Facts and fancies about early fossil chordates and vertebrates

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The interrelationships between major living vertebrate, and even chordate, groups are now reasonably well resolved thanks to a large amount of generally congruent data derived from molecular sequences, anatomy and physiology. But fossils provide unexpected combinations of characters that help us to understand how the anatomy of modern groups was progressively shaped over millions of years. The dawn of vertebrates is documented by fossils that are preserved as either soft–tissue imprints, or minute skeletal fragments, and it is sometimes difficult for palaeontologists to tell which of them are reliable vertebrate remains and which merely reflect our idea of an ancestral vertebrate.

Vertebrates are a very small group among animals, but they show, along with arthropods and possibly echinoderms, a large number of 'fossilizable' complex characters that can be analysed to reconstruct their relationships; however, most of their anatomically informative fossil record appeared relatively late, about 470 million years ago (Ma). During the past 20 years or so, the fossil record of Palaeozoic era, 535–250 million year (Myr) old, jawless vertebrates has been enriched by the discovery of spectacular soft-bodied fossils preserved as imprints in famous fossil sites such as Chengjiang (535 Myr old) in China[1] and the Burgess Shale in Canada[2] (510 Myr old), but also in other, younger sites that yield exceptional preservation of soft tissues (referred to as 'Konservat-Lagerstätte'). These fossils, long considered to be trivial by palaeoanatomists, have gained a new dimension thanks to investigation and imaging techniques that allow the actual nature of the preserved tissues to be identified, as well as a better understanding of the processes involved in decay and fossilization, thereby avoiding their overinterpretation[3–6].

Palaeontologists have been extensively tracing the earliest evidence for typical vertebrate hard tissues, such as bone, calcified cartilage, dentine (the 'ivory' of our teeth) or enamel, generally in the form of bone fragments, isolated scales or denticles made up of bioapatite (calcium phosphate) and found scattered in early Palaeozoic sediments[7,8]. This search for vertebrate 'microremains' or 'ichthyoliths' (often the only available vertebrate remains in the early Palaeozoic) yielded a large diversity of skeletal elements that could be compared with those of previously known, younger, complete fossils that belong to the major vertebrate groups, and provided evidence for the antiquity of most classic vertebrate hard tissues at least since the Lower or Middle Ordovician (about 477 Ma). However, this research also yielded some skeletal elements that, although suggesting the shape of scales or teeth, do not show all the characteristics of hitherto recognized vertebrate hard tissues. Such cases are frequent among Ordovician to Silurian (480–420 Myr old) microremains, which are dismissed by some, but regarded as possible vertebrates by others. The vertebrate fossil record is documented by an abundance of articulated specimens from periods since the late Silurian (about 430 Ma), but is either poorly represented or very puzzling in earlier periods. However, late Silurian (430 Myr old) articulated vertebrates still turn up (in Scotland, Canada and China[9,10]), and hint at exciting issues in deeper vertebrate history.

This may give the reader the impression that the early history (before the late Silurian) of vertebrate evolution is documented by fossils that look rather like squashed slugs and crushed lobster carapaces, although sometimes articulated. Uninformative data indeed, but, practically, it is all we can offer, except for extremely rare three-dimensionally preserved jawless vertebrates, such as the Ordovician astraspids and arandaspids[11–13], which document the first occurrence of an extensive exoskeleton (or dermal skeleton, the superficial skeleton of vertebrates) with site-specific bones and a lateral-line system (the superficial sense organ of fishes).

Living vertebrates fall into two major clades, the cyclostomes (hagfishes and lampreys) and the gnathostomes (jawed vertebrates). Only the latter produce bone and dentine. Therefore, current vertebrate phylogenies that include fossils suggest that all the Palaeozoic jawless vertebrates that display at least an exoskeleton are more closely related to gnathostomes than to cyclostomes, and are thus 'stem gnathostomes', although lacking jaws[14]. These jawless stem gnathostomes that possess a calcified skeleton are informally referred to as 'ostracoderms' for historical reasons, but form
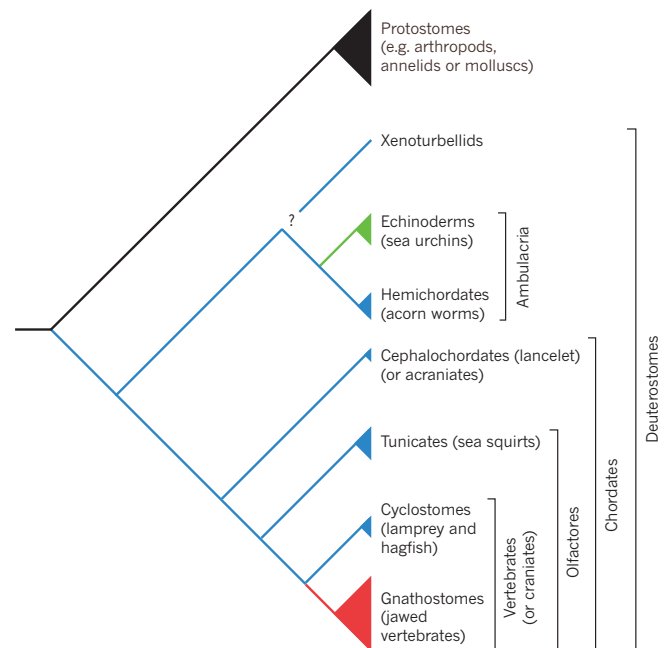
Figure 1 | Interrelationships of the major extant deuterostome clades. Distribution of the major tissues potentially preserved in fossil deuterostomes: no calcified hard tissue except for occasional calcified cartilage in vertebrates (blue), calcitic skeleton (green) and bone, dentine, enamel or enameloid (red).

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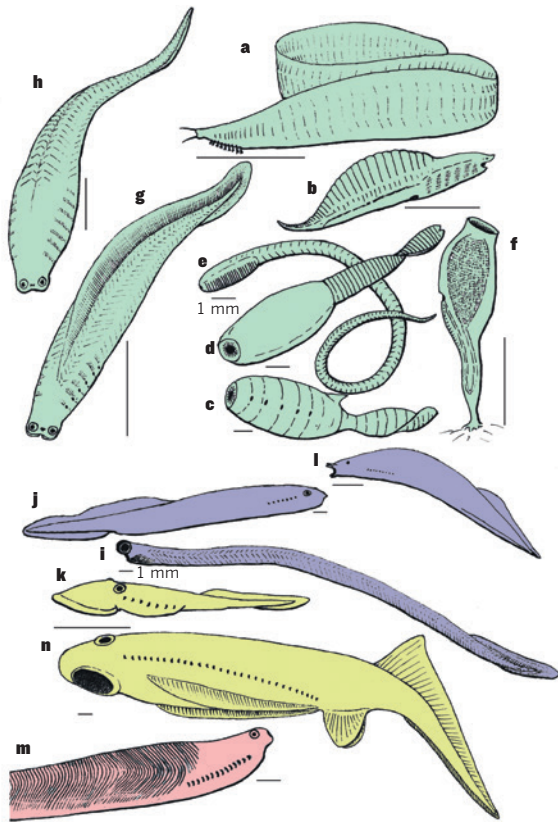
Figure 2 | Soft-bodied presumed fossil chordates and vertebrates, from the Cambrian (green), Silurian (pink), Devonian (yellow) and Carboniferous (purple) periods. a, *Pikaia* was long regarded as a chordate, but is now considered to be either of uncertain affinity, or possibly a close relative of yunnanozoans (adapted from ref. 22). **b**, The yunnanozoan *Haikouella* is a possible stem deuterostome or stem vertebrate (adapted from ref. 28). **c, d**, The vetulicolans *Didazoon* (**c**) and *Banffia* (**d**) are possible stem chordates, stem deuterostomes or stem protostomes (adapted from refs 31, 33). **e**, *Cathaymyrus* is a possible stem cephalochordate (adapted from ref. 34). **f**, *Shankouclava* is a likely tunicate (adapted from ref. 36). **g, h**, *Haikouichthys* (**g**) and *Metaspriggina* (**h**) are stem vertebrates (based on refs 40, 41). **i**, *Clydagnathus* is a euconodont (adapted from ref. 46). **j, k**, *Mayomyzon* (**j**) and *Priscomyzon* (**k**) are two fossil lampreys (adapted from refs 15, 17). **l**, *Myxinikela* is a probable hagfish (adapted from ref. 19). **m**, *Jamoytius* is a jawless stem gnathostome with thin mineralized body scales (adapted from ref. 60). **n**, *Euphanerops*, a jawless vertebrate whose calcified cartilage displays a lamprey-like annular cartilage and branchial basket (adapted from refs 61, 64). Scale bars are 10 mm (**a–d, f–h, j–n**) and 1 mm (**e, i**).

a grade: an array of groups that are more and more closely related to jawed vertebrates and whose anatomy documents the progressive assembly of the gnathostome body plan before the rise of jaws. By contrast, there is no evidence that cyclostomes have ever produced a mineralized skeleton, and neither the four fossil lampreys[15–18], nor the two possible fossil hagfishes[19,20] show any clear indication of a mineralized skeleton.

Soft-bodied chordates and wishful thinking

The bestiary of the Chengjiang and Burgess Shale sites[1,2] comprises a number of animals that have been referred to as either chordates or other deuterostome groups (Fig. 1). Most of these fossils have been referred to as chordates because they show at least some indication of either a notochord (the axial support of chordates, and precursor of the vertebral column), a segmented body structure or gill slits. Although the segmentation of the body musculature and gill apparatus has different developmental causes[21], it is often regarded as a 'signature' of the chordates, but is readily distinguished from the metamery (repeated parts) of arthropods or annelids. Notably, this was the case for *Pikaia* (Fig. 2a), from the Burgess Shale, whose body shows indications of a series of myomeres (muscle blocks)

and a notochord, but whose head bears peculiar appendages (regarded as respiratory organs) and tentacles that are at odds with vertebrate anatomy[22]. Despite the exquisite preservation of numerous specimens of *Pikaia*, this long iconic 'vertebrate ancestor'[23] remains an enigma, and opinions about its affinities oscillate between the chordate hypothesis and a convergent morphology in some protostomes (the sister group of deuterostomes)[22] (Fig. 1). Yunnanozoans (*Yunnanozoon* and *Haikouella*; Fig. 2b) from Chengjiang have also been referred to as chordates[24] because of their presumed notochord, segmented body musculature covered by a cuticle and their seemingly vertebrate-like series of six gill pairs. Notably, they have been referred to as either stem deuterostomes[25], hemichordates, cephalochordates or stem vertebrates[26–28]. The controversy between the advocates of the stem-vertebrate[29] and stem-deuterostome[30] hypotheses reflects the difficulty in assessing the nature of the actual tissues and anatomical characters observed in these fossils. Vetulicolans[31,32] (*Vetulicola*, *Xidazoon*, *Didazoon* and *Pomatrum*; Fig. 2c) from Chengjiang and the somewhat similar *Banffia* (Fig. 2d) from the Burgess Shale display a bipartite structure, with a balloon-shaped, cuticle-covered head laterally pierced by five presumed gill openings, and a flattened segmented tail[33]. *Banffia*, however, seems devoid of gill openings and displays mid-gut diverticulae that rather suggest a protostome anatomy[33]. Again, the vetulicolan's gill openings might suggest a stem deuterostome, but the purported presence of an endostyle (a gland unique to chordates) suggests stem chordate affinity[32]. *Cathaymyrus* (Fig. 2e), from Chengjiang, was described as "*Pikaia*-like"[34]. It has a worm-shaped body with a long series of myomeres, and a distinct row of closely set pharyngeal slits that resemble those of cephalochordates. Other presumed chordates from Chengjiang are the debated tunicates *Cheungkongella*[35] and *Shankouclava*[36] (Fig. 2f). As a whole, all these presumed chordates from the Cambrian, mostly preserved as soft-tissue imprints, only provide tenuous information about their possible phylogenetic relationships. And, despite their often spectacular preservation, there is a risk of overinterpreting their anatomy in the light of widely different living organisms. A notable example of this problem is *Ainiktozoon* (a much younger fossil from the Silurian (430 Ma) of Scotland), which has been interpreted both as a possible chordate because of its segmented body[37] and as a thylacocephalan — a peculiar extinct arthropod group[38].

The myllokunmingiids (for example, *Myllokunmingia* and *Haikouichthys*; Fig. 2g)[39,40] from Chengjiang and the similar *Metaspriggina*[41] (Fig. 2h) from the Burgess Shale look more familiar to vertebrate specialists, as they are clearly 'fish-like'. Despite their similarities, *Metaspriggina* provides better information about the arrangement of gill bars and eye structure. Although only a small number of characters can actually be observed on this kind of material, character analyses have resolved myllokunmingiids as paraphyletic, with *Myllokunmingia* as a stem vertebrate, and *Haikouichthys* as a stem lamprey[39]. More recent analyses suggest that all myllokunmingiids, and probably *Metaspriggina*, are stem vertebrates, but appear in a basal polytomy in the vertebrate tree, more crownward than *Pikaia*, but less so than any crown-group vertebrate (the last common ancestor to living vertebrates and all their fossil relatives)[41]. By combining myllokunmingiids and *Metaspriggina* data, a better reconstruction of the most likely Cambrian vertebrates is possible — a jawless 'fish' with a pair of large, anterodorsally facing camera eyes, a small median olfactory organ, 5–7 pairs of gill arches, a stomach, a series of chevron-shaped myomeres and a median fin web (Fig. 2g, h), thereby remotely resembling old hypothetical reconstructions of ancestral vertebrates[42] (Box 1).

The soft-bodied fossil record of the vertebrates is not limited to the Cambrian, and after the Cambrian 'squashed slug' episode comes the saga of the conodonts. Conodonts are minute tooth- or comb-like elements, or denticles, that are made up of bioapatite (like vertebrate teeth) and occur in marine sediments from the Cambrian to the Late Triassic (about 530–200 Ma). Depending on their internal structure, conodonts fall into three groups: protoconodonts, paraconodonts and euconodonts, the latter being the only monophyletic one[43]. For more than a century, conodonts have received diverse, sometimes fanciful interpretations, until the 1983 publication of the first 'conodont-bearing animal', from the Carboniferous

(330 Ma): a conodont assemblage located in the mouth of an eel-shaped animal preserved as a soft-tissue imprint[44]. Other specimens have since turned up[45], but so far all known articulated conodont-bearing animals are euconodonts. Anatomically, a euconodont-bearing animal has a small head with large paired eyes, a mouth or pharynx containing a large number of denticles, an elongated eel-shaped body with chevron-shaped myomeres, and a small caudal fin supported by possibly cartilaginous rods (Fig. 2i)[46,47]. Superficially, this agrees with vertebrate morphology, although the absence of more typical vertebrate structures, such as gill arches, remains puzzling. The most contentious question was whether euconodont denticle tissues were homologous with vertebrate teeth and odontodes (skin denticles; Fig. 3a), a scenario that was advocated by some[48], but rejected by others[49]. This controversy was finally resolved with the demonstration, by means of high-resolution microtomographic techniques, that euconodont denticle structure and growth were largely at odds with that of vertebrate odontodes[43]. Nevertheless, there remains a chordate- or vertebrate-like aspect to the euconodont body imprints, which does not preclude their position as either stem vertebrates or stem cyclostomes (Fig. 4). During the past 15 years, euconodonts were almost constantly considered in phylogenetic analyses of early vertebrates, and their position as basal-most stem gnathostomes was essentially supported by the presence of the phosphatic denticles[50], which were then assumed to be homologues of gnathostome hard tissues, but lacking in all cyclostomes. However, an old hypothesis that euconodonts might be allied to cyclostomes, and more specifically hagfishes, periodically reappears in the literature[51–53]. For example, the enigmatic Carboniferous protoconodont-like soft-bodied fossil *Conopiscius*[54] shows, like euconodont-bearing animals, a series of chevron-shaped myomeres, but a single pair of hollow, weakly mineralized denticles[52]. It has been suggested that conodont denticles were partly or entirely capped with a keratinous tissue[51,52], which would remain in living cyclostomes. This hypothesis has now been dismissed[55]. The controversy about the homology of the para- and euconodont elements now seems to be settled, and all that soft-tissue data can currently suggest is that euconodonts might be either stem vertebrates, stem cyclostomes (Fig. 4) or, less likely, stem lampreys or stem hagfishes.

Other possible soft-bodied fossil chordates occur here and there, notably in Silurian to Carboniferous rocks, and some are more readily recognized as vertebrates, because they superficially resemble living hagfishes or lampreys. However, the risk of being misled by wishful thinking when making such comparisons is much the same as with odd Cambrian fossils. The fossil lampreys came as a surprise when first discovered in Carboniferous 300-Myr-old rocks, because of their striking overall resemblance to modern forms. *Mayomyzon*[15] (Fig. 2j), preserved as an imprint from the Mazon Creek Lagerstätte in Illinois, looks somewhat like a radiograph of a small modern lamprey. The image shows the outline of the body, the gill pouches and the characteristic cartilages of the 'tongue' apparatus. Other fossil lampreys turned up in the Carboniferous[16] and the Late Devonian (around 360 Ma)[17]. The latter, *Priscomyzon* (Fig. 2k), shows annular cartilage that supports the characteristic oral funnel. The two presumed fossil hagfishes, both coeval with *Mayomyzon*, are more questionable. *Myxinikela*[19] (Fig. 2l) has cartilage imprints and tentacles that do resemble those of hagfishes, but *Myxineidus*[20] was referred to as a hagfish based only on the impression of two V-shaped rows of keratinous teeth that resemble those of living hagfishes. The Mazon Creek Lagerstätte has also yielded peculiar presumed soft-bodied jawless vertebrates, *Pipiscius* and *Gilpichthys*[56]. The former has a lamprey-like oral funnel, and the latter shows possible impressions of sharp, non-mineralized teeth that resemble those of hagfishes[57]. Yet this interpretation remains controversial[58].

Another peculiar Palaeozoic soft-bodied vertebrate is *Jamoytius* (Fig. 2m)[59], from the Silurian (about 438 Ma) of Scotland, which was first regarded as an 'ancestral chordate'. New investigations show that the series of W-shaped imprints on the trunk of *Jamoytius* are not merely soft-tissue imprints of myomeres, but weakly mineralized scales[60]. With its median nostril and about ten gill openings, *Jamoytius* is otherwise suggestive of a lamprey and is often regarded as closely related to the younger, Devonian euphaneropids (*Euphanerops*, *Cornovichthys*, *Achanarella*; Fig. 2n),

whose morphology is now best known from well-preserved 380-Myr-old *Euphanerops* material from the Late Devonian Miguasha Lagerstätte in Canada. Young individuals of *Euphanerops* are preserved as soft-tissue stains, but large individuals also show peculiar spongy calcifications of various elements of the endoskeleton (the internal, cartilaginous or bony skeleton of vertebrates), notably the fin radials, gill bars, vertebral elements, and elements that resemble the 'tongue' and annular cartilages of lampreys[61]. The most peculiar feature of *Euphanerops* is the large number (about 30 pairs) of gill bars that form its lamprey-like gill basket and extend back to the anal region. This is confirmed by a three dimensionally preserved specimen that shows impressions of the gill filaments[62]. Besides this feature, the overall appearance of *Euphanerops* resembles that of an anaspid, a group of Silurian–Devonian 'ostracoderms' that were long thought to be ancestral to lampreys, but are now regarded as being among the basal-most stem gnathostomes[60,61,63] (Fig. 4). Like anaspids, *Euphanerops* displays a long, posteroventrally slanting tail and a large anal fin, suggested to be paired — a unique case among vertebrates[64]. However, this requires confirmation, as does the elongate, paired ventrolateral fins that seem to have extended ventrally to the gill basket[61]. Whatever their relationships to *Jamoytius*, euphaneropids did not possess mineralized scales, but do have some endoskeletal characters uniquely shared with lampreys[65].

Finally, *Palaeospondylus*, from the Middle Devonian (390 Ma) of Scotland is still the most enigmatic early vertebrate, although it is known by hundreds of specimens. It is not preserved as a mere imprint, but clearly displays a vertebral column, a caudal fin with radials and fin supports, possible paired appendages, and its skull consists of several peculiar skeletal elements that cannot be clearly homologized with classic components of the vertebrate skull, be it a cyclostome or a gnathostome[66,67]. All of its skeletal elements are exclusively made up of a spongy calcified matter, which resembles that of the calcified endoskeleton of *Euphanerops*[61], and

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BOX 1

Fossils and 'ancestors'

When the first description of the myllokunmingiids was published[39], early vertebrate palaeontologists were struck by the resemblance between these Lower Cambrian soft-bodied fossils from Chengjiang and various imaginary reconstructions of an ancestral vertebrate published during the twentieth century. For example, myllokunmingiids surprisingly resemble this imaginary reconstruction of an 'ancestral cephalochordate' (amphioxus) (see Figure) published at a time when some zoologists considered the absence of a complex head in living cephalochordates could be secondary. This reconstruction is a curious mix of a rather vertebrate-like, and even a 'ostracoderm'-like head, and some cephalochordate characters. It was thus intended to suggest that the overall morphology of the common ancestor to cephalochordates and vertebrates was rather vertebrate-like. Do such reconstructions of an entirely hypothetical 'ancestor', essentially based on inferences from extant and some fossil vertebrates, influence the way we interpret odd and poorly preserved soft-bodied fossils? Or do such fossils lead us to search for such old and supposedly prophetic reconstructions to justify intuitions? Although palaeontologists try to take a cold look at characters, it is probable that such reconstructions, based on the tree of life in vogue at a given time, unconsciously affect the way researchers look at certain fossils and favour wishful thinking when in search of ancestors. This was probably also the case for the interpretation of *Pikaia*. Image adapted with permission from ref. 42.
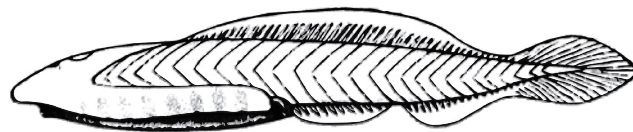
is therefore interpreted as calcified cartilage. Its resemblance to embryonic cartilage of extant osteichthyans (bony jawed vertebrates) has even led to the suggestion that *Palaeospondylus* might be a peculiar bony fish that failed to develop bone[68]. The anatomy of *Palaeospondylus* has been described, and this 'fish' has been tentatively referred to as practically all major fossil and extant vertebrate groups: hagfishes, lampreys, 'placoderms' (extinct armoured jawed fish), chondrichthyans (sharks, rays and chimaeras), teleosts, lungfish larvae and amphibian tadpoles[67,68]. All these interpretations are either dismissed or still debated. However, data on hagfish skeletal development[69] seem to enhance the superficial resemblance, already alluded to by some early authors, between the arrangement of certain elements of the *Palaeospondylus* skull and that of the cranial cartilages of late hagfish embryos. In addition, developmental data suggest that the absence of vertebral elements in hagfishes is probably secondary[70], and the vertebral column of *Palaeospondylus* may thus not preclude close relationships to hagfishes. Yet, no unambiguous character seems to be uniquely shared by hagfishes and *Palaeospondylus*.

These presumed soft-bodied chordates and vertebrates that were mostly devoid of hard tissue, except for occasional calcified cartilage, are generally collapsed and preserved as traces of variously transformed soft tissue[3,6]. Their reconstruction in 3D is often difficult, even by means of sophisticated techniques[60], and their descriptions are characteristically cautious. Should we simply forget about them? Do they provide us with any useful information? Or are they merely material support to our imagination, which is in turn guided by current views about the interrelationships of living animal groups? The art of reconstruction for palaeontologists is usually to put flesh on bones, but it is difficult when there is only decayed flesh and no bone! However, it is worth trying.

Hard–tissue data

Early vertebrate hard tissues are reputedly easier to identify. Their structure can be studied in detail by means of material or virtual (microtomographic) sections, eventually in 3D[71], and classic scanning electron microscopy techniques. Their characteristics can then be compared with those of living or more recent and well-known species. Nevertheless, palaeontologists are confronted with many of the same problems as for soft-tissue preservations when dealing with the earliest presumed vertebrate skeletal remains. The first clues to vertebrate hard tissues are that they are made of bioapatite; the tissues often show an ornamentation of tubercles (odontodes), or ridges, with a structure that resembles that of our teeth;

they have dentine that contains thin canals for cell processes; eventually enamel (enameloid) is present; and there is a pulp cavity (Fig. 3a). Other useful characters may be the surface ultra-sculpture, the small spaces that housed bone cells, and the grooves or canals that housed lateral-line sense organs. The exoskeleton of the earliest, articulated and duly recognized vertebrates, such as arandaspids or astraspids (Fig. 3b, c), show at least some of these characters[13,72,73]. However, younger vertebrates known from complete specimens, such as the Silurian and Devonian anaspids or galeaspids[73,74], lack dentine, and many of the Cambrian to Silurian 'microremains', referred to as vertebrates owing to the aspect of their ornamentation or their scale-like shape, lack some of these characteristic tissues. Instead, they show other hard tissues that no longer exist, such as lamelline (acellular dentine)[8,73]. Therefore, the earliest evidence for possible vertebrate hard-tissue remains are barely less puzzling than the Cambrian soft-bodied animals.

The first controversy about these problematic skeletal fragments arose with the discovery of *Anatolepis* from the Lower Ordovician and Upper Cambrian[75,76]. *Anatolepis* is represented by minute phosphatic fragments ornamented with elongate tubercles (Fig. 3d), which vaguely resemble the exoskeletal ornamentation of certain Silurian–Devonian ostracoderms, notably heterostracans (Fig. 4). Therefore, *Anatolepis* was first regarded as a possible heterostracan; this was immediately contested by some, whereas others considered it plausible. At around the same time, *Anatolepis* was tentatively referred to an arthropod, but again this raised debate. Later studies of the tissue structure of these fragments using new techniques showed that the tubercles of *Anatolepis* were in fact hollowed by a pulp cavity capped by a somewhat dentine-like tissue, and connected by a lamellar tissue, which was perforated by thin vertical canals (Fig. 3e)[77]. Nevertheless, these new data failed to convince the sceptics[78]. *Anatolepis* may remain an enigma — as long as no articulated individual turns up. Other alleged Late Cambrian vertebrate bone fragments have been described from Australia[79] and superficially resemble the exoskeletal bone ornamentation of the Ordovician arandaspid *Porophoraspis*[11]; however, they are also strikingly similar to some Palaeozoic arthropod carapaces[78]. In sum, apart from the euconodonts, whose possible vertebrate affinities essentially rest on soft-tissue characters, there is no undisputed evidence for Cambrian vertebrates that possess a mineralized skeleton. By contrast, the following Ordovician period not only yields articulated vertebrates covered with extensive mineralized armour and scales, but also numerous isolated bone fragments and scales[80]. Most of these microremains, such as
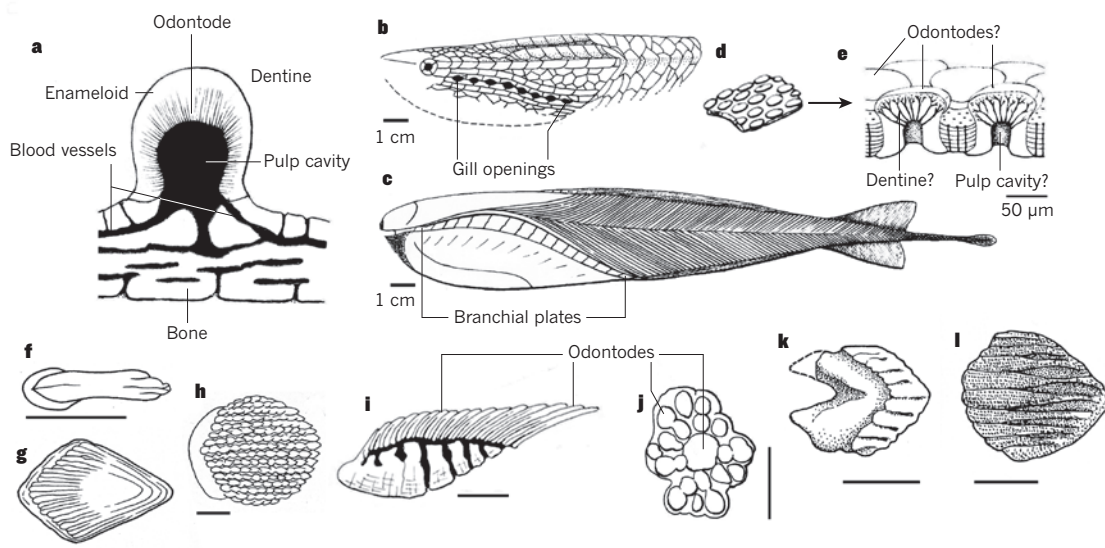
Figure 3 | Late Cambrian, Ordovician and early Silurian vertebrate exoskeletons. **a**, Ideal vertical section through a typical, ornamented vertebrate exoskeleton showing a tubercle (odontode) attached to a bony base (not to scale). **b, c**, The most complete articulated Ordovician vertebrates, *Astraspis* (**b**) and *Sacabambaspis* (**c**) (adapted from refs 86, 93). **d, e**, Exoskeleton fragment of the debated vertebrate *Anatolepis* (**d**) and vertical section of the possible odontodes (**e**) (adapted from ref. 77). **f–l**, Major types of isolated vertebrate scales retrieved from Upper Ordovician and Lower Silurian rocks: a thelodont (**f**), an 'acanthodian' (**g**), the possible chondrichthyan *Mongolepis* as an external view (**h**) and vertical section (**i**), and the vertebrates of uncertain affinities *Tesakoviaspis* (**j**), *Apedolepis* (**k**) and *Areyongalepis* (**l**). (**f–j** adapted from ref. 8 and **k, l** from ref. 82) Scale bars are 1 cm (**b, c**), 0.5 mm (**f–l**) and 50 μm (**e**).
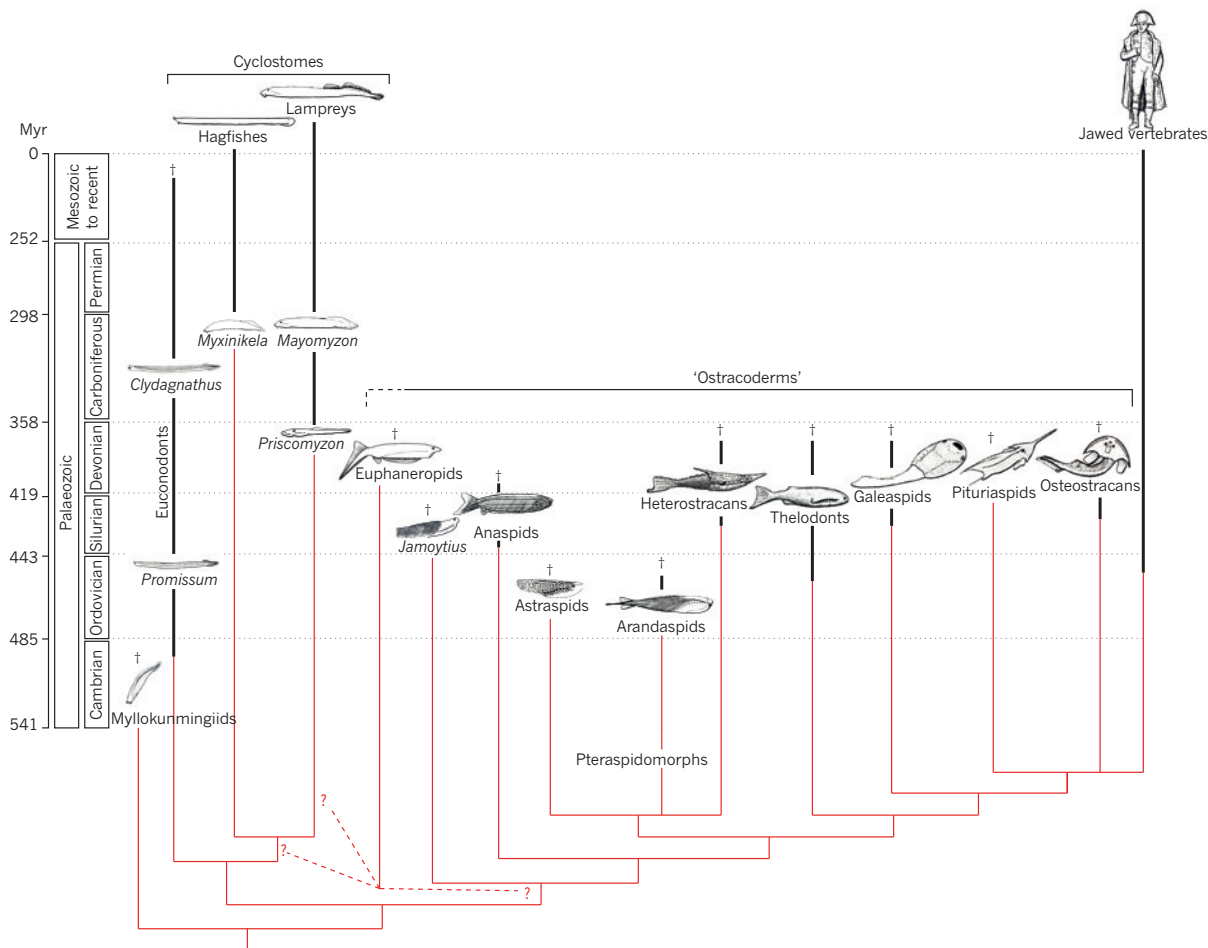
Figure 4 | Distribution through geological time (black bars), and patterns of interrelationships (red) of the major Palaeozoic jawless vertebrate groups and their extant relatives. Pattern of relationships adapted from ref. 60, except for the position of the euphaneropids. *Promissum* and *Clydagnathus* adapted from ref. 47; lampreys, hagfishes, *Myxinikela*, *Mayomyzon*, *Priscomyzon*, Euphaneropids, Anaspids, Heterostracans and Thelodonts adapted from ref. 65; *Jamoytius* adapted from ref. 60; *Astraspids* adapted from ref. 86; Arandaspids adapted from ref. 93. Not to scale. †Extinct groups.

Skiichthys[81] (a possible 'placoderm') or other scale-like elements, show at least some hard-tissue characters that are shared with younger vertebrate groups. However, others, such as *Areyongalepis* (Fig. 3k) and *Apedolepis* (Fig. 3l) are very puzzling[82]. Isolated vertebrate remains occur sporadically throughout most of the Ordovician and early Silurian and, despite their amazing diversity of hard-tissue structures, show an increasingly close resemblance to structures and ornamentations of the late Silurian and Devonian vertebrate groups, which are known from complete skeletons.

The three articulated Ordovician vertebrates, *Astraspis* (Fig. 3b), *Arandaspis* and *Sacabambaspis* (Fig. 3c)[11–13], and the bone assemblages of *Eriptychius*[83] and *Ritchieichthys*[84] show the overall morphology of the earliest vertebrates that have an extensive exoskeleton with a large head shield composed of either large plates or polygonal platelets, a posteriorly slanting series of numerous gill openings, and a scale-covered body and tail[85,86]. However, they provide no information about internal anatomy, apart from uninformative fragments of calcified cartilage in *Eriptychius*[83], and faint internal impressions of the gill pouches in *Astraspis* and *Sacabambaspis*. Orbits indicate the presence of eyes, and paired dorsal openings in arandaspids are interpreted as pineal foramina, but the position of nasal openings is unclear[57]. The lower lip of arandaspids is covered with a series of minute platelets, suggesting a filtering function, as in the younger heterostracans[87]. These articulated fossils may give the impression that all Ordovician fishes looked like big armoured tadpoles. However, the diversity of the scales and other microremains retrieved from coeval Ordovician rocks suggests that different morphologies may have existed already. *Porophoraspis* is regarded as an arandaspid, but some relatively large plates referred as this genus are difficult to reconcile with the head-skeleton

morphology of either *Arandaspis* or *Sacabambaspis*[11]. Among the isolated scales retrieved from Ordovician and Early Silurian rocks, some clearly belong to thelodonts (a group of 'ostracoderms'; Figs 3f, 4) and 'acanthodians' (Fig. 3g; presumed stem chondrichthyans). Both of these were known later by complete specimens, whereas others, such as *Mongolepis* (Fig. 3h, i), *Teslepis*, *Sodolepis* and *Tesakoviaspis* (Fig. 3j)[8], all presumed chondrichthyans (shark relatives), and still-unnamed forms[80] may have belonged to vertebrates that had an entirely micromeric (composed of minute scales) exoskeleton like that of sharks. Their body structure will remain unknown unless articulated material is discovered in some still-elusive Lagerstätte. Although some of these scales are, by default, referred to as chondrichthyans, they are in fact vertebrates in limbo.

After the Middle Ordovician, no articulated vertebrate turns up until the mid-Silurian (around 433 Ma), apart from the Late Ordovician euconodont *Promissum*[45]. Then, relatively complete representatives of the six major Silurian–Devonian 'ostracoderm' groups (anaspids, heterostracans, thelodonts, galeaspids, pituriaspids and osteostracans; Fig. 4) occur, and, shortly after (about 430 Ma) the earliest complete jawed vertebrates, notably 'placoderms'[10], 'acanthodians' and osteichthyans (bony fishes)[9]. Such articulated or well-preserved material is generally the key to suggesting a systematic position for some of the microremains from the Ordovician and early Silurian, and tracing back the distribution of these major groups through time (Fig. 4). Moreover, the number of anatomical characters that this material now offers us allows for better supported reconstructions of the interrelationships of these groups.

The phylogenetic trees of fossil and living vertebrates generally agree on the position of the 'ostracoderms' as a series of jawless stem gnathostomes,

with galeaspids, osteostracans (and possibly pituriaspids) as successive sister groups of the jawed vertebrates[50,57,60,88] (Fig. 4). This is partly because galeaspids and osteostracans have an extensively calcified or ossified endoskeleton, which preserves the cavities and canals that housed the brain, sensory capsules, nerves and blood vessels, including the pectoral girdles and fins in osteostracans, thereby providing a wealth of anatomical characters that can be compared with their homologues in jawed vertebrates[57,88,89]. However, the relationships of other 'ostracoderm' groups is poorly supported because they are devoid of a calcified endoskeleton, and their exoskeleton, which is sometimes entirely micromeric, provides indirect information about their internal anatomy in the form of faint impressions of, for example, gill pouches, brain, olfactory organs or labyrinth[57]. As is the case for heterostracans, but there are no data for anaspids, and only a few thelodonts provide some information[57,90,91]. Heterostracans are characterized by a single pair of common branchial openings, and are gathered with astraspids and arandaspids in the pteraspidomorphs (Fig. 4)[57,72]. However, apart from the presence of large median dorsal and ventral head plates made of acellular bone, and a similar honeycomb-like layer in the exoskeleton of heterostracans and arandaspids, shared derived characters that are unique to these three groups are scarce.

For almost a century, most debates about the relationships of the various 'ostracoderm' groups have been centred on the structure of the rostral part of the head: the olfactory organs, their relation to the hypophysis (pituitary) and the oral region. Classically, the dorsal position of the common nasal and hypophyseal duct of osteostracans and anaspids was compared with the condition in lampreys[92,93]. However, the recent description of the same region of the head in galeaspids has provided new insights[94]. The still elusive heterostracan and thelodont internal anatomy could possibly be reconstructed on the basis of that of galeaspids, with paired nasal sacs and an anteriorly directed hypophyseal duct. This would mean that a galeaspid-like anatomy might have been widespread among stem gnathostomes, and that the allegedly lamprey-like nasohypophyseal complex of osteostracans is independently derived from such a condition.

Fossils, phylogeny and technologies

It is sometimes said that fossils never, or rarely, overturn patterns of relationships based on extant organisms. Patterson[95] mentioned a few possible exceptions, notably the 'calcichordate theory'[96], which assumed that an ensemble of Palaeozoic echinoderm-like groups classically referred to as stylophorans are a paraphyletic array of stem chordates, stem cephalochordates, stem tunicates and stem vertebrates, the calcitic skeleton of which has been lost several times. It also suggested that tunicates, and not cephalochordates, were the closest extant relatives of vertebrates (contra to the then accepted relationships). This theory has raised heated controversies[97], but all stylophorans are now regarded as stem echinoderms. However, recent molecular phylogenies strongly support this tunicate–vertebrate relationship[98]. Tunicates and vertebrates are therefore gathered in a group called Olfactores, a name that, paradoxically, was erected in the framework of the calcichordate theory[96], because some stylophorans that were thought to be stem tunicates display internal structures that resemble vertebrate olfactory organs. Patterson[95] predicted that molecular sequence data would be the best test of the 'calcichordate theory', and, coincidentally, the test seems to have been positive regarding tunicate relationships.

Regarding vertebrates, the hypothesis of living cyclostome paraphyly (that lampreys are more closely related to gnathostomes than to hagfishes) was only based on phenotypic data derived from extant species[99]. Palaeontological data have been merely adapted to this pattern of relationships, because of the long-lasting conviction that certain 'ostracoderms' (osteostracans and anaspids) were most closely related to lampreys[57,93]. More accurate character analyses later showed that 'ostracoderms' were exclusively stem gnathostomes, and the recent revival of cyclostome monophyly had no major bearing on their interrelationships[60]. None of the fossils discussed earlier, be they soft-body imprints, bone fragments, scales or articulated skeletons, seems currently liable to overturn the interrelationships of the major extant vertebrate groups. However, they provide a minimal age for certain characters (thus the groups they define), and

may reveal unsuspected character combinations that allow the reconstruction of the stepwise assembly of novel body plans that foreshadow major evolutionary transitions. This is, for example, what 'ostracoderms' document with the succession of characters that make up the jawed vertebrate body: the rise of the exoskeleton, cellular bone, endoskeletal bone, enlarged cerebellum or pectoral fins, but they are still rather powerless in providing a scenario for the rise of jaws, which is largely left in the hands of evolutionary developmental biologists. Nevertheless, the recent consideration of braincase anatomy in the basal-most 'placoderms' suggests that the anatomical gap between such 'ostracoderms' as galeaspids and osteostracans, and the earliest jawed vertebrates, may not have been that large, and that the prerequisites to the rise of jaws were already there[100].

The future of early vertebrate palaeontology rests on the quality of the data it can provide, especially on fossils derived from crucial periods, such as the Late Cambrian, Early Ordovician and early Silurian. Early vertebrates are generally difficult material, compressed or crushed in hard rocks. Throughout the twentieth century, some early vertebrate palaeontologists gave much weight to the then new preparation techniques[57]. Nowadays, they would be amazed by the quality of the data obtained from high-resolution X-ray microtomography. Also, soft tissues preserved as mere stains can be studied by element mapping that provides information on the fossilization process and sometimes the nature of the preserved tissues themselves. Armed with these non-destructive techniques, early vertebrate palaeontologists can considerably refine their observations and must not be afraid of proposing audacious interpretations of these miserable remains, even though 'squashed slugs' may be slippery! ∎

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