

CONODONTS: PAST, PRESENT, FUTURE

WALTER C. SWEET AND PHILIP C. J. DONOGHUE

Department of Geological Sciences, The Ohio State University, Columbus 43210, <sweet.2@osu.edu>, and
School of Earth Sciences, University of Birmingham, Edgbaston, Birmingham B15 2TT, UK, <p.c.j.donoghue@bham.ac.uk>

ABSTRACT—Conodonts were mostly small, elongate, eel-shaped marine animals that inhabited a variety of environments in Paleozoic and Triassic seas. Although long enigmatic, conodonts are now regarded as vertebrates and their closely controlled fossil record is not only the most extensive of all vertebrates, but it also makes conodonts the fossils of choice in upper Cambrian through Triassic biostratigraphy. Conodonts were soft-bodied except for a variety of phosphatic elements that formed a distinctive feeding apparatus. Post-mortal dissociation of the apparatus and subsequent jumbling of its elements on the sea floor led, from 1856 to about 1966, to development of an artificial, form-based taxonomy that was utilitarian, but clearly unsatisfactory as a vehicle for understanding the group in biologic terms. *Natural assemblages* of elements, discovered between 1879 and 1952, have been interpreted as undisturbed skeletal apparatuses, and in the mid-1960s it was determined that original composition of the apparatuses of many species could be reconstructed and statistically evaluated from collections of disjunct elements by various grouping procedures. These determinations led to an emphasis on *multielement taxonomy* by most (but not all) students of conodonts. Even so, only about a third of the approximately 550 valid conodont genera, have been established (or re-interpreted) in multielement terms and this makes any of the several extant schemes of suprageneric classification phylogenetically suspect. We comment on a recent scheme that recognizes 41 families assigned to some 7 orders, and suggest how it might be modified so as to square with principles of phylogenetic systematics.

INTRODUCTION

THE FIRST report of conodonts in the *Journal of Paleontology* was a short note in volume 4 (1930) by Clinton Stauffer on their occurrence in Ordovician rocks on the University of Minnesota campus, in Minneapolis. Since then, every volume of the *Journal* has included at least one paper dealing with conodonts, to a grand total (through November of 2000) of 415. In 1930, conodonts were paleontologic curiosities, thought probably to be the teeth, jaws, or dermal scales of an extinct group of Paleozoic fishes and of interest to only a few students anywhere in the world. Shortly after Stauffer's report appeared, however, interest in conodonts grew dramatically and the number of paleontologists interested in this enigmatic group increased greatly, due primarily to establishment of a major research program at the University of Missouri. At present, several hundred persons are involved in conodont research and the former curiosities have come to be not only the fossils of choice in Paleozoic and Triassic biostratigraphy but also the group of fossil chordates with the best-documented fossil record.

In the present contribution, we briefly summarize the history of conodont research; detail current ideas about the anatomy and zoologic affinities of conodonts; consider the scope and origin of the Conodonta; discuss the appropriate base for a species-level taxonomy of conodonts; and comment on the status of suprageneric categories and the problems, both real and methodological, involved in their development and use in phylogenetic systematics.

BRIEF HISTORY OF CONODONT RESEARCH

Conodonts were named and first described in 1856 by Christian Heinrich Pander (Fig. 1), one of the founders of embryology and paleontology in Russia. Pander regarded the specimens from which he derived the concept of *Conodonten* as the teeth and/or jaws of an unknown group of fossil fishes. Although Pander used the term *Conodonten* informally to refer to a group of animals, to individuals of that group, and to the mineralized objects on which he based his concepts, we will use *conodont* only for the complete animal. Following Sweet et al. (1959), and most subsequent students of conodonts, we will use *element* (or *conodont element*) for the mineralized skeletal structures most commonly preserved as fossils. We specifically reject terms such as “conodont-bearing animal” or “conodont animal”—at least until our colleagues who study brachiopods or dinosaurs adopt the rubrics

“brachiopod animal” or “dinosaur animal” to distinguish between the shells or bones of those creatures and the entire organism!

Conodonts received scant attention from paleontologists from 1856 until 1926, when E. O. Ulrich and R. S. Bassler, of the U.S. National Museum, summarized what was then known of the group; proposed a classification modeled on, but considerably more extensive than the one devised by Pander; and noted that conodont elements were common fossils in the body of Devonian-Mississippian black shale that blankets much of eastern United States.

In the early 1930s, E. B. Branson and M. G. Mehl and their students, at the University of Missouri, began an extensive program of conodont research, which, in the next two decades, led to an enlarged taxonomy and a greatly expanded knowledge of the nature and distribution of conodonts in North American Paleozoic rocks.

Prior to 1950, most of the collections used to document the nature, range and distribution of conodonts were derived from easily disaggregated sandstones and shales. But, at least as early as 1952, it was found that well-preserved specimens could also be obtained from the residues of carbonate rocks dissolved in dilute acetic acid, and this discovery greatly expanded the size and stratigraphic distribution of conodont-element collections. Indeed, addition of this technique to routine laboratory procedures meant that conodont elements could be expected in (and extracted from) almost any type of marine sedimentary rock.

In 1934, Hermann Schmidt (in Germany) and Harold Scott (in Illinois) discovered clusters of Carboniferous conodont elements on black-shale bedding surfaces. These, like the Devonian one described by Hinde in 1879, and additional ones described in 1952 from the Pennsylvanian of Illinois by Frank Rhodes (Fig. 2), were interpreted as the skeletal apparatuses of individual conodonts. The significance of these Carboniferous *natural assemblages* was not fully appreciated by students of conodonts, however, until the late 1950s and early 1960s, when it was realized independently by Huckriede (1958) and Walliser (1964) (in Germany) and by Webers (1966) and Bergström and Sweet (1966) (in the United States) that the composition of recurrent groups of elements in their large collections of discrete elements in many ways matched or closely approximated that of the natural assemblages. Huckriede and Walliser commented on this interesting observation, but did not follow its lead in the taxonomic treatment



FIGURE 1—Christian Heinrich Pander (1794–1865), first student of conodonts. Portrait is black-and-white reproduction of an oil painting by Julius Hagen-Schwartz that hangs in the Dom Museum, Riga, Latvia.

of their collections. Webers, and Bergström and Sweet, however, based the species they recognized on the clusters generated empirically from their collections. Thus, in 1966, there began a shift in conodont systematics from *form taxonomy* to *multielement taxonomy* and, in 1969, Sweet and Bergström predicted that this new *modus operandi* would ultimately replace form taxonomy. Kohut's (1969) statistical studies of the recurrent groups Bergström and Sweet recognized in their Ordovician collections; Sweet's (1970) cluster analysis of the groups he recognized in collections from the lower Triassic of Pakistan; and von Bitter's (1972) elegant analysis of collections from the Pennsylvanian of Kansas served to confirm the idea that the skeletal apparatuses of conodonts could be reconstructed with some fidelity from collections of discrete elements, and that many of the reconstructed apparatuses closely matched those seen in the natural assemblages described by Schmidt, Scott, and Rhodes. Thus, in 1971, at an international conference of conodont workers in Marburg, Germany, it was decided that multielement taxonomy was to be preferred over form taxonomy, and this was the systematic methodology chosen by authors of revised volume W of the influential *Treatise on Invertebrate Paleontology* (Clark et al., 1981).

The latest, and certainly the most exciting era in conodont research began inauspiciously in 1983 with description by Briggs, Clarkson and Aldridge of a Dinantian specimen from Scotland (Fig. 3.1) that represents a more or less complete conodont. This, and additional specimens from the same locality (Aldridge et al., 1986, 1987, 1993) and the Upper Ordovician of South Africa

(Aldridge et al., 1993; Gabbott et al., 1995) have enabled an expanded understanding of conodont anatomy and now provide the basis for establishing the vertebrate affinities of this group so confidently assumed by Pander in 1856.

CONODONT ANATOMY AND AFFINITY

Our current knowledge of the anatomy of conodonts derives from the form, composition, and histology of a wide variety of skeletal elements and from a small number of specimens from two localities that preserve features of the soft tissues in which the elements were formed and contained. Anatomic information derived from these sources has been exhaustively described, discussed, and interpreted in the recent literature (e.g., Aldridge et al., 1993; Pridmore et al., 1997; Donoghue et al., 1998, 2000), and we rely heavily on the conclusions of these authors. Previous ideas with respect to the affinities of conodonts were summarized by Sweet (1988) and all that needs to be said here is that a majority of those who have ventured an opinion favor either a chordate or an annelid assignment. Current opinion, supported by cladistic analysis, overwhelmingly opts for the former, a result that would certainly please Rigby (1983), whose conclusions, based on similar procedures, were presented only in abstract form and have thus been ignored by later writers.

Although there is general agreement now as to the chordate affinities of conodonts, agreement is by no means unanimous. The chief competing hypothesis (Kasatkina and Buryi, 1996a, 1996b, 1997, 1999) regards conodonts as chaetognaths. But deciding between the chordate and chaetognath hypotheses of affinity involves a number of imponderables. That is, chaetognaths are no longer considered deuterostomes, but are now thought to belong to the Ecdysozoa (e.g., Littlewood et al., 1998), a recently discovered superclade of protostomes united by the possession of a molting cuticle (Aguinaldo et al., 1997). Thus, characters shared by chaetognaths and chordates are only those shared by all triploblastic metazoans and resolution of affinities depends upon adopting a preferred hypothesis of relationship. Homologies between conodonts and either chordates or chaetognaths can be made only in this light. This means that the chordate and chaetognath hypotheses of affinity are mutually exclusive because the preserved anatomic structures of conodonts are interpreted differently depending on which model is followed. For example, paired axial lines that extend much of the length of the soft-tissue remains of *Clydagnathus windsorensis* would be interpreted as a through-gut in the chaetognath model, but as a notochord in the chordate model (although interpretation as a 'through-gut' is also compatible with the chordate model). Given these intangibles, we briefly describe and provide only a limited interpretation of the remains of conodonts before justifying their interpretation in the light of a specific anatomic model.

Description of the anatomic remains.—Aside from the readily fossilized skeletal remains, knowledge of conodont anatomy is based almost entirely upon a handful of specimens from two localities. These are attributable to *Clydagnathus windsorensis* (Globensky), from the Lower Carboniferous Granton Shrimp Bed of Edinburgh, Scotland (Fig. 3.1–4; Briggs et al., 1983; Aldridge et al., 1986, 1987, 1993), and *Promissum pulchrum* Kovács-Endrődy, from the Upper Ordovician Soom Shale of South Africa (Gabbott et al., 1995). Based on hard-tissue characters, these taxa are only remotely related (members of the Cavusgnathidae and Balognathidae, respectively), so the features that are preserved in both can be taken as general for a wide range of conodonts, rather than as specific to just the two species (see Fig. 6).

Specimens of *Clydagnathus windsorensis* (Fig. 3) are slightly more than 40 mm long and about 2 mm wide, whereas reconstruction of the preserved anterior part of the only specimen of *Promissum pulchrum* (Fig. 3.6) suggests the entire conodont was



FIGURE 2—A natural assemblage of conodont elements, $\times 52$. Assemblage is holotype of *Scottognathus typicus* (Rhodes) from Pennsylvanian rocks in Illinois. (*Scottognathus* is a jr. subjective synonym of *Idiognathodus*). White letters indicate some of the components of the S, M, and P regions of the apparatus. Black and white print from a color diapositive furnished by Rodney Norby, Illinois Geological Survey.

at least 400 mm long (Gabbott et al., 1995; Purnell, 1995a; Fig. 3). Specimens of both species are elongate, laterally compressed, and enclose in a bulbous anterior region natural assemblages of skeletal elements now interpreted as a complex feeding apparatus (Fig. 3.4). The bulbous, apparatus-bearing region of the body is interpreted as rostral, and the bilateral arrangement of the anterior lobes and component elements of the feeding apparatus provides a means of establishing the sagittal plane.

Both taxa preserve evidence of segmentation in the form of chevron-shaped structures that are oriented with their apex directed rostrally and overlap such that the apex of each chevron occupies the base of its rostral neighbor (Figs. 3.3, 6). In *Clydagnathus windsorensis* the segments are preserved in phosphate (Aldridge et al., 1993), whereas in *Promissum pulchrum* the segments are preserved in clay minerals (Gabbott et al., 1995); in both, the segments were originally fibrous in nature. The apex of segments is missing in the only specimen of *P. pulchrum*, but in *C. windsorensis* the segments are intersected by a pair of axial lines (Fig. 3.3) that extend the length of the fossil and end short of the feeding apparatus (Conway Morris, 1989). The other end of the fossil is absent in *P. pulchrum*, but in *C. windsorensis* the segments reduce in height until they are no longer distinguishable in a homogeneous mass of phosphate, which is surrounded by a ray-supported fin that is asymmetrically developed (Fig. 3.2). The axial trace provided by the segments and intersecting lines, and their relationship to the axis of bilateral symmetry defined by the apparatus and anterior 'lobes,' indicates that the fin is positioned in the sagittal plane.

The soft-tissue remains of both *Promissum pulchrum* and *Clydagnathus windsorensis* exhibit a pair of lobelike organic structures at the anterior end, one on either side of the plane of bilateral symmetry (Fig. 3.4; Aldridge et al., 1993). The lobes, which are

preserved as carbonized remains of round or ovate outline, have a thickened or darkened rim. They have been reconstructed in three dimensions as a pair of outwardly expanding cups (Aldridge and Theron, 1993). In *C. windsorensis*, the lobes are intimately associated with amorphous patches of phosphate (Donoghue et al., 1998), whereas in *P. pulchrum* the lobes occur in direct association with fibrous clay minerals that are directly comparable to those preserving the segmental structures (Fig. 3.6; Gabbott et al., 1995). In one specimen of *C. windsorensis* (BGS GSE 13821 (part)) the lobes are closely associated with a pair of similar, but smaller structures, and four pairs of rectangular organic traces (Fig. 3.4; Briggs et al., 1983). There is also evidence of a sediment-filled trace independent of the paired axial lines in BGS GSE 13822 (c'part) (Donoghue, *personal observation*).

Elements of the feeding apparatus are phosphatic and have two distinct parts, crown and base (Fig. 4.3). Crowns are composed of lamellar tissue, which may or may not include a core of opaque, cancellated tissue commonly described as "white matter." Lamellar tissue of the crown is typically formed of thin layers of francolite crystallites outlined by and separated from adjacent layers by surfaces that indicate incremental growth. Element bases are more coarsely lamellar in structure than crowns and are composed of much finer crystallites. Most of the basal tissues that have been examined histologically are lamellar, although others are spheroidal, tubular, or combinations of these microfabrics.

Interpretation of the anatomic remains.—At first sight, a hypothesis of relationships that depends on the identification of homologies, which, in turn, depends on a hypothesis of relationships, is a *prima facie* example of circular reasoning. But this is not the case because the reasoning process is not linear (inductive), but reciprocal (deductive) (see e.g., Rieppel, 1988). Given

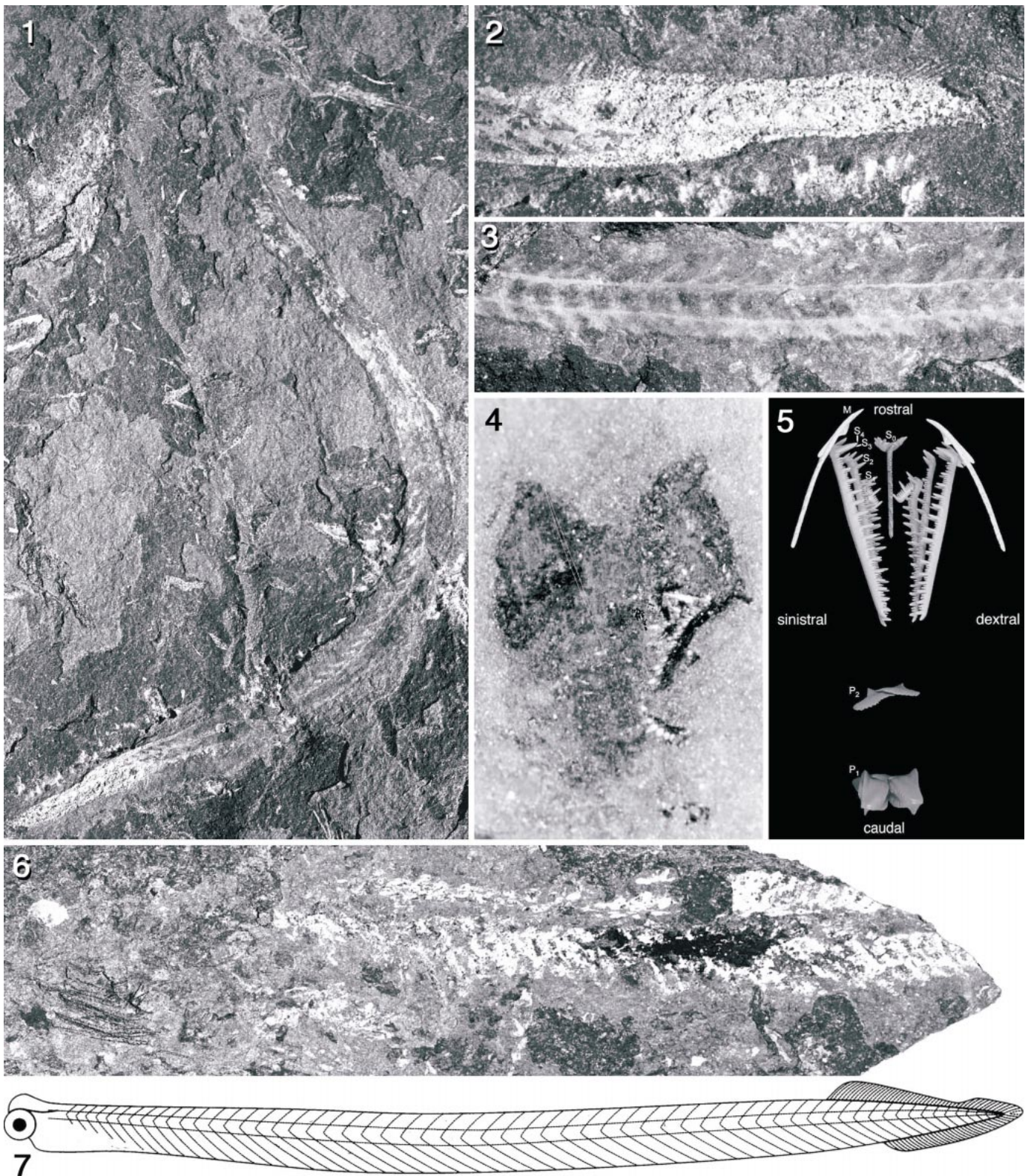


FIGURE 3—1–4, *Clydagnathus windsorensis* (Globensky) from the Dinantian of Scotland. 1, whole animal [BGS IGSE 13821 (part)]; 2, detail of tail and ray-supported fin [BGS IGSE13821 (part)]; 3, trunk region detailing the paired axial lines, interpreted as the remains of a notochord and the superimposed chevrons that are interpreted as the remains of segmental muscles [RMS GY 1992.41.1]; 4, head region detailing the dark organic ‘lobes’ and associated structures including a natural assemblage of elements [BGS IGSE 13821 (part)]. 5, model of the 3D architecture of the feeding apparatus of *Idiognathodus*, a close relative of *C. windsorensis* (from Purnell et al., 2000). 6, *Promissum pulchrum* Kovács-Endrödy from the Upper Ordovician of South Africa [GSSA C721a] (from Gabbott et al., 1995); rostral to left, dorsal to top. 7, reconstruction of the anatomy of *C. windsorensis* (from Purnell, 1995a).

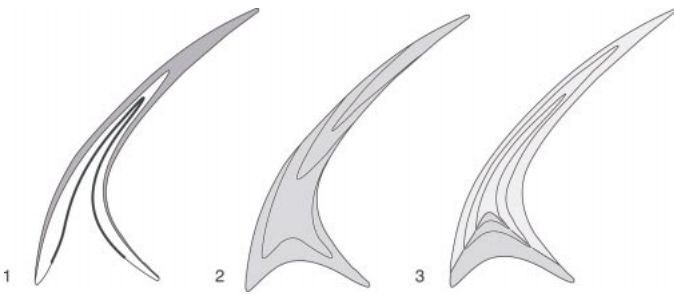


FIGURE 4—Diagrammatic cross-sections of: 1, a protoconodont element; 2, a paraconodont element; and 3, a euconodont element. Different shadings reflect different tissue layers within the elements. 1, the tissue layers of protoconodonts have no counterparts in paraconodonts (2), and/or euconodonts (3). Light shading in 3 represents the euconodont crown; the dark shading represents basal tissue in euconodonts (3) and its putative homologue in paraconodonts (2). From Donoghue et al. (2000), after Bengtson (1976).

that the identification of homologies is deductive, it is possible to determine the appropriateness of using chordates or chaetognaths as the best model for interpreting the fossilized remains of conodonts. In Table 1, we list features of conodonts and their supposed homologies in the two models. The precise justification for each of the interpretations can be found elsewhere (Aldridge et al., 1993; Donoghue et al., 1998; Kasatkina and Buryi, 1996a, 1996b, 1997, 1999). But, in brief, the chordate model represents a stronger hypothesis because it is better able to account for the characteristics of conodont soft-tissue anatomy and hard-tissue histology without recourse to numerous *ad hoc* interpretations of autapomorphies. This conclusion is not based on a subjective interpretation of structures, but on an attempt objectively to assess which model provides the best expository *milieu* within which to interpret conodont anatomy (*contra* Ziegler and Weddige, 1998).

Conodonts as vertebrates.—Once the chordate model is accepted as the most appropriate for interpretation of conodont anatomic remains, the significance of these characters is much more straightforward. Thus conodonts are inferred to possess a generalized chordate anatomy, typical of the living invertebrate chordates (i.e., *Branchiostoma*), but with an anatomically distinct head, paired sensory organs (both optic and otic) and a ray-supported fin akin to hagfishes and lampreys, the most primitive living vertebrates (Fig. 3.7; see Aldridge et al., 1993, for detailed arguments). In detail, conodonts possessed eye musculature (Gabbott et al., 1995) that is otherwise found only in the lampreys and more derived vertebrates, as well as the characteristic feeding apparatus that indicates possession of a biomineralized skeleton that

is otherwise found only in vertebrates more derived than lampreys. This skeleton was composed of homologues of enamel and dentine (both exclusively vertebrate hard-tissue types) that appear to have grown in a manner comparable to the teeth and scales of all vertebrates, including ourselves (Donoghue, 1998). The phylogenetic significance of these characters is supported by formal cladistic analysis of conodonts and other chordates (Donoghue et al., 2000). In short, this analysis finds that conodonts are more derived than any of the living jawless vertebrates. However, conodonts are less derived than jawed vertebrates, or any of the extinct groups of jawless vertebrates that possessed a mineralized dermal skeleton, which was invariably developed in the form of an extensive dermal armor. This reinterpretation of conodont affinity takes on added significance in light of the implied narrative for origin of the mineralized vertebrate skeleton. Unequivocal evidence indicates that conodont elements performed a tooth function in a predator/scavenger, and this, together with our current understanding of conodont affinity, has led to a new scenario that indicates the vertebrate skeleton evolved first to enhance active feeding in a predator/scavenger (Purnell, 1995b). This dramatically overturns the conventional wisdom, which has it that the vertebrate skeleton evolved first for protection against predators (Romer, 1933).

SCOPE AND ORIGIN OF CONODONTA

Rocks of late Precambrian and early Paleozoic age have yielded a variety of tiny spine-like fossils of dominantly organic or weakly phosphatic composition. At one time or another, most of these have been regarded as conodont elements. Histologic studies of some of these fossils, all regarded as conodont elements, led Bengtson (1976) to recognize three histologic categories he termed protoconodonts (Fig. 4.1), paraconodonts (Fig. 4.2), and euconodonts (=“true” conodonts, i.e., those organisms usually referred to as conodonts; Fig. 4.3). Bengtson proposed that protoconodonts evolved into paraconodonts and, ultimately, into euconodonts.

The principal differences between the proto-, para-, and euconodont grades of organization are the number of tissue layers comprising the skeletal elements, the pattern of histogeny exhibited by the elements, and the relationship between these two characteristics. As we have already mentioned, euconodonts are composed of two tissue layers that exhibit synchronous growth, thus increasing the size of the element by outer apposition. The paraconodont grade differs in that there is only one tissue layer, although there may be an external organic coating (Szaniawski, 1987). Bengtson (1976) argued that the main tissue layer of paraconodonts is homologous to the basal tissue of euconodonts. In contrast to these organizational grades, the protoconodont grade

TABLE 1—A selection of the preserved anatomic structures of conodonts and their interpretation in light of a chordate or chaetognath model. Note that the chaetognath model can not provide as many interpretations as the chordate model and requires recourse to the identification of conodont ‘autapomorphies’. Thus, the gross anatomy of conodonts can be deemed to be more similar to chordates than chaetognaths. Even following the chordate hypothesis, conodonts, nevertheless, exhibit a significant autapomorphy: the possession of conodont elements. Based upon the available evidence we can, therefore, conclude that conodonts comprise a monophyletic group.

| Structure | Chaetognath model | Chordate model |
|---------------------------------------|---------------------------------|---------------------------|
| Paired axial lines | Through-gut | Notochord |
| Segmentation | Transverse muscles | Transverse muscles |
| Elements | Grasping spines/Skeletal plates | Odontode homologues |
| Regenerative growth | ? | Dental succession |
| Paired rostral ‘lobes’ | Laterally-oriented hood | Laterally-oriented eyes |
| Accessory ‘lobes’ in BGS GSE 13821 pt | ? | Otic capsules |
| Fin-like extensions | Lateral fins | Dorso-ventral fins |
| Phosphatic biomineralization | Autapomorphy of conodonts | Craniate synaplesiomorphy |
| Crown tissue | Autapomorphy of conodonts | Enamel |
| Basal tissue | Autapomorphy of conodonts | Dentine |
| Paired rectangular structures | ? | Gill pouches |

has three more or less distinct tissue layers; the bulk of the element is composed of the middle layer; and growth is limited to inner apposition in the cone-shaped basal cavity. Szaniawski (1987) argued that the middle layer of protoconodonts is homologous to paraconodont elements and to the basal tissue of euconodonts.

In 1982, Szaniawski demonstrated that the coniform elements of *Phakelodus tenuis*, a protoconodont, are histologically similar to the grasping spines of the living chaetognath, *Sagitta*. Szaniawski further suggested that this chaetognath-like structure might also characterize the coniform elements of other protoconodont species.

In Volume W, supplement 2 of the *Treatise on Invertebrate Paleontology* (Clark et al., 1981) protoconodonts and paraconodonts are included in the Paraconodontida and regarded as conodonts. Sweet (1988), however, excluded both protoconodonts and paraconodonts and thus restricted the Conodontata to forms whose elements have euconodont-like histology. *Proconodontus* and *Terodontus*, founders of the two euconodont clades recognized by Sweet, are more similar to each other than either is to the paraconodonts or protoconodonts, both in terms of histology and what little is known of apparatus composition. Thus, it is most likely that, contrary to dogma, *Proconodontus* and *Terodontus* have a common ancestor that is a euconodont, rather than a paraconodont or protoconodont. In turn, euconodont and paraconodont elements are more similar, in terms of histology and histogeny, than either is to protoconodont elements. Thus, euconodonts and paraconodonts plausibly comprise a natural group that excludes the protoconodonts. Even if we agree with Szaniawski (1982) that *Phakelodus tenuis* and paraconodonts are stem-group chaetognaths, it does not necessarily follow that conodonts and chaetognaths are closely related (cf. Bengtson, 1976, 1983). In fact, conodonts (=“paraconodonts” + “euconodonts”) have more features in common with hagfish, lampreys, and cephalochordates than they do with chaetognaths (see above).

How do the conodonts (=eu- + paraconodonts) fit into the chordate tree? Did conodonts and all the more-derived vertebrates have a feeding apparatus like that of conodonts? The likely answer is “yes.” Both hagfish and lampreys have a bilaterally symmetrical and bilaterally acting feeding apparatus that exhibits considerable similarity to that of conodonts, and many independent workers (e.g., Janvier, 1981; Jefferies, 1986) have argued that this character is primitive for vertebrates. Whether the common ancestor of conodonts and all more derived vertebrates had a feeding apparatus composed of elements with an histology precisely similar to the paraconodont grade will require data on the anatomy of these early members of the Conodontata. But this implication is not beyond the realm of possibility, particularly given recent discoveries on the histology of hagfish toothlets (Diekwisch and Vahadi, 1997). Just to be provocative, we point out that this outcome would not only render the Conodontata (eu- + paraconodonts) paraphyletic, but would also imply that, in cladistic terms, we, too, are conodonts!

TAXONOMIC BASE

From 1856 to about 1966, specific and generic concepts for conodonts were based on shapes of the individual components of what is now interpreted as a complex feeding apparatus. Most students of conodonts understood this practice to be artificial and without any particular value in phylogenetic analysis (e.g., Müller, 1956), but a majority evidently assumed that reconstruction of skeletal apparatuses from collections of jumbled discrete elements was impossible, despite evidence from natural assemblages that suggested that a more natural taxonomy should include all components of those apparatuses.

Analysis of large collections by several authors (e.g., Huckle, 1958; Walliser, 1964; Webers, 1966; Bergström and Sweet, 1966) revealed a striking constancy in association in them between certain types of elements. Furthermore, some of these “recurrent associations” were seen to include elements whose shapes resembled, or could readily be compared with those in certain of the natural assemblages described by Schmidt (1934), Scott (1934) and Rhodes (1952). Thus, it occurred to some of these authors that the recurrent groups identified empirically in their collections might more realistically reflect the skeletal apparatuses of conodont species than would the individual components of those apparatuses.

Webers (1966) and Bergström and Sweet (1966) were the first to use recurrent groups of elements in the diagnosis of conodont species and the latter introduced the epithet *multielement species* to distinguish those taxa from ones based on the shape of discrete elements. In naming multielement species, both Webers and Bergström and Sweet advocated adherence to rules of nomenclature promulgated by the ICZN and, in at least the early stages of transition from form to multielement taxonomy, this resulted in long synonymies, the use of unfamiliar names for otherwise familiar species, and problems in the nomenclature of certain biostratigraphic zones.

In 1969, Sweet and Bergström predicted that transition to a multielement taxonomy for all conodonts could be accomplished in five years. This prediction is now seen to have been well off the mark. That is, a rough survey of the conodont literature indicates that in the years since 1969 only about a third of the more than 550 valid conodont genera have been diagnosed or rigorously re-interpreted in multielement terms. This number might be increased if we were to accept as correct the view that only P elements exhibit characters useful in distinguishing those apparatuses taxonomically. However, this view has yet to be demonstrated, so we have not counted those species (or genera) in our canvass.

Apparatus structure is known from intact natural assemblages for only a few conodont species. In all of these, including those associated with the more anatomically instructive ones, the apparatus is bilaterally symmetrical and composed of 15 to 19 discrete components. In natural assemblages that represent taxa that formed complex elements, the apparatus is divisible structurally into three parts, termed S, M, and P (Fig. 5.1–2). In the best-known natural assemblages, like the one in Figure 2, there are two pairs of elements in the P position. P-region elements were commonly the stoutest, were approximate mirror images of one another, had their long axes oriented dorso-ventrally and their denticulated surfaces opposed (Fig. 3.5; Purnell et al., 2000).

In most natural assemblages, and in clusters generated from collections of discrete specimens, one element in the S region is itself bilaterally symmetrical and unpaired; the remainder are fragile, paired, profusely denticulated structures, elongate antero-posteriorly (or along a rostral-caudal axis in terminology advocated by Purnell et al., 2000) and with members of each pair opposed on opposite sides of the plane of bilateral symmetry. A pair of pick-shaped elements, commonly with one or two long denticulated processes, is situated outboard of the S group. These elements occupy the M position in the feeding apparatus.

Natural assemblages that represent taxa that formed only coniform elements are exceedingly rare. These apparatuses differ from their more complex, more derived, relatives in lacking obvious structural division into distinct suites of elements that may compare to the P M S divisions (Sansom et al., 1994). Indeed, the identification of homologies between species with coniform-only apparatuses and those with apparatuses composed of more complex elements is at present an intractable problem that hinders resolution of the intra- and interrelationships of those species.

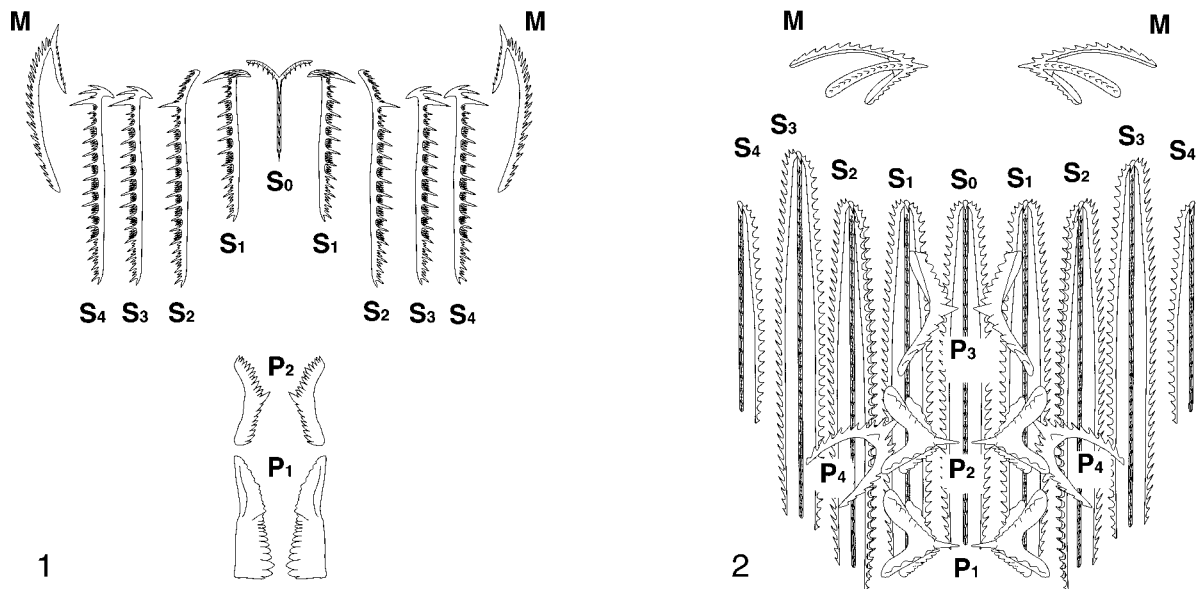


FIGURE 5—1–2, Apparatus plans for 1, *Ozarkodina*; and 2, *Promissum pulchrum* (and possibly other balognathids). From Aldridge et al. (1995), modified to show element notation and homology according to Purnell et al. (2000).

In detail, morphology of elements that form the conodont feeding apparatus varies greatly (e.g., compare Fig. 5.1 with Fig. 5.2) and an elaborate terminology has been devised to handle this variation (see Clark et al., 1981; Sweet, 1988, for glossaries and definitions). In fact, major categories of element shape are few and a review of the terminology currently applied to these categories and their many variants is unnecessary here. We should note, however, that Purnell et al. (2000) provide a set of new terms (and a re-definition of some old ones) for the orientation and anatomic notation of elements within the conodont feeding apparatus. This new terminology incorporates some terms in general use for elements before development of present-day understanding of conodont anatomy, and squares with current interpretations of soft-tissue anatomy. We urge use of the new terminology in future descriptions of conodonts and their feeding-apparatus elements.

SUPRAGENERIC CLASSIFICATIONS

Most of us who have worked with conodonts have done so as biostratigraphers and we have thus paid scant attention to the suprageneric classification of the species reconstructed in our studies. Families and more inclusive taxa, like the form-species on which they were based, were merely devices to aid in the identification of elements of similar or identical form and there is little evidence that anyone familiar with conodonts took those devices to represent entities of any particular biologic significance. With the advent of multielement taxonomy, however, it became possible to regard species established through use of this methodology as “real” biologic entities and thus to address construction of a classificatory scheme that might truly be of some phylogenetic significance.

Lindström (1970), the first to give serious attention to a suprageneric classification of conodonts, distributed 21 families among two orders and eight superfamilies, all based on similarities in the multielement apparatuses of the genera and species included. Lindström’s scheme is basic to the one adopted by authors of the influential volume W, supplement 2, of the *Treatise on Invertebrate Paleontology* (Clark et al., 1981) and underlies, at least philosophically, the one published later by Sweet (1988). The latter, which follows the *Treatise* classification in regarding the

conodonts as a phylum, recognizes 206 genera, in 41 families and seven orders very unevenly divided into two classes. Aldridge and Smith (1993) noted, correctly, that Sweet’s scheme was not “. . . based on well-formulated cladistic or other methodological principles.” Nevertheless, in summarizing the stratigraphic distribution of conodonts for *The Fossil Record 2* (Benton, 1993), they adopted it, with minor rearrangement in content of several of the families Sweet recognized and addition of seven new, but fortunately unnamed families, mostly for genera even yet not diagnosed in multielement terms.

Sweet’s classification, with modifications in Dzik (1991) and Aldridge and Smith (1993), is the one that has been used most widely. However, it embodies a number of taxonomic problems that will sooner or later require revision. For example, the Conodontia of this classification, is a grade of organization acquired independently in two apparently distinct lineages that make their appearance in the fossil-record almost concurrently in Upper Cambrian rocks (Miller, 1980, 1984) (but see above). The *Teridontus* lineage is thought to have been ancestral to all familiar conodont taxa, whereas the *Proconodontus* lineage is generally perceived to have been relatively depauperate. Taxa of the *Teridontus* lineage were included by Sweet (1988) in the Class Conodonti, which embraced five orders and 34 families. Some of these grades are monophyletic (that is, they include the ancestral taxon and all its descendants), but the majority are paraphyletic in being made up of a number of monophyletic subgroups and paraphyletic lineages that lead to other clades.

Because of a general trend in phylogenetic systematics toward removal of paraphyletic taxa, it is appropriate to consider the implications for conodont classification. Rejection of paraphyletic taxa is justified on the basis that such groupings are selected on an *ad hoc* basis from among a set of mutually exclusive possibilities and are neither biologically nor historically coherent (Patterson, 1982). Invariably, these taxa are united not just by the possession of some characters, but by the absence of others. In most paraphyletic groups, however, taxa are united to the exclusion of others on the presence of characters known to be shared primitively ones; that is, by characters primitively absent in some taxa but missing only secondarily in others.

As noted, the *Teridontus* lineage is divided in Sweet’s (1988)

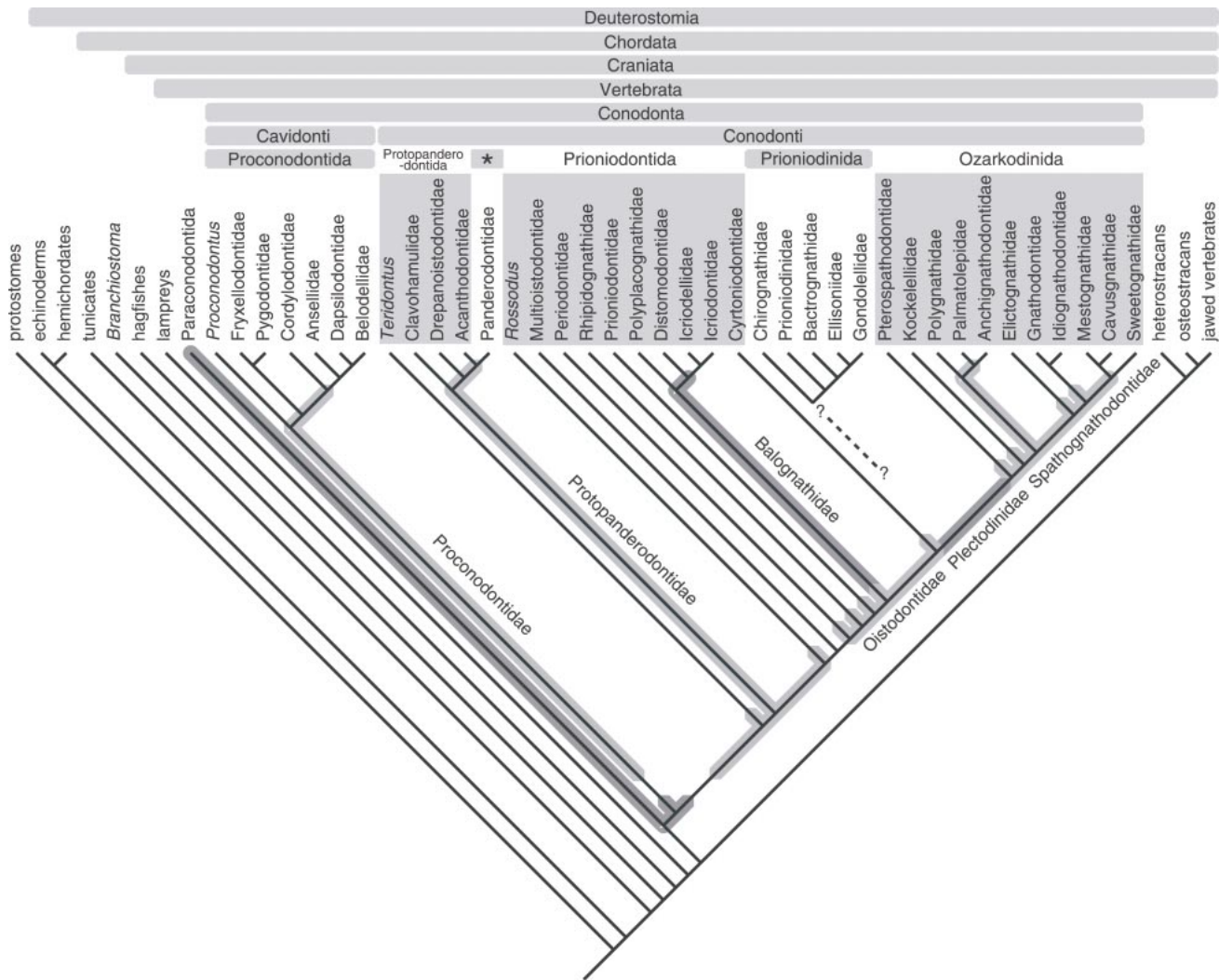


FIGURE 6—Interrelationships and attempted reconstruction of the intrarelationships of conodonts based on Donoghue et al. (2000) and Sweet (1988; with amendment), respectively. Current understanding of conodont intrarelationships, presented here at family level and above, is not based on cladistic analysis. However, we have attempted to derive a cladogram compatible with the phylogenetic hypotheses expressed by Sweet (1988). Note, however, that Sweet (1988) did not express an opinion with regard to the relationships of prioniodinide conodonts. The taxon indicated by an asterisk is the Order Panderodontida.

classification into five orders (Fig. 6), Protopanderodontida, Panderodontida, Prioniodontida, Prioniodinida, and Ozarkodinida. The Protopanderodontida includes families of conodonts with coniform elements in presumably all regions of the feeding apparatus. It includes the ancestral Protopanderodontidae, but excludes the probably derived Panderodontidae (the sole family of the Panderodontida), which is distinguished largely by a feeding apparatus composed of laterally furrowed coniform elements. Paraphyly of the Protopanderodontida could be somewhat reduced by regarding the Panderodontida as a superfamily, rather than an order, and by suitable rewording of the diagnoses of its constituent subordinate taxa. However, the Protopanderodontida remains paraphyletic because it does not include the Prioniodontida (however defined), which is inferred to have been derived from the Protopanderodontida. Rather than suggest further modifications of the Protopanderodontida, we note only that conodonts with feeding apparatuses formed entirely of coniform elements are an especially difficult group to work with; homologies between coniform elements are not easy to establish; species-level taxonomy is beset

with many problems; and, as a result, many supraspecific categories are suspect.

The Prioniodontida, Prioniodinida, and Ozarkodinida present other problems. That is, prioniodinides and ozarkodinides are monophyletic taxa that are thought (Sweet, 1988; Dzik, 1991) to have been derived independently from the Prioniodontida, a group united on the possession in the P region of pastinate elements or their platformed equivalents. The Prioniodinida, which have digyrate elements in the P region, and Ozarkodinida, which lack both pastinate and digyrate elements but have P-region elements that are basically carminate and angulate, are widely recognized as monophyletic taxa. However, that recognition renders the presumably ancestral Prioniodontida clearly paraphyletic (Fig. 6).

Although the Prioniodontida is united on the possession of pastinate P elements, this obscures the fact that some prioniodontides are more closely related to ozarkodinides than they are to other prioniodontides (Fig. 6); that is, they share a common ancestor with ozarkodinides that they do not share with other prioniodontides. For instance, from the hypothesis of relationships in Figure

6, it is clear that despite a gross similarity between *Rossodus* and the multioistodontids, the latter share a common ancestor with ozarkodinides they do not share with *Rossodus*. Thus, multioistodontids are more closely related to ozarkodinides than to *Rossodus*. Similarly, periodontids share a common ancestor with ozarkodinides that they do not share with either *Rossodus* or the multioistodontids and, for this reason, are more closely related to ozarkodinides than to either *Rossodus* or any of the multioistodontids.

One way to rid current conodont classification of paraphyletic taxa would be to change the relative ranks of individual taxa (thereby subtly changing their meaning) such that their hierarchical relationship would reflect evolutionary relationships. As noted in our remarks about the Protopanderodontida, this approach cannot easily be extended to removal of all paraphyletic genera or species, for there are too few ranks available and increasing the number of ranks to a realistic level would result in an unwieldy and ultimately unusable classification (e.g., Farris, 1976; see also Kron, 1997). Thus, we advocate the degree of pragmatism recently espoused by Benton (2001). In our proposal, the overall structure of relationships above the family level should directly reflect the evolutionary relationships of taxa, and less inclusive taxa should be ranked more subjectively to maintain taxonomic stability. In this scheme, it is possible to retain the entities Prioniodontida, Prioniodinida, and Ozarkodinida by adjusting their relative rank and meaning such that the Prioniodontida would include the suborders/superfamilies Prioniodinina (or Prioniodinacea) and Ozarkodinina (or Ozarkodinacea) plus a residue of taxa that are members of neither clade (i.e., those taxa comprising a group equivalent to the old meaning of Prioniodontida). Similarly, the explicitly paraphyletic Spathognathodontidae (sensu Sweet, 1988) could be raised in rank relative to the other mostly monophyletic ozarkodinide families thought to be rooted in it. A revised Spathognathodontacea would embrace a number of monophyletic families/subfamilies, plus an ensemble of plesiomorphic taxa that are interleaved phylogenetically between the constituent clades.

A complete review and revision of suprageneric classification is obviously beyond the scope of this contribution. It would also be premature in that all of these deliberations assume that existing hypotheses of relationship are correct and, most recently, attempts have begun to test these and other assumptions with respect to the quality of the fossil record of conodonts (e.g., Donoghue, 2001). Nevertheless, as more rigorous phylogenetic (or "cladistic") analyses are made of clades at various hierarchical levels it should be possible to establish an overall classification that will be more realistic biologically than the ones at hand in charting the evolutionary history of this major animal group.

CONODONTS, BIOSTRATIGRAPHY, AND PHYLOGENY

In their 1926 report, Ulrich and Bassler noted that "... if carefully prepared and discriminated, [conodonts] will be found as valuable in stratigraphic work as any group of organisms and because of their minute size they will be as useful in subsurface investigations as the foraminifera, bryozoa, and ostracoda." In subsequent years, this prediction has been amply confirmed and conodonts are now the fossil group of choice for biostratigraphic work in rocks of Late Cambrian through Triassic age. Indeed, in many parts of the Paleozoic and Triassic conodonts provide the relative dating against which all else is calibrated and graphic correlation has been used to constrain taxon durations through much of the Ordovician and Silurian (Sweet, 1995; Kleffner, 1995), parts of the Devonian (Klapper, 1989), and the lower part of the Triassic (Sweet, 1989).

An extensive discussion of conodont-based biostratigraphies and the methods by which they have been constructed would be

out of place in a summary of conodont systematics. However, it is appropriate to emphasize the fact that current phylogenetic schemes and virtually all of our present-day perception of conodont interrelationships derive from a basically biostratigraphic tradition in which phylogeny is not only read from the rock record but has also, in many cases, been used in assembling that record.

If the fossil record of conodonts is more than adequate for biostratigraphy (which, after all, requires only the qualities of repeatability and reproducibility), is it also adequate as the basis for unravelling the patterns and processes of both macro- and micro-evolution? Studies of these topics require measures of completeness that approach the absolute—and assessing the degree of completeness of the fossil record is difficult because it requires knowledge of the complete record for comparison! One test of the completeness of the fossil record that would not include stratigraphic data in its formulation might be to compare existing phylogenetic arguments derived from the biostratigraphic record with those from cladistic analyses based on morphologic data alone. This type of test is possible, and more appropriate now than previously. That is, recent advances in our understanding of conodont anatomy, and revision by Purnell et al. (2000) of the terminology to describe its most commonly fossilized parts, have paved the way for development of the entirely homology-based taxonomy long sought by conodont workers. Conodonts with a feeding apparatus of skeletal elements that can be homologized individually, or in part, between taxa, are eminently suitable for cladistic analysis. Consequently, combined with their rich fossil record, conodonts can now make a significant contribution to the debate about the relative importance of stratigraphic and morphologic data in phylogenetic reconstruction (e.g., Smith, 1998, 2000). This is particularly so because conodont taxonomy currently straddles the opposing camps of vertebrate paleontology, which has championed phylogenetic systematics more than any other paleontologic discipline, and micropaleontology, which is steeped in the tradition of inferring phylogenies from a stratigraphically organized data base.

SUGGESTIONS FOR THE FUTURE

In addition to our suggestion that cladistic analyses divorced from a stratigraphic framework might aid in clarifying (or solidifying) conodont relationships at several taxonomic levels, we recommend a number of additional topics for future conodont research. To begin with, if conodont species are to be diagnosed on the basis of the component morphology and architecture of their multielement feeding apparatuses, then careful attention needs to be paid to description and illustration of all parts of those apparatuses. While it may turn out that conformation of individual elemental components is sufficient to distinguish closely related species, there is no defensible reason to assume this *a priori* and very good reasons to believe the assumption to be generally erroneous. For example, Klapper (1989) and Klapper and Foster (1993) have demonstrated that species of *Ancyrognathus* and *Palmatolepis*, founded initially on characters of one of their two pairs of P elements, may be revised and substantially reinterpreted following even incomplete multielement analysis, and that this more sophisticated mode of taxonomy may have rather important biostratigraphic implications.

A problem that lingers concerns the fact that many collections of discrete conodont elements are dominated by pectiniform elements like those in P regions of many natural assemblages—but there are just not enough ramiform elements in those collections to fill the positions in the S and M regions indicated by the natural-assemblage templates, many of which include P elements closely similar to those in discrete-element collections. The puzzling insufficiency of candidate S and M elements in these collections results in recognition of recurrent groups that may be

incomplete as a result of post-mortal attrition. Or, if the recurrent groups are complete, they may represent species whose apparatuses were reduced ontogenetically or as a consequence of environmental adaptation. In any case, the existence of these collections dictates caution in using them taxonomically, and suggests to us that a very fruitful area of future research might involve critically re-sampling stratigraphic intervals that yield both natural assemblages and large collections of discrete elements to determine if all components are really present in suitable numbers, or if features of the enclosing rock shed any light on reasons for disparities in expected frequencies.

Carefully made and tabulated Ordovician collections contain distinctive elements of the sort that occur in the P region of later-Paleozoic species known from natural assemblages, but lack any elements that might be homologized with components of the S or M regions of those assemblages. For this reason, species of, for example, *Cahabagnathus*, *Eoplacognathus*, and *Polyplacognathus* have been interpreted to have had feeding apparatuses of just two pairs of pectiniform elements. Because it is unlikely that re-examination of these collections, which are large and have been carefully tabulated, will produce the 'missing' components, the systematic implications of this possibly variant apparatus architecture will need to be seriously considered.

Above all, if we are to understand anything of the significance of conodonts to early evolutionary history of vertebrate skeletal, nervous, sensory, locomotory, or digestive systems, we must be able to calibrate the fossil record of the group against a rigorously defined scheme of phylogenetic relationships. The greatest barrier to this goal is a firm understanding of positional homology between the apparatuses of the major conodont groups, particularly among the most pleisiomorphic taxa. These homologies can be firmly established only through the discovery and interpretation of natural assemblages. We enter this plea to our colleagues with the hope that, together, we can realize the fundamental significance of otherwise unassuming fused clusters lying undescribed in the corners of our conodont residues.

Finally, it is surely true that a more defensible phylogenetic understanding of the conodonts will be good news for biostratigraphy, paleogeography, and paleoceanography. With a data base that is currently unrivaled among Paleozoic and Triassic fossil groups, it would be a shame if future studies failed to use and expand this resource not only to better understand the conodonts themselves but also the environments in which they lived.

ACKNOWLEDGMENTS

We thank fellow members of the Pander Society who have helped make conodontology so much fun. In particular, we thank R. J. Aldridge (Leicester), S. M. Bergström (Ohio State University), Rod Norby (Illinois Geological Survey), M. A. Purnell (Leicester), and M. P. Smith (Birmingham) for stimulating discussions through the years and/or for figures used in this contribution. Purnell also provided a thorough review of an early draft of this manuscript, which we have found very useful in revising it. Donoghue is funded by NERC postdoctoral research fellowship (GT5/99/ES/2).

REFERENCES

- AGUINALDO, A. M. A., J. M. TURBEVILLE, L. J. LINFORD, M. C. RIVERA, J. R. GAREY, R. A. RAFF, AND J. A. LAKE. 1997. Evidence for a clade of nematodes, arthropods and other moulting animals. *Nature*, 387: 489–493.
- ALDRIDGE, R. J., AND M. P. SMITH. 1993. Conodonts, p. 563–572. *In* M. J. Benton (ed.), *The Fossil Record 2*. Chapman and Hall, London.
- ALDRIDGE, R. J., AND J. N. THERON. 1993. Conodonts with preserved soft tissue from a new Upper Ordovician *Konservat-Lagerstätte*. *Journal of Micropalaeontology*, 12:113–117.
- ALDRIDGE, R. J., D. E. G. BRIGGS, E. N. K. CLARKSON, AND M. P. SMITH. 1986. The affinities of conodonts—new evidence from the Carboniferous of Edinburgh, Scotland. *Lethaia*, 19:279–291.
- ALDRIDGE, R. J., D. E. K. BRIGGS, M. P. SMITH, E. N. K. CLARKSON, AND N. D. L. CLARK. 1993. The anatomy of conodonts. *Philosophical Transactions of the Royal Society of London*, series B, 340:405–421.
- ALDRIDGE, R. J., M. A. PURNELL, S. E. GABBOTT, AND J. N. THERON. 1995. The apparatus architecture and function of *Promissum pulchrum* Kovács-Endrödy (Conodonts, Upper Ordovician) and the prioniodontid plan. *Philosophical Transactions of the Royal Society of London*, series B, 347:275–291.
- ALDRIDGE, R. J., M. P. SMITH, R. D. NORBY, AND D. E. G. BRIGGS. 1987. The architecture and function of Carboniferous polygnathacean conodont apparatuses, p. 63–75. *In* R. J. Aldridge (ed.), *Palaeobiology of conodonts*. Ellis Horwood Limited, Chichester.
- BENGTSON, S. 1976. The structure of some Middle Cambrian conodonts and the early evolution of conodont structure and function. *Lethaia*, 9: 185–206.
- BENGTSON, S. 1983. The early history of the Conodonts. *Fossils and Strata*, 15:5–19.
- BENTON, M. J. (ed.). 1993. *The Fossil Record 2*. Chapman and Hall, London.
- BENTON, M. J. 2001. Stems, nodes, crown clades, and rank-free lists: is Linnaeus dead? *Biological Reviews*, 76 (in press).
- BERGSTRÖM, S. M., AND W. C. SWEET. 1966. Conodonts from the Lexington Limestone (Middle Ordovician) of Kentucky and its lateral equivalents in Ohio and Indiana. *Bulletins of American Paleontology*, 50(229):271–441.
- BRIGGS, D. E. G., E. N. CLARKSON, AND R. J. ALDRIDGE. 1983. The conodont animal. *Lethaia*, 16:1–14.
- CLARK, D. L., W. C. SWEET, S. M. BERGSTRÖM, G. KLAPPER, R. L. AUSTIN, F. H. T. RHODES, K. J. MÜLLER, W. ZIEGLER, M. LINDSTRÖM, J. F. MILLER, AND A. G. HARRIS. 1981. Conodonts. *In* R. A. Robison, (ed.), *Treatise on Invertebrate Paleontology*, Pt. W, Supplement 2, W1–W202. Geological Society of America and University of Kansas, 202 p.
- CONWAY MORRIS, S. 1989. Conodont palaeobiology: recent progress and unsolved problems. *Terra Nova*, 1:135–150.
- DIECKWISCH, T. G. H., AND R. VAHADI. 1997. Do hagfish have teeth? *Journal of Morphology*, 232:247.
- DONOGHUE, P. C. J. 1998. Growth and patterning in the conodont skeleton. *Philosophical Transactions of the Royal Society of London*, series B, 353:633–666.
- DONOGHUE, P. C. J. 2001. Conodonts meet cladistics: recovering relationships and assessing the quality of the fossil record. *Palaeontology*, 44 (in press).
- DONOGHUE, P. C. J., P. L. FOREY, AND R. J. ALDRIDGE. 2000. Conodont affinity and chordate phylogeny. *Biological Reviews*, 75:191–251.
- DONOGHUE, P. C. J., M. A. PURNELL, AND R. J. ALDRIDGE. 1998. Conodont anatomy, chordate phylogeny and vertebrate classification. *Lethaia*, 32:211–219.
- DZIK, J. 1991. Evolution of the oral apparatuses in the conodont chordates. *Acta Palaeontologica Polonica*, 21:265–323.
- FARRIS, J. S. 1976. Phylogenetic classification of fossils with Recent species. *Systematic Zoology*, 25:271–282.
- GABBOTT, S. E., R. J. ALDRIDGE, AND J. N. THERON. 1995. A giant conodont with preserved muscle tissue from the Upper Ordovician of South Africa. *Nature*, 374:800–803.
- HINDE, G. J. 1879. On conodonts from the Chazy and Cincinnati group of the Cambro-Silurian, and from the Hamilton and Genesee-shale divisions of the Devonian in Canada and the United States. *Quarterly Journal of the Geological Society of London*, 35:351–369.
- HUCKRIEDE, R. 1958. Die Conodonten der Mediterranen Trias und ihr stratigraphischer Wert. *Paläontologische Zeitschrift*, 32:141–175.
- JANVIER, P. 1981. The phylogeny of the Craniata, with particular reference to the significance of fossil 'agnathans'. *Journal of Vertebrate Paleontology*, 1:121–159.
- JEFFERIES, R. P. S. 1986. *The Ancestry of the Vertebrates*. Cambridge Univ. Press, Cambridge, 376 pp.
- KASATKINA, A. P., AND G. I. BURYI. 1996a. On the relation of chaetognaths and conodonts. *Albertiana*, 18:21–23.
- KASATKINA, A. P., AND G. I. BURYI. 1996b. About the relationship of the Chaetognatha with conodonts. *In* J. Dzik (ed.), *Sixth European Conodont Symposium (ECOS XI)*, Abstracts, p. 27. Instytut Paleobiologii, Warszawa.

- KASATKINA, A. P., AND G. I. BURYI. 1997. Chaetodonta, a new animal superphylum and its position in animal systematics. *Doklady Biological Sciences*, 356:503–505.
- KASATKINA, A. P., AND G. I. BURYI. 1999. The position of the phyla Chaetognatha and Euconodontophylea in the classification of Metazoa. *Zoosystematica Rossica*, 8(1):21–26.
- KLAPPER, G. 1989. Frasnian species of the Late Devonian conodont genus *Ancyrognathus*. *Journal of Paleontology*, 64:998–1025.
- KLAPPER, G., AND T. FOSTER. 1993. Shape analysis of Frasnian species of the Late Devonian conodont genus *Palmatolepis*. *Paleontological Society Memoir*, 32:35 p. [issued as supplement to *Journal of Paleontology*, 67(4) July 1993.]
- KLEFFNER, M. A. 1995. A conodont- and graptolite-based Silurian chronostratigraphy. In K. O. Mann, H. R. Lane, and P. A. Scholle, (eds.), *Graphic Correlation*. SEPM Society for Sedimentary Geology, Special Publication 53:159–176.
- KOHUT, J. J. 1969. Determination, statistical analysis and interpretation of recurrent conodont groups in Middle and Upper Ordovician strata of the Cincinnati Region (Ohio, Kentucky, and Indiana). *Journal of Paleontology*, 43(2):392–412.
- KRON, K. A. 1997. Exploring alternative systems of classification. *Aliso*, 15:105–112.
- LINDSTRÖM, M. 1970. A suprageneric classification of the conodonts. *Lethaia*, 3:427–445.
- LITTLEWOOD, D. T. J., M. J. TELFORD, K. A. CLOUGH, AND K. ROHDE. 1998. Gnathostomulida—an enigmatic metazoan phylum from both morphological and molecular perspectives. *Molecular Phylogenetics and Evolution*, 9:72–79.
- MILLER, J. R. 1980. Taxonomic revisions of some Upper Cambrian and Lower Ordovician conodonts, with comments on their evolution. *University of Kansas Paleontological Contributions*, Paper 99:44 p.
- MILLER, J. R. 1984. Cambrian and earliest Ordovician conodont evolution, biofacies, and provincialism. *Geological Society of America, Special Paper* 196:43–68.
- MÜLLER, K. J. 1956. Taxonomy, nomenclature, orientation and stratigraphic evaluation of conodonts. *Journal of Paleontology*, 30:1324–1340.
- PANDER, C. H. 1856. *Monographie der fossilen Fische des silurischen Systems der Russisch-Baltischen Gouvernements*. Akademie der Wissenschaften, St. Petersburg, 1–91.
- PATTERSON, C. 1982. Morphological characters and homology. In K. A. Joysey and A. E. Friday (eds.), *Problems of Phylogenetic Reconstruction*. Systematics Association Special Volume 21:21–74. Academic Press, London.
- PRIDMORE, P. A., R. E. BARWICK, AND R. S. NICOLL. 1997. Soft anatomy and the affinities of conodonts. *Lethaia*, 29:317–328.
- PURNELL, M. A. 1995a. Large eyes and vision in conodonts. *Lethaia*, 28:187–188.
- PURNELL, M. A. 1995b. Microwear on conodont elements and macrophagy in the first vertebrates. *Nature*, 374:798–800.
- PURNELL, M. A., P. C. J. DONOGHUE, AND R. J. ALDRIDGE. 2000. Orientation and anatomical notation in conodonts. *Journal of Paleontology*, 74:113–122.
- RHODES, F. H. T. 1952. A classification of Pennsylvanian conodont assemblages. *Journal of Paleontology*, 26:886–901.
- RIEPPPEL, O. 1988. *Fundamentals of comparative biology*. Burkhäuser, Basel.
- RIGBY, J. K., JR. 1983. Conodonts and the early evolution of the vertebrates [Abstract]. *Geological Society of America, Abstracts with Programs*, 15(6):671.
- ROMER, A. S. 1933. Eurypterid influence on vertebrate history. *Science*, 78:114–117.
- SCHMIDT, H. 1934. Conodonten-Funde in ursprünglichem Zusammenhang. *Paläontologische Zeitschrift*, 16:76–85.
- SCOTT, H. W. 1934. The zoological relationships of the conodonts. *Journal of Paleontology*, 8:448–455.
- SMITH, A. B. 1998. Adequacy of the fossil record. *Nature debates* [online]. <http://helix.nature.com/debates/index.html>.
- SMITH, A. B. 2000. Stratigraphy in phylogeny reconstruction. *Journal of Paleontology*, 74:763–766.
- STAUFFER, C. R. 1930. Conodonts from the Decorah Shale. *Journal of Paleontology*, 4:121–128.
- SWEET, W. C. 1970. Uppermost Permian and Lower Triassic conodonts of the Salt Range and Trans-Indus ranges, West Pakistan. In B. Kummel and C. Teichert (eds.), *Stratigraphic Boundary Problems: Permian and Triassic of West Pakistan*. Department of Geology, University of Kansas, Special Publication 4:207–275.
- SWEET, W. C. 1988. The Conodonta: Morphology, Taxonomy, Paleogeology, and evolutionary history of a long-extinct animal phylum. *Oxford Monographs on Geology and Geophysics*, No. 10, 212 p. Clarendon Press, New York, Oxford.
- SWEET, W. C. 1989. A quantitative conodont biostratigraphy for the Lower Triassic. *Senckenbergiana lethaea*, 69:253–273.
- SWEET, W. C. 1995. Graphic assembly of a conodont-based composite standard for the Ordovician System of North America. In K. O. Mann, H. R. Lane, and P. A. Scholle (eds.), *Graphic Correlation*. SEPM Society for Sedimentary Geology, Special Publication 53:139–150.
- SWEET, W. C., AND S. M. BERGSTRÖM. 1969. The generic concept in conodont taxonomy. *Proceedings North American Paleontological Convention*, 1:29–42.
- SWEET, W. C., C. A. TURCO, E. WARNER, JR., AND L. WILLKIE. 1959. The American Upper Ordovician standard. I, Eden conodonts from the Cincinnati Region of Ohio and Kentucky. *Journal of Paleontology*, 33:1029–1068.
- SZANIAWSKI, H. 1982. Chaetognath grasping spines recognized among Cambrian protoconodonts. *Journal of Paleontology*, 56:806–810.
- SZANIAWSKI, H. 1987. Preliminary structural comparisons of protoconodont, paraconodonts, and euconodont elements, p. 35–47. In R. J. Aldridge (ed.), *Palaeobiology of Conodonts*. Ellis Horwood, Chichester.
- ULRICH, E. O., AND R. S. BASSLER. 1926. A classification of the toothlike fossils, conodonts, with descriptions of American Devonian and Mississippian species. *United States National Museum Proceedings*, 68, Art. 12:63 p.
- VON BITTER, P. H. 1972. Environmental control of conodont distribution in the Shawnee Group (Upper Pennsylvanian) of eastern Kansas. *University of Kansas Paleontological Contributions*, 59:105 p.
- WALLISER, O. H. 1964. Conodonten des Silurs. *Abhandlungen der Hessischen Landesamtes Bodenforschung*, 41:1–106.
- WEBERS, G. F. 1966. The Middle and Upper Ordovician conodont faunas of Minnesota. *Minnesota Geological Survey Special Publication Series*, 4:123 p.
- ZIEGLER, W., AND K. WEDDIGE. 1998. Zur Biologie, Taxonomie und Chronologie der Conodonten. *Paläontologische Zeitschrift*, 73:1–38.