Conodont anatomy, chordate phylogeny and vertebrate classification
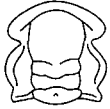
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Interpretations of conodont anatomy and affinity continue to generate controversy. Fossilized soft-tissue evidence indicates that conodonts possessed eyes, extrinsic eye muscles, a notochord, myomeres, a differentiated tail with fin radials, possible otic capsules and possible branchial structures. Indirect evidence suggests a differentiated brain and cartilaginous head skeleton. The multi-component phosphatic tissue complexes of the conodont feeding apparatus cannot be compared to the amorphous apatite of extant agnathan otoliths. By limiting cladistic analysis to a restricted selection of these characters the hypothesis that conodonts are a sister group of the clade comprising extant hagfish, lampreys and gnathostomes can be supported. However, exhaustive analysis of a more complete character-set strongly supports the hypothesis that conodonts are more derived than hagfish. From a taxonomic perspective, these two hypotheses have no effect on how conodonts should be classified. Whether they are a stem group (the former hypothesis) or part of the crown group (the latter), conodonts are clearly part of the total group Vertebrata (=Craniata). □*Chordates, craniates, vertebrates, Agnatha, conodonts, cladistic analysis, phylogeny, anatomy, palaeobiology.*

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Conodonts are provocative fossils. Their discovery by Pander in 1856 initiated a debate regarding conodont biology and affinities that has sometimes been heated and that continues to this day (see Aldridge 1987; Aldridge *et al.* 1993; Janvier 1995; Aldridge & Purnell 1996). The recent paper by Pridmore *et al.* (1997) demonstrates that consensus remains elusive, and raises points that demand a response.

A number of aspects of the debate are, however, no longer controversial. The discovery of conodont fossils preserving remains of myomeres and a notochord (Briggs *et al.* 1983; Aldridge *et al.* 1986, 1993; Briggs & Kear 1994; Gabbott *et al.* 1995) has provided widely accepted evidence that the affinities of the conodonts (used here=euconodonts *sensu* Bengtson 1976) lie among the chordates (Pridmore *et al.* 1997 and references therein). Controversy is now focused primarily on details of conodont biology, such as soft-tissue anatomy, element histology and the functional morphology of the feeding apparatus, particularly centering on the emotive question 'were conodonts vertebrates?'

The case for a vertebrate affinity for conodonts was most fully advanced by Aldridge *et al.* (1993), supported by investigations of element histology (Sansom *et al.* 1992, 1994) and supplemented by further soft-tissue evidence published by Gabbott *et al.* (1995). Pridmore *et al.* (1997) have taken issue with this conclusion and have argued that the evidence of the preserved anatomy of the fossil conodonts places them outside the Craniata (=Vertebrata in the usage of many authors). Their paper considers three separate but related aspects of the debate: conodont anatomy, chordate inter-relationships and the classification of vertebrates. Here we set out to reconsider conodonts in the light of the points raised by Pridmore *et al.* (1997).

Conodont anatomy

Interpretation of the anatomy of fossil specimens is often difficult, especially where there are no undisputed close modern relatives. The vagaries of preservation invariably result in the loss of some information, and the features that survive decomposition become transformed during compaction and mineralization. Hence, absence of evi-

dence should not be taken as evidence of absence. Inter-pretation necessarily relies on comparisons with struc-tures in extant organisms, but it is important to avoid circularity: the choice of a modern comparator controls the interpretation of anatomical characters, which, if then used in a phylogenetic analysis, will inevitably link the fos-sil and modern forms. To minimize these dangers, the most rigorous approach is to use a few unequivocal char-acters to set a broad phylogenetic context within which to interpret other features of the fossils. The best placement within the selected clade can then be determined by an analysis involving all the anatomical characters. In the case of conodonts, the starting point is the presence of a notochord and myomeres, characters unique to the phy-lum Chordata.

The tail

The tail bears a clear caudal fin, within which fin radials are observable (Briggs et al. 1983; Aldridge et al. 1986, 1993), comparable in their position, length, orientation and number to the fin radials of vertebrates (Briggs & Kear 1994; Pridmore et al. 1997). There is currently no evidence to determine whether musculature was present at radial bases. The fin on one side of the animal is appar-ently divided into at least two lobes (Briggs et al. 1983).

Trunk musculature

The trunk muscles of conodonts preserve the characteris-tic inflection of chordate myomeres (Aldridge et al. 1993; Gabbott et al. 1995), but as the fossils lack clear body mar-gins it is more difficult to determine whether the myo-meres were originally V- or W-shaped. The preserved portions are, however, clearly V-shaped. V-shaped myo-meres are preserved in the Carboniferous fossils Gilpich-thys and Pipiscius (Bardack & Richardson 1977), a possi-ble hagfish and a possible lamprey, respectively (Janvier 1981, 1996b), but as Pridmore et al. (1997) indicated, this is unparalleled by any extant adult vertebrate. However, embryonic and hatchling hagfishes have V-shaped myo-meres (Dean 1899), and they are widespread among larval stages of gnathostomes, including teleosts and anurans.

As Pridmore et al. (1997) have pointed out, it is possible that the apparent V-shape of the conodont myomeres reflects post mortem decay of originally more complex structures. They considered, however, that the dorsal por-tions of the myomeres are complete and that only M-shaped myomeres could be produced if additional chev-rons of ventral musculature were postulated. An alterna-tive would be that the preserved portion represents the axial inflection of the W, with the ventral limb lost and a shorter dorsal limb either unpreserved or concealed in the known lateral views of the trunk. The structures would

then compare with the myomeres of ammocoetes, which are cryptically W-shaped with the outer limbs of the W acutely deflected anteriorly as they approach the dorsal and ventral margins of the body. However, there is cur-rently no evidence, either direct or indirect, to suggest that conodont myomeres were anything other than V-shaped. Interestingly, it has been shown that the angle of inflection of chordate myomeres is related to function (Van Der Stelt 1968). The angle of inflection in the cono-donts (80°–90°) is similar to values measured in teleost larvae (Van Raamsdonk et al. 1977) but greater than angles in Branchiostoma (60°–70°). Measurements taken from the figures of Briggs & Kear (1994) suggest that these angles do not change significantly during decay.

Pridmore et al. (1997) suggested that the relative dispo-sition of myomeres on either side of the trunk might be an important feature. In Branchiostoma, and possibly in Myxine, these are staggered, whereas in the hagfish Eptatretus and in other vertebrates they are aligned. It is a functional requirement of the axial locomotory system of chordates that the apices of V-shaped myomeres are aligned with the notochord or vertebral column (see Bone et al. 1995), but in the conodont fossils the axes of the Vs are displaced. There must, therefore, have been some rel-ative dislocation of the myomeres and the notochord post mortem, and details of original myomere disposition appear to be beyond the resolution of the known fossil material.

Paired structures in the head

Not all chordates possess a head, but there is clearly a degree of anatomical elaboration at the anterior end of the conodont body that warrants use of the term. This should not be taken as an a priori implication that conodonts were craniates or vertebrates; we use the term merely as shorthand for the collection of organs and structures at the anterior of the animal.

Prominent among the soft-tissue features of the cono-dont head is a pair of lobate or doughnut-shaped struc-tures, which have been interpreted as the remnants of sclerotic eye capsules (Aldridge & Theron 1993; Aldridge et al. 1993; Gabbott et al. 1995; Purnell 1995a). Pridmore et al. (1997) considered these structures to be more rea-sonably interpreted as otic capsules, based on the size, shape and position of the lobes, on the relative preserva-tion potential of agnathan eyes and otic capsules, and on the interpretation of associated musculature.

Relative size alone may not be a reliable indicator for differentiating eyes from otic capsules in extant agnathans (Pridmore et al. 1997), although diagrams of dissections published by Marinelli & Strenger (1954) show that the eyes of the lamprey Lampetra fluviatilis are considerably larger than the otic capsules (contra Pridmore et al. 1997, Fig. 2). However, Pridmore et al. (1997) considered that

the paired lobes in conodonts are more similar in size to the otic capsules of fossil hagfish and lampreys than they are to their eyes. The data here are limited to two taxa: the fossil lamprey *Mayomyzon* and the fossil hagfish *Myxinikela*. In *Mayomyzon*, there is little difference in size between the eyes and otic capsules, and both are of similar size to the paired lobes of conodonts (Pridmore *et al.* 1997). In *Myxinikela*, however, the otic capsules were shown by Pridmore *et al.* (1997, p. 321) to be similar in size to conodont lobes, 'depending upon how the specimen is interpreted'. It is pertinent to note here that the darkly pigmented spots they interpreted as otic capsules in *Myxinikela* were regarded to be eyes in the original description of the animal (Bardack 1991; see Pridmore *et al.* 1997, caption to Fig. 3). Moreover, in their discussion of eye size in extant myxinoids, Pridmore *et al.* (1997) omitted mention of the eyes of *Eptatretus*, which are considerably larger than those of *Myxine*. Thus, only by selective use of the evidence can size be considered to support an interpretation of the conodont lobes as otic capsules.

Reconstruction of the three-dimensional shape of the lobes requires fossils preserved in different orientations. Where the configuration of the feeding apparatus shows the head to be in lateral or near-lateral orientation, the lobes are ring-shaped (Aldridge & Theron 1993; Aldridge *et al.* 1993; Pridmore *et al.* 1997). Two fossils (IGSE 13821/13822 from Granton and C358 from South Africa) show orientations that are not close to lateral; the former reflects collapse of the head at approximately 45° (Purnell & Donoghue 1998), and the latter is also oblique rather than dorsoventral. However, the sub-rhomboid or trapezoid shape of the paired lobes in these specimens provides strong evidence that their original three-dimensional shape was not ovoid (Aldridge & Theron 1993; Aldridge *et al.* 1993; contra Pridmore *et al.* 1997), as are the otic capsules of extant agnathans (Pridmore *et al.* 1997).

The lobes are positioned at the anterior extremity of the preserved animal, slightly in front of the anterior end of the notochord (Aldridge *et al.* 1993, Figs 4, 6). Pridmore *et al.* (1997, p. 322) argued that 'the positioning of the paired structures with respect to the notochord is in very good agreement with the close approximation of the otic capsules and the anterior margin of the notochord in both lampreys and hagfishes'. This argument assumes that the proportions of the agnathan head have remained constant for the 500 million or more years since it was developed in the common ancestor of the conodonts, lampreys and hagfishes. It also requires either that the otic capsules were located at the anterior end of the body (a situation unknown among chordates) or that the anteriormost part of the conodont head has not been preserved (see also Janvier 1995). An interpretation of the lobes as the remains of eyes avoids these difficulties; their position is comparable to the anterior eyes in other early agnathans such as the arandaspids (Gagnier 1993), and there is no

need to resort to *ad hoc* speculations regarding unpreserved anterior extensions to the head.

The original interpretation of the conodont lobes as sclerotic cartilages surrounding eyes (Aldridge & Theron 1993) was influenced by comparisons with similar organic traces in the head of the fossil agnathan *Jamoytius*, which Ritchie (1968) regarded as the remnants of eyes. Ritchie's hypothesis was partly derived from the location of these structures at the anterolateral extremities of the head, but it also drew on comparisons with cephalaspids, in which the eyeballs were 'almost completely encapsulated by a subspherical, sclerotic ossification' (Ritchie 1968, p. 28). Ritchie (1968) also cited a number of examples of preserved eyes from among fossils associated with *Jamoytius*, such as *Lasanius, Birkenia, Thelodus* and *Lanarkia*. In addition, unossified eye remnants have been reported in a number of taxa from several Palaeozoic Lagerstätten, for example *Hardistiella* from the Bear Gulch (Janvier & Lund 1983; Lund & Janvier 1986), *Mayomyzon, Gilpichthys, Pipiscius* and *Myxinikela* from the Mazon Creek (Bardack & Zangerl 1968; Bardack & Richardson 1977; Bardack 1991), and *Euphanerops* and *Legendrelepis* from Miguasha (Arsenault & Janvier 1991). In most of these examples, the eyes are preserved but the otic capsules are not. Nonetheless, Pridmore *et al.* (1997, p. 322) considered that 'the eyes of cyclostomes, and indeed of fossil forms closely related to them, are less likely to be preserved than their auditory capsules'. This conflicts with the fossil record; in the few instances where traces of the otic capsules are preserved they are mouldic or more faintly preserved than the eye remnants (e.g., *Myxinikela* as interpreted by Bardack 1991; contra Pridmore *et al.* 1997). Clearly, unless the eyes of most or all fossil agnathans are re-interpreted as otic capsules, the hypothesis of differential preservation forwarded by Pridmore *et al.* (1997) is refuted by this evidence.

Fibrous musculature in the position of the lobes was first described in specimen C721 of *Promissum* from the Soom Shale by Gabbott *et al.* (1995), who interpreted it as extrinsic eye musculature. Some additional specimens with preserved musculature have been discovered subsequently from the same locality. These fibrous tissues are restricted to the position occupied by the carbonized lobes in other specimens and appear to be intimately related with the lobes rather than just representing fortuitously preserved underlying or overlying musculature. Pridmore *et al.* (1997) noted that muscles overlie, but do not attach to, the otic capsules of extant agnathans, and to some degree the interpretation of the nature of the conodont musculature must be controlled by the interpretation of the capsules. However, the close association of the muscles and capsules in *Promissum* attests to a close anatomical link and cannot be dismissed as coincidental.

The nature of the paired structures, as suggested by Pridmore *et al.* (1997), may be resolved by the discovery

of otoliths. Examination of the most fully preserved conodont specimen (IGSE 13822) has revealed that the region of the anterior lobes is littered with small crystal bundles, but these also occur throughout the head, in the trunk and in the tail. Bundles of this type are associated with the preservation of soft tissues by phosphate replication (Briggs 1996; Briggs & Wilby 1996); they are not fossil otoliths (statoconia). However, excavation of Granton specimen RMS GY 1992.41.3 has revealed a possible otolith (statolith) (Aldridge & Donoghue 1998). This structure is located dorsal of the feeding apparatus, but the specimen does not preserve anterior paired capsules and it is not possible to determine whether it lies within or posterior to them. Unfortunately, therefore, it provides no evidence to support or refute otic or optic interpretations of the capsules.

A number of structures in addition to the optic capsules are evident on specimen IGSE 13822. These include a pair of circular organic traces, immediately posterior of the larger paired lobes; these traces were interpreted by Aldridge *et al.* (1993) as the remains of otic capsules. If this interpretation is correct, and alternatives have not been suggested, then the larger lobes cannot be otic capsules. Pridmore *et al.* (1997, p. 323) dismissed these features on the basis that they are lacking on the counterpart and have not been found in other specimens, but the frequency of their preservation is irrelevant. They are clearly present in the most completely preserved specimen found to date, they preserve definite features of the head, and no interpretation of conodont anatomy can simply ignore them.

On the same specimen, at least four pairs of rectangular structures are faintly evident posterior of the circular traces (Briggs *et al.* 1983, Fig. 3). These have been interpreted tentatively as gill pouches or branchial structures (Aldridge *et al.* 1993). Taken together, the layout of structures in the head of specimen IGSE 13822 is closely comparable with the arrangement of preserved features in the head of the fossil lamprey *Mayomyzon* (Aldridge & Donoghue 1998).

Despite the arguments put forward by Pridmore *et al.* (1997), the evidence still indicates that the larger paired capsules are best interpreted as remnants of eyes. Irrespective of this conclusion, however, it is evident that conodonts possessed large, paired sensory organs, implying that they had a brain of sufficient complexity to process the information gathered by these structures.

Other head cartilages

Apart from an indistinct organic trace surrounding the head structures in specimen IGSE 13822 (Aldridge & Donoghue 1998), there is no evidence of other preserved head cartilages in any conodont specimen. As pointed out by Pridmore *et al.* (1997), some fossil lampreys and hag-fishes show dark stains that have been interpreted as cranial cartilages, and it is perhaps surprising that they are not preserved in conodont specimens that display the sensory capsules. However, closer examination of the fossil record reveals that preservation of cranial cartilages is rare and selective. In neither of the two genera that do have preserved cartilage traces (*Mayomyzon* Bardack & Zangerl 1968, 1971; *Myxinikela* Bardack 1991) are all the cephalic cartilages represented when compared with living agnathans. Furthermore, the oldest fossil lamprey, *Hardistiella*, preserves only equivocal traces of its cranial skeleton (Janvier & Lund 1983; Lund & Janvier 1986), and the same is true of most other fossil naked agnathans such as *Jamoytius* (except for sensory capsules and the annular cartilage), *Gilpichthys* and *Pipiscius*. The differential preservation of cartilages in these fossil agnathans may be due to their composition. Ultrastructural and chemical analyses of the cartilages in the two groups of extant agnathans have shown that they lack collagen and are autapomorphic to their respective groups (Wright *et al.* 1983, 1984; Robson *et al.* 1993; McBurney *et al.* 1996); even within these groups different cartilages are composed of distinct cartilage types (Wright *et al.* 1984). This may explain why some fossil taxa preserve only some cartilages, while others preserve none.

Direct evidence is currently lacking, but the non-preservation of cranial cartilages or musculature in conodont fossils cannot be taken as evidence that they were absent (contra Pridmore *et al.* 1997); in fact, work on functional morphology implies strongly that they were present. Recent functional hypotheses agree that at least some parts of the conodont apparatus moved (e.g., Aldridge *et al.* 1987; Nicoll 1987, 1995; Purnell & Donoghue 1997), and this has been corroborated by the discovery of *in vivo* wear on element surfaces (Purnell 1995b). In chordates, such movement requires muscles and a skeletal framework.

The feeding apparatus

The feeding apparatus of conodonts comprises a bilateral array of morphologically differentiated elements composed of calcium phosphate. Despite controversy over the nature of these tissues (see Aldridge & Purnell 1996 for a review) they clearly make up a multi-component complex of different histological types, differing fundamentally from the amorphous phosphate of the otoliths of hagfishes and lampreys, and spicules of tunicates.

Chordate inter-relationships

Determination of the most parsimonious position of the conodonts in the chordate clade is best achieved by a cla-

Table 1. Scoring of character states for Branchiostoma, conodonts, myxinoids, petromyzontids and gnathostomes, extended from the data matrix presented by Pridmore *et al.* (1997). Hard-tissue complexes may or may not be present in petromyzontids (see text)..

Character	Branchiostoma	Conodonts	Myxinoids	Petromyzontids	Gnathostomes
1 Trunk muscles arranged in myomeres	+	+	+	+	+
2 Apatite secretion	–	+	+	+	+
3 Paired sense organs	–	+	+	+	+
4 Radials in caudal fin	–	+	+	+	+
5 Head skeleton of cartilage or bone	–	?	+	+	+
6 Myomere shape	v	v	w	w	w
7 Vertebrae/arcualia	–	?	–	+	+
8 Caudal fin radial muscles	–	?	–	+	+
9 Hard tissues arranged in complexes	–	+	–	–/+	+
10 Caudal fin differentiated into lobes	–	+	–	+	+
11 Extrinsic eye musculature	–	+	–	+	+

distic analysis involving all the available characters. This has been attempted, for example, by Janvier (1996a, Text-fig. 5C), whose analysis places the conodonts firmly within the vertebrates (as a sister group to lampreys). Pridmore *et al.* (1997), however, have taken a different approach. Although they couched some of their discussion in cladistic terms, they preferred to take each anatomical attribute in turn and to consider its value as a defining character of a particular group within the chordates. For example, the statement that 'conodonts may have lacked the array of cartilages and muscle that characterize the head region in living craniates' (p. 323) concerns the use of the character in classification, not in the analysis of relationships. Similarly, they stated (p. 323) that 'while the presence of both caudal fin radials and what are evidently paired sensory capsules aligns conodonts with craniates rather than other chordates, both features ... are entirely consistent with conodonts being the sister group of the craniates'. This again does not consider relationships, it considers whether these attributes should be regarded as diagnostic of craniates or of a broader grouping within the chordates. In this way, they have reduced their discussion to a series of *a priori* hypotheses of the polarity of isolated anatomical attributes; their phylogenetic conclusions, therefore, are not derived from an analysis of relationships based on the overall distribution of characters.

Although Pridmore *et al.* (1997, Fig. 5) presented their conclusions in the form of a cladogram, this was not based on a formal analysis of their data matrix (Table 1). Despite our reservations regarding some of their interpretations of conodont anatomy, we have used their data matrix as the starting point for a more formal analysis, introducing just one small correction (Table 1). They scored the character 'vertebrae' as absent in conodonts, whereas it should be more accurately scored as unknown. Extant lampreys possess arcualia, which were presumably present in fossil lampreys but have not been found preserved, suggesting a very low preservation potential; they may or may not have been present in the conodonts. An

exhaustive analysis of this data matrix using PAUP (Swofford 1990) with *Branchiostoma* as the outgroup produces one most parsimonious tree (Fig. 1A; tree length=7, 8 characters, consistency [CI] and retention [RI] indices of 1.00). This cladogram supports the interpretation of relationships forwarded by Pridmore *et al.* (1997).

However, although Pridmore *et al.* (1997) correctly stated that the number of characters that have been used to produce hypotheses of conodont affinity are small, it is not as limited as their selection implies. For example, the hard tissues of conodont elements clearly comprise a multi-component phosphatic complex. Addition of a character 'multi-component hard tissue complexes' (conodonts and gnathostomes score as present, other taxa score absent; 9 characters in total) produces two most parsimonious trees: the first (tree length=10, CI 0.9, RI 0.8) places conodonts as a sister group to gnathostomes (Fig. 1B); the second (tree length=11, CI 0.8, RI 0.62) agrees with Pridmore *et al.*'s tree (Fig. 1A).

Tail shape is another important character, used in all cladistic analyses of lower chordates (e.g., Janvier 1996a). The caudal fin of conodonts appears to be differentiated into lobes, and addition of this character (present in conodonts, lampreys and gnathostomes, absent in *Branchiostoma* and myxinoids; 9 characters in total) to the original Pridmore *et al.* data matrix produces three equally parsimonious trees. The first (tree length=10+, CI 0.9, RI 0.8) places conodonts in a polytomous relationship with lampreys and gnathostomes (Fig. 1C); the second (tree length=11, CI 0.82, RI 0.6) places conodonts as sister group to lampreys plus gnathostomes (Fig. 1D); the third (tree length=11, CI 0.82, RI 0.6) agrees with that of Pridmore *et al.* (1997). Fifty-percent majority rule consensus supports placement of conodonts as sister group to lampreys plus gnathostomes (Fig. 1D). Addition of both this character and 'multi-component hard-tissue complex' to the matrix places conodonts as the sister group to gnathostomes (Fig. 1D; tree length=10, 10 characters, CI 0.9, RI 0.8).

If we accept the evidence that the cephalic lobes of conodonts are the remains of eyes, and that the patches of muscle tissue in *Promissum* are extrinsic eye musculature, this provides another character. Addition of the character 'extrinsic eye muscle' to the original matrix (present in conodonts, lampreys and gnathostomes, absent in *Branchiostoma* and myxinoids; 9 characters in total) produces three equally parsimonious trees: the first (tree length=10+, CI 0.9, RI 0.8) places conodonts in a polytomous relationship with lampreys and gnathostomes (Fig. 1C); the second (tree length=11, CI 0.82, RI 0.6) places conodonts as a sister group to lampreys plus gnathostomes (Fig. 1D); the third (tree length=11, CI 0.82, RI 0.6) concurs with that of Pridmore *et al.* (Fig. 1A). Fifty percent majority rule consensus again supports placement of conodonts as sister group to lampreys plus gnathostomes (Fig. 1D). Inclusion of all three characters produces a single most-parsimonious tree (tree length=10, 11 characters, CI 0.9, RI 0.8), placing conodonts as sister group to gnathostomes (Fig. 1B).

Lampreys have been shown to be capable of calcifying cartilage in experimental situations (Langille & Hall 1993) and in life (Bardack & Zangerl 1971), although this occurs in warm conditions beyond their present physiological range (Langille & Hall 1993). These observations may support the hypothesis, mentioned by Pridmore *et al.* (1997), that lack of a dermal skeleton in extant lampreys may be secondary. To test the effect of this hypothesis, we have analysed a data matrix of all 11 characters, with 'multi-component hard tissue complex' scored present for lampreys. This produces two equally parsimonious trees: in the first (tree length=11+, CI 0.91, RI 0.83) conodonts form a polytomy with lampreys and gnathostomes (Fig. 1C); in the second (tree length=11, CI 0.91, RI 0.83) the conodonts form a sister group to lampreys plus gnathostomes (Fig. 1D).

It is evident from these analyses that inclusion of any or all of the additional characters in the data matrix places the conodonts within the crown group containing myxinoids, lampreys and gnathostomes. They also show that the postulated secondary loss of scales in lampreys does not demand that conodonts lie outside the vertebrates (contra Pridmore *et al.* 1997). Further elaboration of these analyses largely awaits new evidence from conodonts. Some refinement may, however, be gained from more careful consideration of some of the characters. For example, coding of myomere shape could be more complex than division into the simple V and W categories employed by Pridmore *et al.* (1997). Myomeres in lampreys, sharks and teleosts are not the same, and the single
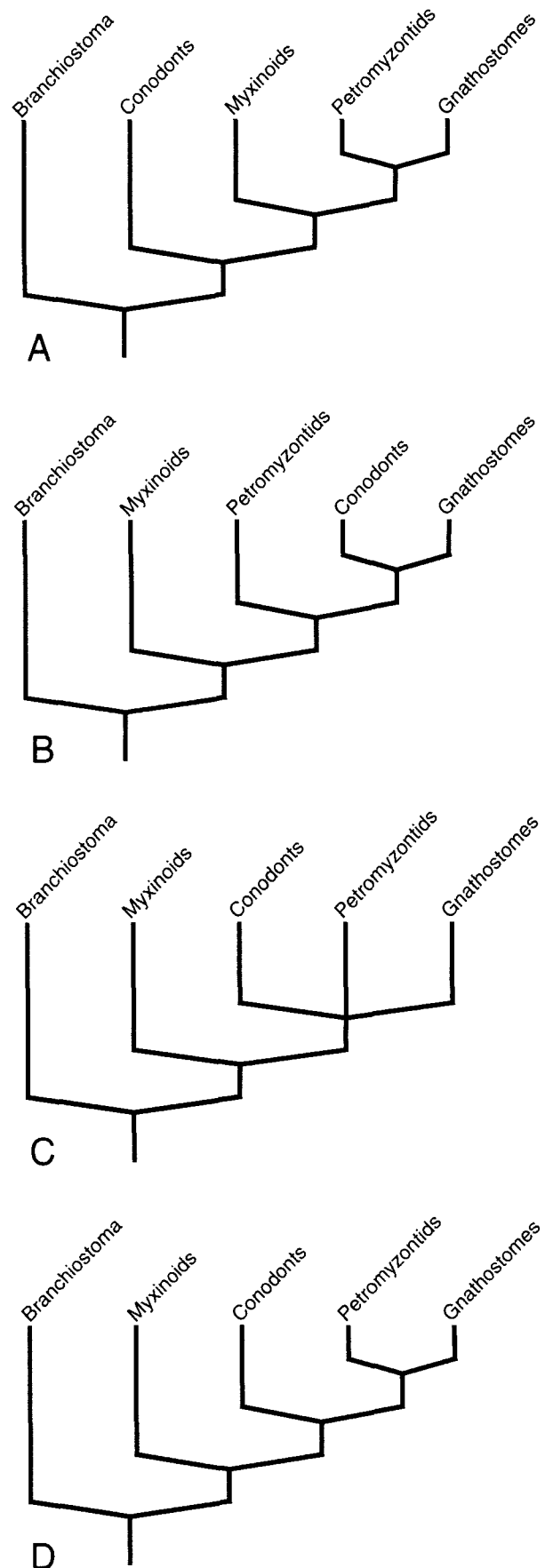
Fig. 1. Alternative relationship between Branchiostoma, conodonts, myxinoids, petromyzontids and gnathostomes. For characters and coding, see text and Table 1.

categorization 'W-shaped' conceals shape differences that have important functional implications (see Van Leeuwen 1994).

The analysis could also be refined, albeit more controversially, by coding for the different hard tissues in the multi-component complexes and in coding eyes and otic capsules as separate characters. The significance of eyes was questioned by Pridmore *et al.* (1997), who argued that the simple eyes of myxinoids are likely to be degenerate and that evidence for a common genetic programme for eye morphogenesis in various invertebrates and vertebrates raised the possibility that eyes could have been independently evolved by conodonts and vertebrates. The question whether hagfish eyes are primitively simple or secondarily degenerate is a matter of considerable current debate (see, e.g., Wicht & Northcutt 1995) and a judgement on polarity should not be made before this is resolved. The issue of the homology of metazoan eyes is less of a problem, as shared patterns of regulatory gene expression do not necessarily equate with homology of the resultant morphological structures (Müller & Wagner 1996). The problem of developmental genetics and the homology of eyes has recently been reviewed by Abouheif (1997), and recent work on echinoderms indicates that co-option of regulatory genes into new developmental roles may be much more widespread than has been realized (Lowe & Wray 1997). In the present context, it is only the development and distribution of eyes within the chordate clade that is relevant, and analysis of this should be untainted by *a priori* hypotheses of multiple origins.

Vertebrate classification

With the widespread acceptance that only monophyletic taxa should be erected as groups within biological classifications, the objective of a classification is to represent relationships using a system of names (see, e.g., Wiley 1979; de Queiroz & Gaulthier 1992; Smith 1994). Given a cladogram of inferred relationships, the most informative classification is that which provides a summary of the maximum number of attributes of the taxa included (Smith 1994). Were we to accept the cladogram forwarded by Pridmore *et al.* (1997, Fig. 5; Fig. 1A), we would not, in this regard, accept their classificatory conclusions. The clade they labelled as 'Craniates' is united on their diagram by only two synapomorphies, 'head skeleton of cartilage or bone' and 'W-shaped myomeres', although the former character is unknown in conodonts, not absent. The clade conodonts + myxinoids + petromyzontids + gnathostomes, on the other hand, is united by the synapomorphies 'apatite secretion', 'paired sense organs' and 'radials in caudal fin', but was not recognized as a taxon in the Pridmore *et al.* classification. Pridmore *et al.* (1997) rejected the use of the term 'Craniata' for this

clade because of the lack of evidence for a full suite of cranial cartilages in the conodont fossils (i.e. on the basis of a character which is unknown). However, it is clear that the taxon Craniata *sensu* Pridmore *et al.* is less informative than the alternative including the conodonts, especially considering the broader implications of the paired sense organs for the presence of a differentiated brain and the possession of neural crest and epidermal placodes (Northcutt & Gans 1983). Acceptance of the classification presented by Pridmore *et al.* would almost certainly require the erection of an additional term for this clade in order to communicate a useful taxonomic concept. This would result in separate names for the total group and crown group within this clade when only the total group need be given a formal name (see also Peterson 1994). A better solution in such cases is to extend the name given to the taxa comprising the crown group to include all stem group members of the clade (see Smith 1994).

However, our analyses suggest that this discussion is unnecessary: conodonts appear to be firmly sited within the crown group, as has been argued by previous authors (e.g., Aldridge *et al.* 1986, 1993; Briggs 1992; Janvier 1995, 1996a; Aldridge & Purnell 1996). Some authorities (e.g., Janvier 1996b) recognize this clade (comprising the living taxa myxinoids + lampreys + gnathostomes) as the Craniata, and restrict the term Vertebrata to the clade comprising lampreys + gnathostomes. But the terms are widely used as synonyms (e.g., Kardong 1995; Nielsen 1995; Young 1995), and this usage has been largely influenced by the realization that the acquisition of a head (i.e. the traditional acraniate–craniate transition) was linked with a number of genetic, developmental, morphological and functional changes that represent key innovations in chordate evolution. These include gene duplications in several gene families (e.g., Garcia-Fernandez & Holland 1994), and the acquisition of neural crest, epidermal placodes, paired sensory structures, and a differentiated brain (e.g., Northcutt & Gans 1983). Continued recognition of Vertebrata and Craniata as distinct taxa communicates little apart from the historical origins of the terms, and we therefore follow common usage of Vertebrata as the senior synonym.

Conclusions

Although we have extended the restricted list of characters used by Pridmore *et al.* (1997), the number we have utilized is still small. It would be preferable to use more characters, but the addition of attributes for which presence or absence in conodonts cannot be presently determined would serve only to increase tree length and decrease tree stability. Inclusion of more fossil taxa (cf. Janvier 1996a) would result in a more robust analysis, but this is beyond the scope of the present paper. We have also

made the presumption that the taxa under investigation represent monophyletic clades. Notwithstanding these caveats, our extended analyses provide strong support for the hypothesis that conodonts are more derived than myxinoids.

We are pleased that our work on conodonts continues to engender the lively interest shown by Pridmore et al. (1997) and other authors, but maintain that the hypothesis of a vertebrate affinity remains unrefuted.

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