

THE APPARATUS COMPOSITION AND ARCHITECTURE OF *CORDYLODUS* PANDER—CONCEPTS OF HOMOLOGY IN PRIMITIVE CONODONTS

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ABSTRACT

A clear distinction may be drawn between the perpendicular architecture of the feeding apparatus of ozarkodinid, prioniodontid and prioniodontid conodonts, in which the P elements are situated at a high angle to the M and S elements, and the parallel architecture of panderodontid and other coniform apparatuses, where two suites of coniform elements lie parallel to each other and oppose across the midline. The quest for homologies between the two architectures has been fraught with difficulty, at least in part because of the paucity of natural assemblages of coniform taxa. A diagenetically fused apparatus of *Cordylodus lindstromi* elements is here described which is made up of one rounded and two compressed element morphotypes. One of the compressed elements is bowed and asymmetrical and the other is unbowed and more symmetrical. These compressed elements are considered to be homologous with those of panderodontid apparatuses and would have lain at the caudal end of the parallel arrays, with the more symmetrical morphotypes located rostrally to the asymmetrical ones. The bowed and unbowed compressed elements of *Cordylodus* thus correspond, respectively, to the pt and pf positions of panderodontid apparatuses. In addition, the presence of symmetry transition within the rounded elements of *Cordylodus*, but not the compressed morphotypes, enables correlation of these with the S and M element locations of ozarkodinid apparatuses. By extension, the compressed elements must be homologues of the P elements. Specifically, the asymmetrical pt morphotype is homologous with the P₁ of ozarkodinids and the more symmetrical and rostral pf morphotype is homologous with the P₂ position. However, because of uncertainties over the nature of topological transformation of the rostral element array (the “rounded” or “costate” suites), it is not possible to recognize specific homologies between these elements and the M and S elements of ozarkodinids. Morphologic differentiation of P from M and S element suites thus preceded the topological transformation from parallel to perpendicular apparatus architectures.

INTRODUCTION

The discovery of conodont soft tissue remains has revolutionized the scientific perception of this long-enigmatic and extinct animal group. Conodonts are now almost universally recognized as chordates and, furthermore, the available evidence indicates that they are the most primitive vertebrates to possess a mineralized skeleton (Donoghue *et al.*, 2000). Thus, the phylogeny of conodonts is no longer a subject of interest

only to a specialist group of paleontologists but extends beyond, to the evolutionary and developmental biology of vertebrates. Unfortunately, conodont phylogeny is rather poorly understood in a detailed sense—and it is only through the resolution of conodont relationships that we can begin to elucidate the early stages of evolution in vertebrate skeletons. The key to recovering relationships is the identification of homology between the apparatuses of different taxa. In the absence of soft tissues, the crucial first step is

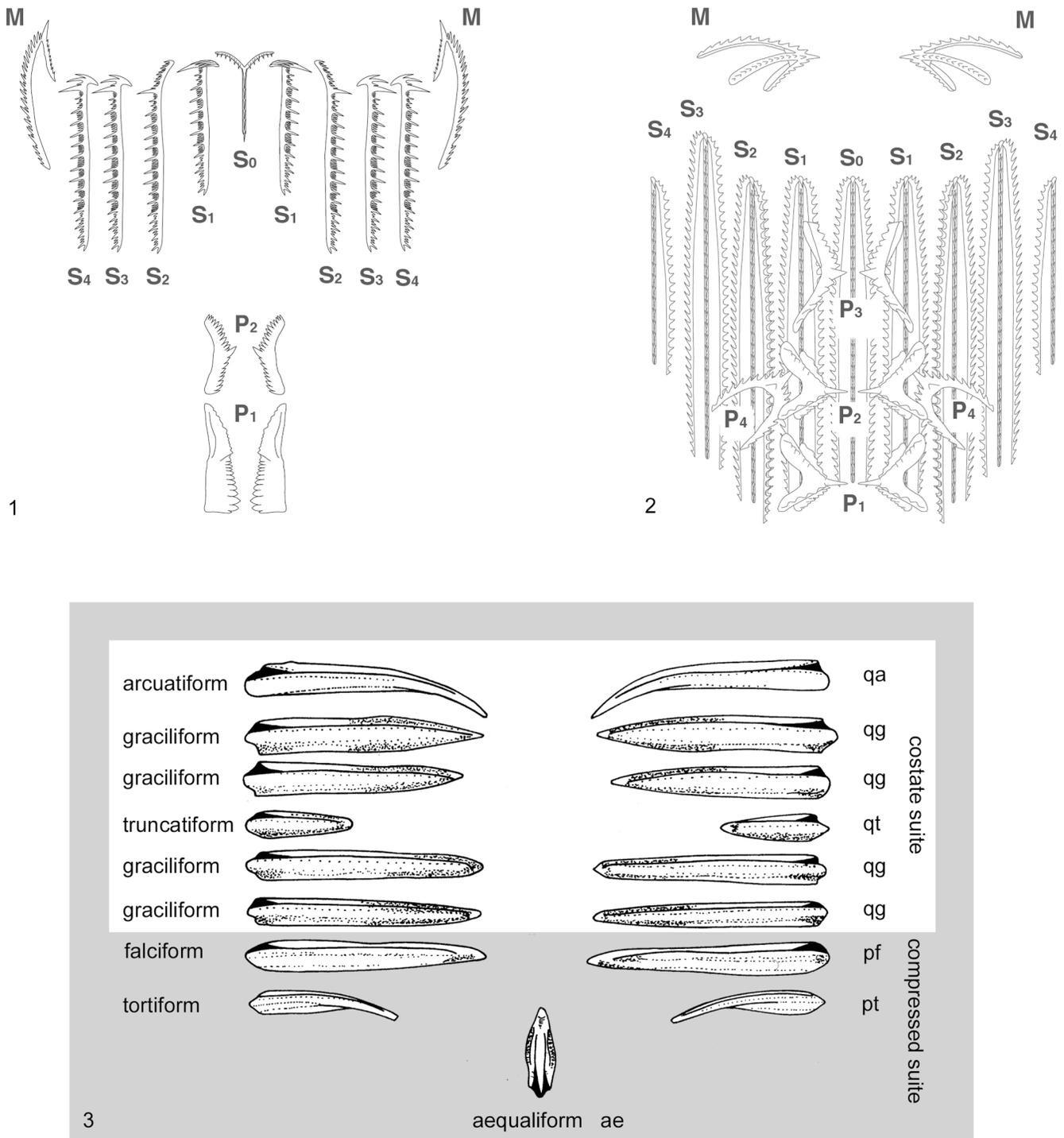
to seek homology in the apparatus composition and architecture of individual taxa. Although some success has been achieved in assessing homologies between taxa with complex apparatuses (Purnell *et al.*, 2000 and references therein), it is far less certain how the apparatus composition and architecture of primitive coniform conodonts relates to that of the more derived prioniodontids, ozarkodinids and prioniodinids. As an aside, it should be noted that preliminary cladistic analysis (Sweet and Donoghue, 2001) indicates that these taxa cannot be sustained at equal, ordinal, rank—the Prioniodontida is paraphyletic with respect to Ozarkodinida + Prioniodinida. Nevertheless, these terms encapsulate useful grades of apparatus organization and, in the interim, their use is informally maintained in this paper.

Although the multielement revolution in conodont studies began with the seminal works of Huckreide (1958), Walliser (1964), Webers (1966), and Bergström and Sweet (1966), multielement taxonomy was, and to some extent remains, slow to be taken up by workers on post-Early Paleozoic faunas. Gilbert Klapper, initially in collaboration with Graeme Philip (Klapper and Philip, 1971, 1972), was a pioneer in extending multielement taxonomy to the younger portions of the conodont record. Together with a concept of homology within the apparatus, Klapper was among the first to impress upon his peers the importance of this advance not only for systematic studies, but also for biostratigraphy. Although we remain far from a Utopian ideal in which all conodont taxa are known in a multielement sense, the early work of Klapper and others has served as a solid foundation from which later workers have been able to begin elucidating conodont diversity and disparity. For instance, conodont workers are now in a position to conclude, with a degree of certainty, that all ozarkodinids shared a common apparatus plan and architecture (Text-fig. 1.1; Nicoll and Rexroad, 1987; Purnell and Donoghue, 1998). It is also possible that this plan may be much more widely applicable among other conodont groups (Purnell and Donoghue, 1998; Purnell *et al.*, 2000). However, forays into resolving the apparatus structure of coniform conodont taxa have revealed that some possessed an apparatus of seventeen elements that were arranged within a radically different architecture (Text-fig. 1.3; Smith *et al.*, 1987; Sansom *et al.*, 1994), and the recognition of homology between the two architectural types remains far from resolution (Sansom *et al.*, 1994; Purnell and Donoghue, 1998; Purnell *et al.*, 2000). The reasons behind the failure to recognize homologies are multifarious, but include the difficulty of identifying P homologues in relatively simple coniform morphologies; the problems associated with de-

termining the total number of individual elements within apparatuses in the absence of complete natural assemblages; and the fact that most natural assemblages represent relatively derived members of each group. A key step would be to determine the apparatus composition and architecture of less derived taxa that are more likely to be representative of the common ancestor of the two groups. The composition of these apparatuses is often well understood in terms of the number of element morphotypes but, in distinct contrast, the locational homologies of these morphotypes are poorly constrained.

As progress is made in comparing the apparatus plans and architecture of coniform conodonts with those of ozarkodinids and other derived groups, it is essential that a clear distinction be made between different degrees of inference when assessing homology within apparatuses. Homologies between conodont apparatuses can be arrived at through direct or indirect approaches, which correspond to more or less precise hypotheses of homology. The direct approach requires evidence of the relative position of each component element of an apparatus. Such evidence is sparse and relies upon the fortuitous discovery of articulated remains of conodont apparatuses on bedding plane surfaces, or cemented together by early diagenetic minerals in the form of a “fused cluster.” The indirect approach extrapolates direct evidence of locational homologies to the apparatuses of taxa that are known only from collections of discrete elements. This may be achieved by comparing element morphotypes in known apparatus positions to morphotypes in discrete-element collections. However, as the phylogenetic distance between taxa grows, the likelihood is greater that dissimilar morphologies of elements will occupy homologous element positions, and extrapolations of locational homology then become more tenuous. Nevertheless, it is possible in such instances to infer homology based upon element morphotypes possessed mutually by closely related taxa for which there is no appropriate architectural template. Thus, although it will not be possible to infer locational homologies and relationships with better known taxa represented by natural assemblages, it remains possible to undertake phylogenetic analysis within these groups. Furthermore, it is possible that through the identification of common element morphotypes between taxa, connections to taxa whose locational homologies are well constrained may be made. It should be noted, however, that these are among the weakest hypotheses of homology and the most likely to be subject to radical reinterpretation upon the discovery of natural assemblages of closely related taxa.

In the past, hypotheses of locational homology be-



Text-figure 1.—1 Apparatus architecture of ozarkodinid conodonts (after Purnell and Donoghue, 1998). 2 Apparatus architecture of balognathid prioniodontid conodonts (from Aldridge *et al.*, 1995). 3 Apparatus architecture of panderodontid conodonts (from Sansom *et al.*, 1994). Reproduced with the permission of the Palaeontological Association.

tween taxa have been conceptualized in a variety of notational schemes (e.g., Klapper and Philip, 1971; Jeppsson, 1971; Sweet and Schönlaub, 1975; Barnes *et al.*, 1979; Sweet, 1981, 1988; Armstrong, 1990;

Sansom *et al.*, 1994; Purnell and Donoghue, 1998; Purnell *et al.*, 2000). At the inception of the majority of these schemes, little was known regarding apparatus architecture, and the number and variety of notational

schemes erected underscores the difficulty in establishing homology in the absence of locational data. This situation has been remedied in recent years through the elucidation of apparatus architecture based on data derived from natural assemblages (Aldridge *et al.*, 1987; Smith *et al.*, 1987; Purnell, 1993; Sansom *et al.*, 1994; Aldridge *et al.*, 1995; Purnell and Donoghue, 1997, 1998). This has, in turn, enabled the erection of an entirely apparatus location based scheme of element homology that directly reflects homology independently of element morphology (Purnell *et al.*, 2000).

Despite these advances, the number of taxa for which locational homologies are known directly remains small. Furthermore, the implicit assumption that the earlier conceptual schemes reflected statements of homology has broken down and the explanatory content of the associated nomenclature has been lost through overzealous use and misapplication (Purnell *et al.*, 2000).

Three approaches have been manifest with respect to the use of homology within early euconodont faunas. Some authors (*e.g.*, Nicoll, 1990, 1994; Nicoll *et al.*, 1999; Löfgren, 1997a, b, 1999) have adopted a utilitarian approach in which the P, M, S notation of Sweet and Schönlaub (1975) and Sweet (1981, 1988) is used, although in many instances homology may not be certain. Others (*e.g.*, Smith, 1990, 1991; Sansom *et al.*, 1994) have urged caution and stressed the need to be certain of locational homology before using ozarkodinid notation. This latter approach has been allied to the creation of alternative notational schemes, of which those introduced by Barnes *et al.* (1979), and modified by Armstrong (1990), Ji and Barnes (1994) and Sansom *et al.* (1994) are most applicable to coniform conodonts. A third approach has been to use adjectival descriptors for element morphotypes, which are often based on form-taxonomic names, without any attempt to identify locational homologues between genera (*e.g.*, Kennedy, 1980). All of these approaches have disadvantages. The utilitarian use of ozarkodinid notation may imply homology where none is present or the evidence is very weak; the use of alternative schemes tends to overlook homology with more derived conodonts even where the evidence seems strong (for example with Sa and M elements) and the third approach may fail to recognize homology between even closely related taxa. Clearly, it would be ideal to establish homology between at least some coniform taxa and the better-constrained architecture of ozarkodinid taxa, but this has proved to be an intractable problem given the available dataset of natural assemblages. Even where coniform architecture is well understood, as is the case with *Panderodus* (Sansom *et*

al., 1994), the element morphologies are highly derived and comparison with ozarkodinid templates (Text-fig. 1) is difficult. Architectural information from a primitive taxon, ideally one that is closely related to the latest common ancestor of the prioniodontids and coniform groups, would offer the best opportunity for comparing apparatus architecture and establishing more secure homologies.

In this contribution it is our aim to re-examine what is known regarding the apparatus composition, architecture and homologies of the Late Cambrian–Early Ordovician genus *Cordylodus*, based upon discrete-element collections and upon what little is known from natural assemblages. *Cordylodus* is a key taxon across a range of conodont research—it is an important biozonal index in the Cambrian–Ordovician boundary interval; it is one of the earliest conodonts with denticulated elements and its youngest representatives co-occur with the earliest prioniodontids (*sensu* Sweet, 1988). As part of this review we describe and figure for the first time an incomplete fused cluster of the apparatus of *Cordylodus lindstromi* Druce and Jones, 1971.

ACKNOWLEDGMENTS

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EVOLVING CONCEPTS OF APPARATUS COMPOSITION IN *CORDYLODUS*

Cordylodus was one of the first conodonts to be described (Pander, 1856), and is one of three, apparently unrelated, denticulate euconodont genera that occur in the Late Cambrian and earliest Ordovician, the others being *Eodentatus* Nicoll and Shergold, 1991, and *Iapetognathus* Landing in Fortey *et al.*, 1982 (see Nicoll *et al.*, 1999 for review). In considering the taxonomy of *Cordylodus*, Pander (1856) adopted a form-element approach but the history of, and degree of conflict between, multielement apparatus reconstructions of the genus is perhaps more complex than for any other conodont genus (Table 1). Early apparatus reconstructions invoked a bimembrate apparatus plan that included either two “rounded” elements of different morphology (Bergström and Sweet, 1966) or one “rounded” and one “compressed” element (Mill-

Table 1.—Development of apparatus concepts within *Cordylodus* Pander, 1856, and correlations of individual morphotypes made by successive authors.

	Rounded suite	Compressed suite
Bergström & Sweet 1966	rounded, rounded	
Miller 1980	rounded	compressed
Fortey <i>et al.</i> , 1982	rounded, rounded	compressed
Viira <i>et al.</i> , 1987	rounded a, rounded b, rounded g	compressed
Bagnoli <i>et al.</i> , 1987	$p'a', p'b', p'c'$	q
Barnes 1988	p 1, p 2, p 3	q
Nicoll 1990	Sa, Sb, Sc, Sd	M, Pa, Pb
Ji & Barnes 1994	a, c	e, e
Huselbee 1997	ae, r 1, r 2, r 3	compressed

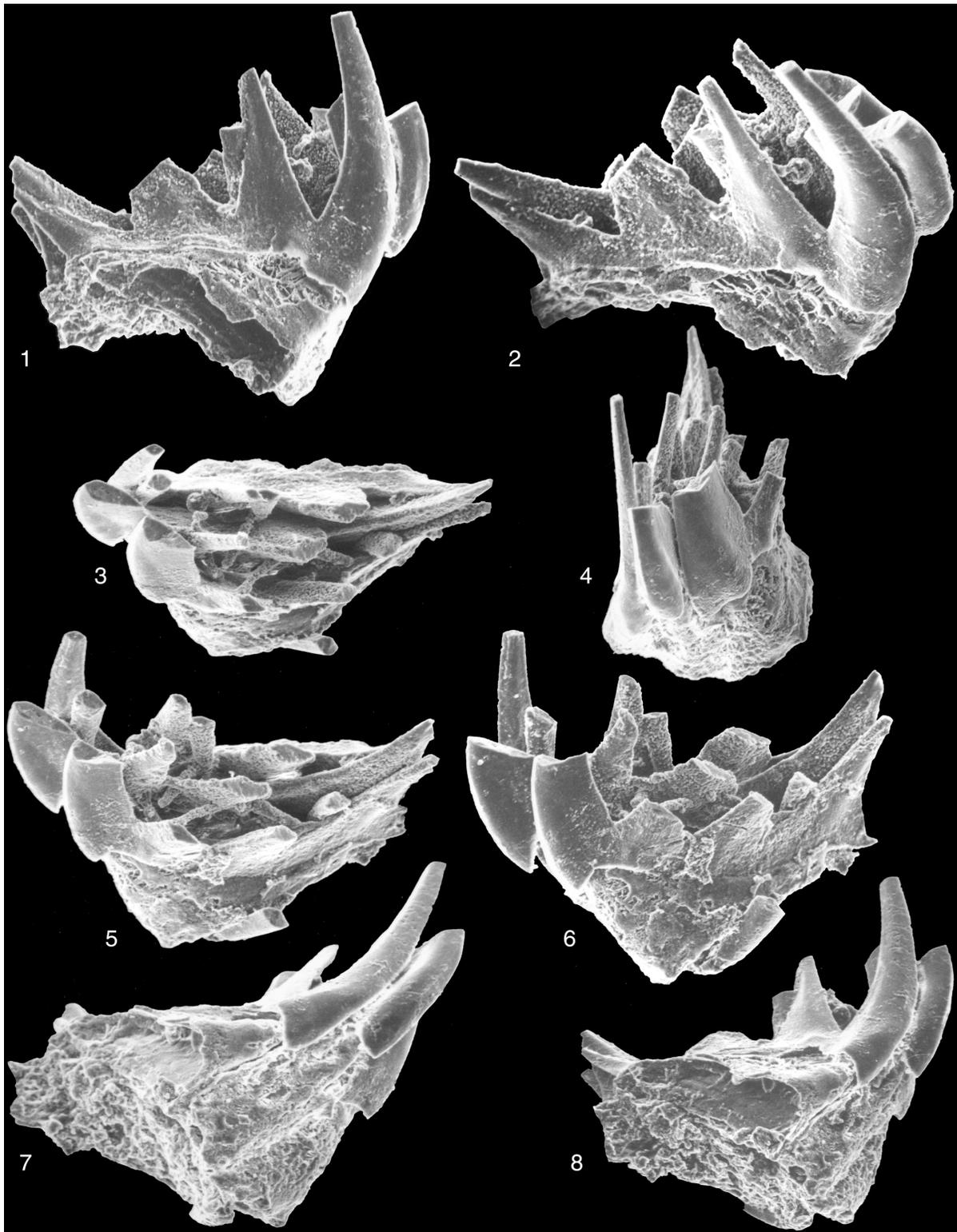
er, 1980; Landing *et al.*, 1980). In both instances, the terminology employed referred to the cross-sectional profile of the cusp. A second rounded element was later recognized in *C. angulatus* Pander, 1856, suggesting that at least the younger species of the genus had a trimembrate apparatus (Fortey *et al.*, 1982). A more complex apparatus was proposed by Bagnoli *et al.* (1987), who recognized the rounded and compressed categories of earlier authors but also suggested that a symmetry transition series could be identified within the rounded category. This was composed of laterally compressed symmetrical elements, slightly asymmetrical forms with a flat inner lateral face and markedly asymmetrical types in which the inner lateral face bears a low carina and the outer face is broadly rounded. Bagnoli *et al.* recognized this apparatus structure in all but the oldest representatives of the genus, in which less morphological differentiation seemed to be present. The apparatus reconstruction of Bagnoli *et al.* (1987) was formalized by Barnes (1988), who proposed the terms *p1*, *p2* and *p3* for the variants in the symmetry transition series. However, Barnes preferred to express the variation in terms of both cusp curvature and posterior process orientation and morphology, rather than symmetry as Bagnoli *et al.* had done, and *C. lindstromi* was not specifically divided in this way.

A trimembrate apparatus was proposed for *Cordylodus proavus* Müller, 1959, and *C. lindstromi* by Andres (1988). This plan was extended by Ji and Barnes (1994) who identified the three basic element types—

a subrounded “*a*” element, a suberect “*c*” element, and a compressed “*e*” element—but also recorded two variants for each of their *a* and *e* elements, essentially creating a quinquemembrate apparatus. The *a* elements were considered to be equivalents of the *p1* and *p2* of Barnes (1988), the *c* to be that of the *q*, and the *e* elements to be variants of the *p3*. This differs markedly from the scheme of Bagnoli *et al.* (1987) who considered the compressed element to be the *q*, not a *p*.

The most complex apparatus plan proposed to date for *Cordylodus* is that of Nicoll (1990, 1991, 1992). Employing the ramiform-pectiniform notation of Sweet and Schönlaub (1975), Nicoll suggested that the apparatus of *Cordylodus* was septimembrate, with Pa, Pb and Sa-Sd elements, together with an M element that was thought to be either adenticulate (*C. angulatus*, *C. caseyi* Druce and Jones, 1971, *C. proavus*) or denticulate (*C. lindstromi*). Miller and Repetski (1993) attempted to test the Nicoll model using topotype material together with comparative collections of *C. proavus* and other early *Cordylodus* species. They had only partial success; they did not recognize four separate S elements *sensu* Nicoll nor did their material contain an adenticulate M element.

Huselbee (1997) did recognize a series of four rounded elements on the basis of their symmetry, similar to the “Sa-Sd” suite of Nicoll (1990) but found no evidence for makelliform elements and only one morphotype of compressed element within her rather



Text-figure 2.—Fused cluster of *Cordylodus lindstromi* Druce and Jones, 1971 (USNM 516997) from Ibexian (Early Ordovician) strata of the Vinini Formation, Nevada, USA. Specimen recovered from USGS sample 9446-CO and deposited in the National Museum of Natural History, Washington DC, USA. **1** Lateral view of the rounded element (Element 3), $\times 200$; the cusp of the P_2 homologue is visible behind the rounded element on the right hand side of the figure. **2** Oblique view of cluster showing the two compressed elements behind the rounded one, $\times 250$. **3** Axial view of the cluster, $\times 200$. The asymmetrical P_1 homologue (Element 1) is situated at the bottom of the figure, adjacent to the less bowed P_2 homologue (Element 2) which in turn abuts the rounded element (Element 3). **4** “Anterior” view of the cluster, $\times 230$;

low-abundance faunas from NW Scotland and Greenland.

The youngest representatives of *Cordylodus*, *C. angulatus*, *C. intermedius* Furnish, 1938, *C. lindstromi*, and *C. prion* Lindström, 1955, have their last appearances in the *angulatus* Biozone (early Tremadoc). Younger species have been assigned to the genus but are based on homeomorphic elements that are present in taxa not closely related to *Cordylodus*. These include “*Cordylodus*” *horridus* Barnes and Poplawski, 1973, which is based on a denticulated Llanvirn species of *Paroistodus* (Löfgren, 1995; Albanesi and Barnes, 2000), and “*Cordylodus*” *ramosus* Hadding which is now considered to be part of the apparatus of *Spinodus spinatus* (Hadding, 1913), a Middle Ordovician genus of uncertain affinity (Dzik, 1976; Armstrong, 1997).

Clearly, there has been little concordance over the apparatus composition of, and taxonomic concepts for, *Cordylodus* despite intensive work related to selection of the Cambrian–Ordovician global boundary stratotype and point. Although there is mounting consensus from Bagnoli *et al.* (1987) through Nicoll (1990) to Huselbee (1997) for the presence of a suite of rounded elements defined by differences in symmetry, there is little agreement on the number of compressed elements (including makelliform elements) within the apparatus. Natural assemblages have the capacity to provide tests for these competing apparatus models.

NATURAL ASSEMBLAGES OF *CORDYLODUS*

Only two natural assemblages of *Cordylodus* have been recorded to date, both of which are fused clusters. Andres (1988, pl. 13, figs. 1, 2) figured a cluster assigned to *C. proavus* Müller elements that incorporates at least three elements. However, it is not possible to interpret the element morphologies present from the plate alone and recourse to the original material will be necessary for detailed reappraisal. Preliminary notes on another cluster of elements referred to *Cordylodus* were made by Repetski (1980) and Repetski and Szaniawski (1981), but the specimen has never before been figured or described in detail. The fused cluster includes three complete elements and three element fragments assigned to *C. lindstromi* Druce and Jones (Text-figs. 2, 3). It was recovered through acid digestion of U.S. Geological Survey sample 9446-CO from the Vinini Formation, Elko County, Nevada,

U. S. A. (SE¼, sec. 19, T 35 N, R 53 E). The associated fauna includes *Cordylodus angulatus* Pander, 1856, *Cordylodus intermedius* Furnish, 1938, *Iapetognathus sprakersi* (Landing in Landing *et al.*, 1996) and *Variabiloconus bassleri* (Furnish, 1938), indicating an *angulatus* or early *manitouensis* Biozone age (Skull-rockian, early Ibexian, earliest Ordovician; Ross *et al.*, 1997). The protoconodont *Phakelodus tenuis* (Müller, 1959) is also present, both as isolated elements and clusters, together with the phosphatized embryos of bilaterian metazoans.

DESCRIPTION OF *CORDYLODUS LINDSTROMI* CLUSTER

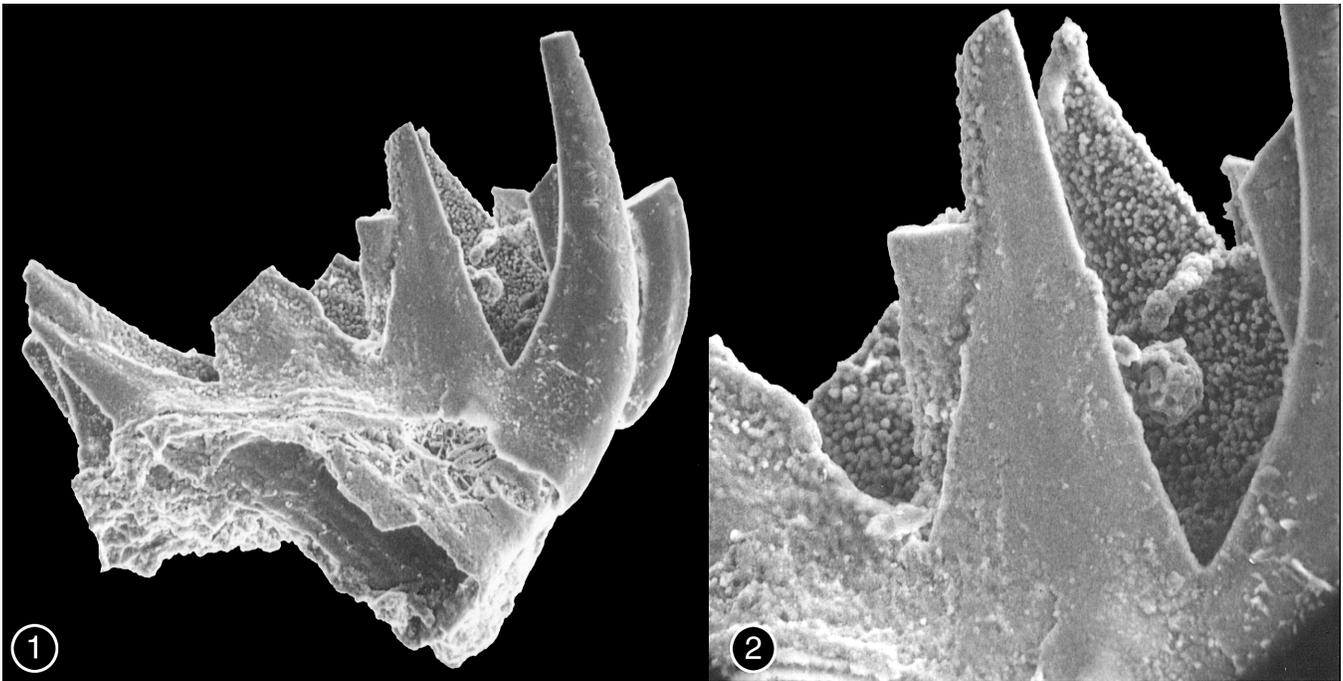
The cluster (Text-fig. 2) comprises three complete elements, together with cusp and denticle fragments of at least two others—the latter fragments oppose the more complete elements with the long axes of the cusps and denticles parallel to each other. The complete elements are fused by their lateral faces and there is no evidence of *post mortem* disruption. Element 1 (Text-fig. 2.3–2.6) has compressed cusp which is proclined-erect in the preserved portion. Faint carina at base of outer face. Outer face broadly convex toward posterior margin, but more tightly convex at anterior margin. Inner face flat; cusp therefore asymmetrical in cross-section and twisted inwards relative to posterior process. Element strongly bowed. In lateral aspect, basal margin has marked 100° inflection. Three denticles. First and second denticles are asymmetrically triangular in lateral profile with steeper posterior margin. Third denticle is more slender and reclined than more anterior denticles. First denticle has convex outer face and flat inner face. Denticles two and three are more symmetrical and biconvex in cross-section.

Element 2 (Text-fig. 2.3–2.6) is sandwiched between the other two elements and, in consequence, the morphology is partly obscured. Cusp as broad as Element 1 and strongly compressed; erect to proclined in preserved portion. Outer and inner faces broadly convex resulting in more symmetrical cross-section than Element 1; element gently bowed. Basal margin has similar inflection to Element 1 when viewed in lateral profile. Three denticles. First denticle is complete, narrow and short. Second denticle is more triangular with steeper posterior margin than anterior margin. Third denticle more reclined than other two.

Element 3 (Text-figs. 2, 3) is the most complete element. Cusp narrower and markedly less compressed

←

P₁ homologue on the right. **5, 6** Oblique axial and oblique “anterior” views, ×200; the P₁ homologue is the nearest element. **7, 8** Each element has a distinct basal body, which remains separate until the basal part of the cluster where they become fused into a single mass; ×225, ×200. It is unclear whether this is a primary feature relating to the apparatus or a consequence of the early diagenesis that produced the cluster.



Text-figure 3.—Opposed cusp and denticle tips in the fused cluster of *Cordylodus lindstromi* Druce and Jones, 1971 (USNM 516997). **1** Lateral view of the rounded element (Element 3 showing the fused cusp and first denticle of the opposing element, $\times 225$. **2** Close-up of the cusps and denticles showing the precise alignment, $\times 500$. The similarity in cusp and denticle cross-sections can be seen in Text-figure 2.3.

than Elements 1 and 2; slightly bowed to inner. Inflection in basal margin beneath posterior margin of cusp. Three denticles. First denticle is narrow and triangular, with posterior margin markedly steeper than anterior. Junction of cusp with first denticle lower than that between first and second denticles. Second denticle more broadly triangular in lateral profile than either of other denticles. Denticles symmetrically biconvex in cross-section. Third denticle more reclined than first two.

All elements have a basal body, which in Element 3 has a hollow, conical interior surface. Incremental growth lines are apparent on the inner surface of the basal body (Text-figs. 2.8, 3.1) The basal bodies of each element remain distinct for almost their entire lengths but are fused into a single mass at the base; it is not certain whether this is a primary or diagenetic feature.

An opposed and inverted cusp fragment is attached to the cusp of Element 3 and is of similar morphology; an inverted denticle, which may belong to the same element, is attached to the first denticle of Element 3 (Text-fig. 3). An additional inverted denticle is attached to the flank of Element 1, and a third inverted denticle is attached between Elements 1 and 2 at the anterior end of the third denticles of these two elements. The opposing cusp and denticle fragments are parallel to their counterparts.

Microspheres, of phosphatic composition and probable bacterial origin, coat many of the element surfaces (Text-fig. 3.2) and were presumably involved in the early *post mortem* mineralization that resulted in element fusion.

COMPARISON WITH MULTIELEMENT RECONSTRUCTIONS OF *CORDYLODUS*

Elements 1 and 2 are compressed elements. The only apparatus reconstructions of *Cordylodus* to have included two morphotypes of compressed element are those of Nicoll (1990) and Ji and Barnes (1994). Element 1 resembles the Pa element of Nicoll (1990) in that the cusp is twisted inwards relative to the posterior process. In turn, Element 2 conforms to the description of Nicoll's Pb element type in being more symmetrical in cross-section and in being untwisted relative to the posterior margin. As in Nicoll's material, the cusps of the compressed elements are keeled on their anterior and posterior margins, and the basal cavity extends along the posterior process. Ji and Barnes (1994) also documented variations in the compressed elements and recognized two types based on differences in cusp curvature, basal cavity shape and symmetry. In particular, one compressed element morphotype was considered to be more compressed than the other (Ji and Barnes, 1994, p. 31) and, on this basis, the less compressed morphotype may correlate with the Element 1. It is

not, however, possible on the basis of their figures to correlate directly with the elements in the cluster.

Element 3 is a “rounded” element and is probably equivalent to Nicoll’s (1990) Sb element. The first denticle is deflected outwards relative to the cusp and second denticle; the cusp is biconvex in cross-section and the anterior margin is rounded in its lower part. It corresponds to one of the two categories of “a” morphotype recognized by Ji and Barnes (1994).

The two compressed elements within the half apparatus of *Cordylodus lindstromi* are closely comparable to the pf and pt elements of the compressed suite in *Panderodus* described by Sansom *et al.* (1994). Furthermore, the posteriormost pt pair in *Panderodus* is markedly asymmetrical and the elements have twisted cusps similar to that of Element 1.

COMPARATIVE APPARATUS ARCHITECTURE OF *CORDYLODUS*

The construction of apparatus architecture models depends to a large degree on the availability of bedding plane assemblages and fused clusters, which can provide three-dimensional data on element disposition once the effects of collapse generated by decay are removed (see Briggs and Williams, 1981; Aldridge *et al.*, 1987; Purnell and Donoghue, 1999 for reviews of the technique). The vast majority of natural assemblages described to date are of prioniodontid, prioniodinid and ozarkodinid taxa, with a relatively very small number of coniform taxa represented. Partly because of the relative abundance of natural assemblages and partly because of the presence of associated soft tissues in the Granton *Lagerstätte*, ozarkodinids have tended to be used as the *Bauplan* for complex conodonts (Aldridge *et al.*, 1987; Purnell and Donoghue, 1998). Ozarkodinid apparatuses contain two pairs of P elements located at the caudal end of the apparatus, with the P₂ pair rostral to the P₁ elements (Text-fig. 1.1). The ramiform S elements are oriented with their long caudal (“posterior”) processes parallel to the long axis of the trunk. M elements flank the battery of S elements but lie, at rest, in an oblique rostro-lateral orientation. The long axes of the S and M elements lie at a high angle to those of the P elements, producing an approximately “perpendicular” architecture.

Prioniodontid conodonts are less derived than ozarkodinids and a smaller number are represented by natural assemblages. *Promissum* has the best-constrained architecture (Text-fig. 1.2), and it has been suggested that its architecture could be typical of the Prioniodontida as a whole (Aldridge *et al.*, 1995). Four pairs of P elements lie in pairs along the midline, but were located between, and dorsal to, the sinistral and dextral

suites of S elements, not caudal to them (Aldridge *et al.*, 1995). The M elements occupy a rostro-lateral position similar to those in ozarkodinids. However, the element morphology of *Promissum*, whilst potentially typical of the Balognathidae, is not typical of the Prioniodontida as a whole and the small number of available natural assemblages from other prioniodontid taxa suggests that a simpler architecture was characteristic of the group. Clusters and associated isolated collections of *Oepikodus* (Smith, 1991), *Paracordylodus* (Stouge and Bagnoli, 1988, pl. 8, figs. 17a, b; Tolmacheva and Purnell, 2002) and *Phragmodus* (Repetski *et al.*, 1998; Barrett, 2000) suggest that the possession of four pairs of P elements was not general for prioniodontids, and that the more common architecture for the group may have been more similar to that of ozarkodinids than to *Promissum*.

The only well-constrained architectural model for a coniform taxon is that of *Panderodus* (Text-fig. 1.3). A large number of fused clusters and a bedding plane assemblage with associated soft tissue from the Waukesha *Lagerstätte* of Wisconsin, U. S. A., have been used to produce a detailed model for the apparatus of *Panderodus* (Smith *et al.*, 1987; Sansom *et al.*, 1994). Eight pairs of elements oppose across the midline of the apparatus, and Smith *et al.* (1987, p. 100) concluded that they must have been arranged in life as parallel and opposed arrays, with either the rostral elements more closely spaced or with all of the elements located on an arched support. This arrangement contrasts markedly with the geometry of S elements in prioniodontids, prioniodinids and ozarkodinids, which are parallel to the midline. Some morphological differentiation is evident in the elements of *Panderodus*; Sansom *et al.* (1994) recognized two principal locational domains—a rostral costate suite and a caudal compressed suite—and all of these elements are parallel to each other, contrasting with the perpendicular architecture of the ozarkodinids. A third domain occupied by a single symmetrical element lies on the midline. It is immediately tempting to consider the compressed suite as the homologues of the P locations in ozarkodinid apparatuses. However, *Panderodus* lacks a clearly defined “symmetry transition series” of morphologically intergrading elements, making unequivocal identification of S homologues difficult. In consequence, it remains a possibility that the two pairs of compressed elements may be homologues not of P elements but of other members of the apparatus. Sansom *et al.* (1994) therefore argued for a conservative approach until supporting evidence was forthcoming. Parenthetically, the concept of symmetry transition has been principally used to differentiate suites of elements rather than to imply locational homology. Neverthe-



Text-figure 4.—*Besselodus arcticus* Aldridge, 1982, from the Cincinnatian (Late Ordovician) Aleqatsiaq Fjord Formation of Washington Land, western North Greenland (MGUH 15071) showing a single cluster that split into two during original preparation. **1, 2** Lateral views of sub-cluster “a” ($\times 330$). **3, 4** Lateral views of sub-cluster “b” ($\times 330$). The original plane of fusion between the two sub-clusters lay between the lateral faces of the uppermost elements in Text-figures 4.1 and 4.3. The full array comprises six laterally costate, bilaterally symmetrical non-geniculate elements and one geniculate element, which is located at the end of the array. Reproduced with the permission of the Palaeontological Association.

less, some authors have used this concept to infer location directly, despite the fact that all available evidence indicates the contrary—symmetry transition cannot be used as a tool in predicting the sequence of S elements within the ramiform array (Aldridge *et al.*, 1987; Purnell and Donoghue, 1998). It is clear, however, that morphologically intergrading elements do frequently comprise the suite of S elements and, thus, this character provides a predictive tool in distinguishing S from M or P elements from elements in other positions (although this tool appears to be inapplicable to prioniodinids; Purnell and von Bitter, 1996).

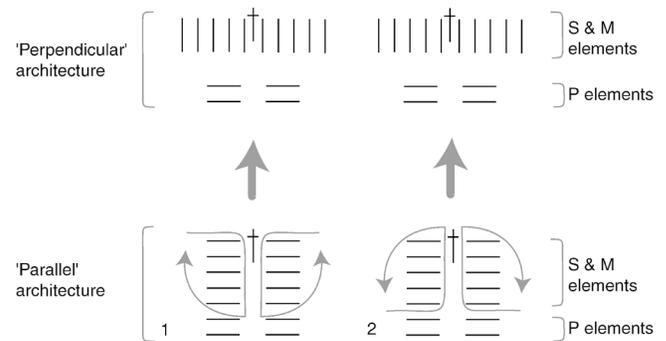
The availability of a well-constrained architectural model for at least one coniform taxon, albeit a rather

derived form, enables the appraisal of less well-preserved and/or less plentiful cluster material of other taxa. A cluster of *Besselodus* elements (Text-fig. 4) figured by Aldridge (1982) is a single half apparatus with little morphological differentiation. It includes six laterally costate, bilaterally symmetrical elements fused by their lateral faces and a single geniculate element at one end of the array. In the absence of elements from the opposing half of the apparatus this cluster could be incorporated into either a pandero-dontid or an ozarkodinid architectural model and there is also no direct control over rostro-caudal polarity in the array. However, Sansom *et al.* (1994) concluded that the architecture of *Besselodus* conformed to the

panderodontid model on the basis of correlations between elements present in isolated collections and would thus be expected to have a parallel architecture. Critical evidence for the conformity of a given apparatus to either the panderodontid or the ramiform-pectiniform model thus lies in the geometry of the respective halves of the apparatus. In the panderodontid architectural model, elements are arranged along the rostral-caudal axis and are opposed cusp tip to cusp tip, a geometry referred to as parallel-reversed by Landing (1976, p. 1078).

Although far from complete, the fused cluster of *Cordylodus lindstromi* elements may be used to provide some constraints on the apparatus architecture of the genus. Firstly, given the presence of a distinct suite of morphologically intergrading “symmetry transition” elements in the apparatus of *Cordylodus*, we can discriminate a suite of homologues to the S elements of ozarkodinids. This leaves a suite of compressed elements that represent either P or M elements. Given that the compressed elements occur paired in the cluster, it is likely that they represent a pair of P homologues. The occurrence of P homologues aligned in parallel and in juxtaposition to an S homologue indicates that *Cordylodus* possessed overall apparatus geometry that was more similar to panderodontids than to ozarkodinids. Finally, the presence of two compressed elements adjacent to each other, with the more asymmetrical morphotype at the end of the array, is consistent with them being locational homologues of the compressed domain in the apparatus architecture of *Panderodus*. Therefore, it follows that the compressed suite in *Panderodus* is homologous with the P positions in ozarkodinids and their kin. More specifically, we can identify the asymmetrical compressed elements of *Panderodus* and *Cordylodus* apparatuses as P₁ homologues (*sensu* Purnell *et al.*, 2000), and the more rostral symmetrical elements are P₂ homologues.

It is tempting to extend from these homologues and identify specific S₀₋₄ and M locational homologues among the apparatuses of *Cordylodus* and *Panderodus*. However, because of the architectural differences between the “parallel” apparatuses of *Cordylodus* and *Panderodus*, and the “perpendicular” apparatuses of prioniodontids and their kin, this is not possible because we have no knowledge of the transformational relationship between the S and M *versus* P locations in these two fundamentally different architectural types. For instance, the element position immediately adjacent to the putative P₂ of *Cordylodus* and *Panderodus* could represent either the S₁ or S₄ depending upon the direction in which the left and right halves of the S array have rotated relative to each other (Text-figure 5). The possibility must also be entertained, how-

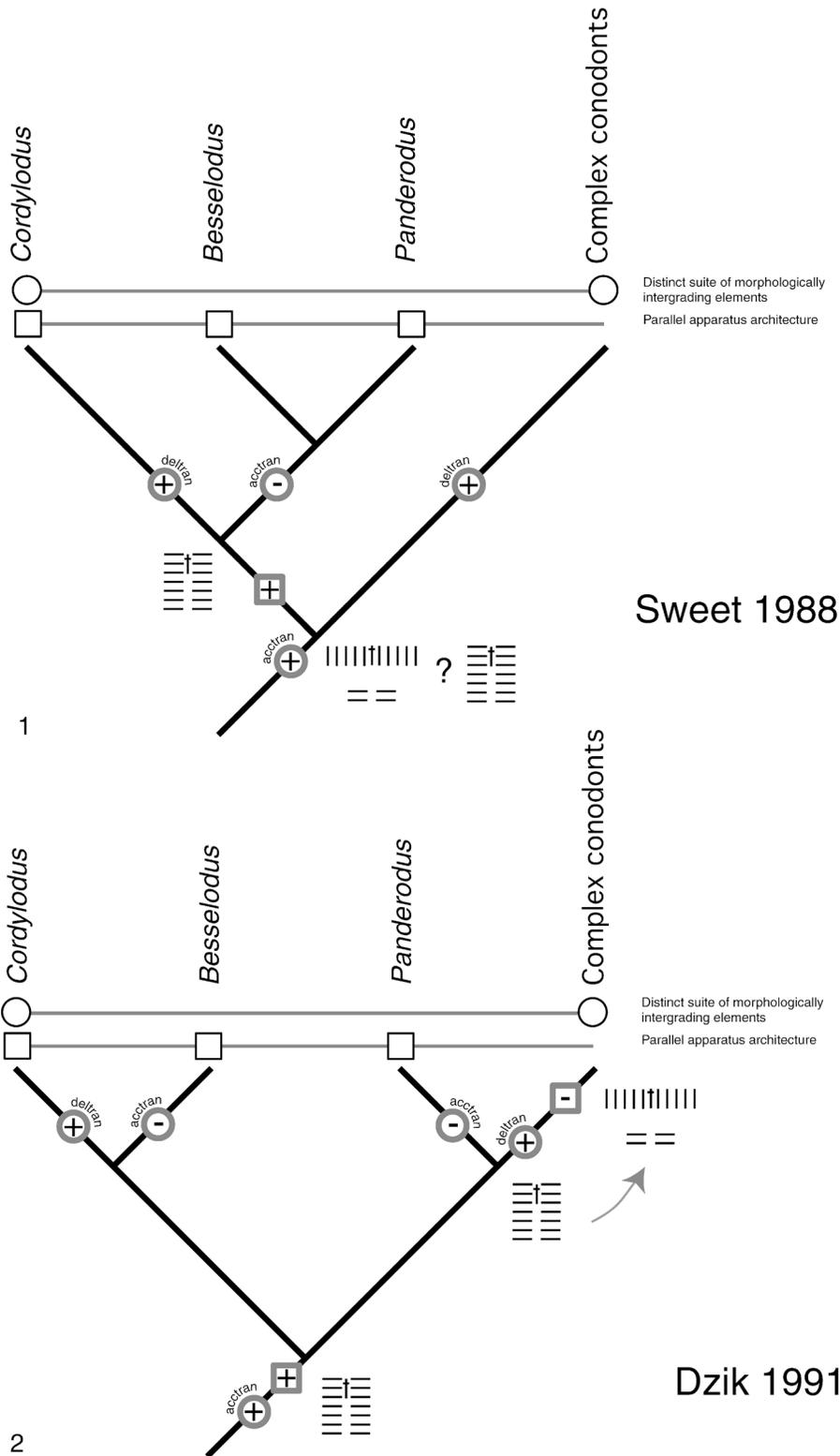


Text-figure 5.—Alternative patterns of transformation from the parallel architecture of *Cordylodus*, *Panderodus* and *Besselodus*, to the perpendicular apparatus architecture typical of prioniodontids, prioniodinids and ozarkodinids. The differing methods of transforming the parallel architecture are illustrated in the left and right halves of the figure. Given these alternatives, it is not possible to identify specific M and S element homologues in parallel and perpendicular apparatuses, although it is possible to recognize P₁ and P₂ homologues and the overall homology of the M and S array of perpendicular apparatus architecture with the anterior suite of elements (“costate” or “rounded”) in parallel architectures.

ever, that the element position immediately adjacent to the P₂ in parallel apparatuses represents the M location, or even another P location. In addition, Dzik (1991) has suggested that the axial (and therefore unpaired) S₀ location of prioniodontids may be homologous to paired abaxial S₀ locations in apparatuses with parallel architecture. There is simply insufficient evidence to reconcile these competing hypotheses.

One direction in which progress can be made is in attempting to resolve the primitive apparatus architecture of the earliest euconodonts and its relationship to locational homologues. To do this, parallel and perpendicular architectures must be considered with respect to one or more phylogenetic trees. In the absence of a generally accepted hypothesis of relationships for conodonts, we have adopted and compared the rival schemes of Sweet (1988) and Dzik (1991) and mapped onto these trees the architectural characteristics of those taxa for which data are available. The differing implications for architectural evolution of the conodont apparatus under these schemes can be seen in Text-figure 6. Under the hypothesis of relationships proposed by Sweet (1988), it is not possible to resolve unequivocally whether parallel or perpendicular architectures are representative of the latest common ancestor of the taxa concerned; both hypotheses are equally likely. However, under the scheme of relationships proposed by Dzik (1991), it is possible to resolve unequivocally that the latest common ancestor of all four taxa possessed a parallel, rather than perpendicular apparatus architecture.

The functional implications of architectural trans-



Text-figure 6.—Inferences of the relative phylogenetic timing of apparatus architectural transformation in taxa for which data are available, based upon the hypotheses of relationships proposed by (1) Sweet (1988) and (2) Dzik (1991). Given that it is not possible to unequivocally infer the relative timing of transformation and/or the primitive apparatus architecture of all the conodonts considered, we have presented the alternative implications of early (ACCTRAN) and late (DELTRAN) transformation. Whilst it is not possible to reconcile primacy between parallel and perpendicular architectures under the scheme proposed by Sweet (1988), following Dzik (1991) it is possible to infer unequivocally that parallel architecture is primitive with respect to perpendicular architecture.

formation of the apparatus, from parallel to perpendicular, are unclear. However, it is clear that morphological and, by implication, functional differentiation of P from M and S elements preceded the transformation from parallel to perpendicular architectures. Indeed, since morphological differentiation of the apparatus is common to all of the taxa considered, it is possible to conclude that their latest common ancestor possessed an apparatus composed of morphologically distinct element suites.

FUTURE DEVELOPMENTS

Further resolution of locational homology in primitive conodonts will require better quality data in the form of complete natural assemblages. More specifically, these data are required for taxa that can provide insight into the transformational pattern/s through which apparatus architecture was remodelled from the plesiomorphic parallel arrangement to the perpendicular architecture that is characteristic of all prioniodontids currently known from natural assemblages. Nevertheless, the further resolution and refinement of locational homologies and architectures among parallel apparatus-bearing taxa will help to provide a much clearer understanding of plesiomorphic euconodont characteristics.

CONCLUSIONS

1) Elements 1 and 2 are “compressed” elements. Element 1 has an asymmetrical cusp cross-section and is bowed. Element 2 is symmetrical in cross-section and only gently bowed. The presence of

two morphotypes of compressed element in the cluster affirms the apparatus reconstructions of Nicoll (1990) and Ji and Barnes (1994), the only apparatus reconstructions of *Cordylodus* that have incorporated two morphotypes of compressed elements.

- 2) The compressed element suite of the *Panderodus* apparatus (*sensu* Sansom *et al.*, 1994) may, with some confidence, be considered as a homologue of the compressed elements in *Cordylodus*. The rounded and compressed elements lay parallel to each other in the apparatus and, together with the closely aligned opposing cusp and denticle tips of the rounded elements, this indicates that *Cordylodus lindstromi* had a parallel panderodontid architecture rather than a perpendicular ozarkodinid type.
- 3) Consideration of the available natural assemblage material allows a hypothesis to be advanced that elements in the compressed suite of *Cordylodus* (and *Panderodus*) may be considered as reasonable candidates for locational homologues of ozarkodinid P₁ and P₂ elements.
- 4) Although it is possible to differentiate between homologues of P and S/M elements, it is not possible to identify specific S₁–S₄ and M homologues.
- 5) The morphological differentiation of elements into P, M and S homologues preceded the topological transformation of the apparatus that produced the characteristic ramiform-pectiniform apparatus architecture of ozarkodinids, prioniodontids and prioniodinids.

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