

ORIENTATION AND ANATOMICAL NOTATION IN CONODONTS

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ABSTRACT—All aspects of conodont paleontology rely on the identification and description of homologous anatomical units or elements. But the current schemes of anatomical notation and terms for orientation were formulated at a time when little was known of conodont anatomy or skeletal architecture, resulting in some confusion and difficulties in their application. With improving knowledge of conodonts, these problems are becoming increasingly acute.

In an attempt to address current problems, we introduce new terms for orientation in conodonts and their elements, and a modified scheme of anatomical notation. The principal axes of the conodont body are identified as rostrocaudal, dorsoventral, and mediolateral, with opposite lateral sides designated dextral and sinistral. Anatomical notation is defined according to topological relationships between elements with reference to the principal axes of the body and takes the form of letters with numeric subscripts (e.g., P₁, P₂, S₀–S₄). The ozarkodinid apparatus serves as a standard, but the P_n–S_n scheme can be applied rigorously to all taxa that are known from natural assemblages or where an hypothesis of topological homology can be inferred from secondary morphological criteria.

INTRODUCTION

ALL ASPECTS of conodont paleontology rely ultimately on the description of elements, and this requires a means of identifying direction and communicating the relative disposition of morphological features. Equally important is a scheme for identifying the various elements of the conodont apparatus. Such schemes allow the formulation and testing of hypotheses of homology, the development of multielement taxonomy, and the analysis of phylogenies and evolutionary patterns. But the current systems of terminology for orientation and anatomical notation were formulated when little was known about conodont anatomy and biology. With the discovery and interpretation of conodonts with preserved soft-tissues (e.g., Aldridge et al., 1993; Gabbott et al., 1995), we now have direct evidence of the orientation of the feeding apparatus within animals of different taxa. From detailed analysis of natural assemblages, the architecture of the apparatus in ozarkodinids, prioniodontids, and prioniodinids is now known in some detail (Aldridge et al., 1987, 1995; Purnell and Donoghue, 1997, 1998; Repetski et al., 1998; Purnell and von Bitter, 1996). These new data have shown that several historical assumptions were in error, and continuing traditional usage of terms is misleading for comparisons within the conodonts, and between conodonts and other animals. In this contribution we propose a new terminology for element orientation and anatomical notation based on the biological information now known.

Although this paper is aimed specifically at current problems in conodonts, we cannot avoid a brief discussion of general terminology. Conodonts are not unique in having evolved a complex and sometimes contradictory terminology. Aspects of anatomical nomenclature in birds, for example, have been somewhat confused by different authors applying different names to the same structure, or the same name to different structures. Rowe (1986) discussed this problem in detail. His review of the literature on avian anatomical nomenclature concluded that anatomical terminology should be based on homology and that prevailing terms founded on inaccurate anatomy or incorrect hypotheses of homology should be replaced (Rowe, 1986, p. 343, and references therein). But what is homology? The meaning of homology is the subject of continuing debate (see, e.g., Hall, 1994; Tautz, 1998), and a precise definition remains elusive. For the purposes of this paper we adopt an operational concept of

homology as an hypothesis of similarity that is based on topological relations and which contains potential phylogenetic information (see Rieppel, 1994 for discussion). Topology refers to the numbers of, and the relative spatial relationships between, recognizable anatomical units. Similarity, in this context, does not mean morphological similarity of the units under consideration. We should also point out that homology is hierarchical, operating at different levels including genes, development, and structure. It is also contextual as illustrated by the classic example of batwings and birdwings; these structures are homologous as tetrapod forelimbs but not as wings. In this paper we deal only with homology of whole elements within the conodont apparatus (not homology of the apparatus, nor homology of parts of elements).

CURRENT PROBLEMS

Difficulties with conventions of orientation.—The basic terms of orientation currently applied to conodont elements include anterior, posterior, oral, aboral, upper, lower, inner, outer, left, right, sinistral, and dextral. These terms have universal biological meanings, but as applied to conodont elements they have distinct and different meanings. The orientation of conodont elements is currently determined according to arbitrary morphological criteria, based on a datum defined as “an imaginary surface that includes the apexes of the cusp and basal cavity” (Sweet, 1981a, p. W6). In most cases the concave side of the cusp within this plane is “posterior,” the tip of the cavity is “up,” and the upper margin of the element’s base or posterior process indicates “horizontal” (for more precise definitions see Sweet, 1981a, p. W6–W9). This convention has a number of potential problems (see, e.g., Müller, 1956 for discussion), but until now the scheme has persisted without causing serious difficulty. This is primarily because terms can generally be applied consistently; because comparisons have been made only between different conodont elements, not between conodonts and other organisms; and because there has been little need to describe the orientation of elements in life. However, conodonts no longer exist as a discrete group outside comparative biology, and with increasing knowledge of conodont biology the problems associated with conventional arbitrary terminology have become more acute. Purnell and Donoghue (1998, p. 89) recently noted that “In no apparatuses for which the architecture is known do . . . conventional designations coincide fully or consistently with true biological orientations.” The evidence that the P elements of the ozarkodinid apparatus, for example, were oriented with their “posterior” process directed dorsally is now overwhelming. Dzik (1994) has also expressed similar concerns,

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but his proposal for a biological system of orientation was derived from an hypothesis of apparatus architecture (Dzik, 1991) that is contradicted by natural assemblages preserving intact apparatuses (Purnell and Donoghue, 1998). Consequently some of Dzik's terminology for element orientation is incorrect. Jeppsson (1997) has also proposed new biological terms for orientation, but his mesial-distal terminology for panderodontids is also based on an hypothesis of element orientation that is contradicted by natural assemblages; he identifies the furrow on panderodontid elements as distal, but in reconstructions of the *Panderodus* apparatus (see Smith et al., 1987; Sansom et al., 1994) it faces forwards, not distally. Nevertheless, we agree with Dzik and Jeppsson that our knowledge of conodont anatomy and apparatus architecture has reached the point where the use of an arbitrary scheme can no longer be justified, and in certain circumstances the use of biological terms cannot be avoided (see e.g., Donoghue and Purnell, 1999a, 1999b).

Difficulties with anatomical notation.—Anatomical notation in conodonts takes on particular significance because of its importance in disentangling biologically-valid "multielement taxonomy" from the taxonomically illegal practice of erecting discrete component elements as taxa without regard for the fact that several different "taxa" came from a single individual. It is no coincidence that the advent and proliferation of multielement taxonomy in the 1960s and 1970s (e.g., Bergström and Sweet, 1966; Webers, 1966; Jeppsson, 1971; Klapper and Philip, 1971) was accompanied by the development of several schemes of anatomical notation designed to identify and communicate which elements comprised multielement taxa and, usually by inference, what was homologous with what (e.g., Klapper and Phillip, 1971; Jeppsson, 1971; Sweet and Schönlaub, 1975; Barnes et al., 1979; for a review see Sweet, 1981b). All of these schemes derived the criteria for the application of a notation, and in some cases the notation itself, from the morphology of the elements. Sweet (1981b, p. W6) criticized them all on these grounds, because they did not clearly distinguish element form from apparatus location. He proposed a scheme modified from that of Sweet and Schönlaub (1975), in which "major positions in a common type of skeletal apparatus are designated by letters" (our emphasis). However, although Sweet's P, M, S scheme was intended to be a locational notation, at the time it was erected knowledge of apparatus architecture (i.e., the actual positions of elements) was almost nonexistent, and Sweet's aim of separating location from element morphology could not be realized. There was simply no way to define the principal "positions" except by reference to the morphology of the elements that usually occupied them. Furthermore, although one of the reasons he rejected previous schemes was that they obscured homologies, Sweet (1981b, p. W19) added the caveat that identification of elements in different taxa as occupants of the same position in his scheme "does not (or should not) imply that [they] are necessarily homologous." He continued, however, that "with time and increased understanding . . . it is hoped that the connotation of homology can be attached to locational notation." We are now in the period of transition that Sweet anticipated; the problem is that the same notation is now used differently in different contexts and by different authors, sometimes to indicate homology, other times not.

S element notation exemplifies this problem. Sweet (1981b) recognized only three major positions in the S series (Sa, Sb, Sc), the occupants of which were thought to form a transition series of increasing asymmetry away from the Sa. He realized that "there may be more than three morphologically distinct components of the S series and, to describe and locate them, it

may be necessary to invent intermediate categories such as Sa-b or Sb-c" (Sweet, 1988, p. 25), but S notation is applied inconsistently and can be confusing, with the same term having different meanings in different contexts. A number of authors (e.g., Aldridge et al., 1987; Nicoll, 1985, 1987) have applied the notation "Sd" to the element that is intermediate in location (but not symmetry) between the Sa and the Sb positions. According to Sweet (1981b, 1988), however, "Sd" refers to an axial position occupied by a quadriramate element and should not be applied to ozarkodinids (Sweet, 1988; Over, 1992). Purnell and Donoghue (1998) suggested that the four lateral S positions in ozarkodinids be identified as Sb₁, Sb₂, Sc₁, and Sc₂ (see also Aldridge et al., 1995, fig. 1), but this is not without difficulties. The architectures of the S arrays in ozarkodinids and in the prionodontid *Promissum pulchrum* are known in detail from natural assemblages, and both contain the same number of elements in the same relative positions (Aldridge et al., 1995; Purnell and Donoghue, 1998). But despite the clear homologies (see below) Aldridge et al. (1995) labeled those of *Promissum* Sb₁, Sd, Sb₂, Sc rather than Sb₁, Sb₂, Sc₁, Sc₂. This was explicitly to avoid applying the term "Sb₂" to quadriramate elements, which on morphological grounds are widely designated as Sd elements in the literature. Thus the Sd element of *Promissum* is homologous with the Sb₂ in ozarkodinids, and the Sb₂ of *Promissum* is homologous with the ozarkodinid Sc₁. This is not a satisfactory situation.

Similar problems are encountered if Sweet's P, M, S notation is applied to apparatuses composed of coniform elements or scalelike forms such as *Fungulodus*. Ji and Ziegler (1992), for example, identified Pa, Pb, and M elements of *F. rotundus* and *F. centrodus*, but they did not discuss homologies. It is not clear if their use of notation should be taken to imply homologies of the elements, either between these two taxa or with the morphologically-complex elements in better known apparatuses.

Except for the symmetrical axial element of the S array, morphology alone is not a reliable guide to element position. If it is used to infer position by comparison with natural assemblages, reliability generally declines as element morphology becomes increasingly different from that of a typical derived ozarkodinid such as *Ozarkodina* or *Idiognathodus*. Thus, the discovery of a natural assemblage of *Kladognathus*, for example, indicated that the occupants of P positions in the assemblage had been previously identified as Sb and Sd elements (Purnell, 1993). Ideally, recognition of homologous structures and the application of anatomical notation must be based on evidence of topology, and this cannot be deduced from morphology (contra Nicoll, 1995). Only in the absence of topological data should morphology be used to infer indirectly a weaker hypothesis of homology (see below). One of the principal difficulties with the current terminology is that morphology and topology cannot be disentangled; they are inextricably linked in the definitions of terms and in the process of their application. Our knowledge of apparatus architecture in different groups of conodonts has now reached the point where the ultimate objective of previous notational schemes (e.g., Barnes et al., 1979; Sweet, 1981b) can be realized: we are now able to propose a scheme in which notation is defined and can be applied on the basis of topology, independently of element morphology.

NEW TERMS FOR ORIENTATION AND ANATOMICAL NOTATION

Orientation.—The group of conodonts for which we have the best evidence of absolute orientation in three dimensions is the Ozarkodinida. This evidence comes from fossils preserving the apparatus in different orientations of in situ collapse within the outline of the conodont body (Briggs et al., 1983; Aldridge et al., 1986, 1993; Purnell and Donoghue, 1997, 1998). Figures 1–3

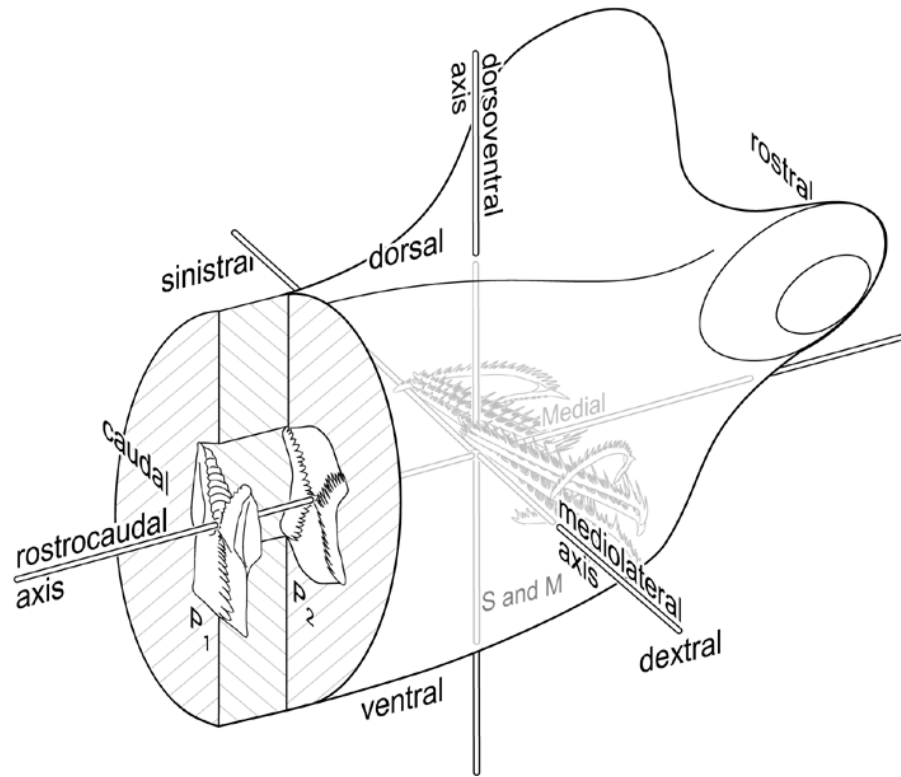


FIGURE 1—Biological orientation in conodonts; the new terminology as applied to the head and apparatus of an ozarkodinid conodont.

provide a graphical summary of the terminology that we propose and Table 1 provides a glossary of the basic terms. The terms “anterior” and “posterior” are not used because their conventional meaning in conodonts does not coincide consistently with true orientation (see Table 2). Rather than introduce potentially confusing new definitions for these terms, we use “rostral” and “caudal” to indicate front and rear respectively. Both terms are in common biological usage. The terms “dorsal” and “ventral” are not part of conventional conodont orientation, so no confusion arises. “Sinistral” and “dextral” (and “left” and “right”) have the same meaning according to both conodont convention and biology; use of the Latin-derived terms “sinistral” and “dextral” maximizes consistency with the other terms for orientation. Thus, use of these six basic biological terms ensures minimal overlap between conventional and biological terminology and should result in no ambiguity in the way an author describes orientation. Table 2 and Figure 4 indicate how the new biological terms relate to the conventional, arbitrary system.

Anatomical notation.—With few exceptions (e.g., Dzik, 1991, 1994) Sweet’s P, M, S scheme is now universally applied to conodonts with apparatuses composed of elements with complex multidenticulate morphology (i.e., taxa assigned to the Orders Ozarkodinida, Prioniodinida, and Prioniodontida), and some authors also apply it to apparatuses composed entirely of elements of coniform morphology (e.g., Barrick, 1977; Nicoll, 1994; Löfgren, 1997). Because this scheme represents such universal currency among conodont workers, to propose its outright replacement would probably be a backward step. Similarly, redefinition of terms such as “Pa,” “Pb,” and “Sa” would simply perpetuate and possibly exacerbate the current state of confusion, with the same terms of notation used to mean different things by different authors. We propose a new notation that retains Sweet’s useful tripartite division of the apparatus, while introducing a firm locational (i.e., topological) foundation based on apparatus

architecture (Fig. 2). In this scheme, position refers to the position of an element’s cusp; S positions form a symmetrical rostral array across the sagittal plane; M positions are not part of this array, generally lying rostral, lateral, and/or dorsal to the outermost S position; P positions lie caudal to the S positions, usually somewhat more dorsal. Within these groups, positions are identified by numeric subscripts (P_n - S_n), the S positions are numbered from the median axis outwards (medial position = S_0); P positions are numbered from caudal to rostral (caudal element = P_1) (see Figs. 2, 3). The definition of position is completely independent of element morphology. Where necessary or desirable, elements from the sinistral and dextral sides of the apparatus can be differentiated using superscripts (e.g., S_1^d = the first element lateral to the medial element on the dextral side of the apparatus).

Sweet (1981b, p. W20) was clear that the Pa, Pb, Sa-Sc scheme was “designed to be a vehicle for expressing analogy . . . no general system in which locational notation expresses both homology and analogy is apparent or suggested.” We propose that use of the terms “Pa,” “Pb” etc. be limited to expressing analogy in the way Sweet seems to have intended, as there is still a need for this scheme where homologies are not known. P_n - S_n terminology is topologically defined with the express purpose of indicating homology, and in ideal situations element homologies can be recognized from direct topological evidence (i.e., natural assemblages). For most taxa, however, this evidence is unavailable and *application* of P_n - S_n terms must be based on an hypothesis of homology inferred from indirect morphological evidence, i.e., by comparison of element morphology with the morphology of elements in an apparatus that is known from natural assemblage material. The closer the similarities between the apparatuses being compared and the morphology of their elements, the stronger the hypothesis of homology. Thus, in practice, hypotheses of homology will generally become

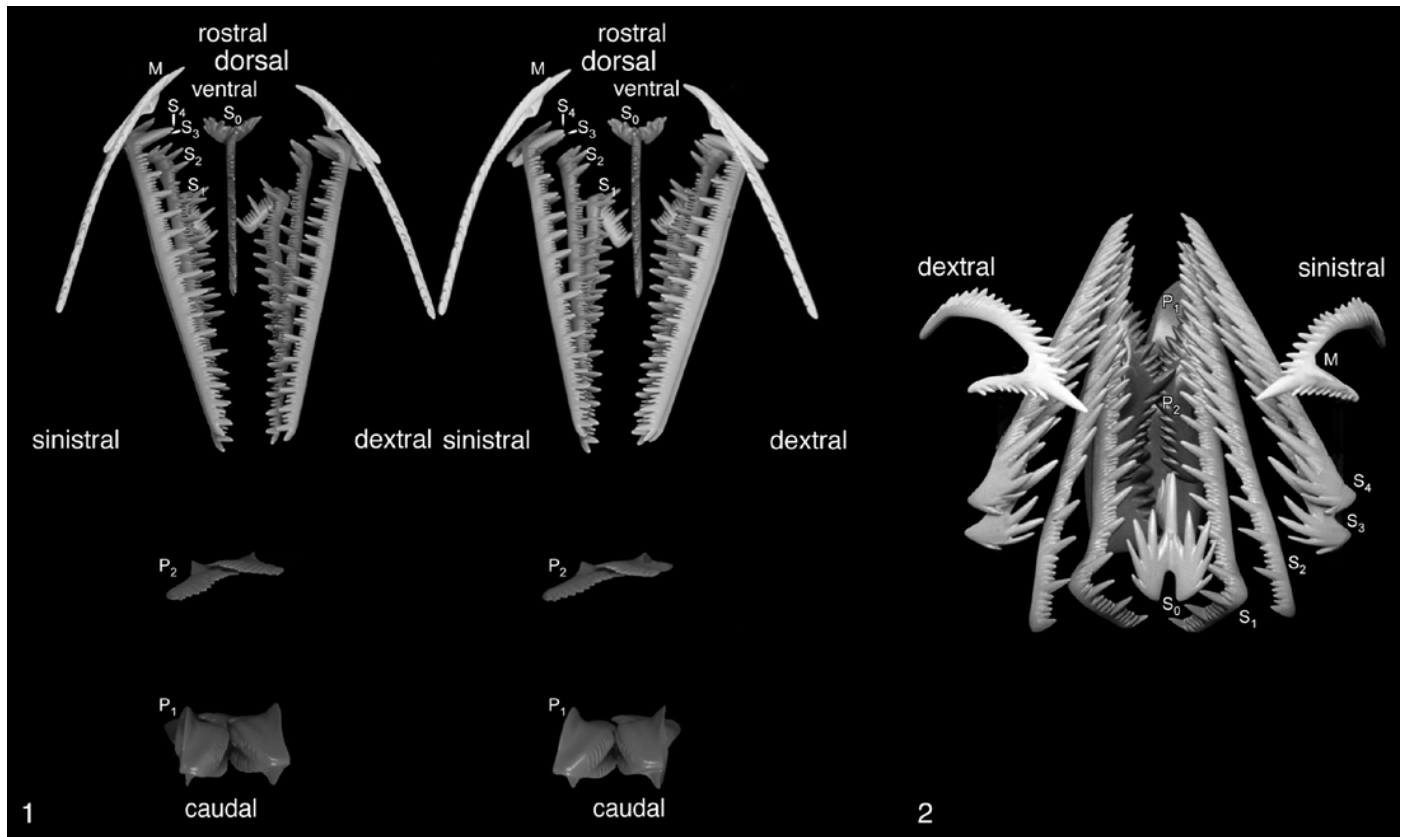


FIGURE 2—Biological orientation and topological anatomical notation and orientation. 1, Stereo pair of the ozarkodinid apparatus viewed from dorsal to ventral. 2, The ozarkodinid apparatus viewed from rostral to caudal.

weaker and less direct with increasing taxonomic distance between a species and the closest comparable taxon for which homologies are known directly. Morphological evidence alone will not always allow precise position to be identified; e.g., in some taxa occupants of S₃ and S₄ positions are morphologically similar and it may only be possible to identify them as S_{3/4}.

The new notation is based primarily on the topology of the

ozarkodinid apparatus and we propose that the ozarkodinid apparatus be taken as the standard against which to compare other apparatuses (cf. Dzik, 1991). Ideally, it would be better to use a more plesiomorphic taxon, but several factors support the use of ozarkodinids: the ozarkodinid apparatus is known from more specimens representing more taxa than any other group of conodonts; the architecture of the apparatus is known in precise

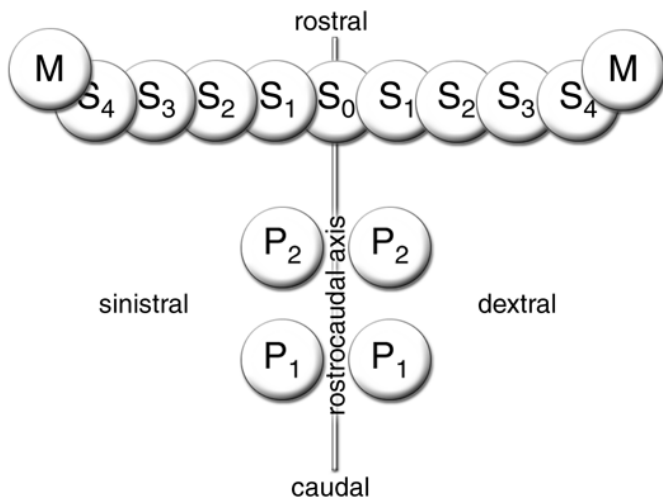


FIGURE 3—Schematic map of the relative positions of elements in the topological scheme of notation (cf. Sweet, 1981b, fig. 13; 1988, fig. 2.10).

TABLE 1—Glossary of terms for basic biological orientation in conodonts.

Useful compound terms can also be formed, such as medioventral (on the midline of the ventral surface), dorsolateral (relating to the back and side), and dorsocaudal (to or towards the dorsal surface and the caudal end). For the derivation of terms see, for example, Brown (1956).

Term	Definition
rostral	pertaining to or nearer front or head end (rostrad: directed towards rostral end)
caudal	pertaining to or nearer rear or tail end (caudad: directed towards end)
dorsal	pertaining to or nearer back or upper surface (dorsad: directed towards dorsal)
ventral	pertaining to or nearer belly or undersurface (ventrad: directed towards ventral)
medial	pertaining to or nearer sagittal plane (mediad: directed towards sagittal plane)
lateral	pertaining to or nearer side (laterad: directed towards side, away from medial axis)
adaxial	pertaining to or nearer rostrocaudal axis
abaxial	away from rostrocaudal axis
oral	pertaining to or nearer mouth or oropharyngeal cavity; corresponds to denticulated functional surface of element
aboral	away from or opposite to mouth or oropharyngeal cavity; corresponds to element surface bearing pit or cavity occupied in life by "aboral body" (=basal body)

TABLE 2—Comparison between conventional terms for orientation, our suggestion for identifying relative disposition of process on elements without implications of *in vivo* orientation (see Figs. 4, 6), and true biological orientation in ozarkodinid conodonts (Figs. 1, 2). Terminology can also be applied to other conodonts as discussed in the text. Strictly speaking S_1 - S_4 elements in the ozarkodinid apparatus are oriented obliquely with their long axis dorsocaudad. Where biological orientation could be expressed using two terms the less ambiguous term is emboldened. Note that the conventional meanings of oral and aboral correspond to their meaning in biological usage. Similarly, elements designated dextral/right and sinistral/left according to conventional criteria of element curvature were actually located on the dextral and sinistral sides of the body respectively.

Element position	Conventional term	Disposition relative to cusp	True biological orientation
P	anterior (based on cusp and aboral cavity)	"anterior"	ventral
	posterior (based on cusp and aboral cavity)	"posterior"	dorsal
	inner (based on curvature)	"inner"	caudal
	outer (based on curvature)	"outer"	rostral
	upper		oral or adaxial
S	lower		aboral or abaxial
	anterior (based on cusp and aboral cavity)	"anterior"	rostral
	posterior (based on cusp and aboral cavity)	"posterior"	caudal
	inner (based on curvature)	"inner"	adaxial or medial or inner
	outer (based on curvature)	"outer"	abaxial or lateral or outer
M	upper		oral or dorsal
	lower		aboral or ventral
	anterior (based on cusp and aboral cavity)	"anterior"	abaxial or lateral
	posterior (based on cusp and aboral cavity)	"posterior"	adaxial or medial
	inner (based on curvature)	"inner"	dorsal
	outer (based on curvature)	"outer"	ventral
	upper		rostral
	lower		caudal

detail, and the available evidence suggests that architecture did not vary significantly among ozarkodinids (Purnell and Donoghue, 1998); the ozarkodinids are the only group for which we have a number of fossils preserving the apparatus *in situ* within the outlines of the body, providing unequivocal evidence of both relative and absolute spatial relationships. Further support comes from the historical derivation of the P, M, S scheme: it was first applied to *Oulodus*, a prioniodinid, but it was based on the recognition of principal categories of elements in natural assemblages (Sweet, 1988); given the material available at the time the scheme was developed, it must have been *derived* primarily from the arrangement of elements in ozarkodinid assemblages (Purnell, 1993).

APPLICATION OF NEW TERMS

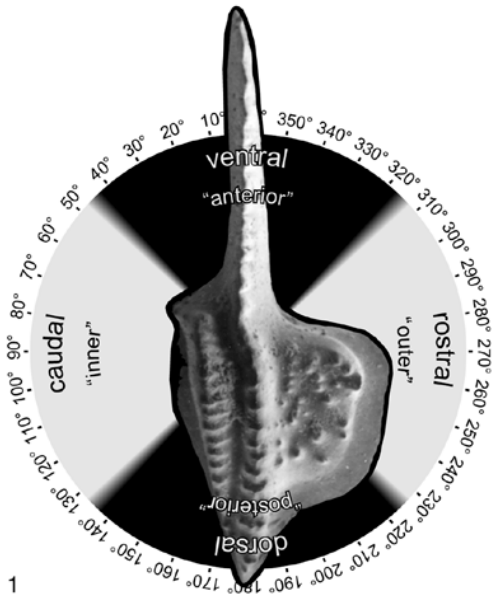
Orientation and notation in prioniodinids.—Natural assemblages of taxa assigned to the Prioniodinida (*sensu* Sweet, 1988) are much scarcer than those of ozarkodinids: they are known from a single *Hibbardella angulata* from the Upper Devonian Gogo Formation of Western Australia (Nicoll, 1977), an incomplete *Idioprioniodus* from the lower Namurian of Germany (Schmidt and Müller, 1964; Purnell and von Bitter, 1996), a few *Neogondolella* from the Middle Triassic of Switzerland (Rieber, 1980; Orchard and Rieber, 1996; Orchard, 1998), and a *Kladognathus* from the Mississippian of the USA (Purnell, 1993). There are also a number of fused clusters known (e.g., Lange, 1968; Ramovš, 1977, 1978; Mietto, 1982; Igo, 1988) but most of these are incomplete and have yet to be interpreted architecturally. The fecal assemblages of *Gondolella* described by von Bitter and Merrill (1998) preserve little if any direct evidence of apparatus topology (von Bitter and Merrill, 1998).

The precise three-dimensional architecture of the prioniodinid apparatus has yet to be reconstructed, but the data provide strong evidence that it was essentially the same as that of ozarkodinids (Purnell and von Bitter, 1996). None of the natural assemblages of prioniodinid taxa preserves any traces of soft tissues that could provide direct evidence of *in vivo* orientation, but given the detailed similarities between prioniodinid and ozarkodinid apparatuses it would be very surprising if their position and orientation were significantly different. Thus the biological terms for orientation can be applied to prioniodinid taxa with a high degree of confidence.

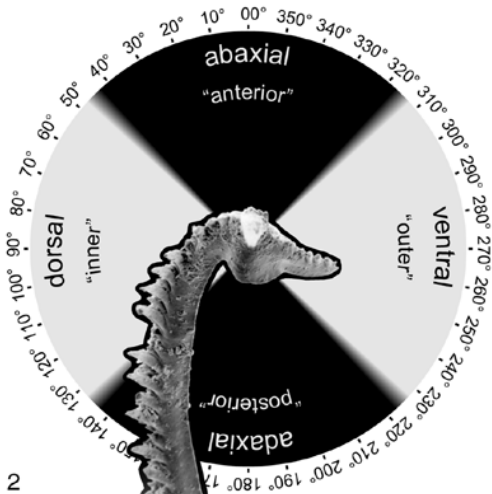
Application of the new anatomical notation relies on recognition of homologies with ozarkodinids. The available data from natural assemblages indicate that the apparatuses of *Hibbardella* and *Kladognathus* were arranged according to the same basic skeletal plan as that of ozarkodinids (Purnell, 1993), and the same is true of *Idioprioniodus* (Purnell and von Bitter, 1996) and *Neogondolella* (Orchard and Rieber, 1996; Orchard, 1998). Thus the P_n - S_n notation can be applied with some confidence to prioniodinids, even though the morphology of the occupants of some of the 15 positions in the apparatus is completely different from the morphology of those in ozarkodinid apparatuses.

Orientation and notation in prioniodontids.—Natural assemblages of taxa assigned to the Prioniodontida now number in excess of 400, but almost all are of *Promissum pulchrum*. Consequently, the architecture of the apparatus of *Promissum* is known with a high degree of confidence. Moreover, *Promissum pulchrum* not only furnishes evidence for a well-constrained model of apparatus architecture (Aldridge et al., 1995) but also unequivocal direct evidence for absolute orientation in three dimensions: a single specimen preserves traces of the eyes and trunk with the apparatus (Gabbott et al., 1995) and numerous specimens preserve the apparatus with remains of eyes (Aldridge and Theron, 1993). These specimens indicate that, although the angular relationships between the long axes of the elements and the rostrocaudal axis of the animal were a little different from those in ozarkodinids (cf. Aldridge et al., 1995), the S elements were oriented with their cusps rostral, and denticles directed obliquely dorsal (Fig. 5). The extent to which apparatuses of other prioniodontids reflect the architecture of *Promissum* is, however, uncertain. Prioniodontid assemblages from the Ordovician of Australia (Nowlan, 1993; Stewart, 1995) are probably fecal (Stewart, 1995; Purnell and Donoghue, 1998), and provide no evidence for orientation. Preliminary work on natural assemblages of *Phragmodus inflexus*, however, indicates that other taxa currently assigned to the prioniodontids bore an apparatus which, in terms of architecture, was very similar to ozarkodinid apparatuses (Repetski et al., 1998). This evidence combined with that from *Promissum* provides strong support for application of the same biological terms for orientation.

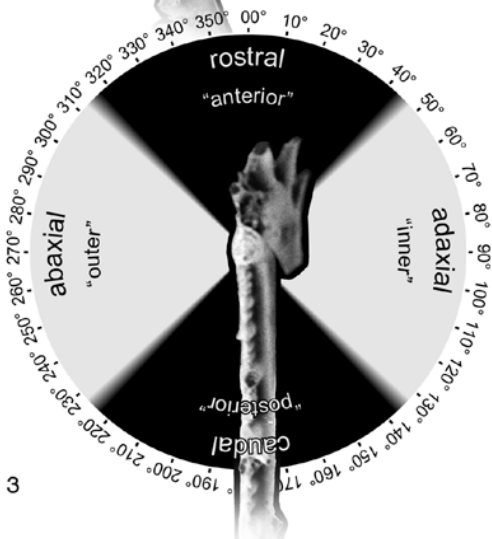
Topological comparisons between the apparatuses of *Promissum pulchrum* and ozarkodinids indicate a number of homologies (Aldridge et al., 1995; Purnell and Donoghue, 1998). Anatomical notation can therefore be applied to the apparatus of



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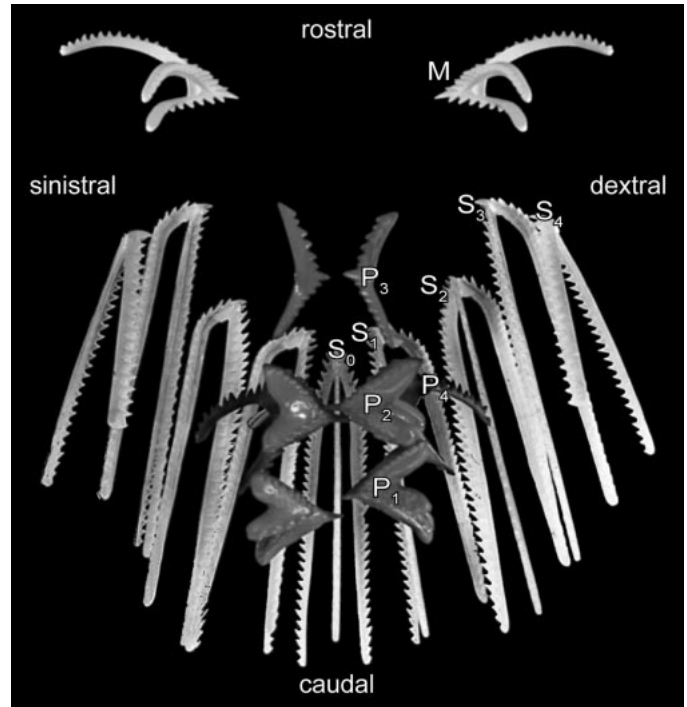


FIGURE 5—Notation applied to the apparatus of *Promissum pulchrum* (viewed from dorsal to ventral).

Promissum as indicated in Figure 5; however, *Promissum* bore more P elements than ozarkodinids, so homologies between the P elements of *Promissum* and those of ozarkodinids are not certain. Figure 5 follows the hypothesis of homology advocated by Aldridge et al. (1995), which was based primarily on element orientation. However, it is also possible that the two pairs of caudal pastinate platform elements in *Promissum* are serial homologues, arising by duplication of the P₁ element of an hypothetical ancestor. Determining which of these hypotheses is correct is a problem of iterative or serial homology (see, e.g., Roth, 1991) that cannot be resolved using topological criteria alone. Tests based on additional evidence derived from developmental/ontogenetic or phylogenetic analysis may overturn the current hypothesis of homology.

The architecture of the *Promissum* apparatus is probably typical of the family Balognathidae (Aldridge et al., 1995), but the question remains of the extent to which the skeletal plan of *Promissum* represents a standard for the prioniodontids. Fecal assemblages of other prioniodontid taxa (Nowlan, 1993; Stewart,

FIGURE 4—Comparison of biological orientation in ozarkodinid conodonts and conventional terms for orientation. Conventional terms are surrounded by quotation marks to indicate that they show the disposition of processes relative to the conventional, arbitrary datum (i.e., the plane that includes the apices of the cusp and basal cavity defines the "anterior-posterior" datum, the 0–180° plane) not in vivo orientation. All elements are *Gnathodus bilineatus*. 1, P₁ element (Leicester University Specimen LEIUG 114246); 2, M element, (Natural History Museum (London) specimen PM X 3076); 3, S₄ element, (specimen PM X 3077); all illustrated in apical view, "anterior" towards top of page. Note that the M element process identified as "inner" by strict application of conventional criteria for orientation is often mistakenly described as the "posterior" process.

1995) suggest that the apparatuses of these taxa had fewer elements (Stewart, personal commun., 1996; personal observation) and may have been less complex than that of *Promissum*. Natural assemblages of *Phragmodus inflexus* support this hypothesis (Repetski et al., 1998); the topology of the *Phragmodus* apparatus does not differ significantly from that of ozarkodinids and the P_n - S_n notation can be applied without equivocation.

Orientation and notation in other conodonts.—Among taxa that bore an apparatus composed of essentially coniform elements, there is direct evidence for orientation in *Panderodus* alone. The architecture of the apparatus of *Panderodus* was reconstructed by Smith et al. (1987) and Sansom et al. (1994), and the soft tissue traces from the Brandon Bridge Formation of Waukesha, Wisconsin indicate the approximate orientation of the elements relative to the rostrocaudal and mediolateral axes. Dorsal and ventral, however, cannot be determined. There is no other evidence for orientation in apparatuses of coniform elements and it would thus be premature to apply any biological terminology to taxa other than close relatives of *Panderodus*. Morphology alone cannot be used as a reliable guide to life orientation, and until more biological constraints are in place, it may be better to describe elements using a system which identifies the position of morphological features relative to cusp curvature without any implications (intended or otherwise) for in vivo orientation; such a system is described below.

Notation in coniform taxa is also problematic. Several authorities apply Sweet's P, M, S notation to apparatuses composed entirely of elements of coniform morphology (e.g., Barrick, 1977; Nicoll, 1994; Löfgren, 1997), but we are unaware of any topological evidence upon which to base hypotheses of homology. Sansom et al. (1994) introduced a new locational notation for coniform conodonts based on the spatial differentiation of the elements in their reconstructed apparatus, but due to the paucity of natural assemblages of coniform taxa they were forced to rely heavily on morphological criteria in applying their notation beyond *Panderodus*. They recognized the value of identifying homologies between the panderodontid apparatus and the apparatuses of conodonts with more complex element morphology, but it was precisely because such homologies could not be recognized that they introduced their new notational scheme. Purnell and Donoghue (1998) suggested that their model of the ozarkodinid apparatus reduced some of the topological differences between *Panderodus* and ozarkodinids, but we concur with Sansom et al. (1994) that it would be premature to apply a notation designed to express homologies with ozarkodinids to *Panderodus*, or indeed to any apparatus composed of coniform elements. Leslie's (1997) scheme of element notation using numeric subscripts (applied to fused clusters of *Belodella*) was intended to identify morphological categories of elements without implying homology. This contrasts directly with the P_n - S_n scheme we are proposing, the purpose of which is to identify homologies. If the Pa, Pb, Sa-Sc terminology is used as Sweet (1981b, p. W19) recommended (i.e., to indicate analogy but not firm topological homology), then it can express what Sansom et al. (1994) and Leslie (1997) intended, and provides a means of comparing elements in different taxa without indicating homology with better known taxa.

IMPLICATIONS AND ADVANTAGES

Orientation and the description of element morphology.—The new terms for orientation also have implications for other descriptive terms applied to conodont elements. In particular the widely-used shape categories (such as "carminate," "angulate," "dolabrate," and "bipennate;" see Sweet, 1981b, p. W6-W16, 1981a, p. W60-W67) are defined on the basis of the numbers and the orientation (according to convention) of processes. To

translate conventional aspects of description into biological orientations would probably cause more problems than it would solve. For example, in many prioniodinid apparatuses, occupants of some S positions are morphologically similar to the occupants of P positions; both would be considered digyrate. Yet the orientation of these elements in the apparatus is markedly different, with the "posterior" process dorsal on the elements in P positions and approximately caudal in the S positions. A scheme of biological orientation also begs the question of how element morphology is to be described if position and orientation are unknown (see above); application of strictly biological terminology would be speculative and misleading, suggesting homologies between elements where none exists. In such cases it would be useful to have some way of indicating the relative disposition of morphological features without using terminology that implies in vivo orientation of the element. In some respects, the introduction of new, unambiguous terms would be the best solution, but this is probably impracticable. A more pragmatic solution is to use the conventional terms but to enclose them within quotation marks to indicate that they are being used to indicate arbitrary designations, not biological orientation. Thus, "anterior," "posterior," "inner," and "outer" are defined according to the current arbitrary scheme (i.e., the plane that intersects the apexes of the cusp and basal cavity defines the "anterior-posterior" datum) (see Figs. 4, 6). This approach reduces ambiguity without introducing additional cumbersome nomenclature and provides a convenient solution to the problems of shape categories and elements of unknown orientation. However, where true element orientation is known or can be inferred by direct comparison with natural assemblages, biological terms that carry the full weight of topological homology provide a better means of description (see Fig. 4). The Appendix includes illustrative examples of systematic descriptions of elements using the terminological conventions we propose.

Symmetry transition and notation.—The concept of the "symmetry-transition series" is based on an hypothesis of a progressive increase in asymmetry away from the axial element of the S array, but in no case where articulated fossil material provides direct evidence does symmetry transition occur. Symmetry transition has certainly been invaluable as a method for identifying possible occupants of S positions in collections of disarticulated elements, but it fails as a guide to their position in the S array. Symmetry transition cannot be taken to have any significance for element topology or homology; it cannot be used to assign elements to positions within the P_n - S_n scheme.

CONCLUSIONS

The difficulties associated with co-opting and redefining standard biological terms for use in conodonts were anticipated decades ago (Müller, 1956), but with increasing knowledge of conodont anatomy and skeletal architecture this problem has become more acute. Similarly, the conflation of morphological and topological criteria in the prevailing scheme of anatomical notation means that the application of terms can become subjective and ambiguous; real topological homologies can be obscured when anatomical notation is applied according to morphological criteria.

Rather than proposing new definitions or prescribing new criteria for the application of existing terms, the solution we are suggesting relies on the erection of a few new terms for biological orientation and anatomical notation. Terms such as "dorsal", "ventral", "rostral", "caudal", "medial" and "lateral", "abaxial" and "adaxial" can be applied in specific situations that warrant their use, or more generally by authors who prefer a more biological terminology. These terms have the advantage of being based on universal biological criteria, and have the

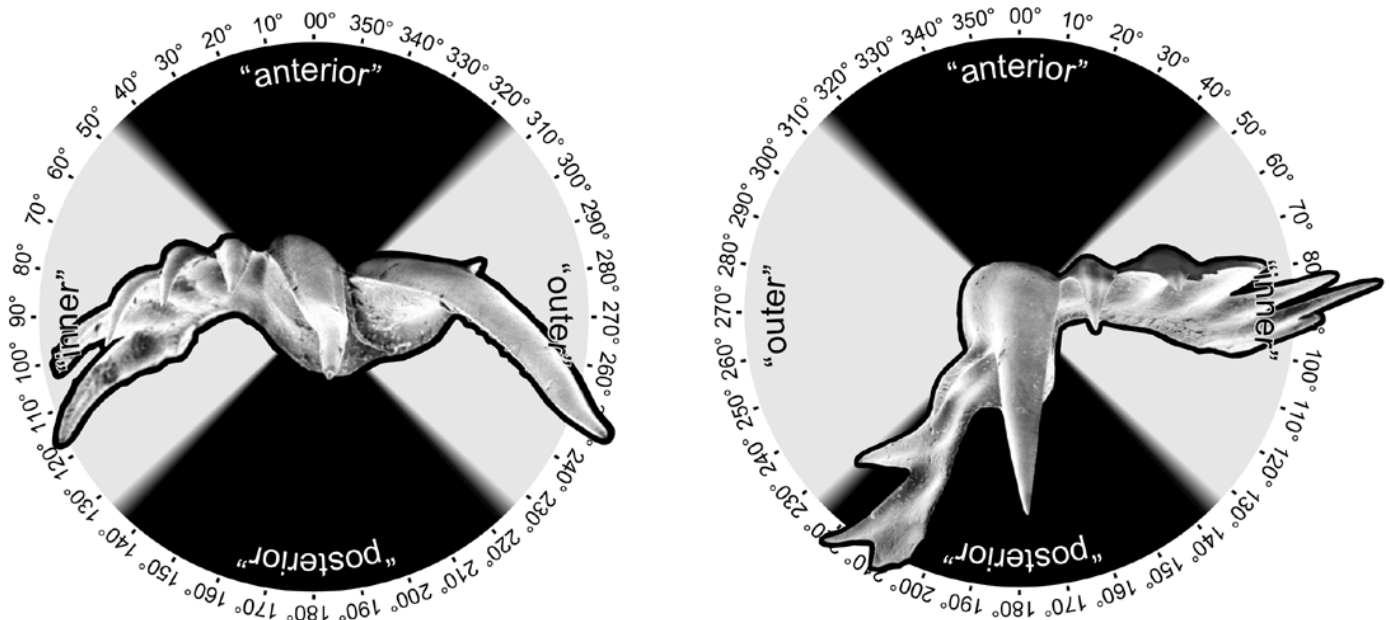


FIGURE 6—Use of terms indicating disposition of processes relative to the conventional arbitrary datum without implications of in vivo orientation (i.e., the plane that includes the apexes of the cusp and basal cavity defines the “anterior-posterior” datum, the 0–180° plane). The use of quotation marks reduces ambiguity without adding to the existing terminological confusion.

same meaning as the same terms in other chordates. The new terms can be used in parallel with the conventional schemes without exacerbating the difficulties we are seeking to resolve. We have tried to avoid ambiguity and overlap with existing terminology so that it should be implicitly clear whether an author is describing an element using biological or conventional terms. Our modified anatomical notation has similar aims. The P_n - S_n scheme is based on clear topological definitions and can be applied rigorously to taxa which are known from natural assemblages or where an hypothesis of topological homology can be inferred from secondary morphological criteria. Where homologies are not known, the existing scheme (i.e., Pa, Pb, Sa-Sc) can be used as Sweet (1981b, p. W19) originally intended.

We concede that conodont paleontology is already burdened with a considerable weight of arcane jargon, but it is our hope that the use of the few new terms we are proposing will reduce ambiguity and significantly improve clarity of communication.

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APPENDIX

1) The following descriptions of the S₂ element of *Clydagnathus windsorensis* (Fig. 7.1; description modified from Purnell 1992) illustrate, firstly, the use of quotation marks to show that conventional, non-biological terms are being used to indicate the disposition of morphological features, and, secondly, the use of biological terminology.

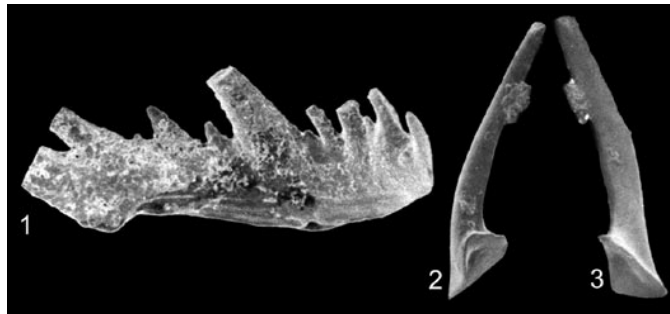


FIGURE 7—Conodont elements described in Appendix to illustrate use of traditional and biological terminology. 1, S_2 element of *Clydagnathus windsorensis*, “inner” or adaxial view, $\times 100$ (Royal Ontario Museum specimen ROM 48804; from Purnell, 1992, plate 2, figure 14). 2, 3, Element of *Eucharodus apion*, “outer lateral” and “inner lateral” views, $\times 35$ (University of Copenhagen Geological Museum specimen MGUH 18.764; from Smith, 1991, figure 19a, 19b).

Nonbiological terms.—The “anterior” process is laterally compressed and straight or slightly curved “inwardly.” It bears six or more laterally compressed denticles, free for most of their length, which curve “inwards” and become increasingly reclined “posteriorly.” The sharply pointed cusp is laterally compressed, reclined, and curved “inwards.” It is larger than the denticles of the “anterior” process. The “posterior” process is laterally compressed, straight, and longer than the “anterior” process, bearing up to approximately 10 laterally compressed denticles. The denticles increase in size and reclination towards the “posterior-most” denticles, which may be larger than the cusp. The “posterobasal” termination beneath these denticles may be curved aborally. The aboral cavity is small, located just “anterior” of the cusp, aligned with its long axis. It continues as a narrow groove along the sharp lower edge of the “posterior” process and part way along the “anterior” process. In larger specimens, the groove is flanked by recessive basal margin.

Biological terms.—The rostral process is laterally compressed and straight or slightly curved adaxially. It bears six or more laterally compressed denticles, free for most of their length, which curve adaxially and become increasingly reclined caudally. The sharply pointed cusp is laterally compressed, reclined, and curved adaxially. It is larger than the denticles of the rostral process. The caudal process is laterally compressed, straight, and longer than the rostral process, bearing up to approximately 10 laterally compressed denticles. The denticles increase in size and reclination towards the caudalmost denticles, which may be larger than the cusp. The caudobasal termination beneath these denticles

may be curved towards the aboral surface. The aboral cavity is small, located just rostral to the cusp, aligned with its long axis. It continues as a narrow groove along the sharp lower edge of the caudal process and part way along the rostral process. In larger specimens, the groove is flanked by recessive basal margin.

2) The following description of the P element of *Eucharodus apion* (Figs. 7.2, 7.3; description modified from Smith 1991) illustrates the use of quotation marks to show that conventional, nonbiological terms are being used to indicate the disposition of morphological features. Note that, because of the lack of evidence for biological orientation in *Eucharodus* and many other coniform taxa, description using biological terms is not currently possible.

Cusp proclined to erect, upper edge of base very short, flat to broadly convex, curving round evenly into cusp. “Posterior” margin sharp, straight or very slightly curved, may continue across base as a costa. “Anterior” margin sharp, straight in lower half, gently curved at mid-height, straight distally. Cusp symmetrically biconvex, strongly deflected “inwards.” Aboral margin straight “anteriorly,” curving up “posteriorly” so that cavity opens to “posterior.” Aboral outline pear-shaped, narrow “anteriorly,” broadening rapidly at one third of the distance to the “posterior.” Base gently expanded laterally, “anterior” margin sharply rounded and a continuation of “anterior” keel. Cavity very shallow, apex “posterior.” Hyaline, thin growth axis runs from aboral cavity apex to cusp tip parallel to “posterior” margin.