

Fossils explained 64



Comprehending conodonts

Conodonts were small, thin, elongate jawless creatures that were a common component of the marine fauna from the late Cambrian, throughout the Palaeozoic and into the Triassic. For the majority of conodont research history, speculations on conodont affinity were restricted to the histology and arrangement of their mineralized tissues—‘conodont elements’. These conodont elements comprise millimetre-scale phosphatic microfossils that superficially resemble teeth, and are commonly recovered from the residues of appropriately aged, disaggregated sedimentary rocks. It has only been in the last three decades, since the discovery of exceptionally preserved soft tissues, that the debate on conodont affinity has been refined, though it has hardly been less vigorously debated. Despite being studied extensively for over more than a century and a half, conodonts retain significant enigmatic qualities. Although many geologists today are familiar with the name, knowledge of conodont biology and ecology are often surprisingly lacking or confused, and conodonts remain as largely disembodied microfossil curiosities. Despite this, conodont elements are extensively and variously used in biostratigraphy, thermal maturation studies and palaeoenvironmental reconstructions, while conodonts themselves occupy a potentially critical position in the evolutionary tree of our own phylum—the chordates.

Since conodont elements were first reported as dental apparatuses of some unknown Palaeozoic fish by Christian Heinrich Pander in 1856, these fossils have been ascribed to a plethora of taxa, ranging from algae to vertebrates and virtually everything in between. It wasn't until some 70 years after their discovery that conodonts were recognized for their significant biostratigraphical potential, and from this point their investigation really flourished.

Prior to the 1960s, with continuing uncertainty over their arrangement in life, conodont elements were largely considered in isolation and given their own taxonomic designation based on morphology: ‘form taxonomy’. With careful investigation, recurrent conodont element associations were recognized, matching natural assemblages on bedding planes and in fused clusters. The new systematic work saw the recognition of a varied and complex arrangement of different element morphologies in a single feeding apparatus for an individual animal, and a shift from ‘form taxonomy’ to ‘multi-element taxonomy’.

In spite of 125 years of research and significant

advances in understanding, in 1981 the origin of conodonts was still considered by Klaus Müller as ‘one of the most fundamental unanswered questions in systematic palaeontology’. As if in reply to this call for new data, in 1983 the first ever unequivocal conodont specimen with preserved soft tissues was reported from museum specimens collected from the Carboniferous Granton Shrimp Beds of Scotland (Fig. 1). Over subsequent years, more specimens in various states of completeness have been recovered from the same lagerstätte, proving that the initial find was not a fluke of imposed preservation or a ‘conodontophage’ (a creature that had consumed the actual conodont organism). Despite the proliferation of studies into exceptional fossilization processes since the original find, only two sites have subsequently yielded indisputable evidence of conodont soft-bodied preservation. In 1985, a single incomplete coniform-bearing conodont was reported from the Silurian of Wisconsin, USA, while in 1995, another incomplete conodont was described from the Ordovician Soom Shale of South Africa. This later discovery was made

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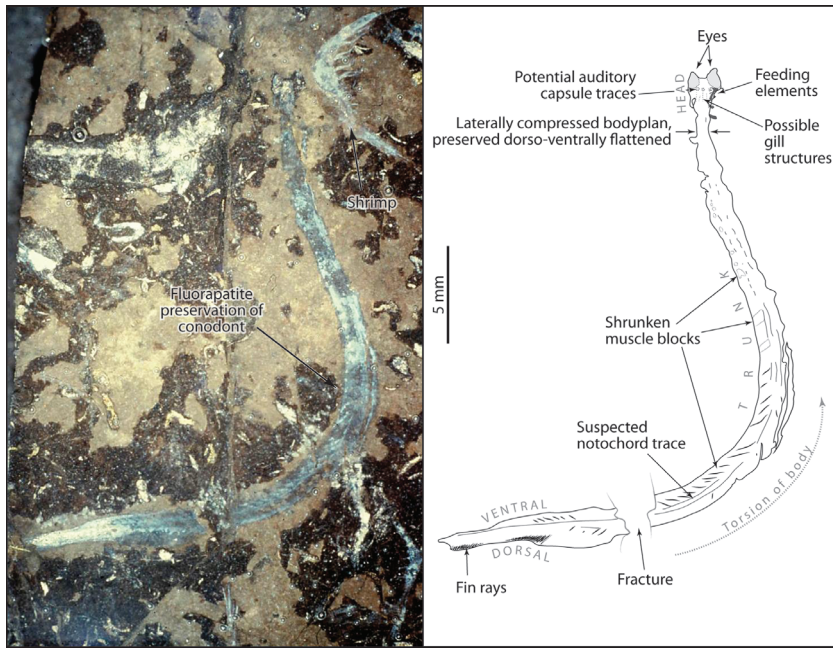


Fig. 1. Soft-bodied anatomy of conodonts. Photograph on left shows the original conodont impression from the Granton Shrimp Beds of Scotland (image courtesy of the late Richard Aldridge and Derek Briggs). A line drawing interpretation of key features is shown on the right.

especially notable by the size of the animal (perhaps an order of magnitude larger than previous discoveries), as well as the preservation of muscle fibres.

Biology and phylogeny

Hard tissues

Historically, proto-, para- and eu-conodont elements were thought to represent the phosphatic microfossil remains of related taxa that were differentiated by their histology (Fig. 2). Proto-conodonts have since convincingly been shown to have belonged to chaetognaths (predatory marine worms) based on their element structure, morphology and arrangement in fused clusters with other diagnostic structures. However, a chaetognath taxonomic determination for proto-conodonts cannot inform our understanding of the more derived para- and eu-conodont taxa that are thought to share an evolutionary lineage. For simplicity, the term conodont is generally used to

refer to the euconodonts (true conodonts) and will be used as such for the remainder of the text.

Conodont elements are small denticulate microfossils generally < 2 mm in size. They comprise dominantly calcium carbonate fluorapatite [$\text{Ca}_5\text{Na}_{0.14}(\text{PO}_4)_{3.01}(\text{CO}_3)_{0.16}\text{F}_{0.73}(\text{H}_2\text{O})_{0.85}$] with a matrix of collagen and other organic material. Internally, conodont elements are divisible into three distinct tissues—a basal body (commonly absent due to preservation bias and being less common in post-Devonian taxa), white matter and lamellar crown.

Conodont elements come in a variety of morphologies (Fig. 3) but can typically be described as: (1) coniform—simple and cone-like; (2) ramiform—bar-like elements where part of the structure is drawn out with the oral surface adorned with numerous denticles; and (3) pectiniform—commonly expanded into some ornamented ‘platform’ area attached to a comb-like blade. Although there are only a limited number of conodonts whose element arrangements are well understood, conodont feeding apparatuses are thought to comprise 15 elements in general (apparatuses with 17 and 19 elements are also known). A universal system to describe the orientation and anatomical location of elements has been established (Fig. 4) based on the most well-known arrangements of ozarkodinitid (a dominant order of conodonts throughout much of the Palaeozoic) Granton Shrimp Bed conodonts. All elements (excepting one that sits on the plane of symmetry) are arranged in pairs in an unusual bilaterally occlusal (closing) fashion. The terms sinistral and dextral are used to define elements found on the left and right sides of the conodont respectively (when viewed from the perspective of the creature itself). Three anatomical positions are defined (Fig. 4):

- 1 P-elements—single pairs of occluding elements, which lie caudal of the main feeding array within the oropharyngeal cavity. Numeric subscripts (P_1 , P_2 , etc.) increase in value for each pair of elements further towards the anterior of the creature.
- 2 S-elements—complex array of elements arranged

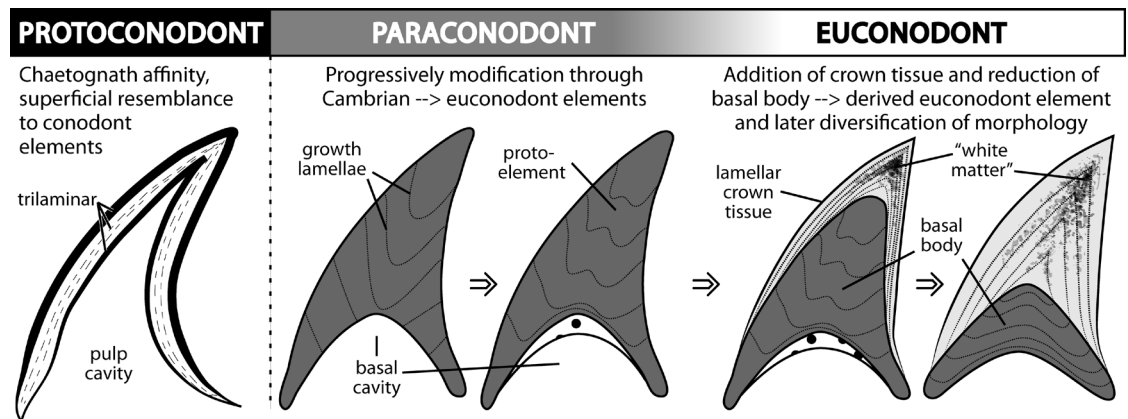


Fig. 2. Simplified diagram showing the proposed relationships of simple coniform elements belonging to proto-, para- and eu-conodonts.

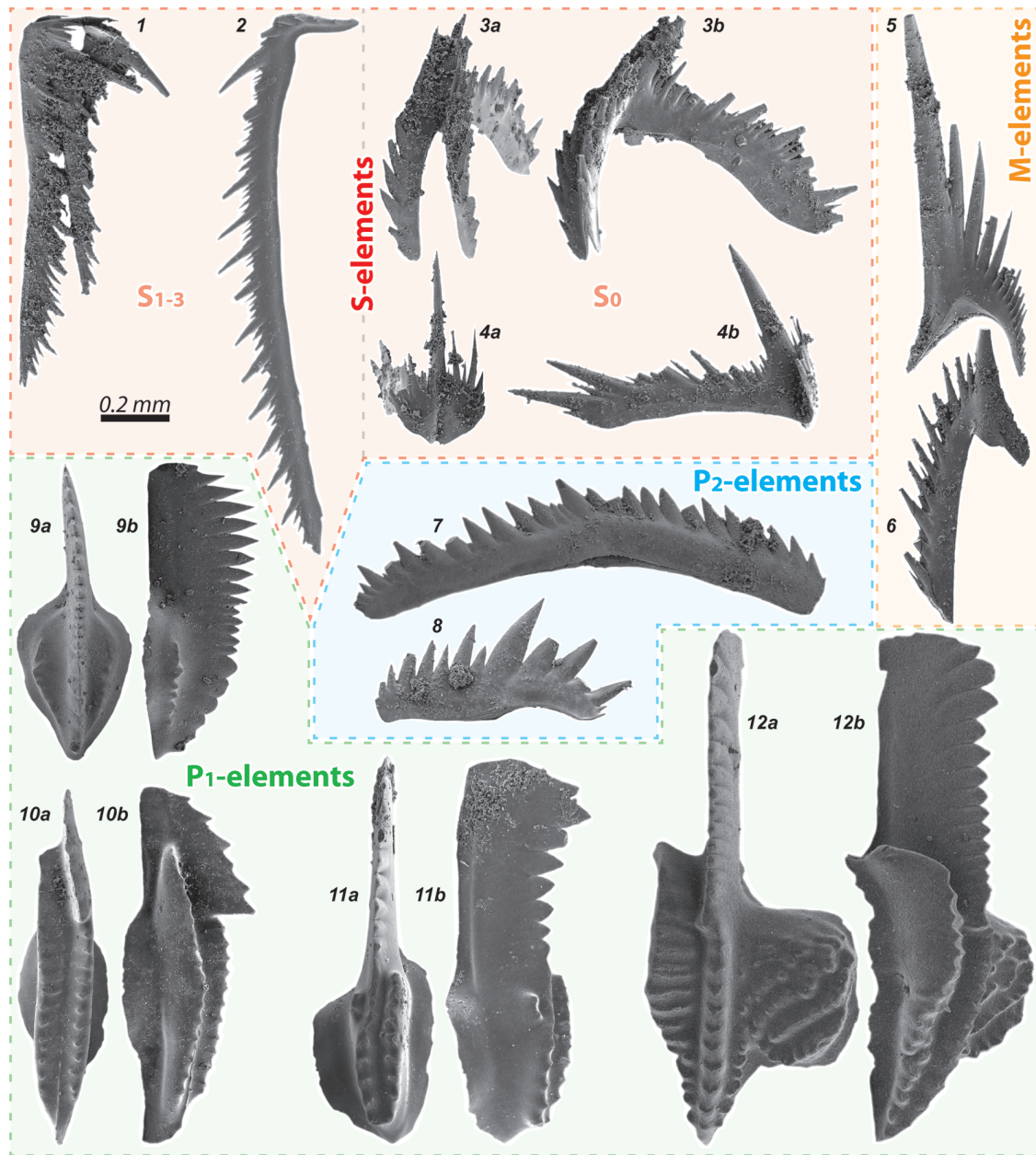


Fig. 3. Example scanning electron microscopy images of selected ozarkodinid Carboniferous conodonts. Relative positions in the feeding apparatus are indicated by letters and colours (refer to Fig. 4). Scale bar represents 0.2 mm. **1–4**, example ramiform S-elements that constituted part of the anterior ‘grasping’ component of the apparatus. **1**. Fused cluster of several S-elements. **2**. Isolated S-element. **3, 4**. Symmetrical S_0 elements in oblique rostral and lateral views. **5, 6**. Ramiform M-elements of *Lochriea* and *Gnathodus* genera (respectively) that occupied dorso-lateral positions in the anterior feeding array. **7, 8**. P_2 -elements of *Gnathodus* and *Lochriea* genera respectively. **9–12**. Occlusal and lateral views of four diagnostic pectiniform P_1 -elements belonging to different species. **9a,b**. *Lochriea homopunctatus*. **10a,b**. *Cavusgnathus naviculus*. **11a,b**. *Declinognathodus noduliferous*. **12a,b**. *Gnathodus bilineatus*.

symmetrically in pairs about a single unpaired S_0 -element along the plane of bilateral symmetry. Numeric subscripts 1, 2, 3, etc. apply to symmetrically paired (but separated) elements increasingly further laterally and dorsally from the axis of symmetry.

- 3** M-elements—single pair of elements that are bilaterally symmetrically paired (but separated) and positioned both rostral and dorsal of the main S-element array.

Ideally, conodont studies should consider the full feeding apparatus. However, complete apparatuses are still unknown for many taxa. Since P-elements are typically the most morphologically distinct, they

are often used independently for species identification, reconstructions of evolutionary lineages, and species abundances. S- and M-elements are commonly more fragile in construction and so tend not to be preserved as well, or are more morphologically conservative preventing species-specific diagnoses.

Soft tissues

Despite the significant age, as well as taxonomic differences between each of the three sites that have reported exceptional preservation of the conodont animal, their preserved soft-bodied anatomy is highly comparable. Conodonts appear to have been bilaterally symmetrical, thin and elongate—bearing

a superficial similarity to eels. Apart from the Soom Shale specimen, which appears to be some 10-fold larger than the norm (based on an extrapolation of size from the elements and preserved trunk width relative to the better known Granton specimens), conodonts had a general body width of just a few millimetres and a body length of a little over 40 mm (Fig. 1).

Where preserved, the anterior of the specimens (associated with feeding assemblages) display two large bilaterally symmetrical sub-circular mineralized patches that are interpreted as sclerotic cartilages that surrounded the eyes. In the South African Soom Shale example, muscle fibres associated with similar preserved traces are interpreted as extrinsic eye musculature and relatively advanced vision. Only in the original conodont soft-part specimen are additional head structures preserved. Small, paired sub-circular dark-patches located posterior to the eyes have been tentatively interpreted as auditory capsules and faint transverse traces could be interpreted as branchial (gill) structures.

The trunk region of many specimens show well-defined chevrons that represent shrunken V-shaped myomeres (muscle blocks), with the Vs pointing anteriorly. Where preserved, the tail exhibits dorsal and ventral fins, apparently with supportive fin rays. The dorsal fin appears to extend further along the trunk than the ventral, although only limited specimens display this feature at present so it could be a taphonomic (preservation) effect. A distinct set of parallel lines, interpreted as the margins of a notochord (flexible axial support structure), is preserved running through the centre of most specimens. The lines converge towards the anterior and posterior of the specimen and are not preserved anterior of the feeding apparatus. In two of the Granton specimens, thickening of the axial lines and separation by a darker line is speculatively interpreted as superimposed preservation of a dorsal nerve cord on the notochord. However, without clearer specimens this remains equivocal.

Affinity

Despite a fantastic fossil record, the discovery of soft-bodied preservation and extensive study for over 170 years, conodonts remain one of the most controversial fossil groups, with opinions on their exact taxonomic affinity divided. Conodonts were undeniably extremely successful and exhibit many characters that are shared with our own ancestors. For this reason conodonts are seen as an important study group to better understand the factors that drove our own evolutionary path and the ultimate success of the chordate phylum.

In the past it was argued that homologies (shared ancestries) were recognizable between conodont

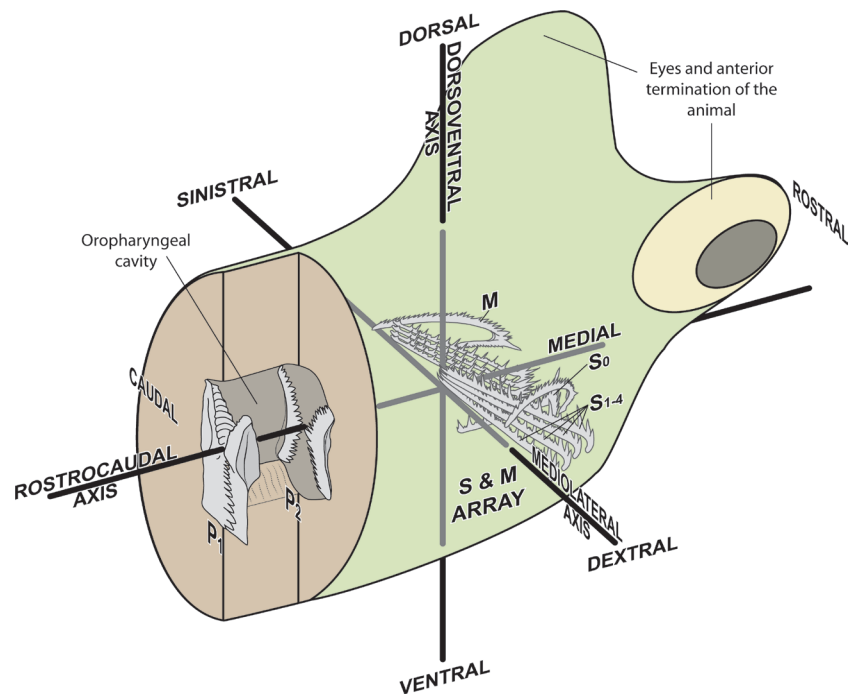


Fig. 4. Cut-away of the anterior of an idealized ozarkodinid conodont showing the element arrangement and notation.

elements and classic vertebrate mineralised tissues. In particular, lamellar crown tissue was compared with enamel, white matter was interpreted as cellular bone and the basal body as containing dentine. However, histological similarities between conodont elements and vertebrate scales and teeth are now largely interpreted as coincidental or the product of diagenesis or evolutionary convergence.

The presence of a notochord represents significant evidence for the recognition of conodonts as chordates while the fact that the structure apparently tapers posteriorly and does not reach the anterior termination, supports a more evolved craniate status. In support of a more derived position within the chordates are the interpretations of sensory organs and extrinsic eye musculature, which suggests a high degree of encephalization (brain development) as well as the tentatively identified ray-supported fins, auditory capsules and gill structures. However, it has been argued that the simplicity of muscle blocks ('V' rather than 'W'-shaped as for most vertebrates), lack of true vertebrate hard tissues, lack of musculature or basal articulation for the fin rays and lack of clearer gill preservation, all point to a non-vertebrate condition for conodonts.

Part of the issue may be taphonomic. Different tissues are known to have different preservation potential and it has been demonstrated that more evolved characters are often those that are least likely to be preserved. This non-random decay of characters tends to cause partially decomposed creatures to 'appear' at lower positions in the family tree. Despite the continued disagreement, there appears

to be almost universal recognition of the chordate affinity of conodonts and a growing acceptance that conodonts represent some form of jawless craniate or primitive vertebrate (within an expanded view of the group) (Fig. 5).

Ecology

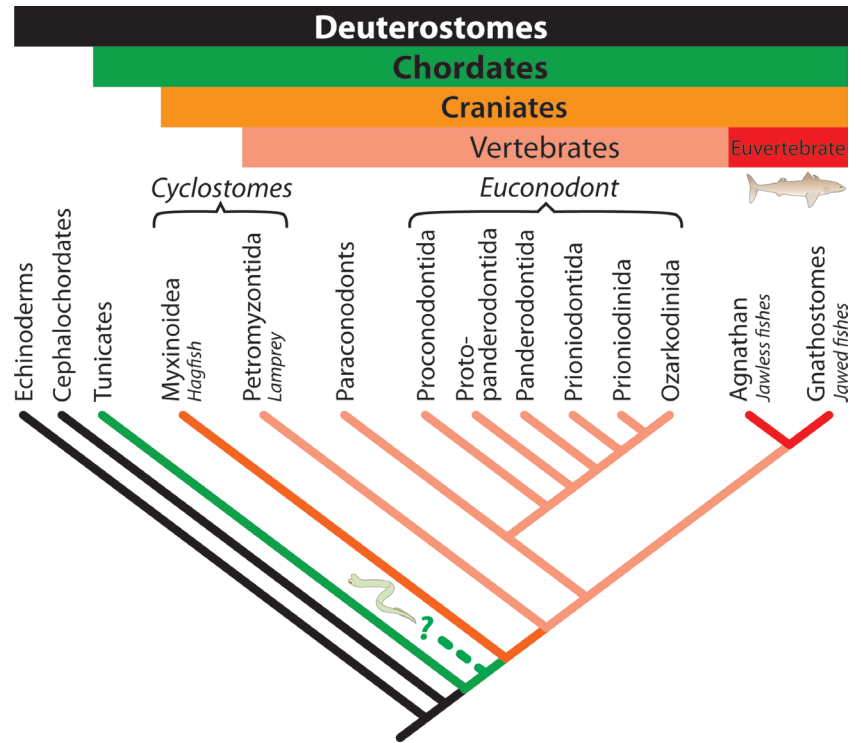
Conodont fossils are exclusively found in marine environments ranging from restricted near-shore to abyssal facies. The presence of fins, well-defined muscle blocks and suspected lateral flattening of the body, suggests the conodonts were mobile anguilliform swimmers (moving with wave-like motions in the body; Fig. 6). The ubiquitous development of many species around the globe, and their recovery from deep marine sediments deposited below the carbonate compensation depth, strongly supports a nektonic (free-swimming) mode of life.

In some cases taxa are found to exhibit particular environmental and/or palaeogeographical associations, which are suggestive of niche/temperature sensitivity and forms the basis for biofacies models. Although many biofacies models suggest that conodonts lived close to the water–sediment interface, geochemical analyses (oxygen isotopes) of a range of conodont taxa belonging to different biofacies (restricted and open-marine) have largely failed to distinguish any significant difference in the water-masses inhabited by the extinct creatures. This has led to the suggestion that conodonts were largely photic-zone surface dwellers, representative of sea-surface conditions. Conodonts with preserved soft-tissue and interpreted eye-structures support a nektonic photic zone existence.

The exact function of the conodont elements themselves has been the subject of significant debate, which prior to the discovery of soft-bodied preservation, was central to determining conodont biological affinity. Two main models of conodont function have been proposed:

Microphagous—soft tissue supports

The conodont elements were permanently enclosed in soft tissue that acted as a filter feeding array or microphagous structure. S- and M-elements supported tissue which selectively directed fine organic matter towards the P-elements where they were gently crushed prior to digestion. The main support for a microphagous model comes from the internal centrifugal-accretion lamination patterns observed in conodont elements that requires the element to have been covered entirely in secretory tissue. Such soft-tissue envelopment also explains numerous examples of apparent repair of fractures or broken denticle tips. However, although it would likely have comprised extremely labile tissue, no evidence for any conodont element covering has ever been reported.



Macrophagous—exposed teeth array

Elements were exposed and functioned as predatory teeth. S- and M-elements actively grasped prey, which was then directly processed via the P-elements. Several lines of evidence suggest that conodont elements were exposed (at least) for periods when they actively functioned as food processing structures:

- 1 Functional analysis (e.g. Finite Element Analysis and Synchrotron-aided in-life element reconstructions) of associated elements is strongly suggestive of directly occluding paired elements.
- 2 Wear patterns on functional surfaces that correspond to impact points on opposing element pairs have identified cutting, crushing and shearing feeding designs in various taxa.
- 3 Analysis of skeletal ontogeny (morphology through various stages of maturation) demonstrates that the functional platform area of conodont elements increased at, or above, the rate required in order to maintain sufficient feeding efficiency as teeth. The length and effective area of S- and M-elements, on the other hand, did not increase at a rate sufficient to feed the growing conodont animal if operating purely as a filter-feeding array.

Exactly how the conodonts controlled precise element occlusion without guiding jaws is still uncertain; however, recurrent patterns of damage punctuated by episodes of growth and repair strongly suggests cyclical alternations of precise microphagous use followed by re-envelopment by secretory tissue. No evidence has been found for the replacement or

Fig. 5. Simplified evolutionary tree of conodonts and relevant related taxa. The dashed line and question mark indicates a lower taxonomic position for the conodonts that is argued by some workers.

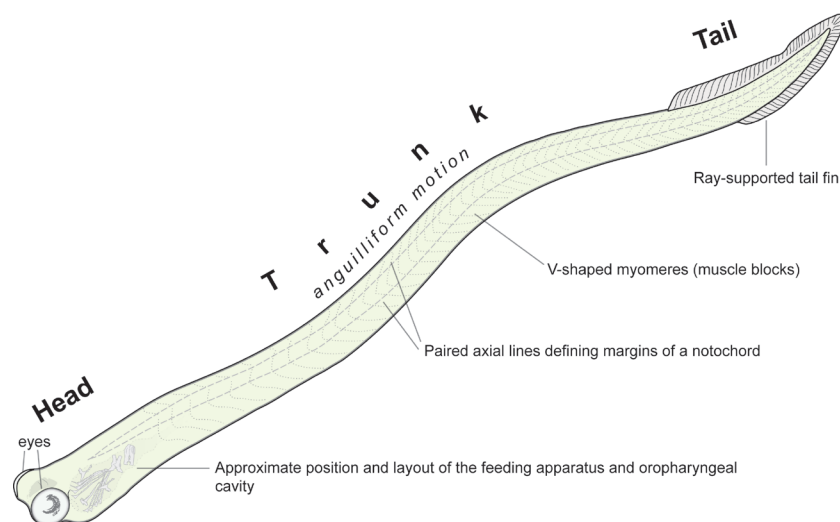
shedding of elements within a conodont apparatus and the truncation of growth laminations on relict occlusal surfaces suggests a retention of elements throughout the lifetime of the individual. Elements can therefore be broadly used as a proxy for conodont abundances, while P_1 (platform elements) can be used as a proxy for creature size.

The large size and rostral location of the eyes, anterior to the internal position of the feeding array, has been used to support a reconstruction of conodonts as active predators. These interpretations have important implications for the chordates; as one of the earliest members to develop mineralised tissues, conodonts apparently evolved their hard parts originally for predation rather than protection (armour).

Applications

The earliest significant recognition of the practicality of conodonts, other than as curiosities that may inform understanding of ancient life, was as biostratigraphical tools in the 1930s. It was quite rapidly recognized that conodont elements varied through geological sequences via progressive modification or origination of morphology and ornamentation. Difficulties associated with the taxonomy and evolutionary study of a group whose fossil record is almost exclusively restricted to mineralized tissues is not unique to conodonts. Using the morphological diversity of conodont elements as a proxy for true biological differentiation assumes that their mineralised morphology is directly related to the biology of the organism and gets faithfully inherited from generation to generation. However, the issues raised are insignificant enough to prevent the hugely successful practical application of conodonts to biostratigraphy. Refined rock processing and concentration techniques have been established that maximize the potential to recover conodont elements from marine sandstone, shale and limestone. The systematic sampling, processing and recording of elements from sections all over the world has established a detailed picture of the diversity of conodont taxa through time. Conodonts arose in the late Cambrian, peaked in diversity in the Ordovician and went extinct at the end of the Triassic. Conodonts represent the most refined stratigraphic tools for, and are used to define, numerous chronostratigraphic intervals throughout the Palaeozoic and over 150 conodont biozones are defined across their ~300 Ma history.

Despite being reconstructed as swimmers, certain conodont taxa still display particular affinities for specific depositional settings, a fact that has been applied in countless palaeoenvironmental interpretations. Conodont biofacies proposals have evolved through various iterations of lateral-



segregation models with distance from shore, depth stratification models or some combination of the two. The factors driving the choice of habitat by conodonts are still poorly understood, and it should be noted that it is rare for any species found to be wholly confined to any specific palaeoenvironmental niche. More generally, a biofacies is manifest in the relative abundance of a particular species, rather than its presence or exclusion. Conodont biofacies play an important role in facies analysis and reconstructions of palaeoenvironmental and palaeogeographical evolution.

Conodont elements also have the useful attribute of varying in texture and colour with increasing exposure to temperature. As the organics bound within the element are heated, the elements vary from pale amber through to black, while the element's crystallites tend to coarsen. During metamorphism, the organic materials responsible for the colour change begin to volatilize and the elements progressively whiten and become translucent. This has made the elements extremely useful indicators of thermal maturation, with a universal conodont Colour Alteration Index (CAI) widely used in the hydrocarbon industry.

Oxygen-isotope analysis of microfossils for palaeoenvironmental work has seen a significant proliferation in recent decades due to advances in sample preparation and analytical precision. Due to their abundance, biostratigraphical application and long evolutionary range, conodont elements have been recognized as particularly prospective geochemical archives. The biogenic apatite that constitutes the conodont elements is particularly robust and more resistant to diagenetic alteration than coeval fish apatite or shelly biogenic carbonate, making them an ideal reservoir for O-isotope studies. Oxygen-isotope studies of conodonts have demonstrated them to be

Fig. 6. Reconstruction of a conodont in life that measures ~40 mm long.

particularly useful at discerning variations in the original isotopic composition of the host marine water body (i.e. changes in hydrology—salinity, extent of freshwater locked into ice-sheets, etc.) as well as ancient sea-surface temperatures. Oxygen isotope analyses of conodont apatite have yielded important insights into the dynamics of Palaeozoic glaciations and clarified our understanding of the climatic backdrops to some of the most significant periods of evolution (Great Ordovician Biodiversification Event) and extinction (end Ordovician, Late Devonian, end Permian, etc.).

Given the ever-refining appreciation of conodonts in terms of biology, ecology, biostratigraphy, etc. and their ever-expanding application to our understanding of the evolution of life, environments and sedimentary basins on the Earth, the future for conodont research remains bright.

Suggestions for further reading

- Aldridge, R.J., Briggs, D.E.G., Smith, M.P., Clarkson, E.N.K. & Clark, N.D.L. 1993. The anatomy of conodonts. *Philosophical Transactions of the Royal Society of London, B.*, v.340, pp.405–421.
- Briggs, D.E.G., Clarkson, E.N.K. & Aldridge, R.J. 1983. The conodont animal. *Lethaia*, v.16, pp.1–14.
- Epstein, A.G., Epstein, J.B. & Harris, L.D. 1977. Conodont colour alteration - an index to diagenesis of organic matter. *US Geological Survey Professional Papers*, v.995, pp.20.
- Gabbot, S.E., Aldridge, R.J. & Theron, J.N. 1995. A giant conodont with preserved muscle tissue from the Upper Ordovician of South Africa. *Nature*, v.374, pp.800–803.
- Jones, D., Evans, A.R., Siu, K.K.W., Rayfield, E.J. & Donoghue, P.C.J. 2012. The sharpest tools in the box? Quantitative analysis of conodont element functional morphology. *Proceedings of the Royal Society B: Biological Sciences*, v.279, pp.2849–2854.
- Purnell, M.A., Donoghue, P.C.J. & Aldridge, R.J. 2000. Orientation and anatomical notation in conodonts. *Journal of Paleontology*, v.74, pp.113–122.
- Turner, S., Burrow, C.J., Schultze, H.-P., Blicek, A., Reif, W.-E., Rexroad, C.B., Bultynck, P. & Nowlan, G.S. 2010. False teeth: conodont-vertebrate phylogenetic relationships revisited. *Geodiversitas*, v.32, pp.545–594.