

Chapter 2

The First Vertebrates, Jawless Fishes, the Agnathans

2.1 Ostracoderms

Vertebrates arose over 500 million years ago (MYA) but traces of their appearance only occur during the Ordovician period about 460 MYA. These primeval, small fish-like vertebrates are popularly known as the ostracoderms and during the 100 million years of their existence they were comprised of about 600 species. Ostracoderms are especially important in the history and evolution of vertebrates. As undoubted vertebrates they possessed a backbone, were bilaterally symmetrical and had a nervous system divided into brain and spinal cord (partly enclosed within the backbone). They are also characterized by the possession of no more than two pairs of limbs and muscular system consisting primarily of bilaterally paired masses and a well-developed coelom, which contained the organs. In appearance, ostracoderms were dorsoventrally flattened and, quite extraordinarily, they lacked jaws, a condition so important that the classification of modern vertebrates is recognized by two major groups, the agnathans (without jaws) and the gnathostomes (literally, jaw-mouths) (Figs. 2.1 and 2.2). Ostracoderms are now regarded as an artificial designation that includes perhaps four distinct superclasses of jawless craniate fishes, the Pteraspidomorphi, Anaspida, Thelodonti, and Osteostrachomorphi. Despite an apparently inauspicious beginning, these simple animals would be responsible for two events of major importance in the history of the vertebrates—the evolution of a tough outer protective layer, the integument, and the evolution of bone. Remarkably, in the beginning the histories of these seemingly disparate structures were intrinsically linked.

Ostracoderms possessed an external bony head shield or armor but its internal skeleton was probably not ossified to any great extent. Debate over the origin of the vertebrate skeleton has revolved around the question of which group was the first to exhibit evidence of skeletonization and mineralization. The vertebrate skeleton is comprised of at least two distinct skeletal systems: the dermoskeleton (arising from the dermis; widely perceived to encompass teeth, scales, fin spines, etc.) and the endoskeleton (the braincase, branchial skeleton, axial, and appendicular skeletons). It has been argued that although elements of the skeleton can be

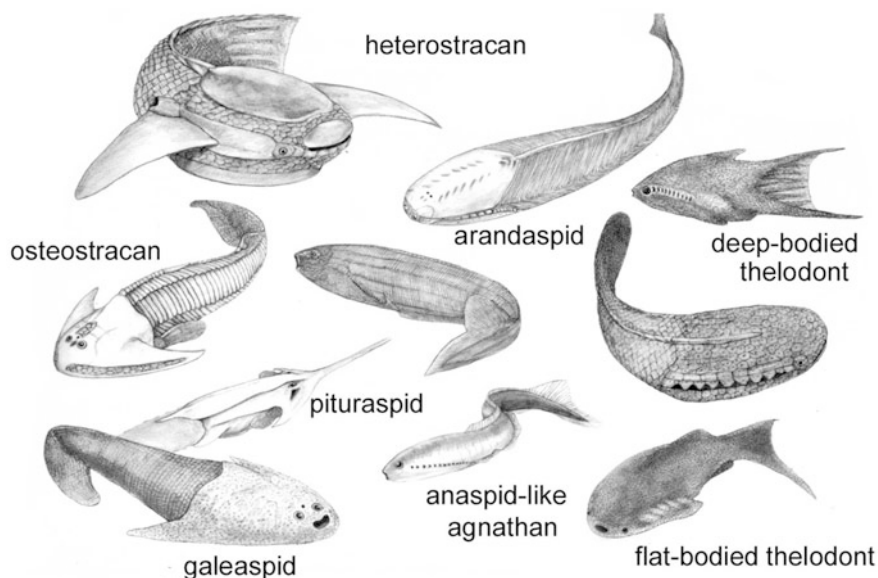


Fig. 2.1 Ostracoderms evolved into a wide variety of shapes and sizes during their 100 MYR reign on earth. The nearly 600 species of ostracoderms can be classified into one of nine or ten groups. From Forey and Janvier (1994)



Fig. 2.2 The fossilized impression left by the head shield and body scales of a 400-million-year-old ostracoderm from Great Britain. The specimen is about 15 cm long and shows the location of the eye sockets and special sensory fields on the head. From Forey and Janvier (1994)

interchangeably derived from either system, the two systems have remained distinct throughout vertebrate phylogeny (Donoghue and Sansom 2002), of which more will be said later (Fig. 2.2).

2.2 Marine or Freshwater Origins?

The environment of early vertebrates in the Ordovician was of enormous importance in the question of how these vertebrate characters came about and how their roles would later take very separate paths. There had been much early discussion by geologists and zoologists on whether the first vertebrates evolved in a marine or freshwater habitat (Halstead 1969a). The prevailing view among zoologists was that vertebrates had originated in the sea. This view was challenged when fragments of bony armor were discovered in the freshwater Middle Ordovician Harding Sandstone of Colorado. This new evidence presented a number of questions on how the early vertebrates would cope with living in a freshwater habitat (Halstead 1985), which literally involved a sea change in scientific thinking. Halstead (1985) showed how despite an originally purely marine habitat these early vertebrates, e.g., the thelodonts showed an ability to deal with variations in salinity and were able to colonize both brackish and fresh waters and by the lower Devonian were able to spread globally. Among other groups that made freshwater colonizations of non-marine habitats during the Wenlock or Ludlovian times were the galeaspid, a group of cephalaspidomorphs, known only from South China (Figs. 2.3 and 2.4).

In the sea the concentration of salts in the body fluids of animals and that of the water is approximately the same, hence there is no appreciable osmotic gradient between the two. In freshwater on the other hand the concentration of salts is negligible. The idea that a bony integument could serve as waterproofing was proposed by Berrill (1955) and Homer Smith (1963), i.e., to prevent waterlogging of the body. The drawback to this hypothesis is that the bony integument was present when the ostracoderms colonized marine environments where there was no need for waterproofing. In support of the idea of a freshwater habitat, Homer Smith and others suggested that the glomerular kidney was developed principally to control osmoregulation.

Prior to the freshwater problems of osmoregulation the development of a bony armor, as the name implies, led to the hypothesis that it may have evolved in vertebrates for protection. Alfred Sherwood Romer (Romer and Grove 1935; Romer 1971) was one of the strongest supporters of this hypothesis. Romer also believed in a freshwater origin of vertebrates and contended that the bony integument would have protected the ostracoderms from the formidable pincers of the giant freshwater scorpions or eurypterids that inhabited the lakes and rivers of the time, although other workers such as Halstead (1969a) suggested that there was no evidence to show the eurypterids and ostracoderms ever shared the same locations. Romer, like Homer Smith, believed that the glomerular kidney originated to help control osmoregulation. The stumbling block to this hypothesis is that hagfishes, which possess a glomerular kidney have always had a marine environment. The British physiologist Robertson (1957) further showed that a similar filtration system was also present in a number of marine invertebrates that are stenohaline (low tolerance to salinity changes) and consequently have little need to modify intracellular osmolality. Maintaining internal salt conditions like that of the sea water was widely

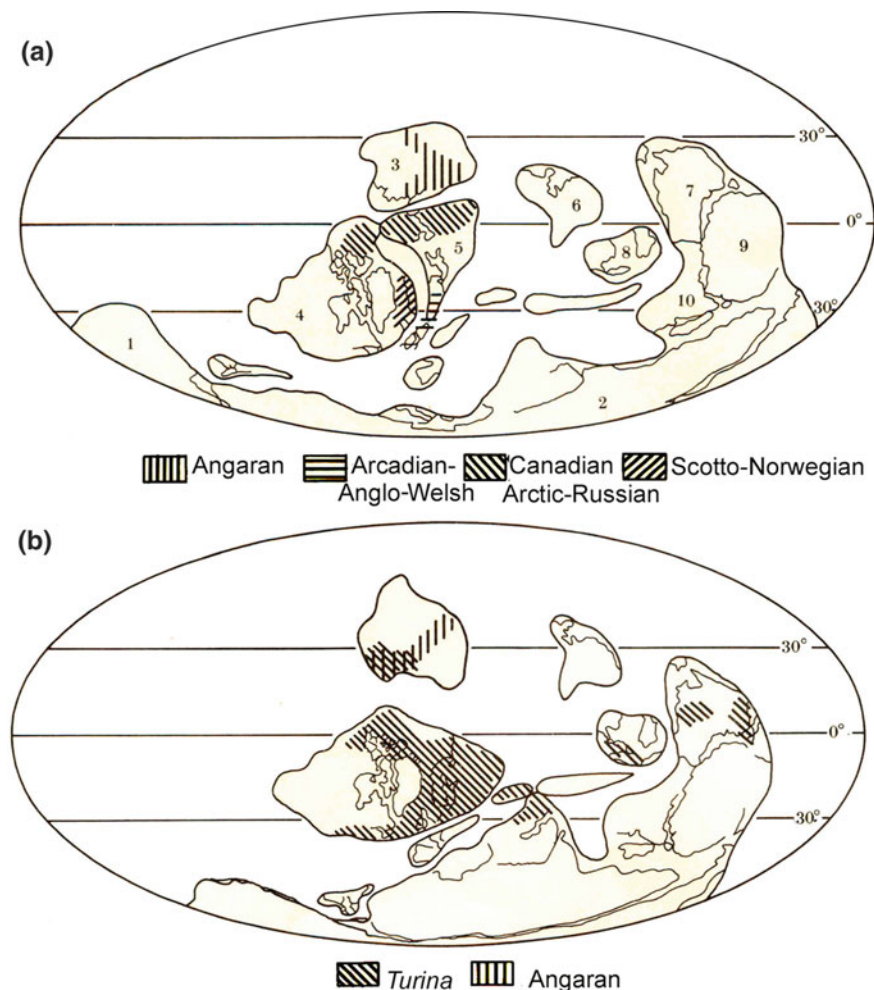


Fig. 2.3 Thelodont faunal provinces and palaeogeography. **a** Silurian. **b** Lower Devonian. 1 South America; 2 Africa; 3 Angaraland; 4 North America; 5 Baltica; 6 North China; 7 Australia; 8 South China; 9 Antarctica; 10 India. From Halstead (1985)

regarded as a strong argument against the freshwater origin of vertebrates. However, the physiological arguments and counter arguments seemed redundant when it was subsequently shown that the Harding Sandstone, rather than a freshwater deposit, extended over thousands of miles and was in fact an offshore deposit. Indeed, the matter should have been settled by the even older deposits from the Lower Ordovician rocks of Russia that showed unequivocally shallow marine conditions. Halstead (1985) noted that it was unfortunate that the Harding Sandstone's mistaken association with a freshwater system had led effectively to such a waste of time and energy and a number of erroneous zoological explanations and he unequivocally

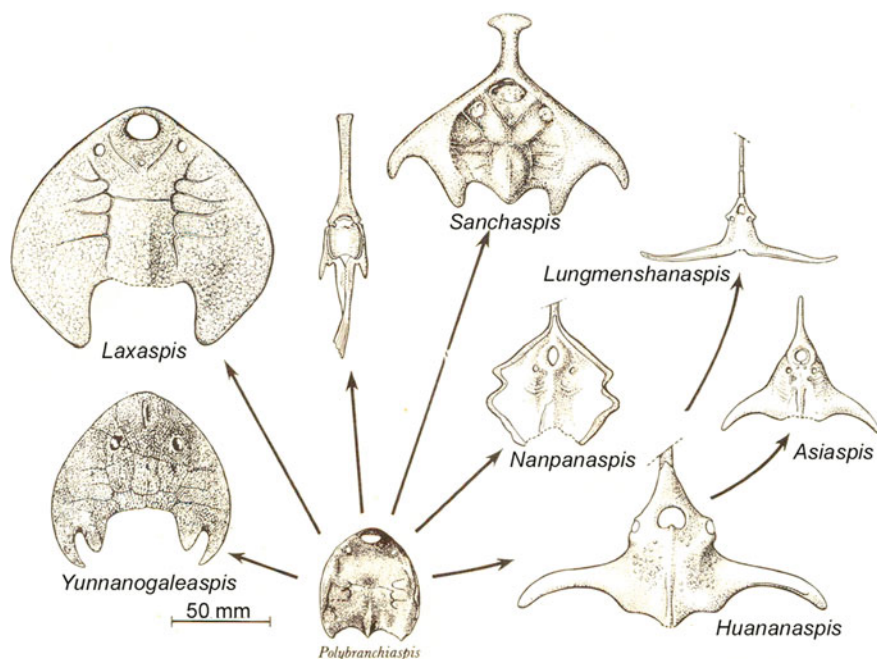


Fig. 2.4 Radiation of galeaspid from South China. From Halstead (1985)

stated that the origin and early evolution of the vertebrates took place in exclusively marine conditions. He cited little evidence of non-marine vertebrate faunas extending as far back as the Middle-Cambrian chordate *Pikaia* (a possible cephalochordate from the Middle-Cambrian Burgess Shale, about 550 million years ago), through to the Upper Cambrian, Ordovician, and early Silurian records.

Despite this apparent resolution, over time it is not unusual to see that ideas once unfashionable become acceptable, or at least in part, with renewed research. For instance, Griffiths (1985) has suggested that there is more to this than just the simple salt content of the habitat and that the glomerular kidney may have originally been a feature of a freshwater and ion-regulatory function. Griffiths also suggested that the first vertebrates may have been anadromous (marine fish that migrate to freshwater to breed) like the lamprey and that the rivers and estuaries may have provided a safe haven for reproduction and early development of the young with a move to the coastal marine waters to feed after they had grown big enough to compete with marine species (see Foreman et al. 1985). This is an intriguing hypothesis and whether the marine stage came first or the freshwater what seems undeniable is that the invasion of fresh waters, as Beverly Halstead (1985) emphasized, marked perhaps one of the most important advances in the evolution of the physiology of vertebrates and that these jawless oddly looking animals, microphagous detrital feeders, would herald the invasion of predators, the benthonic placoderms, and nektonic acanthodian fishes.

2.3 Feeding

Many zoologists believe that the bony ostracoderms were in the main line of vertebrate evolution (Moy-Thomas and Miles 1971). While defense or even predatory behavior are not excluded because they almost certainly would have helped to protect the animal, the consensus of opinion seems to be that as a primary function, a heavy bony armor would be incompatible with an active predatory lifestyle. At a major stage in their evolution, vertebrates had arrived at a crossroads. Glover et al. (2011) proposed that they had to make an evolutionary choice between nutrient absorption via the skin as in hagfish and many invertebrates or forms of filter feeding (Jollie 1982), to a form of feeding that limited exchanges across permeable surfaces and was associated with more active feeding methods and specialized digestive systems. The view that there was a long-term ecological trend toward increasingly active and predatory habits in the heterostracans was contradicted by Purnell (2001) who contended that heterostracans were microphagous suspension feeders and that this was a relatively advanced development in feeding. He based it on his observations on heterostracan feeding structures, which exhibit recurrent patterns of *in vivo* wear and covered internally by microscopic oral denticles. The functional significance of the denticles derives from the fact that their tips are consistently directed outwards, i.e., the entrance to the heterostracan mouth would have been lined with imbricate rows of anteriorly directed barbs, which would have prevented grasping, biting, or any other form of macrophagy (Fig. 2.5).

2.4 Bone, a Chemical Store

As we saw above, the seemingly obvious answer that bone on the outside of an animal provides protection has nevertheless been a source of much debate. Many of the notable paleontologists and biologists of the time were not distracted by what might have seemed the most obvious answers. Halstead (1969a) put his finger on the pulse when he observed that during the course of evolution a structure necessary for survival under new conditions may invariably already be present or had begun its development in its original environment although for a different reason. Answers with respect to the function of the bony armor in the jawless vertebrates came from the most unlikely source. On the basis of work on protozoans, it was shown that a conveniently accessible phosphate store is likely to have been needed by an animal with much muscular activity (Pautard 1961). We know that bone in humans and many terrestrial vertebrates is a reservoir for calcium and phosphate and it is reasonable to postulate that bone evolved originally as such a store. Calcium phosphate, e.g., is a convenient way of storing phosphate.

The need for a phosphate store in the early vertebrates may be connected with the seasonal changes in the sea and different levels of availability. Free phosphates

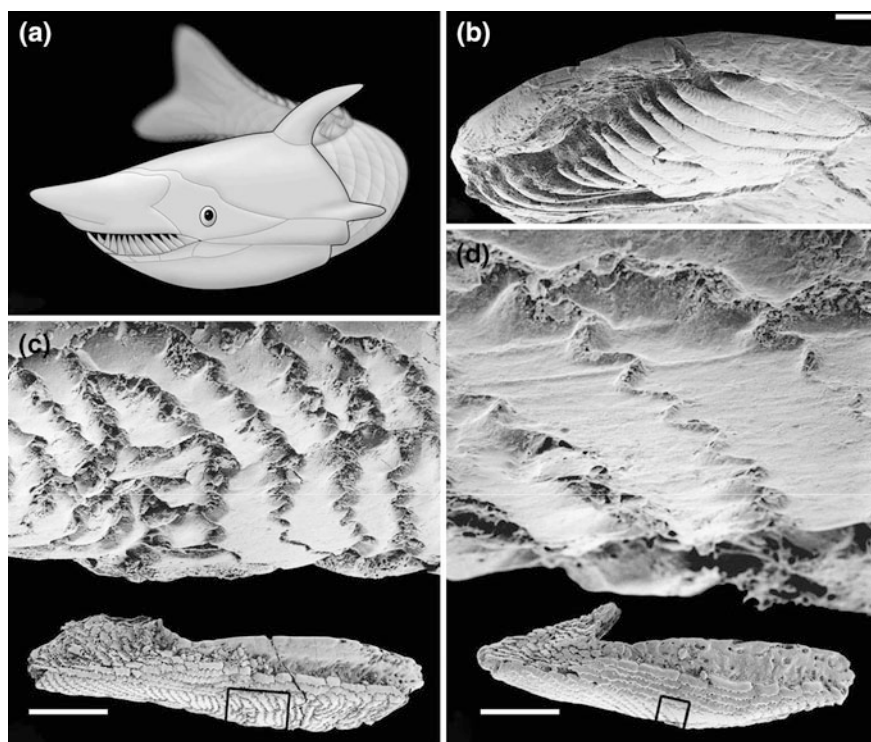
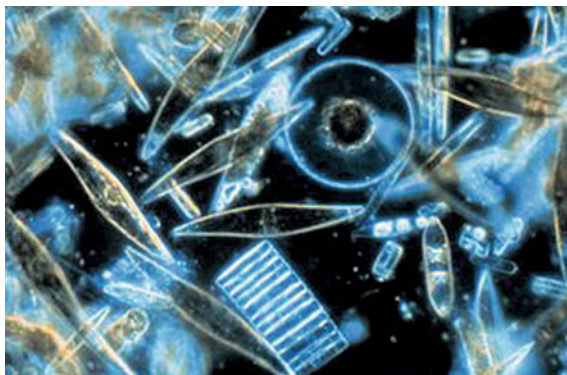


Fig. 2.5 Oral plates of heterostracans. **a** Oblique anterior view of a pteraspid heterostracran showing the configuration of the oral plates forming the lower margin of the mouth. The illustration is based on a reconstruction of *Errivaspis waynensis* Bleick. **b** Oblique anterior view of the mouth of *Protopteraspis vogti* preserving oral plates in situ. The image is a montage of scanning electron micrographs of an epoxy replica of specimen A28720/2 (Paleontologisk Museum, Oslo; Devonian, Ben Nevis Formation, Spitzbergen). **c** Oblique view of isolated oral plate of *Loricopteraspis dairydinglensis* (White), specimen NHM P43713. **d** Oblique view of isolated oral plate of *L. dairydinglensis*, specimen NHM P43711. Both **(c)** and **(d)** show typical patterns of wear developed on the ventral surface of oral plates (*anterior to left*). The enlarged views of the areas outlined by the *boxes* show worn dentine ridges and parallel scratches (NHM P43711 and NHM P43713, Lower Devonian, Ditton Group, Dairy Dingle, near Neenton, Shropshire, UK). Scale bars, 1 mm. From Purnell (2001)

are most plentiful in the sea during the winter months. Phytoplankton (Phylum Bacillariophyta) have the ability to utilize the free phosphates. Because they are free floating, these microscopic algae of the ocean are capable of developing in the surface layers since light of photosynthetically effective wavelengths is largely filtered out at a depth of about 50 feet (Stanier et al. 1989) (Fig. 2.6). Where the environment is favorable their growth is largely limited by the relative scarcity of two elements phosphorus and nitrogen. These elements are made available as phosphates and nitrates by the runoff of rainwater from the continents and subsequent distribution by ocean currents, when profuse development of

Fig. 2.6 Diatoms.

Microscopic one-celled alga (may be colonial) found in water. They are frequently called jewels of the seas because of their shapes and are among the most important and prolific sea organisms. They are photosynthetic and serve directly or indirectly as food for many animals



phytoplankton occurs. In the past, as now, a heavy intake of phosphates occurs during spring and summer months by the phytoplankton. Free phosphates on the other hand, even when abundant, cannot be directly utilized by animals. Animals obtain their phosphates by feeding on phytoplankton and others by feeding on the latter the whole process serving to lock the phosphates into the marine plant and animal fauna. Thus at the end of the summer months when there was a dearth of phosphates in the sea, their presence in the animal cycle could be utilized by the bottom-dwelling ostracoderms feeding either on the decaying phytoplankton that sinks to the bottom or other animals. Thus, a means for storing phosphates at times when it is abundant in their diet would be of considerable advantage in the relatively long-living ostracoderms. Workers such as Pautard (1961, 1962) and Halstead (1969a, b) concluded that bone originated as a simple store of phosphates laid down in the skin of the earliest vertebrates.

Griffiths (1985) agreed that a calcium and phosphate store has advantages during times of food shortage. He demonstrated in a number of animal including in fishes in which phosphates stored in bone are reabsorbed into the blood that they play a vital role during reproduction (in humans mineralization and reabsorption are under the control of hormones from the parathyroid and thyroid glands). He made a compelling case for his hypothesis concerning an anadromous freshwater origin of vertebrates. Most living anadromous fishes feed little during their migrations. He compared this with periods in the early Paleozoic when the rivers had even less food and the hypothetical anadromous ancestral vertebrates would have been unable to acquire phosphate or other minerals through the diet during their upstream spawning migrations. The capacity of the female proto vertebrates to synthesize vitellin, which was vital to reproductive success, would have depended on body phosphate reservoirs. This would have provided a strong selective pressure for the evolution of dermal bone as a reservoir.

Either way, whether the first vertebrates had a freshwater or marine origin, the above arguments indicate the most likely reasons for the origin of bone was that it served as a store of vital minerals. It is not difficult to see that such a store of calcium phosphate in the outermost layer of these animals would rapidly have

assumed the secondary role of a protective armor. Thus this would conform to the classic of an original function being co-opted to a new one, i.e., protection of the body. Yet, even more profound was how that store of calcium phosphate shifted from the outside of the animal to the inside and eventually to a fundamentally different primary role, that of an internal bony skeletal support system, which would revolutionize life on earth.

This transition took a while and it was only considerably later in vertebrate evolution that bone came to replace the cartilaginous endoskeleton (not in an evolutionary sense)—and change the course of vertebrate evolution. It is for this very important reason that the earliest jawless vertebrates are pivotal to the story of vertebrate evolution and why so many eminent paleontologists, zoologists, and geologists devoted so many years of research to trying to find answers to vertebrate origins. Also important, in resolving these mechanostuctural and physiological problems we are coming closer to understanding the phylogenetic origins of modern fishes.

Simpson (1950) in his book *The Meaning of Evolution* showed how the accidents that occur during evolution may have resulted in the development and rise of novel and successful types of organization that allow unimagined possibilities and enable certain groups of animals to overshadow all other life forms put together. The evolution of bone may be regarded as one of those accidental events in nature that defines evolutionary theory. We may be surprised that bone started its journey not on the inside of our vertebrate ancestors but on the outside and more so for the seemingly mundane purpose of a storehouse for calcium and phosphate. This is what the evidence points to, as we see amply demonstrated in the fossil record, but it brought with it a whole bundle of new problems, which is why we need to look a little closer at these curiously odd ancestors of ours.

Fragments of bony armor are found historically in horizons of Ordovician age in the US and Russia, and more recently Australia. They belong to the primitive jawless vertebrates the ostracoderms whose nearest living relatives are the present-day cyclostomes, which, however, are naked (more will be said later). The ostracoderms possessed a bony carapace and as we have already indicated, their vertebrate status is beyond question.

2.5 Heterostraci

The heterostracans, among the most primitive agnathans, include the earliest known vertebrates, the arandaspids from the late Cambrian of the US and the earliest Middle Ordovician of Spitsbergen and Australia and the astraspids and erptychids (Figs. 2.7 and 2.8) from the Middle Ordovician of America (Jarvik 1980). Their long held importance as a possible ancestor of the extant myxinooids has recently been called in question and a number of workers have placed them

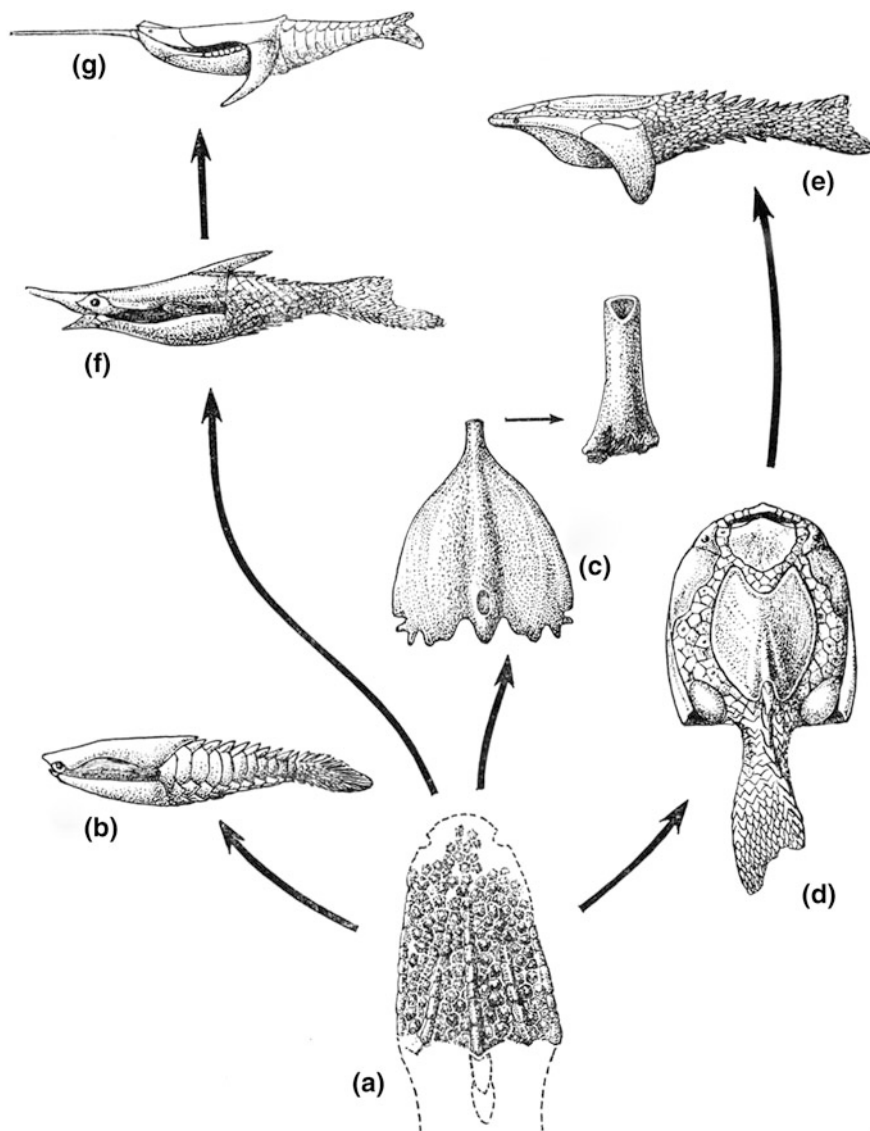
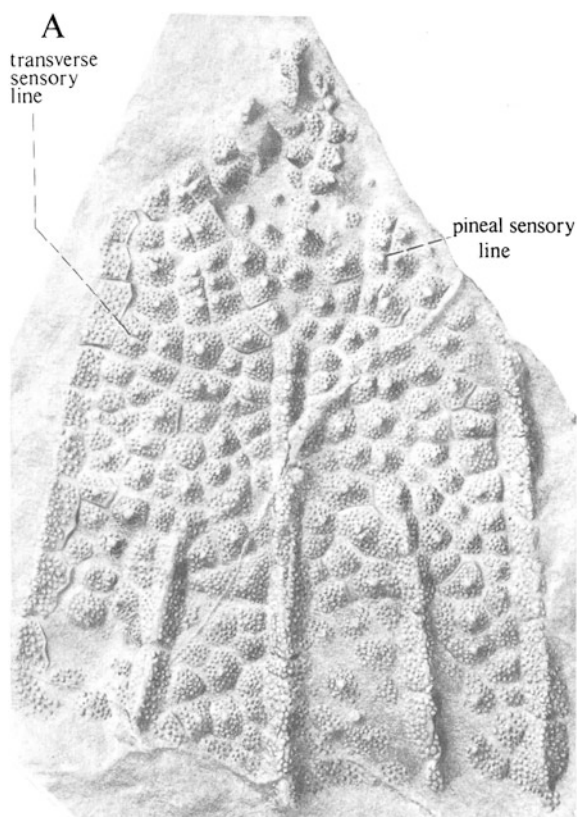


Fig. 2.7 Heterostracan ostracoderms. **a** *Astraspis* (Ordovician). **b** *Cyathaspid* (Silurian-Devonian). **c** *Eglonaspis*, showing tubular mouth (Devonian). **d** *Drepanaspis* (Lower Devonian). **e** *Pycnosteus* (Middle Devonian). **f** *Pteraspis*, showing oral plates splayed out to form a scoop (Lower Devonian). **g** *Doryaspis* (Lower Devonian). From Halstead (1969a)

outside the main line of potential ancestors (Janvier 1996a). Unlike in the cyclostomes, in heterostracans the head and anterior part of the trunk are encased in a bony armor, the shield or carapace (Fig. 2.8). To anyone who has flipped through a

Fig. 2.8 Imperfect dorsal shield of the astrapid *Astrapis desiderata*. From Jarvik (1980)



book with pictures of these animals they could easily be perceived as formidable monsters of the oceans. However, most were small, no more than a few centimeters long. At the anterior end there is an opening for the mouth, generally bounded ventrally by oral plates, and small laterally placed orbital fenestrae but unlike the osteostracans (Fig. 2.8) there is no nasohypophysial opening on the dorsal side of the carapace and only one branchial opening on each side. Behind the carapace, the trunk and tail are covered in scales. There are no paired fins but spines or ridge-scales in the position of the median and ventrolateral fin fold. There is nothing to indicate that true moveable folds with radial muscles were developed (Jarvik 1980). However, these agnathans had developed a number of features that affirmed their vertebrate status even more such as an efficient nasal apparatus, eyes, a pineal organ, an advanced acoustic-lateralis system and a lateral line system (Halstead 1969a; Jarvik 1980; see Chap. 4).

The various genera and species can be distinguished mainly by differences in proportion and in the development of the superficial layer of the dorsal and ventral shields. From studies in the development of the armor of the carapace in the

various groups the overall shape can be reconstructed. It shows that despite the apparently limited potential of the animals, they underwent a remarkable radiation, and a surprisingly large number of unusual modifications of the basic form of the carapace evolved. Halstead (1962) demonstrated that it was possible to show from the carapace the way in which these groups are related to one another, and hence to be able to trace the main evolutionary lineages within the Heterostraci (Fig. 2.6). Halstead (=Tarlo 1960) also showed that what had once been considered to be three distinct types of growth of dermal plates in the Heterostraci, are in fact all related. This will be dealt with in detail further on.

From the perspective of mobility it would appear that the heterostracans were rather limited. The absence of fins indicates that they had little active maneuverability in the three-dimensional environment. Compared to the flattened and broad anterior regions of the body the posterior trunk was much narrower and deeper, suggesting that the animal was propelled forward by lateral movements of the tail. Halstead (1969a) suggested that the markedly convex ventral surface of the carapace (Fig. 2.6) meant that forward movement would have automatically lifted the body free of the bottom as the animal bounded from one mud patch to another, a form of movement he described as resembling the slow-motion bounding motion of a finch. Consistent with this type of movement, it seems likely that the convex shaped ventral surface was more connected with the body's hydrodynamics and to remaining above the mud for a longer period.

Jarvik (1980) summed up the importance of the heterostracans with respect to six major developments, four of which are mentioned here within the context of the integument and the origin of bone.

- (1) In the microstructure of the dermal skeleton of the earliest heterostracans they show practically all the types of hard tissue (calcified cartilage, bone, dentine, and enamel-like structures), characteristics of the later appearing vertebrates. In the histologic structure of the skeleton they are thus typical vertebrates.
- (2) In pre-Silurian and later heterostracans, the bone is of the acellular type known as aspidin which has been the source of considerable debate and which some authors considered primitive (Halstead 1973) while others considered to be a secondary derivative of bone (Orvig 1967) (see below).
- (3) Distinct grooves for sensory lines present in *Astraspis* and *Arandaspis* prove a lateral line system was developed and that modifications of the brain had already taken place.
- (4) Given that the dorsal shield in both astraspid and eriptichids is composed of polygonal scales ("tesserae"), it has been considered by several workers to be primitive. Despite numerous attempts based on this hypothesis, often based on the time of the first appearance of the various groups in the geological record, there is uncertainty. For instance, certain authors (Denison 1951, 1964, 1967; Miles, and others; see Jarvik 1980) have indicated that statements as to primitiveness based on geological age is not necessarily the case, a subject that has been the source of much debate (below).

2.6 Osteostraci

The cephalaspids (Osteostracomorphi) are the best known group of the ostracoderms (Fig. 2.9). For a long time, they were the only early members in which the internal anatomy of the head was known (Jarvik 1980). Cephalaspids possessed a solid cephalic shield and a scale covered trunk and tail. A major advance in some forms was the presence of paired pectoral fins, replaced by a ventrolateral crest, one or two dorsal fins and a heterocercal caudal fin with occasionally a paired horizontal flap (Heintz 1939). These features indicate a more efficient benthic mode of life than in the heterostracans. The cephalic shield varies considerably in shape and is comprised of an outer exoskeletal and inner endoskeletal part. The endoskeletal component furnishes equivalent comparison data not only with the neurocranium of gnathostomes but also with the dorsal parts of the visceral endoskeleton, the shoulder girdle and possible anterior parts of the pectoral fins (Jarvik 1980), which will be discussed further below. Near the center of the shield is a pair of orbital fenestrae (located as far away from the mud as possible in a benthic mud-grubber) and between them lies the pineal foramen. In front of the latter is the nasohypophysial opening. The fact that distinct grooves are present in *Astraspis* (Jarvik 1980) (Fig. 2.8) as well as in *Arandispis* (Fig. 2.1) proves not only that the lateral line system (we will see it more fully developed in advanced fishes) developed in these early vertebrates but also implies that the modifications of the brain and cranial nerves connected with the development of this system had already taken place. It seems almost certain that these forms had undergone the same specializations as later heterostracans in most important respects. Ventrally, there is a large, hollow oralo-branchial chamber, which apart from the mouth and paired series of external branchial apertures, is covered by small dermal bones (Fig. 2.10).

A third major group of ostracoderms were the anaspids (Anaspida), a group that includes the early Silurian *Jamoytius kerwoodi* (Fig. 2.11). The body shape is much more fish-like than the other groups, indicating a more active mode of life. Possession of both a hypocercal tail and paired fins (Ritchie 1964) may indicate that the group was surface feeders. Although the anaspids were agnathan, there are signs that the lower margins of the mouth were bounded by strong plates of dermal armor analogous to jaws and teeth (Ritchie 1964). Despite these novelties Halstead (1969a) thought this group was closest to the living cyclostomes and several authors believed that the origin of modern agnathans may be found among them. However, Strahan's (1958) view, based on plotting developmental stages, which suggests that it is not possible to derive the modern lampreys, let alone the hagfishes from the anaspids, is becoming increasingly apparent in recent studies.

The taxonomic position of *Jamoytius kerwoodi* has been a source of considerable discussion (Ritchie 1968, 1984). Most recently, Sansom et al. (2010) re-examined the well-known specimen (Figs. 2.12 and 2.13). Taking into account

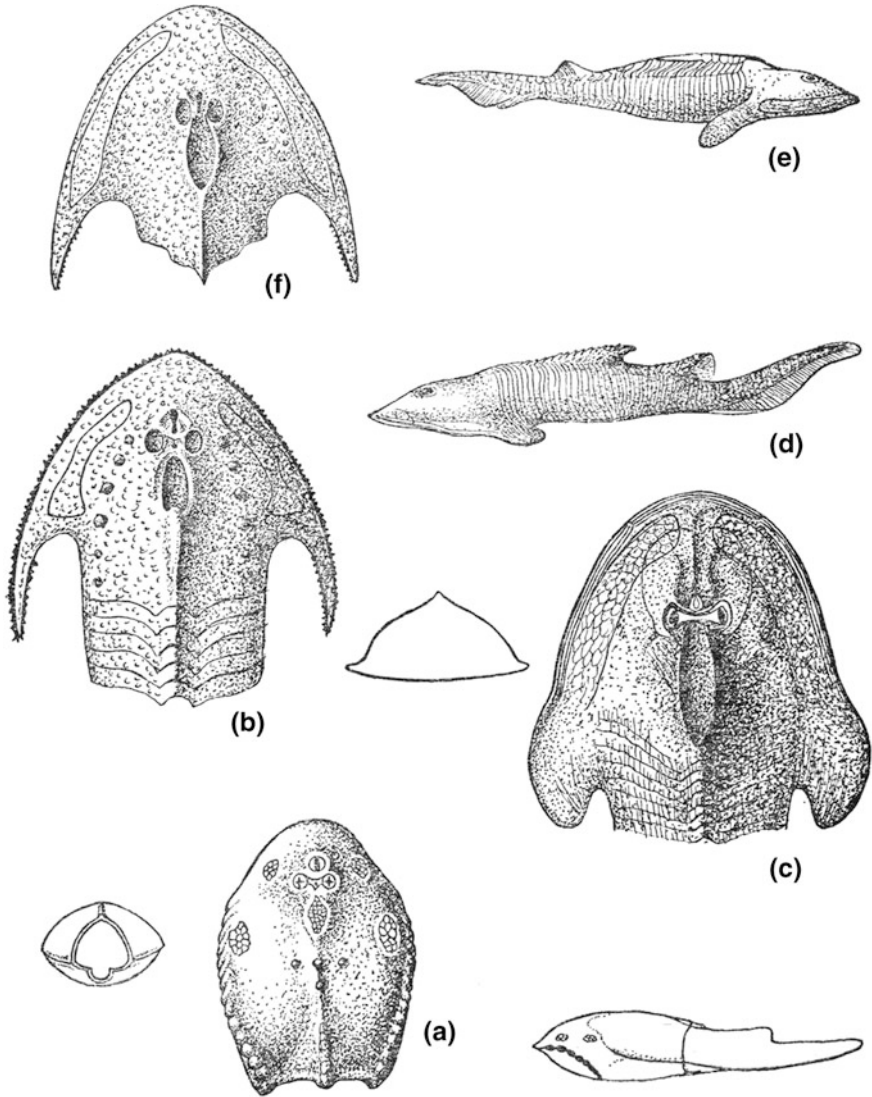
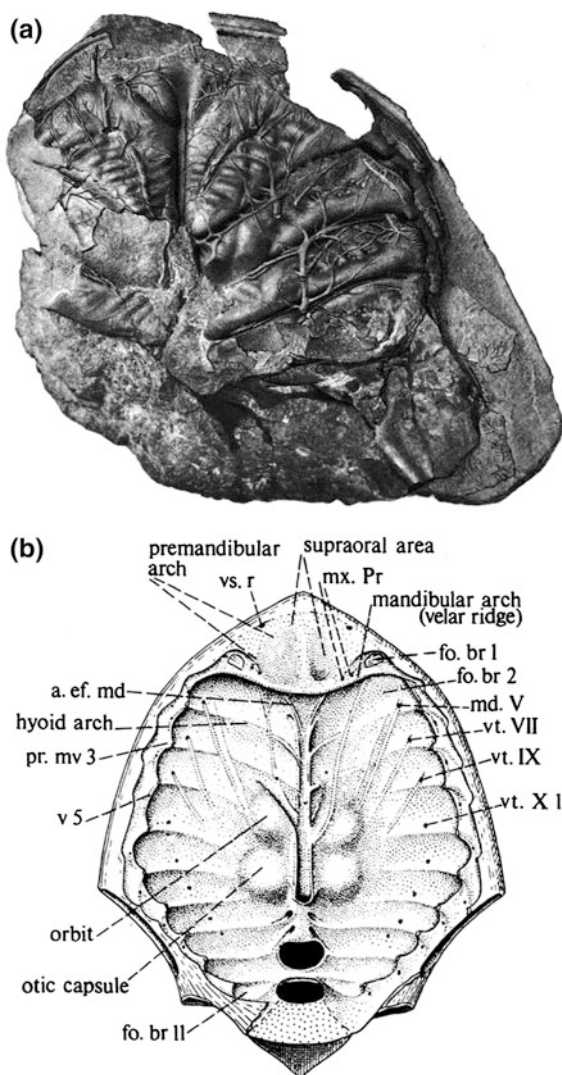


Fig. 2.9 Cephalaspid ostracoderms. **a** *Tremataspis* (Silurian). **b** *Thyestes* (Silurian). **c**, **d** *Aceraspis* (Silurian-Devonian). **e** *Hemicyclaspis* (Silurian-Devonian). **f** *Cephalaspis* (Devonian). From Halstead (1969a)

taphonomic studies, topological analysis, model reconstruction, and elemental analysis, they arrived at a more rigorously tested anatomical interpretation. On the basis of their analysis they provided a new cladistic analysis which showed that *Jamoytius*, a jawless vertebrate, and *Euphanerops* (= *Endeiolepis*) form a clade,

Fig. 2.10 *Cephalaspis signata* (Lower Devonian).
a Photograph of natural cast of oralo-branchial chamber in dorsal view. Cephalaspid *Nectaspis areolata* (Lower Devonian). **b** ventral aspect.
 From Jarvik (1980)



which they named Jamoytiiformes. They proposed that they are stem-gnathostomes rather than proto-lampreys or Anaspida. Their cladogram also revealed the Anaspida to be similarly along the line to gnathostomes, and not related to Petromyzoniformes (lampreys) (Fig. 2.14). Philippe Janvier (1996a) has also shown that the anatomy and physiology of lampreys and hagfishes are so different that it is difficult to reconstruct an ancestral morphotype of the cyclostomes, and there is no clear evidence of any fossil taxon that is neither a fossil hagfish or a fossil lamprey, but would be more closely related to the cyclostomes than to the

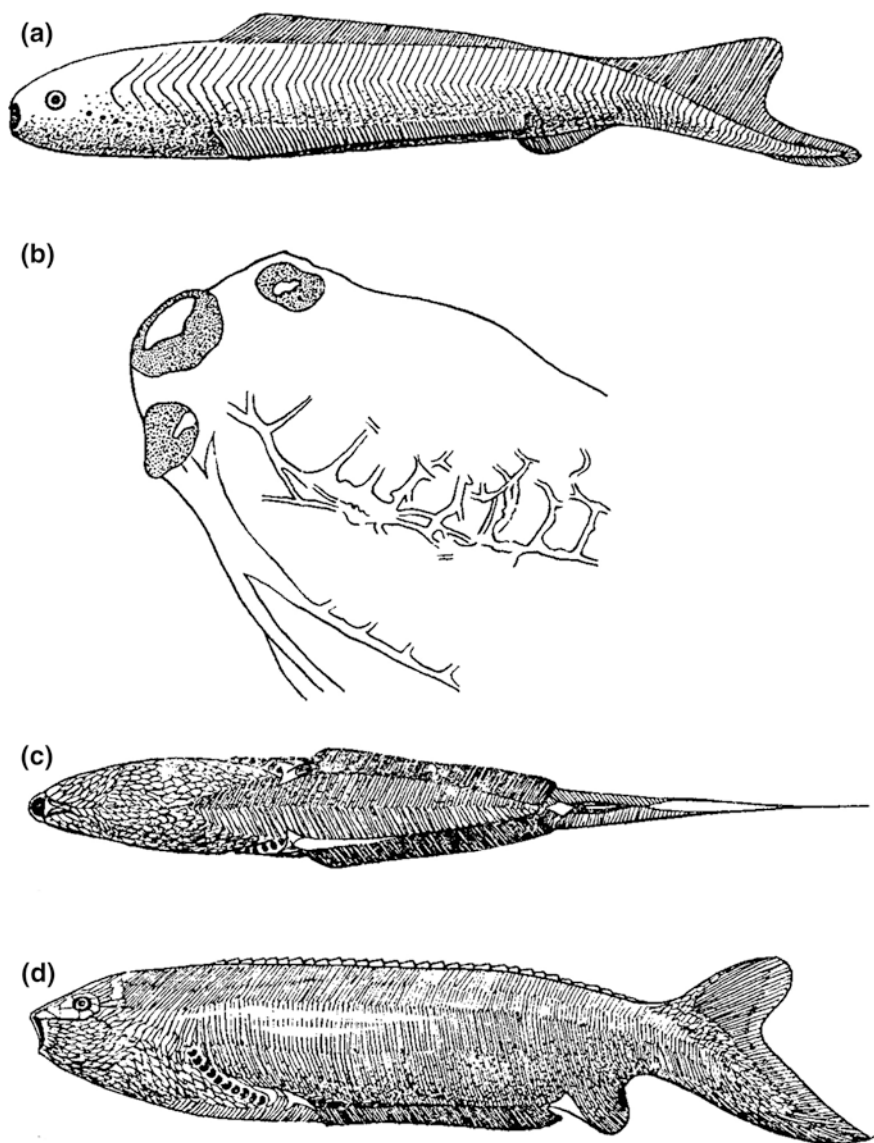


Fig. 2.11 Anaspids. **a, b** *Jamoytius* (Silurian). **a** Restoration (complete). **b** Head region to show branchial basket, eyes and mouth. **c, d** *Pharyngolepis* (Silurian), (**c**) ventral view showing lateral fins, (**d**) lateral view. From Halstead (1969a)

gnathostomes. For instance, he points out that the dorsal, median, nasohypophysial complex of osteostracans, which has been regarded as identical and homologous to that of lampreys, instead that recent investigations (notably on the galeaspid braincase) now suggest that this resemblance is in fact a convergence.

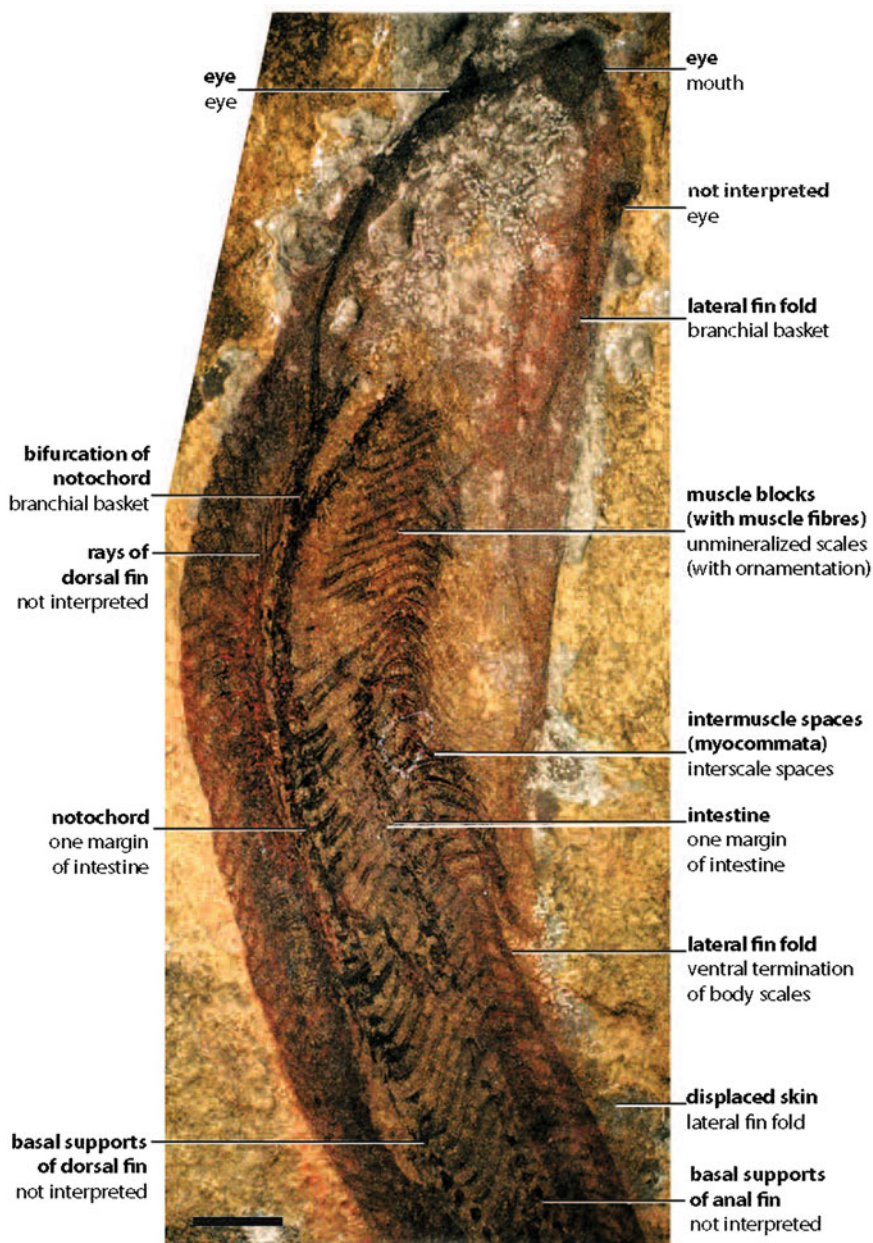
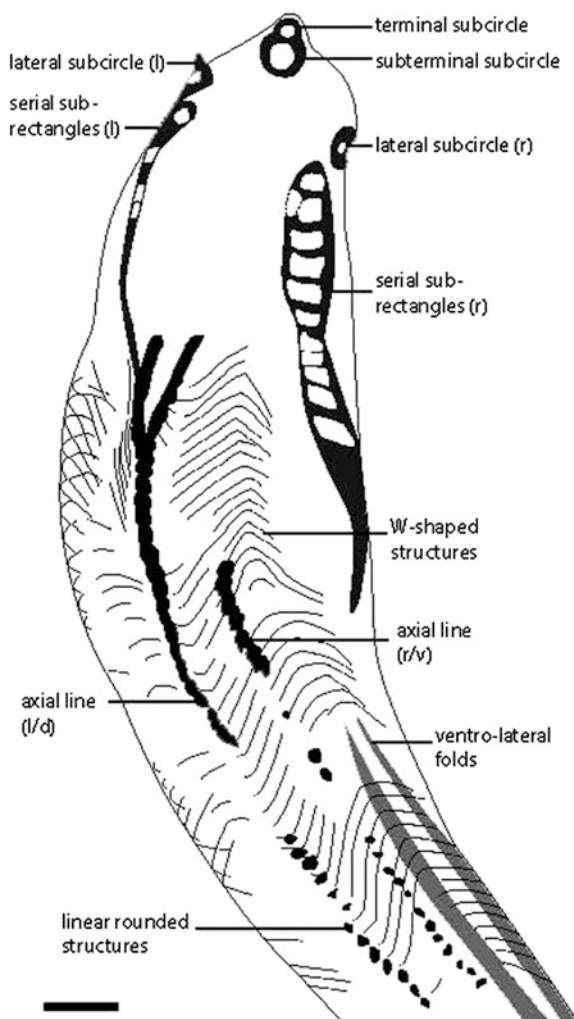


Fig. 2.12 *Jamoytius kerwoodi* White holotype (NHM P11284a) immersed in 90 % ethanol with incident polarized light and filter, illustrating the conflicting interpretations of White (1946), in bold, and Ritchie (1960, 1963, 1968, 1984) in plain text. Scale bar represents 10 mm. From Sansom et al. (2010) and references therein. Copyright Palaeontology

Fig. 2.13 Body parts and topological interpretation of the holotype (NHM P11284a) of *Jamoytius*. Scale bar represents 10 mm. From Sansom et al. (2010). Copyright Palaeontology



Recent findings also show that although there are variations as to the position of certain taxa, the Galeaspida and Osteostraci constantly group together with the Gnathostomes (Forey and Janvier 1993, 1994, Janvier 1996b). Until now an intermediate stage between the separation of the olfactory ducts of agnathans and gnathostomes was not known but evidence from the jawless galeaspids, a 435–370 million-year-old group of ostracoderms from China to Vietnam (Gai et al. 2011), provide the earliest evidence for the clear separation of the paired olfactory organs from the hypophyseal duct as in jawed vertebrates but unlike in the cyclostomes and osteostracans (Fig. 2.15). In vertebrate phylogenetic terms it is regarded as a prerequisite condition for evolutionary developmental biology models for the origin of complete diplorhiny (clear separation of the olfactory organs from the

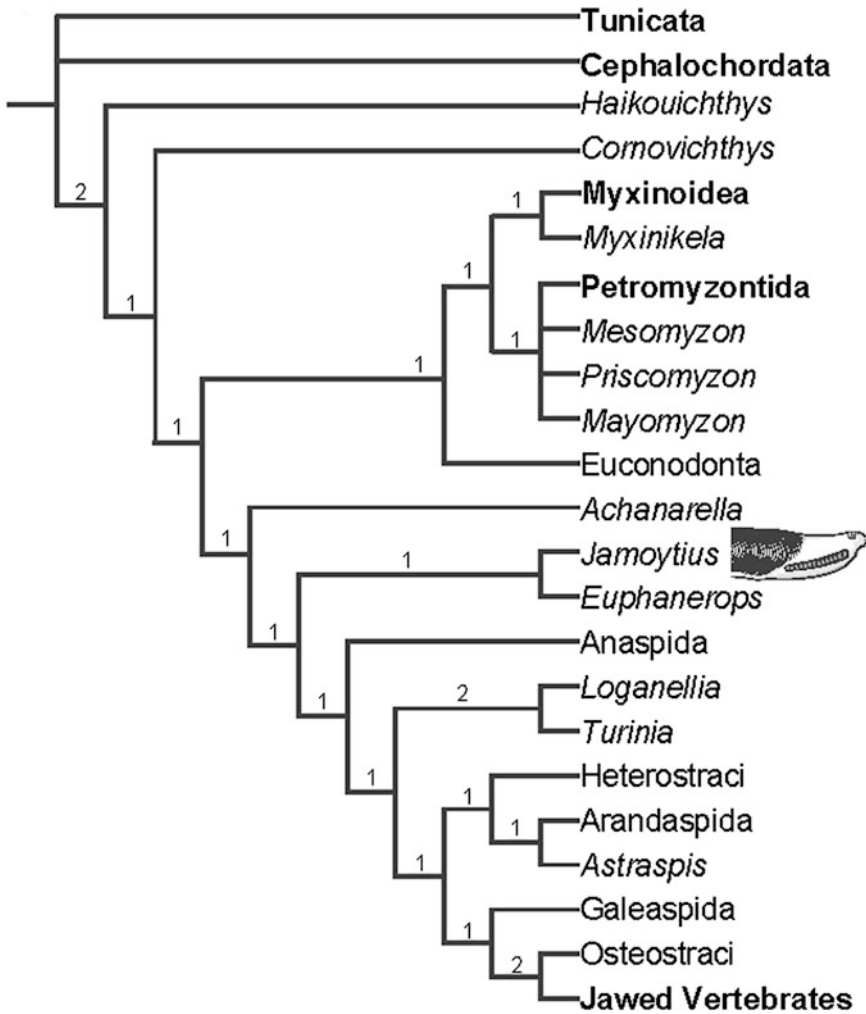


Fig. 2.14 *Jamoytius*. **a** single most parsimonious tree from the unconstrained phylogenetic analysis with decay support indices. **b** Strict consensus of trees resulting from analysis constrained for cyclostome monophyly with decay indices. From Sansom et al. (2010). Copyright Palaeontology

hypophyseal duct) and jaws (Gai et al. 2011). These authors propose this as an intermediate condition in the establishment of diplorhiny and jaws in which this barrier to the forward growth of (neural-crest-derived) craniofacial (ectomesenchyme) development was removed. The way to the possession of jaws was paved by these forms and in the next chapter we will see the emergence of true jaws.

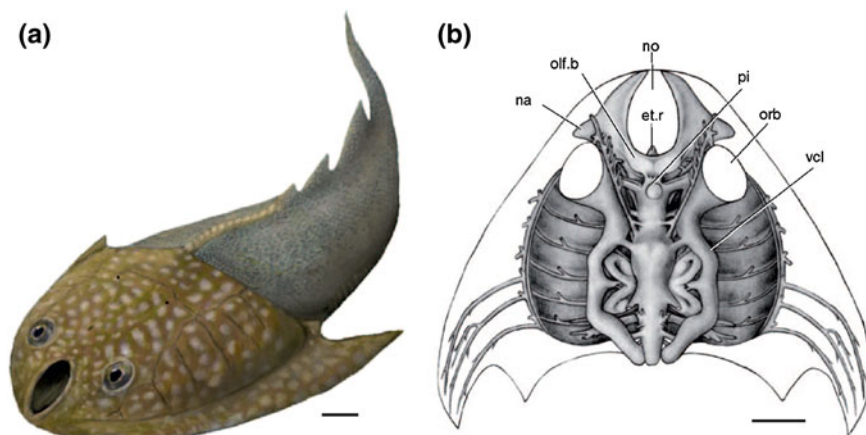


Fig. 2.15 *Shuyu zhejiangensis*, Silurian of Zhejiang, China. **a** Restoration of external morphology. **b** Synthetic restoration of nasal and hypophyseal region. *na* nasal sacs; *no* nostril; *olf.b* olfactory bulb; *et.r* ethmoid rod; *orb* orbital opening; *pi* pineal organ; *vcl* lateral head vein or dorsal jugular vein. Reprinted with permission of Gai et al. (2011). Copyright Macmillan Publishers, Ltd

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