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The conodont controversies

Richard J. Aldridge and Mark A. Purnell

Some biologists may still not have heard of the conodonts. Although their apatitic skeletal elements (Fig. 1) were first found as microscopic fossils in the middle of the last century, for a long time their study was the domain of geologists, who found them useful for dating and correlating the strata in which they occurred. Biologically, conodonts provided some curiosity value, their affinities being an intriguing mystery; however, they were largely ignored in zoological texts. This was all changed by the discovery in 1982 of a fossil specimen of a nearly complete conodont animal, preserving much of the soft tissue as well as the skeletal elements¹. From this renaissance, new evidence on the nature of conodonts has accumulated dramatically, and has propelled the conodonts into the centre of the debate on the origin of the vertebrates.

Conodont anatomy

By 1995, the number of fossilized conodont animal specimens known had risen to 12. Ten of these came from the Carboniferous rocks of the Granton shore in Edinburgh, UK² (Fig. 2), augmented by a single, partially preserved fossil from Silurian deposits of Wisconsin, USA^{3,4}, and the well-preserved anterior portion of a giant specimen from Ordovician shales of South Africa⁵ (Fig. 3). The Carboniferous specimens clearly show that the conodonts were chordates. A series of chevrons preserved along the trunk of each specimen represents the muscle blocks, and there is a ray-supported caudal fin². Paired axial lines are interpreted as the remains of the notochord^{2,6}, a conclusion corroborated by decay experiments on the extant cephalochordate *Branchiostoma*⁷. The phosphatic skeletal elements form a bilaterally symmetrical feeding apparatus at the anterior end of the animal, set a little ventral to the trace of the trunk; there is no other biomineralized skeleton.

The discovery of fossilized conodont soft tissues has led to suggestions that these enigmatic animals were among the earliest vertebrates and that they were macrophagous, using their oropharyngeal skeletal apparatus to capture and process prey. These conclusions have proved controversial. There is now a consensus that conodonts belong within the chordates, but their position within the clade is hotly debated. Resolution of these questions has major implications for our understanding of the origin of the vertebrates and the selective pressures that led to the development of the vertebrate skeleton.

Richard Aldridge and Mark Purnell are at the
Dept of Geology, University of Leicester,
Leicester, UK LE1 7RH.

Two of the Granton specimens preserve details of the head region, above and anterior to the feeding apparatus. Most prominent is a pair of lobes at the front of the animal, behind which two small discs may represent the otic capsules². Indistinct transverse traces behind the head may be the remains of branchial structures^{1,2}. The geometry of the anterior lobes has been confirmed by specimens from the Ordovician Soom Shale of South Africa, where completely preserved feeding apparatuses are relatively common, and more than 40 have been found with associated ring-like structures. These structures can be reconstructed as a pair of deep, hollow rings expanding outwards away from the axis of the animal and have been interpreted as sclerotic cartilages that surrounded the eyes⁸. Fibrous patches preserved in the same position on the more complete animal specimen from the Soom Shale (Fig. 3) appear to represent extrinsic eye musculature⁵. This specimen also displays exquisite preservation of the trunk muscle blocks, showing details of the rod-like muscle fibres, myofibrils, and even possibly the sarcomeres⁵.

Conodont hard tissues

The recognition that the conodonts were chordates has prompted a re-evaluation of the histology of the phosphatic elements of their feeding apparatuses. Most pre-Carboniferous conodont elements are constructed of two parts, the crown and the basal body. The crown commonly comprises two tissues: a hyaline portion comprising apatitic lamellae with incremental growth lines, and an opaque tissue, traditionally known as 'white matter', which is present in the centres or cores of cusps and denticles. The basal body is more variable and may be lamellar or spherulitic, and may or may not contain tubules. Examination of sectioned and etched specimens using light and scanning



Fig. 1. The conodont fossil record consists almost entirely of dissociated elements such as these, which became scattered in the sediment on death and decay of the animal. The elements are composed of apatite, the form of calcium phosphate from which bones and teeth are constructed. Element morphology varies widely, from simple coniform types (b), to ramiform bars (a), blades (d) and platforms (c). The earliest fossils of true conodonts are of Late Cambrian age, and they became extinct in the latest Triassic. Magnifications: (a) $\times 44$, (b) $\times 60$, (c) $\times 42$, (d) $\times 47.5$.

electron microscopy has led to the suggestion that the lamellar tissue of the crown is homologous with enamel and that the white matter is cellular bone⁹. Tissues in the basal bodies of some species compare with globular calcified cartilage⁹, whereas others appear to be formed from a variety of dentine types^{10,11}.

These interpretations have not been universally accepted. Forey and Janvier^{12,13}, for example, pointed out that similarities between conodont hard tissues and those of vertebrates may be superficial. The cell spaces in white matter are particularly problematic; they are similar not only to those of dermal bone, but also to those found in the mesodentine of early fossil vertebrates¹⁴. It has also been claimed

that they are too small to have housed eukaryotic cells¹⁵. Recently, attempts have been made to determine the nature of conodont tissues using histochemical tests^{16,17}. Partially demineralized conodont element surfaces were found to stain with picosirius red, and this was taken to indicate the presence of collagen^{16,17}, a result at odds with the interpretation of this tissue as enamel. Conversely, white matter did not stain, but if this tissue is bone or dentine, collagen should have been present during life. These results are intriguing, as are results of staining tests suggesting among other things the presence of DNA in conodonts¹⁶, but they are difficult to reconcile with the Ordovician and Devonian ages of the conodonts tested. This material is hundreds of millions of years old, yet peptide-peptide bonds decompose over much shorter time scales (e.g. Ref. 18). The possibility of preserving intact, histochemically active proteins in material of more than a few million years old seems remote (e.g. Ref. 19), and even intracrystalline proteins decompose in a few million years²⁰. The issue can only be settled by geochemical tests to determine directly the nature of the preserved organic components in conodont elements.

Conodont affinities

The soft tissues preserved in the conodont animals from the Granton Shrimp Bed and the Soom Shale provide severe constraints on any hypothesis addressing the phylogenetic position of the Conodonts. The presence of a notochord is a plesiomorphic chordate character shared by the protochordates (Urochordata + Cephalochordata) and the craniates, whereas the chevron-shaped muscle blocks are normally regarded as limited to the cephalochordates and craniates (e.g. Ref. 21). In extant chordates, only the craniates possess a caudal fin with radial supports and only the vertebrates possess eyes with extrinsic musculature and secrete apatitic skeletal elements. In addition, the presence of homologues of enamel, bone and dentine in conodont elements, if substantiated, would be powerful corroboration of a vertebrate affinity.

In recent years, analyses of chordate phylogeny and vertebrate origins have focused attention on the evidence that almost all vertebrate synapomorphies are derived embryologically from neural crest, epidermal placodes or muscularized hypomere (e.g. Ref. 22). Many vertebrate characters have a negligible preservation potential and will never be found in fossils, but the recognition of features in conodonts that depend for their formation on any of these key embryological tissues has clear implications for hypotheses about affinity. Herein, for example, lies the significance of the interpreted presence of neural-crest-derived skeletal tissues, such as bone and dentine, in conodont elements². Also, conodonts possessed sclerotic eye capsules^{2,8}, extrinsic eye musculature⁵, and probably had good vision²³, characters that implicate neural crest and epidermal placode involvement in the development of conodont eyes.

Despite all the new evidence, however, there is continuing debate in the literature regarding the placement of the conodonts within the chordate clade (see Fig. 4). Dzik²⁴, for example, while accepting that they had well-developed eyes, has suggested that conodonts may be more primitive than both the Urochordates and the Cephalochordates. Kemp and Nicoll^{16,17}, however, prefer an affinity with cephalochordates, citing their histochemical evidence that conodont hard tissues are not homologous with those of vertebrates; these authors did not address the soft-tissue evidence for conodont relationships. Others who doubt a craniate affinity include Insom *et al.*²⁵, who considered the case to be based on cladistic methods, an approach they regard as flawed.

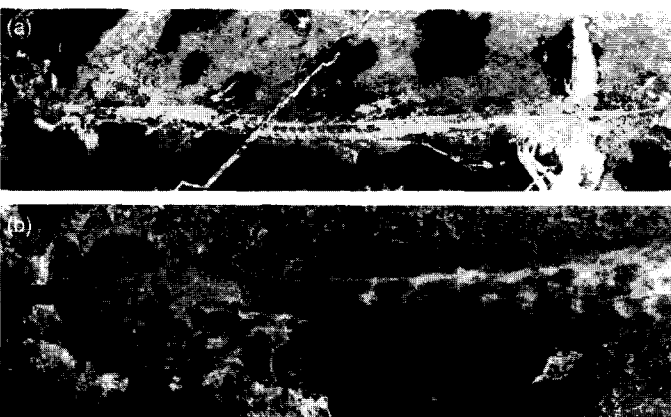


Fig. 2. A Carboniferous conodont from Granton, Edinburgh, UK. (a) A nearly complete specimen of *Clydagnathus windsorensis* (Globensky) ($\times 2.7$); the anterior is to the left, the tail is not preserved. (b) The anterior end, showing elements of the apatitic feeding apparatus ventral to and behind two lobate structures, interpreted as eye capsules ($\times 12$). Specimen RMS GY 1992.41.1, Royal Museum of Scotland, UK. Reproduced, with permission, from Ref. 2.

Authors who have worked on the conodont animal specimens are united in the view that the conodonts belong within the Craniata (=Vertebrata, if the myxinooids are included in the vertebrates – although the role of neural crest in myxinooid development remains equivocal). The initial interpretation was that the conodonts might be a sistergroup to the myxinooids, or that they might be a stem group immediately crownwards of the myxinooids²⁶. However, the recognition in conodonts of well-developed eyes with extrinsic muscles and of putative vertebrate hard tissues suggests that a sistergroup relationship between conodonts and myxinooids would only be tenable if the latter had lost these characters secondarily. The specialist modes of life of the myxinooids perhaps make this scenario possible, and there is some evidence that the essentially non-functional eyes of extant hagfish may be degenerate²⁷ (but see Ref. 13). But the hard tissues of conodonts may be evidence that a placement further crownwards is more appropriate. The extant petromyzontids (lampreys) lack such tissues, and some authors continue to argue for a monophyletic grouping of myxinooids and petromyzontids on morphological and molecular evidence^{28,29}. Recent cladistic analyses^{13,30} have refuted the idea that hagfish and lampreys form a natural group, but Forey³⁰ has asserted that both groups are primitively naked and cannot be regarded as degenerate in respect of their lack of bony tissues. In this event, conodonts may be more derived than lampreys and may be a sistergroup to the extinct bony agnathans (ostracoderms) plus the gnathostomes⁵. Janvier¹⁴ has even gone so far as to speculate that the conodonts may be more derived than all the ostracoderms other than the most advanced group – the osteostracans.

Clearly more evidence and analysis is required before the precise phylogenetic position of the conodonts is finally resolved. In particular, their relationship to the various groups of naked and armoured agnathans, mostly known only from the fossil record, needs to be clarified. Many important characters are unlikely ever to be known for conodonts or for other extinct chordates, but the accumulat-

ing evidence shows that scenarios of vertebrate origins and early evolution can no longer ignore the Conodonts.

Conodont element function

If the affinities of conodonts have provided fertile ground for debate over the past few years, then the question of the function of the conodont apparatus and its constituent

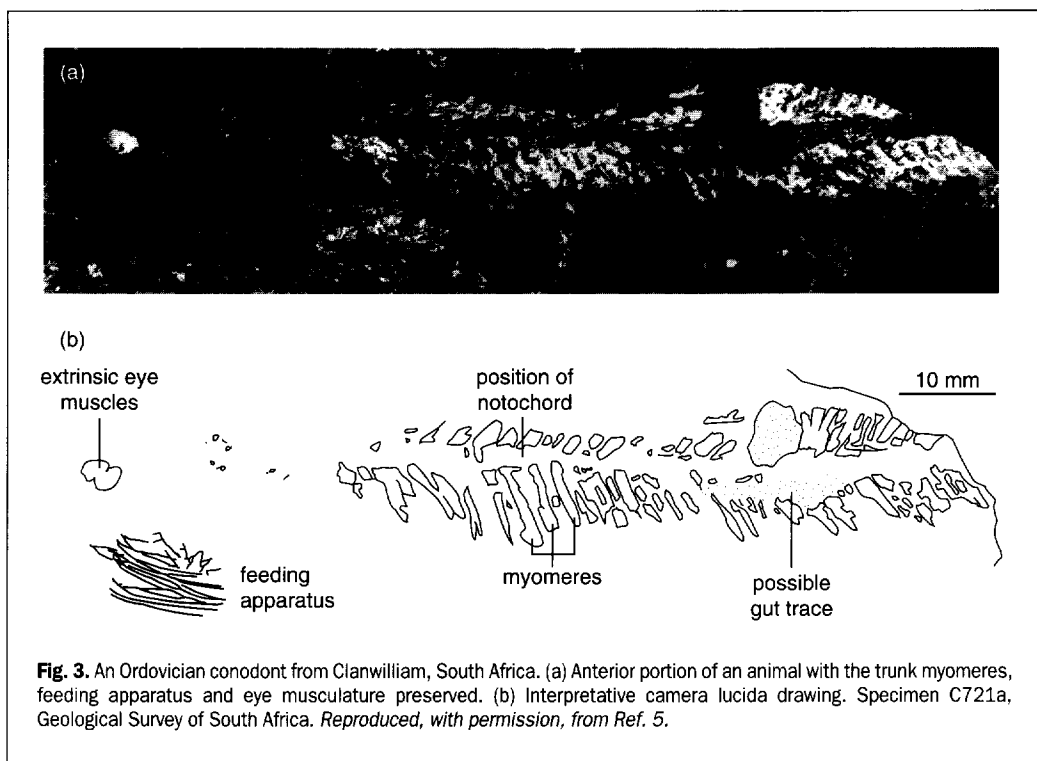


Fig. 3. An Ordovician conodont from Clanwilliam, South Africa. (a) Anterior portion of an animal with the trunk myomeres, feeding apparatus and eye musculature preserved. (b) Interpretative camera lucida drawing. Specimen C721a, Geological Survey of South Africa. Reproduced, with permission, from Ref. 5.

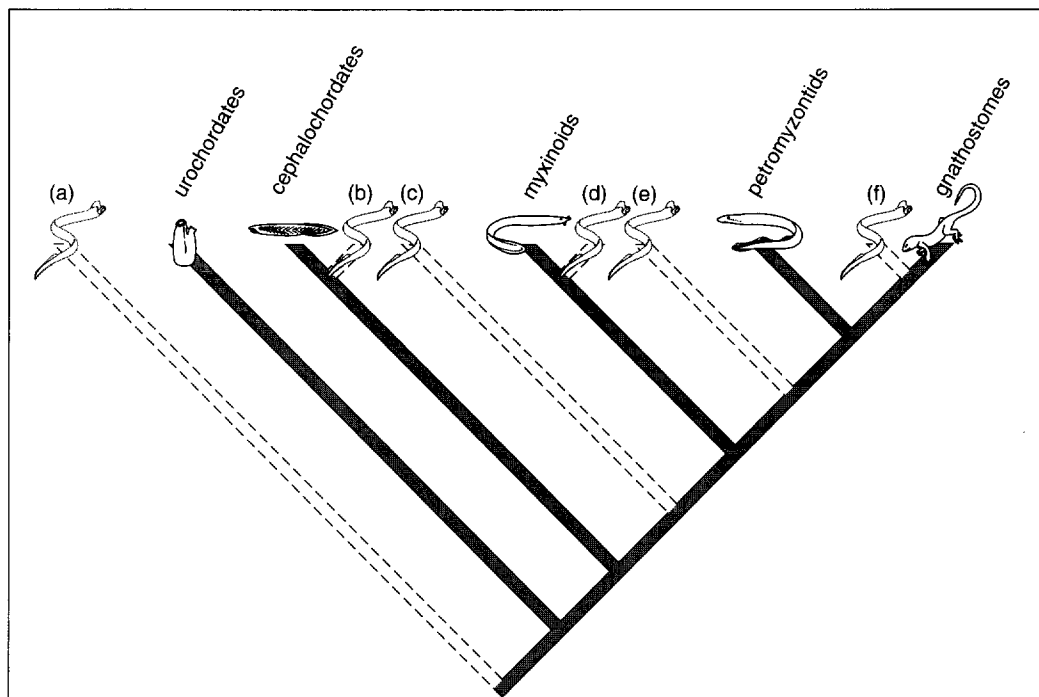


Fig. 4. Hypothesis of relationships between extant chordates (based partly on Ref. 30), with various proposed positions of conodonts indicated: (a) Ref. 24; (b) Ref. 17; (c) Ref. 40; (d) Ref. 26; (e) Ref. 2; (f) Ref. 5. Positions (a), (b) and (c) require that various conodont characters, including eyes with extrinsic musculature, ray-supported fins and phosphatic hard tissues (comparable with enamel, bone, dentine and globular calcified cartilage) were developed independently in the conodonts and in the vertebrates. Position (d) requires either independent development of these characters in the conodonts or their secondary loss in the myxinooids. Position (e) requires secondary loss of the hard tissue characters in the petromyzontids.

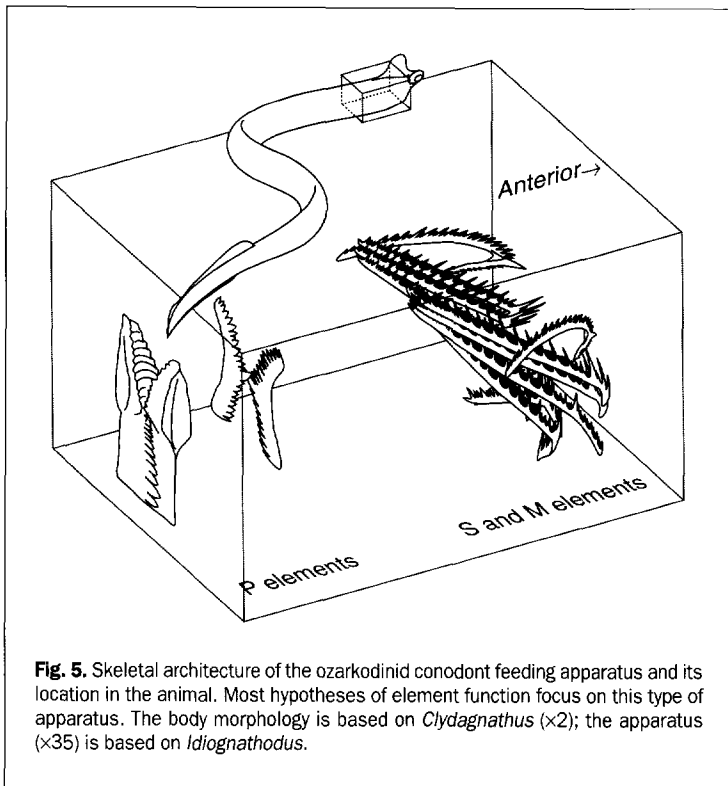


Fig. 5. Skeletal architecture of the ozarkodinid conodont feeding apparatus and its location in the animal. Most hypotheses of element function focus on this type of apparatus. The body morphology is based on *Clydagnathus* (×2); the apparatus (×35) is based on *Idiognathodus*.

elements has been no less controversial. Until the discovery of body traces, there was no way to determine the orientation or location of conodont skeletal elements within the animal, and without even basic developmental, spatial or structural constraints, most hypotheses of element function were pure speculation. The new evidence of conodont anatomy, however, and the now almost universal acceptance of the chordate credentials of conodonts have provided the biological context that was lacking. Conodont elements are

now widely regarded as components of the oropharyngeal feeding apparatus of an eel-shaped chordate, and functional analyses have focused on two hypotheses. According to one model, conodonts were microphagous suspension feeders in which the anterior S and M elements (see Fig. 5) together formed a ciliated sieve structure to capture small particles of food^{31,32}. The posterior P elements then either gently crushed these particles between their tissue-covered surfaces, or simply aided in ingestion³². This hypothesis draws heavily on analogies with *Branchiostoma*. The alternative suggestion is that conodonts were macrophagous, with the S and M elements (located in the oral cavity) actively grasping food that was then sliced or crushed by the P elements (e.g. Refs 1, 33–35); the grasping action of the anterior elements may be analogous to the bilateral biting of the myxinoid lingual apparatus.

Rigorous testing of these hypotheses has proven difficult. The conodont apparatus has no homologue among extant chordates, and critical evaluation of the alternative models has often relied heavily on arguments of functional plausibility. This is partly to blame for the general lack of consensus that characterizes the literature dealing with conodont function, but it is also true that neither hypothesis is without difficulties. The main problem with the microphagous model is that the food intake of the conodont would have been dependent on the surface area of the filtering array formed by the S and M elements. In an isometrically growing animal, this would have increased in proportion to body mass to the power 0.67. Food requirements, however, are linked to metabolic rate, which increases in proportion to body mass to the power 0.75. The increasing metabolic demands of the growing conodont would therefore require positive allometry of the filtering elements, but this does not occur^{34,36}. This conclusion provides some support for macrophagy, but there are also long-standing objections to the hypothesis that conodont elements functioned as teeth. Chief among these has been the observation that the elements do not exhibit surface wear (e.g. Ref. 37; see references in Ref. 35). Recent work, however, has identified microscopic wear features on conodont elements that compare very closely with those documented on the teeth of mammals³⁵.

Mammal teeth exhibit a range of microwear textures produced by abrasives in food and the compressive and shearing forces that act on enamel during feeding³⁸. Similar microwear patterns on a variety of conodont elements, including simple coniform types belonging to some of the most primitive conodonts, and complex molar-like platforms, have been used to interpret precise mechanisms of feeding and food breakdown by conodonts³⁵. Pitting, for example, which is observed on platform elements, indicates that food was crushed between their opposed occlusal surfaces, whereas scratching, observed on blade-shaped elements (Fig. 6) and primitive coniforms, indicates shearing. This has particular significance as shearing is a method of food breakdown that is incompatible with microphagy. Patterns of microwear also suggest that occlusion between P elements in some conodonts was surprisingly precise³⁵; quite how this was achieved in the absence of jaws has yet to be established.

Contrary views of element function, however, still survive. Nicoll³² proposed hypothetical reconstructions of apparatus structure, concluding from these that a cutting action is almost impossible for conodont elements, and although Kemp and Nicoll¹⁶ conceded that microwear indicates element-to-element contact, they did not accept this as evidence of tooth-like function. Other recent work^{14,39} disagreed with

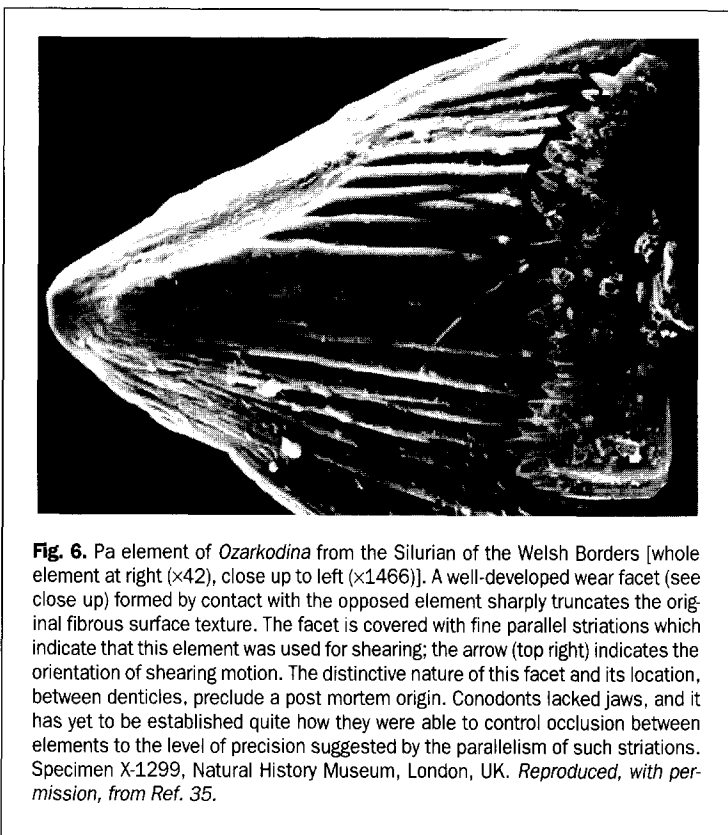


Fig. 6. Pa element of *Ozarkodina* from the Silurian of the Welsh Borders [whole element at right (×42), close up to left (×1466)]. A well-developed wear facet (see close up) formed by contact with the opposed element sharply truncates the original fibrous surface texture. The facet is covered with fine parallel striations which indicate that this element was used for shearing; the arrow (top right) indicates the orientation of shearing motion. The distinctive nature of this facet and its location, between denticles, preclude a post mortem origin. Conodonts lacked jaws, and it has yet to be established quite how they were able to control occlusion between elements to the level of precision suggested by the parallelism of such striations. Specimen X-1299, Natural History Museum, London, UK. Reproduced, with permission, from Ref. 35.

the reconstruction of the conodont S and M elements as an oral raptorial array, and took the position of the apparatus, beneath and slightly posterior to the eyes, to suggest that it lay in the pharynx. Janvier¹⁴ even speculated that conodonts developed suction feeding; without jaws, however, agnathans are incapable of generating strong suction³⁹. The hypothesis that the conodont apparatus lay entirely in the pharynx requires either that the rostral region of the conodont head has not been preserved, or that conodonts lacked an oral cavity. However, the eyes of conodonts may have been situated in front of the oral cavity, a position consistent with their more forward situation in some other early agnathans such as the Ordovician arandaspids (e.g. see Refs 12, 13, 30).

Although most recent analyses of element function are independent of hypotheses of affinity, each has clear implications for the other. The debate certainly continues, but the emerging picture of conodonts as macrophagous animals with anguilliform locomotion and good vision suggests that they were probably predators. If this hypothesis is sustained, such habits in a group as primitive and ancient as the Conodonta lend strong support to scenarios that suggest that an ecological shift from suspension feeding to predation played a crucial role in the origin of vertebrates²².

The importance of fossils

Recent years have seen tremendous advances in the use of genetic, biomolecular and cladistic methods for assessing relationships between organisms. The data from the fossil record will never be as complete as that obtainable from extant animals, but the conodonts provide an excellent example of how evidence from an extinct group can challenge existing phylogenetic views and enrich evolutionary interpretations. Without our knowledge of the conodonts and of the bony ostracoderms, questions regarding the pattern and timing of the origin of key vertebrate features could not be adequately addressed or resolved, nor could we attempt to interpret the selective pressures and pathways driving the historical development of the vertebrate skeleton. Palaeontology and biology have much to offer each other.

Acknowledgements

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How do animals choose their mates?

Robert M. Gibson and Tom A. Langen

Sexual selection has been such an intensive focus of research over the past decade that one might expect there to be a well-established answer to the question posed in our title. On the contrary, researchers have focused their efforts primarily on determining which mates are chosen and why, largely ignoring the processes by which prospective mates are evaluated. It has been apparent for well over a decade that studying the process of mate choice would be instructive. Simply demonstrating that mate choice involves complex assessment provides convincing evidence for adaptive choice¹. More-detailed analyses promise to

How animals search for and evaluate prospective mates has, until recently, been a neglected aspect of sexual selection. Theory and field data suggest that discrimination varies with the costs and benefits of choice, but a consensus has yet to be reached on the tactics by which prospective mates are evaluated. This intriguing issue may be clarified by new studies that deal explicitly with the process of information acquisition.

Robert Gibson and Tom Langen are at the Dept of Biology, University of California, Los Angeles, CA 90095-1606, USA. (rgibson@ucla.edu) (tlangen@ucla.edu)

sharpen understanding of the associated costs and benefits of mate choice, clarify the ways in which mate choice affects the evolution of a range of sexually selected characters and illuminate general mechanisms of decision making². Yet until 1990, tactical aspects of mate choice were ignored by all but a handful of researchers^{2–6}. Since then, interest in this topic has been stimulated by new theory and data. Our purpose here is to highlight these developments, identify areas of debate, and point to some unanswered questions.

Active choice

A starting premise of most work in this area is that animals are engaged in a process of active choice while searching for mates¹. They examine a number of prospects closely and reject all but one, based on comparisons either among the candidates or to an internal standard (threshold). This is an appealing idea, but mate choice may often entail much simpler mechanisms, such as attraction to mates emitting more conspicuous or intense signals¹. What is the evidence for active choice?

Active choice has been inferred from the observation that individuals visit several prospective mates but choose only one (or a subset) of them, thus implicitly rejecting the remainder. Using this criterion, field workers have documented active choice of males by females in diverse taxa, including insects^{7,8}, crustacea⁹, fish^{10–12}, frogs¹³, birds^{5,14–19} and mammals²⁰. Table 1 summarizes data from 11 well-studied species. In each case, data refer to one mating episode in which a female typically selects a single mate.

Besides illustrating that active choice can be an important component of mate selection, the data also show that females of a number of species do not approach males at random but rather visit a pre-selected subset. This suggests some initial assessment based on long-range cues, although simpler alternative processes such as differences in detect-

ability²⁴ are also possible in some cases. Different cues may be used hierarchically² to narrow down the search at each stage. Fiddler crabs (*Uca annulipes*), for example, preferentially approach larger males but base subsequent choice on burrow dimensions⁹. Female sage grouse (*Centrocercus urophasianus*) (Fig. 1) are attracted by vocal characteristics of male displays but choose among visited males using other cues, including display rate¹⁷. These observations imply that the number of prospective males a female evaluates could substantially exceed the number that she visits.

The economics of finding a mate

Given active choice, are there any generalities that govern how choosy individuals will be, or the way in which prospective mates are evaluated? These two issues have been addressed from a theoretical perspective^{1,4,25–27} and are beginning to be scrutinized empirically. We take up each in turn.

Optimal choosiness

In theory, the fitness gain from choice, and hence optimal choosiness, should be affected by at least three variables: the distribution of mate quality, the costs of searching for mates, and the chooser's quality^{1,25,28}. Quality is used here synonymously with the fitness obtained when choosing a particular partner. The predictions are intuitive: choosiness should increase with the variance in quality of prospective mates and decrease as the costs of locating another mate or delaying choice increase. When both sexes choose their mates, low quality (less desirable) individuals should be less discriminating. This is because their options are limited to lower quality individuals of the opposite sex, capping their benefits and increasing search costs. Data relevant to the first two predictions are beginning to accumulate, though choosiness based on individual quality remains unexplored.

There is some evidence that animals can adaptively track changes in the distribution of mate quality. Female pine engraver beetles (*Ips pini*), searching for a mate in the field, discriminate more strongly in favor of unmated males as the proportion of such males on the log where they are searching increases⁸; this preference probably increases larval viability. Bakker and Milinski²⁹ presented female three-spined sticklebacks (*Gasterosteus aculeatus*) with three males sequentially, the first and last of which had similar nuptial coloration (a cue presumed to indicate male quality).