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Early Jawless Vertebrates and Cyclostome Origins

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Undoubted fossil lampreys are recorded since the Late Devonian (358 Ma), and probable fossil hagfishes since the Late Carboniferous (300 Ma), but molecular clock data suggest a much earlier divergence times for the two groups. In the early 20th century, hagfishes and lampreys were generally thought to have diverged much later from unknown ancestral cyclostomes, in turn derived through 'degeneracy' from some Paleozoic armored jawless vertebrates, or 'ostracoderms.' However, current vertebrate phylogenies suggest that most, if not all, 'ostracoderms' are in fact jawless stem gnathostomes, which retain certain features that were once regarded as unique to the cyclostomes, such as gill pouches or lack of horizontal semicircular canal. The dorsal, median, nasohypophysial complex of osteostracans has been regarded as identical and homologous to that of lampreys, but recent investigation (notably on the galeaspid braincase) now suggests that this resemblance is in fact a convergence. The anatomy and physiology of lampreys and hagfishes are so different that it is difficult to reconstruct an ancestral morphotype of the cyclostomes, assuming that they are a clade, and there is no clear evidence of any fossil taxon that is neither a fossil hagfish nor a fossil lamprey, but would be more closely related to the cyclostomes than to the gnathostomes. A possible exception is the Silurian-Devonian euphaneropids (or 'naked anaspids').

Key words: cyclostomes, hagfish, lamprey, vertebrates, ostracoderms, phylogeny, fossils

INTRODUCTION

The significance of hagfishes and lampreys for vertebrate systematics, then phylogeny, has long been a matter of debate. For Linnaeus (1758) and many naturalists of his time, lampreys were merely "cartilaginous fishes," and their lack of typical, vertically biting jaws was not regarded as an enigma, but a mere modification of the jaws due to their ectoparasitic mode of life. By contrast, Linnaeus curiously classified hagfishes among "intestinal worms" (probably by reference to their legendary endoparasitic mode of life), although they were known to possess much the same large notochord as lampreys. Abildgaard (1792) definitely settled the status of hagfishes as fishes, and akin to lampreys. Duméril (1806) classified hagfishes and lampreys in the group Cyclostomi and pointed out a series of unique anatomical characters they shared (e.g., horny teeth, lingual apparatus, gills enclosed in pouches) that supported a close relationship. Yet Duméril (1812) still alluded to hagfishes as a possible 'intermediate' between polychete worms, and vertebrates. The more detailed anatomical studies by Müller (1839) have led to the clear distinction between the *Hyperotreti* (hagfishes) and *Hyperoartia* (lampreys), but during the entire 19th century, no zoologist made any allusion to the possibility that the cyclostomes were not a "natural group," with the possible exception of Retzius (1881), who was puzzled by the peculiar, and possibly primitive, condition of the hagfish labyrinth. With the rise of the Darwinian view of evo-

lution, and in particular the influence of Haeckel's (1866) tree-like representations of animal relationships, it progressively became common knowledge that the cyclostomes were a primitive offshoot of the vertebrates, and it was finally agreed that, although 'degenerate' in one way or another, they were not derived from a gnathostome-like ancestor or, at any rate, never possessed jaws. However, the old legend of cyclostome 'degeneracy' due to parasitism still underlay all considerations of the group until late in the 20th century.

As comparative anatomy, physiology and embryology progressed, a number of characters shared uniquely by lampreys and gnathostomes (jawed vertebrates) were pointed out, but hagfishes were often left aside from the debate about cyclostome relationships, partly because of their elusive development and their rather odd characters. The two taxa nevertheless remained lumped together in the cyclostomes, for want of a better solution. In Darwinian times, as in the earlier time of Lamarck, all naturalists who dared allude to a historical process of evolutionary transformation were obsessed by the discovery of actual 'transitional forms' between major living taxa. As they were increasingly convinced that the resemblance between living beings was a consequence of a historical process of descent with modification, naturalists searched for taxa that could possibly fill the gaps between what was still intuitively perceived as grades in the Aristotelian Great Chain of Beings. When, in the second half of the 19th century, it progressively became likely that such gaps could no longer be filled by the discovery of new living 'intermediate forms,' scientists turned towards fossils, in hope that deeper in time and closer to the 'origin' such 'intermediate' or 'ancestral' morphologies would turn up.

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Many paleontologists have mulled over the significance of the earliest fossil fishes. The fact that the earliest fossil fishes known around 1850 were heavily armoured forms, superficially resembling sturgeons or catfishes, was most puzzling and somehow seemed to confirm the creationists' view that the earliest fishes were rather similar to what we now call 'bony fishes' (osteichthyans) and that the living cyclostomes are degenerate relatives of such extensively ossified forms. This idea of the "progress of degradation" (i.e., character loss through time) is exemplified by Miller's (1849) desperate attempt at finding, within the Devonian and Silurian (430–360 Myr-old) fossil fishes (and earliest vertebrates known at that time), evidence for what Louis Agassiz later called "the embryonic age of fishes". However, palaeontologists failed to find any transitional form between these early fishes and the cyclostomes. In a straightforward manner, Cope (1889) proposed that, if certain of these peculiar armored fishes, which he called Ostracodermi (ostracoderms), showed no evidence of jaws, they were actually jawless and most closely related to hagfishes and lampreys (still gathered as cyclostomes) (Fig. 1A). Cope therefore coined the name Agnatha (agnathans) for jawless vertebrates, including the fossil ostracoderms and living cyclostomes, which he regarded as what we would now call the sister group of Pisces (fishes). Apparently, Cope was unaware of the fact that the name Gnathostomata (jawed vertebrates) had been erected years before by Gegenbaur (1874), in which he also included the tetrapods. The sister-group relationship between the Agnatha and Pisces (or Gnathostomata) became readily accepted, but, in the earliest years of the 20th century, palaeontologists were still wondering whether the ostracoderms were ancestral to the supposedly degenerate cyclostomes, or to all vertebrates. Kiaer (1924) recognized four major groups of ostracoderms, the Osteostraci, Anaspidi, Heterostraci, and Coelolepida (now known as Thelodonti), and pointed out that the former two shared with lampreys a median dorsal, presumably nasohypophysial opening (an obviously derived condition, considering the then available embryological data for lampreys), whereas the other two (heterostracans and thelodonts) were likely to have possessed paired, separate olfactory capsules (and perhaps nostrils), like the gnathostomes (Fig. 1B). Ostracoderms could therefore be paraphyletic ancestral vertebrates and include stem forms of both the living cyclostomes and gnathostomes. Stensiö (1927) made a thorough morphological study of the extensively ossified osteostracans and apparently confirmed the close anatomical resemblance of the nasohypophysial complex of osteostracans and lampreys, and thus the 'degeneracy' of lampreys relative to their bony fossil jawless relatives or ancestors.

Stensiö (1928, and contra Kiaer, 1924) also made the strange suggestion that hagfishes were derived from another group of armored 'agnathans', the Heterostraci (heterostracans) (Fig. 1C). This theory was based initially on a few, vague arguments, such as the presence of a single common external gill opening and very small eyes in all heterostracans, recalling the condition in myxinid hagfishes (Fig. 2B2). Stensiö and some other paleontologists supported his theory of the "diphyletic origin" of the cyclostomes until the 1970's (Stensiö, 1968; Janvier, 1974; Jarvik, 1980), whereas most other palaeontologists regarded this heterost-

racan-hagfish relationship as unlikely. Instead, there was growing consensus over Kiaer's (1924) theory of a possible relationship of heterostracans to the gnathostomes, based on equally vague arguments, such as the presumably paired olfactory organs and "biting" oral plates that recalled jaws (Kiaer 1928).

Apart from Moy-Thomas and Miles (1971), who still supported agnathan monophyly (Fig. 1D), these remained the dominant views until the late 1970's, when the rise of Hennig's (1950) phylogenetic systematics (now known as 'cladistics') provided a parsimony-based conceptual and methodological framework for reconstructing phylogenies and making them testable. Cladistic analyses of all major fossil and living vertebrate taxa, including ostracoderms, progressively yielded radically new vertebrate trees, showing first the paraphyly of the 'Agnatha' (Fig. 1E), then supporting the status of ostracoderms as paraphyletic stem gnathostomes (Fig. 1F, G); i.e., some, and finally all 'ostracoderms' were more closely related to the gnathostomes than to either hagfishes or lampreys (Janvier, 1978, 1981, 1984, 1993, 1996a, b; Janvier and Blicek, 1979; Maisey, 1986; Gagnier, 1993; Forey 1984, 1995; Forey and Janvier, 1993; Donoghue et al., 2000; Donoghue and Smith, 2001; Gess et al., 2007). Nevertheless, the name 'ostracoderm' is still used informally, but between quotation marks, which indicate that they are not a clade.

At about the same time, the question of cyclostome monophyly was also reconsidered by Løvtrup (1977) on the basis of anatomical and physiological data, and analyzed in the light of outgroup comparison and parsimony. Løvtrup (1977) concluded that the cyclostomes are paraphyletic, with hagfishes being the sister group of lampreys and gnathostomes, a conclusion that had been suspected before, but never clearly expressed (Goodrich, 1909; Brodal and Fänge, 1963). Janvier (1978) erected the name Myopterygii for lampreys and gnathostomes (and some fossil taxa), which share radial muscles in paired and unpaired fins. However, since only lampreys and gnathostomes also share homologous neural arch elements (basidorsals and interdorsals), Janvier (1981) later restricted the name Vertebrata to these two taxa, nested along with hagfishes in the more inclusive taxon Craniata [two names erected simultaneously by Linnaeus (1758) in the diagnosis of what we now classically refer to vertebrates ("Vertebrata-Craniata")]. This classification reflects what is now known as the "vertebrate theory," as opposed to the "cyclostome theory," which assumes cyclostome monophyly (Forey, 1995). The vertebrate theory became soon widely accepted among morphologists (Dingerkus, 1979; Hardisty, 1982), although some still adhered to the cyclostome theory (Yalden, 1985; Schaeffer and Thomson, 1980). Soon after, the rapid rise of molecular phylogenetics began to yield results that either supported the cyclostome theory (Lê et al., 1993; Delarbre et al., 2002), were ambiguous (Stock and Whitt, 1992), or exceptionally supported the vertebrate theory (Gürsoy et al., 2000). Currently, a wealth of gene sequence data analysed by means of various methodologies (notably Bayesian analysis) lend strong support to cyclostome monophyly (Mallatt et al., 2001; Hegdes, 2001; Furlong and Holland, 2002; Mallatt and Winchell, 2007; see also review in Kuraku and Kuratani, 2006). These results leave morphologists and

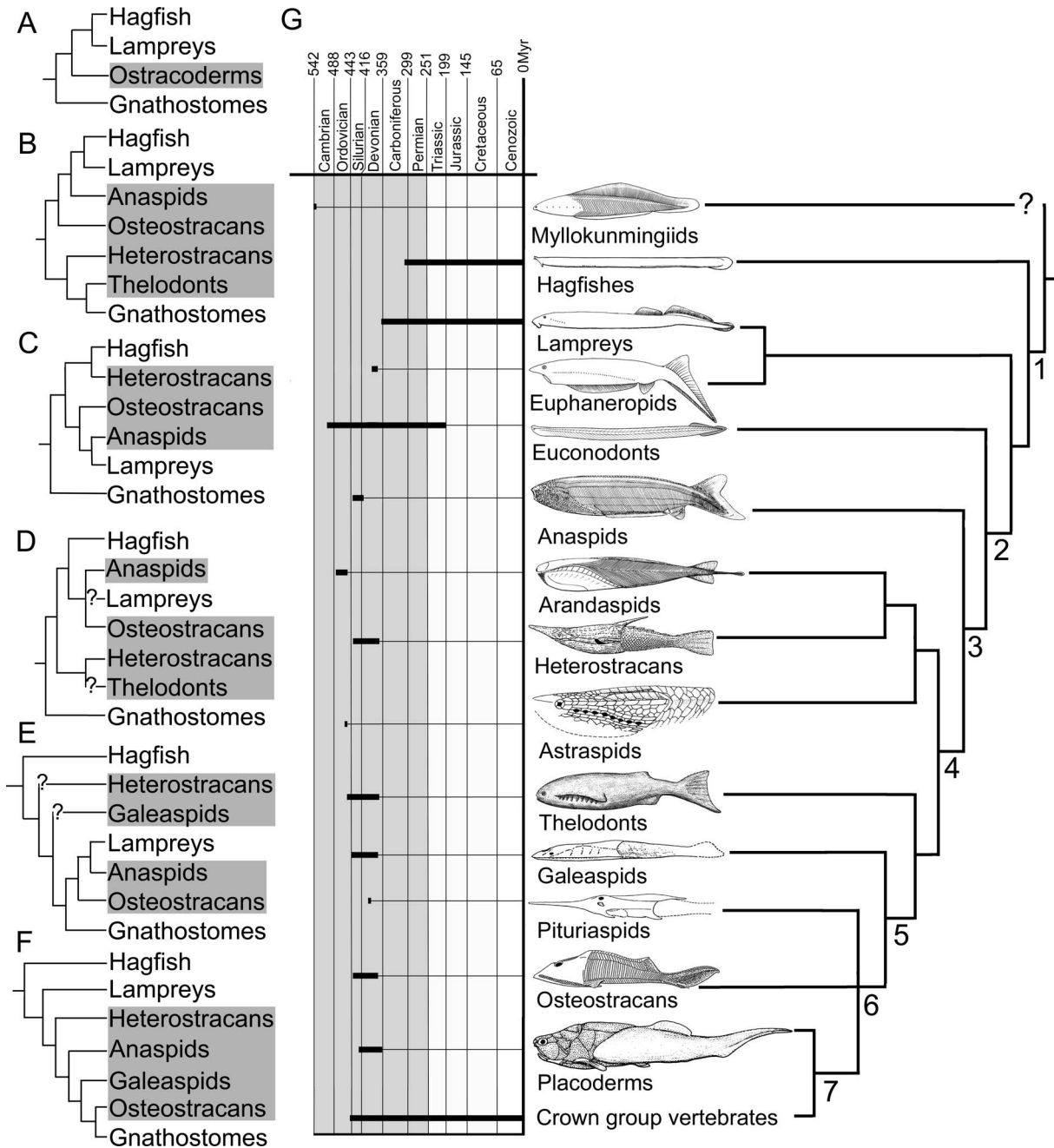


Fig. 1. Interrelationships of the major fossil and living vertebrate taxa since the late 19th century. **(A–F)** Phylogenetic position attributed to the major armored, jawless fossil vertebrate taxa (or ‘ostracoderms’; in grey box) according to various authors, showing the progressive shift from their status of ‘Agnatha’ to that of stem gnathostomes. **(A)** After Cope (1889). **(B)** After Kiaer (1924) and most other authors of the 20th century. **(C)** After Stensiö (1927). **(D)** After Moy-Thomas and Miles (1971). **(E)** After Janvier (1978). **(F)** After Janvier (1996a). **(G)** One of the recently published vertebrate tree topologies that entails cyclostome paraphyly (after Gess et al., 2007; possible position of myllokunmingiids modified according to Janvier, 2003); the distribution of the taxa through time is indicated by bold lines in the time scale to the left. Major synapomorphies at nodes: 1, neural crests, epidermal placodes, fin radials; 2, dermoskeleton in mouth and pharynx; 3, extensive dermoskeleton over the entire body; 4, extensive lateral-line system enclosed in grooves and canals, vertical semicircular canals forming loops, cerebellum; 5, endoskeleton lined with calcified cartilage or perichondral bone; 6, pectoral fins in postbranchial position; 7, jaws. (Illustrations of respective taxa after Janvier, 2007b).

physiologists greatly perplexed, and most of them now turn back to the old ad-hoc explanation of cyclostome ‘degeneracy’ (see contributions in Jørgensen et al., 1998; Hardisty, 2007). Gene sequences may better approach the truth than

other sources of data, but very few authors raise the question of the assumptions underlying the methodologies involved in their analysis, in particular the question of the selected outgroups (Gess et al., 2006).

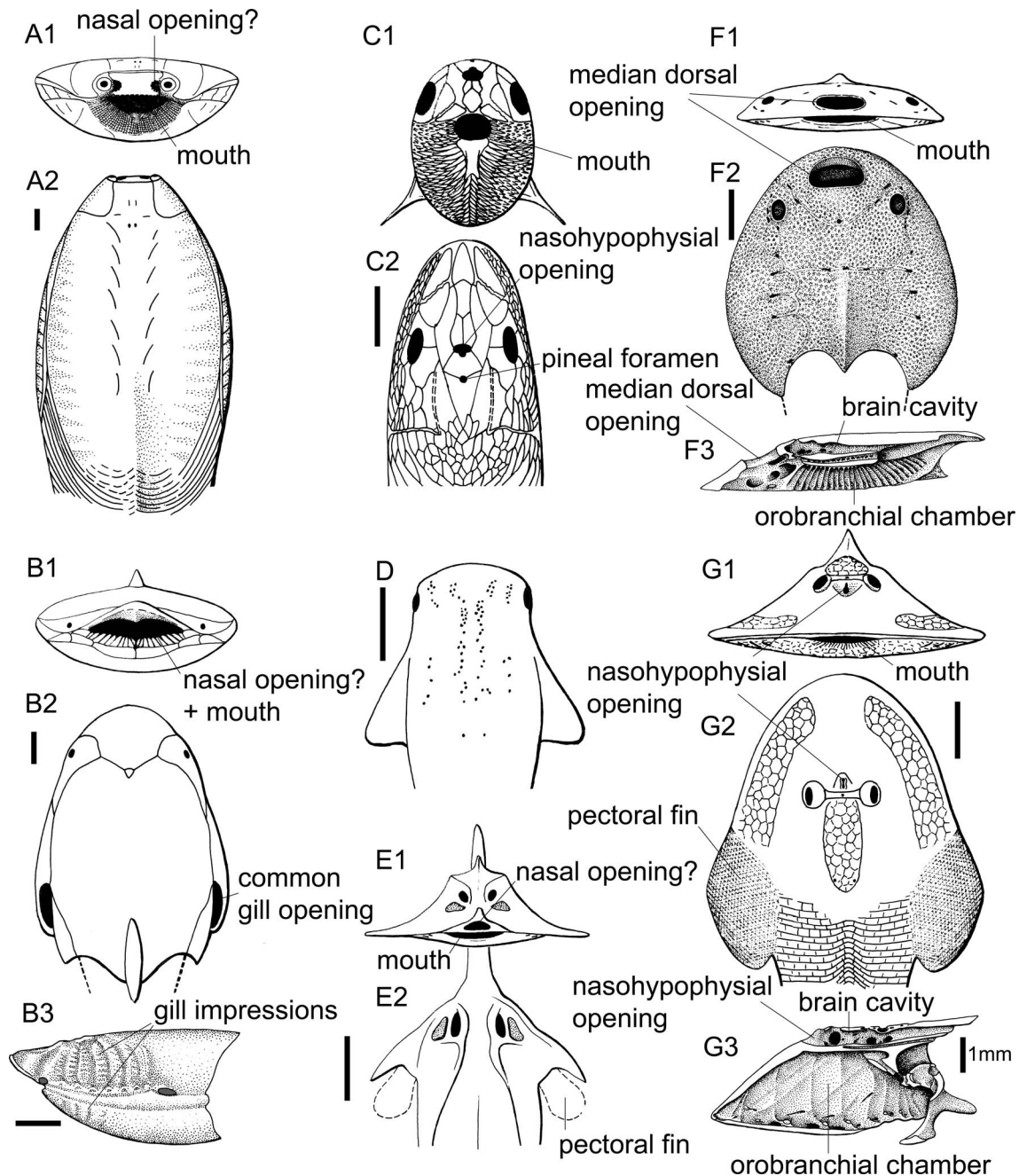


Fig. 2. Head morphology in some of the major 'ostracoderm' taxa from the Ordovician, Silurian and Devonian. **(A)** Arandaspid in anterior (**A1**) and dorsal (**A2**) views. **(B)** Heterostracan in anterior (**B1**) and dorsal (**B2**) views, and internal natural cast of the dermoskeletal head armor, showing gill pouch impressions (**B3**). **(C)** Anaspid in anterior (**C1**) and dorsal (**C2**) views. **(D)** Thelodont in dorsal view. **(E)** Pituriaspid in anterior (**E1**) and dorsal (**E2**) views. **(F)** Galeaspid in anterior (**F1**) and dorsal (**F2**) views, and sagittal section through the braincase (**F3**). **(G)** Osteostracan in anterior (**G1**) and dorsal (**G2**) views, and sagittal section through the braincase (**G3**). Scale bar, 10 mm, unless indicated otherwise. (A, B, D, F1, F2, G2, after Janvier, 1996b; C, based on Ritchie, 1964; E, based on Young, 1991; F3, G3 from Janvier, 2001)

FOSSILS AND BONE: THE PRESERVABLE ANATOMY

The number of the 470–360 million-year-old armored jawless vertebrates taxa that are still informally referred to as 'ostracoderms' has increased since the early 20th century, notably with the discovery of the Ordovician Arandaspida and the Silurian and Devonian Galeaspida and Pituriaspida (Fig. 2A, E, F). 'Ostracoderms' still show no

evidence of vertically biting jaws of gnathostome type, but most of them share with the jawed vertebrates an extensively ossified dermoskeleton, often covered with dentinous tissues, suggesting neural crest contribution, and, in galeaspids and osteostracans, a perichondrally calcified or ossified endoskeleton (Donoghue and Sansom, 2002; Wang et al. 2005) (Fig. 2F3, G3). In the latter two taxa, the preserved endoskeleton provides a rather accurate cast of the

major cranial cavities and canals that housed the brain, labyrinth, optic capsule, and nasohypophysial complex, as well as the cranial nerves, major arteries, veins, and impressions of the gills.

Since Stensiö (1927), and until the 1980's, palaeontologists were impressed by the striking resemblance between the ethmoid cavity of osteostracans and the nasohypophysial complex of lampreys (Janvier, 2007b) (Fig. 2G). This was considered as the best possible example of a synapomorphy shared by two otherwise quite different taxa, and nobody could ever think of interpreting osteostracan anatomy in the light of any other vertebrate group than lampreys (apart from reservations expressed by Gross, 1964). However, very few other characters shared by the two groups turned up, apart from general vertebrate characters (sympleiomorphies) and some characters of uncertain polarity (e.g., the shape of the pericardiac cavity; Janvier, 2007b). In contrast, osteostracans clearly resemble gnathostomes in possessing, e.g., pectoral fins, epicercal tail, ossified sclera, closed braincase, semicircular canals forming large loops, large dorsal jugular vein, open endolymphatic ducts, a large recess for the cerebellum, and cellular bone. In fact, the braincase anatomy of osteostracans displays much the same organisation as that of placoderms, which are extinct jawed vertebrates and currently regarded as the fossil sister group of the living gnathostomes (Janvier, 1984, 1993, 1996a, 2001; Forey and Janvier, 1993; Goujet, 2001). The anatomy of galeaspids is basically similar to that of osteostracans except for their paired, separate nasal capsules, incurrent median dorsal opening (functionally similar to the nasopharyngeal duct of hagfishes), and lack of paired fins (Janvier, 1984, 1996b; Wang 1991) (Fig. 2F). This is confirmed by new data on galeaspids (Zhikun Gai, pers. comm., 2008) and provides strong support to the hypothesis that the nasohypophysial complex of osteostracans and lampreys is homoplastic, however similar it may look (Janvier, 2001, 2007b). The still poorly known pituriaspids, whose braincase may also have been lined with either calcified cartilage or perichondral bone (Young, 1991), show evidence of osteostracan-like pectoral fins, but lack a dorsal nasohypophysial opening (Fig. 2E). Yet it is probable that the rest of their braincase anatomy was basically similar to that of osteostracans and galeaspids. The endoskeleton of arandaspids, astraspids, heterostracans, anaspids, and thelodonts is neither ossified nor calcified (Fig. 2A–D). However, impressions on the internal surface of the dorsal shield of heterostracans (Fig. 2B3), and the “gill pouch” imprints and internal denticles of at least one subset of thelodonts, suggest that their internal anatomy was probably rather similar to that of galeaspids (Van der Bruggen and Janvier 1993; Janvier, 1996b; Donoghue and Smith, 2001). The anatomy of anaspids remains an enigma: their external morphology has been long regarded as “lamprey-like” because of their presumed dorsal nasohypophysial opening, gill openings arranged in slanting row, and hypocercal tail, but they possess elongated ventrolateral paired fins and lack a mineralized endoskeleton. The current consensus about ‘ostracoderm’ relationships thus remains that they represent a grade of jawless stem gnathostomes and that their history is irrelevant to that of the cyclostomes (Janvier 2006). Although ‘ostracoderms’ provide some insights about the

origin of what is frequently referred to as the ‘gnathostome body plan,’ they tell us virtually nothing about the origin of jaws proper, which still essentially rests on development-based scenarios (Shigetani et al., 2005; Janvier 2007b).

SOFT-BODIED FOSSILS AND FOSSIL CYCLOSTOMES

Until the late 1960's, most palaeontologists who rejected Stensiö's (1927) theory of the diphyletic origin of the cyclostomes, but accepted their derivation from some early Palaeozoic ‘ostracoderms’ (preferably ‘monorhinal’ ones), considered that the ‘degeneracy’ of the group had already occurred in an unknown cyclostome ancestor in the late Paleozoic. Palaeontologists were therefore desperately looking for hints at an incipient reduction of the dermoskeleton in some of the latest ‘ostracoderms’ (Stensiö, 1939, 1964; Ørvig, 1968). However, such cases of presumed reduction in late Devonian ‘ostracoderms’ (notably in osteostracans and anaspids) did not seem to be accompanied by any notable modification of the morphology that could possibly have foreshadowed the cyclostome condition. An interesting case is that of the enigmatic Middle Devonian (390 Ma) vertebrate *Palaeospondylus gunni* Traquair, 1890, which, despite its abundance and reasonably good preservation, has raised much debate among paleontologists of early vertebrates (Fig. 3A). *Palaeospondylus* has been variously referred to a stem lamprey, stem hagfish, holocephalan, naked placoderm, larval amphibian, or larval lungfish, the latter interpretation being currently preferred (Thomson et al., 2003) but recently refuted again (Joss and Johanson, 2006; Newman and den Blaauwen, 2008). There is still no unambiguous clue as to its relationships, apart from a frustratingly superficial resemblance to a cyclostome or larval gnathostome skeleton.

Until the 1960's, there was thus, by default, a vague consensus among the supporters of cyclostome monophyly about the idea that the divergence between lampreys and hagfishes took place in the Mesozoic (250–265 Ma) from an unknown cyclostome ancestor whose skeleton was already cartilaginous. Therefore, the discovery of the first fossil lamprey, *Mayomyzon pieckoensis*, in the late Carboniferous (300 Ma) (Bardack and Zangerl, 1968, 1971) came as a surprise, and was subsequently confirmed by earlier lamprey occurrences, namely *Hardistiella montanensis* and *Priscomyzon riniensis* (Janvier and Lund, 1984; Janvier et al., 2004; Janvier, 2006; Gess et al., 2006), the latter being dated at 360 Ma (Fig. 3B, C, E). All these fossil lampreys are preserved as soft-tissue imprints in shale, limestone or concretions deposited in anoxic environments, which prevented them from rapid decay. Similar Paleozoic rocks have also yielded other soft-bodied vertebrates, such as the late Carboniferous *Pipiscius zangerli* and *Gilpichthys greeni* (Bardack and Richardson, 1977) (Fig. 3D, H), whose affinities to lampreys and hagfishes, respectively, have been debated (Janvier, 1993, 1996b). The first plausible fossil hagfish, *Myxinikela siroka* (Fig. 3F), has turned up in the same late Carboniferous locality as *Mayomyzon* (Bardack, 1991), and another presumed hagfish, *Myxineides gononorum* (Fig. 3G), was later discovered, also in the late Carboniferous (Poplin et al., 2001). The early Carboniferous *Conopiscius clarki* (Briggs and Clarkson, 1987) and the Cambrian-Triassic (500–200 Ma) *Euconodonta* (or ‘cono-

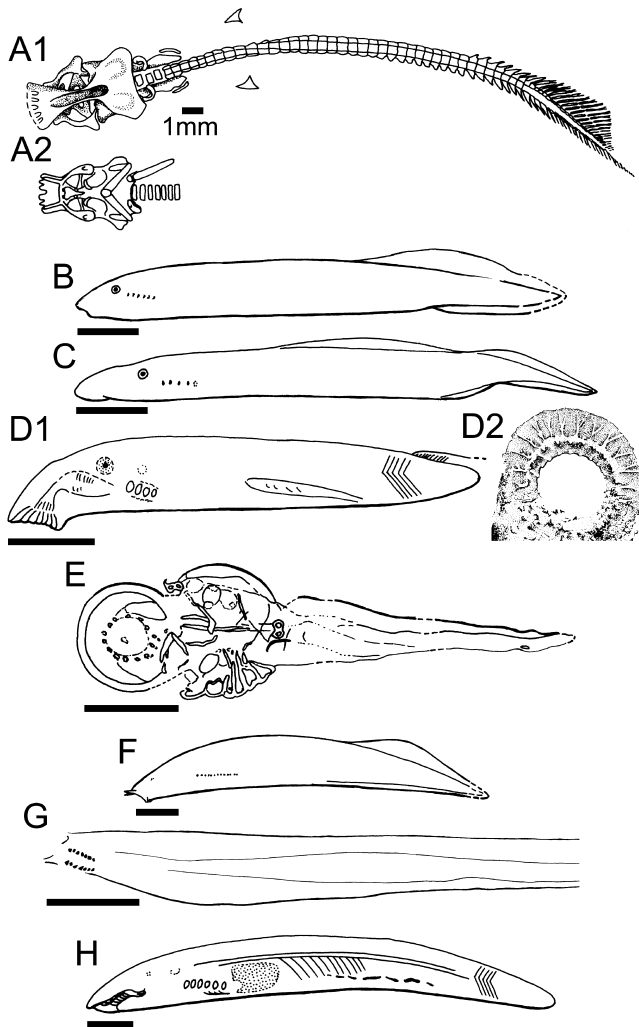


Fig. 3. Palaeozoic fossils preserved as imprints and once referred to the cyclostomes. (A) *Palaeospondylus gunni*, Middle Devonian of Scotland; articulated specimen in dorsal view (A1) and skull in ventral view (A2). (B–E) Fossil lampreys. (B) Reconstruction of *Mayomyzon pieckoensis*, Uppermost Carboniferous of Illinois, USA. (C) Reconstruction of *Hardistiella montanensis*, Lower Carboniferous of Montana, USA. (D) Reconstruction *Pipiscius zangerli*, Uppermost Carboniferous of Illinois of USA (D1) and impression of the oral disc (D2). (E) Sketch of *Priscomyzon riniensis*, Uppermost Devonian of South Africa. (F–H) Presumed fossil hagfishes. (F) Reconstruction of *Myxinikela siroka*, Uppermost Carboniferous of Illinois, USA. (G) Sketch of *Myxineides gononorum*, Uppermost Carboniferous of France. (H) Sketch of *Gilpichthys greeni*, Uppermost Carboniferous of Illinois, USA. Scale bar, 10 mm, unless indicated otherwise. (A1, redrawn after Moy-Thomas and Miles, 1971; A2, redrawn after Thomson et al., 2003; B, after Janvier 1996b; C, from Janvier and Lund, 1983; D1, H, after Bardack and Richardson, 1977; D2, from Janvier, 1996b; E, redrawn after Gess et al., 2007; F, from Poplin et al., 2001 and original specimen.)

donts’) are other examples of partly or completely soft-bodied vertebrates whose affinities are still debated (for a review of the prolific literature on euconodonts, see Briggs et al., 1983; Aldridge and Purnell, 1996; Schultze, 1996; Aldridge and Donoghue, 1998; Donoghue et al., 2000).

Such imprints of soft-bodied vertebrates are generally said to be “carbonaceous,” but contain in fact a variety of

minerals, notably pyrite and clay minerals, and are sometimes spectacular, because they readily recall the actual aspect of living organisms. The holotype of *Mayomyzon pieckoensis* (Bardack and Zangerl, 1968), which is preserved in lateral view, is a good example of such readily interpretable specimens. By contrast, dorsoventrally compressed specimens of the same species would probably not have been interpreted as lampreys if found alone (Bardack and Zangerl, 1971). This is notably the case of the badly squashed *Pipiscius* which, despite its conspicuous, three-dimensionally preserved oral sucker (Fig. 3D), does not show a clearly lamprey-like overall body shape (Bardack and Richardson 1977). However, the recent discovery of exquisitely preserved *Priscomyzon* (Fig. 3E) with its very large oral sucker now provides strong support to the affinity of *Pipiscius* to lampreys (Gess et al., 2006). Finally, the 125 Myr-old Cretaceous lamprey *Mesomyzon mengae* (Chang et al., 2007) shows that the fossil imprint of a lamprey which was almost similar to modern ones is also quite similar to that of a Carboniferous lamprey such as *Mayomyzon*, and that these fossil imprints are, after all, a reliable source of information.

In contrast to these fossil lampreys, the case of *Gilpichthys* was problematic (Fig. 3F). Although Bardack and Richardson (1977) did not refer it to hagfishes, it clearly shows impressions of intra-buccal structures that are suggestive of series of pointed horny teeth similar to those of hagfishes. Bardack (1991, 1998) did not hesitate to refer *Myxinikela* to hagfishes on account of its presumed tentacles, and despite its lack of evidence for typical horny teeth, whereas Poplin et al. (2001) considered that the coeval *Myxineides* shares with hagfishes traces of tentacles, V-shaped series of horny teeth impressions and slender body shape. All these fossil cyclostomes are from marine deposits, except perhaps for *Myxineides*, which is supposed to be from freshwater intramontane lake deposits — strangely so (Janvier, 2007a).

Whatever the reliability of the identification of the fossil hagfishes, that of the Paleozoic fossils referred to lampreys, notably *Mayomyzon* and *Priscomyzon*, leaves little doubt and demonstrates that hagfishes and lampreys had already diverged 360 Myr ago. Considering the stability of lamprey morphology since that time, it would not be too surprising if fossil lampreys turned up 50 or 100 Myr earlier, as suggested by Kuraku and Kuratani (2006). All these presumed fossil hagfishes and lampreys are currently regarded as stem taxa of their respective clades, since none of them can be proved to be members of the crown groups (Gess et al., 2006). There is nevertheless still no unambiguous indication of calcified tissues in fossil cyclostomes, despite possible traces of calcified cartilage in aged individuals of living lampreys that have been inferred from radiographs but never studied further (Bardack and Zangerl, 1971).

ELUSIVE STEM CYCLOSTOMES

Although one can assume that lampreys existed about 360 Myr ago and possible hagfishes about 300 Myr ago, no fossil suggests the existence of ‘intermediate forms’ between these two groups. One may thus wonder if any known fossil could possibly be a stem cyclostome, but neither a lamprey nor a hagfish, through already possessing at

least one cyclostome character. Since there is no clear indication that the two cyclostome groups have ever possessed a mineralized skeleton, and assuming that none of the fully skeletonized 'ostracoderms' shares any unambiguous synapomorphy with the cyclostomes, stem cyclostomes should be looked for among other soft-bodied fossil, jawless vertebrates. Strangely, apart from *Mesomyzon*, no Mesozoic soft-bodied fossil has ever been referred to a jawless vertebrate, possibly because such poorly informative imprints are often overlooked by paleontologists, or because the latter consider they are worth considering only when Paleozoic in age, and thus relevant to deep divergence times. Therefore particular attention has been paid recently to Paleozoic (and especially Lower Paleozoic) soft-bodied vertebrates, notably after the discovery that 'ostracoderms' are stem gnathostomes and that a long, basal segment of vertebrate phylogeny cannot be documented by fully skeletonized fossils (Bleick, 1991; Janvier, 1997; Donoghue and Sansom, 2002; Donoghue et al., 2003). This guess was confirmed in a spectacular way by the discovery of the Lower Cambrian, 535 Myr-old *Myllokunmingiida*, which are currently regarded as the earliest known vertebrates. The first two myllokunmingiids ever described, *Myllokunmingia* and *Haikouichthys*, were regarded as the sister group to lampreys and gnathostomes (*Myllokunmingia*) and to lampreys (*Haikouichthys*), respectively (Shu et al., 1999, 2003), but this rested on very tenuous characters. They are now more likely to be a small clade of stem vertebrates, as may also be the apparently more plesiomorphous yunnanozoans (Mallatt and Chen, 2003; Janvier, 2003, 2007a, b), unless the latter are stem deuterostomes (Shu et al., 2001). Euconodonts had once been envisaged as possible cyclostome or, more precisely, hagfish relatives, despite their mineralized oral denticles, but this hypothesis was later discarded (Kreijtsa et al., 1990; Aldridge and Donoghue, 1998), and there is a consensus over their position as the most inclusive taxon among the stem gnathostomes, that is, basal to all 'ostracoderms' (Donoghue et al., 2000; Gess et al. 2006).

Recently, a consideration of the 370 Myr-old Late Devonian soft-bodied jawless vertebrate *Euphanerops longaevus* Woodward, 1900 (Fig. 4), and its probable junior synonym *Endeiolepis aneri* Stensiö, 1939, has brought forth new insights on the origin of lampreys and, possibly, the cyclostomes in general. These two fossils are referred to the Euphaneropidae and, when first described, were regarded as somewhat similar to the scale-bearing anaspids, a group of Silurian-Devonian 'ostracoderms.' Anaspids were thought to be possible lamprey precursors, because they share with the latter a median dorsal opening (assumed to be nasohypophysial), an elongate body shape, posteriorly slanting series of gill openings, and hypocercal tail (Kiaer, 1924; Stensiö, 1927, 1939, 1964; Ritchie, 1964, 1980) (Fig. 5A, C). Euphaneropids share with anaspids a markedly hypocercal tail with a large epicercal lobe (a presumed homolog of the second dorsal fin of lampreys), and a large anal fin (Fig. 5B, C). Stensiö (1939) interpreted a peculiar series of ventrolateral imprints in *Endeiolepis* as a paired series of ventrolateral scales derived from and ancestral paired fin fold. Curiously, this interpretation seemed further supported decades later by the discovery of similarly placed paired fin webs in anaspids (Ritchie, 1964) (Fig. 5C). New material of

Euphanerops and *Endeiolepis* confirms their overall anaspid-like aspect, but allows a completely different interpretation of what Stensiö (1939) regarded as ventrolateral paired scales. It clearly demonstrates that the presumed 'scale series' is in fact the imprint of a very elongated branchial basket composed of at least 33 pairs of sinuous branchial arches that extend from the anterior limit of the head to the anal region (Arsenault and Janvier, 1991; Janvier, 2004; Janvier and Arsenault, 2007) (Figs. 4A, B, 5B), an interpretation first received with scepticism. At best, some considered that it may recall the structure of the branchial apparatus of cephalochordates (which is unlikely), whereas others considered it as anatomically untenable, until the discovery of an exceptionally preserved specimen showing the imprints of the actual gill filaments supported by gill rays and probably enclosed in closely crowded gill pouches (Janvier et al., 2006) (Fig. 4D). Euphaneropids thus possessed a series of at least 33 gill pouches housing normally developed gills. In addition, large (and presumably aged) individuals of *Euphanerops* show peculiar calcification of various internal structures, notably the fin radials, the gill arches, the vertebral column comprising dorsal and ventral arcualia (like gnathostomes), and a possible braincase (Figs. 4C1, 5B). Although the biogenic or diagenetic nature of these calcified elements remains disputed (Donoghue et al. 2006), their fine structure shows peculiar ovoid cavities embedded in calcium phosphate that are strikingly similar to lamprey chondrocytes, notably in in-vitro calcified cartilage (Langille and Hall, 1993; Janvier and Arsenault, 2002, 2007) (Fig. 4C3). Moreover, these calcified euphaneropid specimens also show evidence for paired calcified radials, suggesting the presence of elongated, ribbon-shaped paired fins, as once mistakenly envisaged by Stensiö (1939) in *Endeiolepis*, but clearly evidenced in anaspids (Fig. 5B, C). Although these paired fin radials seem attached ventrolaterally to the branchial apparatus, they probably arose from a ventral, hypobranchial prolongation of the somatic musculature. Unfortunately, the anterior end of the euphaneropid head is poorly understood. The calcified individuals display a possibly calcified braincase, prolonged anteriorly by three large plates (possible tectal cartilages) (Fig. 5A2, B), an annular structure (a possible annular cartilage) (Figs. 4C2, 5A2, B), and a median ventral bar (a possible homologue of the piston cartilage) (Figs. 4C2, 5A2, B). Contrary to the bony 'ostracoderms', such compressed fossils, though slightly calcified, unfortunately provide no information about such key structures as the nasohypophysial complex or the labyrinth, and one is left with a few hints which suggest either anaspid or lamprey affinities. Yet euphaneropids show no evidence of an enlarged oral sucker (the 'annular cartilage' remains very thin) or a clear-cut piston cartilage (the 'median ventral bar' is a mere anterior prolongation of the basibranchial 'copular' elements; Janvier and Arsenault, 2007). Conversely, the morphology of anaspids is documented only by their dermoskeleton, and nothing is known of their endoskeleton. Are euphaneropids a particular group of secondarily 'naked anaspids' or of stem lampreys? At any rate, apart from their very large number of gills, nothing in their anatomy clearly evokes hagfish characters. Character analyses of fossil and living vertebrates, including euphaneropids, are poorly supported but yield euphaneropids as either derived anaspids,

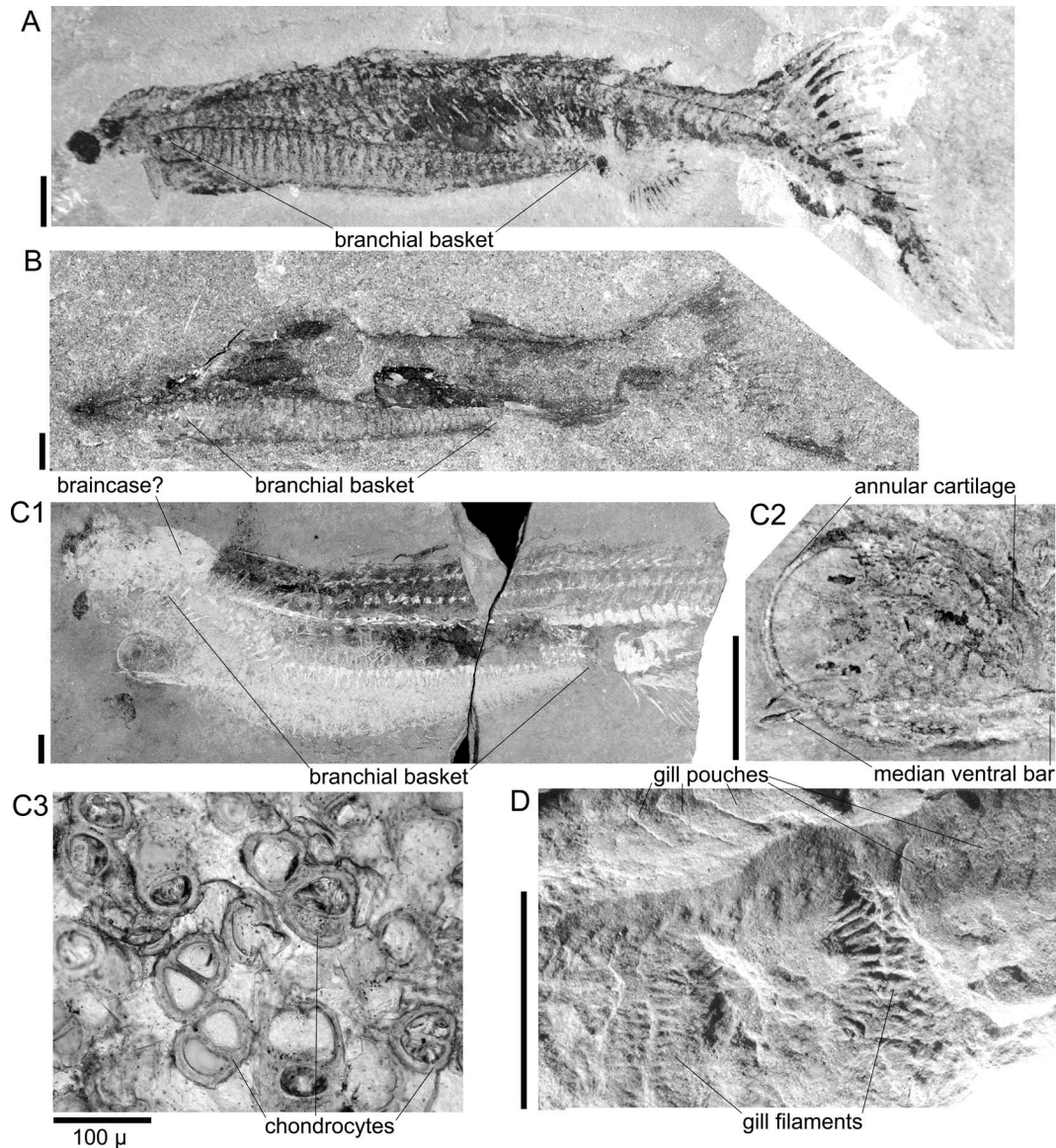


Fig. 4. *Euphanerops longaeus* and *Endeiolepis aneri*, Upper Devonian (Lower Frasnian) of Miguasha, Quebec, Canada. **(A–C)** Specimens preserved as imprints in lateral aspect. **(A)** *Euphanerops longaeus* (Musée d'Histoire Naturelle de Miguasha; MHNM 01-02), showing only traces of mineralized cartilage in the branchial basket. **(B)** *Euphanerops aneri* (MHNM 01-184), showing a three-dimensionally preserved natural cast of the branchial apparatus. **(C)** *Euphanerops longaeus* (MHNM 01-123), large specimen with extensively mineralized cartilage **(C1)**, showing possible evidence of an annular cartilage **(C2)** and a lamprey-like aspect of the mineralized chondrocyte lodges **(C3)**. **(D)** *Euphanerops aneri* (MHNM 01-154) portion of the branchial region, showing exceptional preservation of the gill filaments and gill rays at the limit between the natural mold of adjacent gill pouches. Scale bars, 10 mm, unless indicated otherwise. (A, C, from Janvier and Arsenault, 2007; D, from Janvier et al., 2006)

within the paraphyletic 'ostracoderms' (Donoghue et al., 2000; Donoghue and Smith, 2001), or the sister group of lampreys (Janvier, 1996a, b; Gess et al., 2006). Euphaneropids are now evidenced in the middle Devonian (390 Ma), and it is probable that the early Silurian (430 Ma) *Jamoytius kerwoodi* White, 1945, long regarded as the most primitive vertebrate, then as a 'naked anaspid' (Ritchie, 1968, 1984), is also a euphaneropid that possesses an even more elongated branchial apparatus, and is coeval with the earliest known anaspids.

So far, the relationships of euphaneropids to either lampreys or anaspids remain ambiguous, but there is no evi-

dence that they have any bearing on the relationships of hagfishes to other vertebrates. One possibility is that the somewhat similar overall morphology of euphaneropids and anaspids mirrors that of the ancestral morphotype of lampreys and gnathostomes, in the context of cyclostome paraphyly (Fig. 5B, C). Anaspids may be the most pleiomorphic fully skeletonized stem gnathostomes, and euphaneropids stem lampreys, both sharing the same strongly hypocercal tail (Fig. 5B, C1) and possibly a lamprey-like branchial basket (Fig. 5A2, B). The latter hypothesis would entail the loss of the paired fins and anal fin in lampreys. Yet an anal fin may occur as a possible atavism in

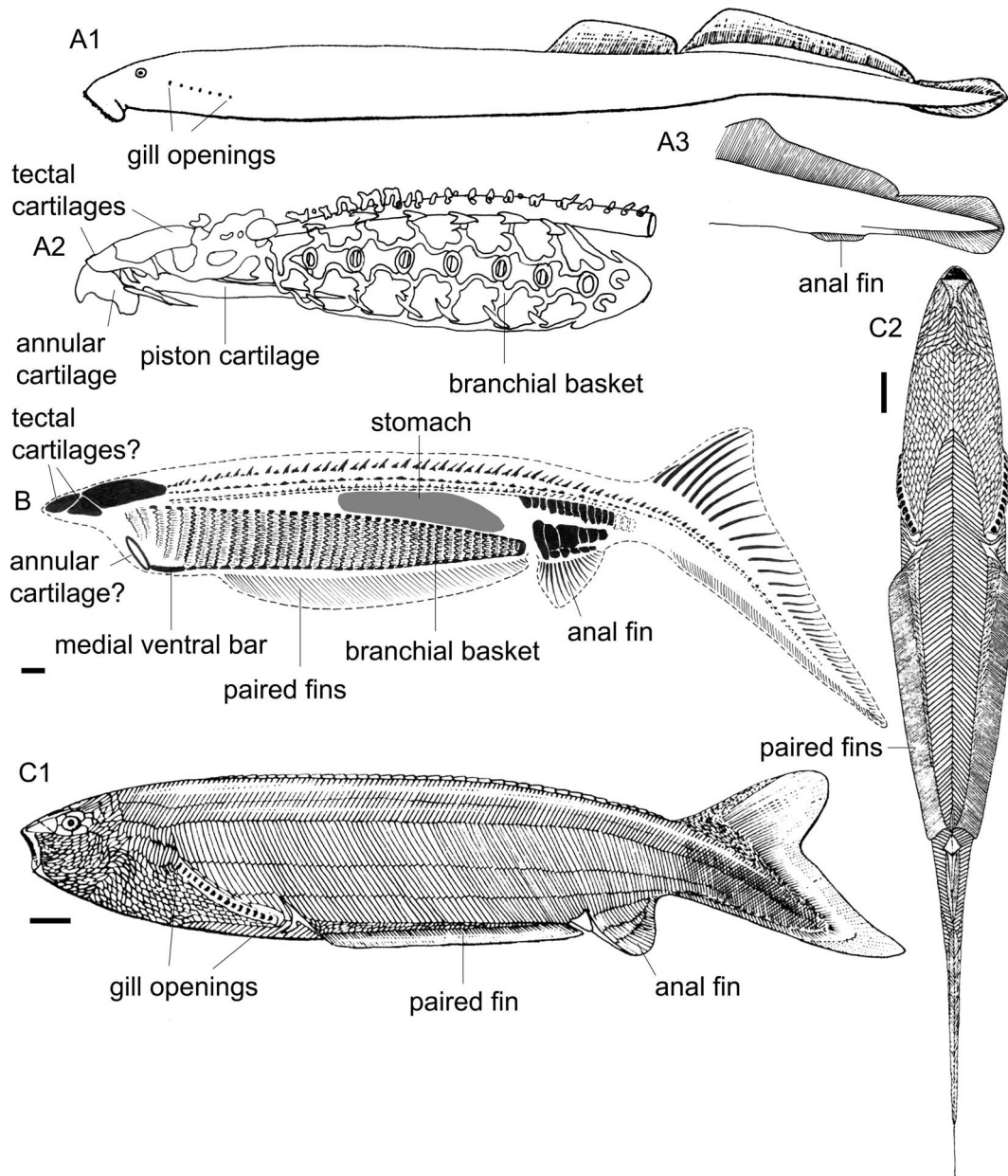


Fig. 5. Lampreys, *Euphanerops*, and anaspids. **(A)** *Petromyzon marinus* in lateral view (**A1**), head skeleton (**A2**), and caudal region of an abnormal specimen showing an anal fin (**A3**). **(B)** The Late Devonian euphaneropid *Euphanerops longaevus*; attempted reconstruction of the endoskeleton, in lateral view, based on specimens whose cartilage is most extensively mineralized. **(C)** The Silurian anaspid *Pharyngolepis oblongus*; reconstruction of the dermoskeleton in lateral (**C1**) and ventral (**C2**) views. Scale bar, 10 mm. (A1, A2, after Janvier, 1996b; A3, based on Vladikov, 1973; B, after Janvier and Arsenault, 2007, modified; C, after Ritchie, 1964)

extant lampreys (Vladikov, 1973) (Fig. 5A3).

CONCLUSIONS

Currently, the question of the monophyly or paraphyly of the cyclostomes rests exclusively on anatomical, physiological and molecular data. Although lampreys are certainly known since 360 Ma, and hagfishes possibly known since 300 Ma, no known fossil taxon could be interpreted as a possible 'intermediate' between the two groups. There is also no clear evidence that hagfishes and lampreys are 'degenerate' descendants of the bony, armoured jawless vertebrates, or 'ostracoderms,' which lived in lower Paleo-

zoic times, before the end of the Devonian, 359 Ma. The only possible hint at relationships between cyclostomes and major extinct jawless vertebrate taxa rests on a rather tenuous resemblance between lampreys and two middle Palaeozoic taxa, the 'naked' euphaneropids and the dermal bone-bearing anaspids. Euphaneropids may share with lampreys an annular cartilage, possible homologs of a piston cartilage and tectal plates, sinuous gill arches, and a quite similar arrangement of the chondrocytes. In contrast, euphaneropids share with anaspids a strongly hypocercal tail, ribbon-like paired fins, and a large anal fin. In addition to paired and anal fins, anaspids share with jawed verte-

brates a fully skeletonized dermoskeleton, but they also share with lampreys a possible dorsal nasohypophysial opening. The available data on euphaneropids and anapids are still too scarce and uncertain for drawing any reliable conclusion as to their relationships. Euphaneropids, despite their possibly autapomorphic, elongated branchial basket, could be plausible stem lampreys, and their resemblance to anaspids could be due to shared general characters of the total-group lamprey and the total-group gnathostome. This evolutionary scenario provides no hint as to the origin of hagfishes, whose relationships to lampreys and hagfishes still need to be reconsidered in the light of new sources of data, notably developmental data.

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