THE APPARATUS ARCHITECTURE OF *PANDERODUS* AND ITS IMPLICATIONS FOR CONIFORM CONODONT CLASSIFICATION

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ABSTRACT. The apparatus composition and architecture of the coniform conodont genus *Panderodus* (Llanvirn–Givetian) has been reconstructed from a bedding plane assemblage associated with soft parts from the Waukesha lagerstätte of Wisconsin, together with published clusters and discrete element collections. This modelling enables a redefinition of the apparatus and species concepts within *Panderodus*, which is now reconstructed as a nonimembrate apparatus, with four subdivisions in the graciliform element category. Architecturally the apparatus falls into three locational domains. The architecture of panderodontid conodonts confirms their status as a distinct ordinal-level group. Extrapolating this architectural model, it has been possible to recognize recurrent apparatus styles within non-panderodontid coniform genera such as *Besselodus* and *Dapsilodus*, lending a firm basis to their suprageneric classification.

THE mineralized oral apparatus is the only commonly preserved part of conodonts, usually as discrete elements in acid residues. The reconstruction of apparatuses from discrete elements provides the basis for a multielement taxonomy and any subsequent palaeobiological work. Features used for reconstruction include common co-occurrence and stratigraphical range, morphological similarities between elements, and comparison with templates provided by previously reconstructed apparatuses and natural assemblages. No attempt is made to reconstruct individuals, but rather to document the range of variation within a given species, independent of age, sex or any other individual factor (Smith *et al.* 1987). Multielement taxonomy has led to a number of major advances in rationalizing the classification and phylogeny of conodonts (Sweet 1988).

The discovery of the Granton conodont specimens with associated soft tissues (Briggs *et al.* 1983) has led to a number of papers (Aldridge *et al.* 1986, 1993; Aldridge 1987; Aldridge and Briggs 1986, 1989; Conway-Morris 1989) which have shown these ozarkodinids to be laterally compressed, some 40 mm long with caudal fins, a well-developed myomeric musculature, notochord and eyes. These animals are presumed to have been active, predatory, nektobenthonic, primitive chordates. The identification of cellular bone, enamel homologues and cartilage in conodont elements has confirmed the vertebrate nature of conodonts (Sansom *et al.* 1992).

Jeppsson (1971) produced a model of element arrangement in *Ozarkodina* Branson and Mehl apparatuses based upon isolated clusters and numerical methods. Work on the Granton animals and bedding plane assemblages (Aldridge *et al.* 1987) largely confirmed Jeppsson's model but, in addition, Aldridge *et al.* (1987) proposed a food gathering and processing function for the ozarkodinid apparatus. The anterior 'ramiform' basket was postulated to have a grasping function and the posterior pectiniform complex a slicing and grinding role. This model has been supported by detailed morphological analyses which propose a tooth-like function for the individual elements (Jeppsson 1979; Purnell and von Bitter 1992; Purnell 1993).

Although substantial advances have been made in reconstructing coniform apparatuses since the first attempts of Webers (1966) and Bergström and Sweet (1966), two major problems remain. Firstly, coniform elements show subtle changes in morphology, particularly in large collections, and it is often very difficult to reconstruct coniform apparatuses and distinguish between inter- and intra-specific characters. Secondly, there are few natural assemblages or diagenetic clusters with

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which to confirm apparatus reconstructions. With the discovery of a number of diagenetically fused clusters of the genus *Panderodus* Ethington (An *et al.* 1983; Kozur 1984; Balogh and Kozur 1985; Dzik and Drygant 1986), and the description of a *Panderodus* bedding plane assemblage with associated soft parts from the Silurian Konservat Lagerstätte of Waukesha, Wisconsin, USA (Smith *et al.* 1987), sufficient data are now available to refine the architectural and functional model for the *Panderodus* apparatus proposed by Smith *et al.* (1987). This is particularly pertinent as there is evidence that species of *Panderodus* had a pelagic rather than nektobenthic mode of life (Barnes, Rexroad and Miller 1973; Barnes and Fåhræus 1975; LeFèvre *et al.* 1976; Aldridge and Mabillard 1981). Additionally, there is some equivocal soft part evidence that suggests they may have had a fundamentally different body plan to that of ozarkodinid species, being dorsoventrally, rather than laterally, flattened (Smith *et al.* 1987; Conway-Morris 1989).

The architectural model presented offers the potential of simplifying the nomenclatural morass that has developed in *Panderodus* taxonomy, allowing a more precise biological diagnosis of constituent species.

DEVELOPMENT OF THE GENERIC AND SPECIES CONCEPT IN *PANDERODUS*

Bergström and Sweet (1966) produced the first multielement reconstruction of *Panderodus*. They recognized *Panderodus gracilis* (Branson and Mehl) as a bielemental apparatus (Text-fig. 1) which

Bergström and Sweet 1966	*Cooper 1975, 1976*	*Barnes 1977*	*Barnick 1977*	*Sweet 1979*	*Barnes et al. 1979*	*Nowlan and Barnes; McCracken and Barnes 1981*
P. gracilis	costate	narrow		arcuatiform	p	arcuatiform
			Sb	asimiliform		graciliform
			Sa	similiform		
P. compressus	simplexiform	wide	M	falciform	q	compressiform
			Sc	tortiform		

Fåhræus and Hunter 1985	*Dzik and Drygant 1986*	*Nowlan and McCracken (in Nowlan et al.) 1988*	*Jeppsson * 1983, 1989*	*Armstrong 1990*	*This Study descriptive*	*This Study locational*
D	hi	a/b	u	eq	arcuatiform	qa
C	ka/pl/tr/oz	b			asym. graciliform	qg
		c		sym. p	sub-sym. graciliform	qg
B	sp		ne	r	truncatiform	qt
A			lr		aequaliform	ae
E	no	e	f	sq	falciform	pf
		a		tp	tortiform	pt

TEXT-FIG. 1. Terminology used by previous authors to describe the *Panderodus* apparatus, and the notation developed herein. Several authors have placed the same elements in different categories, providing a degree of confusion when applying our view of the *Panderodus* apparatus. (* Jeppsson has described some of the elements of *Panderodus* without illustration, but the senior author has had access to his collections, and correlation with other schemes is derived from his proposed homologies between this apparatus and that of *Belodella*).

comprised a slender, elongate element (*P. gracilis* (Branson and Mehl)), and a laterally compressed element (*P. compressus* (Branson and Mehl)).

A bielemental reconstruction was retained by Cooper (1975, 1976) who referred to simplexiform (= compressiform) and costate (= graciliform) elements (Text-fig. 1). Cooper did, however, suggest

that further subdivisions could be made within the latter category. This was later formalized by Barrick (1977), who also tried to apply the nomenclature developed for ramiform-pectiniform apparatuses by Sweet and Schönlaub (1975). Barrick proposed that the compressiform element was homologous with the M element of ramiform-pectiniform apparatuses and the graciliform elements equivalent to the S elements of the first transition series; he gave no reason why the compressiform might not be a P ('platform') element.

Sweet (1979) considered the notational scheme applied to ramiform-pectiniform apparatuses to be inappropriate for coniform taxa, and applied a system based solely on the morphological character of *Panderodus* element (Text-fig. 1). The *Panderodus* apparatus proposed by Sweet (1979) was quinquemembrate, comprising three narrow-based costate elements (the asimiliform, similiform and arcuatiform), a laterally compressed falciform element (the compressiform or simplexiform of previous authors), and a small, twisted, tortiform element.

Barnes *et al.* (1979), in a review of Ordovician conodont genera, introduced a classification scheme specific to coniform apparatuses. They proposed several 'Types' which were defined upon the degree of elemental compression, cross-sectional symmetry and cusp curvature. *Panderodus* was described as a 'Type IIIB', bimembrate, apparatus, where cusp curvature was the most significant feature in delineating morphological transition between elements. In their notation scheme (Text-fig. 1) *Panderodus* comprised an erect p element (the graciliform) and a more highly recurved q element (the compressiform). Although oversimplified, this scheme had the advantage of allowing comparison of apparatuses without presupposing the homology of coniform and ramiform-pectiniform types.

Nowlan and Barnes (1981) suggested that three distinct apparatus types occur within species attributed to *Panderodus*. Group I, typified by *P. unicostatus* (Branson and Mehl), consisted of compressiform elements in association with a suite of variable graciliform and unicostate elements. Group II, included *P. gibber* Nowlan and Barnes, and was bimembrate with symmetrical and asymmetrical elements of similar general morphology. Group III, characterized by *P. liratus* Nowlan and Barnes, was also bimembrate, and divided into broad, laterally compressed, low-based elements, and long, slender, high-based elements.

Nowlan and McCracken (*in* Nowlan *et al.* 1988) applied the Barnes *et al.* (1979) scheme for ramiform-pectiniform apparatuses (Text-fig. 1), and modified the groupings to incorporate the discovery of additional elements. Group I panderodontids were quinquemembrate, with an a/b morphological transition series (Text-fig. 1), equivalent to the arcuatiform, asimiliform and tortiform elements, c subsymmetrical similiform elements. and the e falciform elements. Group II panderodontid apparatuses were trimembrate and consisted of a short unicostate a element, a symmetrical double furrowed c element, and a bicostate b element, similar in form to the a element. Group II apparatuses thus lacked the e (compressiform) element present in Group I species. Group III apparatuses were defined as bimembrate, with laterally compressed, broad, low-based elements (b/c) and long, slender a/b elements. Additional species, such as *Panderodus clinatus* McCracken and Barnes 1981 were found not to fit into any of the above groups.

Jeppsson (1983*a*, 1983*b*) mentioned the presence of eight to ten groups of homologous elements in each *Panderodus* species. Additionally, he implied locational homology between two of these element groups and those present in ozarkodinid apparatuses. One of these elements was totally symmetrical, unpaired and double-furrowed, and this he homologized with the tr element of Jeppsson (1971); the Sa of authors adopting Sweet and Schönlaub's (1975) terminology of other ramiform-pectiniform genera. Subsequently, Jeppsson (1989; Text-fig. 1) introduced a notation scheme for coniform taxa based upon reconstructions of *Belodella*. He proposed homology between certain elements in this apparatus and *Panderodus* species; namely, compressiform (f elements); unicostate, arcuatiform elements (u), symmetrical (tr) and short, twisted (ne) elements.

Fåhræus and Hunter (1985) recognized the presence of five morphological groupings in *Panderodus* apparatuses (Text-fig. 1). Group A consisted of symmetrical bi-furrowed elements, Groups B, C and D were described as asymmetrical 'gracilid' elements (similiform, asimiliform and arcuatiform *sensu* Sweet 1979), and Group E included 'compressid' elements. Additionally,

Fåhræus and Hunter (1985) suggested that a curvature transition series occurred within each element type and they implied that the curvature transition was continuous; thus a very large number of elements could form each series and be present in each individual.

In their description of a diagenetically fused cluster of *Panderodus unicostatus* elements from the Ukraine, Dzik and Drygant (1986) recognized the presence of seven paired element morphotypes, and reconstructed the apparatus in the form of a bilateral size gradation. Discussing the problems of producing a standard notation, they implied homology with other apparatuses by the application of Jeppsson's (1971) scheme, and utilized the descriptive terminology developed for *Panderodus* by Sweet (1979; Text-fig. 1). However, they felt that the compressiform element, the largest present in the Podolia cluster, was locationally equivalent to the ne element, a notable departure from Jeppsson's (1983*a*, 1983*b*, 1989) view. This is based on their assumption that this element was located anteriorly in the apparatus. Dzik and Drygant (1986) also described a pair of tr elements, rather than a single one. Five pairs of graciliform elements were found in the cluster, and were described as arcuatiform (locationally the ke), similiform (pl and tr) and asimiliform (oz and sp, the latter was markedly shorter than the other forms). The unicostate pair were described as tortiform and homologized with hi elements. They suggested that, for practical purposes, 'it seems enough to distinguish only three easily recognizable element types. They may be denominated with location symbols as ne, hi, and ke–sp, respectively' (Dzik and Drygant 1986, p. 138).

Dzik (1991) redefined this locational homology, with the graciliform suite represented by pl–ke elements, and the oz elements being absent. In addition, homology between *Panderodus* and ramiform-pectiniform apparatuses was further pursued, despite Dzik's proposal that *Panderodus* possessed a distinctive 'chaetognath-type' apparatus, lacking a medial element and the 'pharyngeal' components of ramiform-pectiniform apparatus.

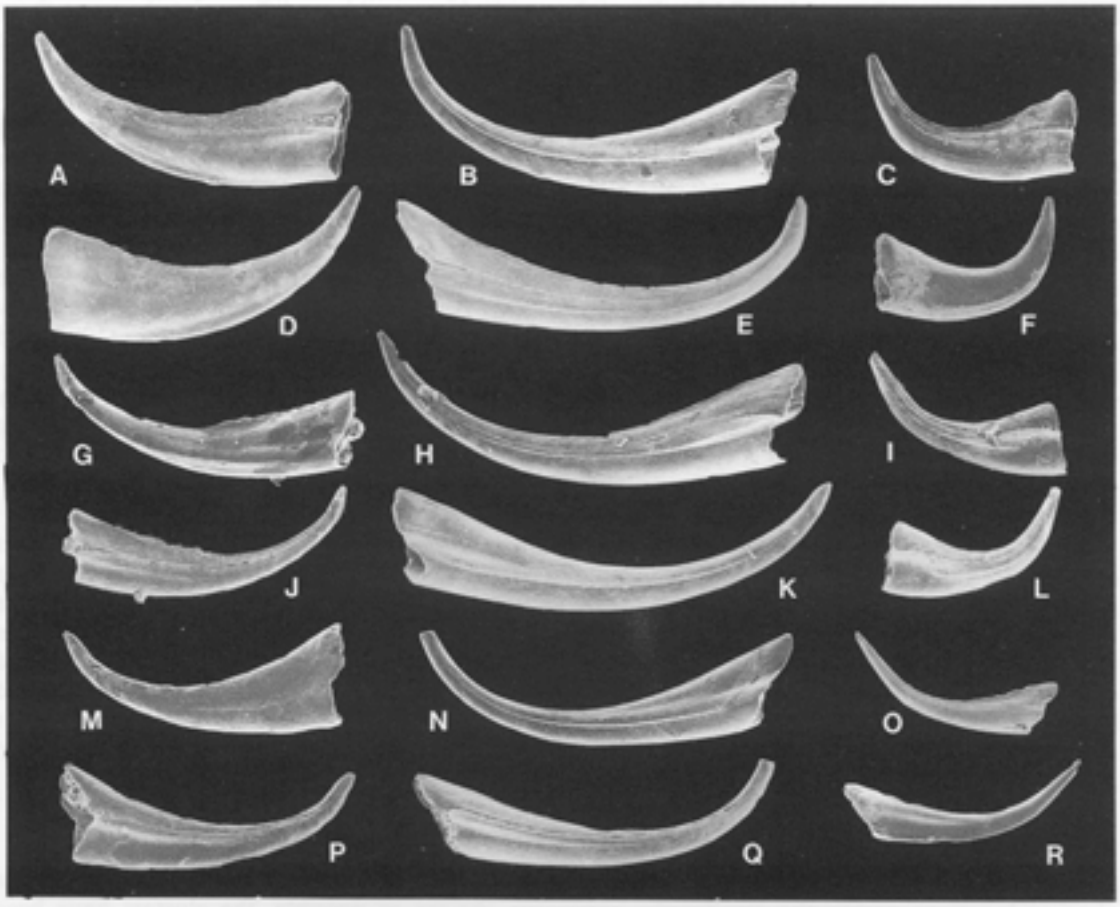
Armstrong (1990) expanded the Barnes *et al.* (1979) coniform scheme by subdividing the p and q categories using cusp cross-section (Text-fig. 1). The *Panderodus* apparatus thus contained sub-symmetrical and asymmetrical p and q elements, a tortiform tp element, and a short recurved r element. He considered the r element to be homologous with the oistodontiform element found in many Ordovician coniform taxa. Using this scheme, Armstrong (1990) proposed a homology of the elements in all Silurian coniform taxa, and suggested that this was the way forward in developing a suprageneric classification for coniform euconodonts.

COMPOSITION OF *PANDERODUS* APPARATUSES

In the following descriptions of *Panderodus* clusters, purely descriptive terms have been adopted. Six element morphotypes have been formalized in this study, although a further four sub-divisions within one element category have been recognized in isolated collections and natural assemblages of *Panderodus*. These categories are recognized on the basis of cusp curvature and cross-sectional symmetry. Eight are found as 'left' and 'right' pairs with single furrows on alternate lateral faces, whilst the ninth is symmetrical, furrowed on each lateral face and is thought to be unpaired. The major shape categories of Sweet (1979) have been modified and expanded, descriptive terminology largely follows Sweet (1981).

Falciform elements. (Text-fig. 2A, D) These have previously been described as simplexiform (Cooper 1975, 1976), compressiform (Nowlan and Barnes 1981; McCracken and Barnes 1981), ne (Dzik and Drygant 1986), e (Nowlan and McCracken *in* Nowlan *et al.* 1988), and f (Jeppsson 1989) elements (Text-fig. 1). In the type species, *Panderodus unicostatus*, these elements are characterized by gradually curved and laterally compressed bases, and have abbreviated cusps. Both the convex and concave edges of the elements are drawn into low keels.

Tortiform elements. (Text-fig. 2O, R) These have been alternatively termed tp by Armstrong (1990; Text-fig. 1). These elements are spatulate, and show torsion of the cusp away from the furrowed



TEXT-FIG. 2. *Panderodus acostatus* (Branson and Branson). Lapworth Museum, University of Birmingham; Kentucky, USA; Brassfield Formation, Silurian, Llandovery; sample collected and donated by R. J. Aldridge, Leicester, UK; ×60. A, D, BU 2258; lateral views of the furrowed and unfurrowed faces of a falciform (pf) element. B, E, BU 2259; lateral views of the unfurrowed and furrowed faces of a high-based asymmetrical graciliform (qg) element. C, F, BU 2260; lateral views of the furrowed and unfurrowed faces of a truncatiform (qt) element. G, J, BU 2261; lateral views of the unfurrowed and furrowed faces of an arcuatiform (qa) element. H, K, BU 2262; lateral views of the furrowed and unfurrowed faces of a low-based symmetrical graciliform (qg) element. I, L, BU 2263; lateral views of an aequaliform (ae) element. M, P, BU 2264; lateral views of the unfurrowed and furrowed faces of a high-based symmetrical graciliform (qg) element. N, Q, BU 2265; lateral views of the unfurrowed and furrowed faces of a low-based asymmetrical graciliform (qg) element. O, R, BU 2266; lateral views of the furrowed and unfurrowed faces of a tortiform (pt) element.

faces. The unfurrowed faces are excavated along their concave margins, while the convex margins are drawn out into sharp edges.

Graciliform elements. (Text-fig. 2B, E, H, K, M, N, P, Q) These have been previously described as asimiliform and similiform (Sweet 1979), ke–pl–tr–oz (Dzik and Drygant 1986), a/b, b, c, (Nowlan and McCracken *in* Nowlan *et al.* 1988), and sym. p (Armstrong 1990; Text-fig. 1). All elements are proclined and generally bicostate. Four morphotypes have been consistently identified in large collections, comprising asymmetric high and low based forms, and sub-symmetrical high and low

based forms. In the clusters described below, it has proved impossible to differentiate between these elements, as their lateral faces are largely obscured. Grouping of graciliform elements as a single category is therefore necessary.

Arcuatiform elements. (Text-fig. 2G, J) These are equivalent to the hi of Dzik and Drygant (1986) and the aq of Armstrong (1990; Text-fig. 1). They are generally unicostate elements which show a varying degree of torsion of their erect cusp towards the unfurrowed face. Occasionally, arcuatiform elements have a serrate keel developed on their concave edge.

Truncatiform elements [*new term*]. (Text-fig. 2C, F) These have been recognized as separate morphotypes by Jeppsson (1983*a*, 1983*b*, 1989) who described them as ne elements, and by Armstrong (1990) who described them as r elements (Text-fig. 1). Fåhræus and Hunter (1985) and Dzik and Drygant (1986) illustrated this form as B and sp elements respectively, but felt that they were merely the smallest end-member of the graciliform suite. Truncatiform elements are generally 50 per cent shorter than the graciliforms, and the unfurrowed face is drawn into a slight edge along their convex margin. The cusp is typically elongate, recurved and varies in torsion with respect to the base from species to species.

Aequaliform [*new term*]. (Text-fig. 2I, L) These bifurrowed elements have been illustrated by Sweet (1979, fig. 7.35) as similiform, and by Nowlan and McCracken (*in* Nowlan *et al.* 1988) variously as b/c (pl. 7, figs 23–24) and c (pl. 6, figs 12–13) elements. The only authors to have recognized the unique and consistent occurrence of this element in all *Panderodus* apparatuses have been Jeppsson (1983*a*, 1983*b*, 1989), who referred to this form as tr, and Fåhræus and Hunter (1985) who described these as Group A elements (Text-fig. 1). Dzik (1991) also discussed the presence of bi-furrowed elements, and considered them to be homologous with paired, asymmetrical elements in other apparatuses. These elements are truly symmetrical, and are similar in size to the truncatiform elements.

CLUSTER DESCRIPTIONS

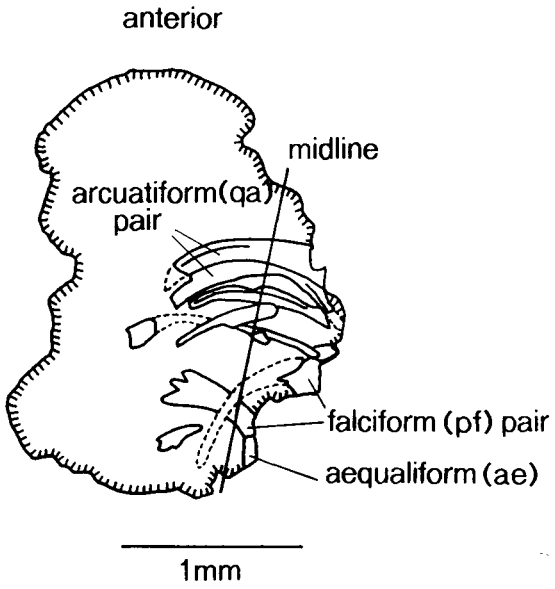
Three clusters and a single bedding plane assemblage are described below in an attempt to elucidate element locations within the *Panderodus* apparatus. As far as possible, the clusters have been selected on the basis of their completeness and structural integrity. Where necessary, sub-clusters within larger specimens have been utilized, but only if they show internal structural consistency *vis-à-vis* consistent element and furrow orientation. The Waukesha bedding plane assemblage provides the necessary architectural framework for the analysis, delineating the anterior and posterior of the apparatus, together with furrow orientation. The remaining clusters serve to fill the gaps in the jigsaw, and thus produce a complete architectural model of the *Panderodus* elemental apparatus.

Waukesha Bedding Plane Assemblage

The single specimen with soft parts preserved (Mikulic *et al.* 1985*a*, 1985*b*; Smith *et al.* 1987), comes from the upper Llandovery Brandon Bridge Konservat Lagerstätte of Waukesha County, Wisconsin, USA, and is the only described coniform euconodont bedding plane assemblage. The presence of a body trace is especially useful as it enables the determination of anterior and posterior in the *Panderodus* apparatus.

The arrangement of elements in the Waukesha bedding plane assemblage (Text-fig. 3) provides constraints for the modelling of three-dimensional apparatus architecture in *Panderodus*, as discussed by Smith *et al.* (1987) and outlined here.

(1) The asymmetrical elements (arcuatiform, graciliform, truncatiform, falciform and tortiform in the terminology used herein) lie in a paired relationship perpendicular to the plane of bilateral symmetry with a posterior and adaxial orientation to the cusp tips.



TEXT-FIG. 3. Camera lucida drawing of the assemblage of elements in the *Panderodus unicostatus* (Branson and Mehl) animal from the Brandon Bridge of Waukesha, Wisconsin, USA, UW4001/7a (part), Geology Museum, University of Wisconsin, Madison; modified from Smith *et al.* (1987, fig. 6.6).

(2) In these elements, the furrowed face shows a consistent orientation, and all the elements on the part have the furrowed faces uppermost.

(3) The arcuatiform element pair lies to the anterior of the assemblage, whilst the falciform element pair lies towards the posterior. An unknown number of pairs of graciliform elements lie between these.

(4) There is no apparent size gradation (*contra* the 'supertooth' model for *Panderodus* presented by Dzik and Drygant (1986)).

(5) The spacing of the elements in the anterior part of the assemblage is closer than that seen at the posterior, which may be either an original feature of the apparatus or the result of flattening of an arched array.

These criteria led Smith *et al.* (1987) to produce an apparatus architecture model for *Panderodus* consisting of two bilaterally opposed, linear and possible arched arrays, which may have been attached to a basal support.

Re-examination of a latex cast of the counterpart and published illustrations of the specimen has enabled the following, additional observations to be made. Firstly, a close study of the overlapping arrangement of the elements shows a consistent stacking with the furrowed faces exposed. Three dimensional modelling of the assemblage has shown that this pattern may only be produced from an opposed linear array by a posterior rotation and collapse of the element cusps with the furrows facing anterior. Secondly, Smith *et al.* (1987) did not recognize the occurrence of the aequaliform element in isolated collections of *Panderodus*, suggesting that such forms were aberrant or extreme morphotypes. However, from studies of discrete collections, it is clear that this element is a consistent and essential component of the apparatus (Jeppsson 1983*a*; Sansom 1992; see also comments by Sweet 1988, p. 57), and must be taken into account in any apparatus reconstruction.

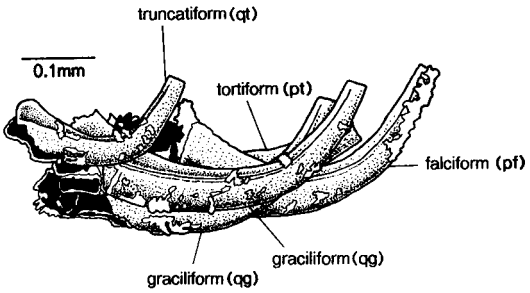
Two small element fragments are found behind the falciform element pair (Text-fig. 3). One of these lies in the same orientation as the paired elements, perpendicular to the plane of symmetry, and would appear to form part of the paired array. The other element is represented by an oblique cross-section, lying parallel to the midline of the assemblage, and the form suggests that this element pointed towards the anterior of the assemblage. Although it may represent the opposing pair of the first element, having been skewed somewhat from its original location, no other pairs show a similar dislocation, as a result this element may be considered as the symmetrical aequaliform element.

Nekézseny Cluster

Described as *Panderodus simplex* (Branson and Mehl) by Kozur (1984) and Balogh and Kozur (1985), this specimen was recovered from a middle Wenlock olistolith within the Devonian Strázsahegy Formation of Nekézseny, northern Hungary.

Panderodus simplex was originally erected as a form taxon and has been synonymized with *Panderodus unicostatus* (Cooper 1976; Armstrong 1990). Although the cluster has been lost (pers. comm. Kozur 1990), the illustrated elements show a number of differences from *Panderodus unicostatus*, notably that they are more recurved and robust. Until additional material is available for study, this specimen is best assigned to *Panderodus* aff. *P. unicostatus* (Branson and Mehl).

Five elements are joined along their lateral faces and they all have the same furrow orientation. Little post-mortem deformation is apparent, although the base of the falciform element is slightly displaced from the bases of the other elements. Text-figure 4 shows the cluster viewed anteriorly,



TEXT-FIG. 4. Cluster of *Panderodus* aff. *P. unicostatus* (Branson and Mehl) elements from a middle Wenlock olistolith within the Devonian Strázsahegy Formation, Nekézseny, northern Hungary. Illustrated by Kozur (1984, pl. 1 fig. 1) and Balogh and Kozur (1985, pl. 1 fig. 1) as *Panderodus simplex* (Branson and Mehl), this specimen has subsequently been lost (Kozur, pers. comm. 1990).

and identifies the element order. Based upon the furrow orientation seen in the Waukesha bedding plane assemblage, the element order from anterior to posterior in this cluster is truncatiform, graciliform, graciliform, falciform and tortiform. The Nekézseny cluster represents a complete posterior portion of half of a *Panderodus* apparatus.

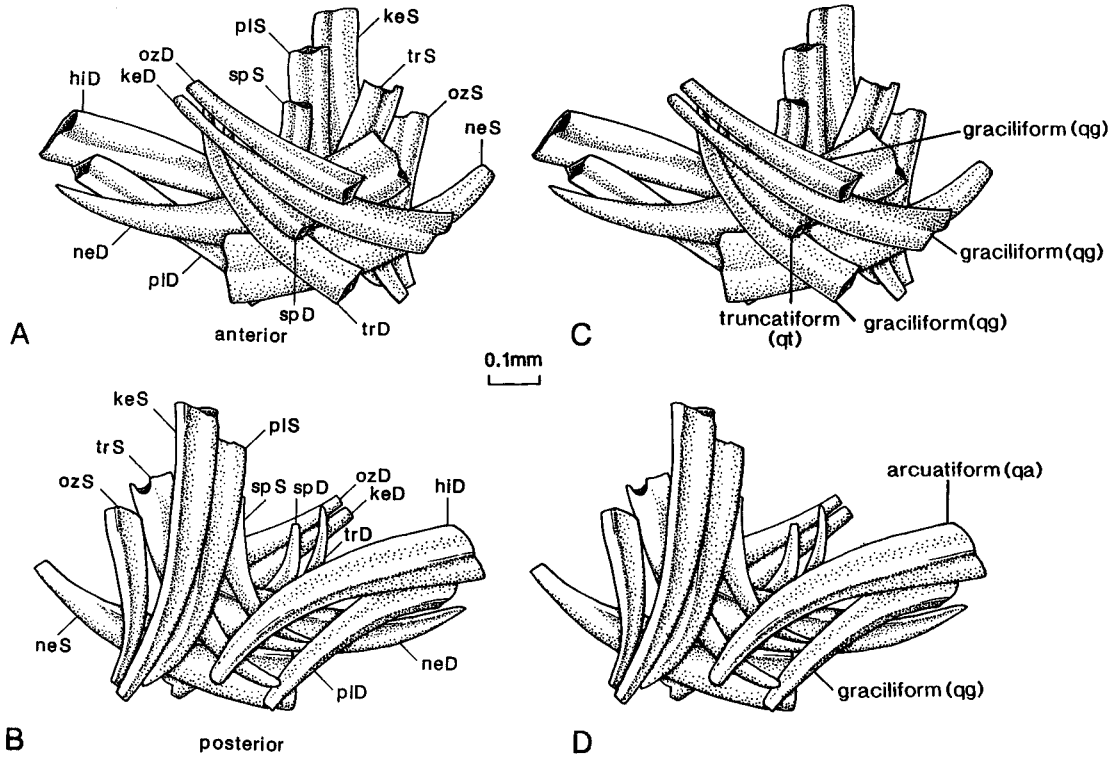
Podolia Cluster

This cluster (Text-fig. 5), consisting of thirteen elements identified as *Panderodus unicostatus* by Dzik and Drygant (1986), is from the Llandovery Teremcy Beds of Podolia, Ukraine. The specimen appears to have undergone considerable taphonomic deformation from the original element arrangement; however, all the elements appear to be asymmetrical and paired. Dzik and Drygant (1986) proposed a three-dimensional model for this cluster based on a size gradation through the elements. This gradation is more conceptual than observable, and the grasping apparatus of protoconodonts and chaetognaths seem to have acted as a template for their reconstruction. In order to explain the preservation of the Podolia cluster, it was necessary for Dzik and Drygant (1986, fig. 2B) to invoke a complex series of apparently random dislocations.

Whilst the cluster has been considerably deformed, two relatively coherent subclusters can be recognized and are of use in architectural restoration. These sub-clusters are selected on the basis of their lateral superposition and spatial arrangement. The similarity in cusp/furrow orientation shows them to have been derived from the same half of the apparatus.

Sub-cluster 1 (Text-fig. 5A, C) consists of four elements. The visible lateral faces of these elements are unfurrowed. The element order is a single graciliform, truncatiform, and two graciliforms. Correlation with the Nekézseny cluster is provided by the presence of two, elongate graciliform elements lying to the posterior of a short, recurved truncatiform element, and from the evidence of the Podolia cluster, an additional graciliform element lies to the anterior of this element.

The smaller sub-cluster 2 (Text-fig. 5B, D) lies on the opposite side of the main cluster, and consists of two elements. Both of the exposed faces are furrowed, the anteriormost is of arcuatiform



TEXT-FIG. 5. Cluster of *Panderodus unicostatus* (Branson and Mehl) elements from the Teremcy Beds, upper Llandovery, Studencyia, Podolia, Ukraine; ZPAL C.XV/2, Zaklad Paleobiologii PAN, Warszawa, Poland. A, B, redrawn from Dzik and Drygant (1986, fig. 3) following their notation; C, sub-cluster 1 of four elements; D, sub-cluster 2 consists of two elements.

morphology, and the element behind is a graciliform. The presence of the arcuatiform element to the anterior of the apparatus is also evident from the Waukesha assemblage.

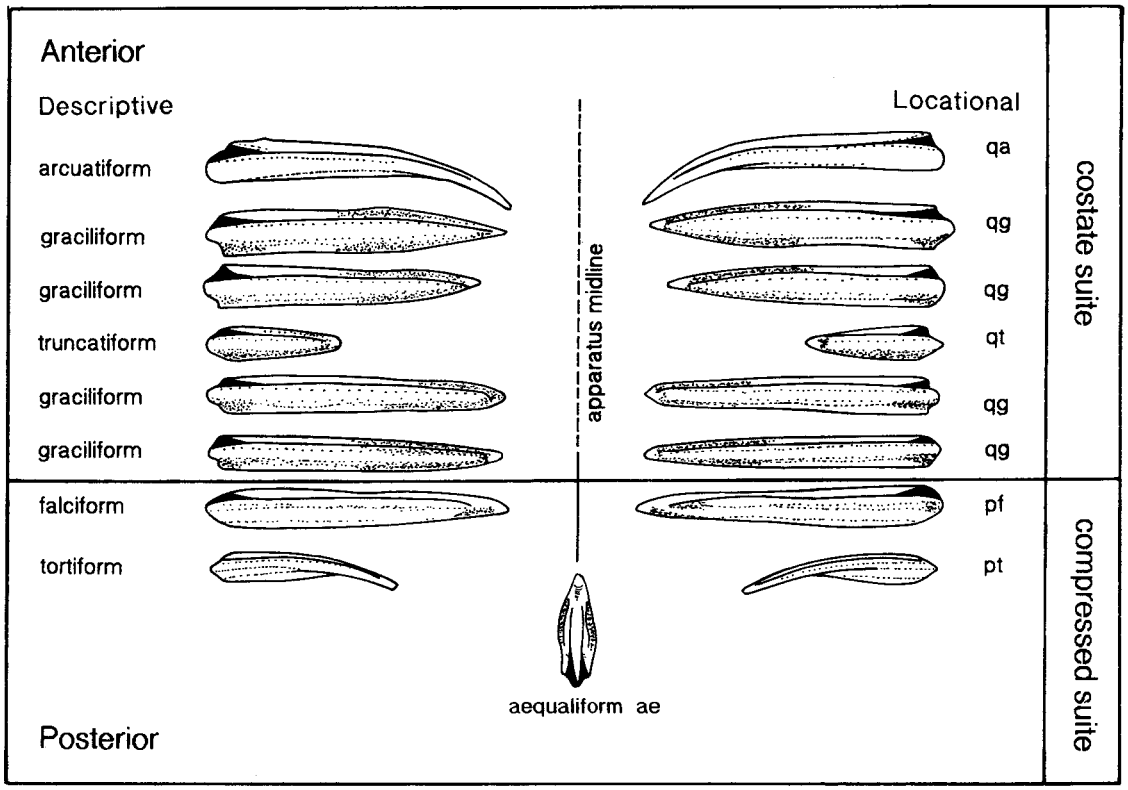
Shandong Cluster

Additional evidence is provided by a three element cluster (An *et al.* 1983; pl. 32, fig. 17*a–c*) from the Shandong Province of North China. This consists of a pair of graciliform elements lying adjacent to a single falciform element.

CLUSTER CORRELATION

Dzik and Drygant (1986) and Smith *et al.* (1987) concluded that the apparatus consisted of fourteen elements, whilst Jeppsson (1983*a*) implied a figure closer to 100. The latter figure was derived from the relative abundance of the symmetrical aequaliform element (tr of Jeppsson 1983*a*) in his discrete collections. Under-representation of this element could be due to its relatively small size and the possibility of selective hydrodynamic sorting in the environment of deposition (McGoff 1991), and/or loss through the sieve during processing (Jeppsson 1983*a*).

The identification and correlation of repeated element sequences in the clusters outlined above, permits formulation of the complete *Panderodus* apparatus (Text-fig. 6). The apparatus consists of seventeen elements, sixteen of which are found in two bilaterally opposed linear arrays. This element number is the same as that which may be inferred from discrete collections, suggesting that each



TEXT-FIG. 6. Architectural reconstruction of the *Panderodus* apparatus showing the differentiation of the paired elements into an anterior costate suite and a posterior compressed suite. The aequaliform ae element is thought to have lain on the midline somewhat to the posterior of the apparatus.

morphotype (including the four sub-divisions within the graciliform category) is a consistent component of the apparatus.

The apparatus plan of *Panderodus* falls into two suites of paired elements, an anterior costate suite and a posterior acostate, compressed suite (Text-fig. 6). The costate suite consists of an anterior pair of twisted unicostate arcuatiform elements, behind which are found four pairs of graciliform elements divided into two units by the truncatiform pair. The posterior compressed suite consists of the falciform and tortiform pairs. The final component of the apparatus is represented by the single aequaliform element lying along the apparatus midline. The medial placement of the aequaliform element is contrary to the interpretation of Dzik (1991) who argued that these elements occurred in pairs orientated perpendicularly across the plane of bilateral symmetry. This is the only truly symmetrical element in the apparatus, supporting a location on the midline.

The integrity of the genus Panderodus

Nowlan and Barnes (1981) and Nowlan and McCracken (*in* Nowlan *et al.* 1988) have suggested that a variety of apparatus styles are present within the genus *Panderodus*, and they questioned the generic assignment of those species which did not follow the *Panderodus unicostatus* apparatus plan. However, the available evidence from cluster data and discrete collections of well known species refutes the presence of more than one apparatus plan within the genus.

In those species of *Panderodus* which are well understood and for which large collections are available, it is possible to homologize all of the elements of the apparatus on morphological criteria

(Text-fig. 7) and identify the presence of a costate suite (arcuatiform and graciliform-truncatiform) and a compressed suite (falciform-tortiform) of paired elements. The symmetrical aequaliform is also consistently present. *Panderodus* is a unified genus based upon a single apparatus architecture, comprising three locational domains. Species can be diagnosed by variations in element morphology.

HOMOLOGY BETWEEN CONIFORM CONODONT APPARATUSES

Coniform locational nomenclature

Having established an architectural model for *Panderodus* it is now possible to propose a locational notation. The modified version of Sweet's (1979) nomenclature employed above is not applicable, since it is purely descriptive rather than locational; the aim here is to demonstrate locational homology, not a morphological comparison of elements. The locational scheme utilized here is an adaptation of the notation of Barnes *et al.* (1979), and subsequently modified by Armstrong (1990). It is important to emphasize that this scheme is now redefined in a locational sense and reference to its previous usage should be made with care.

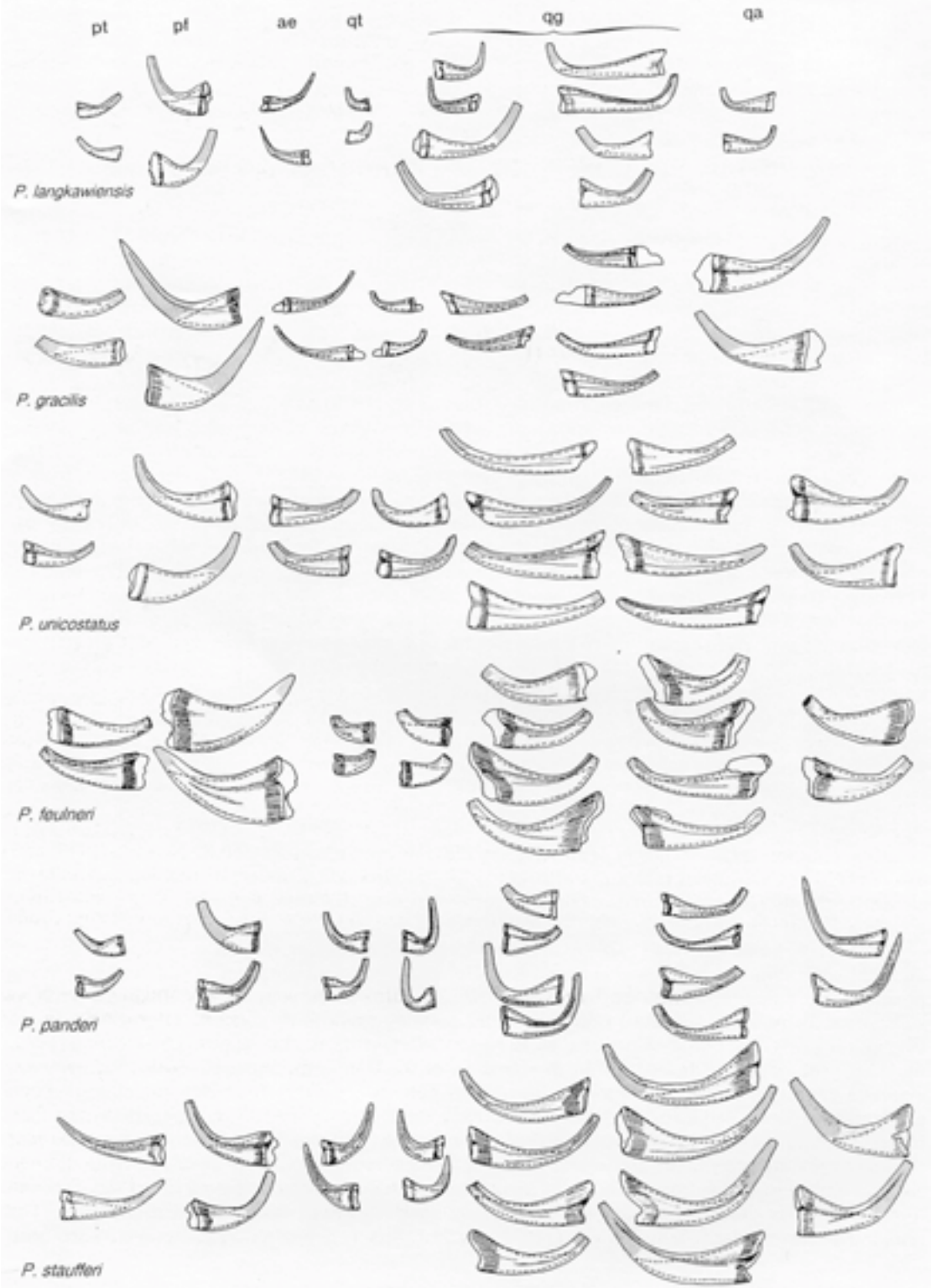
Armstrong (1990) refined the notation of Barnes *et al.* (1979) as a binomial scheme, one letter referring to general element shape and the other to cross-sectional shape and symmetry. As the location of the elements in *Panderodus* has been established, it is possible to further modify this scheme so that it reflects element position. The differentiation of the paired assemblage into two components is recognized by terming the anterior suite as 'q elements' and the posterior suite as 'p elements'. Further subdivisions of the element positions are denoted by a second letter (Text-fig. 6).

This notation, although developed from the element categories in *Panderodus*, has the advantage of being locational, and it is possible to compare coniform architectures where suitable data are available. The identification of homologous elements should lead to a 'natural' suprageneric classification, as suggested by Armstrong (1990), on the basis of apparatus similarities and/or reduction of elements in evolutionary lineages. A number of genera have been studied in an attempt to determine the wider applicability of the *Panderodus* apparatus model, although only genera known from clusters and closely related forms are discussed. Many coniform apparatuses are, as yet, incompletely understood. It is important to establish whether incompleteness of apparatus reconstruction is a result of biological, taphonomic or collection processes, as these characters are used to differentiate between apparatuses at the suprageneric level.

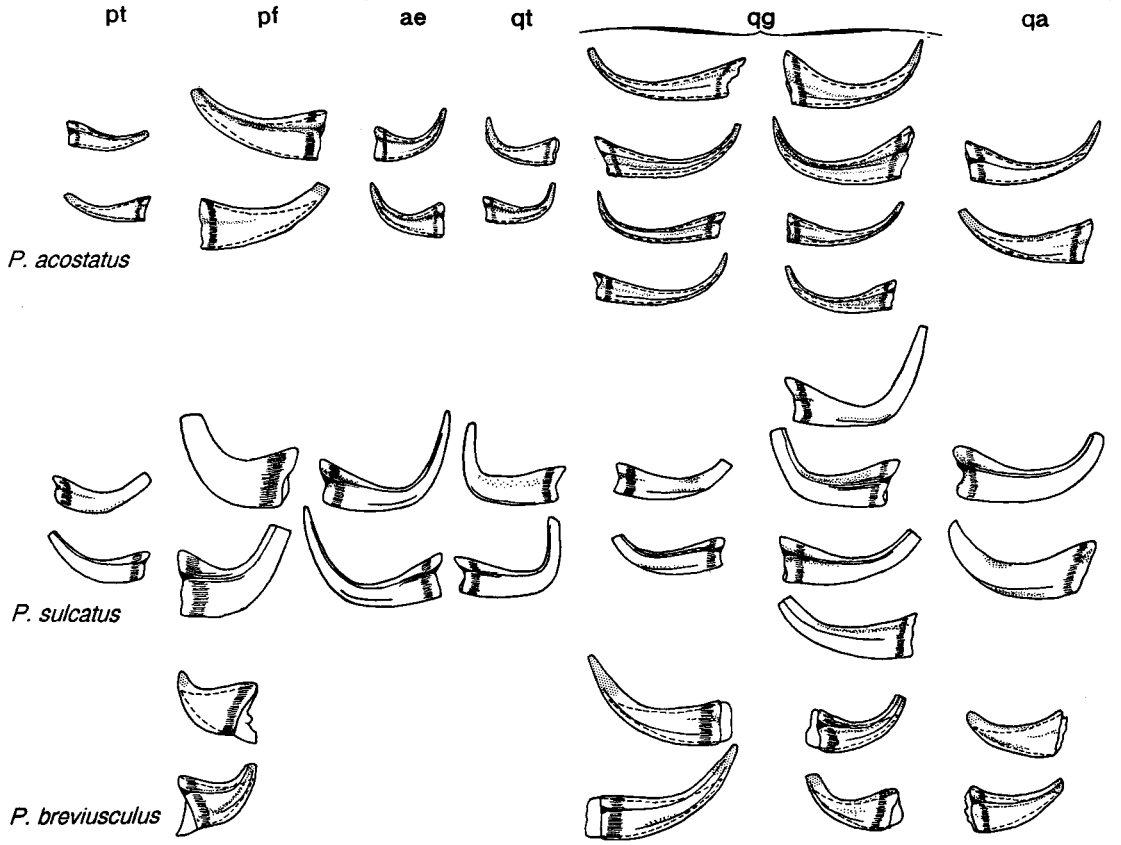
Applicability of the Panderodus *apparatus model to other panderodontid lineages*

Belodina compressa (*Branson and Mehl*). This species has been reconstructed by Nowlan (1979) and Sweet (1979) as a trimembrate apparatus consisting of elongate, slender, denticulate grandiform elements; tightly recurved, broad denticulate compressiform elements; and geniculate adenticulate eobelodiniform elements.

Barnes (1967) and Nowlan (1979) figured three clusters, and using these it is possible to develop an architectural model for *Belodina compressa*. For purposes of orientation, it is assumed that the position and function of lateral furrows in *Belodina* is homologous with *Panderodus*; this is substantiated by the similarity in structure and histology of the two genera (Barnes, Sass and Poplawski 1973). The cluster illustrated by Barnes (1967, text-fig. 2) and refigured by Nowlan (1979, fig. 35.2), shows minor dislocation in the position of the four component elements, but provides evidence for architectural homology with *Panderodus*. Within this four element cluster, three elements were described as grandiform and have the same furrow orientation, suggesting that they represent an undeformed sub-cluster. The anteriormost grandiform element is approximately half the size of the other elements and constitutes a new element not previously described from discrete element collections. The furrowed face of the remaining compressiform element lies in the opposite direction to the others, an orientation probably resulting from post-mortem dislocation. The remaining clusters figured by Nowlan (1979, pl. 35.1, figs 1–5 and pl. 35.1, figs 6–10) are both



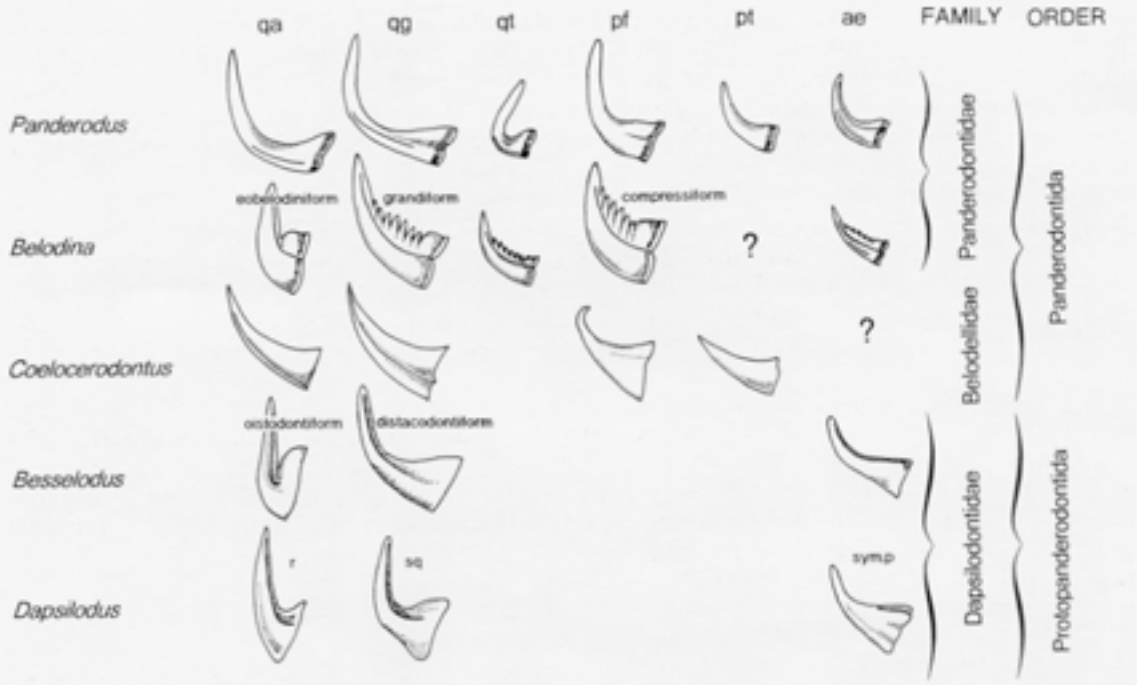
TEXT-FIG. 7. For legend see opposite.



TEXT-FIG. 7. Elements and apparatuses of nine species of *Panderodus*, showing the development of the basal cavity (dashed line) and distribution of white matter (shaded); not drawn to scale. Illustrated apparatuses are based upon elements figured by Sansom (1992), and a revision of the taxonomy of *Panderodus* is currently underway. The internal details of *P. sulcatus* are not known, and the *P. breviusculus* apparatus has not yet been fully reconstructed. *P. langkawiensis* (Igo and Koike); Gotland, Sweden; Lower Visby Beds, Silurian, Llandovery. *P. gracilis* (Branson and Mehl); Washington Land, North Greenland; Lafayette Bugt Formation, Silurian, Llandovery. *P. unicostatus* (Branson and Mehl); Missouri, USA; Bainbridge Formation, Silurian, Ludlow. *P. feulneri* (Glenister); Wulff Land, North Greenland; Morris Bugt Group, Ordovician, Caradoc. *P. panderi* (Stauffer); Leijiatun, China; Xiushan Formation, Silurian, Llandovery. *P. staufferi* (Branson, Mehl and Branson); Gotland, Sweden; Upper Visby Beds, Silurian, Wenlock. *P. acostatus* (Branson and Branson); Kentucky, USA; Brassfield Formation, Silurian, Llandovery. *P. sulcatus* (Fåhræus); Jämtland, Sweden; Flåsjö Formation, Ordovician, Llanvirn. *P. breviusculus* Barnes; Wulff Land, North Greenland; Morris Bugt Group, Ordovician, Caradoc.

formed from two elements, and consist of a grandiform element in juxtaposition with an eobelodiniform element and a broken compressiform or grandiform element respectively. In the former case the furrows are opposed whilst in the latter they face in the same direction.

It is probable that the grandiform elements of *Belodina* and the graciliform elements of *Panderodus* are homologous (Text-fig. 8) and they both occupied the qg positions. In both genera these elements are elongate and slender, and occurred as multiple pairs. The *Belodina* compressiform element is morphologically similar to the falciform element occupying the pf location in *Panderodus*. The small, truncated grandiform element of *Belodina* compares with the truncatiform (qt) element of *Panderodus* in being considerably shorter than the elements occupying the qg locations. The erect cusp of the eobelodiniform element of *Belodina* shows a degree of torsion away from its furrowed lateral face, a feature seen in the arcuatiform elements occupying the qa position in *Panderodus*.



TEXT-FIG. 8. Apparatus homologies and putative suprageneric reclassification of the coniform taxa discussed in the text; not drawn to scale. Descriptive terminology for *Belodina* is from Nowlan (1979), for *Besselodus* from Aldridge (1982) and *Dapsilodus* from Armstrong (1990). The presence of additional elements in *Belodina*, *Coelocerodontus* and *Besselodus* is discussed in the text.

Clusters and published reconstructions of *Belodina compressa* lack tortiform (pt) and aequaliform (ae) homologues. Nowlan and Barnes (1981) included torted, spatulate elements, morphologically similar to the pt, in the grandiform suite of *Belodina arca* Sweet and *Belodina dispansa* (Glenister). In addition, small, double furrowed belodinid elements have been included in Gen. *et*. sp. nov. A of McCracken (1987, pl. 1 figs 16, 21, 22). These occur in samples containing *Belodina confluens* Sweet and it is possible that these elements may be part of a single apparatus. If this is the case, the double furrowed elements would be ae homologues and the apparatus of *Belodina* would comprise the three locational domains identified in *Panderodus*. This new concept is consistent with the familial classifications of Clark (1981), Sweet (1988) and Dzik (1991).

Wider applicability of the Panderodus *apparatus model*

Clusters of coniform elements have also been described for *Coelocerodontus*, a member of the Family Belodellidae (*sensu* Sweet 1988), and *Besselodus* (Family Unknown *sensu* Clark 1981; Family Daposilodontidae *sensu* Sweet 1988; Family Strachanognathidae *sensu* Dzik 1991).

Coelocerodontus *Ethington*. Andres (1988) illustrated clusters of *Coelocerodontus*, from the Tremadoc of Öland, and proposed an apparatus architecture (Andres 1988, fig. 17) which comprised an anterior, unicostate element (equivalent to the qa element in the *Panderodus* apparatus), a suite of at least five, bicostate (qg) elements, a laterally compressed (pf) element and a torted, unicostate (pt) element at the posterior of the paired assemblage. A qt element is not seen in the clusters or has been described as a discrete element. Given the apparent completeness of these clusters, it seems likely that this position was occupied by an element with a similar morphology to those occupying the qg locations in the *Coelocerodontus* apparatus.

Müller and Hinz (1991, pl. 41, figs 11, 14, 16) illustrated two well-preserved clusters of *Coelocerodontus*. In one of these (pl. 41, figs 11, 14), a short element is present. This was not included in their apparatus reconstruction, and has not been previously described from discrete elements collections. The size and shape of this element suggests it may be an ae homologue. If this is the case, then *Coelocerodontus* has elements in the three locational domains described for the Panderodontida (Text-fig. 8).

Besselodus *Aldridge and* Dapsilodus *Cooper*. These two genera are considered to be closely related (Sweet 1988) and are considered together. Aldridge (1982, pl. 44, figs 1–4) described a cluster of *Besselodus* from the Aleqatsiaq Fjord Formation of Washington Land, western North Greenland. This comprises six distacodontiform (qg) element and a single oistodontiform (qa) element. An additional, symmetrical (ae) element was reported by Nowlan and McCracken (*in* Nowlan *et al.* 1988, pl. 2, figs 7–8, 13–15).

Dapsilodus was described as trimembrate by Cooper (1976) and Armstrong (1990). Armstrong separated sym. p elements (ae), sq elements (qg) and r elements (qa). The ae element occurred with a relatively low abundance of one to fifteen qg and qa elements. The apparatus structures of *Dapsilodus* and *Besselodus* are identical and are divisible into a qa pair, a costate qg suite and a single ae element. They differ from *Panderodus* as both *Dapsilodus* and *Besselodus* lack a distinct posterior suite of p elements (Text-fig. 8).

Implications for coniform suprageneric classification

Recent high level classifications (Sweet 1988; Dzik 1991; Aldridge and Smith 1993) have focussed on apparatus structure and morphological homology between elements, but must be considered probationary pending further information (Armstrong 1990; Aldridge and Smith 1993). Although we have only discussed apparatus homology in five coniform genera, it is clear that architectural homology provides one of the few testable ways by which a biologically sound suprageneric classification for conodonts can be established.

The identification of shared apparatus components leads to a re-definition of the Family Panderodontidae, and it is proposed here that all coniform apparatuses whose elements possess a panderodontid furrow and are thought to exhibit a fully developed apparatus (see Text-fig. 8) should be placed within this suprageneric unit. *Panderodus* and, with less certainty, *Belodina* belong here. Other genera which have previously been included within the panderodontids include *Pseudoobelodina*, *Parabelodina*, *Culumbodina* and *Plegagnathus* are known from small collections from the middle and upper Ordovician, and have been reconstructed as quadrimembrate or quinquemembrate apparatuses (Sweet 1988). Given the low abundance of elements referable to these forms, their classification within the Family Panderodontidae is based only upon their development of a panderodontid furrow, and perhaps this should be questioned until further information on their apparatus structure is forthcoming.

It is also proposed that all coniform apparatuses which exhibit differentiation into an anterior qa–qg domain, a posterior pf–pt domain, and a symmetrical ae component should be reclassified within the Order Panderodontida. The presence of a truncated qt element may be a feature of the Panderodontidae, but in other apparatuses it does not appear to be differentiated. Both Sweet (1988) and Aldridge and Smith (1993) rejected any phylogenetic relationship between *Coelocerodontus* and *Panderodus*, placing the former in the Order Belodellida and the latter in the Order Panderodontida. The similarity between the apparatus model of Andres (1988) for *Coelocerodontus*, together with the possible presence of an additional ae component (see discussion above), and the apparatus of *Panderodus* suggests that they should be united within the Order Panderodontida. In addition, Jeppsson (1989) has proposed morphological homology between the apparatuses of *Belodella* and *Panderodus* based upon large discrete element collections. If this observation can be further substantiated with architectural data, then the Family Belodellidae should be transferred to the Order Panderodontida (Dzik 1991).

Besselodus and *Dapsilodus* were classified within the Order Belodellida by Sweet (1988), which was combined with the Order Panderodontida by Dzik (1991), whilst Aldridge and Smith (1993) placed the two genera in their Order Protopanderodontida. The homology proposed here between these two apparatuses and that of *Panderodus* (Text-fig. 8) suggests that *Besselodus* and *Dapsilodus* lack a posterior domain of p elements. This feature of their apparatuses places them outside of the concept of the Order Panderodontida adopted here. McCracken (1989) has reconstructed the apparatus of *Protopanderodus* with a morphological transition series of costate a/b-c elements (?qg homologues) and grooved e elements (morphologically similar to the qa elements of *Besselodus* and *Dapsilodus*). This similarity in apparatus structure argues in favour of following Aldridge and Smith (1993) in including *Besselodus* and *Dapsilodus* within the Order Protopanderodontida.

POSSIBLE HOMOLOGY WITH RAMIFORM-PECTINIFORM APPARATUSES

If conodonts form a monophyletic clade (Conway-Morris 1989), then it is a logical step to try and develop a unified locational apparatus notation, which would allow direct homology to be drawn between ramiform-pectiniform and coniform apparatuses. Many authors have proposed universally applicable schemes (Barrick 1977; Orchard 1980; Sweet 1988; Nowlan and McCracken *in* Nowlan *et al.* 1988) based purely on morphological comparisons of elements, whilst others have used locational models for coniform apparatuses which we consider erroneous (Dzik and Drygant 1986; Dzik 1986, 1991). The proposed unification of a coniform apparatus notation enables comparison with ramiform-pectiniform apparatuses.

Both types of apparatus show a similar broad differentiation into three locational domains. In the ramiform-pectiniform system based upon ozarkodinid architecture, apparatuses can be described as comprising an anterior, symmetry transition series of S elements (including a symmetrical Sa), lateral M elements and posteror P elements. Sb, Sc, Sd and M, and P elements fall into two morphologically, locationally and functionally distinct units. The Sa element is assumed to lie on the midline of the apparatus and is associated with the S and M elements (Aldridge *et al.* 1987). In our locational scheme for coniforms the fully developed apparatus, typified by *Panderodus*, contains the qa–qg–qt–qg domain, the pf–pt domain and the ae element.

Although such a comparison appears to be compelling, it overlooks a potentially crucial difference between the two architectures. The orientation of the anterior paired elements with respect to the apparatus midline is diametrically opposed. In coniform apparatuses they lie perpendicular to the plane of symmetry, and in ramiform-pectiniforms they are parallel (Smith 1990). At present, no intermediates between these architectural types are known. Without relevant architectural information from Lower Ordovician taxa, it is possible that broad agreement in apparatus style may reflect functional convergence rather than actual locational homology. If architectural information is forthcoming for primitive conodonts, it may be possible to derive a universally applicable nomenclatural scheme based upon such a model. Current restriction of our knowledge to two widely divergent clades argues in favour of a conservative approach to apparatus homology.

CONCLUSIONS

Detailed analysis of published clusters and knowledge of element morphologies from large dicrete collections has enabled the development of an apparatus architecture model for *Panderodus*. This enables a redefinition of the species concept for this genus, with the apparatus consisting of eight element pairs and a single symmetrical component. Architecturally, the *Panderodus* apparatus is divisible into three locational domains, the anterior qa–qg–qt–qg paired costate suite, the posterior pf–pt compressed elements, and the symmetrical component which lies along the apparatus midline.

The comparison of other coniform taxa with the *Panderodus* apparatus has initiated a re-assessment of their suprageneric classification. It is proposed that those coniform apparatuses, which exhibit a general differentiation into the same three locational domains identified in *Panderodus*, are placed within the Order Panderodontida. Apparatuses which follow the *Panderodus*

plan precisely, including qt elements, and also possessing panderodontid furrows, are included within the Family Panderodontidae. The identification of homologous apparatus components is aided by the development of unified locational notation specific to coniform conodonts.

Although there are now two well-founded architectural models for conodont apparatuses, these are based upon the morphologically distinct and separate panderodontid and ozarkodinid lineages. This degree of phylogenetic separation and differences in the orientation of the apparatus components with respect to the apparatus midline hampers the recognition of homologous element locations, thus the development of a unified notational scheme is deferred until further data is available. Only with additional architectural data will it be possible to establish a stable suprageneric classification for all conodonts, and hence propose macroevolutionary models for the development of the oral apparatus of the earliest vertebrates.

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