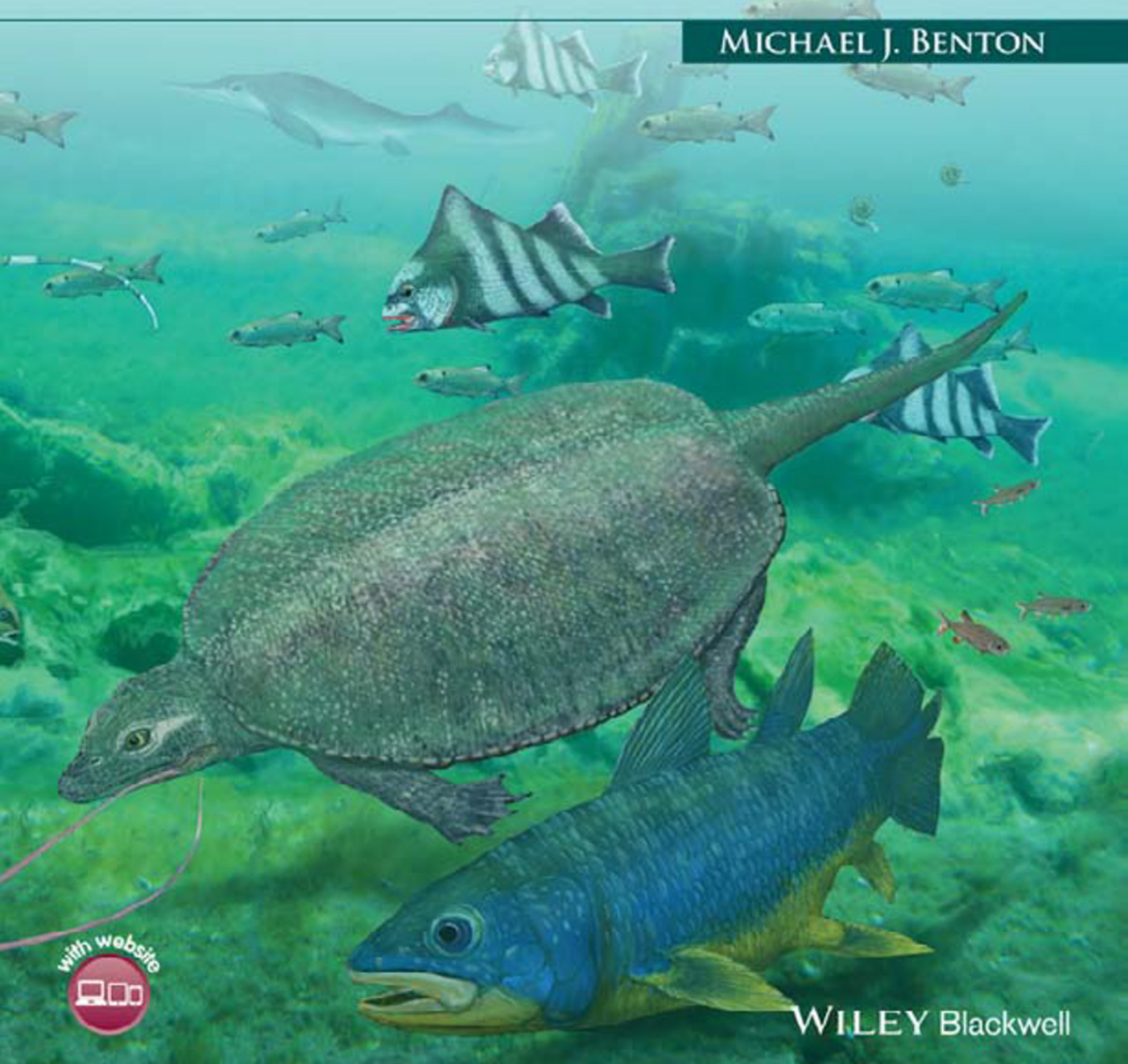


FOURTH EDITION



VERTEBRATE PALAEOONTOLOGY

MICHAEL J. BENTON



with website



WILEY Blackwell

VERTEBRATE PALAEOLOGY

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

VERTEBRATE PALAEOONTOLOGY

Fourth edition

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Chapter opening illustrations drawn by John Sibbick

WILEY Blackwell

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Cover image: Lobster lunch of Luoping; over a muddy seabed during the Middle Triassic (Anisian) 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 *Sinosauropsphargis 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 more so 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 Perfiles, Lleida), the second in Italian in 2000 (*Paleontologia dei Vertebrati*, Franco Lucisano Editore, Milano), and the third in German in 2007 (*Paläontologie der Wirbeltiere*, Dr Friedrich Pfeil, München). This is a measure

of the international appeal of vertebrate palaeontology and the demand from students and instructors for up-to-date information.

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

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

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

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

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

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

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

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

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Michael J. Benton

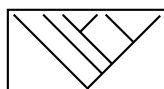
NOTE CONCERNING THE REFERENCES

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/>

†Deceased

List of Boxes



TREE OF LIFE BOXES

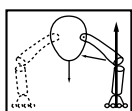
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About the Companion Website

This book is accompanied by a companion website:

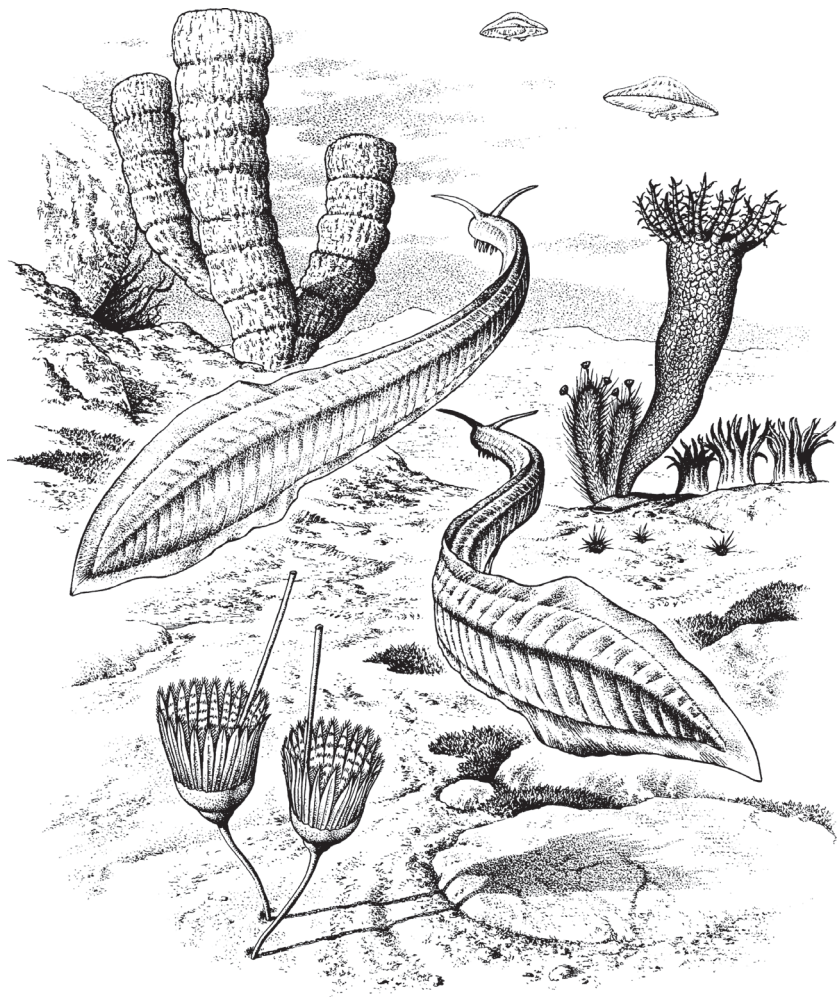
www.wiley.com/go/benton/vertebratepalaeontology

The website includes:

- PowerPoints of all figures from the book for downloading

CHAPTER 1

Vertebrates Originate



KEY QUESTIONS IN THIS CHAPTER

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

INTRODUCTION

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

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

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

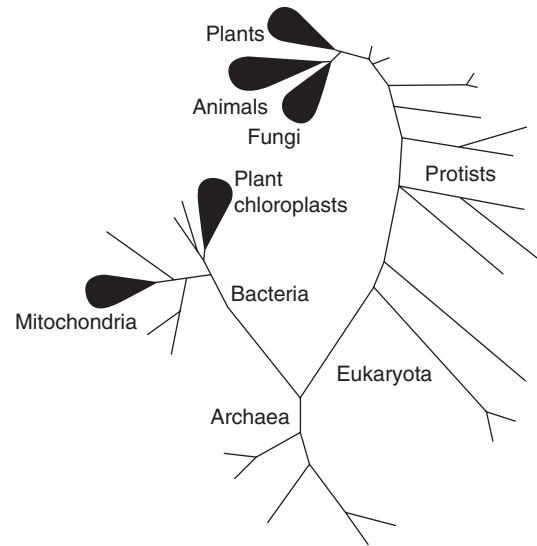


Figure 1.1 The ‘Tree of Life’, the commonly accepted view of the relationships of all organisms. Note the location of ‘Animals’, a minor twig in the tree, close to plants and Fungi. Source: Adapted from various sources.

(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

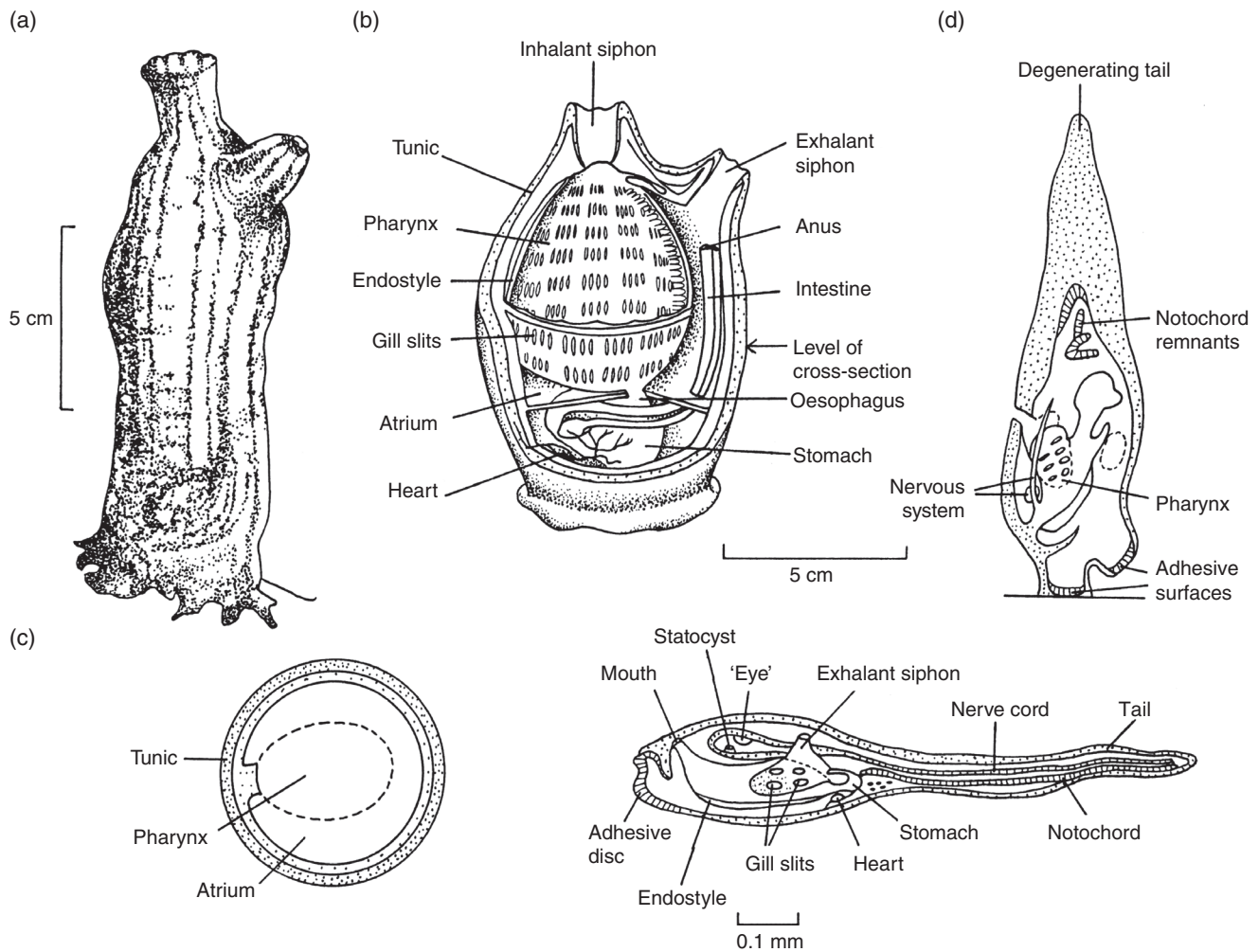


Figure 1.2 The sea squirts: (a) *Ciona*, external view; (b) internal anatomy and cross-section of an adult; (c) swimming larva; (d) metamorphosing form. Source: Adapted from Jefferies (1986) and other sources.

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

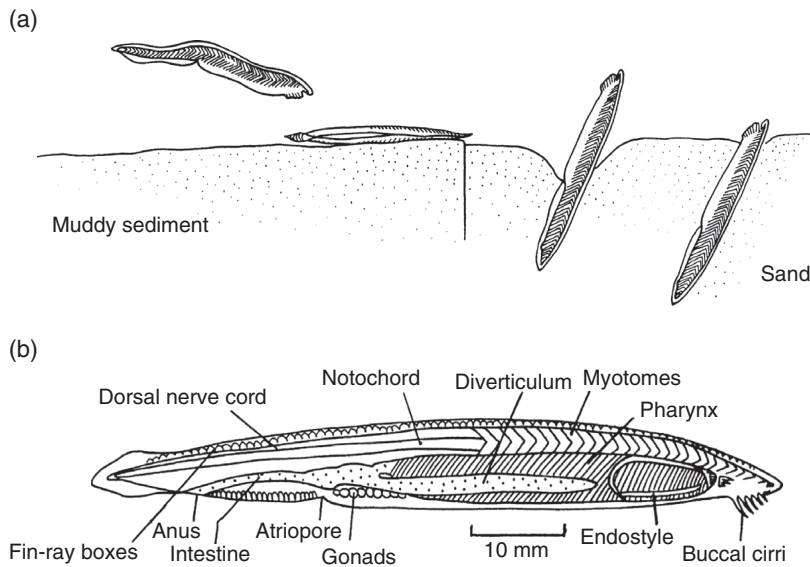


Figure 1.3 Amphioxus, a cephalochordate: (a) modes of life, including swimming and burrowing into sand for protection; (b) internal anatomy. Source: Adapted from Pough *et al.* (2012) and other sources.

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.

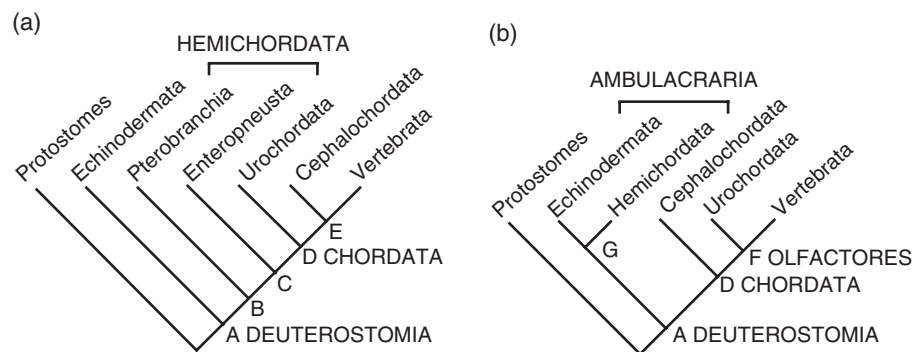
The hemichordates (Röttinger and Lowe, 2012) include two superficially very different kinds of marine animals. The first, the pterobranchs such as *Cephalodiscus* (Figure 1.4(a,b)), are small animals that live in loose colonies on the seabed in the southern hemisphere and in equatorial waters. *Cephalodiscus* 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, diploleula larva with neotroch.

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

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

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

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

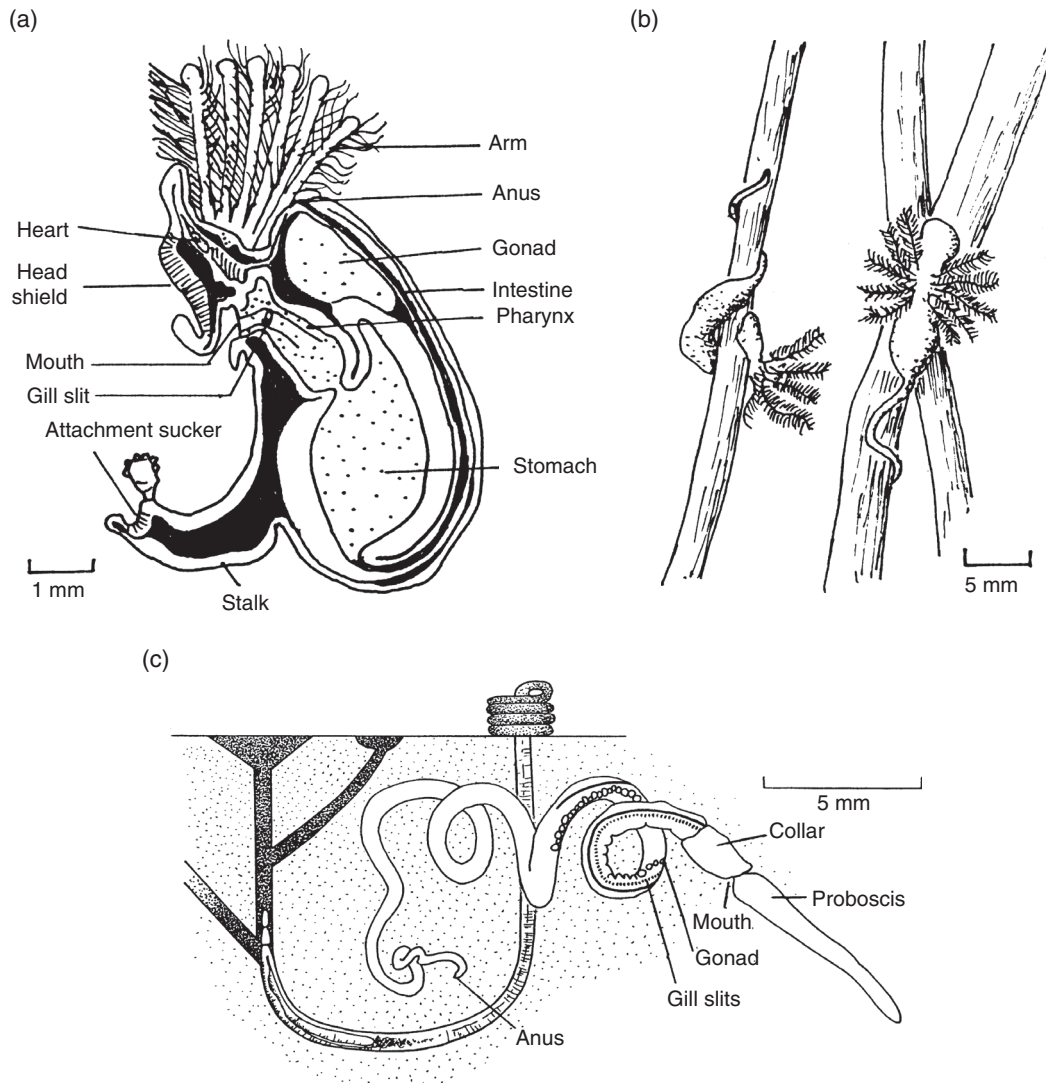


Figure 1.4 Typical hemichordates: (a) the pterobranch *Cephalodiscus*, internal anatomy and (b) mode of life; (c) the enteropneust *Saccoglossus*, mode of life and external anatomy. Source: Adapted from Jefferies (1986) and other sources.

1.3 DEUTEROSTOME RELATIONSHIPS

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

1.3.1 Embryology and the position of the anus

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

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

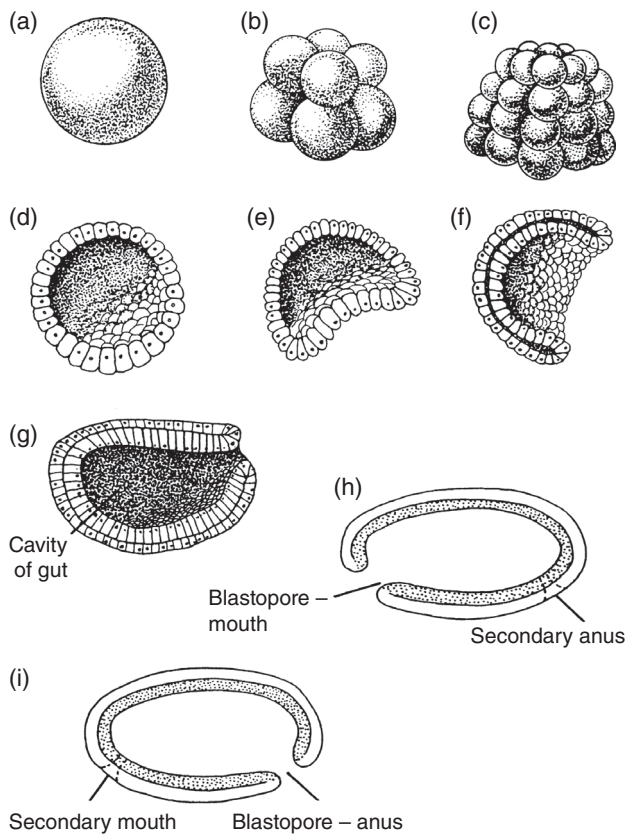


Figure 1.5 Embryonic development: (a–g) sequence of cell division in amphioxus, from the single-cell stage (a), through the blastula stage (d), to the gastrula stage (g). (h) Fate of the blastopore in protostomes, and (i) in deuterostomes. Source: Adapted from Jefferies (1986) and other sources.

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 spiralian 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).

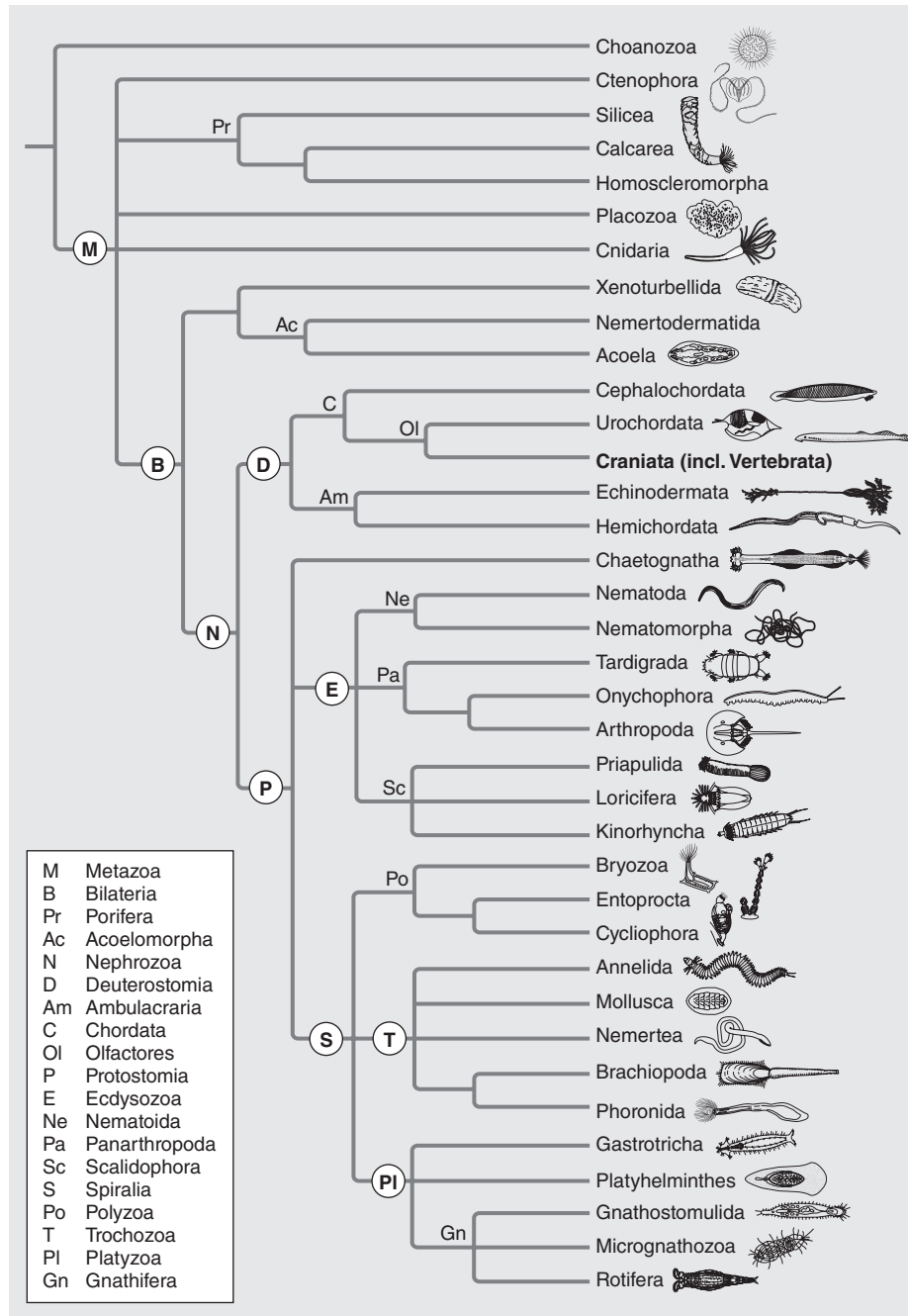


Figure 1.6 Relationships of the major phyla of animals, based on accumulated knowledge from anatomy and embryology, combined with current phylogenomic work. Source: G. Edgecombe, The Natural History Museum, London, UK. Reproduced with permission.

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

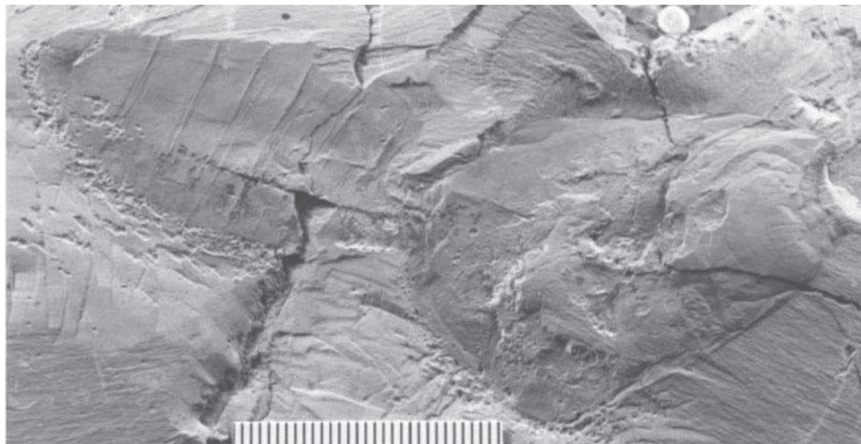
The Chengjiang biota from Yunnan Province, south-west China, is exciting because it is one of the oldest sources of exceptionally preserved organisms, falling early in the great Cambrian radiation of animals in the sea (Hou *et al.*, 2004; Shu *et al.*, 2010). The fossils come from different levels through 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.

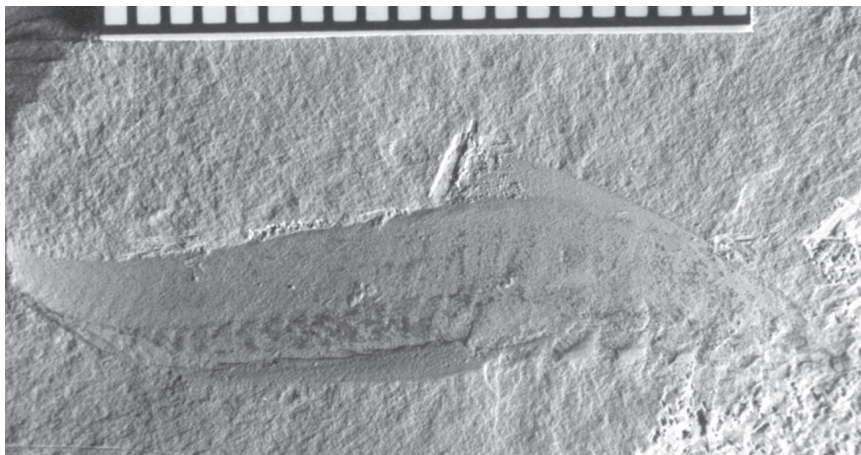
The Chengjiang beds are grey marine mudstones that preserve soft tissues of many animals in exquisite detail, some replaced by phosphate and others by pyrite. Some soft tissues survive as thin organic films. The grey sediment weathers on contact with the air to a light grey or yellow colour, and the 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/chngjiang/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 kinorhynch, 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

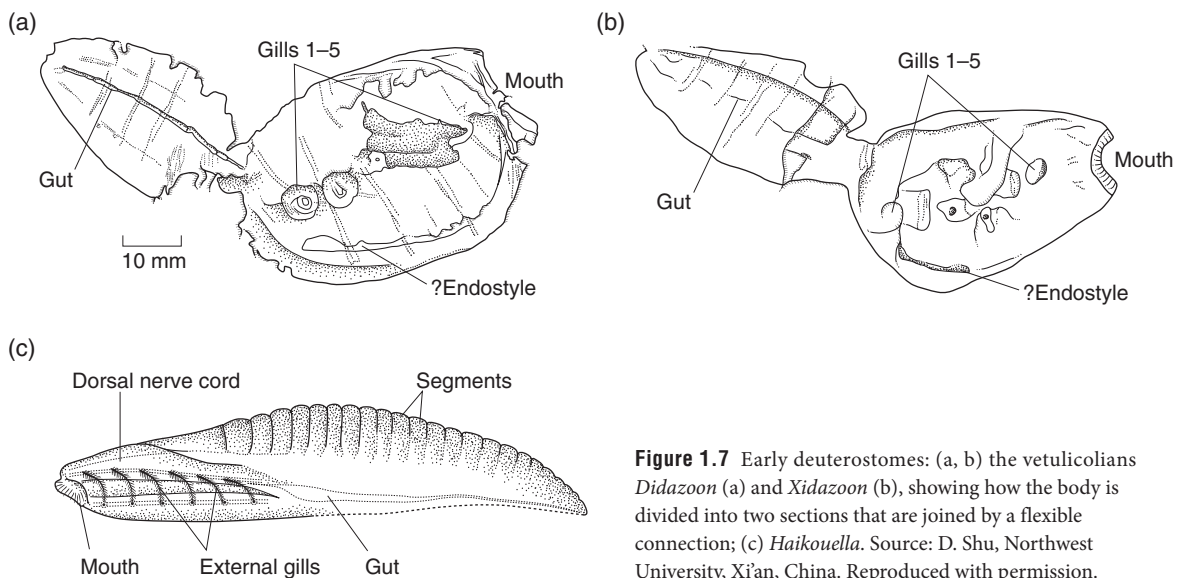


Figure 1.7 Early deuterostomes: (a, b) the vetulicolians *Didazoon* (a) and *Xidazoon* (b), showing how the body is divided into two sections that are joined by a flexible connection; (c) *Haikouella*. Source: D. Shu, Northwest University, Xi'an, China. Reproduced with permission.

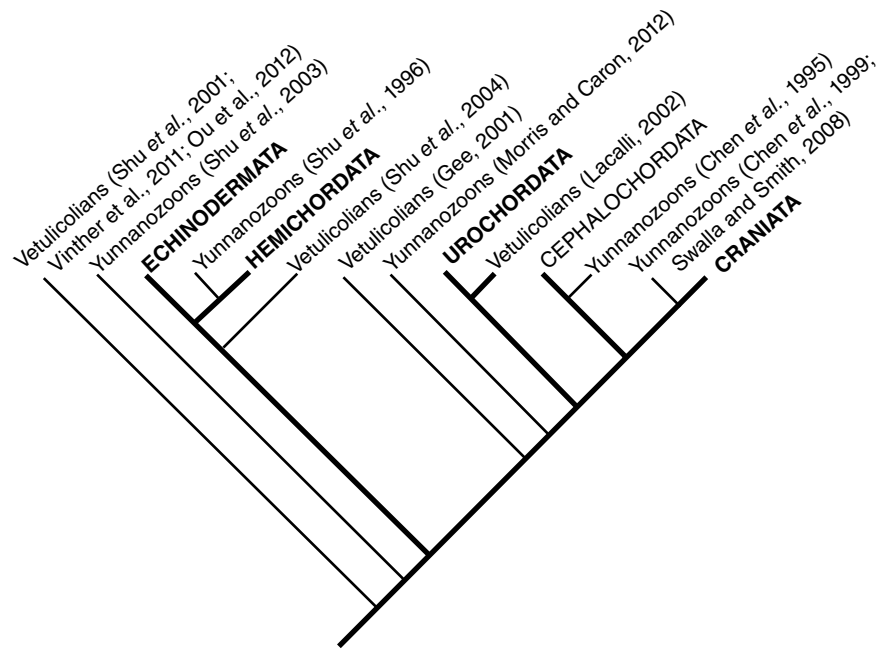


Figure 1.8 Phylogenetic tree of the extant deuterostomes, with suggested locations of the major fossil groups. Source: Adapted from various sources.

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.

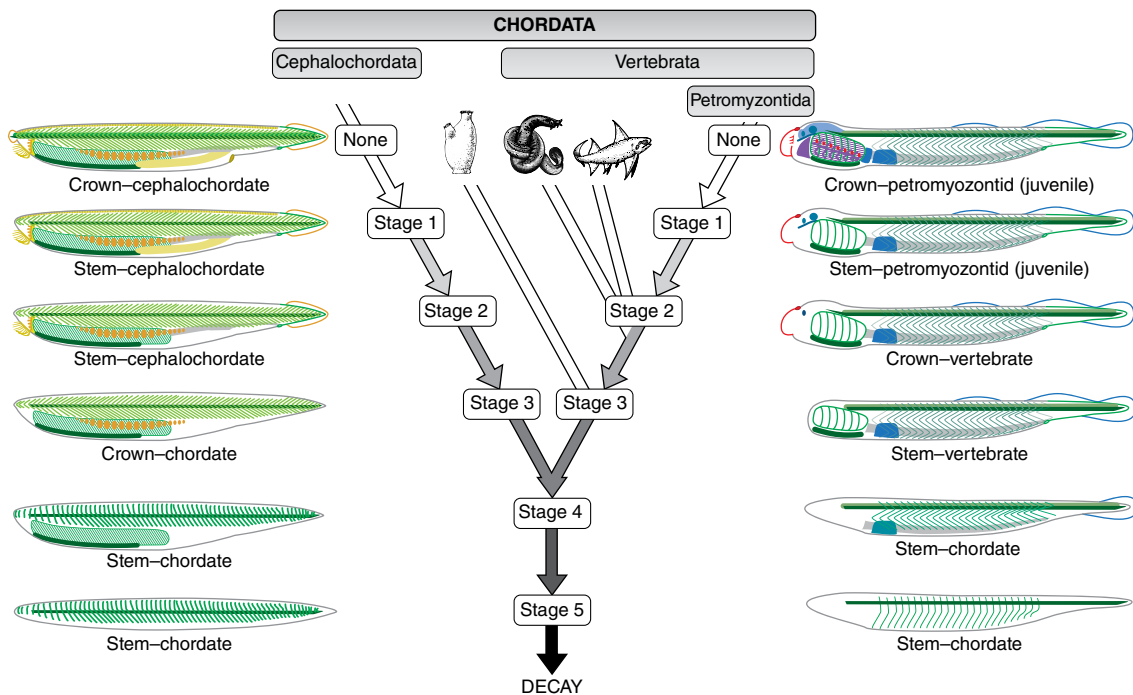
An important note of caution about the interpretation of *Pikaia* and the other early deuterostome fossils is that their phylogenetic placement depends on the identification of key diagnostic characters of the various subclades, such as ambulacrarians, cephalochordates, urochordates, and chordates, and 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 **pseudomorphosis**, the full development of the gonads and



BOX 1.4 GENES AND BRAINS

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

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

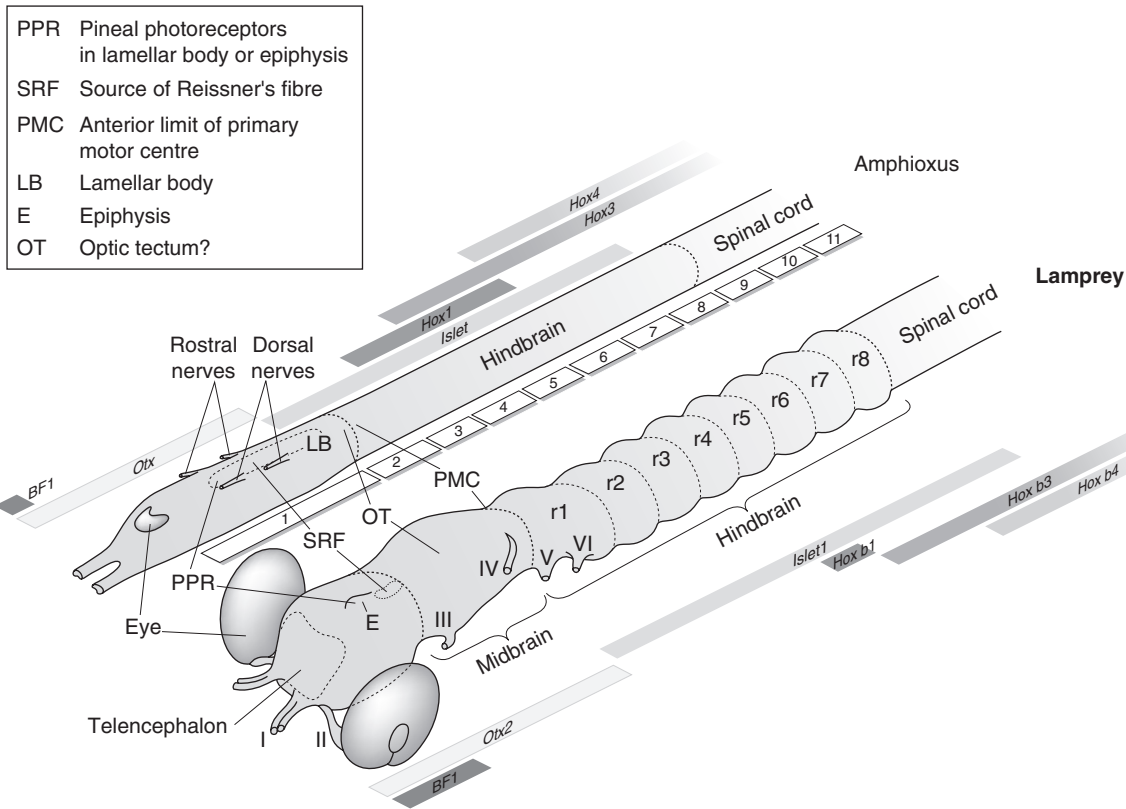
Of particular interest is that, despite over 500 Myr of independent evolution, the amphioxus genome contains a basic set of chordate genes involved in development and cell signalling, including a fifteenth *Hox* gene (Holland *et al.*, 2008b). It turns out that, in places where amphioxus has a single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

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

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

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

Continued



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

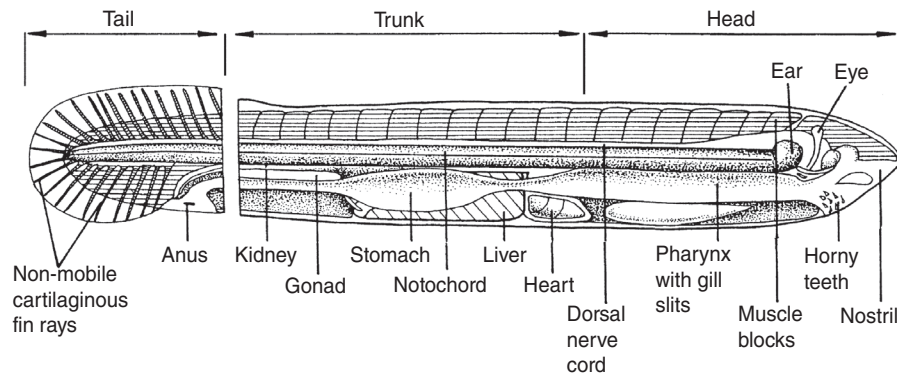


Figure 1.10 The hypothetical 'basic' vertebrate body plan, shown in longitudinal section. Source: Adapted from Jefferies (1986).

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). Waegle *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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