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THE DAWN OF THE VERTEBRATES: CHARACTERS VERSUS COMMON ASCENT IN THE RISE OF CURRENT VERTEBRATE PHYLOGENIES

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ABSTRACT. Armoured fossil jawless fishes, or 'ostracoderms', have long been regarded as being ancestral to Recent hagfishes and lampreys. The latter were supposed to have lost the mineralized exoskeleton and undergone a 'degeneracy' linked with their burrowing or ectoparasitic modes of life. However, recent cladistic analyses suggest that most, if not all 'ostracoderms' are more closely related to jawed vertebrates than to either lampreys or hagfishes, although they are clearly jawless. These views are very similar to those expressed by the early British palaeontologists who made the first attempts at placing these extinct taxa in the classification of the vertebrates. The chaotic history of the phylogenetic position of the 'ostracoderms' seems to be due to varying approaches to the use of either characters or common ascent in phylogeny reconstruction.

ALTHOUGH not very attractive as fossils, the Palaeozoic jawless vertebrates, or agnathans, have always raised interest among both professional palaeontologists and the public. This may be because they often are bizarrely shaped animals, but it is certainly because they are supposed to tell us something about the origin of the vertebrates in general. Therefore, textbooks on vertebrate evolution may sometimes overlook some major fossil taxa, but Palaeozoic jawless vertebrates are always included. During the last 150 years the principal advances in this field of vertebrate palaeontology were triggered essentially by new material and methods which gave access to more characters, in particular those based on internal anatomy and histological structure. The discovery of such new major clades as the galeaspids, arandaspids and pituriaspids has also enriched our perception of the diversity of vertebrate taxa and revealed new character combinations. As well as this progress, the expected result of more thorough investigation of material, the rise of cladistic methodology has given a new analytical dimension to the debates on the interrelationships of these early vertebrates. There is still a wide diversity of opinions on 'basal' vertebrate phylogeny, but most current theories suggest that jawed vertebrates are more closely related to one particular agnathan taxon than to others, i.e. that jawless vertebrates are not a clade.

The purpose of this address is firstly, to highlight the role played by early British vertebrate palaeontologists in the rise of interest in these 'basal' vertebrates, and then to show how circumstances led to the development of a number of long-lived scenarios about their evolution, all these scenarios dependent on the way in which taxa are defined. Finally, I shall deal with propects; suggestions of investigations in this particular field, i.e. how to get more taxa and more characters.

RECENT AND FOSSIL VERTEBRATES: THE CLADES

Recent vertebrates (or craniates, depending on which theory of their interrelationships and nomenclature is accepted) comprise three major clades: the jawed vertebrates, or Gnathostomata, and two clades of jawless vertebrates, the Hyperotreti (hagfishes) and the Hyperoartia (Lampreys). As discussed below, the latter two clades have long been united in the taxon Cyclostomi Duméril,

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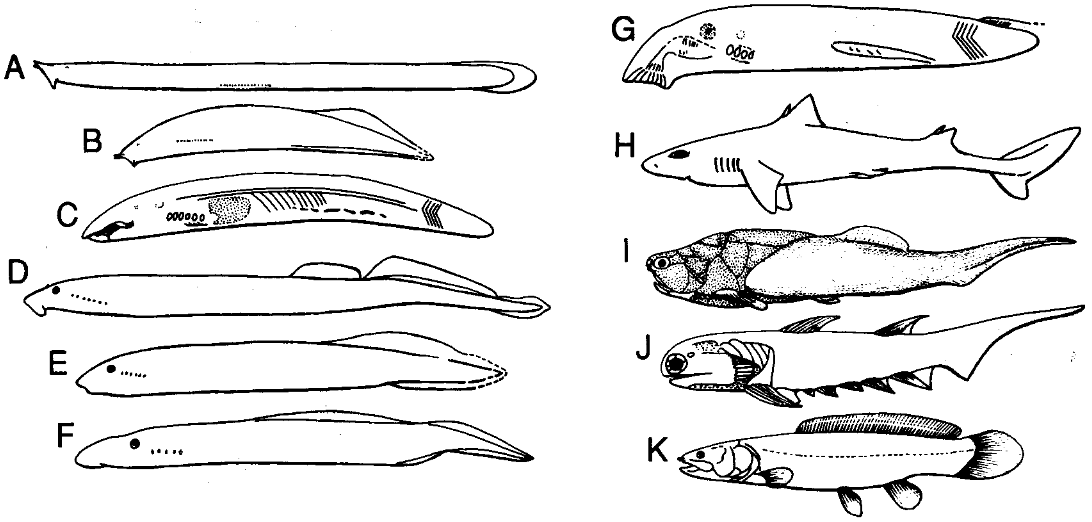
1806, which was subsequently treated as a clade by most authors (e.g. Jarvik 1981), until the late 1970s, by which time the numerous unique characters shared by lampreys and the gnathostomes were regarded as evidence for cyclostome paraphyly.

Lampreys and hagfishes are known as fossils from as early as the Carboniferous. All other jawless vertebrate taxa (except the conodonts if these are regarded as craniates) are pre-Carboniferous in age and, in contrast to lampreys and hagfishes, often possess a strongly calcified exoskeleton. They are, therefore, traditionally referred to as 'ostracoderms', a name erected initially by Aristotle for molluscs, but revived by Cope (1889) who used it to include the armoured jawless vertebrates known at that time. 'Ostracoderms' cannot be shown to be a clade but, for historical reasons, this name is still widely used in Britain and North America. After having fought for years against the use of this term, which is no better than 'pachyderms', I think it is time to surrender and make this concession to the Anglo-American tradition. 'Ostracoderms' range from the Early Ordovician to the Late Devonian (Late Frasnian). They were not recognized as jawless vertebrates until the end of the nineteenth century. Then, in the light of the rising Darwinian theory of evolution, their early age and potentially primitive (jawless) condition raised considerable interest among palaeontologists. This concept, that the presence of jaws was derived relative to their absence, was foreshadowed in early classifications or evolutionary trees based on Recent taxa only (Milne-Edwards 1844; Haeckel 1866). The fact that the earliest known fishes were apparently devoid of jaws gave palaeontological support for this theory. Only two major 'ostracoderm' taxa, the Osteostraci (cephalaspids) and Heterostraci (pteraspids) were defined initially by Lankester (1868), on the basis of the material from Britain referred to earlier as *Cephalaspis* by Agassiz (1835) and as *Pteraspis* by Kner (1847). The latter author, however, regarded the shields of *Pteraspis* as cephalopod shells, and it was Huxley (1858) and Lankester (1864) who showed that they were actually vertebrates, despite the acellular microstructure of the armour. Later, Traquair (1899, 1900) added the unarmoured Anaspida and Thelodonti (or 'coelolepids', which he thought were possibly related to sharks) and, in the second half of the twentieth century, several new major clades were discovered, such as the Silurian and Devonian Galeaspida (Liu 1965), the Ordovician Arandaspida (Ritchie and Gilbert-Tomlinson 1977) and the Devonian Pituriaspida (Young 1991). Many of the controversies about the relationships of the major 'ostracoderm' clades stem from the fact that some taxa (thelodonts, anaspids and heterostracans in their original sense, i.e. including the poorly known Ordovician forms) could not be defined by unique characters, and, consequently, were not taxa in the sense that cladists recognize. I shall thus briefly define and comment upon the terminal taxa that we can now recognize in a consideration of vertebrate or craniate phylogeny. All these taxa are craniates, since they share a head, comprising the skull, brain and sensory capsules, and a unique embryonic cell source, the neural crest, which gives rise to the formation of cells and tissues such as the pigment cells, dermal skeleton, gill arches and dorsal nerve ganglia. To date, the presence of the neural crest in hagfishes is only inferred from the presence of the tissues which, in other craniates, are known to be neural crest derivatives. Moreover, the presence of a neural crest in 'ostracoderms' is inferred from the presence of dermal skeleton (Smith and Hall 1991). In some non-mineralized fossils preserved as impressions, the presence of a skull is inferred from that of well-developed eyes (e.g. *Jamoytius*, *Euphanerops*, Conodonta).

1. *Hyperotreti* (*Pennsylvanian to Recent*; Text-fig. 1A–C)

Hagfishes are exclusively marine, slender-bodied fishes, characterized by a large, ventrolateral slime gland, four pairs of tentacles surrounding the mouth and nasal opening, and a duct leading from the oesophagus to the exterior on the left side only (the oesophago-cutaneous duct). In Recent hagfishes, the gill pouches are posteriorly placed and lie well behind the head. There are other characters which are unique to hagfishes, but many of them can be interpreted as general for craniates (e.g. aneural heart, single semicircular canal in the ear, fibrous braincase). Hagfishes display various conditions as to the number of gill openings. The Myxinidae possess a single pair of common gill openings whereas other hagfishes have up to 15 pairs of separate gill openings. The ontogeny of the Myxinidae suggests that separate gill openings is the general condition for the group. The only undoubted fossil (Pennsylvanian) hagfish known to date, *Myxinikela* (Bardack 1991; Text-fig. 1B), differs from extant forms in having a stouter body, a more extensive dorsal fin and a lancet-shaped caudal fin. This condition can be regarded as general for hagfishes on the basis of the palaeontological argument (i.e. the assumption that a character state found only in the geologically older members of a taxon is primitive, relative to the state found in the geologically younger or the Recent members of the same taxon). *Myxinikela* occurs in the same locality (Mazon Creek, Illinois) as another fossil, *Gilpichthys* (Bardack and Richardson 1977; Text-fig. 1C), which seems to display comb-shaped horny teeth and has been regarded by Janvier (1981*a*) as a possible fossil hagfish as well.

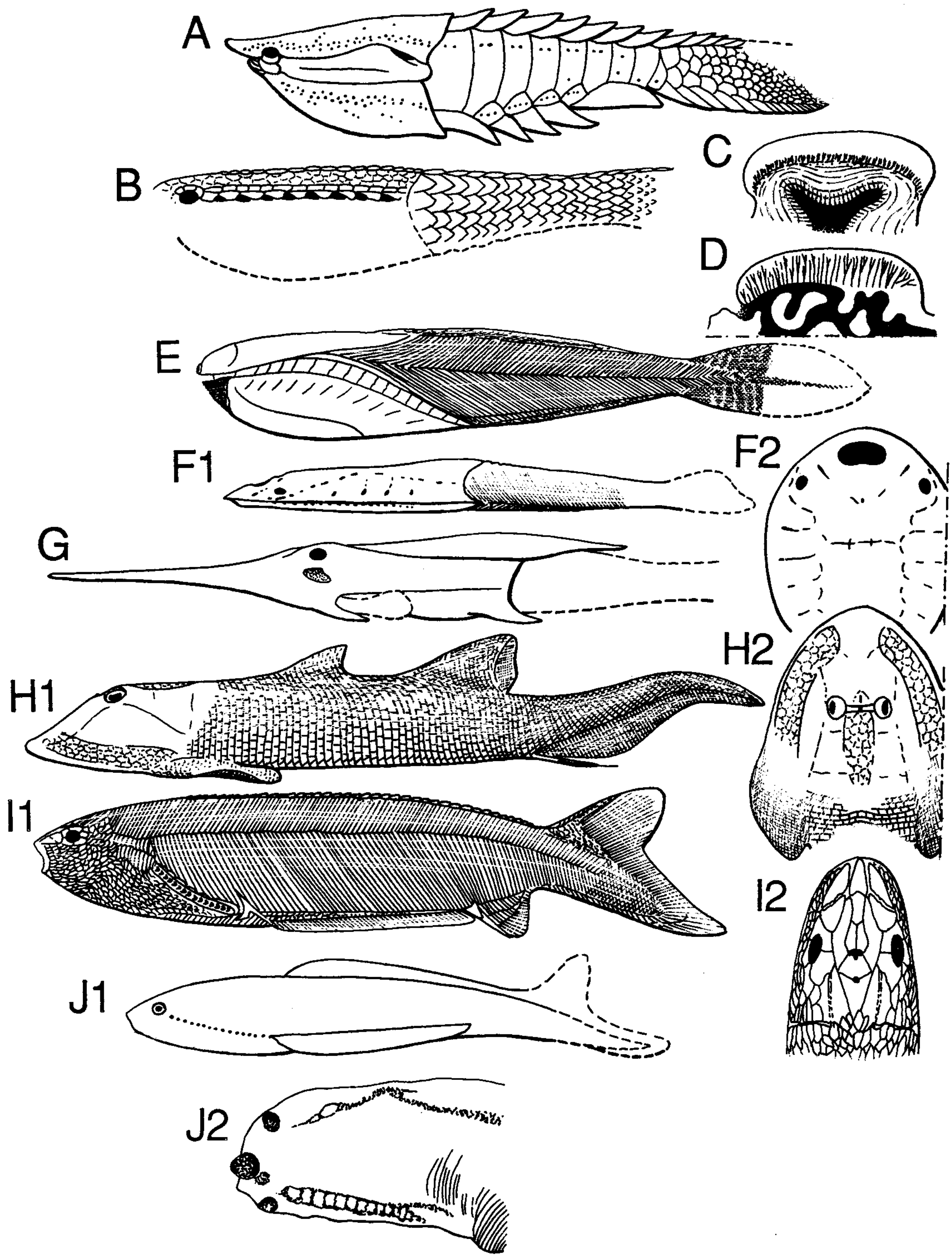


TEXT-FIG. 1. Representatives of the major fossil and Recent craniate taxa, in lateral view, not to scale. A–C, Hagfishes (Hyperotreti) or presumed hagfishes; A, the Recent hagfish *Eptatretus*; B, *Myxinikela*, Pennsylvanian of Illinois (from Bardack 1991); C, *Gilpichthys*, Pennsylvanian of Illinois (from Bardack and Richardson 1977). D–G, Lampreys (Hyperoartia) or presumed lampreys; D, the Recent lamprey *Petromyzon*; E, *Mayomyzon*, Pennsylvanian of Illinois (from Bardack and Zangerl 1971); F, *Hardistiella*, Late Mississippian of Montana (from Janvier and Lund 1983); G, *Pipiscius*, Pennsylvanian of Illinois (from Bardack and Richardson 1977). H–K, the four major gnathostome taxa. H, the Recent chondrichthyan *Squalus*; I, the placoderm (extinct) *Coccosteus* (based on Moy-Thomas and Miles 1971); J, the acanthodian (extinct) *Climatius* (based on Moy-Thomas and Miles 1971); K, the Recent osteichthyan *Amia*.

Since the discovery of the 'conodont animal' (Briggs *et al.* 1983), some authors have tried to revive the old idea that conodont jaw elements are comparable to the horny 'teeth' of hagfishes and that the two groups may be closely related (Krejsa *et al.* 1990). This interpretation had already been argued in the nineteenth century by H. C. Pander, the discoverer of conodonts. Notwithstanding a striking resemblance between the slender body shape of the 'conodont animal' *Clydagnathus* (Text-fig. 3D) and that of extant hagfishes, there is still no conclusive argument to support this relationship, either in the histological structure of the conodonts, or in the anatomy of the soft tissue preserved in the body imprint. The question of conodont relationships will be discussed below.

2. *Hyperoartia* (*Late Mississippian to Recent*; Text-fig. 1D–G)

Lampreys are either freshwater or anadromous eel-shaped fishes, characterized by a sucker surrounding the mouth and a complex rasping and sucking device, usually referred to as a 'tongue'. The latter differs from the 'tongue' of hagfishes in the presence of a piston cartilage which permits



TEXT-FIG. 2. Representatives of the major fossil craniate taxa, not to scale. A, the Early Devonian heterostracan *Anglaspis* (based on Blieck and Heintz 1983); B, the Late Ordovician astraspid *Astraspis* (based on Elliott 1987); C, a vertical section through a tubercle of the presumed astraspid *Pycnaspis* (based on Ørvig 1989);

anteroposterior movement of the entire apparatus. Other characters, which are unique among extant craniates, are the dorsal position of the nasohypophysial opening and the cartilaginous spine-shaped processes on the branchial arches. The dorsally placed nasohypophysial opening can be regarded as a more general condition when fossils are considered. In their life history, lampreys have a larval stage and undergo a metamorphosis. All extant lampreys have seven separate branchial openings.

The three fossil lampreys known to date are *Hardistiella* (Late Mississippian; Text-fig. 1F), *Mayomyzon*, and probably *Pipiscius* (both Middle Pennsylvanian; Text-fig. 1E, G). They are small forms (*c*. 50–100 mm in length) and are found in shallow water marine sediments. Only *Pipiscius* displays a typical sucker armed with horny plates, and only *Mayomyzon* displays a piston cartilage (Bardack and Zangerl 1971; Bardack and Richardson 1977). *Hardistiella* is poorly preserved but appears to retain an anal fin (Janvier and Lund 1983), whereas all other fossil and extant lampreys have no anal fin. The anal fin may reappear in some abnormal individuals of *Petromyzon marinus* (Vladykov 1973). These fossil lampreys differ from extant ones essentially in that their branchial apparatus is situated closer to the skull and may have contained only six gill pouches.

3. *Gnathostomata* (*Llandovery to Recent*; Text-fig. 1H–K)

The jawed vertebrates, or gnathostomes, have a large number of unique characters, such as jaws, medially placed and jointed gill arches, horizontal semicircular canal, united spinal nerve roots, myelinated nerve fibres, etc. There is no reason to interpret these unique characters as general for craniates (and subsequently modified in lampreys and hagfishes) and the Gnathostomata can reliably be regarded as a clade, despite its great diversity. Among extant craniates, only the gnathostomes possess a calcified skeleton. There is, however, a considerable debate as to which Recent or fossil gnathostome displays the most generalized condition for this clade. Using gnathostomes as a single terminal taxon in any cladistic analysis means that many characters, such as scales, unpaired fin structure, or organization of the exoskeletal skull, would be scored as polymorphic. Chondrichthyans (Text-fig. 1H) are often used to reconstruct the morphotype of the gnathostomes, essentially because of the supposedly generalized microsquamose condition of their exoskeleton (i.e. simple, non-growing placoid scales derived from a single odontode). There is, however, no guarantee that this condition is general for either the chondrichthyans or the gnathostomes. The extinct placoderms (Text-fig. 1I), for example, may be the sister-group of all other gnathostomes (Young 1986) and the exoskeleton is always macromeric or macrosquamose (i.e. composed of large dermal plates and compound, growing scales) as in the fossil acanthodians and the osteichthyans (Text-fig. 1J–K). In this review, however, I have scored each state for scale morphology (microsquamose and macrosquamose) as present in the gnathostomes.

4. *Heterostraci* (*Late Llandovery to Frasnian*; Text-fig. 2A)

Heterostracans are exclusively fossil jawless craniates, which possessed a calcified exoskeleton and are characterized by a single, common external branchial opening on either side. This character is admittedly not unique among craniates, and occurs in the hagfish family Myxinidae and in all major

D, vertical section through a tubercle of *Eriptychius*, Late Ordovician (based on Ørvig 1989); E, the Ordovician arandaspid *Sacabambaspis* (after Gagnier 1993*a*); F, the Early Devonian galeaspid *Polybranchiaspis* in lateral view (F1) and dorsal view of head (F2, based on Liu 1965); G, the Early-middle Devonian pituriaspid *Pituriaspis* (based on Young 1991); H, the Silurian osteostracan *Ateleaspis* in lateral view (H1) and dorsal view of head (H2, based on Ritchie 1967); I, the Silurian anaspid *Pharyngolepis* in lateral view (I1; from Ritchie 1964) and dorsal view of head (I2); J, the Early Silurian *Jamoytius* reconstructed in lateral view (J1, from Ritchie 1968) and sketch of a head in a specimen showing the 'branchial basket' (J2, from Ritchie 1984).

gnathostome taxa, the placoderms, holocephalan chondrichthyans, some acanthodians and all osteichthyans. However, considering heterostracans as most closely related to any one of these taxa (as did Stensiö, 1927, with hagfishes) would be unparsimonious with respect to many other characters and would imply too many homoplasies (i.e. it would imply that either hagfishes or the gnathostomes are not clades, or that heterostracans underwent many reversals on other characters).

5. *Astraspida* (*Caradoc to ?Early Llandovery*; Text-fig. 2B–C)

Astraspids, in which I include only *Astraspis* (Text-fig. 2B) and possibly *Pycnaspis* (Text-fig. 2C; if different from the former), are characterized by a dermal ornamentation of large, costulated tubercles made of a thick, glassy enameloid cap. This cap rests directly on the underlying acellular bone, or aspidine, although *Pycnaspis* may show a thin, intervening layer of dentine or mesodentine (Ørvig 1989). Other characters met with in *Astraspis* (polygonal dermal units, longitudinal ridges on the dorsal shield, separate gill openings, large body scales) have a higher degree of generality. Astraspids have long been regarded as heterostracans on the basis of the acellular structure of their exoskeleton, but it is now clear that they differ from the latter in retaining separate external gill openings (Elliott 1987) and that the acellular exoskeleton is more general, as it occurs also in anaspids, galeaspids, and thelodonts.

6. Eriptychius (*Caradoc*; Text-fig. 2D)

This genus has sometimes been associated with astraspids, essentially because they occur together in some North American Ordovician localities and share a dermal armour composed of polygonal platelets. However, *Eriptychius* clearly differs from astraspids in its histological structure, its tubercles being made up of a peculiar type of dentine with large tubules (Ørvig 1989). Whether or not this is mesodentine is uncertain, but it clearly differs from the thin-tubuled orthodentine of heterostracans. *Eriptychius* possesses a partly calcified endoskeleton made up of globular calcified cartilage and pervaded by a network of vascular canals, the walls of which are possibly lined with perichondral bone (Denison 1967).

7. *Arandaspida* (*?Arenig to Ashgill*; Text-fig. 2E)

Arandaspids are characterized by the extreme anterior position of the eyes, which are housed in an elliptical notch of the dorsal dermal shield. All the other characters that they show (oak leaf-shaped tubercles, elongated body scales, large ventral and dorsal exoskeletal 'discs', numerous branchial plates and gill openings, paired pineal opening (if correctly interpreted), tesserae in exoskeleton, cancellar (honeycomb-like) layer of exoskeleton also occur in other taxa. Arandaspids occur essentially in the Llandeilo and Caradoc of Australia, Bolivia, and Argentina, with the genera *Arandaspis*, *Porophoraspis*, *Sacabambaspis*, and perhaps *Andinaspis*, but fragments of arandaspid-like dermal armour occur in Australia from the Arenig to the Ashgill (Young *in* Shergold 1991). They are thus the earliest known undisputed vertebrates.

8. *Galeaspida* (*Llandovery to Famennian*; Text-fig. 2F)

Galeaspids are characterized by large sensory-line canals arranged in a scalloped pattern in the dorsal exoskeleton of the head. These canals lie partly below the level of the exoskeleton and open only at their distal ends and through a few slits (there are no series of sensory-line pores). Another galeaspid character is the dorsal position of the median opening for the prenasal sinus, into which open the olfactory organs, and which communicates ventrally with the oralobranchial cavity (Text-fig. 2F2). However, and notwithstanding the differences in the organization of the nasohypophysial complex, a comparable condition occurs also in lampreys and osteostracans (Text-fig. 2H2), although here the prenasal sinus is continued backwards by a blind hypophysial tube and does not communicate with the underlying oralobranchial cavity. The galeaspid condition may be general relative to that of either osteostracans or lampreys. Galeaspids are known exclusively from China (including Tarim) and Vietnam and seem thus to be endemic to the North and South China continental blocks.

9. *Pituriaspida* (*Emsian to Eifelian*; Text-fig. 2G)

Pituriaspids are known only by a few poorly preserved head-shields from a single locality in Queensland, Australia (Young 1991). Two genera have been recognized, *Pituriaspis* and *Neeyambaspis*, but only *Pituriaspis* shows interpretable morphology. It resembles osteostracans in the overall shape of the head-shield, but is devoid of cephalic fields and a dorsal nasohypophysial opening. The position of the nasal openings is still unknown, but is assumed by Young (1991) to have been situated on the ventral side of the shield, anterior to the mouth. As well as the elongated rostral process, which is known to occur also in some osteostracans (e.g. Boreaspididae) and galeaspids (e.g. Hunnanaspidiformes), the only unique character of the Pituriaspidida is a peculiar pit lying ventrally to each orbit, but these do not communicate with the underlying oralobranchial cavity.

10. *Osteostraci* (*Wenlock to Frasnian*; Text-fig. 2H)

Osteostracans are characterized by paired and median depressions in the dorsal surface of the head endoskeleton, which are linked to the labyrinth cavity by means of large, branching canals. These structures have been variously interpreted as dynamo-sensory or electric organs, but neither of these interpretations is fully satisfactory. Another osteostracan character is the ventral, leaf-shaped horizontal lobe which underlies the caudal fin web, and may possibly be a modified anal fin. However, this horizontal lobe is lacking (supposedly lost) in some osteostracans (Tremataspididae). Other characters met with in osteostracans (dorsal nasohypophysial opening, blind hypophysial tube, paired pectoral fins, epicercal caudal fin, tessellate exoskeleton) may have a higher degree of generality.

11. *Anaspida* (*Llandovery to Přídolí*, Text-fig. 2I)

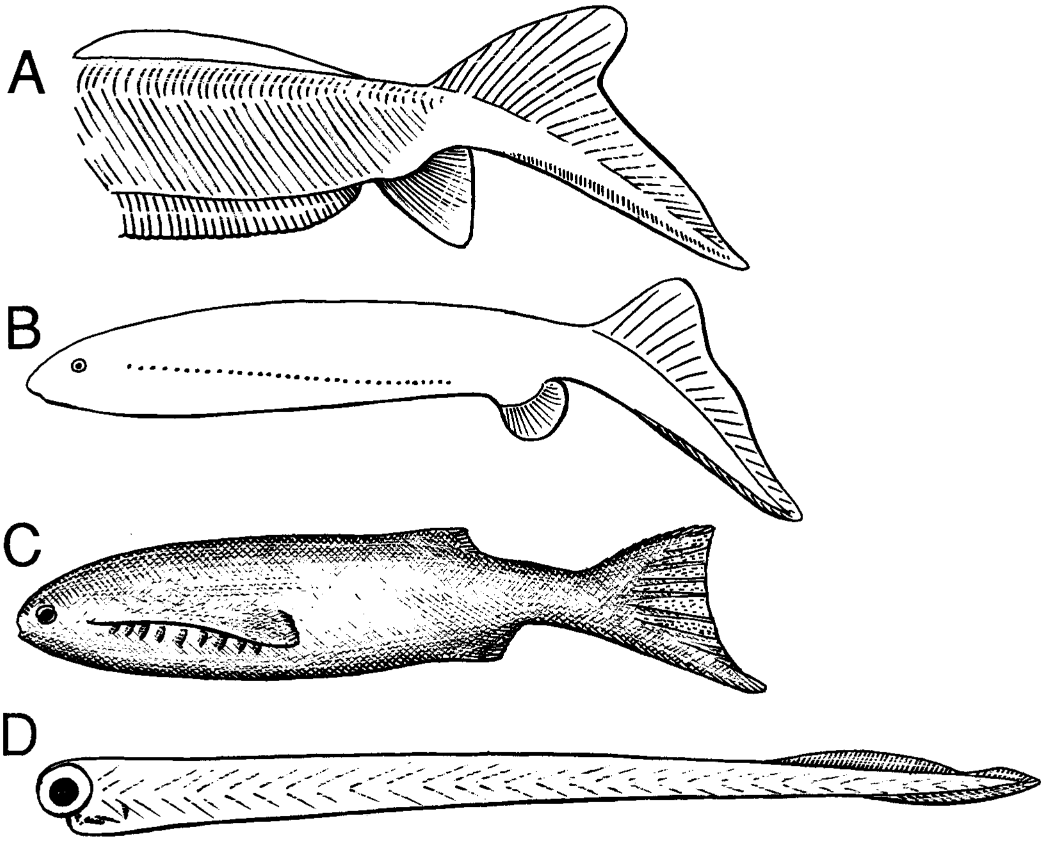
Anaspids are characterized by large triradiate scales or spines, situated behind the series of external branchial openings. Other characters currently used to define anaspids (e.g. strongly hypocercal tail, elongated body scales, presumed dorsal nasohypophysial opening, paired fins, acellular dermal skeleton) have a higher degree of generality. It has been suggested that the lack of a dorsal fin and the presence of a series of enlarged median dorsal scutes are unique to anaspids, but these characters also occur in heterostracans, advanced osteostracans, and some advanced galeaspids.

12. Jamoytius (*Llandovery to ?Early Devonian*; Text-fig. 2J)

Jamoytius has variously been interpreted as the most generalized craniate, a naked anaspid, or a lamprey. It is non-mineralized, preserved in the form of organic films, and shows no unique characters. It is only defined by an association of characters which are unique for this period: nakedness and lamprey-like body with paired fins. If restricted to the material of *J. kerwoodi* from Scotland, it is probably a clade. It is uncertain whether the Early Devonian material from New York referred to by Janvier and Busch (1984) as a '*Jamoytius*'-like craniate belongs here.

13. Endeiolepis (*Frasnian*; Text-fig. 3A)

Endeiolepis is characterized by a peculiar, undulating, ventrolateral series of weakly mineralized 'scales'. It shares with anaspids a strongly hypocercal caudal fin. Although often regarded as an anaspid, it shows no evidence of triradiate postbranchial spines.



TEXT-FIG. 3. Reconstructions of the representatives of the major fossil craniate taxa, not to scale. A, the Late Devonian *Endeiolepis* (head virtually unknown; from Arsenault and Janvier 1991); B, the Late Devonian *Euphanerops* (based on Arsenault and Janvier 1991); C, the Silurian thelodont *Loganellia* (modified from Turner 1991); D, the Carboniferous conodont *Clydagnathus* (based on Aldridge *et al.* 1993).

14. Euphanerops (Frasnian; Text-fig. 3B)

Euphanerops is also an 'anaspid-like' craniate, with a strongly hypocercal tail and a probably non-mineralized or weakly mineralized exoskeleton. It possesses an astonishingly long 'branchial basket' with more than 30 gill units. *Legendrelepis* (Arsenault and Janvier 1991) occurs at the same locality as *Euphanerops* (Miguasha, Quebec), and closely resembles the latter (they may well be synonyms). Despite the fact that numerous gills occur in another unrelated genus (*Jamoytius*), one may provisionally consider that *Euphanerops* and *Legendrelepis* form a clade.

15. *Thelodonti* (*Latest Ordovician to Frasnian*; Text-fig. 3C)

Thelodonts are represented by an ensemble of forms whose exoskeleton consists of minute scales, sometimes fused side-by-side near the gill openings and around the orbits. Each of these scales is supposed to correspond to a single papillary unit, or odontode. Although thelodont scales occur in abundance in marine sediments, the overall shape of the entire animal is known only from a few specimens from Scotland, Estonia and Canada, and provides evidence for a rather wide range of form, some animals being flat-bodied and others deep-bodied (Turner 1991; Wilson and Caldwell 1993). Turner (1991) considered the thelodonts to be monophyletic on the basis of the anchoring devices (processes) around the roots of the scales. This character, however, is not general to all thelodont scales. Other authors (Karatayute-Talimaa 1978; Janvier 1981*a*) considered that thelodonts do not represent a clade but include microsquamose members of other taxa (possibly stem-heterostracans, stem-galeaspids, stem-anaspids, and even stem-gnathostomes). Some thelodonts are unique among jawless craniates in having internal denticles lining the pharynx, like the gnathostomes (Van der Brugghen and Janvier 1993). Most thelodonts have a hypocercal tail (Text-fig. 3C) but some forms have an apparently diphycercal tail (Wilson and Caldwell's 'fork-tailed thelodonts') which is similar to that of heterostracans and may support the idea that some thelodonts are stem-heterostracans. One must, however, keep in mind that this type of diphycercy is only superficial, since the notochord was probably prolonged into the ventral lobe, as in hypocercal thelodonts.

16. *Conodonta* (*Late Cambrian to Triassic*; Text-fig. 3D)

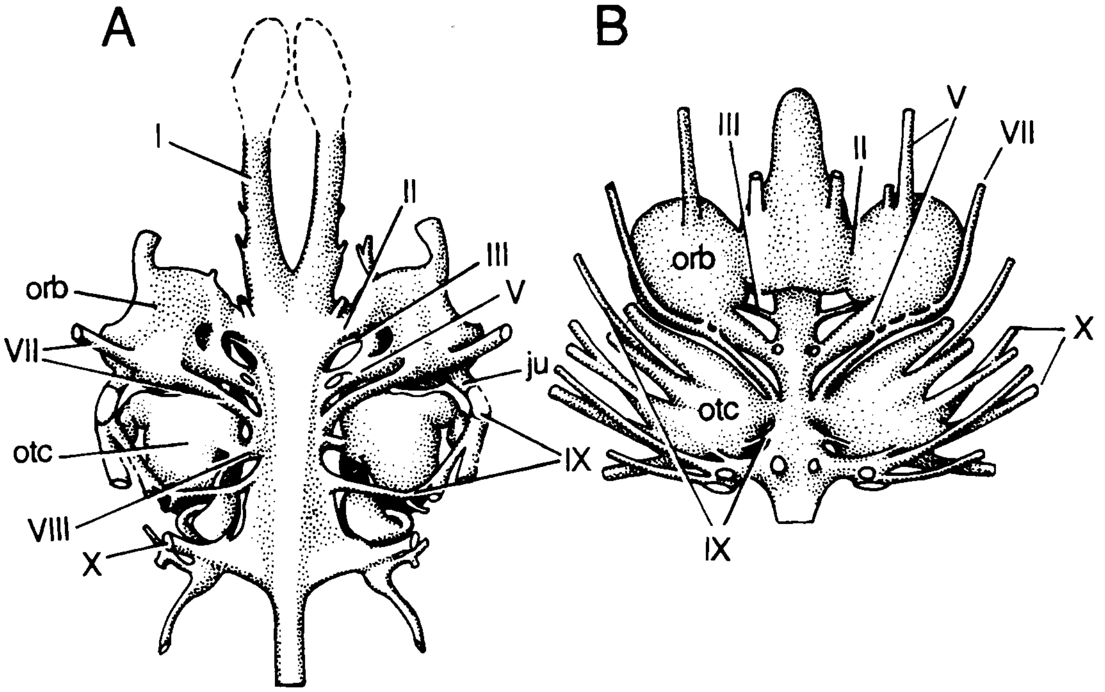
The controversy about the vertebrate affinities of the conodonts continues, following the discovery of the first articulated 'conodont animal' (Briggs *et al.* 1983). Although I have long been among the sceptics, I admit that there is now impressive evidence for the vertebrate affinities of this group, in particular the chevron-shaped myomeres, median fin with radials, and the large eyeballs. The histological structure and the organization of the conodont elements remains ambiguous, although they are likely to have contained osteocytes or odontocytes. In other respects, the conodont elements seem to represent a highly specialized feeding device, with no clear homologue in other craniates. At any rate, the vertebrate or craniate affinity of the conodonts can be accepted only for the para- and euconodonts, the protoconodonts being almost certainly of a different nature (Aldridge *et al.* 1993).

VERTEBRATE CLASSIFICATION AND INTERRELATIONSHIPS: HISTORICAL ACCOUNT

There are various ways of considering the history of theories about fossil and Recent vertebrate interrelationships, but here I shall divide it into four periods: from Agassiz (1835) to Cope (1889), Cope to Stensiö (1927), Stensiö to Løvtrup (1977), and Løvtrup to the present.

During the first of these four periods, Recent jawless vertebrates (or cyclostomes), first regarded as either 'degenerate' fishes or intermediate in some way between some invertebrates (e.g. worms) and fishes, became progressively considered as an early offshoot from the vertebrate tree. Their jawlessness was acknowledged as primitive, but their single nostril and pouch-shaped gills were viewed as specializations. The only fossil forms known during this period were osteostracans and heterostracans, almost unanimously regarded as peculiar bony fishes, possibly related to sturgeons and catfishes. Only a few authors, such as Schmidt (1866) alluded to the possible presence of a single, median olfactory organ in osteostracans, and compared it with the condition in lampreys, with no further bearing on their systematic position. The advent of Darwinian evolutionary theory, which had a significant influence on the interpretation of other fossil taxa (e.g. sarcopterygians), had no major impact on the interpretation of these early forms. The only consequence was that they supported T. H. Huxley's opinion that bony fishes were very ancient (Huxley 1861).

The second period began with a note on vertebrate classification by Cope (1889), where all the fossil vertebrates in which no evidence of jaws had been found (i.e. osteostracans, heterostracans, and also antiarchs, a group of placoderms which later turned out to have jaws) were placed in a taxon 'Agnatha', along with hagfishes and lampreys. Contrary to Agassiz, Huxley, and Lankester, who referred osteostracans and heterostracans to osteichthyans on the basis of characters (large bony scales and dermal bones, fin rays), Cope defined his 'Agnatha' on the basis of the absence of



TEXT-FIG. 4. Ventral aspect of the internal cast of the cavities and canals of the braincase of the placoderm *Macropetalichthys* (A, from Stensiö 1969) and the osteostracan *Nectaspis* (B, from Janvier 1981*b*), to show the basically similar relationships between the main cranial nerves and the sensory capsules. I–X, cranial nerves; ju, dorsal jugular vein; orb, orbital cavity; otc, otic capsule.

gnathostome characters. By erecting such a 'non-group', Cope hindered our understanding of vertebrate interrelationships.

The following period was a period of controversies. Firstly, Traquair (1899, 1900) described two new 'ostracoderm' taxa, the Thelodonti and Anaspida. He regarded the minute, placoid-like scales of thelodonts as evidence for a relationship between 'ostracoderms' and sharks. Goodrich (1909) remained convinced that osteostracans were bony fishes, but he was inclined to accept Traquair's views that 'pteraspidomorphs' (i.e. heterostracans and thelodonts) were related to sharks. A third ensemble was that of Cope, including Dean (1895) and later Woodward (1898), who considered that all 'ostracoderms' were definitely jawless. This period shows little consideration for characters, but instead a great desire for scenarios of anatomical transformation and adaptation, owing to the burgeoning enthusiasm for evolutionary theories (the two review articles by Kemna (1903, 1904) reflect precisely the kind of debates taking place and questions being asked during this period). This period ended with a major discovery by Kiaer (1924), who showed that anaspids possess a median opening on the dorsal surface of the head (Text-fig. 2I2), anterior to the pineal opening, which he regarded as a nasohypophysial opening, similar to that of lampreys. He also extended this interpretation to osteostracans, though with some reservation. In contrast, Kiaer considered that heterostracans possessed two separate olfactory organs, as in the gnathostomes. He thus classified vertebrates into two taxa, the Monorhina (anaspids, osteostracans, lampreys, and hagfishes) and the Diplorhina (heterostracans, thelodonts, and gnathostomes), thereby implying that jawlessness is not a character and cannot define a taxon.

A few years later, Stensiö (1927) opened the third period with a major work on the Devonian osteostracans from Spitsbergen. By using Sollas' grinding section method, Stensiö unravelled the internal anatomy of the endoskeletal cephalic head shield of osteostracans, and thereby confirmed the striking resemblance of the cavities in their ethmoid region with the nasohypophysial complex of lampreys. Although he had described a few years earlier (Stensiö 1925) the internal anatomy of the skull of an early gnathostome, the placoderm *Macropetalichthys*, he does not seem to have been impressed by the striking resemblance (which he may have considered as a general craniate condition) between the organization of the cranial nerves of this placoderm and that of osteostracans (Text-fig. 4). On the contrary, he focused on a point-by-point comparison with the anatomy of lampreys and pointed out some resemblances between the these two taxa, some of which are merely general vertebrate characters. The massive, perichondrally ossified head-shield of osteostracans was regarded by Stensiö as a general vertebrate character, remaining in lampreys in the form of the muco-cartilage of the ammocoete larva. The radically different skull of adult lampreys, made up of cartilaginous bars and plates, was thus viewed by him as the result of a 'degeneracy' or 'regression'. The same skeletal regression had been invoked by him (Stensiö 1925) to justify the evolution of sharks from placoderms. Today, Stensiö would probably have invoked heterochrony or paedomorphosis to justify such a difference between fossil and modern forms. Clearly, all of Stensiö's reasoning was strongly influenced by one character, the dorsal nasohypophysial opening. He then adapted other, less convincing, characters (e.g. the asymmetry of the dorsal aortic groove or of the habenula) to his initial theory. I shall leave aside the heated debates engendered by Stensiö's interpretation of the cranial nerves in osteostracans, linked with the premandibular arch theory. Since osteostracans displayed the earliest known vertebrate internal anatomy, they had to be primitive and thus meet the expectations of such embryology-based theories on head segmentation. Later studies on osteostracans have shown that there is no reason to believe that they possessed a visceral arch anterior to the mandibular arch. Their branchial organization was probably quite similar to that of larval lampreys (Whiting 1977; Janvier 1985). Having grouped osteostracans and anaspids with lampreys in the taxon Cephalaspidomorphi, on the basis of the dorsal position of the naso-hypophysial opening, Stensiö was left with hagfishes, whose nasohypophysial region is quite different from that of lampreys. In particular, the nasohypophysial duct communicates posteriorly with the pharynx (nasopharyngeal duct) and the median 'nostril' (nasohypophysial opening) has a terminal position. He thus suggested that hagfishes were related to heterostracans (including the thelodonts) and *Palaeospondylus* (an enigmatic fossil now regarded as a larval sarcopterygian) in the taxon Pteraspidomorphi, initially with some reservation and on very tenuous grounds (the pair of common external branchial openings of *Myxine*, and the vague resemblance between the embryos of *Eptatretus* and the shield of pteraspids). In subsequent works, Stensiö (1932, 1964, 1968) added more conviction to this suggestion and the poorly known internal anatomy of heterostracans was interpreted to match that of hagfishes. The Recent cyclostomes were thus diphyletic when considered together with the fossil jawless vertebrates, i.e. their nakedness, 'rasping tongue', and elongated body shape were viewed as homoplastic. For Stensiö, however it was absolutely clear that all known fossil and Recent agnathans formed a clade (Stensiö 1927, fig. 103), and thus that none of them could be regarded as more closely related to the gnathostomes than to other agnathans. This was the generally accepted view at that time, and was validated by the structure of the branchial apparatus in agnathans, where the endoderm-derived gills were situated medially to the gill arches. This condition was regarded as irreconcilable with that in the gnathostomes, where the gills are derived from the ectoderm and are lateral to the gill arches. Whether one or the other of these two conditions could be general for all craniates was, however, never questioned, and Jarvik (1980, 1981) still considered agnathans and gnathostomes to be two sister-clades that arose from a hypothetical gill-less ancestor. Although many palaeontologists rejected Stensiö's theory that hagfishes are relatives or descendants of heterostracans, there was a consensus that agnathans were a 'natural group'. Some evolutionary 'spindle' diagrams, however, often showed heterostracans as arising slightly closer to the gnathostomes (e.g. Romer 1945), essentially because of their restored paired olfactory organs, but also mainly because of their lack of cephalaspidomorph characters. It is unclear how important the weight of Cope's taxon 'Agnatha' may have been to this way of considering 'ostracoderms' in craniate phylogeny, but the history of palaeontology shows many similar instances (e.g.

Crossopterygii, Dinosauria, Condylarthra, etc.), where groups based on overall, presumed primitive, resemblance may sit like monoliths and hinder further research for years.

Until the late 1970s, very little changed in the phylogenetic position of the various 'ostracoderm' groups, apart from debates about the affinities of heterostracans which, while retaining their 'agnathan' status, were preferably put closer to the gnathostomes by Russian and some Anglo-American authors (e.g. Halstead 1973, 1982; Novitskaya 1983; see also review in Janvier and Blieck 1993). Those who did not accept the heterostracan-hagfish relationship generally regarded cyclostomes as either a clade characterized by a 'rasping tongue' and pouch-shaped gills, but nevertheless derived from some ostracoderms, or closely allied to anaspids and osteostracans only. The discovery of the galeaspids in China raised some interest but this new group was soon 'shoe-horned' either into the Cephalaspidomorphi (Janvier 1975) or the Heterostraci (Moy-Thomas and Miles 1971). Halstead (as Tarlo 1967) was the first to recognize them as clade, yet within the Cephalaspidomorphi. In the same way, the first arandaspids described by Ritchie and Gilbert-Tomlinson (1977) were regarded as just a new order (Arandaspidiformes) of the Heterostraci. In sum, by the mid-1970s, the widely used taxon Agnatha was still defined by its common ascent from some supposedly agnathous ancestral vertebrate, and not by characters.

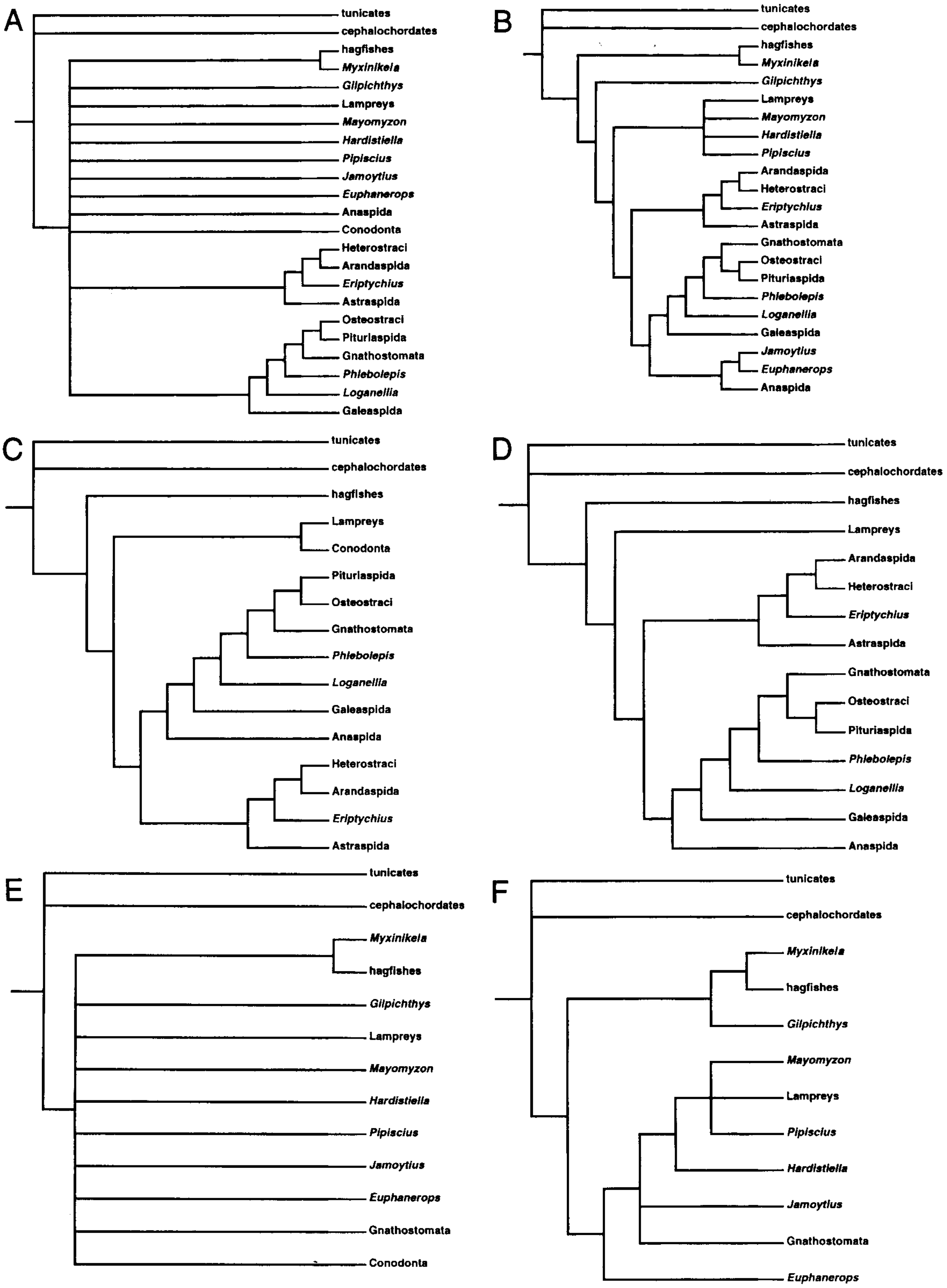
At the end of this third period, some biologists working on Recent lampreys and hagfishes began to consider hagfishes as the 'most primitive vertebrates' (see e.g. Brodal and Fänge 1963), essentially because of their numerous physiological and biochemical peculiarities. This was also the era when phylogenetic systematics, now know as cladistics, began to develop, in particular among lower vertebrate specialists. Løvtrup (1977) opened the fourth period by publishing a cladogram in which lampreys were shown to be more closely related to the gnathostomes than to hagfishes. This was the first clear attempt at breaking through the 'agnathan barrier'. He was immediately followed by a number of biologists and also some palaeontologists. Janvier (1981) suggested that the name Vertebrata should be used only for the taxon including some fossil taxa, lampreys and the gnathostomes, all of which possess vertebral elements (arcualia), and the taxon Craniata would include hagfishes and the Vertebrata, all of which possess a skull. Although many biologists and palaeontologists considered that this solution solved some problems (i.e. it avoids assumptions about the 'degeneracy' of hagfishes') they were reluctant to accept the conclusions of character distribution and break through other barriers, such as that of the Cephalaspidomorphi. It took nearly six years for me (Janvier 1978, 1981, 1984; see also Forey and Janvier 1993) to accept that the characters shared only by osteostracans and the gnathostomes (cellular bone, epicercal tail, pectoral fins, etc.) had not been lost by lampreys and, consequently, that cephalaspidomorphs are either paraphyletic or diphyletic. In these first cladograms published in the mid-1980s, lampreys are still assumed to have lost their paired fins and exoskeleton, being the sister-group of anaspids or osteostracans. However, the suggestion that the naked Silurian form *Jamoytius* may be either the closest relative of lampreys (Forey and Gardiner 1981) or 'intermediate' between anaspids and lampreys (Ritchie 1968, 1984) implied that the loss of exoskeleton, if any, must have occurred very early. The addition of yet another new taxon, the pituriaspids (Young 1991), and better knowledge of the arandaspids (Gagnier 1993*a*), galeaspids (Wang 1991), and thelodonts (Turner 1991; Van der Brugghen and Janvier 1993) allowed researchers to make larger and more complete data matrices and produce cladograms and trees that implied that it was less and less likely that lampreys had undergone some skeletal regression. One may see this fourth period as ending with the publication of a cladogram by Gagnier (1993*b*), where all 'ostracoderms' are placed more crownward than lampreys, implying thus that lampreys never possessed paired fins nor exoskeleton. This solution has recently been accepted by Forey and Janvier (1994) and Forey (1995). In other words, 'ostracoderms' would be stem-group gnathostomes.

This brief review of the research on vertebrate or craniate phylogeny shows, as usual, that theories about relationships are supported and defended for a time, by means of *ad hoc* explanations involving preservation, evolutionary scenarios (assumptions about common ancestry, paths of character evolution and/or character reversions), and they collapse suddenly when they go too far beyond the bounds of parsimony. Their fall is often caused by the discovery of new taxa and new assemblages of characters, and also by a cold look at characters, as free as possible from assumptions about transformation processes.

'OSTRACODERMS' AND CRANIATE PHYLOGENY: CURRENT PROBLEMS

Future tasks in research on vertebrate or craniate phylogeny are obviously to test this latest phylogeny by using other characters, or by finding new associations of characters in new or still poorly known taxa, such as galeaspids, pituriaspids and thelodonts. To begin with, however, the first task is to settle more clearly the question of the interrelationships of extant taxa, i.e. hagfishes, lampreys and the gnathostomes. Løvtrup's 'vertebrate theory' (the Vertebrata being composed of the lampreys and gnathostomes alone) is fairly well supported by anatomical and physiological characters (Hardisty 1982), but molecular sequence data still provide ambiguous results (Stock and Whitt 1992; Lecointre 1994), which depend on the out-group used in the analysis (those generally used are the cephalochordates or tunicates). There are admittedly some characters shared by hagfishes and lampreys which cannot clearly be proved to be general craniate characters. The most impressive of these is the complex musculature and skeleton of the 'lingual' apparatus, which acts to move the horny teeth back and forth. The resemblance in structure between the 'tongue' of hagfishes and lampreys suggests homology (Yalden 1985), although that of hagfishes is certainly more simple than that of lampreys. The mechanism of the hagfish 'tongue' may represent a general craniate condition, further modified in lampreys, and lost in the gnathostomes. However similar this organ may look in hagfishes and lampreys, this potential homology is outnumbered by many other characters shared by lampreys and the gnathostomes, and which cannot be rejected by means of an appeal to either convergences (in lampreys and gnathostomes), or reversions due to 'degeneracy' (in hagfishes). Whatever the status of the cyclostome versus vertebrate problem, this does not influence the relationships between 'ostracoderms' and the gnathostomes if these are regarded as a clade, characterized by, for example, the ability to produce a dermal skeleton.

The major problem in this phylogeny reconstruction is the heterogeneity of the available characters. The characters used in elucidating the interrelationships of extant craniates concern essentially the soft tissue anatomy and physiology, whereas histological and morphological characters of hard tissues are widely used when fossils are considered. Moreover, 'ostracoderms' display very few informative characters: that is, those that are not either unique characters of the terminal taxa, or general craniate or vertebrate characters. As an example of this problem, the conodonts display some general characters of the myomerozoans (i.e. craniates + cephalochordates), craniates or vertebrates, such as the chevron-shaped myomeres, the notochord, and the large eyes, respectively, along with unique characters, such as the morphology and histology of the conodont elements. Only the presence of a phosphatic dermal skeleton with possible dentine or bone cells (osteocytes or odontocytes) is shared only by the conodonts, osteostracans, and the gnathostomes. Also, some anatomical characters are known to some extent in some taxa, as a result of good conditions of fossilization or to extensive endoskeletal ossification, whereas their homologue in other taxa is known only from impressions or indirect evidence. The olfactory organs and associated hypophysial region, for example, are important character-bearing structures and are reasonably well known in osteostracans and galeaspids but not known, or poorly so, in anaspids, arandaspids, astraspids, heterostracans and thelodonts. This imbalance in the quality of the characters is perhaps worse than mere question marks (missing data) in a data matrix, since each palaeontologist has his own propensity to follow one or another interpretation, inferred from such tenuous evidence as impressions of the internal surface of the exoskeleton or poorly defined tarry imprints. This is a general problem with fossils, but here it becomes crucial, due to the paucity of the available characters. Such questions as whether arandaspids have two separate external nostrils, whether anaspids have a dorsal nasohypophysial opening, or whether thelodonts and heterostracans have a nasopharyngeal duct are subjects of controversies but have decisive bearings on the resulting phylogeny. A solution would be to use exclusively histological characters of the dermal skeleton, which are a widespread source of data in 'ostracoderms', but this requires assumptions about the


A
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Gilpichthys
Lampreys
Mayomyzon
Hardistiella
Pipiscius
Jamoytius
Euphanerops
Anaspida
Conodonta
Heterostraci
Arandaspida
Eriptychius
Astraspida
Osteostraci
Pituriaspida
Gnathostomata
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Lampreys
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Hardistiella
Jamoytius
Gnathostomata
Euphanerops

degree of generality of some of them, which are often difficult to make because of the lack of dermal skeleton in hagfishes, lampreys, and cephalochordates/tunicates, the possible outgroups.

We are now in a situation where no clade, apart from the terminal taxa mentioned above (except thelodonts, which may not be a clade), can be regarded as satisfactorily robust. None of those which includes fossils is supported by more than five characters actually observable in all terminal taxa. The most robust clade is perhaps that including osteostracans (+pituriaspids) and the gnathostomes. Even the Pteraspidomorphi (*sensu* Gagnier 1993*b*, i.e. including the Arandaspida, Astraspida, Heterostraci, and *Eriptychius*) is a poorly supported clade (Text-fig. 5A–C), which rests on the assumption that the large median ventral and dorsal shields of their head armour are homologous, although quite different in structure. The peculiar 'naked anaspids' *Euphanerops* and *Endeiolepis* are classically regarded as highly derived anaspids, because of their typical strongly hypocercal tail and geological age (Late Devonian). However, their numerous gill units (up to 30), also found in the Silurian *Jamoytius*, are suggestive of the condition in cephalochordates (Wickstead 1969) and may thus represent a general craniate condition. The data matrix in Table 2 is slightly different from that used by Gagnier (1993*b*) and Forey (1995), since I have tried to include all the terminal taxa mentioned above, including those for which we have very little data, such as *Eriptychius*, pituriaspids, thelodonts and conodonts. The thelodonts are represented by two genera (*Loganellia* and *Phlebolepis*) which differ in some histological and anatomical characters. Only *Endeiolepis* is not included in this matrix because we know nothing of its head, and it would appear as redundant as *Euphanerops* with respect to all other characters. I have also reduced the number of soft anatomy and physiological characters for extant taxa, and some anatomical characters of fossils are inferred (from neighbouring structures linked in some way to these characters, e.g. scales and myomeres) but not directly observed. Table 1 (see Appendix) provides an annotated list of the characters used in the matrix. Characters are classified according to their availability in Recent taxa only, in all taxa, in mineralized taxa only, and in non-mineralized taxa only. The reader may run this data matrix with any program, any option, and any weight or ordering given to the character states. The strict consensus tree (of 79 shortest trees) in Text-figure 5A is produced by using the program HENNIG86 (Farris 1988), options mhennig, branch-breaking*, with character 35 as non-additive (unordered), and tunicates as an outgroup. In order to avoid imbalance in the nature of the characters and fossil taxa, I have run five other data matrices, where some taxa or characters are deleted. In the first modified matrix, only conodonts are deleted, and the strict consensus tree (of 5 shortest trees) is much better resolved (Text-fig. 5B). In the second modified matrix, only extant taxa and fossil mineralized taxa are considered. The only shortest tree obtained (Text-fig. 5C) shows no difference as to the relationships of the mineralized taxa, except for conodonts which appear as the sister-group of lampreys. The third modified matrix is the same as the preceding one, but conodonts are deleted. The only shortest tree (Text-fig. 5D) shows no difference as to other relationships. In the fourth modified matrix, only the extant taxa, the non-mineralized taxa, and the conodonts are considered. The strict consensus tree (Text-fig. 5E) is largely unresolved and remains the same, whether or not characters 42–81 (irrelevant to non-mineralized fossils, but relevant to extant taxa) are deleted. Finally, the fifth modified matrix is the same as the preceding one, but conodonts are deleted. The resulting strict consensus tree (of six shortest trees) differs in some respects from the relationships of the corresponding taxa in the tree derived from the first modified matrix, whether or not characters 42–81 are deleted (Text-fig. 5F). This seems to show that

TEXT-FIG. 5. Strict consensus trees of the equally most parsimonious trees of the Craniata, obtained from the data matrix in Table 2 with the program HENNIG86 (Farris 1988). See text for options. A, all fossil and Recent terminal taxa cited in the text, except *Endeiolepis*; thelodonts are represented by the two genera *Loganellia* and *Phlebolepis* (tree length 150, consistency index 60, retention index 72); B, as for A, but conodonts deleted (t.l. = 148, ci.i. = 61, r.i. = 73); C, only Recent craniates and mineralized fossil taxa (t.l. = 145, ci.i. = 62, r.i. = 70); D, as for C, but conodonts deleted (t.l. = 143, ci.i. = 63, r.i. = 70); E, only Recent taxa, non-mineralized fossils, and conodonts (t.l. = 103, ci.i. = 81, r.i. = 77); F, as for E, but conodonts deleted (t.l. = 101, c.i. = 83, r.i. = 79).

conodonts generate a great uncertainty, probably because of their large number of unknown characters.

It is probable that different specialists of 'ostracoderms' would propose somewhat different matrices, but most of the characters used here would appear with much the same codings, and I doubt that the position of osteostracans, for example, would change, unless a high weight is given to the dorsal nasohypophysial opening, for example. One could also add more anatomical or biochemical characters relevant to extant taxa but, again, they would just reinforce the node (lampreys ('ostracoderms'+gnathostomes)). Certainly, controversies about character interpretation or weighting will continue for a long time, and other theories will be proposed. When considering the imbalance in the quality of the available data, the uncertainties about some histological characters (dentine or mesodentine in Ordovician forms and conodonts, enameloid in galeaspids, etc.) and about the morphotype (most generalized condition) of the gnathostomes, a 'stabilization' of craniate phylogeny cannot be expected in the near future.

THE 'OSTRACODERMS' AS STEM-GROUP GNATHOSTOMES: THE IMPLICATIONS

The well-resolved strict consensus tree in Text-figure 5B reflects the most parsimonious distribution of characters, but it has many implications for their history. The tree is roughly consistent with the distribution of the mineralized exoskeleton or body sensory-lines which appear as unique to 'ostracoderms' and the gnathostomes, yet it implies a loss of the exoskeleton in *Jamoytius*, *Endeiolepis* and *Euphanerops*. It suggests homoplasies for other characters, previously regarded as having a high weight as synapomorphies of some clades. The most surprising of these homoplasies is the dorsal position of the nasohypophysial opening in lampreys and osteostracans (the condition in anaspids remains uncertain, as there is no endoskeleton to tell whether the hypophysial tube was posteriorly closed, as in lampreys and osteostracans, or open toward the pharynx, as in hagfishes and galeaspids). The dorsal position and posteriorly closed nasohypophysial tube of osteostracans may be regarded as a convergence with lampreys, resulting from the loss of the inhalent function of the hypophysial tube and a subsequent close association of the two nasal sacs. One may assume that the common ancestor to osteostracans and the gnathostomes had a large, inhalent terminal duct (the prenasal sinus), like those of hagfishes, galeaspids, and probably also heterostracans and some thelodonts. The two separate nasal sacs opened into the duct, more or less as in galeaspids. Whether the external opening of this duct was slightly dorsal (as in galeaspids) or terminal (as in hagfishes) cannot be decided on the basis of direct evidence, but the history of this character (character 24) in the equally most parsimonious trees suggests that a terminal position could be primitive for the clade including the gnathostomes and osteostracans. Conversely, a primitively dorsal position may find support in the fact that the Rathke's pouch of embryonic gnathostomes (from which the prenasal sinus and hypophysial duct of lampreys is derived and, presumably, also in all 'ostracoderms') has a dorsal position in early osteichthyan embryos (Bemis and Grande 1992). It is thus the loss of the inhalent function of this duct in the osteostracans and gnathostomes that triggered the development of the nasal sacs in two different ways: reduction and close association in osteostracans, separation and direct opening to the exterior in the gnathostomes. The hypothetical common ancestor of osteostracans+pituriaspids and the gnathostomes probably looked more like a flat-bodied 'thelodont' with a microsquamose exoskeleton and true paired fins, than either an osteostracan or a shark.

Another question raised by this tree is that of the appearance of the paired fins. Janvier (1978) regarded true paired fins (with musculature and possibly radials) as a character unique to osteostracans, anaspids, lampreys and the gnathostomes, and supposedly lost in lampreys. If we consider the tree proposed by Forey and Janvier (1994) or Forey (1995), in which anaspids are the sister-group of all other 'ostracoderms' and the gnathostomes, we are faced with the problem of having paired fins either arising twice (in anaspids and in the common ancestor to osteostracans, pituriaspids and gnathostomes), or having been lost in heterostracans and galeaspids (without any evidence). In the tree in Text-figure 5B, the same discrepancy remains, since galeaspids have no paired fins and it is uncertain whether the lateral flaps of thelodonts are really paired fins. The implication of the analysis is that anaspids never possessed true paired fins but merely ventrolateral fin-folds devoid of musculature. What is unique to osteostracans, pituriaspids and the gnathostomes is the presence of muscularized and 'concentrated' pectoral fins in the postbranchial region, which are inserted on an endoskeletal shoulder girdle.

The supposed closest relatives of the gnathostomes, the osteostracans and pituriaspids, possess a massive, shield-shaped head endoskeleton that contrasts with the lightly built skull of chondrichthyans and actinopterygians. This difference fades away when one considers the broadly expanded braincase of most placoderms. This condition is generally regarded as unique to this group but, when considering the fact that placoderms lack a number of unique characters shared only by chondrichthyans and osteichthyans (e.g. their myodome for the superior oblique muscle is posterodorsal, as in osteostracans and lampreys, and not anterodorsal, as in other gnathostomes) and may thus be the sister-group of all other gnathostomes, it is possible that this vague resemblance to osteostracans, pituriaspids and galeaspids in the extension of the braincase over the branchial apparatus is not a convergence but a general gnathostome character.

Although some 'ostracoderms' provide information about the rise of the calcified skeleton, cellular bone, paired and unpaired fins, they tell us nothing about the origin of jaws and medially placed branchial arches of the gnathostomes. The osteostracan braincase may resemble that of a placoderm more than that of a lamprey, but it shows no evidence of any device that might foreshadow jaws. Only the presence of two large pits for the insertion of muscles that may be interpreted as adductor muscles of the lower lip suggests that the mouth of osteostracans opened and closed vertically, like that of the gnathostomes. Jaws probably developed first in microsquamose, thelodont-like forms, and the early stages of their development can be expected to be observed only in exceptionally well preserved fossils of this kind.

Evolutionary patterns

The distribution of the 'ostracoderms' in time is peculiar, since most of them are from the Silurian and Devonian, with a few taxa in the Ordovician, and the in-group relationships of the Siluro–Devonian taxa (in particular osteostracans, anaspids and galeaspids) strongly suggest that their diversification occurred long before their earliest fossil occurrence (Blieck and Janvier 1991). It seems that, being bound to particular, marginal or deltaic environments, their occurrence as fossils largely depends on low-energy conditions of deposition. Nevertheless, there has been some speculation about how they evolved and disappeared. The sudden appearance of most 'ostracoderm' taxa, along with the earliest known gnathostomes, in the Early Silurian shows the kind of pattern that would be called a 'radiation' by most evolutionary palaeontologists. Whether this is a 'recovery' of the vertebrates after the Late Ordovician extinction event, or a consequence of the expansion of marginal marine environments is difficult to tell, and is perhaps not that important. The recent field-work undertaken in Central Asia and Siberia by Karatayute-Talimaa and Predtechenskyj (1995), in continuous sequences which straddle the Ordovician-Silurian boundary, tends to show that such classically Ordovician taxa as astraspids survived into the Silurian, whereas reputedly Siluro–Devonian ones (e.g. thelodonts) were already present in the Late Ordovician. One must keep in mind that a similar 'radiation' was envisaged two decades ago for the gnathostomes in the earliest Devonian, until chondrichthyans, acanthodians, placoderms (including highly derived taxa like antiarchs), and osteichthyans (actinopterygians and lungfishes) were recorded from the Late Silurian, and even the Early Silurian (Llandovery).

There is a widespread belief that 'ostracoderms' were 'outcompeted' by the gnathostomes. However, this ignores the fact that they coexisted with the gnathostomes for 70 million years, and they appear to have been most diverse in the localities where they occur with many gnathostomes (Spitsbergen, Arctic Canada). What may have caused the 'fall' of 'ostracoderms' is perhaps more likely to have been the reduction of their preferred type of environment, that is, vast tidal flats and lagoons, as a consequence of the mid-Devonian transgression. They subsequently survived in disjunct areas until the end of the Frasnian. Whether the end-Frasnian event, which is supposed to have impoverished all invertebrate faunas, played a role in their ultimate extinction is unknown. The fact that the youngest known 'ostracoderms' (*Endeiolepis*, *Euphanerops*, and representatives of osteostracans, heterostracans, galeaspids and thelodonts) are all Frasnian (possibly early Famennian for galeaspids) may well be due to chance, and it would not be surprising to find them in younger levels, when suitable facies are explored. Conversely, and as predicted by the tree in Text-figure 5B, lampreys and hagfishes may be found much earlier than the Carboniferous, at any rate as early as the earliest 'ostracoderms' or perhaps conodonts. As claimed by Forey and Gardiner (1981), the Early Silurian 'naked anaspid' *Jamoytius* is perhaps a lamprey, although in one of the trees shown here (Text-fig. 5B), it comes together with anaspids, *Euphanerops*, and *Endeiolepis*, as classically assumed by previous authors (Ritchie 1968).

In conclusion, the distribution of these early vertebrates in the fossil record tells us little about the timing of the appearance of their characters, except at the scale of minor terminal taxa. It is clear that the Ordovician vertebrate record is abnormally poor and that field palaeontologists have to look carefully for Ordovician vertebrates.

Craniate-related fossils

Paradoxically, the earliest known vertebrates tell us less about the 'dawn' of the vertebrates than do extant hagfishes and lampreys. In fact, as we have seen above, they may tell us more about the dawn of the gnathostomes, although they have no jaws. There have been desperate attempts to plug the systematic gap between the 'protochordates' (tunicates and cephalochordates) and the craniates with fossils. Generally, these attempts have been faithful to the belief that the ancestral craniate was a naked, gracile, fish-like animal, in many ways similar to the extant cephalochordates. The recent assessment of the Conodonta as craniates also follows this trend. A radically different theory is that of Jefferies (see Jefferies 1986 for details) proposing that all recent chordates are rooted in an ensemble of heavily calcified, echinoderm-like fossil creatures, commonly referred to as the 'calcichordates'. Other fossils have been referred to as craniate relatives, or just chordates, such as the Cambrian *Pikaia* or the Silurian *Ainiktozoon* (Ritchie 1985; see Blieck 1992 for a review). The major problem in this field rests on the fact that the characters used to assess the position of these forms are often of a different nature from those commonly used for reconstructing craniate phylogeny. In the case of the conodonts, the characters which are compared with those of craniates are preserved as imprints (fin rays, muscle blocks, eyeballs) and can be interpreted in different ways. In the case of the calcichordates, the characters of the internal anatomy are preserved inside or on the surface of a calcitic endoskeleton which has no homologue in craniates, and the resemblances are remote. Nevertheless, I feel more comfortable with calcichordate anatomy than with conodont anatomy, because, here, there is little ambiguity as to the shape of the structures, whatever their interpretation may be. In many ways, the quality of Jefferies' characters is similar to that which we have for osteostracans or galeaspids. I shall not comment upon the 'calcichordate theory' in the present connection and it is clear that the test, and possible failure of the test, lies in the discovery of characters (other than the calcitic endoskeleton) which would unambiguously prove them to be a sub-group of the echinoderms (see Peterson 1995 for a recent criticism of this theory). Nevertheless, the discovery of a single, unambiguous craniate character (e.g. a labyrinth with at least one semicircular canal) in a mitrate would be more than welcome.

As for conodonts, the series of discoveries on their morphology made during the last twelve years has led many palaeontologists to accept that they are craniates (Briggs *et al.* 1983; Aldridge *et al.* 1986, 1993). My initial enthusiasm for conodonts as craniates (Janvier 1983) had ups and downs (Tillier and Janvier 1986). I now favour this theory, although conodonts still show some ambigous characters. Craniates are defined as having a skull (not necessarily a neurocranium), and otic, optic and olfactory capsules. An important additional character is the neural crest, which is unavailable in fossils, unless interpreted to have been present as a result of its expression in the form of dermal calcified tissues or a cartilaginous branchial apparatus. Conodonts almost certainly had optic capsules, and the recent description of the latter in an Ordovician conodont from South Africa (Aldridge and Theron 1993) provides evidence that these were highly developed, possibly with a lens and extrinsic eye muscles (Gabbott *et al.* 1995). Whether the conodont apparatus can be regarded as evidence for a craniate exoskeleton (and thus a neural crest) is still undecided, despite the description of a somewhat craniate-like histology (Sansom *et al.* 1992, 1994). My impression is that the structure of conodont elements is much derived, relative to that of the classical dentinous tissues of the vertebrates. One must also keep in mind that 'ostracoderms' display a large variety of dermal hard tissues, and that fragments of galeaspid exoskeleton, for example, would never have been referred to the vertebrates if not found on complete skulls (they would probably have been referred to an arthropod). To date, no gill apparatus, either in the form of gill-pouch or gill-arch imprints, has been observed in conodonts, but negative evidence is not evidence. On several occasions, I have played the role of devil's advocate as to the relationships of the conodonts. This time, I shall try to support what is now the current theory, yet with somewhat different viewpoints. Aldridge *et al.* (1993) placed conodonts as the sister-group of the Vertebrata (craniates minus hagfishes) in the cladogram of the craniates of Janvier and Blieck (1979), which assumed that lampreys have lost the mineralized exoskeleton. Conodonts were thus regarded as sharing with lampreys, gnathostomes and all 'ostracoderms' the ability to produce a mineralized exoskeleton and, perhaps, well-developed eyeballs. Now, when considering the extensive consensus tree proposed here (Text-fig. 5A), conodonts appear in a polytomy with lampreys, anaspids and other non-mineralized taxa. When non-mineralized fossil taxa are deleted, conodonts appear as the sister-group of lampreys (Text-fig. 5C). One can, indeed, reconcile the reconstruction of the conodont feeding apparatus as proposed by Purnell (1994) with what may have been the pharyngeal anatomy of the common ancestor to the Vertebrata (lampreys, 'ostracoderms', and the gnathostomes) simply by considering that the ramiform 'M' and 'S' elements were situated near the mouth opening (more or less like the oral plates of many 'ostracoderms', yet internal), and the pectiniform 'Pa' and 'Pb' elements as being attached to a transversely moving structure derived from a velum of larval lamprey type. This suggests that the transformation of the velum into a biting apparatus may have occurred quite early. Yet another possibility is that the conodont apparatus, in particular the S and M elements, is in fact associated with gill arches lying beneath the braincase (or at any rate the eyes). The presence of mineralized dermal denticles in the branchial apparatus would thus make them closer to the gnathostomes than previously believed (Janvier 1995), although such a position does not appear from the present analysis. Finally, the conodont apparatus may turn out to be associated with a 'tongue'-like device homologous to that of lampreys and hagfishes, but this would not necessarily mean that conodonts are particularly close relatives of any of these taxa (contrary to Text-fig. 5C), since such a device is probably general for craniates. The present enthusiasm for research on conodont structure and affinity will certainly provide many new data to argue for and against their position in craniate or chordate phylogeny, but, at the moment, it seems to be firmly established that conodonts possessed a notochord (a chordate character), chevron-shaped muscle blocks (a myomerozoan character), radials and eyes (craniate characters), large eyeballs, possibly with extrinsic eye muscles (vertebrate characters), and a mineralized skeleton (gnathostome, including 'ostracoderms', character). Putting conodonts with the cephalochordates (Nowlan and Carlisle 1987) would imply either that craniates are diphyletic (as suggested by Bjerring 1984), or that cephalochordates have lost the eyes and radials.

A short remark must be made about yet another taxon of supposedly craniate affinities, *Anatolepis*. First recorded from the Ordovician of Spitsbergen (Bockelie and Fortey 1976), then from North America (Repetski 1979), this form is known only from fragments of phosphatic carapace ornamented with small, elongated tubercles and displaying a three-layered structure, with a cancellar middle layer. The tubercles show some ascending tubules which recall the structure of the vertebrate dentine (for a recent reconsideration of *Anatolepis* see Smith and Sansom 1995). These fragments were originally referred to an armoured vertebrate (Bockelie and Fortey 1976; Repetski 1978) and then became the subject of a controversy as to their possible arthropod derivation (Peel and Higgins 1977; Briggs and Fortey 1982). If the structure of *Anatolepis* is somewhat suggestive of that of the heterostracan exoskeleton (Janvier 1981*a*; Ørvig 1989), some of the spine-shaped elements described from the Ordovician of Greenland are difficult to reconcile with what we know in some of the 'ostracoderms' that bear spine-shaped scales or plates. They look too thin-walled and hollow. Putting *Anatolepis* in the vertebrates, and even among 'ostracoderms' should await the discovery of more characteristic elements (e.g. fragments with sensory-line canals or grooves).

Prospects: more characters or more 'ostracoderms'?

The recent history of research on 'ostracoderms' shows that the discovery of new major taxa, such as the galeaspids, pituriaspids and arandaspids, brought forth new viewpoints and new associations of characters. Galeaspids provided the first evidence for an inhalent prenasal sinus associated with separate nasal cavities, and the first evidence of perichondral bone associated with an acellular exoskeleton. Pituriaspids probably provide the first evidence of true paired fins associated with a terminal (at any rate non-dorsal) nasal opening in 'ostracoderms'. Arandaspids are more puzzling in probably having sclerotic rings, a character regarded by Janvier (1984) as unique to osteostracans and gnathostomes, and perhaps two separate nostrils, like the gnathostomes (Gagnier 1993*a*), although some other characters rather support affinities with heterostracans (Text-fig. 5A–B). One of the problems met with in reconstructing the phylogeny of extant and fossil higher vertebrate taxa is the distribution of known characters as opposed to the many question marks. Moreover, as we have seen above, many of the characters observed in 'ostracoderms' are either unique to the respective terminal taxa or general for the vertebrates or craniates. Some more anatomical characters can certainly be obtained from the available 'ostracoderm' material, in particular galeaspids, and one may expect the discovery of exceptionally well preserved material that yields new characters in the body and fin squamation. Histological characters and ornamentation characters are sometimes difficult to assess and polarize, but they are diverse enough to be informative in a data matrix. it is probable that much useful information will be provided by articulated 'thelodonts', and possibly by the examination of large numbers of specimens of non-mineralized forms, such as *Jamoytius* and *Euphanerops*. These provide information on the cartilaginous endoskeleton and soft tissues which can be compared with the skeletons of lampreys or hagfishes.

The ideal future for 'ostracoderm' research would thus be to acquire more characters of equivalent 'quality' (Nelson 1994), but the nature of currently available material has its limits.

CONCLUSIONS

The history of research on early vertebrates since the mid-nineteenth century shows once more that many controversies and perhaps misleading statements have been due to the propensity of palaeontologists to define taxa by their common ascent rather than by the characters that they possess (Nelson and Patterson 1993). Clearly, Huxley and Lankester considered characters (the large scales and bony plates) to put 'ostracoderms' with osteichthyans. Traquair used common ascent (of heterostracans from thelodonts, and of thelodonts from sharks) to suggest chondrichthyan affinities for heterostracans. He accepted the primitiveness of the microsquamose exoskeleton of thelodonts, but used this general gnathostome or vertebrate character to draw relationships with sharks. Cope used absence of jaws (thus ascent from a theoretical jawless craniate ancestor) to put 'ostracoderms' with lampreys and hagfishes, and so did Stensiö when he put the cyclostomes among 'ostracoderms', although he later proposed reasons other than jawlessness to consider agnathans as a clade. Although the early cladograms of the craniates put emphasis on the characters, the common ascent of lampreys, anaspids and osteostracans, for example, was invoked to justify many assumed reversions in lampreys. Common ascent is also underlying many of the assumptions about evolutionary patterns (radiations, extinctions), since they deal with successions of grades. There may be a radiation of heterostracans, but there is no radiation of the 'ostracoderms' or 'agnathans' in general. Similarly, the gnathostomes did not outcompete agnathans but, in the best case, jawed gnathostomes outcompeted several groups of jawless gnathostomes.

This may seem a pointless discussion, largely concerning semantics, but words and names of taxa do have considerable weight when characters are scarce and when the subject concerns the 'origins' of taxa.

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APPENDIX

TABLE 1. Characters and codings.

Characters that can be observed in extant craniates only

0. Eye lens absent = 0; present = 1. (For a recent consideration of this character in hagfishes, see Wicht and Northcutt 1995.)
1. Ribbon-shaped synaptic organelles in retina absent = 0; present = 1.
2. Tubular muscle in 'tongue' musculature absent = 0; present = 1.
3. Lateral-line neuromasts absent = 0; present = 1. (Some fossils are assumed here to have possessed neuromasts when they possess sensory-line canals, since no extant vertebrate is known to have canals but no neuromast. (For a recent consideration of this character in hagfishes, see Wicht and Northcutt 1995.)
4. Nervous control of heart absent = 0; present = 1.
5. Heart response to catecholamine absent = 0; present = 1.
6. Blood system open = 0; closed = 1.
7. Spleen absent = 0; present = 1.
8. Concentrated exocrine pancreas absent = 0; present = 1.
9. Typhlosole in intestine absent = 0; present = 1.
10. Larval stage present = 0; absent = 1.
11. Compartmentalized adenohypophysis absent = 0; present = 1.
12. Pituitary control of melanophores absent = 0; present = 1. (This character may be correlated with the presence/absence of a pineal foramen in fossils. Absence of a pineal foramen and thus of a photosensory pineal organ would preclude pituitary control of melanophores.)
13. Kidney tubules with glomerulae absent = 0; present = 1.
14. Osmoregulation absent = 0; present = 1.
15. Granulocytes and neutrophils absent = 0; present = 1.
16. Two types of giant Mauthner cells in the central nervous system absent = 0; present = 1.
17. Electroreceptive cells absent = 0; present = 1.
18. Sperm not shed through coelomic cavity = 0; shed through coelomic cavity = 1.

Characters that can potentially be observed or inferred in all extant and fossil craniates

19. Skull absent = 0; present = 1. (This refers to any cranial component, i.e. splanchno- or neurocranial.)
20. Cartilaginous or calcified braincase (neurocranium) absent = 0; present = 1.
21. Dorsally closed cartilaginous or calcified braincase (neurocranium) absent = 0; present = 1.
22. Olfactory organ absent = 0; present = 1.
23. Terminal nasohypophysial opening (inhalent or not) absent = 0; present = 1. (The nasohypophysial opening is assumed to be terminal when there is no evidence that it is dorsal. This is the situation in e.g. astraspids or heterostracans.)
24. Dorsal nasohypophysial opening (inhalent or not) absent = 0; present = 1. (It is assumed to be dorsal in *Mayomyzon*, on account of the position of the imprint of the olfactory capsule.)
25. Optic capsules (exclusive of the lens) absent = 0; present = 1.
26. Transversely biting teeth absent = 0; present = 1. (This generally refers to horny teeth of lampreys and hagfishes, but can potentially be extended to the mineralized teeth of conodonts.)
27. Heart absent = 0; present = 1.
28. Closed pericardium absent = 0; present = 1. (The pericardium of *Mayomyzon* is assumed to have been similar to that of modern lampreys, i.e. closed, because of the shape of its imprint.)
29. Trunk and tail musculature with chevron-shaped muscle blocks absent = 0; present = 1. (In mineralized fossils, the arrangement of the musculature may be inferred from that of the scales, as in anaspids, arandaspids, etc.)
30. Radials in fins absent = 0; present = 1. (In many mineralized fossils, the presence of radials is inferred from the alignment of the overlying scales or fin rays.)
31. Numerous and closely set radials in unpaired fins absent = 0; present = 1. (In many fossils, this character is inferred from the arrangement of the scale rows corresponding to the position of the underlying radials.)

TABLE 1 (*cont.*)

32. Radial muscles in fins absent = 0; present = 1. (The presence of radial musculature is mainly inferred from the muscle insertions on the surface of the endoskeleton, e.g. in osteostracans and possibly pituriaspids, but imprints of muscles can potentially be preserved in non-mineralized fossils, such as *Jamoytius*.)
33. Separate dorsal fin absent = 0; present = 1. (This refers to a separate fin anterior to epichordal lobe in the case of forms having a hypocercal tail.)
34. Anal fin absent = 0; present = 1.
35. Tail isocercal = 0; hypocercal = 1; epicercal = 2. (Although apparently pad-shaped, isocercal or diphycercal, the tail of heterostracans is coded here as hypocercal, because it is assumed to be derived from the hypocercal tail of generalized thelodont type by enlargement of the epichordal radials, as suggested by the 'fork-tailed' thelodonts which display the same tail morphology as heterostracans. The actual path of the notochord has, however, never been observed in heterostracans.)
36. Paired fin folds or fins absent = 0; present = 1. (This refers to any lateral skin fold, be it with radials and radial musculature or not. The small lateral skin fold of the extant hagfish *Neomyxine* is not considered here as a fin fold.)
37. Paired fin folds or fins concentrated in the pectoral or epibranchial regions absent = 0; present = 1.
38. Muscles in paired fins absent = 0; present = 1. (In fossils, this can mainly be inferred from the muscle insertions on the endoskeletal girdle.)
39. Arcualia absent = 0; present = 1. (Arcualia are assumed to be present in heterostracans on the basis of the series of median impressions observed in some species, e.g. *Seretaspis*.)
40. Gill openings arranged in a posteriorly slanting line absent = 0; present = 1. (In some non-mineralized fossils, e.g. *Euphanerops*, the position of the gill openings are inferred from that of the series of rounded imprints regarded here as trematic rings.)
41. More than ten gill units = 0; less than ten = 1.

Characters that can be observed in extant craniates and mineralized fossil craniates only

42. Olfactory tract absent = 0; present = 1. (An olfactory tract is assumed to be present in heterostracans on account of the two divergent ridges that link the impressions of the olfactory organs to the pineal, or diencephalic region. Moreover, the distance between these two impressions is such that it implies the presence of a long tract, as in galeaspids and gnathostomes.)
43. Olfactory organ unpaired or with closely set and confluent nasal sacs, absent = 0; present = 1.
44. Olfactory organ paired with entirely separated nasal sacs, absent = 0; present = 1.
45. Nasohypophysial duct serving branchial respiration, absent = 0; present = 1. (This character is assumed to be present in *Loganellia*, because of the similarity between its denticle-covered median duct and that of galeaspids.)
46. Nasohypophysial duct posteriorly closed and serving only as a common 'nostril', absent = 0; present = 1.
47. Extrinsic eye muscles absent = 0; present = 1. (This character is coded as present in conodonts, but the evidence for muscle fibres associated with the optic capsules remains very slight. It is assumed to be present in osteostracans and galeaspids on the basis of the presence of myodomes.)
48. Photosensory pineal organ (or pineal foramen) absent = 0; present = 1. (In fossils, the pineal organ is assumed to be photosensory when there is a distinct pineal foramen.)
49. Semicircular canals absent = 0; present = 1.
50. Single semicircular canal absent = 0; present = 1. (This character is present only in hagfishes, but there is debate as to whether this is a general craniate condition or a uniquely derived condition.)
51. Two vertical semicircular canals absent = 0; present = 1.
52. Two vertical semicircular canals forming distinct loops, absent = 0; present = 1. (This refers to the distinct canals of e.g. osteostracans, galeaspids or gnathostomes, in contrast to those of lampreys, which lie against the vestibular division of the labyrinth.)
53. Lateral lines enclosed in canals, absent = 0; present = 1.

TABLE 1 (*cont.*)

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54. Lateral-line grooves or canals, absent = 0; present on head = 1; present on head and body = 2. (The presence of sensory-line grooves on the body is not clearly shown in anaspids, but nevertheless is coded here as present based on the description made by Smith 1957. In galeaspids, it is not observed, but inferred from the orientation of the main lateral-line canal in the posterior part of the head shield, which suggests that it continued on the body. In hagfishes, the peculiar grooves on the head are now regarded by Wicht and Northcutt 1995, as true lateral-line grooves, associated with the lateralis nerve fibres, although they show no evidence of neuromasts.)
55. Cerebellum absent = 0; present = 1.
56. Large and paired cerebellum absent = 0; present = 1. (This is based on the assumption that the large, dorsal, paired swellings in the brain cavity of osteostracans and galeaspids, and the similarly placed paired impression in heterostracans actually corresponds to the position of the metencephalon, as proposed by Stensiö in 1927. This character is coded as present in pituriaspids, based on the reconstruction proposed by Young 1991.)
57. Vagus and glossopharyngeus nerves included in occipital region, absent = 0; present = 1.
58. Closely set atrium and ventricle, absent = 0; present = 1. (In fossils, this character is known only in osteostracans, where the heart was enclosed in an ossified pericardium.)
59. Large dorsal jugular vein absent = 0; present = 1.
60. Subaponeurotic vascular system absent = 0; present = 1. (This refers to the vascular network which lies at the limit between the exo- and endoskeleton. It is assumed here to be present in heterostracans on the basis of the vascular impressions in the cyathaspidiform *Torpedaspis*.)
61. Calcified cartilage absent = 0; present = 1. (Calcifications of the cartilage are now known to occur in adult lampreys.)
62. Perichondral bone absent = 0; present = 1. (Perichondral bone may be present in *Eriptychius* on account of the vascular canals of the subaponeurotic network on the surface of the calcified cartilage, which seem to be lined with perichondral bone. This, however, remains to be checked and this character is coded here as '?'. It is also assumed to be present in pituriaspids on account of the mode of preservation of the internal structures, which is comparable to the condition in osteostracans and galeaspids.)
63. Head endoskeleton expanded into a massive shield covering the gills, absent = 0; present = 1. (This refers to the massive endoskeletal shield that covers that branchial region in osteostracans and galeaspids. The large endoskeletal expansions of the braincase over the branchial region in some placoderms are provisionally regarded here as being not general for the gnathostomes.)
64. Endoskeletal scleral ossification or calcification absent = 0; present = 1. (The remnants of the eye cup described by Gagnier 1993*a* in *Sacabambaspis* are almost certainly evidence for a calcified sclera, but it is uncertain whether it is perichondral bone or calcified cartilage.)
65. Orthodentine or metadentine absent = 0; present = 1. (Conodonts are coded here as '0' for both types of dentinous tissue, since the structure of the conodont organs remains ambiguous in this respect.)
66. Mesodentine absent = 0; present = 1.
67. Enameloid or enamel (hypermineralized superficial layer) absent = 0; present = 1. (In osteostracans, enameloid is known with certainty in thyestiids, but it is probably present also in many other forms with a shiny superficial layer of the exoskeleton. Conodonts possess a fibrous external layer that may be considered here as enamel or enameloid.)
68. Acellular dermal bone absent = 0; present = 1. (Gagnier 1993*a* suggested that the exoskeleton of arandaspids might have been cellular on account of peculiar cavities observed in the dermal bone of *Sacabambaspis*. This, however, remains unconvincing and arandaspids are coded here as having acellular bone.)
69. Cellular dermal bone absent = 0; present = 1. (Conodonts are coded here as having bone cells, although this is still a matter of considerable debate.)
70. Honeycomb-like middle layer of exoskeleton absent = 0; present = 1.
71. Oakleaf-shaped tubercles or odontodes in ornamentation, absent = 0; present = 1. (The scalloped scale crowns of *Phlebolepis* and *Loganellia* might be coded here as being homologues of the oak leaf-shaped tubercles of arandaspids, *Eriptychius* and early heterostracans. However, since scale crowns are not tubercles, this character is coded here as absent.)

TABLE 1 (*cont.*)

72. Large median dorsal and ventral dermal shields in head, absent = 0; present = 1. (Although made up of polygonal units, the dorsal and ventral shields of arandaspids and astraspids are coded here as being homologous to the ventral and dorsal shields of heterostracans. The large median ventral plate of galeaspids is not considered as being a ventral shield.)
73. External opening of endolymphatic duct absent = 0; present = 1. (The opening of the endolymphatic duct is known only in one galeaspid, *Xiushuiaspis*, but since this genus is regarded as quite generalized for the group the character is assumed to have been lost in more advanced galeaspids.)
74. Opercular flaps on external branchial openings absent = 0; present = 1. (This refers to the small scale-covered flaps that extend in front of each gill opening in osteostracans and thelodonts, in contrast to the puncture-shaped gill openings in most other taxa, including arandaspids. The small 'plica trematica' of lampreys is not regarded here as an opercular flap, as it is inside the gill opening.)
75. Preanal skin fold or scale ridge present = 0; absent = 1.
76. Sclerotic ring absent = 0; present = 1. (The ornamented platelets surrounding the eyes in arandaspids are regarded here as true sclerotic rings, as they seem to be independent of the shield and, thus, are probably not circumorbital plates.)
77. Scales made up by a single odontode (microsquamose), absent = 0; present = 1.
78. Scales made up by several odontodes (macrosquamose) and diamond-shaped, absent = 0; present = 1. (The scales of some heterostracans and osteostracans can be rather elongated in shape, but the most generalized members of these taxa have diamond-shaped scales.)
79. Scales made up by several odontodes (macrosquamose) and rod-shaped, absent = 0; present = 1.
80. Pharyngeal dermal denticles absent = 0; present = 1. (Conodonts are coded here as having pharyngeal denticles, as the rearmost conodont organs are likely to have lain relatively far back in the pharynx.)
81. Scale-covered zones on tail absent = 0; present = 1. (This refers to the large, finger-like zonations of small scales in the tail of heterostracans and many thelodonts. The thin and closely set rows of lepidotrich-like scales in osteostracans are not included in this character.)

Characters that can be observed only in extant craniates and potentially in soft-bodied fossil craniates preserved as imprints as well as in mineralized craniates fossilized in anoxic facies (thus preserving imprints of cartilages and keratinized tissues)

82. Horny teeth absent = 0; present = 1.
83. Piston cartilage absent = 0; present = 1. (The peculiar, calcified dumb-bell-shaped element described by Gagnier 1993*b* in *Sacabambaspis* might correspond to a piston cartilage, but it is coded here as '?', because this interpretation is too poorly supported.)
84. Dentigerous cartilage absent = 0; present = 1.
85. Tentacles strengthened by cartilage, absent = 0; present = 1. (Cartilage-supported tentacles are coded as absent in many of the mineralized forms, because the structure of the oral region shows no evidence for the passage of such organs.)
86. Sucking disc with an annular cartilage around mouth, absent = 0; present = 1. (A sucking disc is coded as absent in most of the mineralized forms, such as osteostracans, heterostracans, and galeaspids, because the organization of the dermal oral plates lining their mouth is incompatible with the presence of a sucker. An annular cartilage is clearly present in *Mayomyzon*, and the large rounded snout of *Hardistiella* suggests the presence of some sucker. The presence of an annular cartilage in *Jamoytius* and *Euphanerops* remains controversial and this character is coded here as '?' for these two taxa.)
87. Pouch-shaped gills absent = 0; present = 1. (This refers to pouches that enclose anterior and posterior hemibranchs, as in hagfishes and adult lampreys. Although often depicted as having 'gill pouches', osteostracans, galeaspids and heterostracans show no direct evidence of such pouches. Gill pouches are assumed here to be present in *Mayomyzon*, on account of the aspect of the gill imprints.)
88. Trematic rings absent = 0; present = 1. (The endoskeletal imprints of *Jamoytius* and *Euphanerops* show lateral series of rings, fused side-by-side, that are interpreted here as being trematic rings, rather than branchial arches proper.)

TABLE 2. Data matrix.

		1		2		3		4		5		6		7		8		
	012345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	678
Tunicata	000000	00010	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	000
Cephalochordata	000000	00000	00000	00000	00000	00010	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	000
Hyperotreti (hagfishes)	001000	00001	00000	00110	01101	11011	00000	00000	00101	00011	00010	00000	00000	00000	00000	00000	01011	011
Myxinikela	??????	?????	?????	???1?	?1101	1??1?	??000	0?0??	??101	0????	?????	?????	00000	00000	00???	00000	01011	0??
Gilpichthys	??????	?????	?????	???1?	????1	1??1?	??000	0?000	1????	?????	?????	?????	00000	00000	00???	00000	010?0	0??
Hyperoartia (lampreys)	111111	11111	11111	11111	01011	11111	11101	00011	10100	11110	10001	00111	10000	00000	00001	00000	01110	111
Mayomyzon	??????	?????	?????	???11	?1011	11111	1?00?	0?0??	1?100	1????	?????	?????	00000	00000	00???	00000	0?110	11?
Hardistiella	??????	?????	?????	???11	?1??1	????1	1?111	??0??	?????	?????	?????	?????	00000	00000	00???	00000	0???0	1??
Pipiscius	??????	?????	?????	???1?	????1	???11	1??0?	?????	1????	?????	?????	?????	00000	00000	00???	00000	01??0	1??
Jamoytius	??????	?????	?????	???1?	????1	???11	1??11	1?0??	0????	?????	?????	?????	00000	00000	00???	00000	00??0	??1
Euphanerops	??????	?????	?????	???1?	????1	?1?11	0?011	??0?1	0????	?????	?????	?????	00000	00000	00???	00000	00??0	??1
Anaspida	??????	?????	?????	???1?	?1011	???11	0?011	1?0?1	0????	??1??	??02?	?????	?0000	00100	00?01	00010	1???0	0??
Astraspida	??????	?????	?????	???1?	???01	?????	??00?	000?0	1????	??0??	??0??	?????	????0	01100	01000	?010?	?????	???
Eriptychius	??????	?????	?????	???1?	?????	?????	?????	?????	?????	?????	??0??	????1	1???0	10100	1????	?010?	?????	???
Arandaspida	??????	?????	?????	???1?	?1?01	???1?	??00?	000?1	0????	??1??	??02?	?????	???10	00101	11000	10010	????0	0??
Heterostraci	???1??	?????	?????	???1?	?1?01	???11	0?001	00010	1101?	?0110	11121	1???1	00?01	00101	11000	00100	1???0	0??
Phlebolepis	???1??	?????	?????	???1?	???01	????1	0?111	11??0	1????	?????	??12?	?????	00000	10100	00???	0100?	1???0	???
Loganellia	???1??	?????	?????	???1?	?1101	????1	0?111	11??0	1?011	0????	??12?	?????	00001	00100	00?1?	01001	1???0	???
Galeaspida	???1??	?????	?????	???11	11011	???11	000??	000?0	11011	01110	11121	11?11	?1100	01100	00101	0100?	1???0	0??
Pituriaspida	??????	?????	?????	???11	11??1	?????	?1???	111?0	?????	?????	????1	1????	?11??	?????	00??1	?????	????0	0??
Osteostraci	???1??	?????	?????	???11	11011	?1111	11102	11110	1?100	11110	11121	11111	11110	11010	00111	10100	0???0	0??
Gnathostomata	110111	11110	11111	11011	11001	01111	11112	11110	11010	11110	11121	11111	11011	11010	00111	11101	00000	000
Conodonta	??????	?????	?????	?????	????1	1??11	1?001	000??	?????	?1???	?????	?????	?0000	01000	00???	00001	00??0	0??