1.10 The hypothetical 'basic' vertebrate body plan, shown in longitudinal section. Source: Adapted from Jefferies (1986).

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

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

QUESTIONS FOR FUTURE RESEARCH

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

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CHAPTER 2
How to Study Fossil Vertebrates
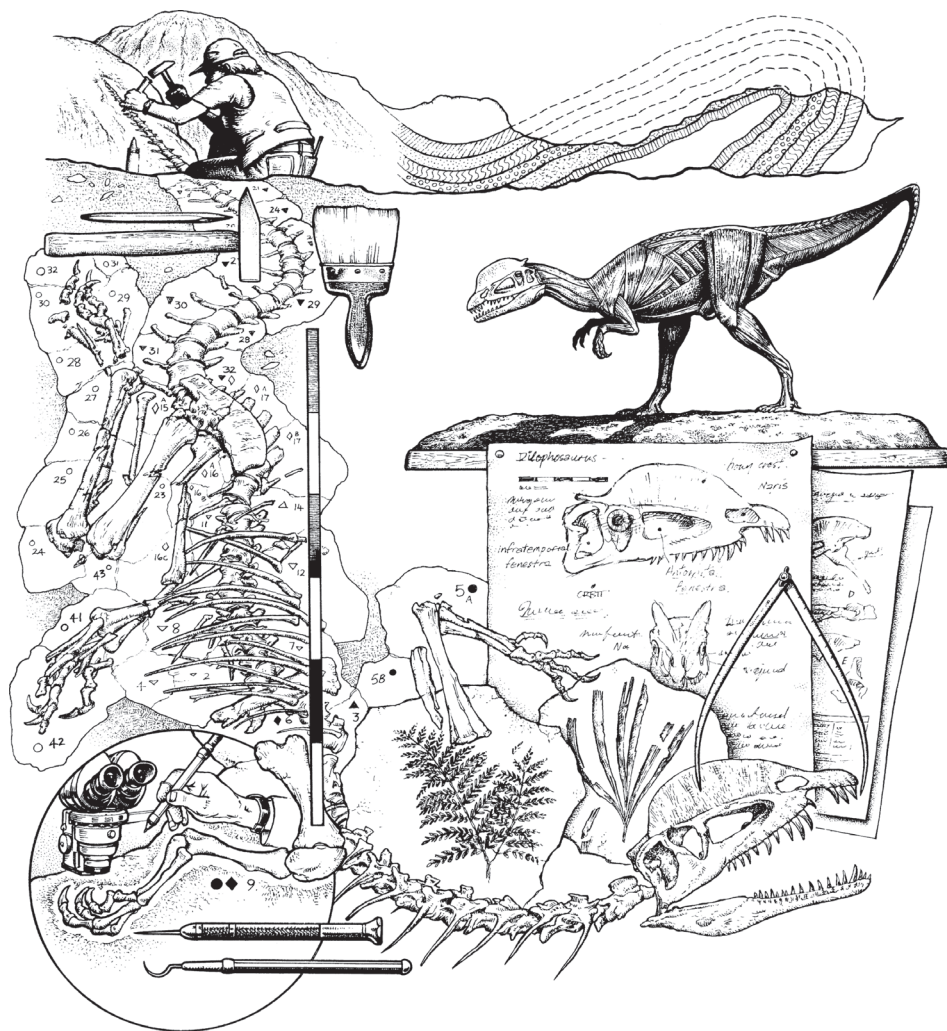
KEY QUESTIONS IN THIS CHAPTER

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

INTRODUCTION

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

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

2.1 DIGGING UP BONES

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

2.1.1 Collecting fossil vertebrates

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

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

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

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

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

(a)

(b)

(c)

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

(a)

(b)

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

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

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

Many small fossil vertebrates are found only as isolated bones and teeth. In certain sedimentary settings, skeletons are tumbled together and broken up. The bones and teeth may be concentrated at particular levels, often in small channel-like

pockets. In cases such as these, palaeontologists dig out the whole bone-bearing layer, and they may sieve it on the spot, picking out the identifiable bones and teeth, or they may transport sacks of bone-rich sediment back to the laboratory for processing.

2.1.2 Preparation and conservation of bones

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

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

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

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

(a)

(b)

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

2.1.3 Display and study

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

In studying a new fossil vertebrate, the palaeontologist tries to reconstruct the skull and the rest of the skeleton in as much detail as possible. This may be a difficult job. If there is a relatively complete and undamaged specimen, the fit of the bones may be tested directly. It may be possible to slot together the bones of the skull like a three-dimensional jigsaw, and to test the stance of the limbs, to some extent, by fitting the bones together end to end. More normally, the palaeontologist must use infor-

mation from several specimens in order to reconstruct the original appearance of an undamaged skeleton. In matching up bones, allowances must be made for differently sized animals, and in difficult cases, scale models of missing bones may be made. Extensive reconstruction is possible because vertebrate skeletons are bilaterally symmetrical, and because many bones, such as vertebrae and ribs, occur in repeating or gradually changing series, and so it is not necessary to find every bone in order to make a reasonably accurate reconstruction of a skeleton.

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

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

(a)

(b)

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

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

2.2 PUBLICATION AND PROFESSIONALISM

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

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

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

2.2.1 The scientific literature

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

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

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

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

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

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

There are three kinds of scientific literature, primary, secondary, and tertiary. The **primary** literature consists of all the

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

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

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

2.2.2 How to write a scientific paper

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

2.2.3 Careers in vertebrate palaeontology

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

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

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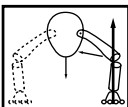
BOX 2.1   VERTEBRATE PALAEONTOLOGY CAREERS

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

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

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

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

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

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

(b)

(a)

(c)

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

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

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

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

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

2.3 GEOLOGY AND FOSSIL VERTEBRATES

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

2.3.1 Taphonomy

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

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

At the same time as the carcass is scavenged, it also begins to decay, a set of processes in which microbes transform and

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

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

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

After transport, the specimen may be buried. Further damage may then occur, such as compaction by the weight of
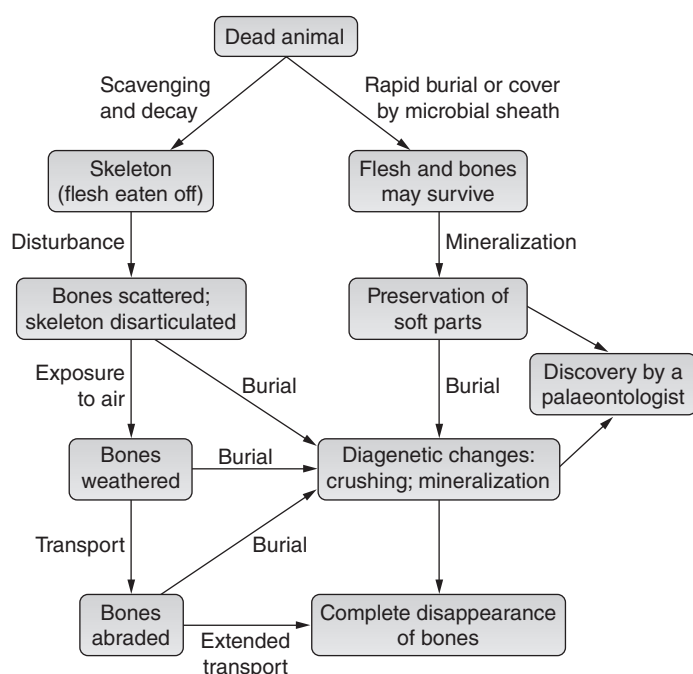
Figure 2.5 Taphonomic processes affecting a fossil vertebrate, from death, through scavenging and decay, and through transport and burial, to eventual discovery by a palaeontologist. Source: M.J. Benton, University of Bristol, UK. Reproduced with permission.

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

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

2.3.2 Continental drift

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

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

BOX 2.2   GEOLOGICAL TIME

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

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

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

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

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

The geological time scale, showing the main divisions of geological time, and current numerical age dates, based on the International Geological Times Scale 2012. Source: Adapted from: http://www.stratigraphy.org/; https://engineering.purdue.edu/Stratigraphy/index.html; http://www.geosociety.org/science/timescale/timescl.pdf; http://www.nhm2.uio.no/norges/GTS_2012.pdf; http://www.geosociety.org/science/timescale/timescl.pdf.
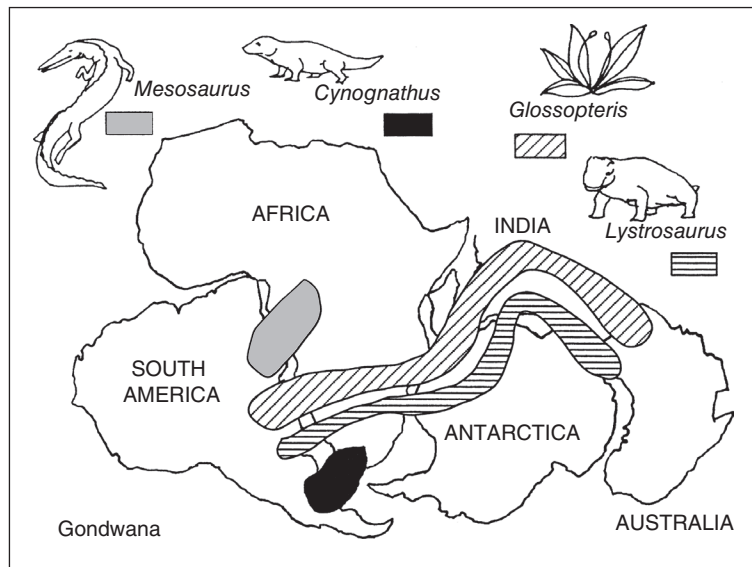
Figure 2.7 Reconstruction of Gondwana as it was from the Late Carboniferous to the Late Triassic, based on the work of Alfred Wegener, showing how this arrangement of continents makes sense of the distributions of Permian reptiles such as *Mesosaurus*, Permian plants such as *Glossopteris*, and Triassic reptiles such as *Lystrosaurus* and *Cynognathus*. Source: M.J. Benton, University of Bristol, UK. Reproduced with permission.

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

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

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

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

Continental drift is crucial in the history of the vertebrates. The geography of Earth has never been stable, and it seems that, through time, the continents have amalgamated and divided

several times. Most is known about the break-up of Pangaea since the Triassic, but it is possible to make good estimates of continental reconstructions for more ancient times. Continental drift has affected animal and plant distributions: biogeographic ranges are sundered at times, and brought together in unpredictable ways. Dinosaurs evolved in a world on one supercontinent, and they could move freely all over Pangaea. By the Cretaceous, however, their movements became restricted, and local, or **endemic**, faunas are found in South America, Africa, and India. During most of the Cenozoic, South America was an island, but 3 million years ago, the Isthmus of Panama was formed, and a great exchange of land animals took place, with profound effects both north and south (see Section 10.6.6).

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

2.3.3 Ancient climates

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

areas, and vegetation was sparse. Coral reefs ringed the continents, and exotic fishes swam in the shallow waters.

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

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

2.4 BIOLOGY AND FOSSIL VERTEBRATES

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

2.4.1 Functional morphology

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

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

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

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

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

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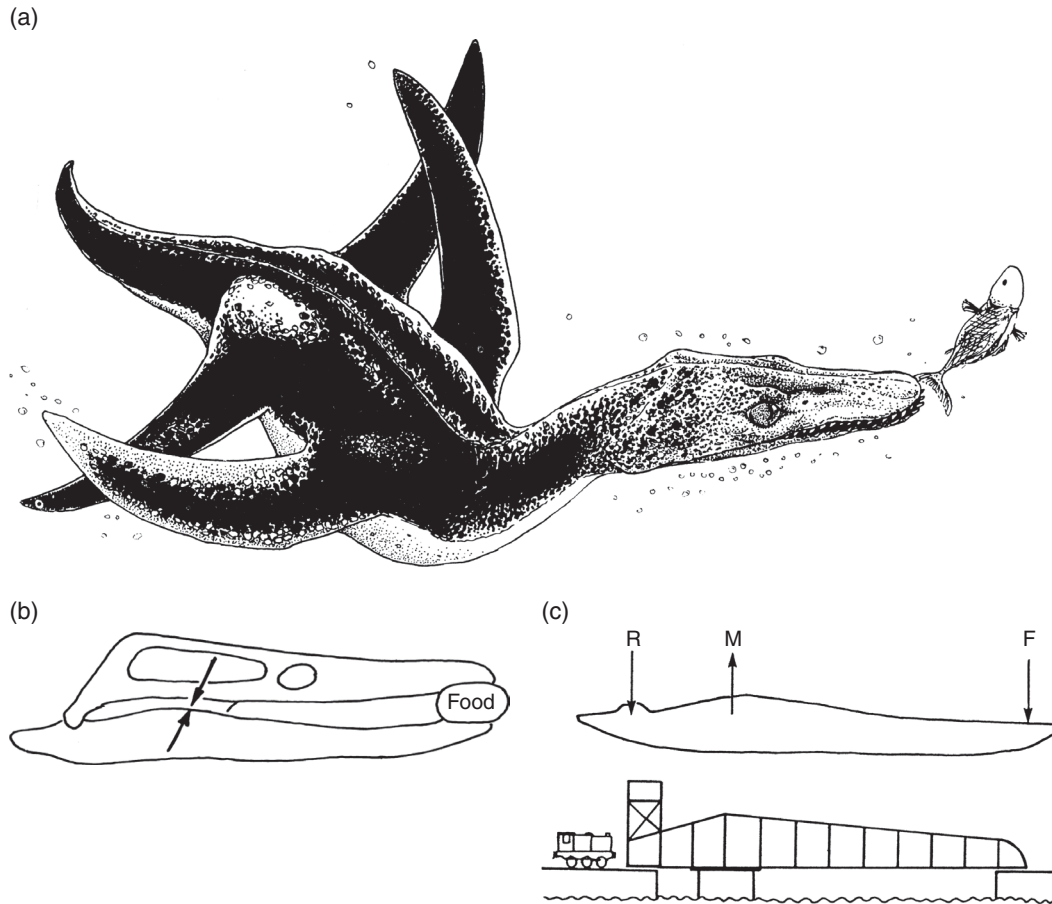
(a)

(b)

(c)

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

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

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

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

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

to the function of extinct organisms, and this is by testing engineering models.

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

2.4.2 Palaeoecology

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

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

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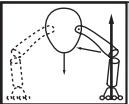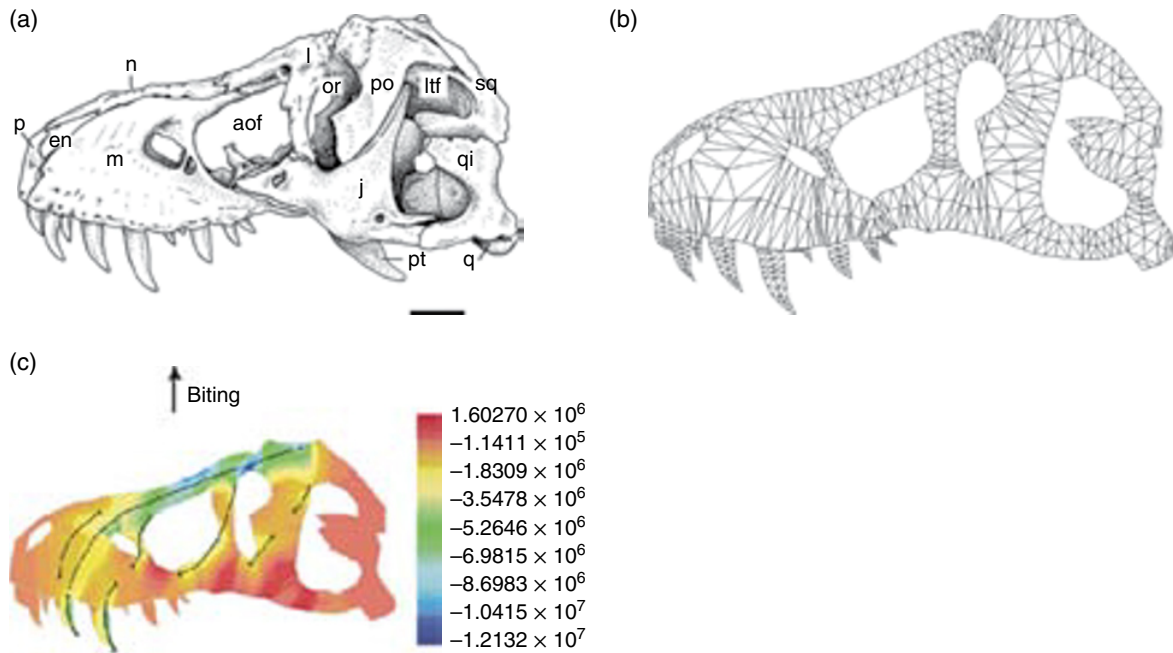

BOX 2.3   ENGINEERING THE SKULL OF *T. REX*

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

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

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

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

(a)

(b)

(c)

Biting

1.60270×10^6
-1.1411×10^5
-1.8309×10^6
-3.5478×10^6
-5.2646×10^6
-6.9815×10^6
-8.6983×10^6
-1.0415×10^7
-1.2132×10^7

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

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

2.5 DISCOVERING PHYLOGENY

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

originated at least 3500 million years ago, and that is probably when the common ancestor lived.

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

2.5.1 Cladistic analysis of morphological characters

Cladistic analysis of morphological characters is the main technique used to determine the relationships of living and fossil vertebrates. The result of a cladistic analysis is a **cladogram**, such as those in Figure 1.8. A cladogram is a branching diagram that links all the species, living and fossil, that are under

investigation, and the branching points, or **nodes**, mark points at which shared characters arose. A cladogram is not an evolutionary tree because there is no *absolute* time-scale, although the *relative* order of nodes is shown. The cladogram shows the closeness of relationship, or recency of a common ancestor shared by two species, by the arrangement of the groups – the closer they are to each other, the closer is the postulated relationship.

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

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

Character discovery and analysis is a complex and time-consuming business. The analyst studies the anatomy of all the organisms of interest in detail, identifying unique and shared characters. There are no objective rules about what is and is not a character. Some are fairly uncontroversial, such as the presence or absence of a particular element, such as the fused clavicles (=furcula/ wishbone) in birds and near-relatives: the fusion of two bones can probably be seen as a single event in evolution,

and so this feature is either present (coded 1) or absent (coded 0). Others may be harder to determine. For example, in looking at theropod dinosaurs and basal birds, some specimens have feathers and others do not. Experts debate whether to code feathers as a single character (feathers present or absent), or as many characters that describe feather anatomy in much more detail, so that full flight feathers are distinguished from other types of feather, such as wispy down 'hairs'. Character states (coded 0, 1, 2…) are listed in a **data matrix**, a table of species/ specimens versus characters. Well-established computer programs, such as TNT, PAUP, NONA, MacClade, and others, are used to process the data matrices and extract patterns of relationships that are expressed as trees. Relationship is determined by shared synapomorphies, and taxa are organized hierarchically to reflect a continuum from most to least proportions of shared synapomorphies.

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

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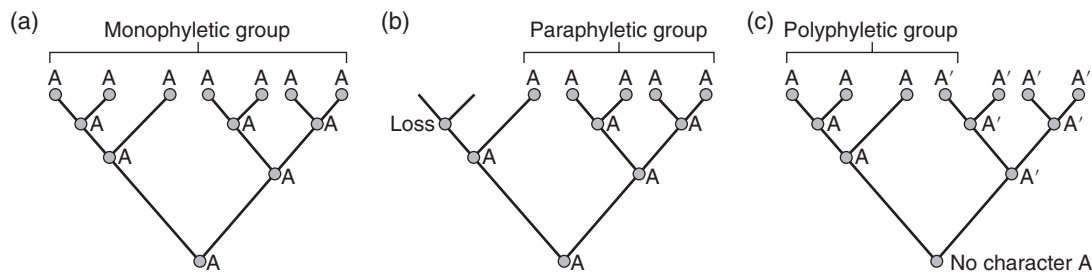

Figure 2.9 Cladograms showing: (a) a monophyletic group, (b) a paraphyletic group, and (c) a polyphyletic group, and the presence and absence of hypothetical characters A and A′ (character A′ is convergent on [very similar to] character A). In the monophyletic group (a), all species have character A,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