CHAPTER 1
Vertebrate Origin

INTRODUCTION

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

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

Looked at more widely, vertebrates are a minor twig on the 'Universal Tree of Life' (Figure 1.1). Molecular studies through the 1990s (e.g. Woese, 2000; Wolf *et al.*, 2002) showed that previous conceptions of the tree
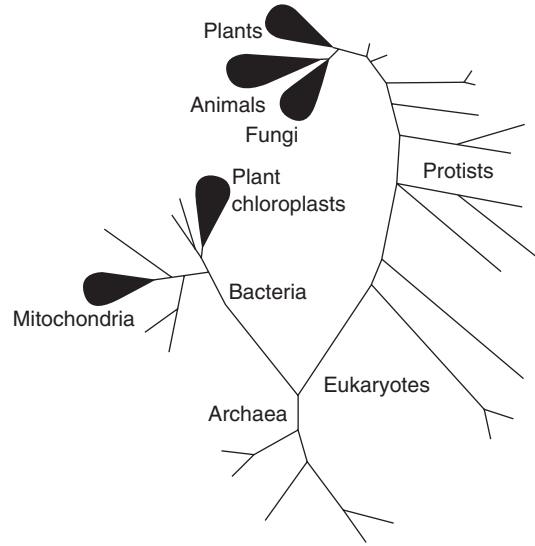

Fig. 1.1 The 'Universal Tree of Life', the commonly accepted view of the relationships of all organisms. Note the location of 'Animals', a minor twig in the tree, close to plants and Fungi. (Based on various sources.)

were wrong, and that the fundamental splits in the tree of life were all among Bacteria, separating the two major groups Bacteria and Archaea. The familiar plants, animals and fungi are part of Eukaryotes, the major group characterized by complex cells with a nucleus, relative late-comers in the broad scheme of things.

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

The purpose of this chapter is to explore the various lines of evidence that can be used to reconstruct the story of the origin of the vertebrates: the study of modern animals that are vertebrate-like in some features, the study of molecular relationships, and fossils.
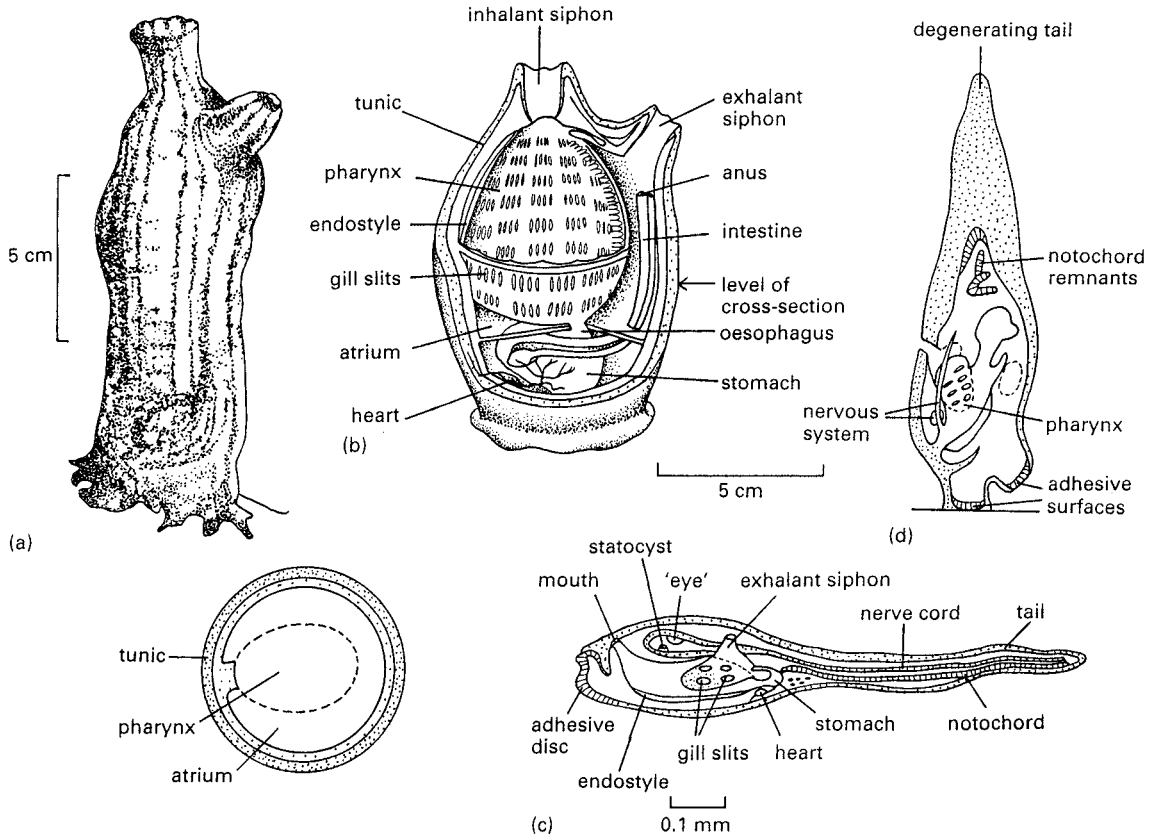
Fig. 1.2 The sea squirts: (a) *Ciona*, external view; (b) internal anatomy and cross-section of an adult; (c) swimming larva; (d) metamorphosing form. (Modified from Jefferies, 1986 and other sources.)

1.1 SEA SQUIRTS AND THE LANCELET

There are two basal groups of living chordates, the sea squirts and the cephalochordates (amphioxus). Amphioxus certainly looks superficially fish-like, but the adult sea squirts could hardly look like less likely relatives of the vertebrates!

1.1.1 Urochordata: sea squirts

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

The internal structure is fairly complex (Figure 1.2(b)). A large **pharynx** fills most of the internal space, and its walls are perforated by hundreds of gill slits, each of which bears a fringe of **cilia**, fine hair-like vibratile structures. Seawater is pumped through the inhalant siphon into the pharynx by beating movements of the cilia, and the water is then passed through a surrounding cavity, the **atrium**, and ejected through the exhalant siphon. The pharynx serves mainly to capture food particles from the stream of seawater that flows through it. The seawater is drawn into a filter bag of mucus, which is produced inside the pharynx by a gland known as the **endostyle**. During feeding, this gland continuously se-
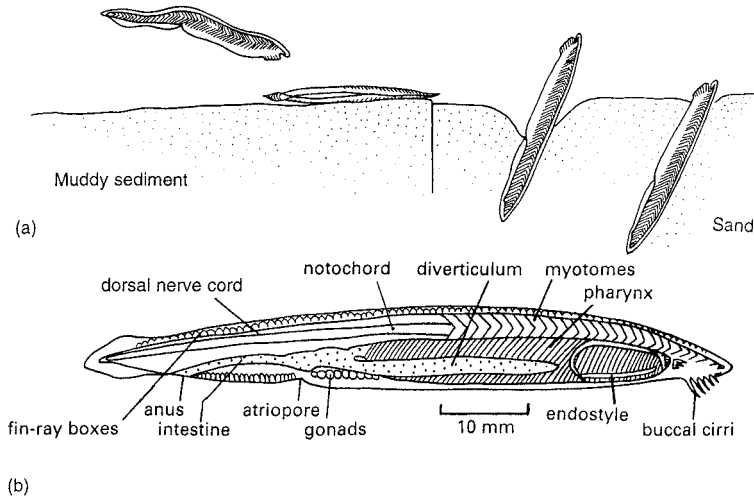
Fig. 1.3 Amphioxus, a cephalochordate: (a) modes of life, including swimming and burrowing into sand for protection; (b) internal anatomy. (Modified from Pough *et al.,* 2002 and other sources.)

cretes mucus into the **oesophagus**, together with the food particles that it has filtered from the seawater, and the food is passed to the stomach for digestion.

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

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

1.1.2 Cephalochordata: amphioxus

Another chordate generally reckoned to be related closely to the vertebrates is the amphioxus or lancelet, *Branchiostoma*, a representative of the Cephalochordata (or Acraniata). The adult amphioxus is convincingly chordate-like, being a 50 mm long cigar-shaped animal which looks like a young lamprey or eel, yet lacking a head. Amphioxus swims freely by undulating its whole body from side to side, and it burrows in the sediment on the sea-floor (Figure 1.3(a)).

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

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

1.2 PHYLUM HEMICHORDATA: PTEROBRANCHS AND ACORN WORMS

Another unusual group of living marine deuterostomes may offer further clues about the origin of the chordates. These are the hemichordates, a **phylum** that in-

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

The second hemichordate group, the acorn worms, or enteropneusts, such as *Saccoglossus*, are worm-like animals varying in length from 20 mm to 1.8 m. They
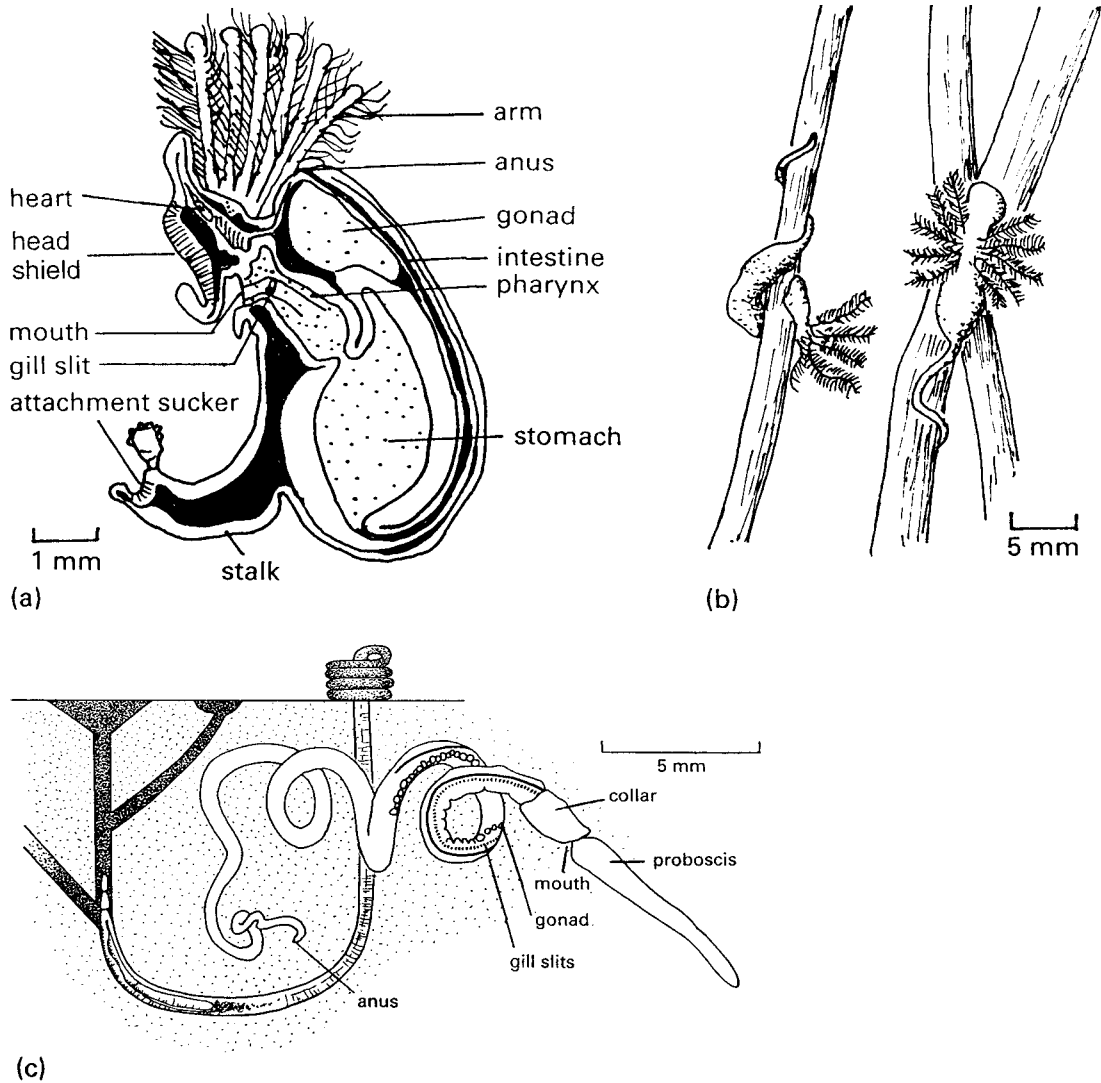

Fig. 1.4 Typical hemichordates: (a) the pterobranch *Cephalodiscus*, internal anatomy and (b) mode of life; (c) the enteropneust *Saccoglossus*, mode of life and external anatomy. (Modified from Jefferies, 1986.)

live in burrows low on the shore in Europe and elsewhere. *Saccoglossus* (Figure 1.4(c)) has a long muscular proboscis that fits into a fleshy ring or collar behind. The mouth is placed beneath this collar, and seawater and sand are pumped through the gut and expelled through an anus at the posterior end of the body. The long body is pierced by small holes at the front end, probably equivalent to the gill slits of *Cephalodiscus*, sea squirts, and amphioxus.

It was suggested that the Pterobranchia and Enteropneusta should be regarded as two separate, but closely-related, groups (Peterson, 1995), although more recent molecular work (Winchell *et al.*, 2002) concurs with morphological data (Smith *et al.*, in press) that Hemichordata is indeed a valid phylum, and more closely related to echinoderms than to chordates. Hemichordates do not have a notochord at any stage, but they possess gill slits, as in chordates, and giant nerve cells in the nerve cord of the collar region that are probably equivalent to similar nerve cells in amphioxus and primitive vertebrates. Both pterobranchs and enteropneusts share morphological characters indicating monophyly of the Hemichordata, such as the stomochord (an anterior buccal tube on the dorsal part of the pharynx) and mesocoelomic ducts.

1.3 DEUTEROSTOME RELATIONSHIPS

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

1.3.1 Embryology and the position of the anus

In early development each animal starts as a single cell. Soon this cell begins to divide, first into two cells, then four, then eight, sixteen, and so on (Figure 1.5(a–c)).

Eventually a hollow ball of cells is produced, called the **blastula** stage (Figure 1.5(d)). A pocket of cells then moves inwards, forming the precursor of the gut and other internal structures. The opening of this deep pocket is called the **blastopore**. You can imagine pushing in the walls of a hollow rubber squash ball with your thumb to produce a model of this embryonic pattern, known as the **gastrula stage** (Figure 1.5(e–g)).

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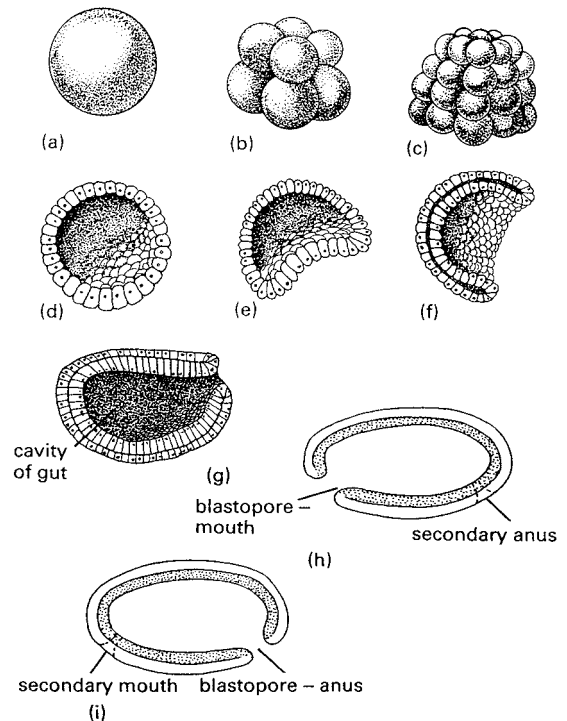

Fig. 1.5 Embryonic development: (a–g) sequence of cell division in amphioxus, from the single-cell stage (a), through the blastula stage (d), to the gastrula stage (g). (h) Fate of the blastophore in protostomes, and (i) in deuterostomes. [Figures (a–g), after Hildebrand and Goslow, 2001, copyright ©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

mouth is a secondary perforation. Such a dramatic turnaround, a switch from mouth to anus, seems incredible. Note, however, that many protostomes show deuterostomy, and this condition may be primitive and shared by all Bilateria (Eernisse and Peterson, in press). Nevertheless, this peculiarity of embryological development appears to solve the question of the broader relationships of chordates.

1.3.2 Relationships of the Deuterostomia

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

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

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

1.4 CHORDATE ORIGINS

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

1.4.1 Diverse early chordates

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

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

The fossil record of cephalochordates is not much better. The Chengjiang locality has also yielded a a superficially amphioxus-like cephalochordate, *Cathaymyrus*, as well as the yunnanozoons, which have also been identified as cephalochordates, although others assign them to the Vetulicolia (see below). In the absence of hard tissues such as bone, these nonvertebrate chordates are not often preserved.

1.4.2 Vetulicolians and yunnanozoons

The Vetulicolia is a newly-named group, one of the most extraordinary findings from the Chengjiang
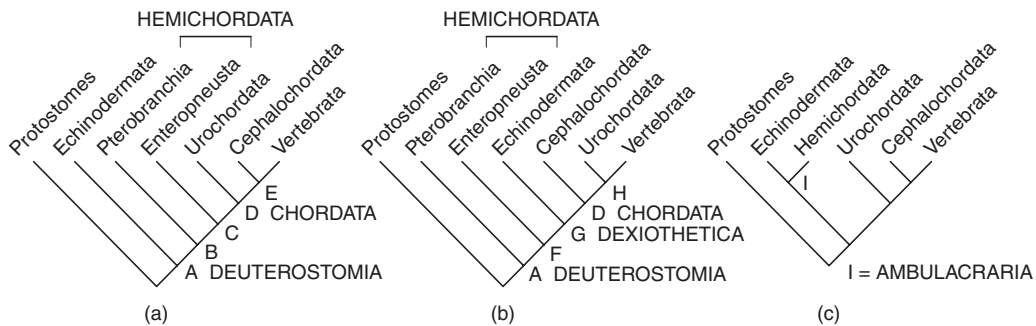
BOX 1.1   DEUTEROSTOME RELATIONSHIPS

Three substantially different schemes for deuterostome relationships have been proposed. The 'traditional' view (e.g. Maisey, 1986; Peterson, 1995; Donoghue *et al.*, 1998; illustration (a)) was to place the hemichordates as basal to chordates since they both share ciliated gill slits and giant nerve cells, as well as other features, which are not seen in echinoderms. Enteropneusts were sometimes said to be closer relatives of chordates since their gill slits are similar, they have a very short dorsal hollow nerve cord, and a number of other features of the gut not seen in pterobranchs (Peterson, 1995). Most authors regard amphioxus as the closest relative of the Vertebrata on the basis of 10–15 features that are not seen in tunicates.

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

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

Cladograms showing the relationships of the main deuterostome groups: (a) the 'traditional' model, (b) the 'calcichordate' model, and (c) the molecular model. Synapomorphies: **A DEUTEROSTOMIA**, blastopore becomes anus during development, bipartite mesocoel, mesocoelomic ducts; **B**, stomochord, paired gill slits; **C**, multiple pairs of gill slits, pharyngeal slits U-shaped, dorsal hollow nerve cord, preoral ciliary organ, mouth anterior and ventral and anus posterior and ventral or dorsal, multiciliated cells; **D CHORDATA**, notochord present and not attached to gut, dorsal hollow nerve cord with neural-plate stage in development, endostyle organ, a true tail used in swimming; **E**, digestive caecum, open capillary junctions, somites present, lateral-plate mesoderm, neural tube differentiated into grey and white matter, cerebral vesicle in brain; **F**, ciliated extensions of the mesocoel either absent or present as water vascular system (but not as lophophore), anus not anterior and dorsal; **G DEXIOTHETICA**, dexiothetism (rotation and partial loss of right side of precursor form), stone canal, calcite skeleton internalization of protostome; **H**, specialized olfactory areas in buccal cavity, hind-tail tripartite, dorsal longitudinal canal connected with notochord; **I AMBULACRARIA**, trimeric arrangement of the adult coelom, axial complex with hydropore, dipleureula larva with neotroch.

Formation, and still highly controversial. The group was named by Shu *et al.* (2001) on the basis of three genera, *Vetulicola*, *Xidazoon* and *Didazoon* (Figure 1.6(a, b)). These animals look like sausage balloons, knotted in the middle: the body is in two parts, with bulbous sections in front of, and behind, a flexible connection. There is a large mouth with a strengthened rim, and preserved internal structures include the guts and a possible endostyle. Both parts of the body appear to be crossed by transverse bands of tissue. On the

BOX 1.2   THE CHENGJIANG FOSSIL SITE

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

(a)

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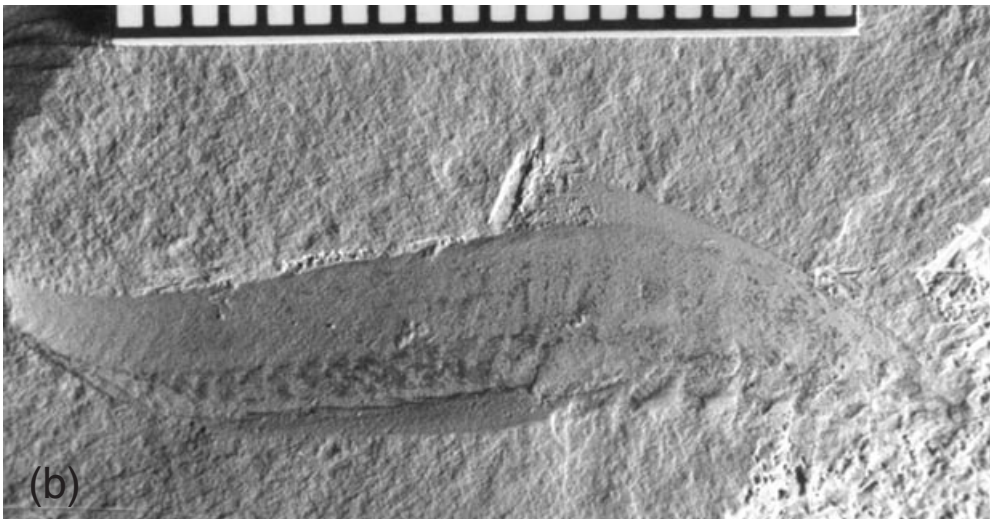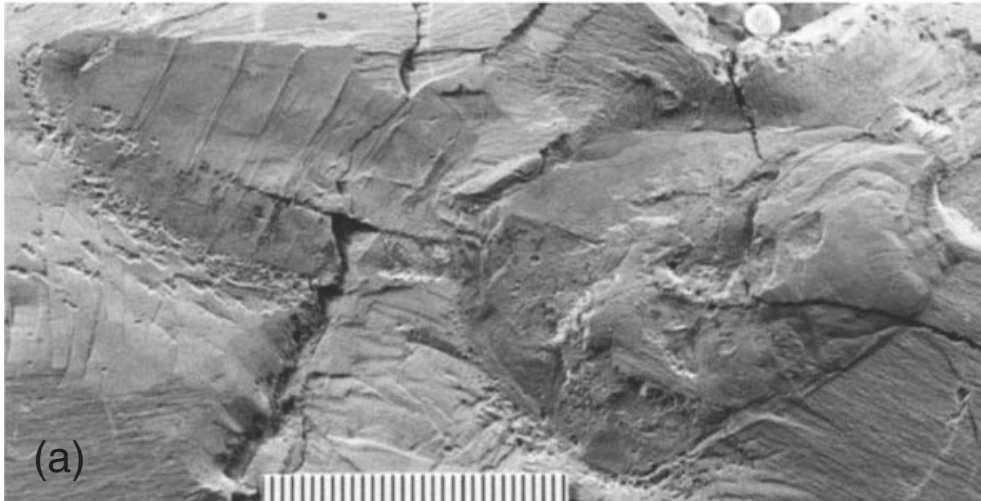
Typical Chengjiang fossils, the vetulicolian *Xidazoon* (a), and the basal vertebrate *Myllokunmingia* (b), both facing right. Scale bars in millimetres. Compare with interpretive drawings in Figures 1.6 (b) and 3.1(a). (Courtesy of Shu Degan.)

The Chengjiang site is rich, having produced more than 10,000 specimens, and the fauna consists of 90 or more species, mainly of arthropods (trilobites and trilobite-like forms), sponges, brachiopods, worms, and other groups, including possible basal deuterostomes, such as the vetulicolians and yunnanozoons (Figure 1.7), as well as the first fishes (Shu, 2003). Some of the arthropods are like Burgess Shale animals, but others, such as the basal deuterostomes, seem to be unique. Most of the animals lived on the bottom of the sea-bed, filtering organic matter from the sediment. There were a few floaters and swimmers, and some of the larger arthropods were clearly predators, feeding on the smaller bottom-dwellers.

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

Read more at http://palaeo.gly.bris.ac.uk/Palaeofiles/Lagerstatten/chngjang/index.html and http://www.palaeos.com/Paleozoic/Cambrian/Chengjiang.html
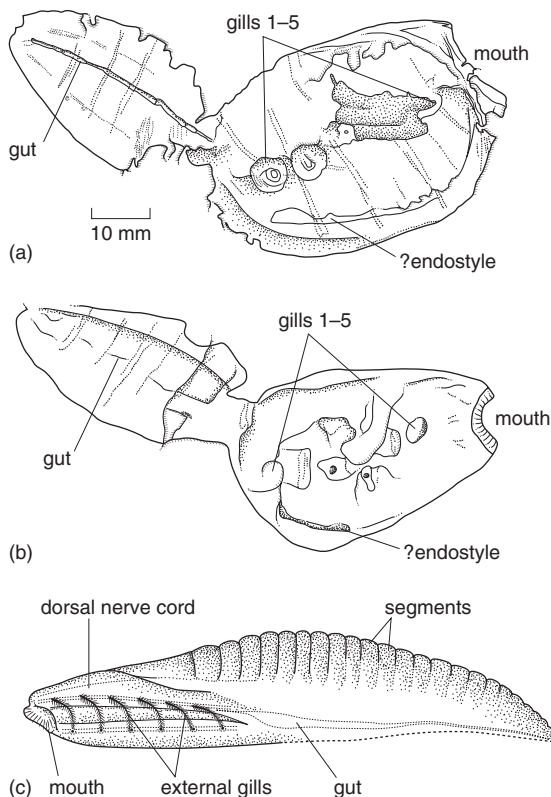

Fig. 1.6 Basal deuterostomes: (a, b) the vetulicolians *Didazoon* (a) and *Xidazoon* (b), showing how the body is divided into two sections that are joined by a flexible connection; (c) *Haikouella*. (Courtesy of Shu Degan.)

mouth-bearing segment, presumably the front part of the body, are five circular structures in a row that have been interpreted as pharyngeal gill slits.

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

Additional invertebrate chordates from Chengjiang, the yunnanozoons *Yunnanozoon* and *Haikouella* (Figure 1.6(c)), have been interpreted by rival researchers both upwards and downwards in the scheme of things (Figure 1.7). One team identified these animals first as possible cephalochordates (Chen *et al.*, 1995), and then upwards as vertebrates (Chen *et al.*, 1999; Holland and Chen, 2001; Mallatt and Chen, 2003). The other team preferred to regard the yunnanozoons first as hemi-
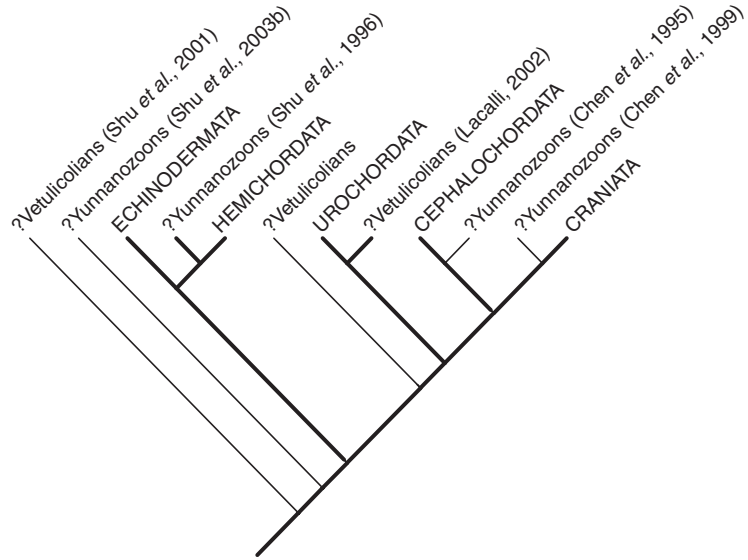
Fig. 1.7 Phylogenetic tree of the extant deuterostomes, with suggested locations of the major fossil groups.

chordates (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.

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

yunnanozoons and the vetulicolians, and moved them down from the hemichordates to a basal position among deuterostomes (Figure 1.7): they could see no evidence of a notochord, a large brain, lateral eyes, or any of the other chordate features previously reported.

1.4.3 Carpoids

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

1 Morphological and molecular phylogenetic analyses agree on a tree of living forms (Box 1.1) that does not
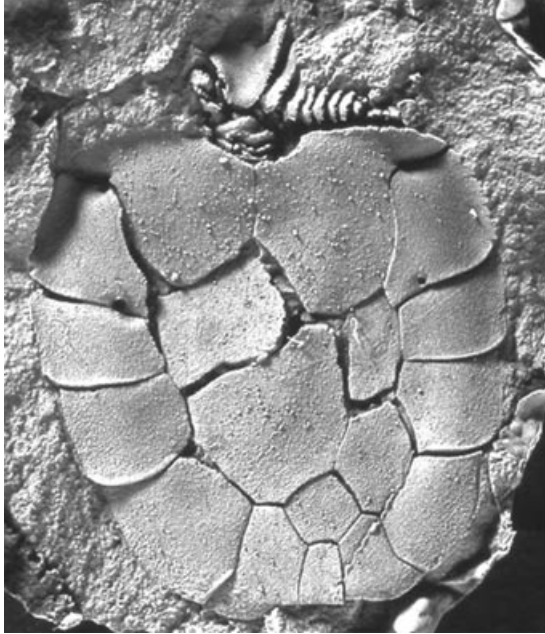
Fig. 1.8 The carpoid *Mitrocystites mitra* from the Mid-Ordovician of Bohemia (Czech Republic), dorsal view, showing the calcite plates that compose the body and the flexible 'arm' folded over at the top. Scale, specimen is about 30 mm long. (Courtesy of Bernard Lefebvre.)

correspond to the requirements of the 'calcichordate' hypothesis.

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

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

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

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

1.4.4 Development and vertebrate origins

The **development** of living vertebrates and basal chordates indicates a great deal about their ancestry. Embryos may be sliced thinly on a microtome, rather like a mini salami-slicer, and three-dimensional reconstructions are made from tracings of the thin-sections by computerized methods. In addition, and most importantly, studies of the **genome** allow developmental biologists to relate specific anatomical structures to genes. In many cases, they have found that genes that code for particular organs or functions are shared among widely different species that may have had enormously long independent histories. So, hypotheses of **homology** between organs can be tested by identifying shared genes, and recent work on amphioxus has been remarkably informative (see Box 1.3).

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

BOX 1.3   GENES AND BRAINS

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

Anatomists have for a long time sought evidence for homologies between the cerebral vesicle of amphioxus and the three-part brain of vertebrates, the frontal eye of amphioxus and the paired eyes of vertebrates and other such structures. New studies by three developmental biologists, who rather confusingly share the homologous surname of Holland—Linda Holland and Nicholas Holland (both at the Scripps Institute of Oceanography, San Diego) and Peter Holland (at the University of Oxford)—have revealed amphioxus homologues of developmental genes on the basis of amino acid sequences of conserved regions (Shimeld and Holland, 2000; Holland and Chen, 2001; Holland and Holland, 2001; Holland *et al.*, 2001). It turns out that developmental genes show remarkable conservation across a wide range of animal phyla—in sequence, expression and in function. In other words, when the Hollands sequence particular segments of the chromosomes of amphioxus and of vertebrates, they find the same genes, and the genes appear to express themselves in comparable parts of the body, hence pointing to potential homologies.
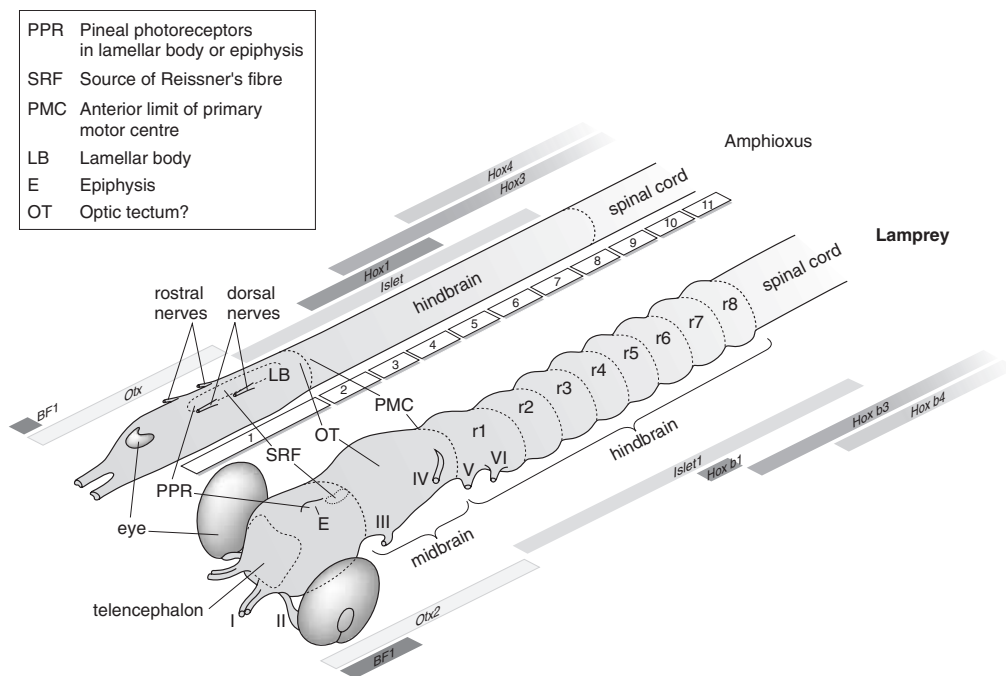
The front part of the developing nerve cords of amphioxus (left) and a vertebrate (right), viewed from above. In amphioxus, the cerebral vesicle, the brain region, is stippled and the numbered rectangles represent the muscular segmentation. Key features of the head and brain of the vertebrate are labelled, and possible homologies with amphioxus are indicated. The zones of expression of developmental genes are indicated to the side, confirming that amphioxus has morphological homologues of the three-part vertebrate brain (forebrain, midbrain, hindbrain), and a segmental structure to the hindbrain, which is composed of eight segments in each case. (Based on information from the cited papers, parts of which are copyright 2001, Holland and Chen; reprinted by permission of John Wiley & Sons Ltd.)

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

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

Most importantly, amphioxus shares embryonic cells that are homologous with the **neural crest** of vertebrates. The neural crest was thought to be a unique developmental feature of vertebrates, and indeed it is a developmental precursor of virtually all the distinctive vertebrate characters. The neural crest starts as a group of cells that forms on either side of the developing spinal cord and migrates to all areas of the body, providing the starting point for much of the head and face, and contributes to many other parts of the body such as the skin, nervous system and limbs, producing the cranial nerves, the fin rays, the pharyngeal gill skeleton, and other key vertebrate characters. The genes *distal-less, snail, Pax-3/7* and *Msx* are expressed in migratory embryonic cells of amphioxus as well as in the neural crest of vertebrates, so the gene homologies point to morphological homologies, and indicate the evolutionary source of the neural crest.

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

larva failed to metamorphose and became adult (i.e. reproductively mature) as a swimming larval form. This elegant theory, however, is rejected by recent molecular phylogenies of tunicates that suggest their developmental characters are unique and did not give rise to the vertebrates.

1.5 VERTEBRATES AND THE HEAD

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

The basic vertebrate body plan (Figure 1.9) shows all of the chordate characters so far described — notochord, dorsal nerve cord, pharyngeal 'gill' slits, postanal tail, myomeres, and so on. The special vertebrate characteristics include a range of features that make up a true head: well-defined sensory organs (nose, eye, ear) with the necessary nervous connections, the **cranial nerves**, and the olfactory, optic, and auditory (otic) regions that make up a true brain. Larval sea
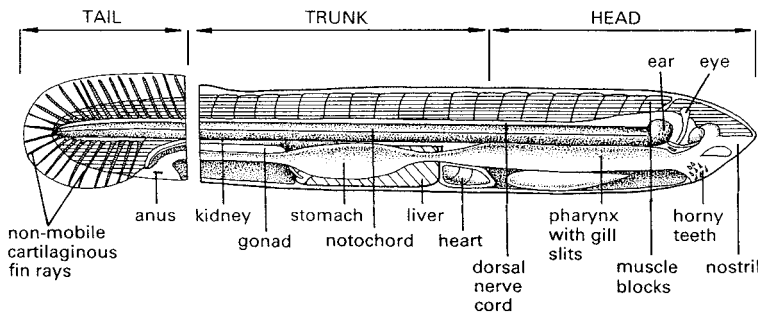

Fig. 1.9 The hypothetical 'basic' vertebrate body plan, shown in longitudinal section. (After Jefferies, 1986.)

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.

1.6 FURTHER READING

You can read more about the palaeontological, embryological, and molecular debates concerning the origins of chordates and vertebrates in Gee (1996) and papers in Ahlberg (2001). Jefferies (1986) presents further detailed information on this topic, and makes an impassioned case for the role of carpoids in linking echinoderms and chordates. Peterson (1995) argues trenchantly against the 'calcichordate' hypothesis, and Holland and Chen (2001) give a good review of the origin of vertebrates. You can find out more about modern invertebrates, and in particular those classified as deuterostomes, in Barnes *et al.* (2001), Nielsen (2001) or Brusca and Brusca (2003). The embryology and anatomy of modern vertebrates is covered by many zoology texts, such as Romer and Parsons (1986), Kent and Miller (1997), Hildebrand and Goslow (2001), Kardong (2001), Liem *et al.* (2001) and Pough *et al.* (2002). Cracraft and Donoghue (in press) presents a review of current thinking on the relationships of the major clades of chordates.