

# CONODONTS: A SISTER GROUP TO HAGFISHES?

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## SUMMARY

Conodonts are an extinct group of naked agnathan fishes which range in age from Cambrian to Triassic. The conodont animal is almost exclusively represented in the fossil record by the phosphatic elements of the feeding apparatus, which was the only mineralized component of the skeleton. Only 12 specimens have been found which preserve the soft tissue anatomy of the animal.

The animal possessed a notochord, myomeres, caudal fin, paired sensory organs (optic and possibly otic) and extrinsic eye musculature; these characters indicate that the animal was a vertebrate. Just posterior of the eyes and ventral of the notochord lay a feeding apparatus of varying complexity that acted bilaterally as in hagfishes, differing from the dorsoventral arrangement and action of gnathostome jaws.

The hard tissues from which the feeding apparatus is composed are comparable with those of vertebrates, particularly other fossil agnathans and corroborate the phylogenetic position established on the basis of the soft tissue anatomy. Although conodont soft tissues suggest a relationship to hagfishes, the elements cannot be homologized with hagfish lingual 'teeth' because of fundamental differences in the modes of growth of these structures.

## 2.1 INTRODUCTION

Conodonts are an extinct group of chordates, represented in the fossil record almost exclusively by the phosphatic elements of their feeding apparatuses. They possessed no other biomineralized skeleton, and remained enigmatic until the discovery of the first of a number of fossils with preserved soft tissues in 1982 (Briggs *et al.*, 1983). Conodont soft tissues are now known from three separate localities: the Ordovician Soom Shale of South Africa (Aldridge and Theron, 1993; Gabbott *et al.*, 1995), the Silurian Brandon Bridge dolomite of Wisconsin, USA (Mikulic *et al.*, 1985a, b; Smith *et al.*, 1987), and the Carboniferous Granton Shrimp Bed of Edinburgh, Scotland (Briggs *et al.*, 1983; Aldridge *et al.*, 1986, 1993). The single Silurian specimen from Wisconsin is very poorly preserved and provides little information about conodont anatomy, but the Soom and Granton specimens preserve several features of the trunk and head. It must be emphasized, however, that the preservation of particular tissues and organs has been highly selective, and the processes of replacement that led to the preservation of non-biomineralized tissues are currently poorly understood. Replacement of muscles by calcium phosphate, as displayed by the Granton specimens, has been replicated in the laboratory by Briggs *et al.* (1993), but the preservation of

muscle fibres by clay minerals, evident in the Soom Shale, is problematic, although it may involve an intermediate phase of phosphate replacement (Gabbott *et al.*, 1995). Whatever the preservational history of these specimens, it is clear that each exhibits only part of the soft anatomy of the original organism, biased by the particular characteristics of the chemical and microbiological environment in which it died and decayed. Using information gleaned from several specimens, however, it has proved possible to reconstruct many of the characters of the living conodont animal, although details of features of low preservation potential remain obscure.

## 2.2 CONODONT SOFT-TISSUE ANATOMY

Ten specimens from the Granton Shrimp Bed exhibit features of the trunk of the animal (Figure 2.1); two of these also preserve the tail, and two show structures in the head (Aldridge *et al.*, 1993). A single giant specimen (Figure 2.2) from the Soom Shale displays part of the trunk and head region (Gabbott *et al.*, 1995), while at least 40 have been found in which lobate structures, interpreted as eye cartilages by Aldridge and Theron (1993), are associated with complete feeding apparatuses. All of these fossils were subject to some decay before the processes of replacement which preserved the tissues commenced, but experimental examination of the pattern of decay in extant primitive chordates, principally *Branchiostoma* (Briggs and Kear, 1994), provides a basis for interpretation of the structures that remain. These features can be compared with those of living and fossil cephalochordates and agnathans to develop hypotheses regarding the phylogenetic position of the Conodonts in relation to the Myxinoidea.

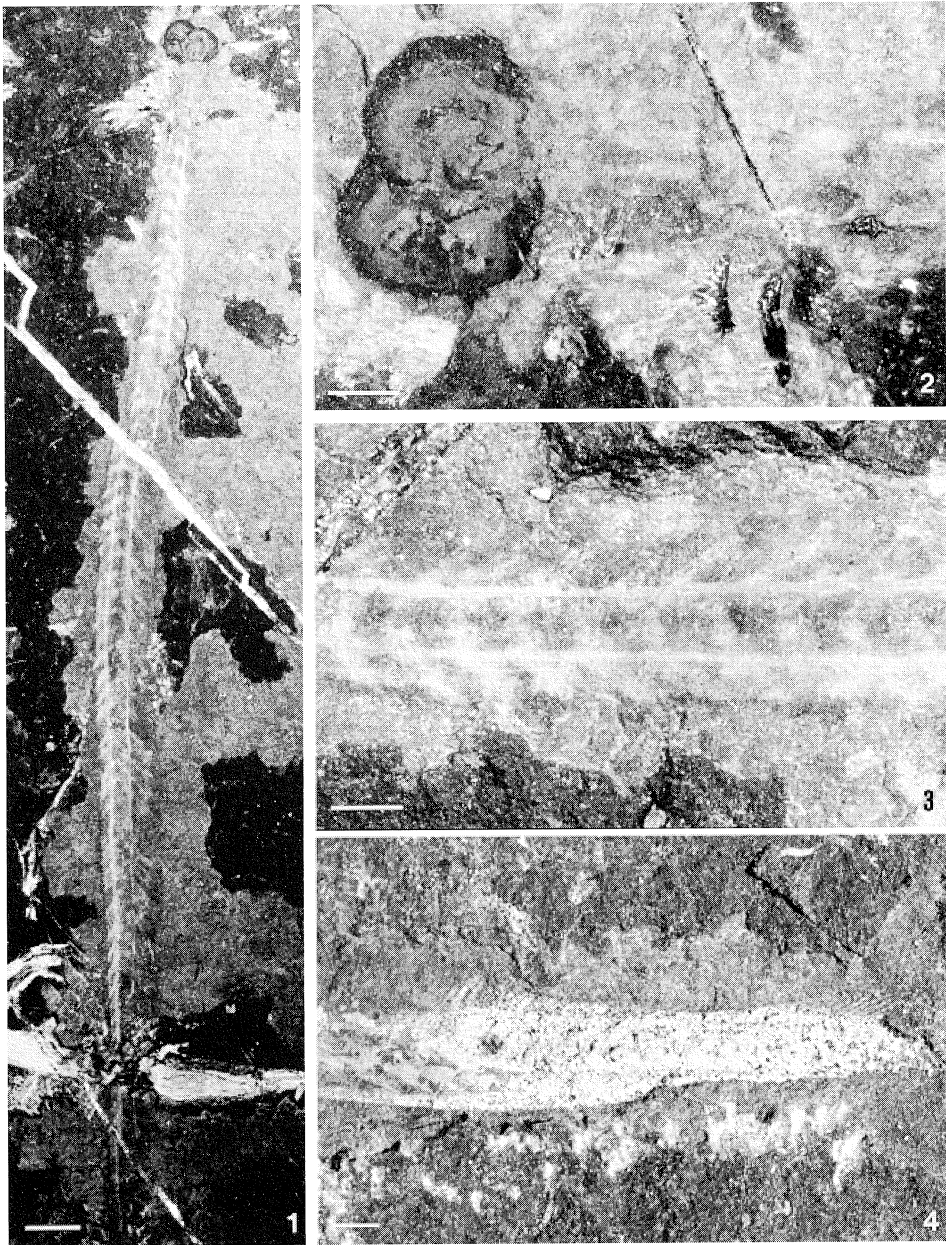
### 2.2.1 General features

The conodont animal specimens from the Ordovician and Carboniferous are all from

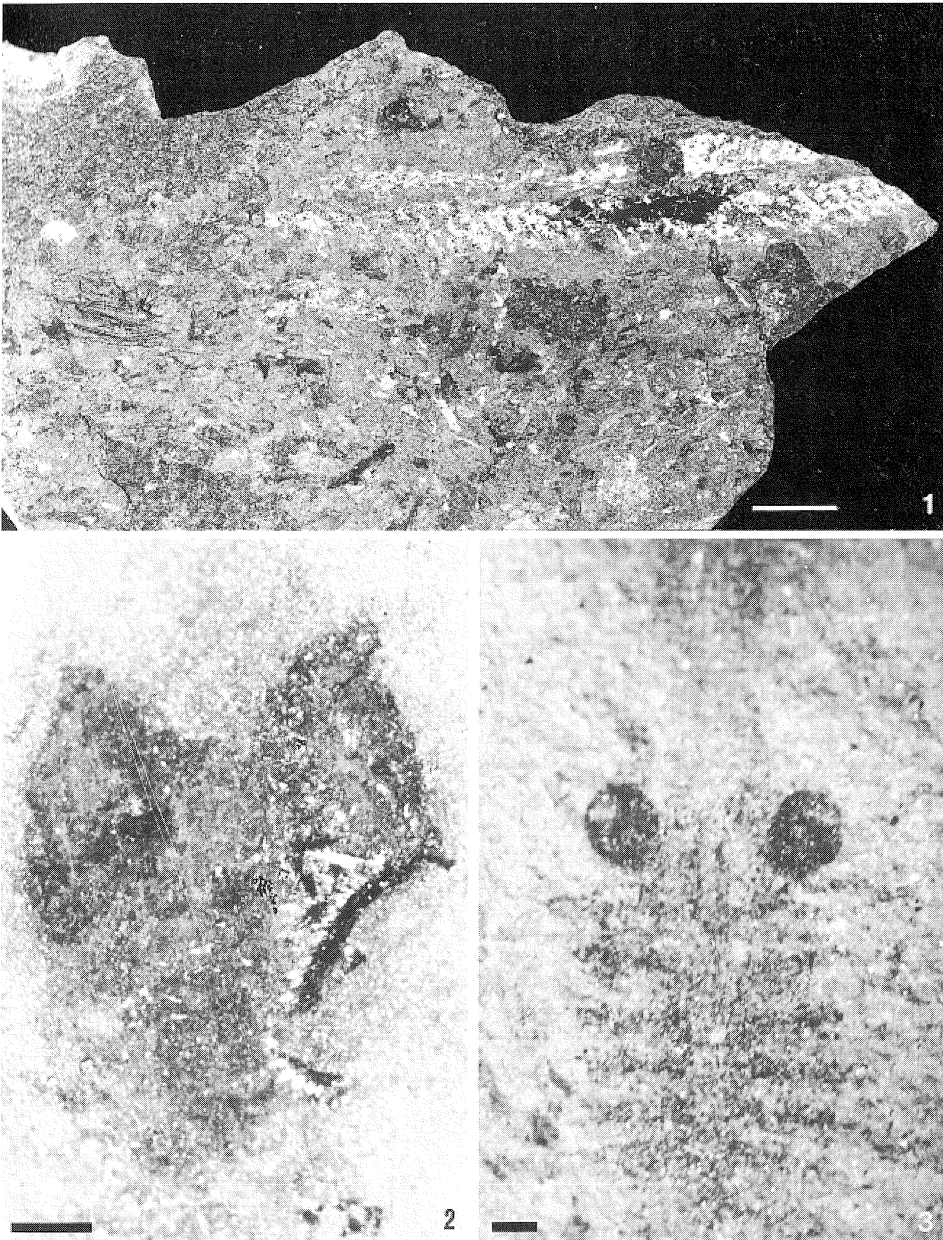
taxa that possessed complicated feeding apparatuses comprising pectiniform and ramiform elements. These taxa represent at least two conodont orders: seven of the specimens from the Granton Shrimp Bed can be assigned to *Clydagnathus*, an ozarkodontid (Aldridge *et al.*, 1993), and the Soom Shale specimen is of the prioniodontid genus *Promissum* (Gabbott *et al.*, 1995). General features of the anatomy are remarkably constant; all are elongate with a short head and a laterally compressed trunk made up of somites (Figure 2.1(1)). These are apparently V-shaped in all specimens, although preservation may be incomplete; they are thus simpler than the W-shaped myomeres of adult hagfishes and lampreys, but comparable with the chevron muscle blocks of *Branchiostoma* and some fossil agnathans (e.g. *Sacabambaspis*, see Gagnier *et al.*, 1986; *Mayomyzon*, see Bardack and Zangerl, 1968, 1971; *Gilpichthys* and *Pipiscius*, see Bardack and Richardson, 1977). The *Clydagnathus* specimens are all small, with the largest a little over 55 mm in total length (Aldridge *et al.*, 1993), whereas the preserved portion of the *Promissum* specimen is 109 mm and the entire length may have approximated 400 mm (Gabbott *et al.*, 1995).

### 2.2.2 The trunk

Paired axial lines occur along the trunk of most of the Granton specimens (Figure 2.1(3)) and represent the margins of the notochord (Aldridge *et al.*, 1993); the notochord of *Branchiostoma* is one of the most decay-resistant features of this animal and collapses to a pair of lateral ridges comparable with those shown by the fossil conodonts (Briggs and Kear, 1994). Preferential preservation of the notochord is also apparent in a number of fossil agnathans from other deposits, including *Gilpichthys* (Bardack and Richardson, 1977) and *Mayomyzon* (Bardack and Zangerl, 1968, 1971) from the Carboniferous Mazon Creek fauna. The notochord is not preserved



**Figure 2.1** *Clydagnathus windsorensis* (Globensky); (1–3) RMS GY 1992.41.1 (refigured from Aldridge *et al.*, 1993, with permission); (4) IGSE 13822 (refigured from Briggs *et al.*, 1983, with permission). (1) Complete specimen, anterior at top and ventral to left; scale bar 2000µm. (2) Anterior portion showing eye cartilages, feeding apparatus (only partially uncovered) and anterior part of trunk with notochord; scale bar 500µm. (3) Detail of trunk at mid-length showing the notochordal sheath and shrunken myotomes; scale bar 500µm. (4) Posterior portion of trunk and tail showing closely set ray supports and tail asymmetry; scale bar 500µm.



**Figure 2.2** (1) *Promissum pulchrum* Kovács-Endrödy (GSSA C721a; refigured from Gabbott *et al.*, 1995, with permission), complete specimen (counterpart) showing the trunk, extrinsic eye musculature and feeding apparatus; anterior to left; scale bar 10 mm. (2) Head of *C. windsorensis* (IGSE 13822; refigured from Briggs *et al.* 1983, with permission) showing eye capsules, otic capsules, possible traces of gill pouches, and feeding apparatus, anterior at top (soft tissues preserved in dorsoventral orientation); scale bar 500  $\mu$ m. (3) Head of *Myomazon pieckoensis* Bardack (FMNH PF 8167) a fossil lamprey from the Carboniferous Mazon Creek lagerstätte, showing nasal and eye capsules, gill pouches and trace of notochord, preserved orientation as (2); scale bar 500  $\mu$ m.

in *Promissum*, but its position is indicated by a 2 mm gap in preservation within the myomeres (Gabbott *et al.*, 1995). A dorsal nerve cord may be represented on two of the Granton specimens by a medial darker trace apparent along the anterior portion of one wall of the notochord, although this interpretation remains equivocal (Aldridge *et al.*, 1993). Details of the structure of the trunk muscles are best preserved in the *Promissum* specimen, in which each myomere displays sets of fibril bundles, together with possible sarcolemmic membranes and collagenous connective tissues (Gabbott *et al.*, 1995). The fibres do not show the extreme flattening characteristic of *Branchiostoma*, and appear more circular in cross-section than those of agnathans and fishes; their size (5  $\mu\text{m}$  in diameter) is consistent with their being slow muscle fibres (Gabbott *et al.*, 1995). Larger, fast muscle fibres have not been recognized, although these may be present outside the plane along which the fossil has split.

### 2.2.3 The tail

Closely spaced fin rays are apparent at the posterior end of two of the Granton fossils (Briggs *et al.*, 1983, figs 4, 5; Aldridge *et al.*, 1986, fig. 4; Figure 2.1(4)), but their configuration is not clear on either. From one of the specimens it is evident that fins occur on both the dorsal and ventral margins; more examples are required before we can ascertain for certain if the disposition is symmetrical, or if the apparent extension of the fin further on one of the margins is genuine. There is no evidence of articulating musculature at the base of the fin rays, suggesting that they resemble the unsupported fin folds of myxinioids (Aldridge *et al.*, 1993).

### 2.2.4 The head

Apart from the phosphatic feeding apparatus, the most commonly preserved features of the head are the two lobate structures interpreted

by Aldridge and Theron (1993) to represent sclerotic cartilages which surrounded the eyes (Figures 2.1(2) and 2.2(2)). In specimens from Granton and from South Africa, these are evident as apparently carbonized impressions, commonly thickened marginally and with some phosphatization; they can be reconstructed as deep, inwardly tapering hollow rings (Aldridge *et al.*, 1993). They are positioned above and immediately anterior to the feeding apparatus and are closely comparable morphologically with structures that have been interpreted as eye capsules in fossil agnathans, for example *Jamoytius* (Ritchie, 1968), and as altered retinal pigments in the hagfish *Myxinikela* (Bardack, 1991), the lampreys *Mayomyzon* (Figure 2.2) and *Hardistiella* (Bardack, this volume), and larval gnathostomes such as *Esconichthys* (Bardack, 1974), *Bandringa* and *Rhabdoderma* (Richardson and Johnson, 1971). Optic capsules in living craniates are embryologically derived from ectodermal placodes (Gans and Northcutt, 1983).

The most complete *Promissum* specimen displays solid white oval patches anterior to and above the feeding apparatus, in a similar position to the sclerotic rings on other specimens (Figure 2.2(1)). These patches have a fibrous texture and were interpreted as representing extrinsic eye musculature by Gabbott *et al.* (1995); the development of such muscles is entirely patterned by connective tissue derived from neural crest (Noden, 1991; Couly *et al.*, 1992).

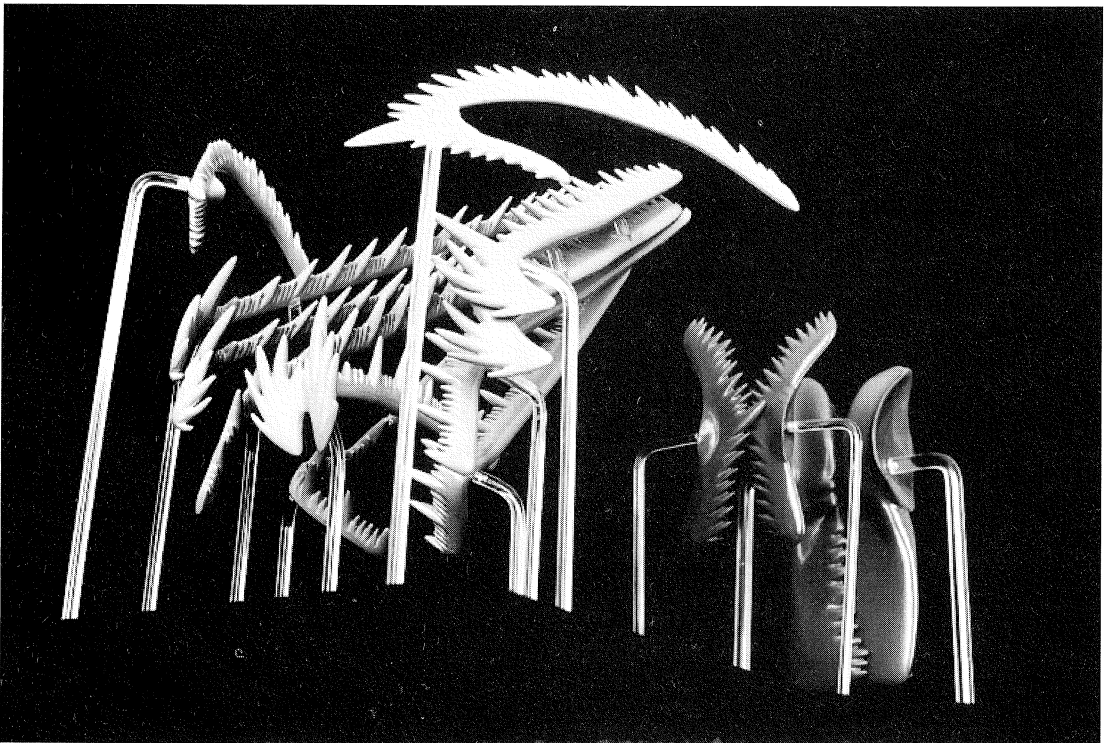
Other than indistinct and indecipherable patches, only the first specimen discovered from Granton has additional soft-tissue features in the head region (Briggs *et al.*, 1983, figs 2C and 3A; Aldridge *et al.*, 1993; Figure 2.2). A pair of small subcircular dark patches behind the sclerotic rings may represent the otic capsules, similar to those reported in the Carboniferous lamprey *Mayomyzon* (Bardack and Zangerl, 1971) and hagfish *Myxinikela* (Bardack, 1991). The presence of otic capsules is further supported by the occurrence of a

phosphatic structure, strongly resembling the statoliths of modern lampreys, in the vicinity of the feeding apparatus in the head of another of the Granton conodont animals (Figure 2.4(2)). Transverse traces posterior to the eyes of the first specimen may be branchial structures, comparable with features so interpreted in *Mayomyzon* (Bardack and Zangerl, 1968, 1971). There is no preserved evidence of pharyngeal slits.

The relative arrangement of the structures in the head of the conodont animal is closely comparable with that shown by fossil and recent lampreys and hagfishes (Figures 2.2(2) and 2.2(3)). The otic capsules are positioned just posterior of the optic capsules, and the putative gill pouches are located very close to the head structures, as in *Mayomyzon*. The first Granton conodont animal also preserves

an indistinct organic trace surrounding the head structures that resembles the unmineralized head cartilage of the fossil lampreys from the Mazon Creek fauna.

The feeding apparatus is only partly exposed in most of the specimens from Granton, but its architecture has been reconstructed using additional evidence from undisturbed assemblages of elements found occasionally on Carboniferous shale surfaces. The apparatus was bilaterally symmetrical, comprising a set of 11 ramiform elements that formed an anterior basket, behind which lay two pairs of pectiniform elements with their long axes directed dorsoventrally (Aldridge *et al.*, 1987; Purnell and Donoghue, *in press*; Figure 2.3). The anterior half of the apparatus has been interpreted as an oral raptorial array (Aldridge and Briggs, 1986; Purnell and von



**Figure 2.3** Model of the conodont (ozarkodinid) feeding apparatus in oblique anteroventral view. From Purnell and Donoghue (*in press*).

Bitter, 1992), but this has recently been challenged (Mallatt, 1996). Mallatt contended that the position of this portion of the apparatus posterior of the eyes suggests that it lay in the pharynx. However, if the interpretation of gill pouches in the first Granton specimen is correct (Figure 2.2(2)), the position of the anterior array, anterior of the first gill pouch, and the pectiniform elements posterior, implies that the two portions of the apparatus were located in the oral cavity and pharynx respectively, thus falling into the 'old' and 'new' mouths of Mallatt (1996).

The *Promissum* apparatus was similar to that of ozarkodinids, but more complicated, with 11 ramiform elements positioned below an array of four pairs of pectiniform elements (Aldridge *et al.*, 1995). Both types of apparatus are more complex than those found in any other agnathan, and they do not compare with the jaws of fishes. However, more primitive conodonts, and their putative ancestors the paraconodonts (Szaniawski and Bengtson, 1993), had simpler apparatuses made up of conical elements which may be more readily comparable with the lingual and palatal teeth of hagfishes. The multicuspid lingual laminae of some lampreys (Potter and Hilliard, 1987) also bear a broad resemblance to some ramiform conodont elements.

### 2.2.5 Phylogenetic interpretations

Of the preserved soft tissues, the notochord and the chevron-shaped myomeres clearly show that the conodonts belong within the euchordates (Cephalochordata + Craniata) (although for a contrary view see Dzik, 1995). Their precise affinities are controversial, with some authorities still maintaining that they are closest to the protochordates (Urochordata + Cephalochordata) (Kemp and Nicoll, 1995), although the radials in the caudal fin, the presence of eyes and the termination of the notochord behind them, the bilaterally operative feeding apparatus, and the phosphatic skeletal biomineralization are all craniate

characters (Aldridge *et al.*, 1993; Janvier, 1995).

The possession of paired external sensory organs and a distinct head anterior of the notochord are also indications of vertebrate grade. The 'new head' hypothesis for the origin of the vertebrates (Gans and Northcutt, 1983) recognizes that most of the functional and morphological differences between vertebrates and other chordates are located in the head, and contends that the vertebrate head is a new structure. Most of the new structures in the vertebrate head are embryologically derived from neural crest and ectodermal placodes.

More recently, a single colinear cluster of *Hox* genes has been identified in *Amphioxus*, the traditional proxy for a vertebrate ancestor, matching four paralogous clusters in gnathostomes (Garcia-Fernández and Holland, 1994; Holland and Garcia-Fernández, 1996). The expression of these clusters in mice never occurs more anteriorly than the rhombomeres of the hindbrain, and expression of *Hox* genes in *Amphioxus* too has distinct anterior limits, indicating a significant portion of the animal equivalent to the craniate head. Furthermore, the single cluster in *Amphioxus* also points to a gene duplication at the acraniate–craniate transition, emphasizing the fundamental importance of this event in chordate evolution. Determination of *Hox* gene clusters in hagfish and lampreys is at a preliminary stage, but multiple clusters, up to four in number, appear to be present in each group (Holland and Garcia-Fernández, 1996).

Much of the opposition to the interpretation of conodonts as vertebrates stems from the lack of consensus over what constitutes a vertebrate or a craniate; many workers consider these to be synonymous (Kardong, 1995; Nielsen, 1995; Young, 1995). The 'new head' hypothesis for the origin of the vertebrates places myxinoids as the first crown-group vertebrates (Gans, 1993). Janvier (1981, 1993), however, considered the lack of arcualia in hagfishes to exclude them from

the vertebrates, placing them in the craniates; the lampreys were regarded to be crown-group vertebrates. On this basis, much of the controversy surrounding the interpretation of conodont affinities becomes semantic. In the present context, it is pertinent to assess the evidence for and against a close relationship between the conodonts and the hagfishes.

Aldridge *et al.* (1986) forwarded two possible phylogenetic positions for the conodonts on the basis of the soft tissues characters: as a sister group to the Myxinoidea, or immediately crownwards of them. Other placements have been suggested (see Aldridge and Purnell, 1996), including immediately anti-crownwards of the Myxinoidea, as stem-group craniates (Peterson, 1994). Conodonts differ from myxinoids in having eyes with apparent extrinsic musculature and in bearing phosphatic, not keratinous, oral elements. Large eyes with extrinsic eye muscles are a vertebrate characteristic, but their absence in myxinoids may be degenerate rather than primitive (Northcutt, 1985). The lack of a phosphatic skeleton in hagfish may also be secondary, or it might be argued that the development of phosphatic structures in conodonts was a separate, convergent feature, unrelated to the origin of skeletons in other craniates. The mode of growth of conodont elements and the nature of their phosphatic tissues are of crucial importance in resolving this particular question.

### 2.3 CONODONT HARD TISSUES

A typical euconodont ('true conodont') element is constructed of two structurally distinct components, a basal body and an overlying crown, which grew by the addition of calcium phosphate on their outer surfaces (Furnish, 1938; Hass, 1941). Post-Devonian elements do not have a basal body, suggesting that its function was fulfilled by unmineralized tissue in more derived forms. The crown is composed of a crystalline, hyaline tissue punctuated by numerous incremental

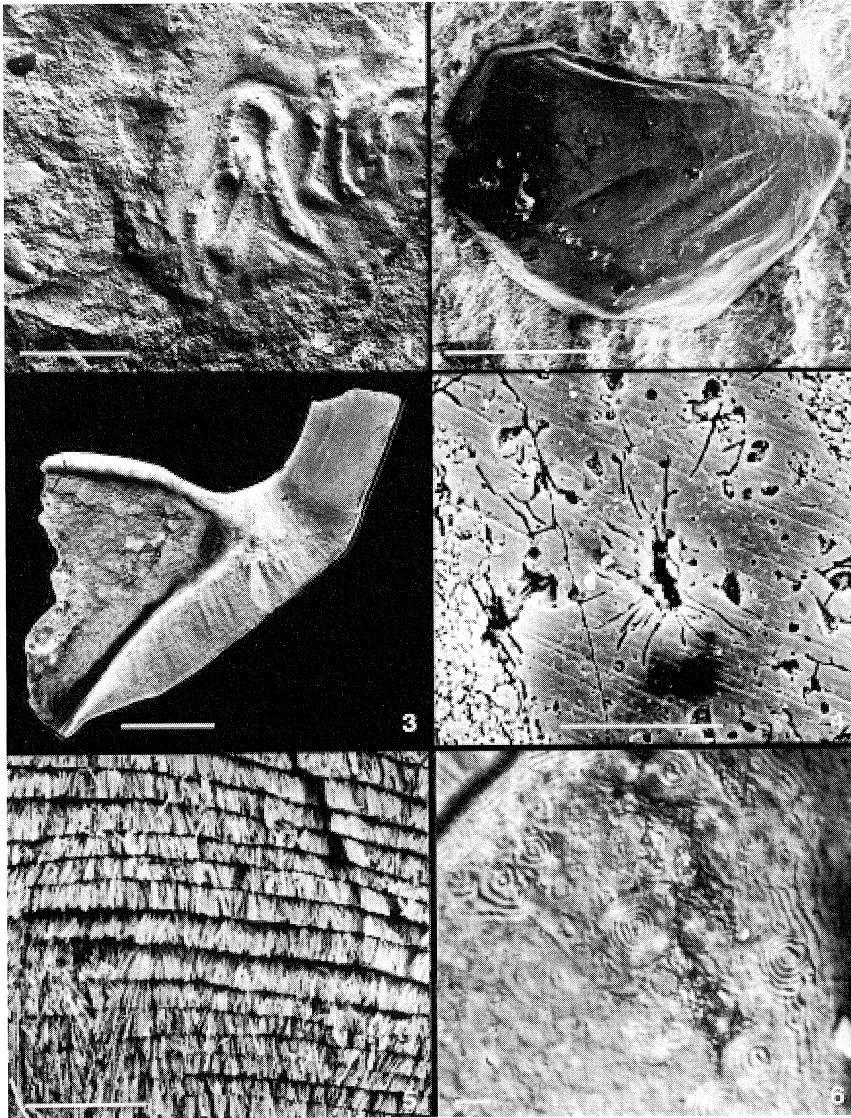
growth lines (Figure 2.4(5)); in most conodonts the crown also includes areas of opaque tissue, traditionally known as 'white matter' because it appears albid in incident light. The cores and tips of the cusps and denticles of conodont elements are commonly composed of this white matter (Figure 2.4(4)), which is relatively fine-grained and massive, but contains numerous cavities and fine tubules (see Lindström and Ziegler, 1981). The basal body is also finely crystalline, but much more variable in structure; it commonly displays growth increments and may show spherical or tubular features (Figure 2.4(6)).

#### 2.3.1 Lamellar crown tissue

A homology between conodont crown tissue and the enamel of vertebrates has been suggested several times (e.g. Schmidt and Müller, 1964; Dzik, 1986; Sansom *et al.*, 1992). Although only a few taxa have as yet been examined in detail, there is considerable variability in the orientation of crystallites in the hyaline lamellae with respect to the incremental growth lines. In most, the crystallites are more or less perpendicular to the growth increments (*contra* Schultze, 1996), as in true enamel, whereas one area of the crown tissue figured by Sansom *et al.* (1992) from *Parapanderodus* (fig. 3F) showed crystallites arranged at a shallower angle and this was considered outside the range of known enamel types by Forey and Janvier (1993). However, crystallite arrangement in enamel is known to vary, particularly in primitive forms of prismatic enamel (Smith, 1989, 1992), and Sansom (1996) has described a prismatic form of lamellar crown tissue that compares directly to primitive prismatic enamel from the teeth of a sarcopterygian fish. As is the case with enamel, the lamellar crown of conodont elements exhibits variation in crystallite arrangement within a single specimen.

The interpretation of the conodont tissue as enamel has been contested by Kemp and Nicoll (1995, 1996) on the grounds that etched





**Figure 2.4** (1) Feeding apparatus from one of the Scottish conodont animals (RMS GY 1992.41.3), still partially covered by matrix. The small black asymmetric structure to the upper left of the frame is the putative statolith; scale bar 1000  $\mu\text{m}$ . (2) Close-up of possible statolith, concentric grooves may represent the limit of annual growth increments; scale bar 100  $\mu\text{m}$ . (3) Thin section of *Cordylodus*, a Lower Ordovician conodont, Maardu Beds, Estonia (BU 2614), micrograph taken using differential interference contrast, showing crown (to right) and basal body (to left). The hyaline crown tissue incorporates 'white matter' upper right; scale bar 100  $\mu\text{m}$ . (4) SEM micrograph of an etched thin section through an element of *Ozarkodina* Upper Silurian, Gotland (BU 2615), showing fine grained ground mass and enclosed cell and cell-process spaces characteristic of white matter; scale bar 10  $\mu\text{m}$ . (5) SEM micrograph of an etched thin section through the enamel crown tissue of an element of *Scaliognathus* Carboniferous, North America (BU 2613), showing incremental growth lines and crystallites organized into proto-prisms; scale bar 10  $\mu\text{m}$ . (6) Micrograph of detail of section 3 taken using differential interference contrast, showing lamellar and spheroidal structures in the basal body; scale bar 10  $\mu\text{m}$ .

surfaces are stained by picosirius red, a stain specific for collagen. True enamel does not contain collagen. However, the validity of such histochemical tests on fossil material remains to be established, as they have not been applied to unequivocal fossil vertebrate material. It is possible that the etching of the element surface increases porosity and permits retention of the stain which 'fixes' by electrostatic attraction; further work is required to test the results of this technique. The presence of fibrous tissues, claimed to be collagen, in conodont elements has also been reported by Fåhraeus and Fåhraeus-van Ree (1987, 1993), who demineralized Silurian conodont hard tissues then fixed, dehydrated, sectioned and stained the residue. They commented that the most remarkable result of their study was that tissue more than 400 million years old could remain histochemically intact (Fåhraeus and Fåhraeus-van Ree, 1987, p. 106). There is, however, no certainty as to which of the conodont hard tissues housed the soft tissue they recovered.

### 2.3.2 White matter

Many of the vacuoles within the white matter closely resemble the lacunae of odontocytes or osteocytes (Figure 2.4(4)), and together with evidence of associated canaliculi this led Sansom *et al.* (1992) to interpret this tissue as dermal bone. The vesicles are ubiquitous in white matter and are repeatedly observed in thin sections (*contra* the assertion that they are artefacts, Schultze, 1996); the nature of the tissue is different from cellular dermal bone in other vertebrates, and it is likely that white matter represents a tissue unique to conodonts.

Histochemical staining of the white matter with picosirius red failed to indicate the presence of collagen (Kemp and Nicoll, 1995, 1996), which is present in the dentine and bone of extant vertebrates. However, it is unusual for any fossil bone or dentine to preserve collagen, which normally disintegrates shortly after

death, leaving at best degradation products in the form of amino acids (Fåhraeus and Fåhraeus-van Ree, 1987). Detectable amino acids have been reported in conodont elements by Pietzner *et al.* (1968) and Savage *et al.* (1990), but see Collins *et al.* (1995).

### 2.3.3 The basal body

Schmidt and Müller (1964) suggested that the basal body of conodonts was homologous with the dentine of vertebrate sclerites, and branched or unbranched tubules representing different forms of dentine have been described in the basal bodies of a number of Ordovician taxa (Barnes *et al.*, 1973; Barskov *et al.*, 1982; Dzik, 1986; Sansom *et al.*, 1994). Basal bodies of other species, including most post-Ordovician elements examined, show regular lamination without tubuli or comprise a homogenous alaminated mass, the former having been interpreted as a form of atubular dentine (Sansom, 1996). In some early conodonts, for example *Cordylodus*, the basal material comprises a mass of fused spherical bodies and this has been compared with the globular calcified cartilage of the Ordovician vertebrate *Eriptychius* (Smith *et al.*, 1987; Sansom *et al.*, 1992), although it is just as likely to be an atubular dentine (Figure 2.4(3) and (6)). Such apparent diversity of tissue types in conodonts is unexpected, but parallels experimentation with different tissue combinations by other coeval agnathans (Halstead, 1987).

As with the white matter, basal bodies examined by Kemp and Nicoll (1995, 1996) failed to stain positively for collagen, although they tested positive for mucopolysaccharides.

### 2.3.4 Histogenesis of conodont elements

Published ontogenetic studies of conodont elements have concentrated on the development of the lamellar crown and basal body, which are known to have grown synchronously (Müller and Nogami, 1971). The

pattern of divergent appositional growth between the basal body and the crown is comparable with that of the dentine and enamel of extant vertebrate teeth, and Schmidt and Müller (1964), Dzik (1976, 1986) and Smith *et al.* (1996) have argued for a homology between conodont elements and vertebrate odontodes. Odontodes are the basic building blocks of the dermal skeleton in vertebrates and are formed by interaction of the epithelium, which forms the enamel, and ectomesenchymal cells, derived from the neural crest, which ultimately form the dentine, dermal bone and cartilage. Odontodes are almost exclusively composed of a complex of enamel, dentine and underlying bone of attachment. The bone of attachment is absent in conodonts, but this is also the case in the dermal denticles of thelodonts and in the oral teeth and skin denticles of chondrichthyans (Smith *et al.*, 1996).

### 2.3.5 Comparison with hagfish toothlets

Both conodonts and myxinooids possess a feeding apparatus comprising a bilaterally symmetrical array of cusped elements, and a homology between conodont elements and hagfish lingual toothlets has been proposed by Krejsa *et al.* (1990a, b). Evidence comes from a similarity in overall morphology between simple conodont elements and myxinooid teeth, and an overlap in size range between conodont elements and juvenile hagfish toothlets. The hypothesis requires that the phosphatic lamellar crown of conodont elements should be a mineralized homologue of keratin, with the pores in white matter interpreted as moribund remnants of pokal cells. The basal body is considered to be a developing replacement tooth (Krejsa *et al.*, 1990a, b).

Evidence such as analogous morphology and similarity in size is regarded as weak and circumstantial, and this interpretation of conodont elements has been severely criticized (Szaniawski and Bengtson, 1993; Smith

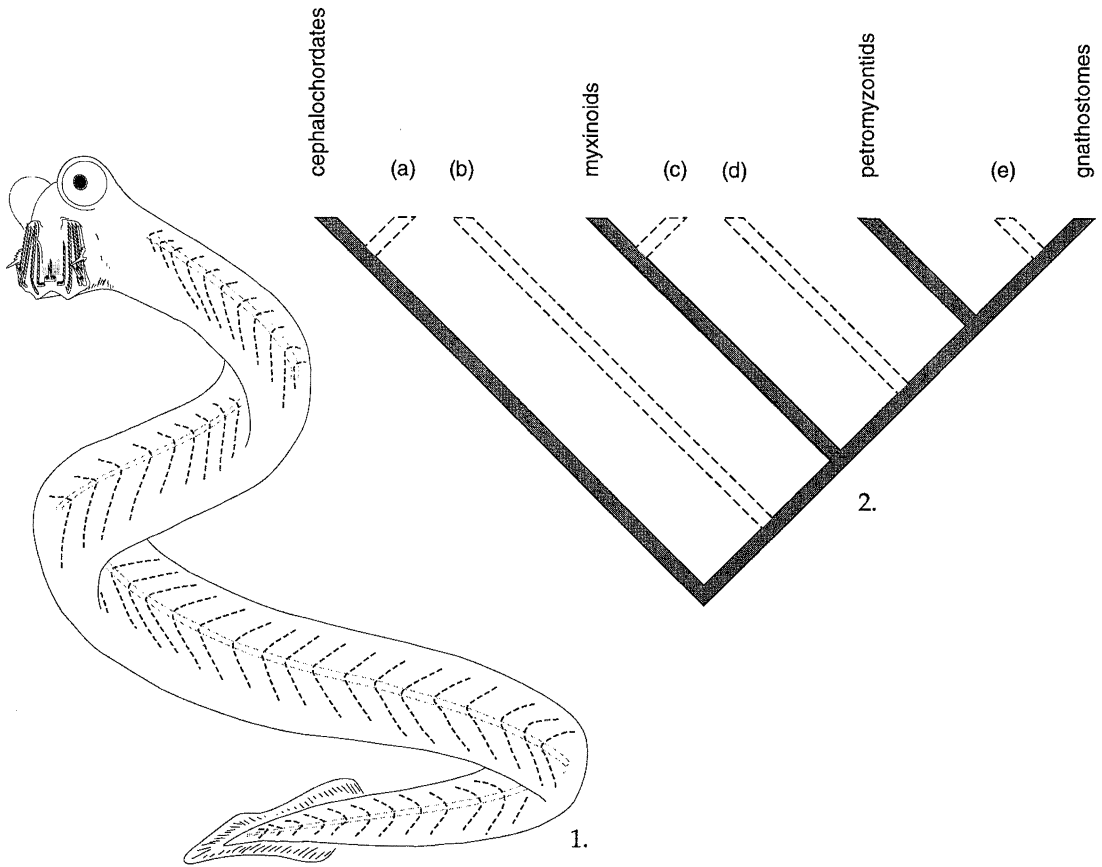
*et al.*, 1996). Histogenetic and ontogenetic studies of conodont elements show that the crown and basal body of conodonts grew synchronously, with appositional growth increments passing confluent between the two structures (Müller and Nogami, 1971); the basal body is clearly not a replacement tooth. Indeed, except in the simplest of conical conodont elements, the upper surface of the basal body bears no morphological resemblance to the upper surface of the crown it would putatively replace.

## 2.4 DISCUSSION

Possible phylogenetic positions of the conodonts relative to the extant euchordates are illustrated in Figure 2.5.

Kemp and Nicoll (1995, 1996) contended that their histochemical tests prove that the hard tissues of conodont elements are not homologous with those of vertebrates, and concluded that conodonts were therefore more closely related to cephalochordates than to craniates. This is not a necessary conclusion from their arguments, even if they were correct. If conodont hard tissues were developed independently from those of vertebrates, then this could have happened at any stage in early chordate history, for example as an offshoot from the myxinooids or from the petromyzontids. The evidence from conodont soft tissues suggests that either of these positions would be more parsimonious than a sister group relationship with the cephalochordates.

How strong, then, is the evidence for the Conodontata to be considered as a sister group to the Myxinoidea? There are two hypotheses to be examined here: either conodont characters are plesiomorphic for this group and have been secondarily lost in the hagfish, or conodont hard and soft tissue features are derived and synapomorphic for the Conodontata. The latter proposal does not seem parsimonious; not only would the enamel- and dentine-like skeletal tissues of conodonts



**Figure 2.5** (1) Reconstruction of a conodont animal, based on current evidence; the feeding apparatus is shown in the 'everted' position according to Purnell and Donoghue (in press). (2) Cladogram of possible conodont relationships; solid branches represent phylogenetic positions of extant groups, dashed lines represent some of the proposed positions of conodonts: (a) Kemp and Nicoll (1995, 1996), (b) Peterson (1994), (c) Krejsa (1990a, b), Aldridge *et al.* (1986), (d) Aldridge *et al.* (1986, 1993) and (e) Gabbott *et al.* (1995), Janvier (1995).

represent a completely independent and fortuitously analogous development from that in other craniates, but the development of eyes with extrinsic muscles would be similarly homoplastic.

It is perhaps more likely that myxinooids separated from the conodonts by secondary loss of conodont characters. The eyes of hagfishes are connected to the brain and sensitive to light (Wicht and Northcutt, 1995) and are probably responsible for the entrainment of the circadian rhythm (Ooka-Souda *et*

*al.*, 1993). They are nevertheless of very limited function, and despite the formation of a lens placode during development, a lens, iris, extrinsic musculature and associated nerves fail to develop (Wicht and Northcutt, 1995). The most likely interpretation is that hagfishes represent a condition degenerate from that of, for example, conodonts, with characters lost in response to their specialized mode of life (Fernholm and Holmberg, 1975; Northcutt, 1985). However, it is quite feasible that the failure of the lens placode to form a

lens is a primitive condition (Wicht and Northcutt, 1995), since the placode is ultimately responsible for the formation of a number of other structures, including the cornea, which are present in hagfishes.

The conversion of phosphatic hard parts to keratin may be more problematic. The recognition of enamel-like antigens (putatively enamelin) in the pokal cell cone beneath the tip of the keratin toothlet of hagfishes (Slavkin *et al.*, 1983) may be of relevance here, and Kresja *et al.* (1990a, b) used this to support a proposal that conodonts were ancestral hagfishes that switched from secreting mineralized keratin to keratin. The occurrence of the fossil hagfish *Myxinikela* in the Mazon Creek (Bardack, 1991) shows that the two groups were distinct by the Carboniferous. The case is weakened, however, by the lack of any demonstrable homology between conodont elements and hagfish toothlets. Smith *et al.* (1996) also cited the lack of developmental support for a switch from an apatitic system to one secreting keratin.

Relatively few myxinoid embryos have been recovered, and there is little evidence to indicate the degree of neural crest involvement in the formation of hagfish skeletal head structures. Conel (1942), however, suggested that neural crest played no role in hagfish cranial skeletal development. If hagfish neural crest is indeed restricted to neuronal derivatives (Langille, 1987), the evidence for neural-crest derived tissues in conodonts would indicate that the conodonts are the more derived.

The placement of the conodonts immediately anticrownwards of myxinoids (Peterson, 1994) suffers from similar drawbacks, involving loss in the myxinoids of the phosphatic tissues, the muscularized eyes and migratory neural crest, and their re-evolution in the post-myxinoid craniates. A position crownwards of the myxinoids poses fewest problems with current evidence of conodont soft and hard tissues (Aldridge *et al.*, 1993). Their precise placement will be influenced by resolution of the controversial relationships between extant

and fossil agnathans. If hagfish and lampreys form a natural group (Yalden, 1985; Stock and Whitt, 1992) or if the hagfish and lampreys are successive paraphyletic groups (Forey and Janvier, 1994; Forey 1995), then conodonts may well occupy a position crownwards of both myxinoids and petromyzontids (Gabbott *et al.*, 1995). However, Langille (1987) has described neural crest involvement in the formation of the head skeleton of lampreys, and the ability of petromyzontids to mineralize their skeleton has been demonstrated by *in vivo* (Bardack and Zangerl, 1971) and *in vitro* studies (Langille and Hall, 1993). This evidence, and the possession of arcualia by lampreys, suggests that of the two groups, the conodonts are the more primitive.

Janvier (1996) recently completed the first full cladistic analysis of the agnatha to incorporate conodonts. Lack of soft tissue characters and equivocation over the interpretation of some characters largely resulted in tree imbalance. However, Janvier's text-fig. 5c, the best resolved of the relevant trees, places the conodonts as a sister group to lampreys, with which they form a sister group to all other agnathans with a mineralized exoskeleton; hagfishes are a sister group to all other craniates. This intriguing solution awaits testing by additional cladistic analyses. Further, the speculation by Janvier (1995, 1996) that conodonts might be closer to the gnathostomes than all the ostracoderms apart from the osteostracans currently seems difficult to sustain, as it would involve secondary loss in the conodonts of the exoskeleton and the paired fins.

Whatever the final position of conodonts within craniate phylogeny, they have clearly influenced recent debates on vertebrate origin and generated a new impetus into long-standing controversies regarding the origin and early evolution of the vertebrate skeleton.

## 2.5 CONODONTS AS LIVING ANIMALS

Aldridge *et al.* (1993) reconstructed the conodont animal as an elongate and laterally

compressed eel-shaped agnathan (Figure 2.5) capable of an anguilliform mode of swimming. Lack of muscle fibres of a size comparable with 'fast' white muscle in the Soom specimen may indicate that conodonts were adapted to sustained swimming and incapable of rapid bursts (Gabbott *et al.*, 1995). However, examination of the musculature in this specimen is at a preliminary stage, and other muscle tissue may be present.

Conodonts had a complex feeding array which performed a number of tooth functions (Aldridge and Briggs, 1986; Purnell and von Bitter, 1992; Purnell, 1995; Purnell and Donoghue, in press). Early forms possessed only conical elements which were capable of grasping and perhaps slicing food (Aldridge and Briggs, 1986; Purnell, 1995); later forms developed more highly differentiated feeding apparatuses which separated grasping from slicing and crushing elements. The great variation in conodont apparatuses suggests that the group adopted a number of different ecological strategies, although with their locomotive capability and differentiated nervous system (including eyes with associated musculature) many would have made effective hunters (Purnell *et al.*, 1995).

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