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THE PALAEOBIOLOGY OF THE PANDERODONTACEA AND SELECTED OTHER EUCONODONTS

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(Graduate Society)

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Acknowledgements

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Dedicated to my mother,

Helen C. Sansom (1939 - 1981)

who pointed me towards academia with the immortal words:

"Ivan, you're a bit of a lazy sod, I think you should consider going to

University"

" Palaeontologists are traditionally famous (or infamous) for reconstructing whole animals from the debris of death. Mostly they cheat."

Stefan Bengtson 1990, Nature vol. 345, p. 765.

Abstract

The apparatus composition and three-dimensional architecture of the coniform conodont genus *Panderodus* (Llanvirn - Givetian) has been reconstructed. This modelling has led to a re-definition of the species concept within *Panderodus*, which is now reconstructed as a septimembrate apparatus. Taxonomic revision enables the recognition of twelve distinct species, characterised on gross morphological criteria. Using the *Panderodus* model, it has been possible to recognise recurrent apparatus styles within other coniform genera. This will provide a basis for future suprageneric classification.

Homology between coniform and ramiform-pectiniform apparatuses has enabled the development of a unified locational notation for conodonts. A new functional model is presented, highlighting the close similarities of conodont oral apparatuses with those of the petromyzontids.

Investigations into the histology of selected conodont elements have identified the presence of cellular bone, two enamel homologues, and globular cartilage. These provide definitive evidence for the vertebrate origins of conodonts, and revised growth models for elements are presented on the basis of these new observations. Cladistic analysis of the expanded character set places conodonts as a sister-group to the "dentineous" craniates. Dentine is no longer recognised as the primitive vertebrate hard tissue. Previous models of early vertebrate hard tissue development, and their significance in evolutionary studies, needs re-evaluation.

Chapter 1

INTRODUCTION

In the Treatise on Invertebrate Paleontology (1981, p. W78), K.J. Müller wrote that the nature of conodonts "is considered by many palaeontologists to be one of the most fundamental unanswered questions in systematic palaeontology".

A brief history of discovery and the development of conodont taxonomy

Conodont elements were first discovered by Pander from the Lower Ordovician and Silurian of Estonia, and the Carboniferous of Russia sometime between 1833 and 1844 (Sweet 1988). When these microscopic, tooth-like fossils were formally described in 1856, Pander referred to them as the teeth and jaws of an hitherto unknown group of fish, which he named *Conodonten*. In classifying his specimens, Pander chose shape as the most important character, thus introducing *form taxonomy* into conodont studies.

Hinde (1879) described a bedding plane cluster from the Devonian of New York, which was composed of multiple element morphologies. Hinde regarded this accumulation as the skeletal apparatus of a single conodont, and named the species *Polygnathus dubius* ("doubtful many jaws"). Thus, Hinde pre-empted subsequent developments in the species concept, although it took nearly a century for his views to become widely accepted (see below).

Until the 1930's, conodonts were largely regarded as palaeontological curios. This changed with the publication by Branson and Mehl (1933) of their *Conodont Studies*. This initiated the widespread use of conodonts in biostratigraphy, a field of study which dominates conodont publications to this day. At this time, the known stratigraphic range of conodont elements was similarly revised, and now they are recorded from the Late Cambrian to the latest Triassic.

Although Schmidt (1934) and Scott (1934) had followed Hinde (1879) in reporting clusters of morphologically distinct elements on the surfaces of bedding planes, form taxonomy remained the predominant style of conodont systematics. With the recognition of recurrent groups of elements in their collections, Bergström and Sweet (1966), and Webers (1966) established taxonomic diagnoses based upon these observations, firmly introducing the concept of *multielement* species that had been nucleated by Hinde.

Multielement apparatus reconstructions are now based upon stratigraphic co-occurrence, similarities of one or more morphological character, and reference to the compositions of apparatuses already described. Statistical clustering has also been used to provide an empirical base for such reconstructions (Sweet 1988). The biological validity of multielement species was confirmed by the discovery of a multielement apparatus in the Granton animal specimens from the Lower Carboniferous of Edinburgh (Briggs *et al.* 1983; Aldridge *et al.* 1986).

The Granton conodont animals

Claims for the discovery of conodont animals have been made by Melton and Scott (1973) and Conway Morris (1976). These reports are now considered erroneous. Melton and Scott's 'conodontochordates' have been reinterpreted as conodontophages (Lindström 1974). *Odontogriphus omalus* Conway Morris does not possess preserved elements and predates the known fossil record of conodonts. Thus the Granton animals were the first direct evidence for the nature of the conodont *bauplan.*

The first specimen was described by Briggs *et al.* (1983) and assigned to *Clydagnathus* ? cf. *cavusformis* Rhodes, Austin and Druce. A further three specimens were reported by Aldridge *et al.* (1986), and an additional five specimens await the publication of a detailed description (Aldridge *et al.* 1988). These animals were elongate, approximately 40 mm in total length and 2 mm across, and the form of the body trace suggested that they were laterally compressed. Oblique v-shaped

2

structures, which are found down the length of the body, are evidence of segmentation, possibly somites, whilst a series longitudinal traces which run from the head region to the tail have been interpreted variously as the remains of a notochord (Conway Morris 1989) or gut walls (Aldridge *et al.* 1986). Two of the described specimens have the remnants of fin rays around their tail region, and Aldridge *et al.* (1986) have suggested that two caudal fins may be present.

The Waukesha *Panderodus* animal

A single specimen of *Panderodus unicostatus* (Branson and Mehl) animal has been recorded from the Silurian of Wisconsin (Mikulic *et al.* 1985a,b). The comparatively poor preservation of this specimen has restricted observations on the whole animal anatomy. However, this specimen has particular relevance as it provides evidence for the nature of the coniform conodont *bauplan*.
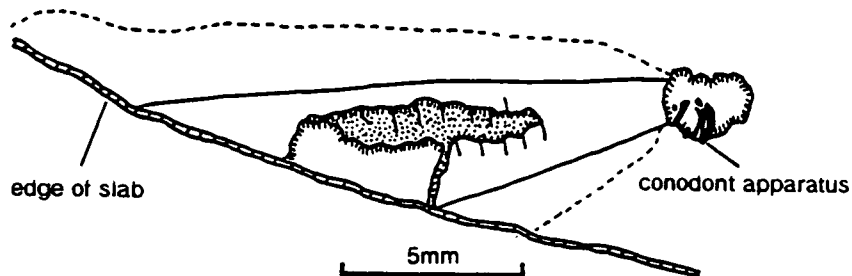
TEXT-FIG. 1.1. Camera-lucida drawing of *Panderodus unicostatus* (Branson and Mehl) animal, UW4001/7a, Geology Museum, University of Wisconsin, Madison, anterior to the right; showing position of the conodont apparatus and segmentation of the trunk (Taken from Smith *et al.* 1987, fig. 6.2).

Smith *et al.* (1987) described the soft parts of this specimen, which possesses a multielement coniform apparatus at the anterior of the specimen (a revised description of element assemblage follows in Chapter 2). The trace of the trunk expands from 1.3mm across just behind the apparatus, to at least 5mm in extrapolated

width before the impression is terminated against the edge of the slab (Text-fig. 1.1). Lateral traces have been interpreted as representing segmentation, and Smith *et al* (1987) have suggested that at least 20 somites were present in the preserved section.

The form of the body trace suggested a more expanded *bauplan* than is evident from the Granton specimens, which have a maximum trunk width of 2mm. Additionally, the orientation of the elements in the apparatus suggests that the body was dorso-ventrally compressed, rather than laterally compressed as in the case of ramiform-bearing conodonts (Smith *et al* 1987).

Conodont phylogeny

The debate on the zoological affinities of conodont elements has included claims that they were the remains of algae (Fahlbusch 1964), vascular plants (Nease 1969), conularids (Bischoff 1973), nematodes (Denham 1944), gnathostomulids (Durden 1969), molluscs (Loomis 1936), annelids (Rhodes 1952), arthropods (Harley 1861), lophophorates (Lindström 1973; Conway-Morris 1976), chaetognaths (Rietschel 1973), and chordates, ranging from planktonic protovertebrates (Halstead 1968) to gnathostomes (Demanet 1939).

The discovery and description of the Granton ramiform-bearing specimens and the Waukesha *Panderodus* animal have produced a number of publications reassessing the origin of the conodonts in the chaetognaths (Bengtson 1983; Szaniawski 1987), aplacophoran molluscs (Tillier and Cuif 1986), and cyclostomes (Aldridge *et al* 1986; Briggs *et al* 1987; Smith *et al* 1987). In addition, it has been suggested that conodonts possess enough unique characters to warrant phylum status (Sweet 1988). Although our knowledge of the conodont bodyplan has been greatly increased by the description of these soft-bodied specimens, and the phylogenetic debate has become somewhat more focus ed, definitive evidence needs to be discovered from other lines of inquiry before conodonts can be conclusively assigned to another group of organisms.

Conodont palaeobiology

The very nature of conodonts leads to a sharp preservational bias in favour of the microscopic phosphatised elements which the animal bore. Thus the conodont palaeobiologist has to extract as much information as possible from the rare, special preservation provided by soft-bodied specimens, element clusters and bedding plane assemblages. Four fields of study can be identified :

      1) Whole animal anatomy

      2) Apparatus architecture

      3) Apparatus function morphology

      4) Element morphology and ultrastructure

All of these techniques have been previously applied in conodont studies, but principally on ramiform-bearing animals. This thesis presents an integrated approach to coniform, 'simple cone', conodonts, using the four techniques outlined above, and attempts to interpret aspects of these animals in a biological context.

This research has been focus ed largely on the genus *Panderodus* as, uniquely among coniform conodonts, a soft-bodied trace and bedding plane assemblage is known (the Waukesha specimen described above). Additionally, an increasing number of element clusters have been described, and these provide a crucial test of apparatus reconstructions and architectural models.

Chapter 2.

THE APPARATUS ARCHITECTURE
OF *PANDERODUS*

2.1 INTRODUCTION

The mineralised oral apparatus is the only commonly preserved part of the conodont animal. Reconstructing this apparatus from discrete elements isolated from sediments provides the basis for multielement taxonomy and any subsequent palaeobiological work. Features such as common co-occurrence and stratigraphical range, morphological similarities between elements, the comparison with previously reconstructed species and natural assemblages are used in the reconstruction of the apparatus. 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) led to a number of papers (Aldridge *et al.* 1986; Aldridge 1987; Aldridge and Briggs 1986, 1989) which have shown these ozarkodinid animals to be laterally compressed, some 40mm long with caudal fins, with a well developed musculature and a putative rudimentary notochord (Conway-Morris 1989). These animals were presumed to be active, predatory, nektobenthonic, primitive chordates.

Jeppsson (1971) produced a model of element arrangement in *Ozarkodina* apparatuses based upon isolated clusters and numerical methods. Work on the Granton animals and previously documented bedding plane assemblages (Aldridge *et al.* 1987) largely confirmed Jeppsson's model. Additionally, Aldridge *et al.* (1987)

proposed a food gathering and processing function for the ozarkodinid apparatus, with an anterior grasping or 'ramiform' basket and a posterior slicing and grinding 'platform' complex. This work has dispelled alternative hypotheses that some conodont elements may have functioned as tentacular supports (Lindström 1974), copulatory structures (Denham 1944) or as internal features of a sieving and milling apparatus (Nicoll 1985; see Chapter 4 for a review).

Despite some Lower Palaeozoic faunas being made up of at least 50% coniform taxa, and the occurrence of many samples where the coniforms vastly out-number ramiform-pectiniform elements, the methodology of multielement taxonomy has proved difficult to apply to coniform collections, thus hampering palaeobiological work on these genera. Two major problems apply to coniform apparatus reconstruction. 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 variable characters. Secondly, there are few natural assemblages or diagenetic clusters with which to confirm apparatus reconstructions. With the recent discovery of a number of diagenetically fused clusters of the genus *Panderodus* (An *et al.* 1983; Kozur 1984; Balogh and Kozur 1985; Dzik and Drygant 1986), and the description of a coniform-bearing *Panderodus* animal from the Silurian Konservat Lagerstätte at Waukesha, Wisconsin (Smith *et al.* 1987), sufficient data are now available to develop an architectural and functional paradigm for the *Panderodus* apparatus. This is particularly pertinent as many workers believe that species of *Panderodus* had a pelagic rather than nektobenthic mode of life (Barnes *et al.* 1973; Barnes and Fåhræus 1975; LeFèvre *et al.* 1976; Aldridge and Mabillard 1981). Additionally, the available soft-part evidence suggests that they may have had a fundamentally different body plan to that of ozarkodinid species, being dorso-ventrally, rather than laterally, flattened (Smith *et al.* 1987; Conway-Morris 1989).

The architectural paradigm presented offers the potential of simplifying the nomenclatural morass that has developed in *Panderodus* taxonomy, allowing a better

diagnosis of species. In addition, it is now possible to demonstrate substantial homology in the elemental locations of *Panderodus* and many other species, including both coniform and ramiform-pectiniform bearing genera.

2.2 GENERIC AND SPECIES CONCEPTS IN *PANDERODUS*

Bergström and Sweet (1966) produced the first multielement reconstruction of *Panderodus*, recognising a bi-elemental apparatus (Text-fig. 2.1). They referred two element types to *Panderodus gracilis* (Branson and Mehl), a graciliform element (previously described as *P. gracilis* s.f.), and a compressiform element (previously described as *P. compressus* s.f. (Branson and Mehl). Cooper (1975, 1976) retained a bi-element reconstruction referring to simplexiform (=compressiform) and costate (=graciliform) elements (Text-fig. 2.1); however, Cooper also suggested that further sub-divisions could be made within the latter category. This was later formalised by Barrick (1977), who also tried to demonstrate homology (Text-fig. 2.1) between these elements and those in ramiform-pectiniform apparatuses developed 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. Barrick 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 therefore he homologised *Panderodus* elements on the basis of independent morphological categories (Text-fig. 2.1). The *Panderodus* apparatus reconstructed by Sweet (1979)

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TEXT-FIG. 2.1. Terminology applied by previous authors to elements of the *Panderodus* apparatus (* terminology used by Jeppsson 1983 a, b, 1989 in discussions of homology between *Panderodus* species and *Belodella* apparatuses).

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

Nowlan & Barnes; McCracken & Barnes 1981	Fåhræus & Hunter 1985	Dzik & Drygant 1986	Nowlan & McCracken (in Nowlan et al) 1988	Jeppsson [a] 1983, 1989	Armstrong 1990	This Study
arcuatiform	D	hi	a/b	u	aq	arcuatiform
graciliform	C	ke/pl/tr/oz	b			asym. graciliform
			c		sym. p	sub-sym. graciliform
	B	sp		ne	r	truncatiform
	A			tr		aequaliform
compressiform	E	ne	e	f	sq	falciform
			a		tp	tortiform

consisted of a number of narrow-based costate forms (the asimiliform, similiform and arcuatiform elements), and a laterally compressed falciform element (the compressiform or simplexiform of previous authors). Additionally, Sweet included a small, twisted, tortiform element. In a more recent publication, Sweet (1988) has implied locational homology between *Panderodus*, other coniform-bearing apparatuses and ramiform-pectiniform apparatuses by the application of Sweet and Schönlaub's (1975) scheme, although without further supporting discussion.

Barnes *et al.* (1979) introduced a classification scheme for coniform genera, with various 'Types' being defined upon the degree of elemental compression, cross-sectional symmetry, and cusp curvature. They considered *Panderodus* to be a 'Type IIIB' bimembrate apparatus, where cusp curvature was the most significant feature in delineating morphological transition between elements. The resulting notation scheme (Text-fig. 2.1) comprised an erect p element (the graciliform) and a more highly recurved q element (the compressiform). *Panderodus* apparently lacked the r (reclined) element, which they included in apparatuses of Type IIIA and Type IIIC. Though this is an oversimplified view of the *Panderodus* plan, the scheme had the advantage of allowing comparison of apparatuses without pre-supposing the homology of coniform and ramiform-pectiniform types.

Nowlan and Barnes (1981) suggested that three distinct apparatus types occur within *Panderodus:*

Group I - typified by *P. unicostatus* (Branson and Mehl) and consisting of compressiform elements in association with a suite of variable graciliform and unicostate elements.

Group II - which included *P. gibber* Nowlan and Barnes, 1981 which was bimembrate and comprised symmetrical and asymmetrical elements of similar morphology.

Group III - characterised by *P. liratus* Nowlan and Barnes, 1981, which was also bimembrate, and divided into broad, laterally compressed, low-based elements, and long, slender, high-based elements.

These sub-divisions were later modified by Nowlan and McCracken (in Nowlan *et al.* 1988) after the discovery of additional elements in the apparatuses of *P. gibber* and *P. liratus*. They adopted the notation developed by Barnes *et al.* (1979) for ramiform-pectiniform apparatuses (Text-fig. 2.1.), suggesting that they believed that homology existed between *Panderodus* and these apparatuses, although they do not present any evidence to substantiate this claim. In their revised scheme (Nowlan and McCracken (in Nowlan *et al.* 1988), the groupings were modified to incorporate the discovery of additional elements. Group I panderodontids were quinquemembrate, with an a/b morphological inter-gradation series, equivalent to the arcuatiform, asimiliform and tortiform elements, c subsymmetrical similiform elements, and the e compressiform/falciform elements (Sweet 1979). 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, b) mentioned the presence of eight to ten groups of homologous elements in each *Panderodus* species. Additionally, he proposed 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 homologised with the tr element (the Sa of authors adopting Sweet and Schönlaub's (1975) terminology) of other ramiform-pectiniform genera. Subsequently, Jeppsson (1989; Text-fig. 2.1) introduced a notation scheme for coniform taxa based upon reconstructions of *Belodella*. He proposed homology between 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) recognised the presence of five morphological groupings in *Panderodus* apparatuses (Text-fig. 2.1). 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, in theory a very large number of elements would form each series.

In their description of a fused cluster of *Panderodus unicostatus* elements from Podolia, Dzik and Drygant (1986) recognised 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 standardized 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. 2.1). 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, 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. 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 homologised with **hi** elements. In a rather confusing passage, they then proceeded to question many of their element homologies, and suggest that "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). What is clear from this work is that Dzik and Drygant had recognised an essentially three fold differentiation in the *Panderodus unicostatus* apparatus, with single pairs of

compressiform (**ne**) and unicostate (**hi**) elements associated with a suite of five graciliform pairs (**ke, pl, tr, oz** and **sp**).

Armstrong (1990) expanded the Barnes *et al.* (1979) coniform scheme by sub-dividing the **p** and **q** categories using cusp cross-section (Text-fig. 2.1). 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 an homology of the elements in all Silurian coniform taxa, and suggested ₐthis was perhaps the way forward in developing a suprageneric classification for coniform euconodonts.

2.3 THE COMPOSITION OF *PANDERODUS* APPARATUSES

In the following descriptions of *Panderodus* clusters, purely descriptive terms have been adopted. Nine element morphotypes have been identified in the *Panderodus unicostatus* apparatus on the basis of cusp curvature and cross-sectional symmetry, eight of these 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 thus thought to be unpaired. The descriptive terminology of Sweet (1979) has been modified and expanded, as this provides a clear morphological impression of the elements under discussion:

<u>**falciform (Pl. 20 figs 1-2)**</u>: 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. 2.1). In the type species, *Panderodus*

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unicostatus, these elements are characterised by gradually curved and laterally compressed bases, and have abbreviated cusps. Both the convex and concave edges of the elements are drawn into shallow keels.

tortiform (Pl. 20 figs 17-18): alternatively termed **tp** by Armstrong (1990) (Text-fig. 2.1). These elements are spatulate, and show torsion away from the furrowed faces. The unfurrowed faces are excavated along their concave margins, while the convex margins are drawn out into . sharp edges.

graciliform (Pl. 20 figs 3-10): those elements which have previously described as asimiliform and similiform (Sweet 1979), **ke-pl-tr-oz** (Dzik and Drygant 1986), **a-b** (Nowlan and McCracken (in Nowlan *et al.* 1988), and **sym. p** (Armstrong 1990) belong in this category (Text-fig. 2.1). All elements are proclined and generally bicostate. Four morphotypes have been consistently identified in large collections, which are divisible into 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 is therefore necessary.

arcuatiform (Pl. 20 figs 11-12): equivalent to the **hi** of Dzik and Drygant (1986) and the **aq** of Armstrong (1990) (Text-fig. 2.1). These are generally unicostate elements which show a varying degree of torsion of their erect cusp towards the unfurrowed face. Occasionally, these elements develop a serrate keel on their concave edge.

truncatiform [new term] (Pl. 20 figs 13-14): these have only been recognised as separate morphotypes by Jeppsson (1983 a, b; 1989) as his **ne** elements, and by Armstrong (1990) who described them as **r** elements (Text-fig. 2.1). Dzik and Drygant (1986) illustrated this form as an

sp, but felt that they were merely the smallest end-member of the **graciliform** suite. **Truncatiform** elements are 50% 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] (Pl. 20 figs 15-16):   these bi-furrowed 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 recognised the unique and consistent occurrence of this element in all *Panderodus* apparatuses have been Jeppsson (1983 a, b; 1989),who referred to this form as **tr** (Text-fig. 2.1) and Fåhræus and Hunter (1985) who described these as Group A elements (Text-fig. 2.1). These elements are truly symmetrical, and are similar in size to the **truncatiform** elements.

2.4 CLUSTER DESCRIPTIONS

A series of clusters are described below in an attempt to elucidate the relative element locations within the *Panderodus* apparatus. As far as has been possible, the clusters have been selected on the basis of their completeness and structural integrity. Where necessary, sub-clusters within larger specimens have been utilised, but only if they show internal structural consistency. The Waukesha bedding plane assemblage provides the necessary architectural framework for the apparatus, delineating anterior, posterior and furrow orientation. The remaining clusters help fill the gaps and produce a complete architectural model of the *Panderodus* elemental apparatus.

2.4.1 Waukesha Bedding Plane Assemblage.

Reported by Mikulic *et al.* (1985 a, b) and subsequently described by Smith *et al.* (1987), this specimen comes from the Llandovery Brandon Bridge Formation Konservat Lagerstätte of Waukesha County, Wisconsin, U.S.A., and is the only known coniform euconodont bedding plane assemblage from the Lower Palaeozoic. It is associated with a poorly preserved impression of a transversely segmented trunk, which represents the soft parts of a *Panderodus* conodont. The presence of this body trace is especially useful as it enables the determination of the anterior and posterior of the conodont element assemblage.
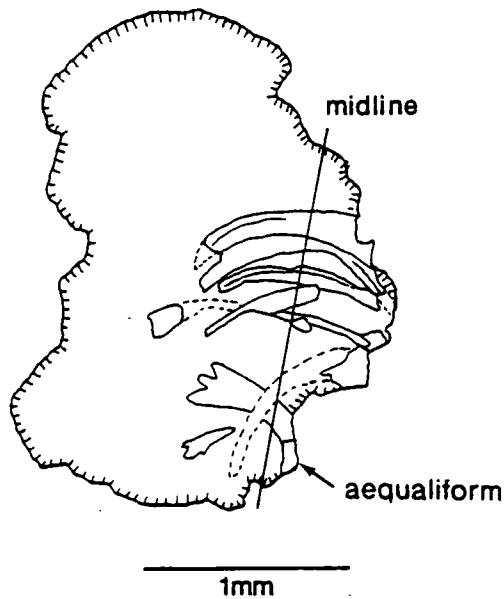
TEXT-FIG. 2.2. Camera-lucida drawing of the conodont bedding plane assemblage associated with the *Panderodus unicostatus* (Branson and Mehl) animal from the Llandovery Brandon Bridge Formation of Waukesha County, Wisconsin (specimen number UW4001/7a, part). The midline and probable aequaliform element are identified (illustration modified from Smith *et al.* 1987, fig. 6.6).

The arrangement of elements in the Waukesha bedding plane assemblage (Pl. 1, fig 1, 2; Text-fig. 2.2) provides constraints for the modelling of three-dimensional apparatus architecture in *Panderodus*, as outlined by Smith *et al.* (1987). These are :

- 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.

- in these elements, the furrowed face shows a consistent orientation, and all the elements on the part have the furrowed faces uppermost.

- 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.

- there is no apparent size gradation (compare with the 'supertooth' model for *Panderodus* presented by Dzik and Drygant (1986).

- the spacing of the elements in the anterior part of the assemblage is closer than that seen at the posterior, this 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 arrays, which may have been attached to an arched basal support.

Re-examination of latex casts of the counterpart (kindly loaned by R.J. Aldridge) and published illustrations of the specimen has enabled the following, additional observations to be made :

1) A close study of the overlapping arrangement of the element tips in the assemblage shows ₐthat the furrowed faces of the elements were anteriormost. The consistent, stacked relationship of the element pairs can only ₐbe produced by a posterior rotation of the element pairs. The Waukesha assemblage represents either a natural, flattened resting position or the result of post-mortem collapse.

2) Smith *et al.* (1987) did not recognise the occurrence of the **aequaliform** element in *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 (see later chapters), and must be

17

taken into account in any apparatus reconstruction. On the part of the Waukesha assemblage (Text-fig. 2.2) lies an oblique cross-section through a small element, which lies parallel to the midline of the assemblage, and to the posterior of the cusps of the falciform element pair. The shape and size of this element suggest that it is a distinct morphotype. Additionally, the form of this cross-section suggests that this element pointed towards the anterior of the assemblage. No other elements show similar dislocation, and this element is considered to be the symmetrical **aequaliform** element.

2.4.2 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.
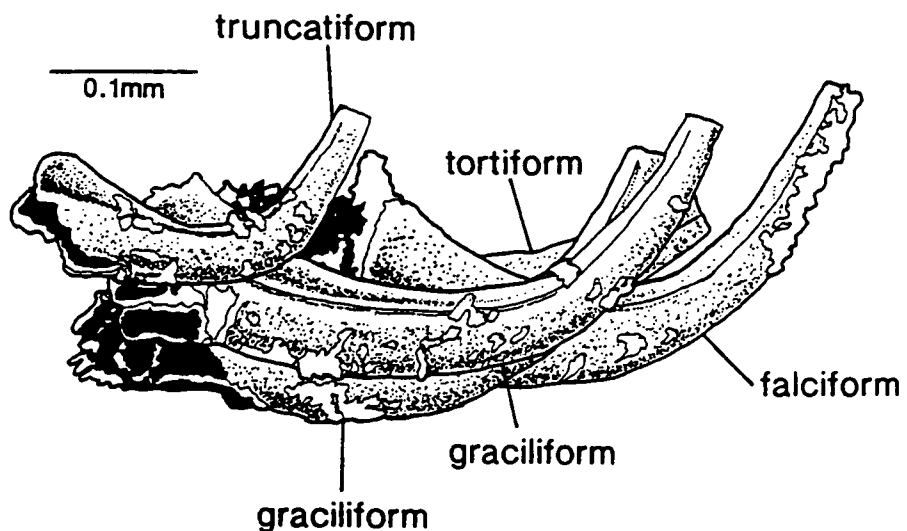
TEXT-FIG. 2.3. Cluster of five elements of *Panderodus* aff. *P. unicostatus* (Branson and Mehl) from a Middle Wenlock olistolith within the Devonian Strázsahegy Formation of Nekézseny, northern Hungary. Specimen is viewed from the anterior, and the elements identified (drawn from Balogh and Kozur 1985, pl. 1 fig. 1).

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

Five elements are joined along their lateral faces (Text-fig. 2.3) 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-fig. 2.3 shows the cluster viewed anteriorly, 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**, two **graciliform**, **falciform** and **tortiform** morphologies. The Nekézseny cluster represents a complete posterior portion of half of a *Panderodus* apparatus.

2.4.3 Podolia Cluster

This cluster (Text-fig. 2.4), 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. All the elements appear to be asymmetrical and paired. Dzik and Drygant (1986) proposed a 3-dimensional model for this cluster based on a size gradation through the elements. As a template, they followed the protoconodont 'supertooth model' (Landing 1977), and the grasping apparatus of extant chaetognaths. In order to explain the preservation of the Podolia cluster, it was necessary for Dzik and Drygant (1986) to invoke a complex series of apparently random dislocations (Text-fig. 2.5).

Whilst the cluster has been considerably deformed, two relatively coherent sub-clusters can be recognised and are of use in apparatus reconstruction. These sub-
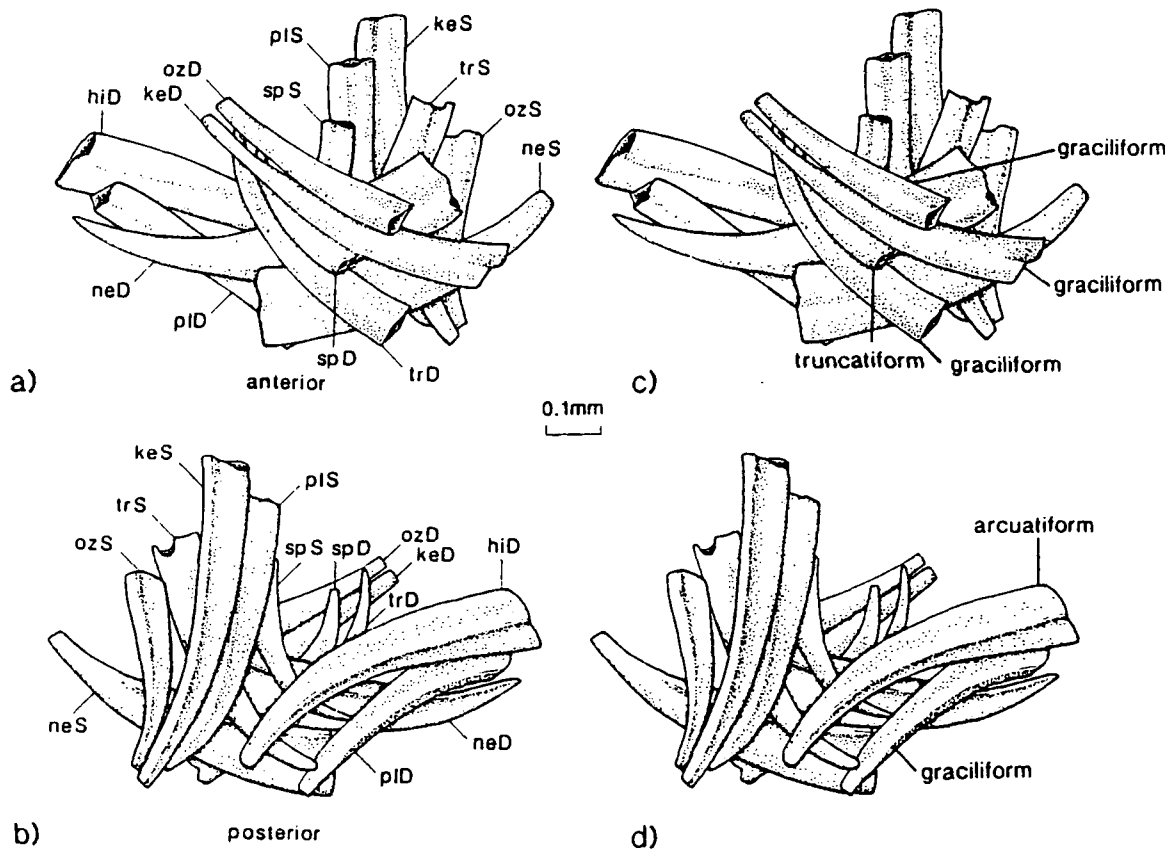
TEXT-FIG. 2.4. Lateral views of a cluster consisting thirteen elements of *Panderodus unicostatus* (Branson and Mehl) described by Dzik and Drygant (1986) from the Teremcy Beds, late Llandovery of Podolia, Ukraine (specimen number ZPAL C.XV/2). Terminology of Dzik and Drygant (1986) in a and b (cf. Text-fig. 2.1.). Element order in Sub-cluster 1 identified in c and Sub-cluster 2 in d (Based on Dzik and Drygant 1986, fig. 3).

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. 2.4a,c) consists of four elements. The visible lateral faces of these elements are unfurrowed, and they are thus viewed from the posterior. The element order from anterior to posterior 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 this evidence, an additional **graciliform** element lies to the anterior of this element.

```
        S        D
      ┌─ ne ─      ── ne ┐
      └─ hi        hi    │
         ke        ── ke ┤
         pl        pl    │
         tr        tr    │
      ┌─ oz ─      oz    │
      │           ┌──    │
      │    sp     ── sp ─┘
      └──────────
```
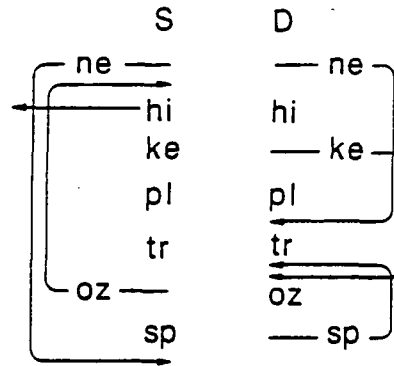
TEXT-FIG. 2.5. Displacements invoked by Dzik and Drygant (1986) to produce an element size gradation from the Podolia cluster (from Dzik and Drygant 1986, fig. 2B).

The smaller sub-cluster 2 (Text-fig. 2.4b,d) lies on the opposite side of the main cluster, and consists of two elements. Both of the exposed faces are furrowed, the anterior-most is of **arcuatiform** 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.

2.4.4 Shandong Cluster

Additional evidence is provided by a three element cluster (Text-fig. 2.6) from the Shandong Province of North China, illustrated by An *et al.* (1983). This consists of a pair of **graciliform** elements lying to the anterior of a single **falciform** element.

2.4.5 Isolated Waukesha Clusters

During the course of this work on the apparatus architecture of *Panderodus*, further evidence was provided by nineteen undescribed clusters from the Waukesha locality, which were kindly loaned by Dr. Rod Norby (Illinois Geological Survey, U.S.A.). These specimens are illustrated on Plates 2, 3 and 4 , and provide supplementary evidence for the architecture of the *Panderodus* apparatus. Fifteen of

the clusters are referable to *Panderodus unicostatus*, the other three are composed of elements of *Panderodus langkawiensis* (Igo and Koike 1967). At least seven clusters represent disrupted assemblages, as they show opposed furrow orientations (Pl. 2, figs 1-7; Pl. 3, figs 1-8; Pl. 4, figs 1-10).
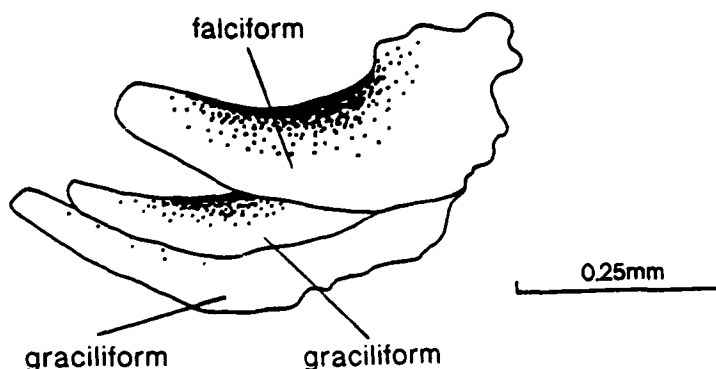
TEXT-FIG. 2.6. Cluster of three elements of *Panderodus unicostatus* (Branson and Mehl) from the Shandong Province of North China (drawn from An *et al.* 1983, pl. 32 fig. 17 a - c).

The undeformed *Panderodus unicostatus* clusters readily fit into the pattern established from the specimens described above. The largest specimen of *P. unicostatus* (Pl. 2, figs 8,9; Text-fig. 2.7) consists of three elongate **graciliform** elements, with a short **truncatiform** nested in front of the posteriormost **graciliform**. The other *P. unicostatus* clusters are, at best, bi-elemental or single elements with fragments of adjacent elements, or appear to be the results of fortuitous superposition. One of these disrupted specimens includes a double-furrowed **aequaliform** element in association with a **falciform** and possible **tortiform** element (Pl. 4, figs 1,2).

Three multielement clusters are referable to the species *Panderodus langkawiensis*. The largest of these specimens (Pl. 3, figs 1-2) consists of at least eleven elements, of which nine appear to be of **graciliform** morphology, and two **falciform** elements. Both halves of the *P. langkawiensis* apparatus are represented, as is evident from the cusp/furrow orientations. Given this opposed furrow

orientation, this cluster is thought to result from post-mortem collapse of a partial apparatus.

truncatiform graciliform

graciliform graciliform

0.2mm
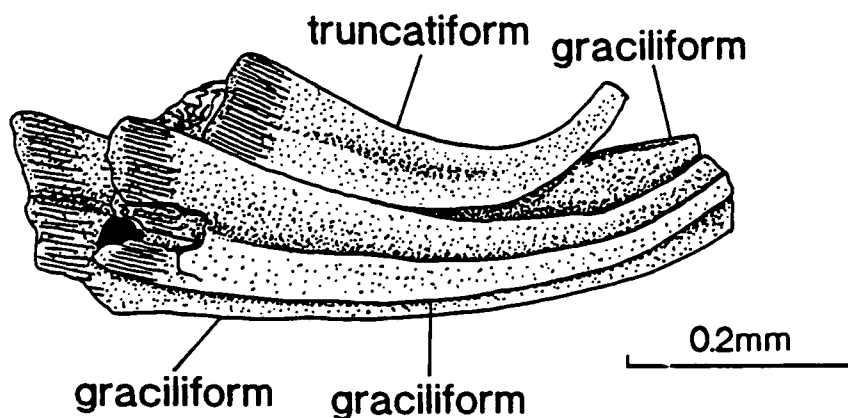
TEXT-FIG. 2.7. Lateral view of a cluster of four elements of *Panderodus unicostatus* (Branson and Mehl) from the Llandovery Brandon Bridge Formation of Waukesha County, Wisconsin. This specimen is also illustrated in Plate 2, figures 8, 9.

The second *P. langkawiensis* cluster (Pl. 4, fig. 7) is tri-elemental, and consists of two elongate graciliform elements in association with a single truncatiform element, which apparently has undergone a degree of rotation with respect to the other elements. Furrow orientation appears to be consistent throughout this specimen.

A third *P. langkawiensis* specimen (Pl. 3, figs 3-5) consists of eight elements; at least four graciliform elements, a single arcuatiform, and one possible truncatiform. The eighth element of this cluster is too fragmentary to confidently identify, although it is possible that this is a graciliform. As is evident from the cusp/furrow orientation, both halves of the apparatus are present.

It is notable that the *Panderodus langkawiensis* clusters all show a degree of radiation of the elements from their bases, perhaps this is a reflection of post-mortem

deformation, or may be an original feature of element displacement in the oral cavity of *P. langkawiensis*.

2.5 CLUSTER CORRELATION

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

Waukesha Assemblage	Nehezsany Cluster	Podolia Subcluster 1	Podolia Subcluster 2	Shandong Cluster	Waukesha Cluster
arcuatiform			arcuatiform		
graciliform			graciliform		graciliform
graciliform		graciliform			graciliform
	truncatiform	truncatiform			truncatiform
	graciliform	graciliform		graciliform	graciliform
	graciliform	graciliform		graciliform	'
	falciform			falciform	
	tortiform				

TEXT-FIG. 2.8. Chart showing the correlation in the paired element orders of the clusters described in the text. It is this correlation which has been used to develop an architectural model for *Panderodus*, and the element order from top to bottom is thought to represent anterior to posterior in the apparatus.

The identification and correlation of repeated element sequences in the clusters outlined above (Text-fig. 2.8), permits formulation of the complete *Panderodus* apparatus (Text-fig. 2.9). The apparatus consists of seventeen elements,

sixteen of which are found in two bilaterally opposed linear arrays. This element number is the same as which may be inferred from discrete collections (see later chapters), suggesting that each morphotype (including 'left' and 'right' pairs) is a consistent component of the apparatus.
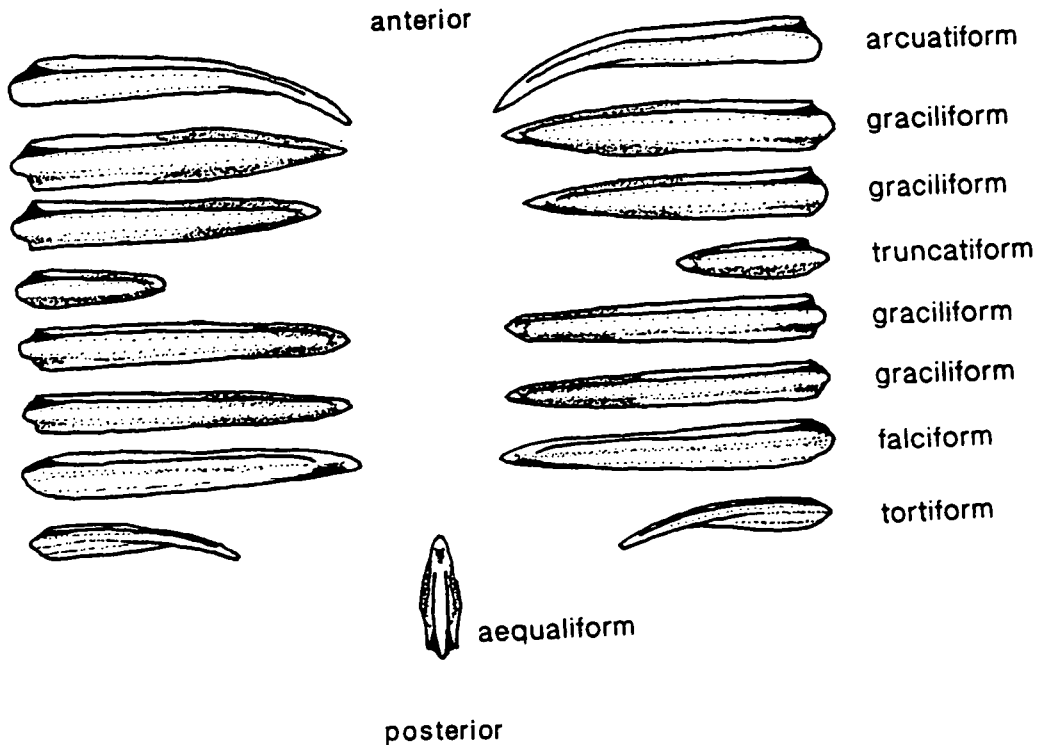
TEXT-FIG. 2.9. Ventral or dorsal view of the generalised apparatus architecture of *Panderodus* developed from the evidence presented in Text-fig. 2.8. The position of the **aequaliform** element is drawn from it's position in the Waukesha bedding plane assemblage (Text-fig. 2.2).

The apparatus plan of *Panderodus* falls into two suites of paired elements, an anterior costate suite and a posterior compressed suite (Text-fig. 2.10). The costate suite is further sub-divisible into an anterior pair of twisted unicostate **arcuatiform** elements, and to the rear of this pair lies a group of morphologically variable costate elements (the **graciliform-truncatiform-graciliform** series). The posterior compressed suite consists of the **falciform** and **tortiform** pairs. The final component of this apparatus is represented by the single **aequaliform** element lying along the

apparatus midline. Thus the apparatus of *Panderodus* consists of four morphological units, three of which fall into two suites within the paired assemblage.
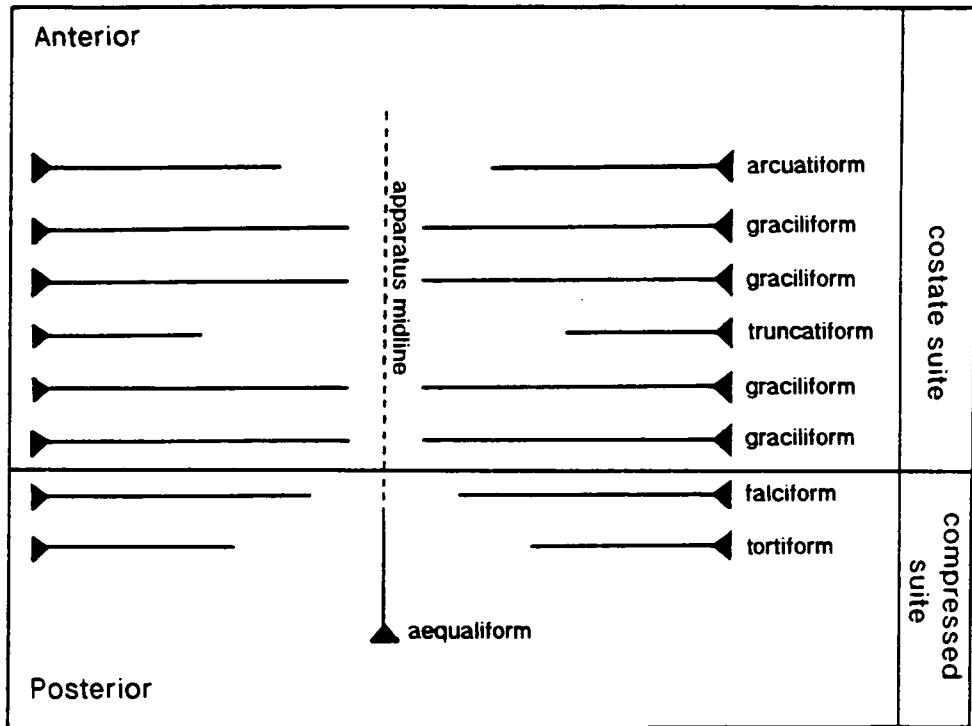
TEXT-FIG. 2.10. Model for the *Panderodus* apparatus showing the architectural differentiation into an anterior costate suite and a posterior compressed suite within the paired assemblage.

2.6 HOMOLOGY BETWEEN CONIFORM GENERA

2.6.1 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 disparate styles within the genus.

In those species of *Panderodus* which are well understood and for which large collections are available, it is possible to homologise all of the elements of the apparatus on morphological criteria (Chapter 7; Text-fig. 7.3) and identify the presence of a costate suite (**arcuatiform** and **graciliform-truncatiform**) and a compressed suite (**falciform-tortiform**) of paired elements. An additional morphological component, the symmetrical **aequaliform**, is consistently present. *Panderodus* is a unified genus based upon apparatus architecture, and species vary in individual element morphology. As such, it is possible to establish those character states which are of use in the suprageneric classification of *Panderodus*.

2.6.2 Applicability of the *Panderodus* apparatus model to other Panderodontid lineages

The model presented for the apparatus architecture of *Panderodus* euconodonts may be tested against future discoveries of undeformed clusters and additional bedding plane assemblages. It may also be compared with other coniform genera to establish whether their apparatuses follow the same basic design. Identification of homologous elements should lead to a 'natural' suprageneric classification, as suggested by Armstrong (1990), on the basis of apparatus similarities, and the addition or reduction of elements in evolutionary lineages.

In an attempt to initiate such work, a number of genera have been studied in an attempt to determine the wider applicability of the *Panderodus* apparatus model. This is not a comprehensive comparison, as only those genera for which clusters are known are discussed. Additional information has been derived from several genera which are taxonomically well founded. Many coniform apparatuses are, as yet, incompletely understood. It is important to establish as to whether incompleteness of apparatus reconstruction is a result of biological or taphonomic processes, as these characters are used to differentiate between apparatuses at the supergeneric level.

Belodina compressa (Branson and Mehl)

Using the clusters illustrated by Barnes (1967) and Nowlan (1979), an apparatus model for *Belodina compressa* (Branson and Mehl) is proposed, this may be tested if and when further clusters are found. An *a priori* assumption that the lateral furrow is homologous with that seen in *Panderodus* has been made, and that this is consistently developed on the anterior face of *Belodina* elements. This assumption can be substantiated as the structure and histology of the furrows in the two genera are the same (Barnes, Sass and Poplawski 1973). *Belodina compressa* 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 non-denticulate eobelodiniform elements.
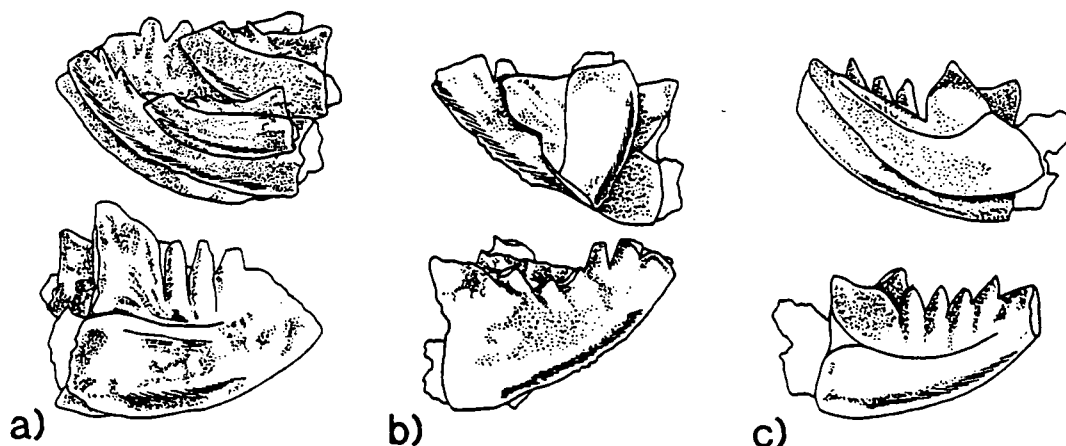
TEXT-FIG. 2.11. Clusters of *Belodina compressa* (Branson and Mehl) illustrated by Barnes (1967, text-fig. 2) and Nowlan (1979, pl. 35.2 and fig. 35.2). a) four element cluster from the Cobourg Formation (Upper Ordovician) of Ottawa, Canada (GSC 21396, x 100). b) and c) bielement clusters from the Thumb Mountain Formation (Middle to Upper Ordovician) of Ellesmere Island, District of Franklin, Canada (GSC 59981 and GSC 59982 respectively, both x 60).

Two of the *Belodina* clusters are seen to be disrupted as they are composed of elements which show opposition of their furrowed faces (Text-fig. 2.11a,b). The third cluster (Text-fig. 2.11c), although comprising of only two elements, is potentially an original association, as the furrowed faces are in a consistent orientation. If the furrow orientation exhibited by the Waukesha bedding plane assemblage is valid for other panderodontids, then the grandiform element in this specimen lies to the anterior of the eobelodiniform element. The cluster assemblage illustrated by Barnes (1967) and refigured by Nowlan (1979), although showing a degree of dislocation in the position of the four component elements (Text-fig. 2.11b), may provide further insight into the *Belodina* apparatus. Three of the elements are grandiform, with considerable variation in size, and all have the same furrow orientation; this may thus be an undeformed sub-cluster. The 'anteriormost' of these elements is roughly 50% of the size of the other grandiform elements. The

compressiform   grandiform   eobelodiniform

aequaliform   falciform   truncatiform   graciliform   arcuatiform
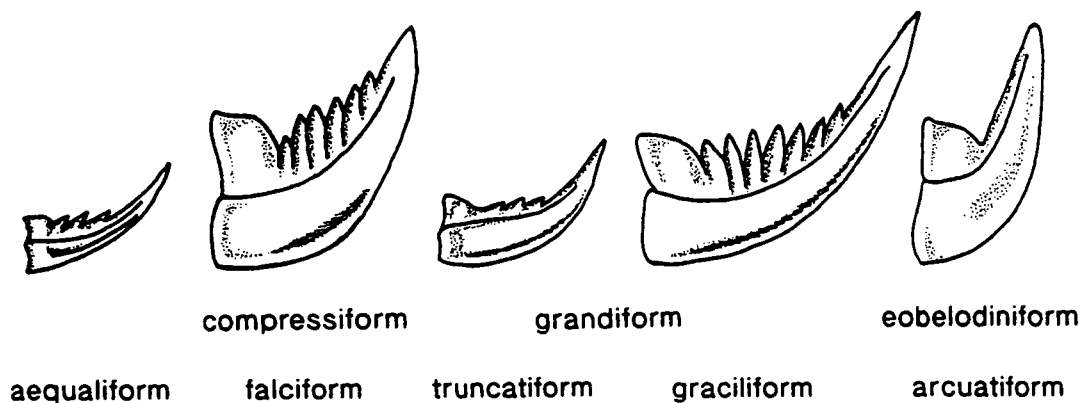
TEXT-FIG. 2.12. Discrete elements of the *Belodina compressa* (Branson and Mehl) apparatus based upon the morphologies present in the clusters illustrated in Text-fig. 2.11 with the terminology employed by Nowlan (1979) overlying the notation scheme developed herein. The aequaliform element is based upon elements illustrated by McCracken (1987, pl. 1, figs 16, 21, 22) as New genus A new species A. All approximately x 60.

furrowed face of the fourth compressiform element is orientated 180° out of phase from the other elements, possibly the result of post-mortem dislocation. It appears from the cluster evidence that *Belodina compressa* bore a number of grandiform elements in association with single pairs of eobelodiniform and compressiform elements. The abbreviated 'grandiform' element seen in Text-fig. 2.11a forms an additional apparatus component that is not present in published reconstructions.

Morphological homology can be identified between the grandiform elements of *Belodina* and the **graciliform** elements of *Panderodus*. Both are comparatively elongate and slender, and the evidence suggests that they occurred in multiple pairs within the apparatus. The laterally compressed and recurved form of the compressiform of *Belodina* is morphologically equivalent to the **falciform** element of *Panderodus*. The abbreviated 'grandiform' element seen in one of the *Belodina* clusters invites homology with the **truncatiform** element of *Panderodus* apparatuses; it is considerably shorter than the grandiform elements, which it resembles in gross morphology, and it appears to be locationally associated with the grandiform elements. The erect cusp of the eobelodiniform element of *Belodina* shows a degree of torsion away from its furrowed lateral face, a feature seen in **arcuatiform** elements in *Panderodus*. Additionally, cluster evidence shows that the eobelodiniform element was located at the anterior of the apparatus; this is also the position occupied by the **arcuatiform** element in *Panderodus*.

The clusters and published reconstructions of *Belodina compressa* lack elements which can be homologized with the **tortiform** and **aequaliform** elements of *Panderodus*. Although **tortiform** elements have yet to be formally differentiated in the *Belodina* apparatus, morphologically homologous elements have been included as grandiform elements in the species *Belodina arca* Sweet, 1979 and *Belodina dispansa* (Glenister) by Nowlan and Barnes (1981). Small, double-furrowed belodinid elements have been figured by McCracken (1987, pl. 1 figs 16, 21, 22) as apparatus components of new belodinid genera; these specimens co-occur with elements of *Belodina confluens* Sweet, 1979 in very limited numbers. Given the

previous doubts as to the existence of such elements in *Panderodus*, and their comparative rarity, it is suggested that these elements may eventually be found associated with all *Belodina* apparatuses and that they represent the *Belodina* **aequaliform** element.

The apparatus of *Belodina* comprises a costate suite and a compressed suite of paired elements, and the full apparatus readily falls into the four morphological groupings identified in *Panderodus*, thus supporting the famial classification of Clark (1981) and Sweet (1988). A testable apparatus model for *Belodina* is presented in Text-fig. 2.13.

anterior

———————< arcuatiform

—————————< graciliform

—————————< graciliform

————————< truncatiform

————————< graciliform

—————————< graciliform

—————————< falciform

– – – – – – –< ? tortiform

∧ aequaliform

posterior
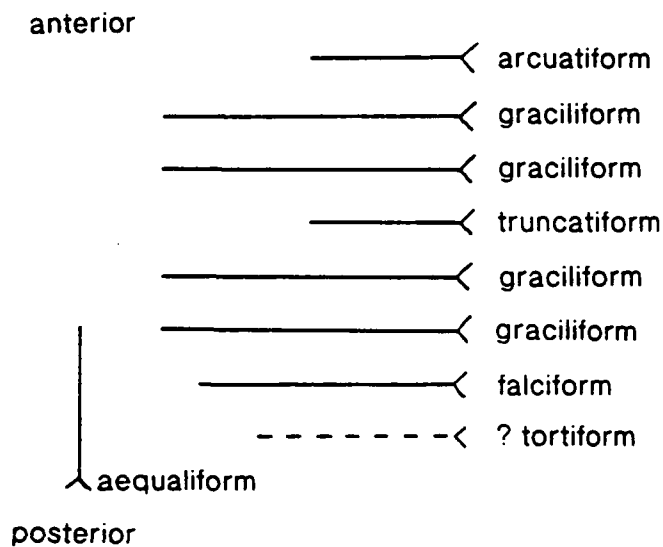
TEXT-FIG. 2.13. Architectural model for *Belodina* Ethington based upon Text-figs 2.11 and 2.12. The presence of a **tortiform** element is considered likely and discussed in the text.

Parapanderodus Stouge

Parapanderodus Stouge is thought to be closely related to *Panderodus;* indeed some authors have suggested that the former is the evolutionary precursor of the latter (Dzik 1976; Löfgren 1978). The transition from one form to the other appears to have been accompanied by the, possibly gradual, transfer of the ventral furrow of *Parapanderodus* to the lateral position seen in *Panderodus*. *Parapanderodus* has recently been reconstructed by M.P. Smith (1991) who

combined a number of monomembrate species into his revised trimembrate apparatus. This divided into a suite of morphologically similar **graciliform** elements (the s elements in Smith's terminology), laterally compressed **falciform** elements (t elements), and symmetrical u elements. The latter component may be an **aequaliform** homologue, but it is considerably larger than these elements in other apparatuses, and lacks two furrows, the principle diagnostic feature of the **aequaliform** in other panderodontid apparatuses. **Arcuatiform, truncatiform** and **tortiform** elements have yet to be recognised in *Parapanderodus*, although their presence should not yet be discounted until the multielement composition of the apparatus is more widely established.
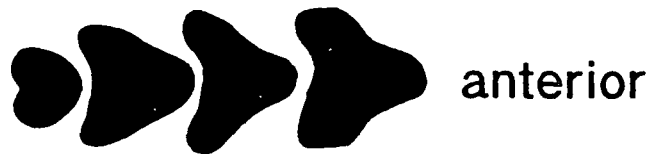
anterior

TEXT-FIG. 2.14. Model presented by M.P. Smith (1991, fig. 30) of anterior-posterior nesting in the graciliform elements of *Parapanderodus striatus* (Graves and Ellison).

Three clusters of *Parapanderodus* have been illustrated by M.P. Smith (1991, fig. 29), and these confirm the presence of a multielement apparatus, though each specimen appears to be somewhat disorganised. This is evident as the element bases are dislocated away from their presumed parallel and linear original arrangement, as seen in *Panderodus*. M.P.Smith (1991) has used one of these specimens (fig. 29 c, d) to propose a nested relationship for the morphological variable **graciliform** elements in the *Parapanderodus* apparatus (Text-fig. 2.14). Smith's illustration of nesting within the **graciliform** suite shows considerable variation in the cross-sections of these elements. However, M.P. Smith (1991) does not formalise them as discrete

anterior

Parapanderodus

anterior
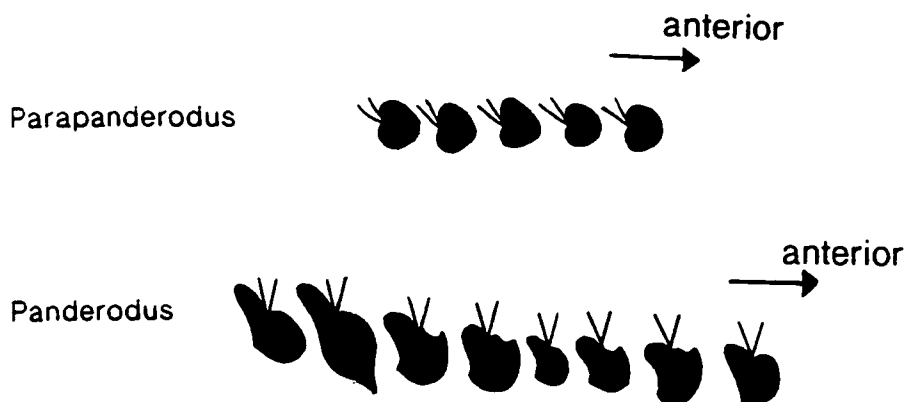
Panderodus

TEXT-FIG. 2.15. Diagram to illustrate a theoretical shift in the insertion of the panderodontid furrow in *Parapanderodus* Stouge and *Panderodus* (Ethington).

morphological entities. If a nested relationship is an original feature and not an artifact of post-mortem deformation, then *Parapanderodus* elements are orientated differently within the apparatus when compared to *Panderodus* (Text-fig. 2.15). A nested elemental arrangement in *Parapanderodus* may explain the relative shift in the furrow suggested above, and is a hypothesis which needs to be tested if and when further specimens are discovered.

Other members of the Panderodontidae have been homologised with the *Panderodus* apparatus by Sweet (1979, 1988), who illustrated morphological homology between the elements of *Parabelodina* Sweet, *Pseudobelodina* Sweet, *Plegagnathus* Ethington and Furnish. However, this work was based upon his quinquemembrate reconstructions of *Panderodus* apparatuses and is not substantiated by cluster data. *Parabelodina, Pseudobelodina* and *Plegagnathus* are only known from small collections and appear to be only partially reconstructed, and lack aequaliform and truncatiform elements. The absence of these comparatively small elements from these apparatuses could be a result of taphonomic sorting or collection bias.

2.6.3 Applicability of the *Panderodus* apparatus model to Non-Panderodontidae coniforms

Clusters of non-Panderodontidae coniform elements have been described for *Coelocerodontus,* a member of the Family Belodellidae (*sensu* Clark 1981), and *Besselodus* (Family Unknown *sensu* Clark 1981, although Sweet has placed the genus in the Family Belodellidae).

Coelocerodontus Ethington, 1959

Andres (1988) illustrated a number of clusters of *Coelocerodontus,* from the Tremadoc of Öland, from which he was able to propose an apparatus architecture for the genus (Text-fig. 2.16). Andres' model places a unicostate element (**arcuatiform** in the *Panderodus* apparatus) anteriorly, followed by a suite of at least five bicostate elements (**graciliform**), a laterally compressed element which can best be described as **falciform**, and a torted unicostate element (**tortiform**) at the posterior of the paired assemblage.
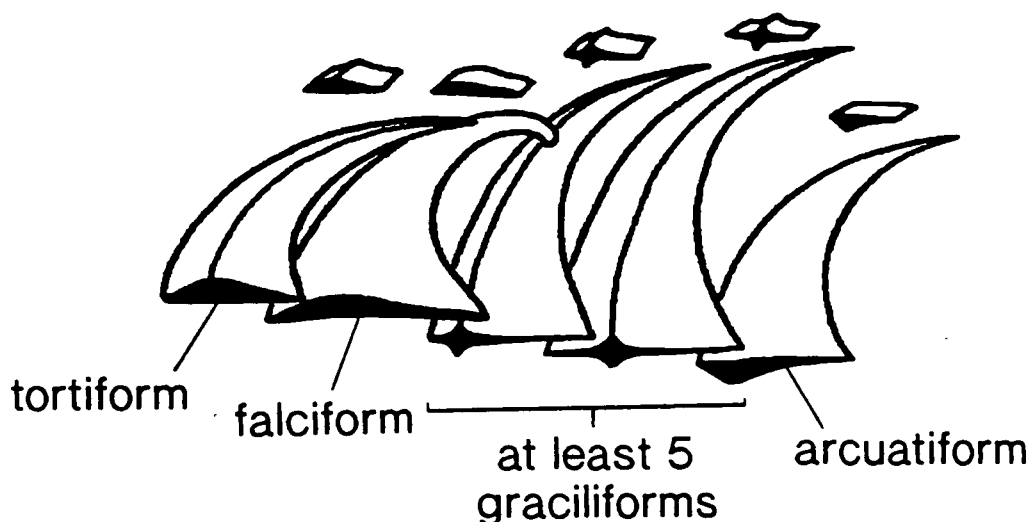
TEXT-FIG. 2.16. Architectural model for *Coelocerodontus* Ethington produced by Andres (1988, fig. 17) based upon a number of clusters from the Tremadoc of Öland, Sweden. Andres did not include an **aequaliform** element in his reconstruction of *Coelocerodontus.*

The morphological variation seen within the *Coelocerodontus* apparatus is directly comparable with that seen in the paired elements of *Panderodus*. The paired apparatus falls again into an anterior costate suite (**arcuatiform** and **graciliform**) and a posterior compressed suite (**falciform-tortiform**), although a **truncatiform** element is not seen.

In a recent paper, Müller and Hinz (1991) have illustrated two well-preserved clusters of *Coelocerodontus* which they interpret as being coprolitic. In one of these (Müller and Hinz 1991, pl. 41, figs 11,14), a short element is present which does not figure in their description or reconstruction of the *Coelocerodontus* apparatus; perhaps this element is an **aequaliform** homologue which has so far evaded description. If this element is an **aequaliform** homologue, then the *Coelcerodontus* apparatus shows the same quadrate morphological division as is seen in the Panderodontidae.

anterior

————————< arcuatiform

————————< graciliform

————————< graciliform

————————< graciliform

————————< graciliform

————————< graciliform

————————< falciform

————————< tortiform

人? aequaliform

posterior

TEXT-FIG. 2.17. Apparatus architectural model for *Coelocerodontus* Ethington based upon Andres' (1988) reconstruction of the paired assemblage (Text-fig. 2.16), and including a possible aequaliform element that has been illustrated by Müller and Hinz (1991, pl. 41, figs 11, 14) in a multielement cluster of *Coelocerodontus*, although they did not identify this element as such.

Armstrong (1990) thoroughly revised and illustrated the apparatus of *Walliserodus*, another member of the Belodellidae, whose apparatus shows notable morphological homology with both *Coelocerodontus* and *Panderodus*. Although Armstrong's homologi es between *Panderodus* and *Walliserodus* are slightly modified in Text-fig. 2.18, it would appear that locational homology and a quadrate division of elements can be traced through apparatuses of the Families Panderodontidae and Belodellidae apparatuses, implying superfamilial connection.

| aequaliform | tortiform | falciform | graciliforms | arcuatiform |
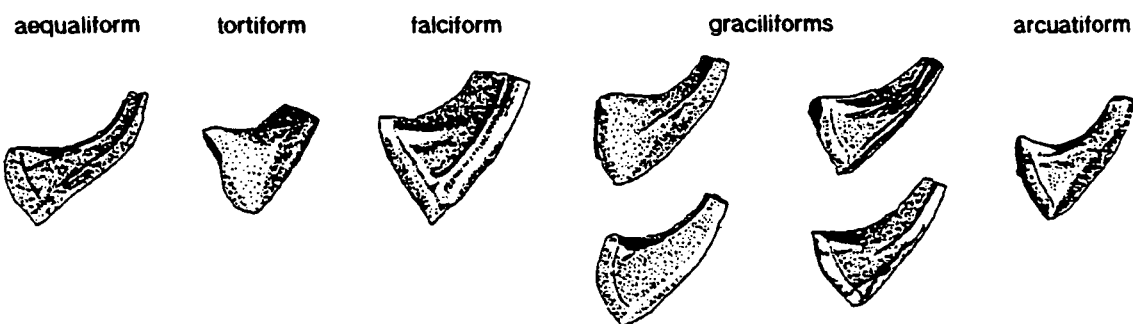
TEXT-FIG. 2.18. Apparatus of *Walliserodus curvatus* (Branson and Mehl) homologised with the *Panderodus* apparatus. Based upon Armstrong (1990, pl. 21, figs 6-8, 11, 13-15) although his homologies are somewhat modified here. All elements are approximately x 30.

Besselodus Aldridge, and *Dapsilodus* Cooper

These two genera are considered together, given their morphological proximity to each other.

A cluster of the coniform genus *Besselodus* has been described by Aldridge (1982) from the Aleqatsiaq Fjord Formation of Washington Land, north Greenland. The cluster consists of a suite of six distacodontiform elements and a single oistodontiform element (Text-fig. 2.19). An additional symmetrical element in the *Besselodus* apparatus has been reported by Nowlan and McCracken (in Nowlan *et al.* 1988) as a c element (Text-fig. 2.20).

Closely related to *Besselodus* is the Silurian genus *Dapsilodus*, which has been described as trimembrate by Cooper (1976) and Armstrong (1990). Armstrong

described the morphological categories of *Dapsilodus* as: sym. p (= c in *Besselodus*), this element being totally symmetrical, with a relatively low abundance (1:15 being the figure quoted) in comparison with other categories; sq (= distacodont in *Besselodus*), which are morphologically conservative, bicostate and occur in the greatest abundance; and unicostate, geniculate r elements. In comparison with the apparatus plans already discussed, the sym. p element is homologous with the **aequaliform**, the sq elements share the characters of the **gracilforms**, and the geniculate r element is consistent with the geniculate **arcuatiform** element of *Belodina* (Text-fig.2.21).

As reconstructed here, the apparatuses of *Besselodus* and *Dapsilodus* are divisible into three morphological units: an anterior geniculate **arcuatiform** component; a costate **graciliform** unit; and a single **aequaliform** element. These apparatuses differ from the quadrate apparatuses of the Panderodontidae and *Coelocerodontus* and *Walliserodus* as they lack a distinct 'compressed' suite of elements (Text-fig. 2.22).
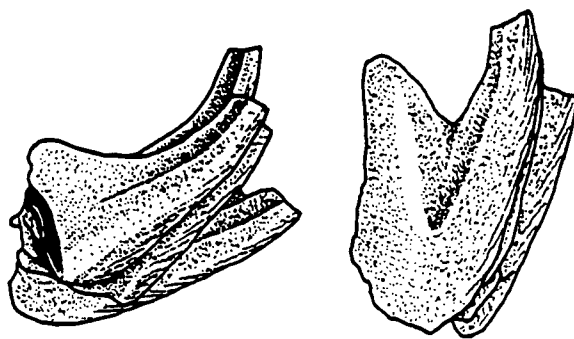
TEXT-FIG. 2.19. Cluster of *Besselodus arcticus* Aldridge from the Aleqatsiaq Fjord Formation (Upper Ordovician) of Washington Land, north Greenland, (Drawn from Aldridge 1982, pl. 44, figs 2, 4; approximately x 200).

distacodontiform

oistodontiform

aequaliform

graciliform

arcuatiform
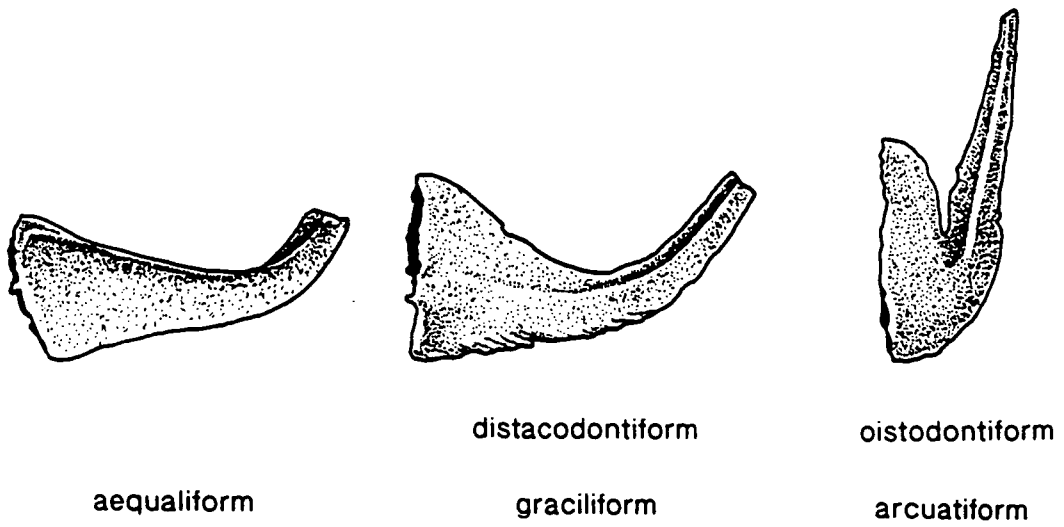
TEXT-FIG. 2.20. Discrete elements of *Besselodus borealis* Nowlan and McCracken from the Whittaker Formation (Upper Ordovician - Early Silurian) of the Mackensie Mountains, N.W. Territories, Canada with the terminology applied by Aldridge (1982) to *Besselodus* overlying the notation scheme developed herein (Drawn from Nowlan et al. 1988, pl. 2, fig. 15 [aequaliform] x 150, fig. 10 [graciliform] x 125, fig. 17 [arcuatiform] x 180).

aequaliform

graciliform

arcuatiform

TEXT-FIG. 2.21. Apparatus of *Dapsilodus obliquicostatus* (Branson and Mehl) homologised with the *Panderodus* apparatus. Based upon Armstrong (1990, pl. 7, figs 8, 10, 12) although his homologies are somewhat modified here. All elements approximately x 45.

anterior

——————————< arcuatiform

——————————< graciliform

——————————< graciliform

——————————< graciliform

——————————< graciliform

——————————< graciliform

⋏ aequaliform

posterior
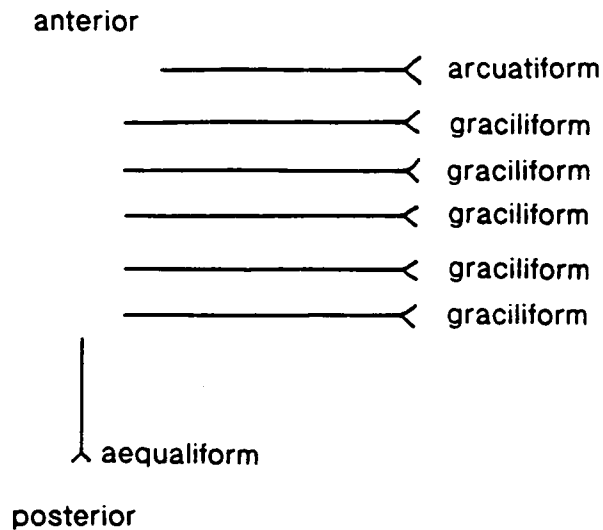
TEXT-FIG. 2.22. Apparatus architecture model for *Besselodus* Aldridge and *Dapsilodus* Cooper based upon the *Besselodus* cluster illustrated by Aldridge (1982; Text-fig. 2.20 and the discrete elements illustrated in Text-fig. 2.21 (*Besselodus*) and Text-fig. 2.22 (*Dapsilodus*). Both *Besselodus* and *Dapsilodus* lack elements which are homologous with the **falciform** and **tortiform** in panderodontid apparatuses.

2.7 IMPLICATIONS FOR PANDERODONTID SUPERGENERIC CLASSIFICATION

The recognition of a comparatively conservative architectural plan in the coniform apparatuses examined above (Text-fig. 2.23) has major implications for the supergeneric classification of these taxa. It is evident that this classification can now be based upon apparatus architecture, and thus follow the same criteria as is employed in the supergeneric classification of ramiform-pectiniform bearing apparatuses.
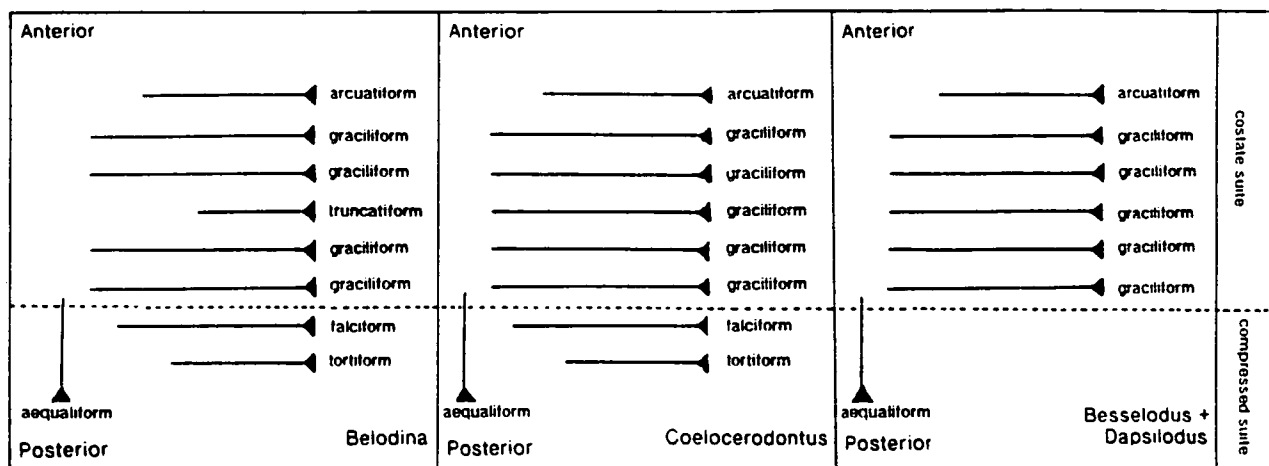
TEXT-FIG. 2.23. Comparison between the apparatus architecture of *Belodina, Coelocerodontus, Besselodus* and *Dapsilodus* based upon element homologies with the *Panderodus* apparatus architecture model presented in Text-fig. 2.10. (the presence of a **tortiform** element in *Belodina* apparatuses is considered likely, though not yet confirmed).

Referring specifically to the higher classification of the Panderodontidae, it is apparent from Text-figs 2.23 and 2.24 that *Panderodus, Belodina, Coelocerodontus* and *Walliserodus* follow the same basic architectural plan. Both *Panderodus* and *Belodina* are united by the presence of a fully developed apparatus. If the apparatuses homologies presented in Text-figs 2.23 and 2.24 are accepted, then the similarities in architecture between the apparatuses of *Coelocerodontus* and *Walliserodus* and the apparatuses of *Panderodus* illustrate that they are united at the Superfamily level, as has been suggested by Clark (1981) in the Treatise by their unification in the Superfamily Panderodontacea. As apparatus homology has now been established within this Superfamily, it is proposed that all coniform apparatuses which exhibit a differentiation into a 'costate suite' of paired elements (consisting of **arcuatiform, graciliform** and **truncatiform** elements), a 'compressed suite' of paired elements (**falciform** and **tortiform**) and symmetrical (**aequaliform**) component should be reclassified within the Panderodontacea. The presence of the

panderodontid furrow has been cited as a character (Sweet 1988; and Dzik 1991) uniting the Family Panderodontidae; this is a view accepted here. Additionally, the **truncatiform** element has so far only been recognised in *Panderodus* and *Belodina*, suggesting that the development of this element could be used as a further diagnostic character, perhaps at the Subfamily level, although additional evidence is required to substantiate this observation.

	aequaliform	tortiform	falciform	truncatiform	graciliform	arcuatiform
Panderodus	■	■	■	■	■	■
Belodina	■	?	■	■	■	■
Walliserodus	■		■	■	■	■
Coelocerodontus	■		■	■	■	■
Besselodus	■				■	■
Dapsilodus	■				■	■

TEXT-FIG. 2.24. Comparison between selected coniform apparatus structures based upon the homologies presented in this chapter.

Besselodus and *Dapsilodus*, although they have recently been classified in the Family Belodellidae by Sweet (1988), show a tripartite apparatus division, lacking a 'compressed suite' of paired elements (see above), whereas other members of the

family, e.g. *Coelocerodontus* and *Walliserodus,* possess a quadrimembrate apparatus including a 'compressed suite' of paired elements. Thus the Belodellidae (*sensu* Sweet 1988) represents a disparate group, and if apparatus differentiation is accepted as the basis for super-familial classification, *Besselodus* and *Dapsilodus* belong outside of Belodellidae.

Chapter 3.

A PRELIMINARY ATTEMPT TO UNIFY CONODONT LOCATIONAL NOMENCLATURE

3.1 INTRODUCTION

Conodonts are thought to form a monophyletic clade (Conway-Morris 1989; see later chapters), consequently it is a logical step to develop a unified nomenclature scheme with which to describe and denote homologies between their elements. Many authors have proposed universally applicable schemes (Barrick 1977; Orchard 1980; Dzik and Drygant 1986; Dzik 1986; Sweet 1988; Nowlan and McCracken (in Nowlan *et al.* 1988), but these have been flawed as they have been based purely on morphological comparison between disparate forms (M.P. Smith 1990). The principle aim of this chapter is to compare the architectural model developed for the Panderodontidae (Chapter 2) and those which have been produced for ramiform-pectiniform taxa, and assess the extent of homology between these apparatuses.

3.2 CONIFORM APPARATUSES

Models of the apparatus architecture of various coniform taxa have been developed (see Chapter 2) on the basis of cluster and bedding plane assemblage evidence, this being supplemented by discrete collections where appropriate. These apparatuses may be classified at the suprageneric level by the extent of apparatus development.
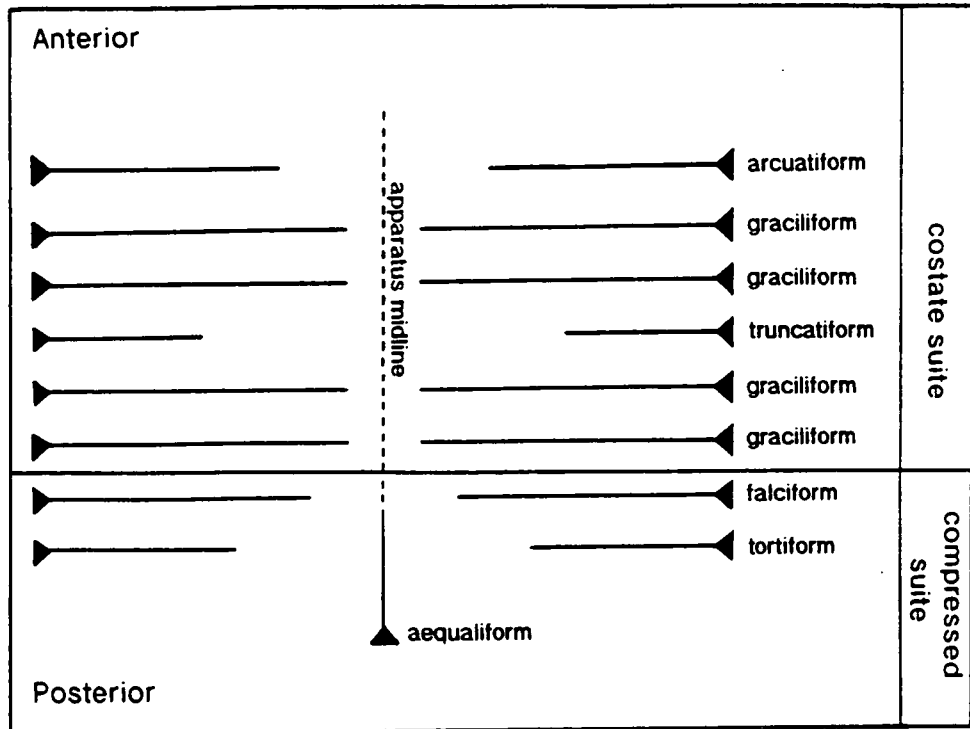
TEXT-FIG. 3.1. Diagrammatic representation of the apparatus architecture of *Panderodus*, showing the differentiation into an anterior costate suite and a posterior compressed suite (reproduced from Text-fig. 2.10.).

Panderodus, for which most architectural information is available, is thought to exhibit a fully developed apparatus structure. The apparatus is divisible into a paired and a symmetrical component, the latter being represented by the **aequaliform**. The paired elements lie perpendicular to the symmetry plane, and can be divided into a costate suite and a compressed suit. The costate suite consists of an anterior **arcuatiform** pair, and the **graciliform-truncatiform** suite, whilst the compressed suite consists of one pair each of **falciform** and **tortiform** morphology. Additionally, soft tissue preserved in association with the Waukesha *Panderodus* bedding plane assemblage has allowed the determination of anterior and posterior in the apparatus. An architectural model for *Panderodus* has been developed where the paired elements are orientated perpendicular to the midline of the apparatus, with the single symmetrical **aequaliform** element orientated parallel to this symmetry plane

(Text-fig. 3.1). In the paired assemblage, the **arcuatiform** elements are located at the anterior of the assemblage, followed by a suite of five costate elements (four **graciliform** pairs with a single **truncatiform** pair inserted between them), and the two pairs of laterally compressed elements (the **falciform** and **tortiform** respectively) lie at the posterior.

Certain other coniform apparatuses follow the *Panderodus* plan to a varying extent. *Belodina* is thought to mimic *Panderodus* closely, with the same element morphologies present, and these are thought to have occupied similar positions in the apparatus (Text-fig. 2.23). The apparatus of *Coelocerodontus*, as reconstructed by Andres (1988; see also Chapter 2), shows morphological and locational homology with *Panderodus*. Although the **truncatiform** element is not developed in this apparatus, an additional, fifth, **graciliform** element is thought to be present in the centre of the costate suite (Text-fig. 2.23). *Besselodus* and *Daspilodus* have been reconstructed from cluster and discrete collection data, these apparatuses are thought to have an essentially trimembrate apparatus, lacking the compressed suite of elements seen in the Panderodontidae (Text-fig. 2.23). As further architectural information becomes available, the expansion of these models to include other genera should provide a basis for the supergeneric classification of coniform apparatuses.

3.3 RAMIFORM-PECTINIFORM APPARATUSES

3.3.1 Order Ozarkodinida Dzik 1976

Numerous multielement clusters of genera belonging to the Order Ozarkodinida have been described and figured (Rexroad and Nicoll 1964; Pollock 1969; Briggs *et al.* 1983; Nicoll 1985, 1987; Nicoll and Rexroad 1987), and bedding plane assemblages are widely illustrated in the literature (Schmidt 1934; Du Bois 1943; Rhodes 1954; Schmidt and Müller 1964; Mashkova 1972; Briggs *et al.* 1983;

Aldridge *et al.* 1986; Ritter and Baesemann 1991). Many of these specimens have provided the data for several architectural models (Jeppsson 1971; Nicoll 1985; Dzik 1986; Aldridge *et al.* 1987), which differ in only a few details. In addition, the Granton conodonts and their associated soft parts enable the identification of anterior and posterior in the assemblages, allowing the formulation of a three-dimensional architectural model, from which all of the available specimens can be derived (Aldridge *et al.* 1987). Aldridge *et al.* (1987) have also identified the location of Sweet and Schönlaub's (1975) element categories within the ozarkodinid apparatus.
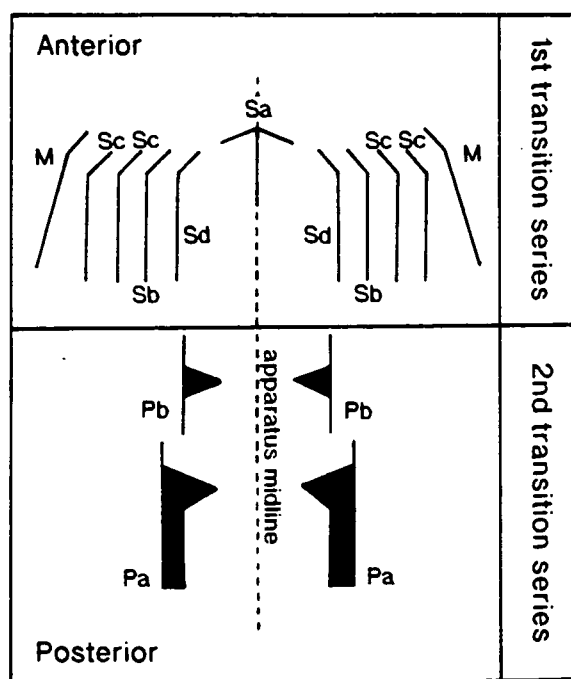
TEXT-FIG. 3.2. Diagrammatic representation of the apparatus architecture of ozarkodinid conodonts. Jeppsson (1971), Nicoll (1985), Dzik (1986) and Aldridge *et al.* (1987) have localised the position of the element morphologies within these apparatuses. Barnes *et al.* (1979) identified the presence of a 1st transition series (M and S elements) and a second transition series (the Pb and Pa elements).

Ozarkodinid apparatuses are differentiated into four morphological components. The notation scheme of Sweet and Schönlaub (1975) designates these categories as **M**, **Sb-Sd**, **Sa** and **Pa-Pb**. The architectural plan of ozarkodinid

apparatuses relating these units to their location, as reconstructed by Aldridge *et al.* (1987), is given in Text-fig. 3.2. The dolabrate ramiform (M) elements occupy an external position at the anterior of the assemblage, and a first symmetry-transition series (*sensu* Barnes *et al.* 1979) of paired and elongate, bipennate ramiform (Sb-Sd) elements lies between the M pairing. The elements of the ramiform suite are all oriented parallel to the apparatus midline. A bilaterally symmetrical, alate element, the Sa, is thought to lie on the apparatus midline at the centre of the ramiform suite. Pairs of Pb and Pa pectiniform elements lie to the posterior of the assemblage and are orientated perpendicularly to the apparatus midline, forming a second transition series (Barnes *et al.* 1979). The model of Aldridge *et al.* (1987) placed the anterior elements at a steep angle to the long axis of the animal, with the posterior elements lying vertically. The Ozarkodinida show varying degrees of morphological differentiation in the S transition series, some species possess two pairs of Sc elements, and single pairs of Sb and Sd elements, others have two pairs each of Sb and Sc elements or a quadrate set of Sc elements (Aldridge *et al.* 1987).

3.3.2 Order Prioniodontida Dzik 1976

Evidence is available for the architecture of another group of ramiform-pectiniform apparatuses in the form of bedding assemblages of *Promissum pulchrum* Kovács-Endrödy, 1986 from the late Ashgill Cedarberg Formation of South Africa (Theron *et al.* 1990). A quadrimembrate apparatus differentiation is seen in this genus, with a symmetrically arched M; a first symmetry transition series of extremely elongate paired Sb-Sd elements, a single, symmetrical, alate Sa; and a second transition series comprising of three P elements (Pa-Pb-Pc). Although no architectural model has yet been published of the *Promissum* apparatus, a number of features have been noted by Theron *et al.* (1990). The components of the first symmetry transition series are all orientated parallel to the apparatus midline, much in the style seen in the Ozarkodinida, with the symmetrical Sa lying to the anterior of this suite. A notable departure from the ozarkodinid plan is the geometrical

association of the M elements with the P elements, rather than the S series. From the available evidence Theron *et al.* (1990) suggested that these components were positioned above or below the first transition series, not in a posterior location as in the ozarkodinids. If the M elements in *Promissum* are positioned in this fashion, the locational homology inferred by Theron *et al.* (1990) with ozarkodinid apparatuses, by the application of Sweet & Schönlaub's (1975) terminology, is thought highly questionable. *Promissum* seems to demonstrate an additional, possible unique, architectural style within the conodonts (Theron *et al.* 1990).
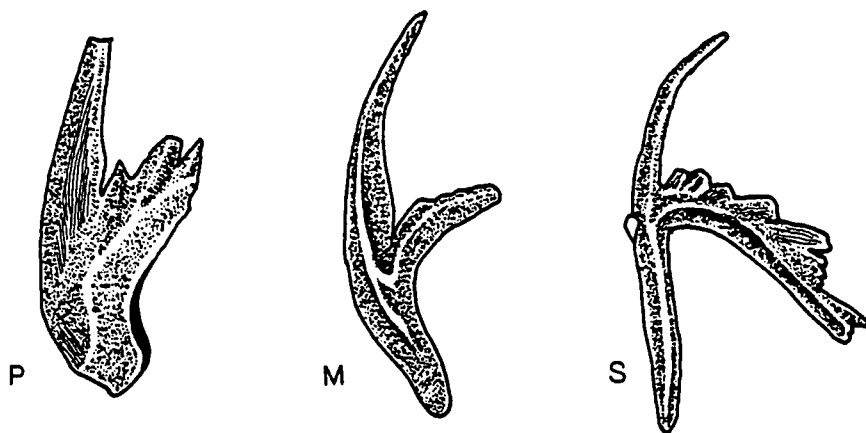
TEXT-FIG. 3.3. Apparatus of *Paracordylodus gracilis* Lindström, as reconstructed by Stouge and Bagnoli (1988; P element traced from pl. 8, fig. 16 [x45]; M element traced from pl. 8, fig. 19 [x35]; S element traced from pl. 8, fig. 18 [x25]).

A cluster of *Paracordylodus gracilis* Lindström, 1955, illustrated by Stouge and Bagnoli (1988: pl. 8, figs 17 A, D), suggests that other architectural plans were also present within the Prioniodontida. *Paracordylodus* has been reconstructed with a suite of morphologically similar S elements, a geniculate M, and a single P component (Text-fig. 3.3). An Sa element has not been recognised. In the cluster illustrated by Stouge & Bagnoli (1988: Text-fig. 3.4), all the elements show the same cusp/base orientation, and it consists of five S elements and a single M, all in lateral juxtaposition. There is little evidence to suggest that the cluster has been deformed in

any sense. The presence of the M element in lateral association with the S suite is a notable departure from the pattern seen in *Promissum*. Because of the isolated nature of this specimen, there is no evidence of the relative orientation of this suite of elements with respect to the apparatus midline. The relative location of the **P** elements is also problematic. Despite these outstanding problems, it is clear that *Paracordylodus* possessed a different architectural plan than that exhibited by *Promissum*, and the architectural integrity of the Prioniodontida is questionable.
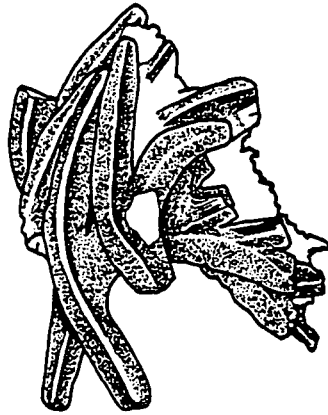
TEXT-FIG. 3.4. Cluster of *Paracordylodus gracilis* Lindström, consisting of five S elements and a single M element (Traced from Stouge and Bagnoli 1988; pl. 8, fig. 17B [x40]).

3.4 COMPARISON BETWEEN OZARKODINID AND PANDERODONTID APPARATUSES

As well-founded architectural models now exist for representatives of the Panderodontidae and the Ozarkodinida, it is appropriate to compare the two architectural styles to establish whether homology is demonstrable between coniform and ramiform-pectiniform bearing apparatuses. The Prioniodontida are considered to be an inappropriate starting point, as they exhibit at least two architectural plans, neither of which is yet fully understood.

The two architectural models are illustrated in Text-figs 3.1 and 3.2. Both apparatuses readily fall into four morphological categories, and these element suites have been localized within the apparatuses.

Both the panderodontids and the ozarkodinids possess a suite of morphologically similar elements to the anterior of their apparatuses, these being termed **graciliform/truncatiform** and **Sb-Sd** respectively. An important morphological feature of ozarkodinid apparatuses is the presence of the first symmetry transition series within the **Sb-Sd** elements. Discrete collections of *Panderodus* yield asymmetrical and sub-symmetrical **graciliform** elements, but these have yet to be localized within the apparatus, therefore the presence or absence of a symmetry transition series remains a matter of conjecture. Given this uncertainty, it seems inappropriate to apply **Sb-Sd** terminology to *Panderodus* elements at this stage. However, given the fact that the **graciliforms & truncatiform** occupy the same position in the apparatus as the **Sb-Sd** suite, locational homology can be highlighted by the use of the terms S_1 (symmetrical **graciliform**), S_2 (sub-symmetrical **graciliform**) and S_3 (**truncatiform**). It is notable that true symmetry transition series have only been demonstrated in those apparatuses where the anterior S suite is located sub-parallel to the midline (e.g. *Ozarkodina, Gnathodus, Promissum* etc.). It is doubtful whether such a transition could ever be demonstrated in *Panderodus* where the elements are orientated perpendicular to the axis of symmetry (Text-fig. 3.5).

Additional paired elements lie to the anterior of this assemblage in both the *Panderodus* (the **arcuatiform**) and the ozarkodinid (**M**) apparatuses. In both of these apparatuses, the elements occupying this external location are morphologically closest to those elements which are situated inside them; this similarity has enabled the inclusion of the arcuatiform within the costate suite in *Panderodus* (see earlier). This is not the case in all forms (for example, see Theron *et al.* 1990 on *Promissum*, and comments above on the validity of homology between the **M** element of this genus and the ozarkodinids). Given the correspondence in relative location and

morphology, the *Panderodus* arcuatiform element is homologised with the M of ozarkodinid apparatuses (Text-fig. 3.5).
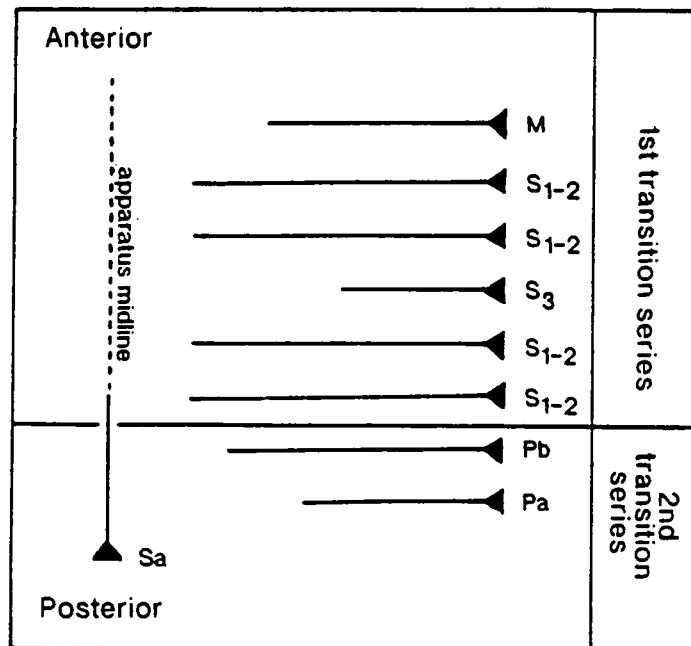
TEXT-FIG. 3.5. Apparatus architecture of *Panderodus*, described with the modified version of Sweet and Schönlaub's (1975) notation scheme developed herein. The 'costate suite' has been homologised with the 1st transition series, and the 'compressed suite' with the 2nd transition series of ozarkodinid apparatuses (compare with Text-fig. 3.1. and 3.2.).

The posterior paired elements in both apparatuses show a degree of morphological specialization. In ozarkodinid apparatuses, these are divided into the anterior **Pb** and posterior **Pa** elements which are united in the second transition series (*sensu* Barnes *et al.* 1979). In the *Panderodus* apparatus, the **falciform** and **tortiform** pairs form the compressed suite. Both are aligned perpendicular to the plane of symmetry, the presence of the morphologically distinct **falciform** and **tortiform** element pairs in the same relative location in the *Panderodus* apparatus suggests homology and it appears to be a reasonable step to apply the terms **Pb** and **Pa** for the **falciform** and **tortiform** elements, respectively, to denote this similarity (Text-fig. 3.5).

Jeppsson (1971) and Aldridge *et al.* (1987) placed the ozarkodinid Sa element medially within the anterior ramiform basket, and thus in the same plane as these

elements. The admittedly scant evidence regarding the position of the symmetrical aequaliform element in the *Panderodus* apparatus suggests that it too lay on the plane of bilateral symmetry. Although it is thought that this element was found to the posterior of the assemblage, the totally symmetrical nature and medial position implies homology, and thus the aequaliform element may be termed Sa (Text-fig. 3.5).

3.5 EVOLUTIONARY DEVELOPMENT OF APPARATUS ARCHITECTURE

Varying degrees of homology may be demonstrated between the apparatuses of the panderodontids and the ozarkodinids. On the basis of this work, Sweet and Schönlaub's (1975) notation scheme has been developed so that it becomes available to most coniform apparatuses (cf. homologies within coniform apparatuses presented in Chapter 2). Other authors have developed homology between a wide range of ramiform-pectiniform apparatuses utilising the scheme of Sweet and Schönlaub (see, for example, Sweet 1988), although these have the drawback of being largely based on morphological homology. Thus it seems likely that this notation can be applied, in modified form, to all multi-element conodont genera.

In Text-fig. 3.6, a simple, hypothetical model is presented to show how it could be possible to evolve from the *Panderodus* condition, with elements opposed to the midline, to the ozarkodinid plan, with the anteriormost elements oriented sub-parallel to the symmetry plane. The passage from one plan to another could theoretically occur in either direction based upon rotation of the anterior paired assemblage. Such developments could be driven by a change in apparatus function or animal shape in response to ecological changes (see discussion in Chapter 4).
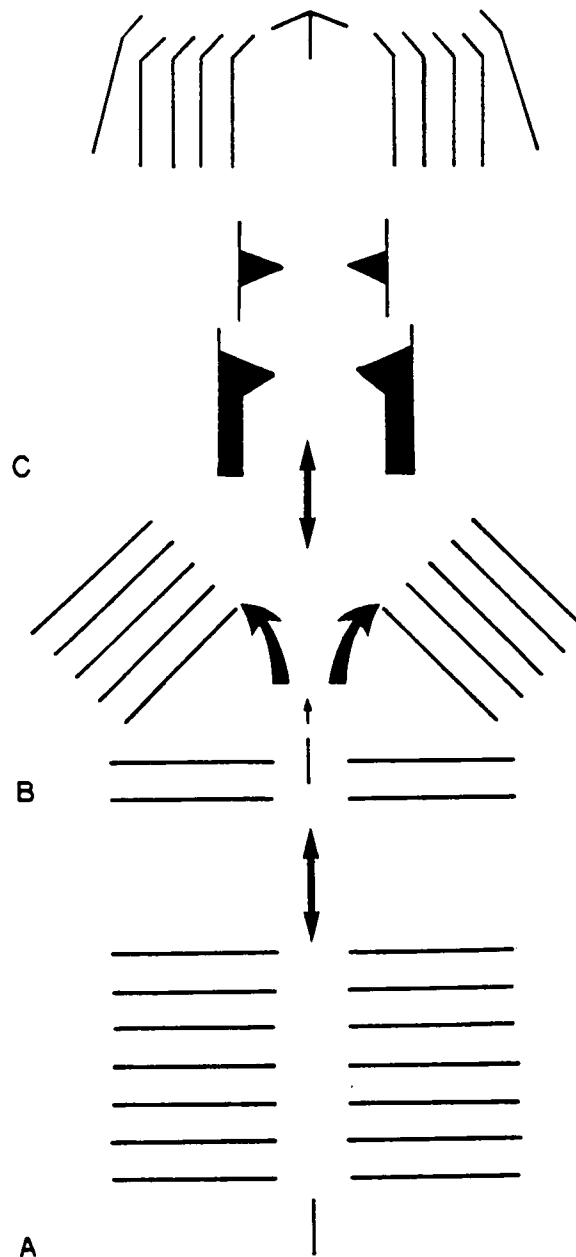
TEXT-FIG. 3.6. Diagrammatic transition from the *Panderodus* condition (A) to the ozarkodinid condition (C) through a hypothetical intermediate stage (B). The elements of the 1st transition series open out within the oral cavity, from a midline-perpendicular position to a midline-parallel position, with a relative anterior shift of the medial Sa element. There is currently no direct evidence as to whether A or C represents the primitive condition, and therefore this hypothetical transition could be followed from A to C, or C to A.

The general architecture of conodont apparatuses appears to be fairly conservative, and is essentially divisible according to the orientation of the anterior S elements, i.e. whether they are sub-parallel or perpendicular to the apparatus midline; this should provide a basis for a higher classification of apparatuses. Sweet (1988), in his revision of conodont classification, utilises at least seven Orders; of these, direct architectural evidence is available for four: the Bellodellida, the Panderodontida, the Prioniodontida and the Ozarkodinida. There is little evidence for the apparatus architecture of major groups such as Sweet's Orders Protopanderodontida and Prioniodinida; the absence of an architectural plan for the latter is especially significant because this order contains the genus *Oulodus*, for which Sweet & Schönlaub's notation scheme was developed. However, the available evidence suggests that the presence of a true symmetry transition series (as developed in *Ozarkodina* and *Promissum*, for example) within the S suite only occurs in those apparatuses where the anterior basket is oriented sub-parallel to the midline, and that the variations seen within the prioniodontids, and between the prioniodontids and ozarkodinids are modifications of this basic plan. A symmetry transition is not seen in the panderodontids, and hence I have been unable to fully apply Sweet & Schönlaub's notation scheme to these apparatuses.

The question of primacy in apparatus style is problematic. Sweet (1988) presents an evolutionary model which centres on the protopanderodontids, because, not only does this order provide the root stock for the panderodontids, but the protopanderodontids also contain the ancestors of the prioniodontids, prioniodinids and ozarkodinids. Sweet envisages this differentiation as occurring during the earliest Ordovician when *Utahconus* evolved into *Rossodus*. If this scenario is accepted, then the basic apparatus architecture of the protopanderodontids would appear to be the primitive condition. Unfortunately, it is here that there is a gap in our knowledge. A cluster of *Protopanderodus* has been illustrated by McCracken (1989: pl. 1 figs 16, 17, 27, pl. 2 figs 1-5), but the specimen has undergone a degree

of torsion since the element bases are in opposition, and the identification of elements is confused by a covering of diagenetic material.

The search for further architectural evidence in disparate taxa assumes great importance to assessments of both the suprageneric classification and evolutionary development of conodont apparatuses.

Chapter 4.

A FUNCTIONAL INTERPRETATION OF
THE *PANDERODUS* APPARATUS

4.1 INTRODUCTION

The function of conodont elements is the subject of much controversy and has frequently been cited as having a central role to play in resolving conodont affinities. Despite this, comparatively little detailed work has been published on this aspect of conodont palaeobiology. In this chapter, a functional paradigm is developed for the *Panderodus* apparatus based upon the architectural model produced in Chapter 2. This is compared against the functional model of Aldridge *et al.* (1987) for ozarkodinid apparatuses and possible extant and fossil models.

Hypotheses of conodont function have followed developments in the generic concept of conodonts. Early studies resulted from the analysis of single morphologies, a consequence of form-taxonomic methodology which dominated conodont systematics until the 1960's. With the advent of multielement taxonomy (Rhodes 1962; Bergström and Sweet 1966), and latterly the discovery of soft-bodied conodont specimens (Briggs *et al.* 1983; Aldridge *et al.* 1986; Smith *et al.* 1987) and reconstructions of apparatus architectures (Jeppsson 1971; Aldridge *et al.* 1987; Chapter 2), new integrated models can be developed (Jeppsson 1979; Nicoll 1985; Aldridge *et al.* 1987).

Rhodes (1954) and Müller (1981) provide a comprehensive review of the various functional interpretations. The following historical review is thus not intended to be comprehensive, but serves rather to highlight the major hypotheses cited in the functional debate.

4.2 HISTORICAL REVIEW

Conodont elements were first described as fish teeth by Pander (1856). Although he did not develop any particular functional model, Pander (1856, p. 8) drew morphological analogy with throat teeth in sharks and the lingual apparatus of the cyclostomes.

Many authors have accepted a tooth-like function for conodont elements and the list of 'toothed organisms' with which they have been compared is quite extensive: including Aschelminthes; Gnathostomulida (Durden 1969; Rodgers 1969); Mollusca (Loomis 1936); Annelida (Scott 1934; DuBois 1943; Rhodes 1954); Chaetognatha; as well as various chordates (see Rhodes 1954; and Müller 1981 for a review).

Huddle (1934) expressed doubts about the external tooth function and cited the lack of wear on the surface of elements. This was supported with the discovery of apparent repair and cusp regeneration by Hass (1941, p. 81) who proposed that elements 'functioned as the internal supports for tissues located at places exposed to stress'.
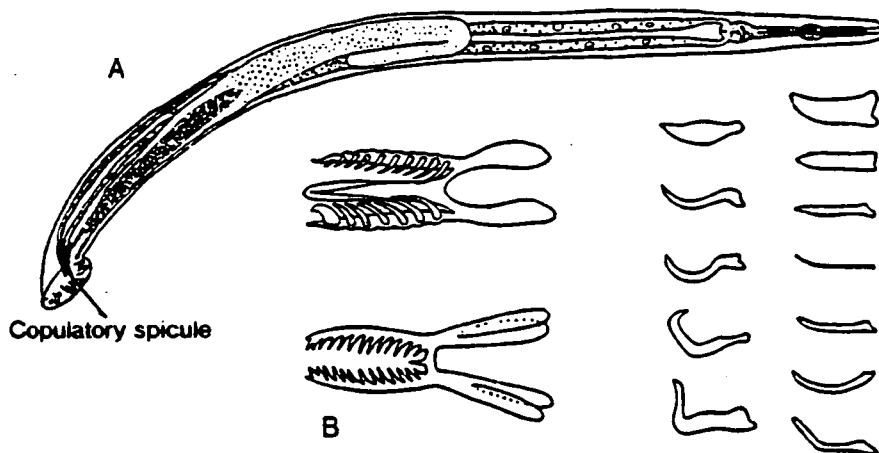
TEXT-FIG. 4.1. A) *Rhabditis* sp., a male nematode showing the location of the copulatory spicule. B) A variety of nematode and turbelarian copulatory structures and spicules (Modified from Denham 1944, fig. 1).

Denham (1944) drew morphological comparison between conodont elements and the paired copulatory structures of the Nematoda. Denham questioned Hass's (1941) conclusion that conodont elements were internal supports, and favoured a grasping or holding function. He suggested that the chitinous copulatory structures of nematodes could be used as a functional analogue for conodont elements. These copulatory structures are positioned at the rear of the animal, and, although normally contained within the worm's body, they are everted during copulation to hold the animals together (Text-fig. 4.1).

Conodont elements grew by external and centrifugal apposition of lamellae, and it has been a long held misconception in conodont literature that this is a unique growth style. Gross (1954) introduced this idea into the conodont literature with the suggestion that enamel grows by internal apposition of lamellae, whereas this tissue actually grows centrifugally (Krejsa *et al.* 1990b). On the basis of his error, Gross (1954) did not believe that conodont elements could function as teeth, instead he suggested they were dermal ossicles, presumably covered by a secretory tissue.

Lindström (1964) promulgated Gross's misconception, and repeatedly cited centrifugal growth as being evidence of an internal support function for elements whilst dismissing any vertebrate connection. Lindström (1973, 1974) extended the internal support hypothesis to produce a theoretical multielement-bearing animal (Text-fig. 4.2). He envisaged the conodont apparatus as a support for a tentaculate lophophore, which served as both a feeding apparatus and a locomotive organ. For these reconstructions, Lindström used the much vaunted conodontochordates, once identified as conodont animals, though now accepted as conodontophages (Conway Morris 1985), to constrain the dimensions of his hypothetical beast. Although this animal seemed to offer solutions to several (non-existent) problems, it was based upon extremely limited data.
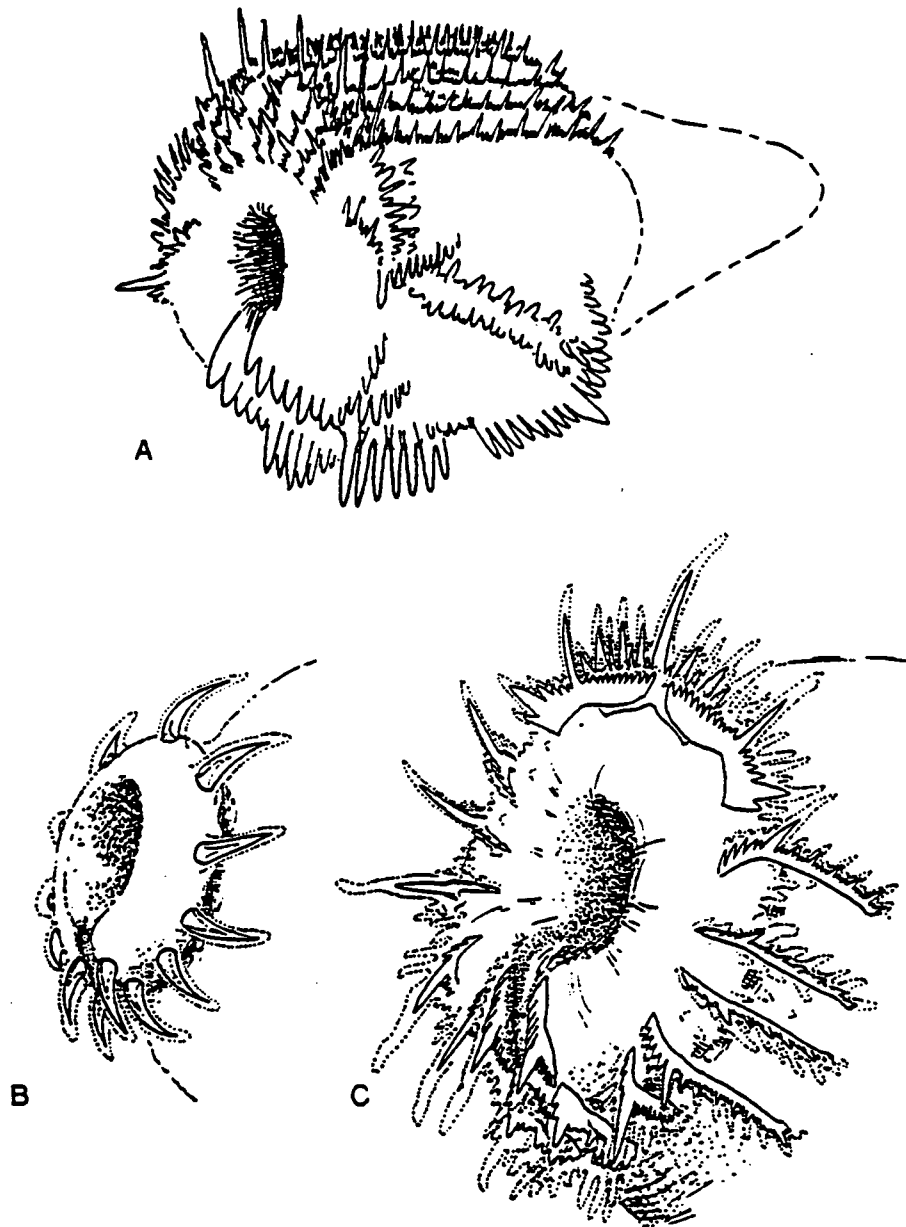
TEXT-FIG. 4.2. A) Lindström's hypothetical reconstruction of an ozarkodinid conodont animal as a lophophorate, approximately 6 mm in maximum length. Oral regions of (B) an ancestral or early growth stage, and (C) an advanced or adult lophophorate conodont (A: From Lindström 1974, text-fig. 4; B and C from Lindström 1973, figure 6).

Priddle (1974) proposed that conodont assemblages, although differing in form, were organised in a similar way to the lingual tongue of myxinoids. However, Priddle suggested that fractured and 'healed' specimens illustrated elsewhere suggested that elements were borne internally, despite recognising that pits and striae on the surface of elements were similar to those seen on mammalian enamel. In order to reconcile their presumed internal location and similarity with myxinoid lingual denticles, Priddle (1974) suggested that conodont elements formed internal supports to horny (presumably keratin-based) cusps (Text-fig. 4.3).
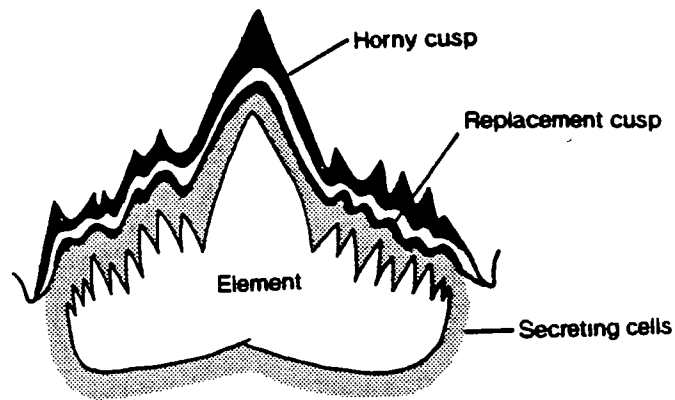
TEXT-FIG. 4.3. An ozarkodinid Pb element acting as an internal support for a 'horny' (presumably keratinous) cusp, presumably homologous with myxinoid lingual denticles (Modified from Priddle 1974, fig. 2).

Conway Morris (1976, 1979) pursued the conodont-lophophorate connection further, proposing that the problematic *Odontogriphus* from the Burgess Shale was a conodont, despite the lack of preserved phosphatic elements and the stratigraphic gap between this genus and the oldest euconodont elements. The coniform impressions in the presumed oral region were proposed as internal supports for a tentacular feeding apparatus.

Bengston (1976) tried to accommodate a tooth-like function with centrifugal growth, by proposing a model of eversion and retraction. During growth the element

was retained within an epithecal pocket, and to function in food gathering and processing was everted from the pocket (Text-fig. 4.4). Problems with accommodating the secretory tissue around complex platform elements has been cited as evidence against this model (Nicoll 1985, 1987).
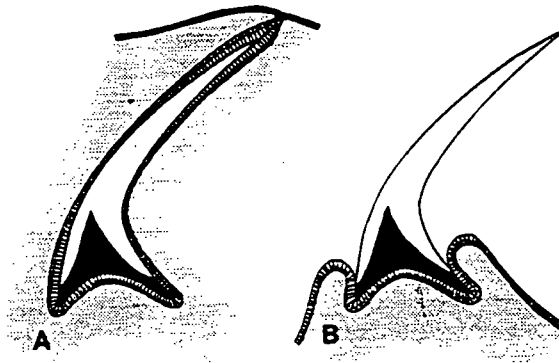
TEXT-FIG. 4.4. Bengtson's model of resting and growth (A), followed by eversion to an external functional position (B) (Taken from Bengtson 1976, fig. 12).

A further model invoking a support function for conodont elements is that of Hitchings and Ramsay (1978). This work was based upon their interpretation of the conodont bedding plane assemblages known at that time. The apparatus was proposed as a filter feeding and respiratory organ with the **Pa** elements anteriorly controlling the opening and closing of the apparatus, the **Pb** pair acted as a sieve, with the **M** and **S** series functioning as a support for ciliated tissue (Text-fig. 4.5).
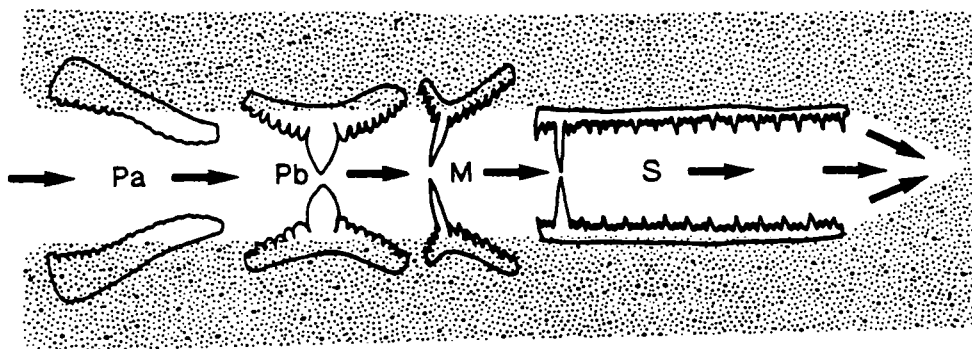
TEXT-FIG. 4.5. Median section through a conodont oral cavity, as reconstructed by Hitchings and Ramsay, indicating the proposed relationship between the elements and soft tissue (stippled). The elements were thought to be covered by ciliated tissue, and the direction of food transfer is indicated by the arrows (Modified from Hitchings and Ramsay 1978, fig. 5).

Jeppsson (1979) highlighted detailed similarities in shape between various conodont elements and vertebrate teeth. In this work he showed that a number of detailed structures occur in both conodont elements and vertebrate teeth, and was able to recognise that a variety of 'bites' occurred within individual apparatuses (*Ozarkodina (Hindeodella)* being one specified example). Jeppsson's (1971) model of the apparatus architecture of *Ozarkodina* could now be interpreted functionally as consisting of a presumed anterior suite of grasping elements (the M and S suite), with the posterior elements fulfilling cutting (Pb pairing) and crushing (Pa elements) roles. Although Jeppsson proposed that conodont elements functioned as teeth, and that individual apparatuses showed functional partitioning, he recognised that shape alone could not be used as evidence for affinity, and that such similarities in morphology were the result of functional convergence.

The discovery of the first Granton specimen (Briggs *et al.* 1983) enabled the orientation of the apparatus to be confirmed as that predicted by Jeppsson (1971), and not the reverse plan invoked by Hitchings and Ramsay (1978). With this new data, Bengston (1983) suggested that in the Granton assemblages the ramiform elements were not in opposition, but in a non-functional resting position. This, he felt, provided confirmatory evidence for his model (Bengston 1976) of elemental growth which predicted periods of external function followed by internal growth.

Two functional models based upon the Granton conodonts and additional clusters or bedding plane assemblages have been presented :

1) Nicoll (1985) produced an integrated model of apparatus function in ozarkodinid animals. This assumed that the elements were covered by ciliated tissue, and the apparatus was located on the ventral surface of the oral cavity. Nicoll (1985) interpreted the architectural differentiation into an anterior ramiform suite and posterior platform pairs as representing a functional partition (Text-fig. 4.6). The ramiform elements acted as a sieve (the 'discerens' elements) and the platforms as crushing and milling units (the 'contundens'). On the basis of this model, Nicoll

(1985) concluded that conodonts were microphagous. This theme was further developed by Nicoll (1987), who proposed functional analogy (and possible phylogenetic affinity) with the microphagous cephalochordates. The oral apparatus of the cephalochordates consists of the buccal cirri, which acts as an anterior sieve, and the ciliated wheel organ lying to the posterior, serving to transfer food particles into the pharynx (Text-fig. 4.7).
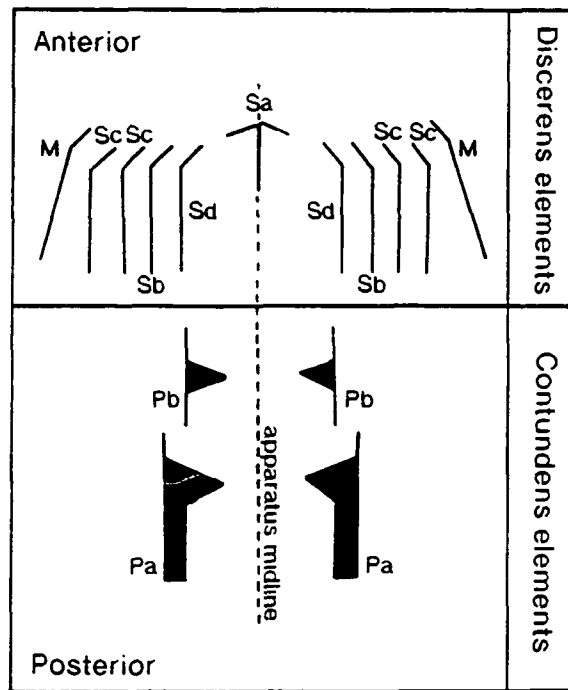
TEXT-FIG. 4.6. Diagrammatic reconstruction of the architecture of an ozarkodinid apparatus, showing the differentiation into an anterior *discerens* assemblage and a posterior *cotundens* assemblage, proposed as a functional partition in a microphagous apparatus by Nicoll (1985).

2) Aldridge *et al.* (1987) interpreted ozarkodinid elements as forming part of a macrophagous feeding apparatus. They suggested that the ramiform elements were exposed to function, and followed Jeppsson's (1971) model of an anterior grasping assemblage followed by posterior slicing and grinding elements (Text-fig. 4.8). In order to grasp, Aldridge *et al.* (1987) proposed that the ramiform basket rotated through 90° from a resting position (as had previously been suggested by Jeppsson

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1971 p. 107). This action was compared with the transverse operation of the myxinoid lingual apparatus, and was also felt to be compatible with the retraction - eversion model of element growth suggested by Bengtson (1976).
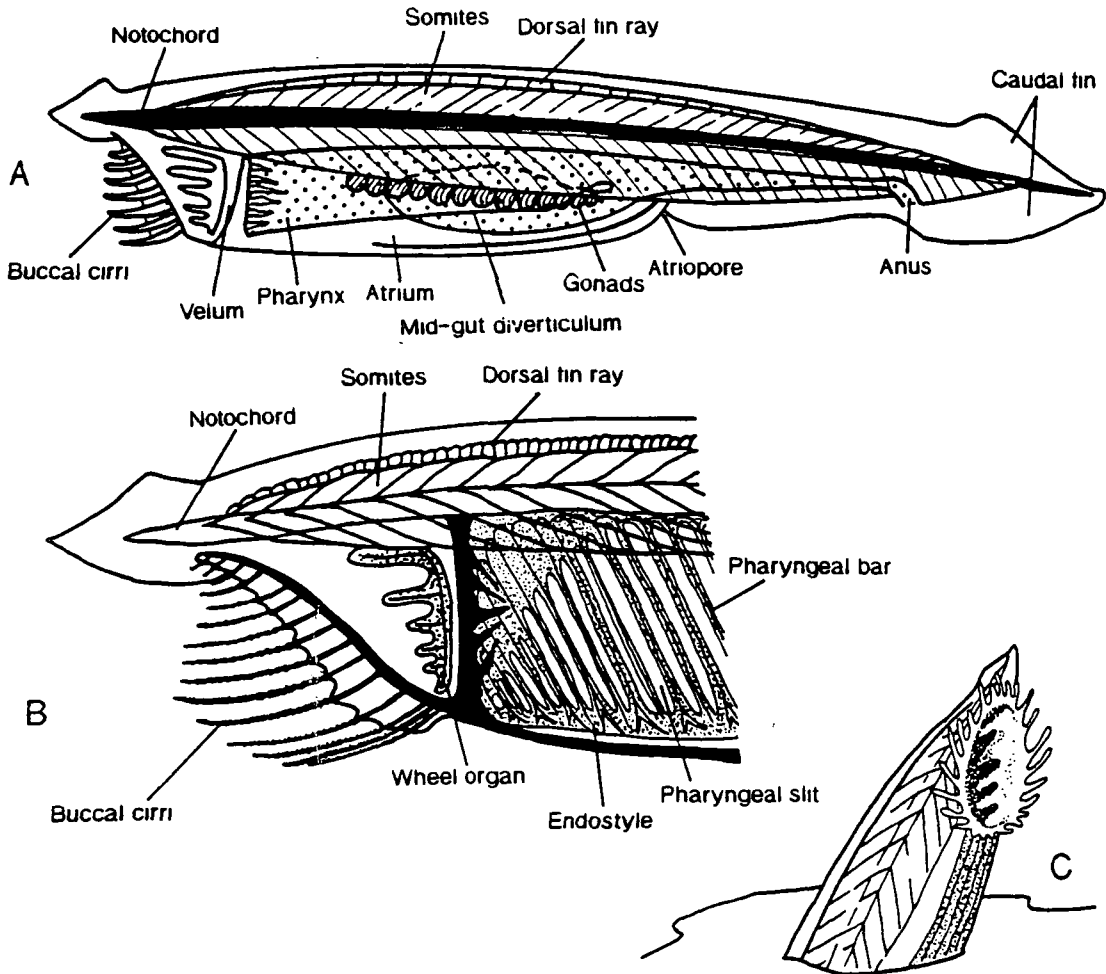
TEXT-FIG. 4.7. A) Body plan of the cephalochordate *Branchiostoma;* B) Detail of the anterior showing principle features of the pharynx; C) Sketch showing *Branchiostoma* in feeding position, partially buried in sediment with it's anterior end protruding. Nicoll (1987) has proposed homology between the *discerens* elements and the buccal cirri and the *contundens* and the wheel organ of conodonts and *Branchiostoma* respectively (Redrawn from Chapman and Barker 1972, (A) fig. 13.4, (B) fig. 13.7 and (C) fig. 13.3).

The presence of a basal support to conodont apparatuses has been argued for by Jeppsson (1979) and Smith *et al.* (1987). Jeppsson (1979) proposed analogy between the flared bases of certain coniform elements and similar structures in basally supported pike teeth. Spherulitic structures in *Panderodus* (Barnes *et al.*

1973; Chapter 5) and *Cordylodus* (Pander 1856; Szaniawski 1987; Sansom *et al.* 1992; Chapter 5) have been homologised with globular calcified cartilage (Smith *et al.* 1987; Sansom *et al.* 1992; Chapter 5). It has been argued that the presence of such a cartilaginous basal support would be more efficient in producing a united apparatus function than individual musculature (Smith *et al.* 1987).
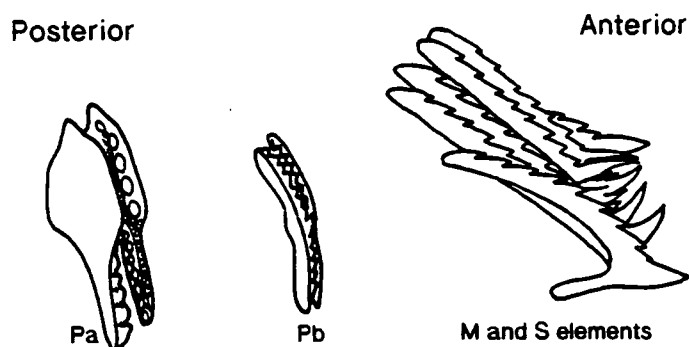
TEXT-FIG. 4.8. Modified lateral view of the architectural model for ozarkodinid apparatuses of Aldridge *et al.* (1987). They proposed functional homology between the M and S elements and the lingual apparatus of *Myxine*.

The recognition of enamel, which grows centrifugally but provides an external cap to vertebrate odontodes, in the lamellar crown of conodont elements Sansom *et al.* (1992; and Chapter 5) weakens models of internal secretion, as they are no longer a necessity (*contra* Nicoll 1987). Similarly, models which invoke eversion and retraction of the elements from a secretory pocket need to be re-examined.

4.3 A FUNCTIONAL MODEL FOR THE *PANDERODUS* APPARATUS

The overall shape of coniform elements is similar to the grasping spines of extant chaetognaths (Dzik and Drygant 1986) and spiders (Müller 1981) suggesting functional convergence. Opening of the *Panderodus* apparatus (Text-fig. 4.9) strongly suggests that the elements fulfilled a primary grasping function. However,

Panderodus species exhibit a variety of element morphotypes, suggesting that a degree of specialisation had been achieved within the apparatus and between species.
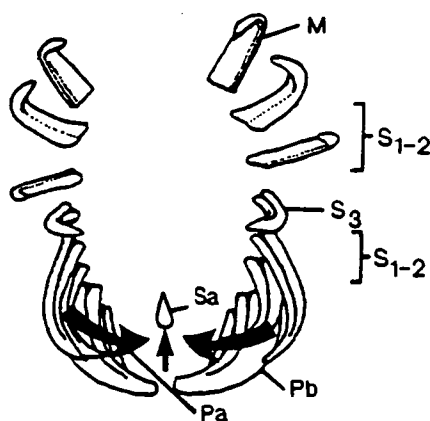
TEXT-FIG. 4.9. Anterior view of a 3-D architectural model for the *Panderodus* apparatus, based upon the reconstruction presented in Chapter 2, and opened out into a functional orientation, with putative motion of the elements indicated by the arrows. The orientation of the apparatus dorsally or ventrally within the oral cavity is not known, although indirect, comparative evidence is discussed in the text.

The apparatus can readily be divided into three units based upon element morphology. The anterior costate M and S elements of the paired array form one morphologically similar unit. The posterior **Pb** and **Pa** elements are more specialised in form, both showing a degree of lateral compression and are acostate and keeled. This suggests the possibility of additional functions. The compressed form and keeled margins of the **Pb** elements seem to be suited to a shearing function upon occlusion; a similar function for keeled elements has been suggested by Aldridge and Briggs (1986). The torted nature of the **Pa** element suggest a refined function, possibly in specialised shearing or the manipulation of food particles towards the posterior. The third apparatus component is the symmetrical **Sa** element which is located towards the posterior of the paired arrays. As far as can be envisaged, the only orientation in which this element may function is in opposition to the paired assemblage; if the Sa lay in the same plane as the other elements it would only have served as a barrier to the posterior transfer of food particles. To function, the paired

linear array can be brought into occlusion by the laterally transverse closure of apparatus, with the symmetrical element operating in a dorso-ventral plane (Text-fig. 4.9). The furrows, which run laterally along the individual elements, may represent scars of ligament insertion or muscle attachments (Lindström and Ziegler 1971); if so these structures could serve to control the motion of individual elements relative to one another.

4.4 POSSIBLE FUNCTIONAL ANALOGUES

In an effort to see whether the functional constraints of the *Panderodus* architectural model are of use in the affinity debate, they can be compared with a number of possible analogues:

4.4.1 Comparison with the chaetognath grasping array

Several authors have attempted to draw functional analogy between chaetognath grasping spines and coniform conodont elements. This has been used to suggest a close phylogenetic relationship (Rietschel 1973; Repetski and Szaniawski 1981; Dzik and Drygant 1986).

Chaetognath grasping spines are located in arrays which exhibit a pronounced size and curvature gradation, and function as a bilaterally opposed radial apparatus. These 'superteeth' emerge from a resting position laterally alongside the animal's head (Text-fig. 4.10C) to form an anterior grasping basket (Text-fig. 4.10A,B; Szaniawski 1982; see also illustrations in Kuhl 1938; Thuesen and Bieri 1987; Kapp and Mathey 1989). From this position the chaetognath is able to move the arrays independently, and they can hold prey with one set and work it into the oral cavity with the other.

Smith *et al.* (1987 fig. 6.8) and I (Chapter 2) have demonstrated that the *Panderodus* apparatus is essentially bilateral and linear, and it is unlikely that any

radial arrangement could produce the Waukesha bedding plane assemblage through a simple collapse. The presence of vertebrate hard tissues in conodont elements (Sansom *et al.* 1992; Chapter 5) dismisses any further arguments of a close conodont - chaetognath phylogenetic relationship.

TEXT-FIG. 4.10. A) and B) Ventral views of the head of the chaetognath *Sagitta.* A) Hood withdraw and grasping spines opened out into a functional position. B) Spines partially covered by hood. C) Dorsal view of the head with grasping spines resting and covered by the hood (Taken from Szaniawski 1982, text-fig. 2).

4.4.2 Comparison with the lingual apparatus of myxinoids

A number of authors have proposed a close relationship between conodonts and myxinoids. This has been based upon analogy between the morphology of ramiform elements and lingual teeth (Priddle 1974; Krejsa and Slavkin 1987; Krejsa

et al. 1987, 1990a,b), and similarities in body structure displayed by the Carboniferous ozarkodinid animals and myxinoids (Briggs *et al.* 1983; Janvier 1983; Aldridge *et al.* 1986; Aldridge and Briggs 1990).

The myxinoid feeding apparatus consists of a series of small, keratinous denticles lying in two rows either side of a cartilaginous dental plate. This lingual apparatus protrudes from the oral cavity with the dental plates opened out like a book. In the biting action, these denticles are brought into opposition with a bilateral motion resulting in a tearing action. The lingual apparatus is then withdrawn into the oral cavity in the closed position (Dawson 1963). A single palatal tooth is found in the roof of the oral cavity, and this may act as a barb preventing the eversion of food particles during subsequent bites (Dawson 1963), or used to impale prey to aid ingestion (Krejsa *et al.* 1990 a).
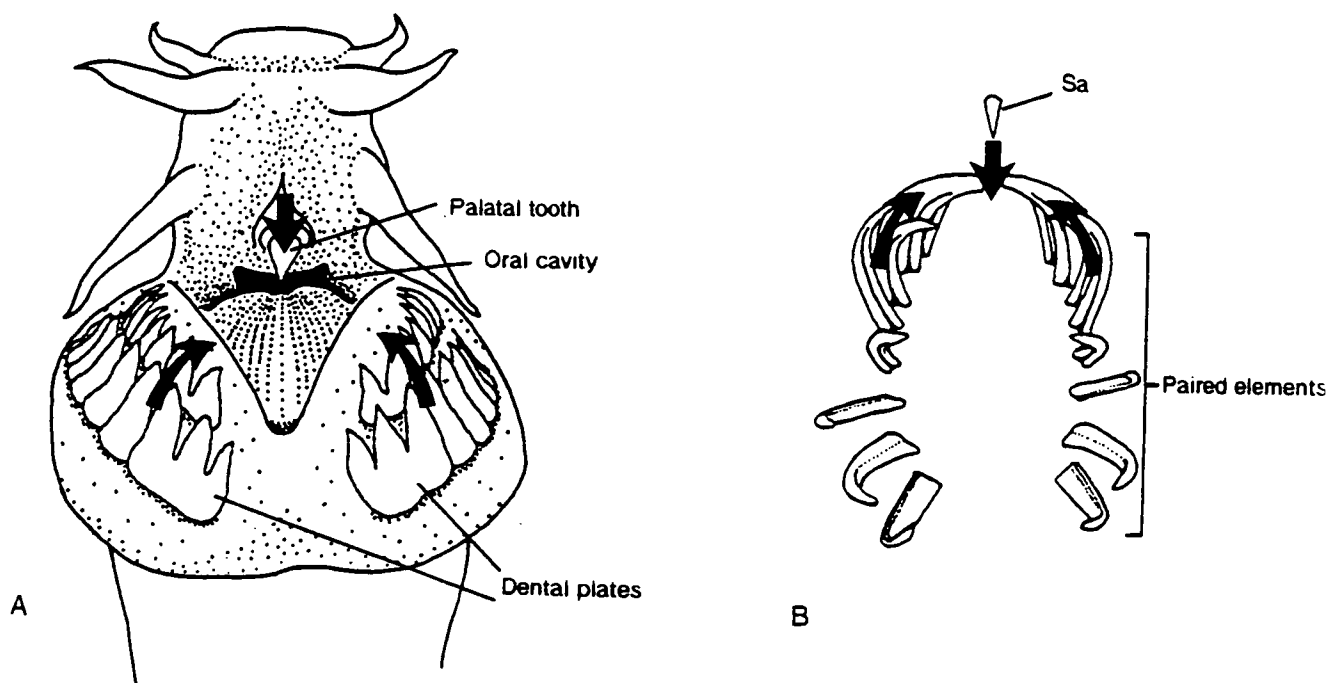
TEXT-FIG. 4.11. Functional comparison between A) the lingual apparatus of *Myxine*, from a "prey's eye view", and B) the apparatus model of *Panderodus* with the paired elements located ventrally. Functional motion in both apparatuses is indicated by the arrows (A: Traced from Krejsa *et al.* 1991, figure 4).

In order to compare the *Panderodus* architectural model with the lingual apparatus of *Myxine*, it is necessary to orient the bilateral array ventrally and the **Sa** medial element dorsally (Text-fig. 4.11). A number of similarities may be noted. Both apparatuses consist of a single dorsal component: the palatal tooth of *Myxine* and the **Sa** element of *Panderodus*; and a paired array: the dental plates (*Myxine*) or bilateral element array (*Panderodus*). The operation of these two apparatuses is essentially bilateral, with the paired elements serving to grasp and the opposed tooth acting as a barb to impale prey (Text-fig. 4.11).

Analogy, and possible phylogenetic homology, between the lingual arrays of myxinoids and ozarkodinid euconodont apparatuses has been suggested by Aldridge *et al.* (1986, 1987) who highlighted similarities in the functional closure of the respective apparatuses. The apparatus is thought to have been located ventrally within the oral cavity, with the cusps of the ramiform basket facing dorsally (Text-fig. 4.12). Functional comparison between myxinoids and this apparatus extends to the bilateral motion inferred for the asymmetric components of the ramiform basket and the book-like closure of the dental plates, respectively (Text-figs 4.11 and 4.12). However, the **Sa** element, placed medially within the ramiform basket, is thought to have functioned in a dorso-ventral sense; no such transverse component is found within the lingual plates of myxinoids. The lack of a structure such as the ozarkodinid **Sa** suggests that analogy with the myxinoid apparatus, rather than homology, is more appropriate.
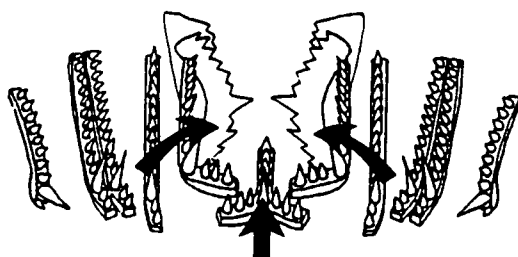
TEXT-FIG. 4.12. Anterior view of the ozarkodinid apparatus model of Aldridge *et al.* (1987). Functional motion within the M and S ramiform basket is indicated by the arrows.

If conodonts do represent a monophyletic clade, as the architectural homologies presented in Chapter 2 and 3 imply, then it is more appropriate to orient the *Panderodus* apparatus dorsally within the oral cavity (Text-fig. 4.9). In this orientation, the Sa element of *Panderodus* acts in a dorso-ventral sense but is directly opposed to the position of the palatal tooth in myxinoids.

4.4.3 Comparison with the oral apparatus of the petromyzontids

The petromyzontids (lampreys) have been classified with the myxinoids as making up the extant representatives of the infraphylum Cyclostomata (Jarvik 1980; Yalden 1985). They have so far escaped detailed comparison with conodonts. However, given the doubt expressed above as to the validity of the myxinoid functional paradigm, comparison with the feeding apparatus of the petromyzontids is thought appropriate.

The biting apparatus of the petromyzontids differs from that possessed by myxinoids in the presence of a median ventral component, the transverse lamina (Jarvik 1980). As outlined above, the myxinoid lingual apparatus functions by the 'book-like' closure of the extruded dental plate. In petromyzontids, the mouth is surrounded by the oral disc, or sucker, which bears a series of keratinous toothlets. The oral cavity is lined by elongate multi-denticulate elements, and these are divided into the bilaterally-symmetrical longitudinal laminae and the ventral transverse lamina. In functioning, the longitudinal laminae bite in bilateral occlusion across each other, whilst the transverse lamina operates with a rasping motion in the dorso-ventral plane (Text-fig. 4.13). Both the longitudinal laminae and transverse lamina evert from the oral cavity on the piston cartilage (Text-fig. 4.13).

Yalden (1985) has argued in favour of cyclostome monophyly by comparison of the oral musculature in petromyzontids and myxinoids. However, the myxinoids lack a structure homologous with the petromyzontid transverse lamina, and the petromyzontids do not possess an equivalent to the myxinoid palatal tooth (Jarvik 1980).
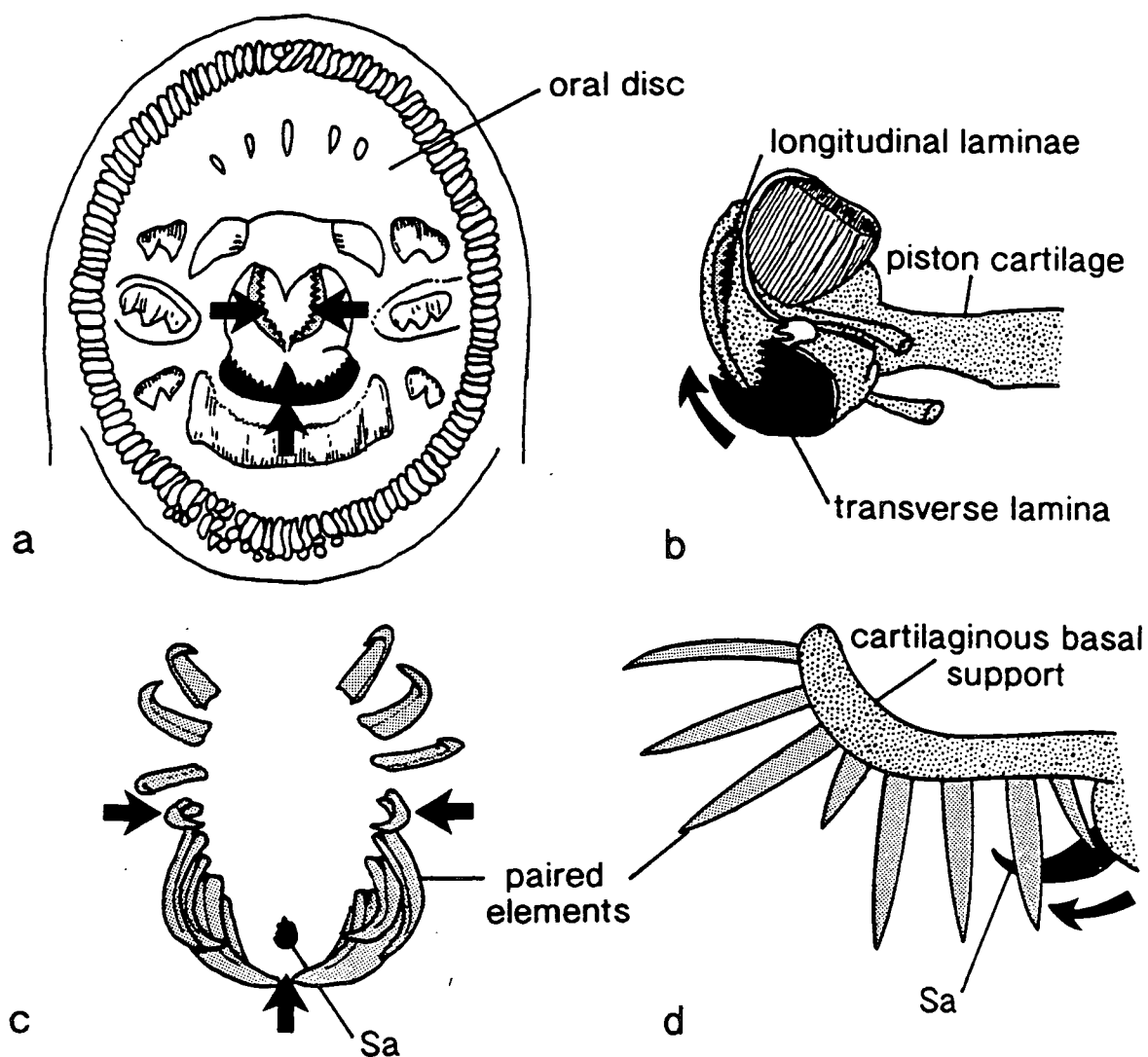
TEXT-FIG. 4.13. a) and b), oral region of the petromyzontid *Lampetra* in anterior and lateral aspects. c) and d) annotated *Panderodus* apparatus model in anterior and lateral aspects, for comparison with a) and b). Functional motion is indicated by the arrows, and is suggested as homologous although there is no evidence of the protrusion of the *Panderodus* apparatus along a piston cartilage as in *Lampetra*. (a) and b) modified from Jarvik 1980, fig. 341).

The presence of a bilateral and dorso-ventral action of the petromyzontid oral laminae is comparable with the function postulated for the *Panderodus* apparatus (Section 4.5). In the *Panderodus* apparatus, bilateral motion appears to have occurred in the linear paired elements, the symmetrical **Sa** element functioned in the dorso-ventral plane (Text-fig. 4.13). In this scenario, the orientation of the *Panderodus* apparatus agrees with that inferred from homology with the ozarkodinid

Granton specimens. There is a lack of positive or negative evidence for the extrusion of the *Panderodus* apparatus by the action of a piston cartilage.

The postulated function of ozarkodinid apparatuses (Aldridge *et al.* 1987) can also be compared with the petromyzontid oral apparatus. Both possess a bilateral bite surrounding the oral cavity, the ramiform basket and the longitudinal laminae respectively. The medial **Sa** element has been reconstructed within the main ramiform basket by Aldridge *et al.* (1987), and thus is thought to lie ventrally within the ozarkodinid apparatus (Text-fig. 4.12). In this orientation, the ozarkodinid **Sa** appears to be homologous with the petromyzontid ventral transverse lamina, as they both have a similar location within the oral apparatus and function in the dorso-ventral plane.

4.5 THE FEEDING APPARATUSES OF EARLY 'AGNATHANS'

Comparatively little is known about the oral apparatuses of the heterostracomorphs and the osteostracans. Despite this, Jarvik (1980) and Janvier (1981) have proposed that they can be divided on the basis of their bite style.

The oral areas of the earliest 'agnathans', *Arandaspis* and *Porophoraspis* from the Llanvirn of central Australia, have yet to be described due to preservational problems, and reconstructions of *Arandaspis* are illustrated with an indistinct oral opening (Ritchie and Gilbert-Tomlinson 1977; Text-fig. 6.11). Similarly, little is known about the feeding apparatuses of the 'agnathans' from the Caradoc Harding Sandstone. Elliott *et al.* (1991) presented a reconstruction of *Astraspis* with a rather enigmatic smile (Text-fig. 6.10), possibly a reflection of this lack of knowledge. Halstead (1969) postulated that the Harding Sandstone vertebrates burrowed through the sediment, although there is only indirect evidence, the presence of large burrows, to suggest this (Spjeldnaes 1979). Presumably, the oral region would have

functioned to sieve food particles in some fashion if this was the case. *Sacabambaspis janvieri* from the Caradoc of Bolivia is known from more complete material (Gagnier *et al.* 1986; Gagnier 1989). In this genus, the oral area is composed of a series of 60 small plates which are thought to have been movable and formed a filter to suck up small food particles from the sediment (Gagnier 1989).

A similar sparsity of evidence exists on the nature of the feeding apparatus of post Ordovician 'agnathans'. Both Jarvik (1980) and Janvier (1981) have inferred a myxinoid bite for the oral apparatuses of the pteraspid heterostracans. In the pteraspids, the oral plates are found lining the ventral margin of the mouth, and these are thought to have opened ventrally and laterally, acting as a scoop to gather sediment to be processed for food particles (Janvier 1981; Text-fig. 4.14).
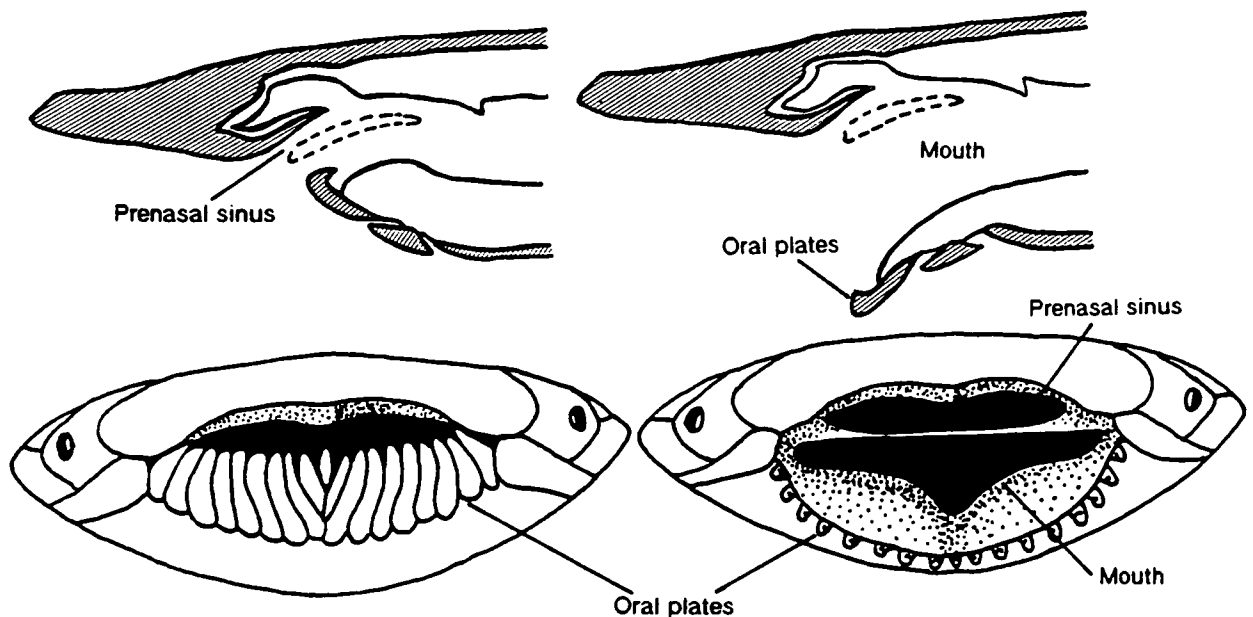
TEXT-FIG. 4.14. Reconstruction of the head of a pteraspid heterostracan in longitudinal section (top) and anterior view (bottom). The oral plates are shown in retracted (left) and open (right) positions. Jarvik (1980) and Janvier (1981) have considered the function of the heterostracan feeding array as homologous with the lingual apparatus of *Myxine*. (Taken from Janvier 1981, figure 12 B_{1-2} and C_{1-2}).

Jarvik (1980) has suggested that a petromyzontid bite, consisting of a bilateral bite with an additional dorso-ventral motion, was present in the anaspids, although a

sucking and rasping action was absent in the later cephalaspid osteostracans. On the basis of these and other morphological comparisons, it has been proposed that heterostracans and myxinoids form one clade, whilst the cephalaspids (osteostracans) and petromyzontids form another (Jarvik 1980).

4.6 CONCLUSIONS

A functional model for the *Panderodus* apparatus has been developed, which infers the bilateral occlusion for the paired elements and a dorso-ventral motion for the Sa element.

This has been compared with chaetognath grasping arrays, and functional analogy has been rejected, because the model predicts an essentially linear motion while the operation of the chaetognath grasping array is radial.

Comparison with the myxinoid lingual apparatus argues against functional homology (*contra* Aldridge *et al.* 1987) as conodonts possess a distinct transverse component in their oral apparatuses, the symmetrical Sa element.

The function of the petromyzontid laminae appears to present a closer homologue for *Panderodus* and ozarkodinid apparatuses as they involve occlusion of bilateral components and a dorso-ventral motion for a ventrally located median element. Differences in the form of the petromyzontid and conodont apparatuses, notably in the wide range in morphologies of individual elements and the lack of an oral disc in conodonts, and the absence of an antero-posterior differentiation in petromyzontids, may result from differences in feeding strategy. Conodonts appear to have been active, grasping predators which processed their food with specialised posterior elements, whilst petromyzontids have adopted a parasitic mode of life with their mouth parts developed into a sucker to attach them to their prey.

The widespread occurrence of *Panderodus* has led to interpretations of the genus as pelagic creatures, whilst the ozarkodinids are thought to have been nektobenthonic in habit (Barnes *et al.* 1973; Barnes and Fåhræus 1975; LèFevre *et al.* 1976; Aldridge and Mabillard 1981). Similarly, ozarkodinids are thought to have possessed a laterally compressed body (Briggs *et al.* 1983; Aldridge *et al.* 1986), whilst the admittedly scant evidence from the Waukesha animal suggests that *Panderodus* had a dorso-ventrally compressed *bauplan* (Smith *et al.* 1987). The different orientation of *Panderodus* and ozarkodinid apparatuses may result from their accommodation within morphologically distinct oral cavities, which, in turn, could reflect divergent ecological habitats and macrophagous prey.

Chapter 5.

THE HISTOLOGY OF SELECTED CONODONT ELEMENTS

5.1 INTRODUCTION

This study was initiated as an attempt to produce a model of elemental growth for *Panderodus*. This comparatively minor project yielded some surprising histological results and, as a result, a phylogenetically wide-ranging group of Lower Palaeozoic conodont genera has been studied in an initial attempt to elucidate histological variability within conodont elements. A preliminary report of this work was published by Sansom *et al.* (1992), and although many of the ideas expressed in that paper are reiterated here, many are developed at greater length and additional specimens are described.

5.1.1 Protoconodonts, Paraconodonts and Euconodonts

In the Treatise on Invertebrate Paleontology Part W, three histologically distinct phosphatic microfossils are classified within two Orders of the Class Conodonta (Clark 1981). Within the Order Paraconodonta, elements are found which have been described elsewhere as protoconodonts and paraconodonts (Bengtson 1976, 1983; Sweet 1988). Although these superficially resemble 'true conodonts' or euconodonts (placed by Clark 1981 in the Order Conodontophorida), their histology and mode of growth are quite distinct.

In protoconodonts (Upper Vendian to Middle Ordovician) the elements were formed of three structural layers (Text-fig. 5.1). The thin inner and outer lamellae were not mineralised. The middle layer appears to have formed by the addition of phosphate along the internal cavity, producing a 'cone-in-cone' structure (Bengtson 1976, 1983; Szaniawski 1983, 1987). Protoconodonts have been identified as

phosphatised chaetognath grasping spines on the basis of histological and morphological comparison by Szaniawski (1982).
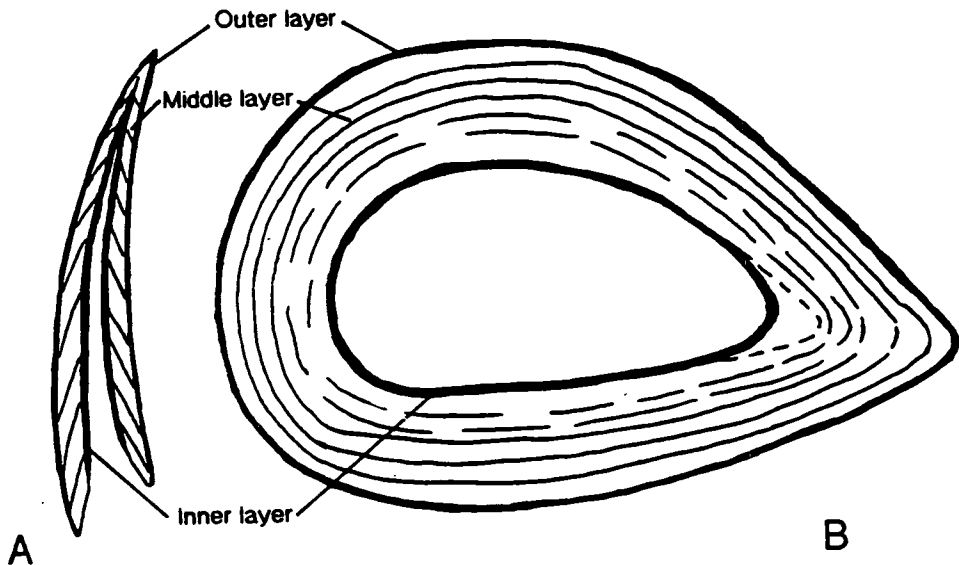
TEXT-FIG. 5.1. Schematic longitudinal section (A) and cross section (B) through a protoconodont element (*'Prooneotodus' tenuis* Müller), showing the differentiation into inner, middle and outer layers and the form of the growth lamellae (Modified from Szaniawski 1983, fig. 1).

Paraconodonts *sensu stricto* (Middle Cambrian to lowest Ordovician) are distinguished by the addition of lamellae around the basal area, along both the interior and exterior surfaces, but not around the external element tips (Müller and Nogami 1971, 1972; Bengtson 1976, 1983; Text-fig. 5.2).

Those elements which are considered here as representing euconodonts (Bengtson 1976, 1983) range from the Late Cambrian to the end Triassic and are formed of two mineralised components. The hyaline crown was formed by the addition of phosphatic lamellae along the outer surface, giving the appearance of essentially centrifugal growth, and concentrically covering the whole element (Text-fig. 5.3A) or concentrated around the basal area (Text-fig. 5.3B). The second component, the basal body is also essentially phosphatic although apparently weakly mineralised and with more included organic material. It too is formed of essentially lamellar (often not continuous) tissue (Müller and Nogami 1971, 1972; Bengtson 1976; Text-fig. 5.3).
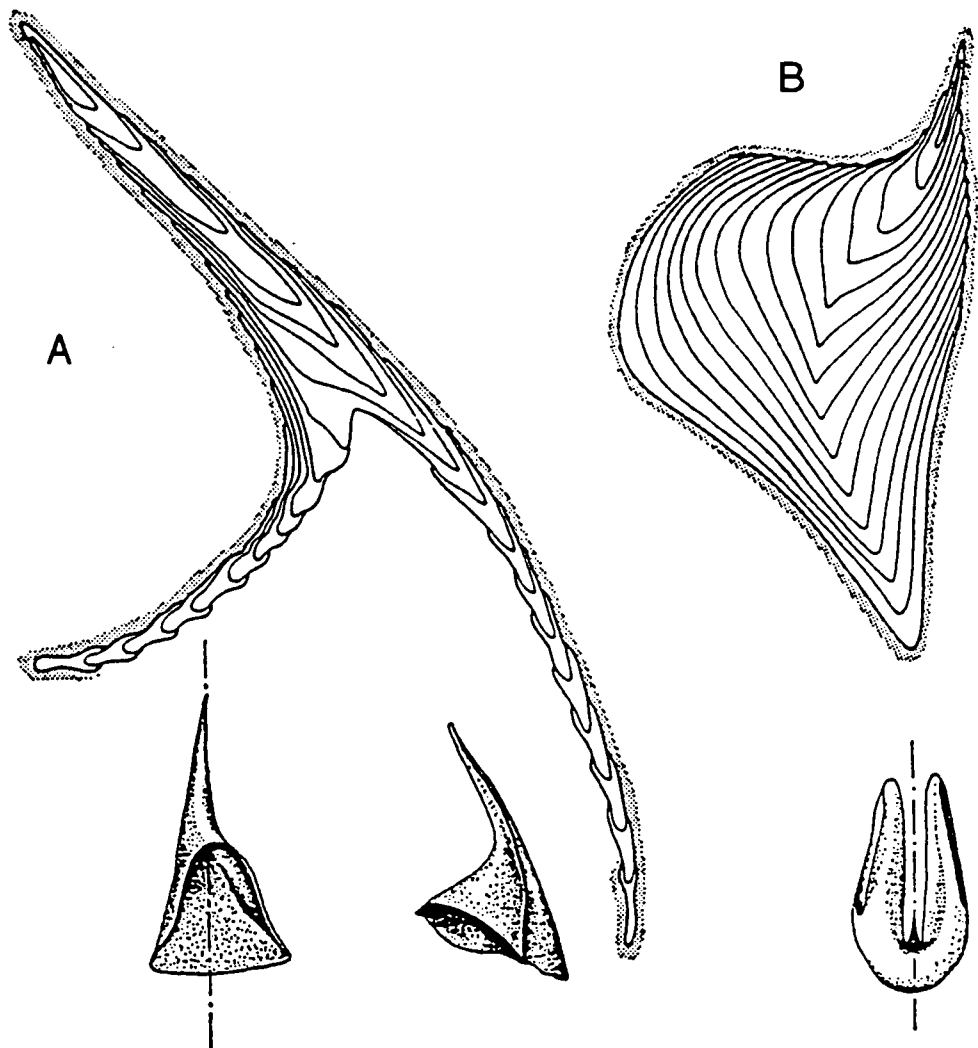
TEXT-FIG. 5.2. Longitudinal sections through the paraconodonts *Furnishina furnishi* Müller (A) and *Westergaardodina bicuspidata* Müller (B) showing the form of the growth lamellae. A thin layer of organic cover is stippled (Taken from Müller and Nogami 1972, figure 1).

Bengtson (1976) has proposed a phylogenetic model by which it is possible to pass from the protoconodont growth style to the euconodont grade through an intermediate paraconodont stage by the gradual retraction of the phosphatic element into a fully-enclosing epithecal pocket (Text-fig. 5.4). In order to function, Bengtson

suggested that the euconodont element was everted from the retracted pocket. However, it has yet to be generally accepted that any link exists between these groups and the euconodonts (Sweet 1988), despite the advocacy of Szaniawski (1982, 1987) and Andres (1988). Histological observations on the euconodonts (simply referred to as conodonts elsewhere in this work) are presented here. The absence of published data on paraconodonts has precluded their inclusion in this discussion.
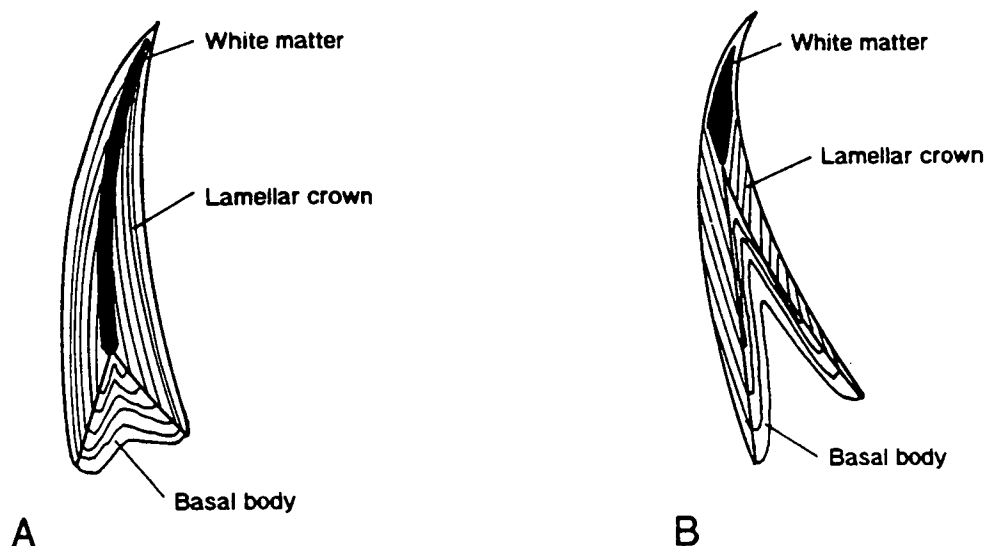
TEXT-FIG. 5.3. Diagrammatic section through two simple euconodont elements showing the distribution of three tissue types and growth increments within the lamellar crown. A) represents a non-*Panderodus* type whilst B) represents a *Panderodus* type element.

The form and function of the conodont apparatus, and evidence from the Granton conodont specimens demonstrates that these animals were chordates (Aldridge *et al.* 1986; Dzik 1986; Aldridge *et al.* 1987; Smith *et al.* 1987; Krejsa *et al.* 1990; see Chapters 2 and 4), although some authors still dispute the evidence (Tillier and Cuif 1986; Szaniawski 1987; Sweet 1988). Within the chordates, only the vertebrates show scleritisation and the development of apatitic hard tissues. Consequently, the histology of conodont elements has been compared with material which is widely accepted as the oldest histologically intact vertebrate hard tissues from the Harding Sandstone of Colorado (Ørvig 1989; Smith and Hall 1989; Elliott *et al.* 1991).

Euconodont

Paraconodont
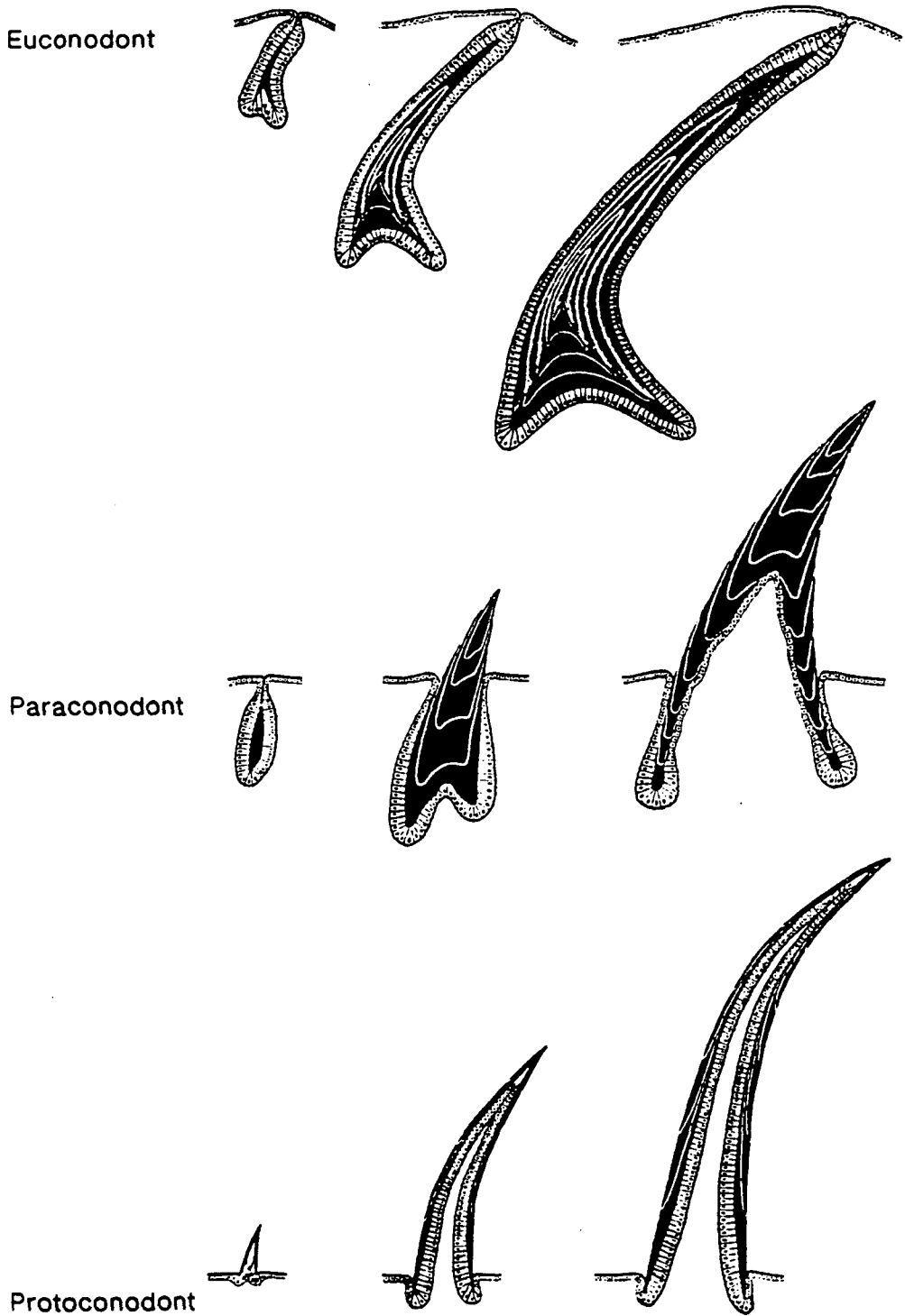
Protoconodont

TEXT-FIG. 5.4. Hypothetical diagrammatic reconstructions of epithelium and elements during growth. This sequence has been proposed by Bengtson (1976) as representing an evolutionary development from proto- through para- to euconodont grade by the gradual retraction of the element into a secretory epithelial pocket (Taken from Bengtson 1976, fig. 11).

5.2 VERTEBRATE ODONTOGENIC TISSUES

The descriptions of vertebrate hard tissues included in this section are of relevance to both the discussion of previous interpretations of conodont histology and the new data and interpretation presented below.

Enamel and Enameloid

Enamel and enameloid form superficial glassy caps of highly mineralised material to many vertebrate odontodes. Both tissues are hypermineralised, formed of more than 95% apatite (Ten Cate 1989). A number of histological criteria have been identified in order to distinguish between enamel and enameloid (Smith 1978; Reif 1979, 1982), centring on the orientation and size of the crystallites forming each tissue, and resulting from their development pattern.

In enamel, the crystallites are orientated perpendicular to the growth surface, or organised into enamel prisms (Smith 1978; Reif 1982; Ten Cate 1989). The presence of growth lines indicate that enamel is not formed in one single event, but over a period of several days. The organic matrix of enamel differs from other vertebrate tissues in lacking significant amounts of collagen, instead it is dominated by amelogens. Individual crystallites in enamel are 0.1 μm thick and 0.5-1.0 μm in length.

Enameloid lacks growth lamellae and contains crystallites that may be orientated randomly, parallel or perpendicular to the growth surface (Reif 1982). The lack of lamellae indicates that mineralisation takes place in a single event. The unmineralised matrix is formed largely of collagen which is degraded during mineralisation. Crystallites in enameloid are 10 times the size of those seen in enamel.

Dentine

Dentine and related tissues are characterised by the presence of polarised tubules radiating from a basal canal opening. Variations in the size of the tubules have been used as a mean of dividing dentine into a wide variety of forms (Shellis 1981). Cell bodies (odontocytes), if present in the mineralised tissue, tend to be pear-shaped (M.M. Smith 1991). Incremental growth is evident from the presence of growth lamellae, and occasionally these lamellae develop a spherulitic structure (Smith and Hall 1990). The lower percentage of mineralised tissues in dentine compared with enamel and enameloid (70% as opposed to 95%+) means that individual crystallites are not resolved in this material (Ten Cate 1989).

Bone

Primary bone (i.e. not resulting from the secondary replacement of cartilage) can be divided on the degree of cellularity of the tissue. In cellular bone, interconnecting tubuli (canaliculi) running between osteocyte cell spaces (lacunae) are randomly orientated, distinguishing this tissue from dentine (Smith and Hall 1990; M.M. Smith 1991). Lamellae may or may not be present, depending upon the rate of mineralisation of the organic matrix. The mineral phase of bone forms between 50 to 60% of the tissue (Ten Cate 1989).

Aspidin

This tissue is only known from the heterostracans and the allied forms found in the Harding Sandstone, where it forms a honeycombed middle layer and basal laminated tissue in the exoskeleton (see below). Aspidin is characterised by coarse fibrous structures and finer spindle shaped cavities within mineralised matrix. These have variously been described as the sites of aspidinocytes (Halstead 1969) or collagen bundles (Ørvig 1965; Halstead 1987). Aspidin seems to be an intermediate tissue between true dentine and bone (Maisey 1988).

Cartilage

Cartilage has a variety of forms, both lamellar and non-lamellar (Smith and Hall 1990), and is a weakly mineralised material formed on a collagen-based organic matrix (Walker 1987). Globular, laminated cartilage is formed from isolated nucleation points to form a spherulitic tissue which appears as linked, scalloped growth lamellae. Globular cartilage has been described from heterostracans (Denison 1967; Halstead 1969; Smith and Hall 1990), placoderms and elasmobranchs (Ørvig 1951).

5.3 THE DEVELOPMENTAL SEQUENCE OF VERTEBRATE ODONTOGENIC TISSUES

In all extant vertebrates, the dental papilla comprises a mass of star-shaped mesenchymal cells enclosed by a cap of epithelium (Shellis 1981; Text-fig. 5.5). Mesenchymal cells are derived form the neural crest. The neural crest forms a pair of ridges in the developing vertebrate embryo, and the interaction between the epidermis and mesoderm, induced by the mobile mesenchymal cells, is thought to produce many of the derived characters of vertebrates (Gans 1987). The epithelial layer next to the inner dental papilla differentiates to form the secretory odontoblasts. Hard tissues are deposited between the mesenchymal cells and the inner dental epithelium (Shellis 1981).

- »

TEXT-FIG. 5.5. Diagrammatic representation of the development of enamel (a,b,c,d), enameloid (a',b',c',d'), dentine and odontogenic bone within the dental papillae of modern vertebrates. Note the comparatively early formation of enameloid with respect to dentine and the late formation of enamel (Modified from Shellis 1981, fig. 6.2).

a) Epithelial cap
Mesenchymal cells

b)

b')

c)

c')

d)

d')

| ▓▓ Enamel | ▒▒ Enameloid | ▐▐ Dentine | ⟨⟩ Odontogenic bone |
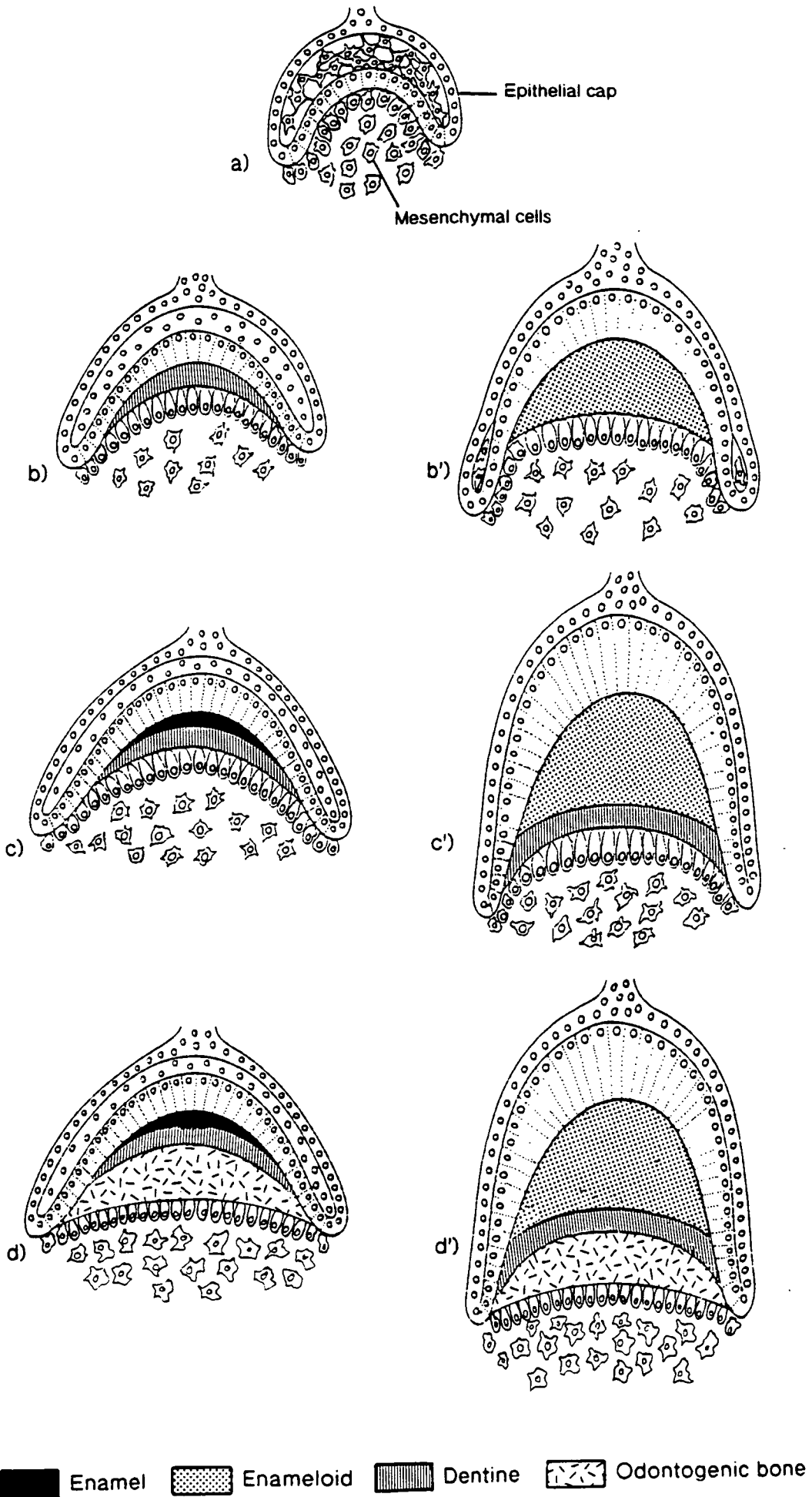
Differences in the relative timing of mineralisation are evident, and serve to produce distinct tissue associations within the final odontode (Shellis 1981; Reif 1982; Smith 1992). In those vertebrates possessing enamel, it is the dentine matrix which is secreted first from the odontoblasts (Text-fig. 5.5b). Soon after, the inner dental epithelial cells are induced to secrete enamel onto the upper surface of the first increment of dentine. Subsequent development involving these tissues is seen in the thickening of the tissues, enamel centrifugally towards the epithelium and the dentine centripetally towards the papilla (Text-fig. 5.5c).

Where the superficial cap is comprised of enameloid, the matrix of this tissue forms first (Text-fig. 5.5b') and continues to grow centrifugally, and, unlike enamel, reaches it's full thickness before any dentine is deposited (Text-fig. 5.5c').

Subsequent development in both cases progresses with the deposition of dentine from the mesenchymal (neural crest) odontoblasts (Smith and Hall 1990). When this ceases, bone associated with these odontodes is deposited from a separate population of mesenchymal osteoblasts (Smith and Hall 1990; Text-fig. 5.5d and d'). Cartilage in the exoskeleton is associated with this bone and it has been suggested that it is derived from the population of neural crest cells (Smith and Hall 1990).

5.4 THE HARDING SANDSTONE VERTEBRATES

The earliest unequivocal fossil vertebrates are late Arenig or early Llanvirn heterostracomorphs (*sensu* Blieck 1992) from central Australia (Ritchie and Gilbert-Tomlinson 1977). These are known to have borne dermal armour which was presumably phosphatic. Known only from moulds and casts, they are not available for histological study. The earliest histologically intact vertebrate skeletal material is that from the Harding Sandstone, Canon City, Colorado (Walcott 1892; Denison 1967; Halstead 1967, 1987; Reif 1979; Ørvig 1989; Smith and Hall 1990; M.M.

Smith 1991) which is of Caradoc age. Specimens of *Sacabambaspis janvieri* Gagnier, from the Caradoc of Bolivia (Gagnier *et al.* 1986; Gagnier 1989) have yet to be histologically studied.

Three genera are present in the Harding Sandstone, and each possesses a distinct histological association (Text-fig. 5.6).

Arandaspis + *Sacabambaspis*	*Astraspis*	*Eriptychius*	3rd unnamed vertebrate
not	enameloid	enamel	enameloid
yet	astraspidin	mesodentine	mesodentine
histologically	aspidin	aspidin	cellular bone
studied	cartilage	cartilage	? cartiliage

TEXT-FIG. 5.6. Tissue distributions within the dermal skeleton of Ordovician heterostracomorphs. Data taken from Smith and Hall (1990) and Smith (1991).

Astraspis Walcott 1892, possesses a thin cap of hypermineralised tissue lacking growth lamellae which is thought to have affinities with enameloid (Denison 1967; Ørvig 1989). This overlies denticles formed of a lamellar tissue penetrated by fine diameter tubules, termed 'astraspidin' (a tissue thought to represent a form of dentine with fibrous tubules Halstead (1987); Smith and Hall (1990): Text-fig. 5.7). *Astraspis* is the only form from the Harding Sandstone which has been reconstructed as a whole animal (Elliott 1987; Chapter 6, Text-fig. 6.10).

Eriptychius Walcott 1892, exhibits denticles capped by a thin birefringent layer which has a weak boundary with the underlying tissue (Smith and Hall 1990). Growth lamellae have yet to be described from the superficial layer, although Smith and Hall (1990) interpret this material as enamel. The body of the denticles are formed from dentine in which growth lamellae (both uniform and sphericular) and polarised wide-calibre tubules are present (Text-fig. 5.10).

TEXT-FIG. 5.7. Colour photomicrograph, taken with partially crossed-nicols, of a section through an *Astraspis* plate fragment from the Caradoc Harding Sandstone, Canon City, Colorado. This shows tubercles of astraspidin (ast) and trabecular tissue (as), overlain with a superficial cap of enameloid (white arrow). Slide BU 2175 (Lapworth Museum, Birmingham University (x100).

The denticles of both *Astraspis* and *Eriptychius* are supported on a honeycomb layer of trabecular tissue, aspidin, which is thought to represent acellular bone or a form of dentine (Smith and Hall 1990; Text-fig. 5.7 and 5.10).
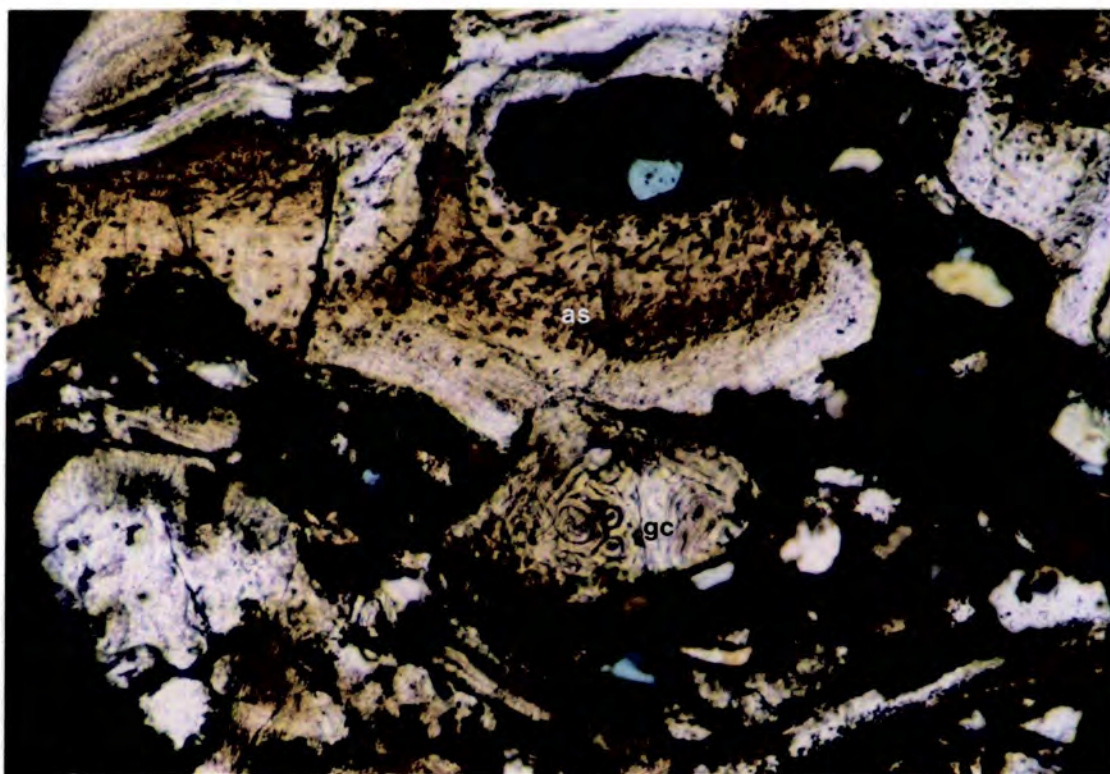
TEXT-FIG. 5.8. Colour photomicrograph of globular cartilage (gc) attached to the aspidin (as) base of an *Astraspis* plate. Slide BU 2175 (x100).
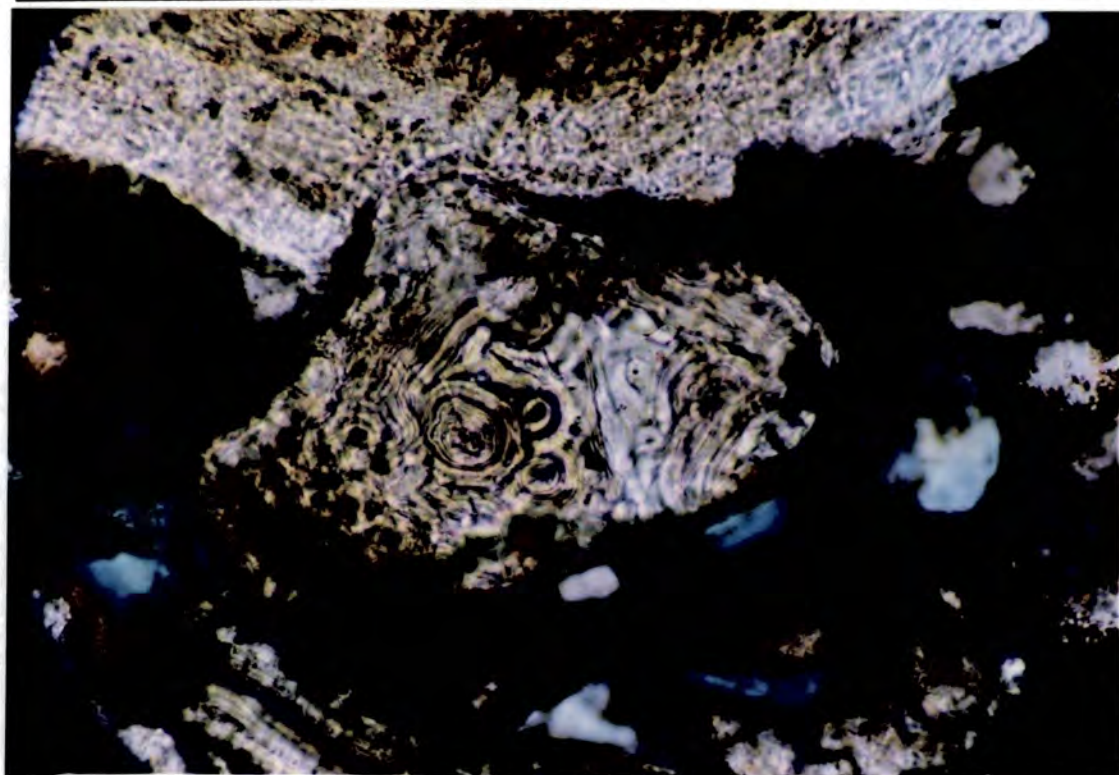
TEXT-FIG. 5.9. Detail of globular cartilage attached to *Astraspis*, showing the transition from a lamellar to scalloped structure away from the attachment surface. Slide BU 2175(x200).
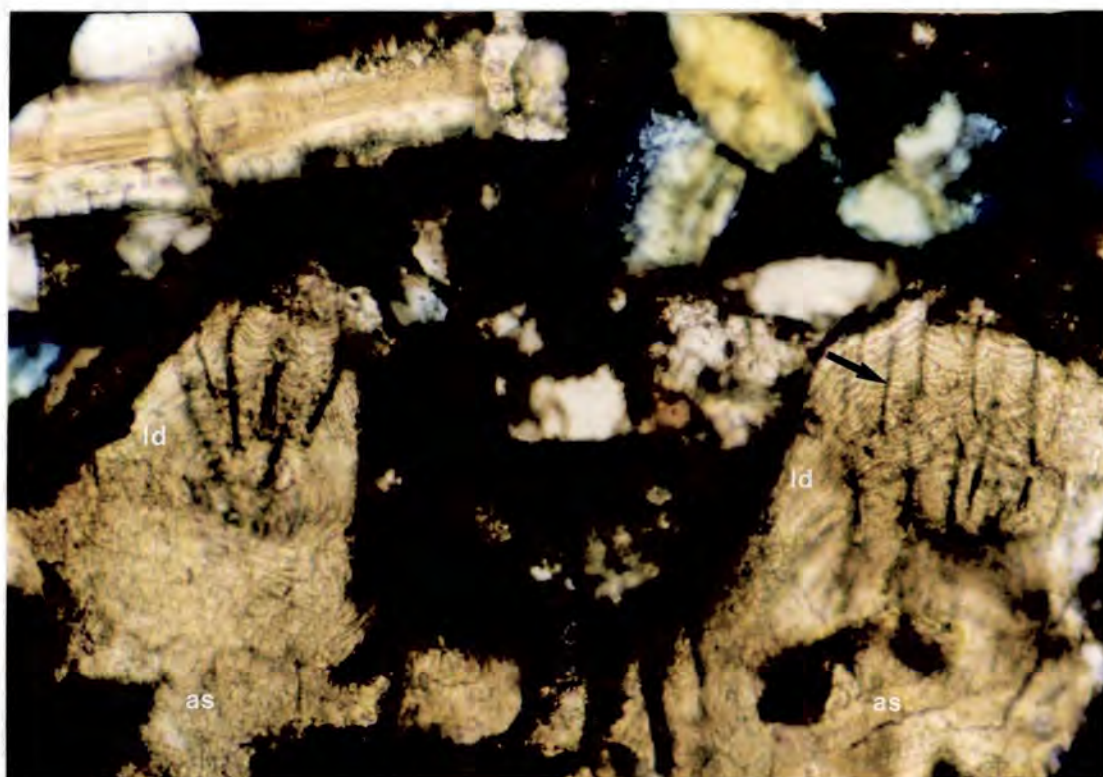
TEXT-FIG. 5.10. Colour photomicrograph, taken with partially crossed-nicols, of tubercles on the surface of an *Eriptychius* plate fragment from the Caradoc Harding Sandstone, Canon City, Colorado (Slide BU 2175). Wide calibre tubules (black arrow) penetrate the lamellar dentine (**ld**), which shows scalloped and globular mineralisation. A superficial cap of enamel is absent in these specimens. These tubercles are borne on a honeycombed layer of trabecular aspidin (**as**) x200 .

A third, as yet unnamed, genus is represented by discrete tubercles (Ørvig 1965; Denison 1967; M.M. Smith 1991) in which a superficial cap of enameloid overlies the rest of the denticle. The upper part of the denticle is characterised by pear-shaped lacunae with polarised tubules, and represents mesodentine with odontocytes (M.M. Smith 1991; Text-fig. 5.11). In the base of the denticle, cell bodies (lacunae) are interconnected by randomly oriented, fine tubules (canaliculi), and this tissue has been described as cellular bone with osteocytes (M.M. Smith 1991).
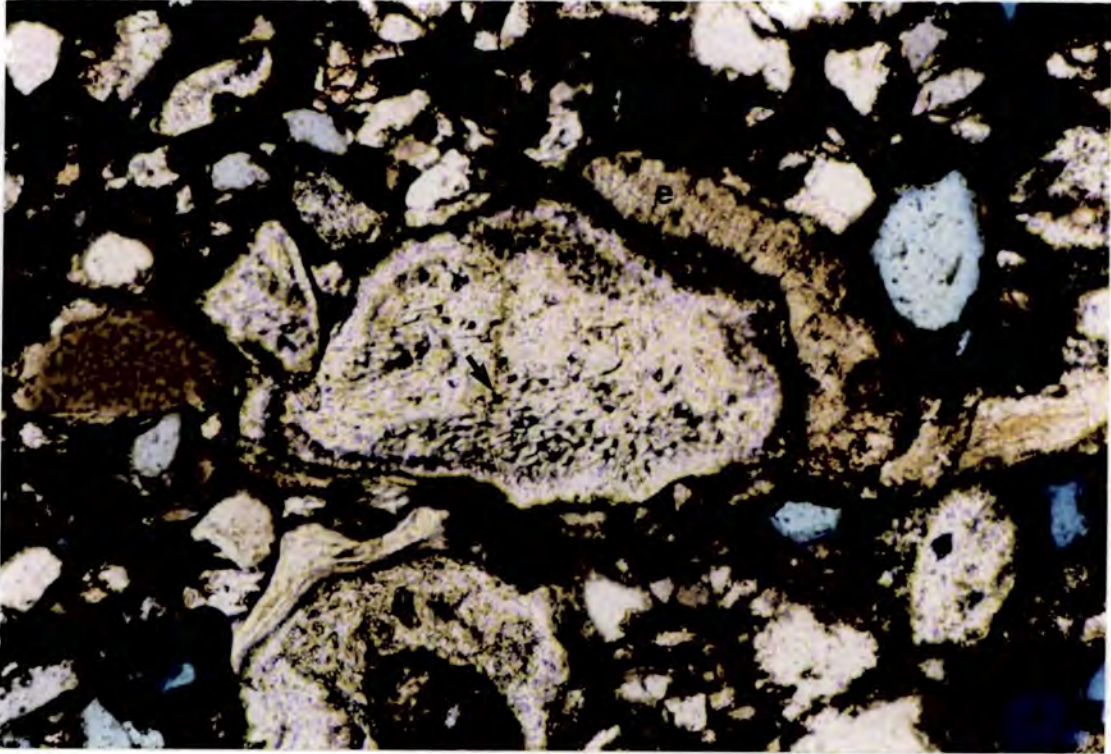
TEXT-FIG. 5.11. Colour photomicrograph, taken with partially crossed-nicols, of an isolated
tubercle of the '3rd unnamed vertebrate' from the Caradoc Harding Sandstone, Canon City,
Colorado (Slide BU 2175). A mass of infilled cell-spaces within the basal cellular bone,
with sphericular cell bodies (lacunae) and radiating processes (canaliculi), are arrowed.
These pass into mesodentine towards the enameloid (e) cap (x100).

Large patches of globular calcified cartilage are found in association with the
Harding Sandstone vertebrates (Denison 1967; Halstead 1973; Ørvig 1989; Smith
and Hall 1990; Text-fig. 5.12). Cartilage is thought to form a weakly mineralised
support to the ossified carapace of each form (Smith and Hall 1990). This tissue has
been identified in association with *Eriptychius* by Denison (1967), and has been seen
underlying a tessera of *Astraspis* during this study (Text-figs 5.8 and 5.9).
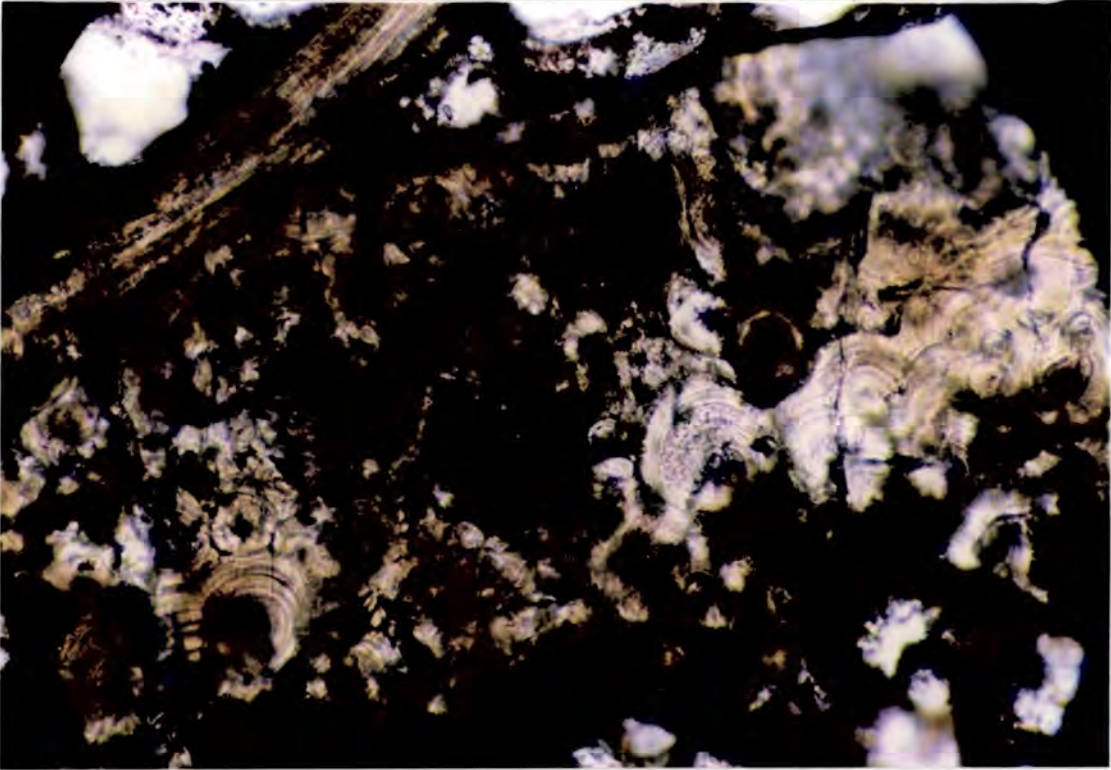
TEXT-FIG. 5.12. Colour photomicrograph, taken with partially crossed-nicols, of an isolated patch of mineralised globular cartilage from the Caradoc Harding Sandstone, Canon City, Colorado (Slide BU 2175 : x200).

5.5 HISTORICAL REVIEW OF CONODONT HISTOLOGICAL WORK

5.5.1 Technological Developments in the Study of Conodont Mineralised Tissues

Histological examinations of conodont elements have featured in many publications since their original discovery (Pander 1856). In the subsequent century and a half, many technical advances have been made in the resolution of ultrastructural features and this is reflected by a shift in the techniques employed by the authors of the reports outlined below. Initial studies were made with the aid of transmitted light microscopes (Hass 1941; Gross 1954, 1957; Lindström 1964).

Although many pertinent observations were made during this period, the resultant illustrations are often indistinct and appear to have lead to some ambiguity in their interpretation. Following their development in the 1950's, there followed a shift from optical studies to investigations utilising scanning electron microscopes (see Pietzner *et al.* 1968), largely to the exclusion of alternative techniques. S.E.M. technology has dramatically increased the resolution of the histological features of conodont elements, although workers have employed different preparation techniques on the material. Some schools have relied on the study of fractured surfaces (Lindström and Ziegler 1971; Ziegler and Lindström 1972; Krejsa *et al.* 1990b), whilst others preferred working with etched orientated sections (Barnes, Sass and Monroe 1970, 1973; Barnes, Sass and Poplawski 1973; Barnes and Slack 1975; Szaniawski 1987). Some studies have experimented with transmission electron microscopy (Barnes, Sass and Monroe 1973, Szaniawski 1987), although this has yet to become a widespread technique for looking at the internal structure of the mineralised crystals (this may be a result of problems in specimen preparation, see Section 5.6). In this study, S.E.M. investigations have been supplemented by using pseudo-3D imaging techniques, such as phase and Nomarski interference optics, on high-powered optical microscopes.

5.5.2 Previous Interpretations of Conodont Histology

Pander (1856), in his original description of conodonts, recognised the importance of the internal structure of conodont elements. He identified the lamellar nature of the conodont element crown, and the presence of small and irregular 'cellules' within white matter. Pander (1856, pl. 3, fig. 10a) also illustrated a specimen of *Cordylodus* which had an intact basal body, infilling the 'pulp cavity'. This shows a globular ultrastructure. On the basis of histology and comparative morphology, Pander (1856, p. 8) concluded that conodont elements were fish teeth, and stated 'with reasonably certainty, that these teeth were inserted into the mucous membrane of the throat, similar to the teeth of cyclostomes and the squalids...'.

Although Pander interpreted conodonts as fish teeth, he did not draw specific comparisons between the hard tissues of the elements and those seen in vertebrates.

Pander (1856) suggested that conodont elements were composed of calcium carbonate, but this error was corrected by Harley (1861) who found that conodont elements were composed largely of calcium phosphate. Hinde (1879) persisted with Pander's view, and doubted the conodont nature of Harley's material. By the 1920's and early 30's, Harley's (1861) conclusions had gained general acceptance, and were later confirmed by Pietzner *et al.* (1968) who established the mineral phase to approximate to the carbonate fluoroapatite, francolite.

Kirk (1929) reported conodont elements from the Harding Sandstone and mentioned their attachment to 'peculiar fragments of bone' (the basal body), but did not describe the fauna. Branson and Mehl (1933) considered the Harding Sandstone material to consist principally of primitive elements, and noted what they considered to be a significant difference in their histology from other, presumably more advanced forms. This differentiation was based upon fracture patterns, the absence of a basal cavity (the 'pulp cavity' of Pander) and the attachment of the element directly onto 'the surface of the hard jaw support by ankylosis' (Branson and Mehl 1933, p. 22). Based on this work Branson and Mehl (1933) divided conodont taxa into 'fibrous' and 'lamellar' forms. These divisions were later formalised as the suborders 'Neurodontiformes' and 'Conodontiformes', respectively (Branson and Mehl 1943).

Hass (1941) recognised and figured discontinuities in the lamellar crown of a number of Carboniferous genera. He interpreted this as evidence for regeneration, and also re-affirmed the presence of a 'cancellate' structure of branched 'cellules' within the white matter.

Gross (1954, 1957) described white matter as being composed of a series of cellules within the laminated tissue, although it is clear that he did not view them as cell spaces because he proposed homology with acellular aspidin (Gross 1954). This work marked the first genuine attempt to homologise the ultrastructure of conodont

elements with specific vertebrate hard tissues. Gross (1957) suggested that the growth of the basal body (*'basiskörper'*) was not synchronous with the lamellar crown and that this was the result of resorption at the crown/base junction.

Lindström (1964), in a review of previous histological work, questioned the presence of interconnecting tubules within white matter, because of the tissue's apparently impermeable nature. Lindström (1964, p. 21-23) suggested that white matter was formed by a series of hollow spaces and particles of unknown origin and stated that 'all conodonts are lamellar *and* fibrous' (a point already proposed by Hass (1962) in his restudy of the Branson and Mehl collections). Lindström also found no evidence for the 'out of phase' growth of the basal filling compared to the crown proposed by Gross (1957) and illustrated specimens that supported his view of the simultaneous addition of lamellae in both the crown and basal filling (Lindström 1964, figs 7, 8).

Schwab (1965) published the results of his work on a number of 'neurodontiform' conodont elements, and also found that they exhibited a lamellar ultrastructure. He described two types of basal body, one characterised by a lamellar ultrastructure and the other by spherules. He suggested that the former was 'cartilage-like', and the latter 'bone-like'.

Pietzner *et al.* (1968) made the first histological study of conodont elements which relied principally on scanning electron microscopy. They described white matter as being characterised by a series of randomly distributed holes, and felt there was little evidence of inter-connection; it was also recognised that white matter was more finely crystalline than lamellar crown tissue.

Müller and Nogami (1971, 1972) concentrated on the growth patterns of primitive conodonts (*sensu lato*), using transmitted light, and demonstrated that the earliest elements formed a separate histological grouping, principally on the basis of their growth pattern, the Suborder Paraconodontida (see Section 5.1.1). Müller and Nogami also proposed that white matter was formed in three ways: by interlamellar spaces; 'peg-like' bubble structures in the centre of denticles; and by layers of bubbles

cutting across the growth lamellae. In addition, they suggested that variation in the distribution of the latter (Text-fig. 5.13) could be utilized in taxonomy.
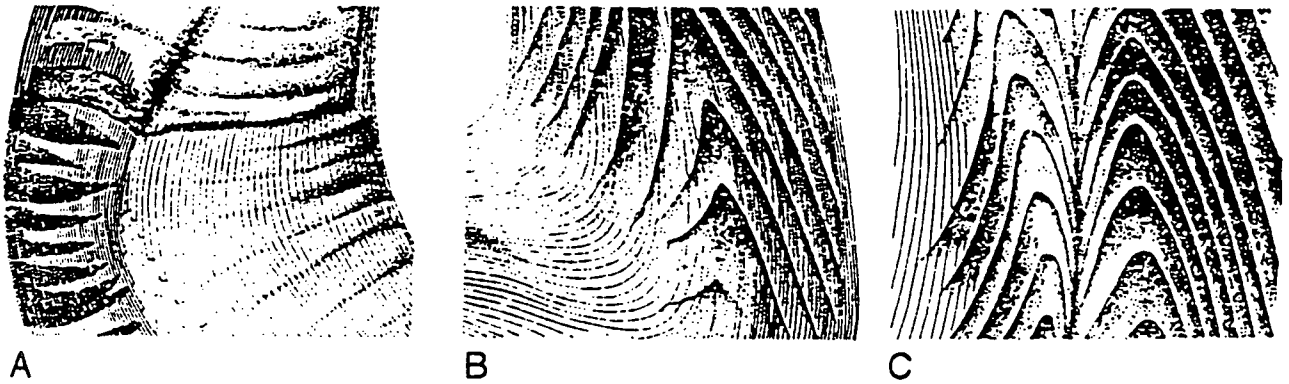
TEXT-FIG. 5.13. Different forms of 'white matter' cross cutting growth lamellae in A) *Cordylodus*, B) and C) *Ligonodina*. It is suggested that these structures are formed from porous enamel rather than discrete areas of cellular bone, as found in 'true white matter' (Taken from Müller and Nogami 1972, figure 5).

Lindström and Ziegler (1971) figured scanning electron micrographs of artificial fracture surfaces from a variety of conodont taxa. They suggested that white matter was a product of recrystallisation of the lamellar crown, and felt that the resultant material retained the same crystallite orientation. Because white matter occurred during all growth stages, Lindström and Ziegler (1971) concluded that it was formed during the growth of the conodont element. In a later publication (Ziegler and Lindström 1972), they confirmed that the fibrous 'neurodontiformes' possessed a lamellar structure.

During the early 1970's, Barnes and his co-workers published the results of a series of studies (Barnes, Sass and Monroe 1970, 1973; Barnes, Sass and Poplawski 1973; Barnes and Slack, 1975) which demonstrated the potential of histology in conodont taxonomy. This work relied almost exclusively on S.E.M. studies of sectioned and etched material. The specimens examined included members of the Family Panderodontidae (Barnes, Sass and Poplawski 1973), the Subfamily

Acanthodontidae (Barnes and Slack 1975), and a number of Ordovician forms including those which previously fell within the 'neurodontiformes' (Barnes, Sass and Monroe 1970, 1973). They also recognised a number of growth styles, notably in the Panderodontidae where the elements appeared to have undergone eruption during growth (Barnes, Sass and Poplawski 1973). This work thus challenged the widely held belief that conodont elements were unified by a concentric and centrifugal growth pattern. Barnes, Sass and Monroe (1970) and Barnes and Slack (1975) concluded that white matter was composed of a series of microspheres rather than holes. Although they agreed with Lindström and Ziegler (1971) and interpreted white matter as a secondary replacement feature, they suggested that it formed after the element had fully developed and served to strengthen the element (Barnes and Slack 1975). Barnes, Sass and Monroe (1970) drew analogy between various features of conodont hard tissues and those found in the earliest vertebrates, and considered that the formation of white matter could be similar to the changes in tissue mineralisation in bone, without drawing any definite conclusions for a vertebrate-conodont connection.

Szaniawski (1982) recognised a close similarity between protoconodont elements and chaetognath grasping spines (see Section 5.1.1). The possibility of a chaetognath-conodont link was further highlighted by the discovery of the first soft bodied conodont specimen from Granton, Edinburgh by Briggs *et al.* (1983) who compared their remains with both chaetognaths and chordates. Bengtson (1983) also noted similarities between the Granton specimen and the chaetognath bodyplan. If the proto-para-euconodont transition proposed by Bengtson (1976; Section 5.1.1) could be proved, then chaetognaths and conodonts probably shared the same ancestor. However, the phylogenetic link between protoconodonts, paraconodonts and euconodonts is far from firmly established, indeed this is strongly refuted by many workers (see Sweet 1985 and Szaniawski 1987 for contrasting views).

Barskov *et al.* (1982) produced a study of the basal filling of the genera *Coleodus* Branson and Mehl, and *Neocoleodus* Branson and Mehl. In this work, they

divided the basal filling into two structure types, 'spongy' and 'lamellar'. They described spherical structures within the spongy layer as osteocytes, and reached the conclusion that the basal material of conodont elements was bone. Sweet (1988) questioned the conodont affinities of this material, incorrectly stating that such spherical features had not been seen in other conodont elements; Pander (1856) had illustrated such structures from *Cordylodus* in his initial description of conodonts, and similar material had been figured by Schwab (1965), Barnes, Sass and Monroe (1973), Szaniawski (1987).

Following the discovery of additional specimens of soft bodied conodonts from Granton and a *Panderodus* animal specimen from the Silurian of Wisconsin (Mikulic *et al.* 1985a, b; see earlier Chapters) with associated soft parts, the craniate affinities of conodonts has gathered credence (Aldridge *et al.* 1986; Smith *et al.* 1987; Blieck 1992).

Dzik (1986, p. 240, fig. 1) identified structures within the basal filling of conodont elements which he considered to be homologous with dentine tubuli. He also compared, but did not formally homologise, the crown with enamel. Dzik (1986, p. 252) concluded that 'there is virtually no feature of the conodonts that would contradict their classification as vertebrates'.

Fåhræus and Fåhræus-van Ree (1987) described a number of biochemically active and intact soft tissues from demineralised elements of *Ozarkodina confluens* from Gotland. The organic material was identified as collagen, possible collagen and various cell bodies. The cellular material varied in size and shape with a number of relatively large cells with nuclei of 3-5 μm and smaller cells with many small nucleoli. The presence of collagen and collagen-like fibrous tissues in the decalcified matrix of these elements suggested that conodont biomineralisation followed the same basic processes as vertebrates (Fåhræus and Fåhræus-van Ree 1987).

Andres (1988) investigated the histology of a number of Cambrian and Lower Ordovician paraconodont and euconodont elements. He described oval structures from the basal cavities of paraconodonts. The presence of basal material in

paraconodonts with a similar structure to that seen in euconodonts suggested homology between the two forms (the assignment of some of Andres' material is questionable; for example he describes *Coelocerodontus* as an advanced paraconodont, whereas, elsewhere (Clark 1981; Sweet 1988) the genus is classified as a euconodont). In addition, Andres (1988) believed that paraconodonts, euconodonts and vertebrates shared the same ancestor. He proposed homology between the basal tissues and lamellar crowns of para- and euconodonts $_\wedge$ dentine and enamel.
and vertebrate

Wright (1989, 1990) suggested that the 'microspheres' identified by Barnes, Sass and Monroe (1970) and Barnes and Slack (1975) within conodont white matter were homologous with those expelled by golgi cells during vertebrate biomineralisation (Pautard 1981). Wright (1990) suggested that white matter represented a site of primary apatite secretion, thus contradicting the resorption models of Lindström and Ziegler (1971), Barnes, Sass and Monroe (1970, 1973), Barnes, Sass and Poplawski (1973), and Barnes and Slack (1975). Wright (1990, p. 281) concluded that 'the same processes of bone and tooth production and formation have been utilized for at least 520 million years'.

Krejsa *et al.* (1990a, b) suggested that the 'peg-like' structures, identified in conodont white matter by previous workers, were homologous with the goblet-shaped pokal cell spaces seen underlying the keratinized denticles of extant myxinoids. These structures were illustrated from the fractured tip of a single specimen of *Ozarkodina* (Krejsa *et al.* 1990b, fig. 7). They felt$_\wedge$this was sufficient evidence to
that
confirm the myxinoid affinities of conodonts, and the hypothesis was supported with a statistical size comparison of conodont elements and myxinoid denticles. Krejsa *et al.* (1990b) also proposed that basal bodies represented primary replacement teeth, indicating that conodont elements grew in a directly homologous fashion to cyclostome denticles.

Burnett and Hall (1992) illustrated and described the etched surfaces of many conodont genera from the Ordovician to Carboniferous. Although they discussed variations in crystallite stacking within the lamellar crown, which was compared with

protoprismatic enamel, and the massive nature of white matter, Burnett and Hall did not draw any homologies. They also noted a variation in the form of the basal body, which has an essentially botyroidal structure with changes in the density of packing of the spheres.

The histological work outlined above has not been widely accepted as conclusive proof of a conodont-vertebrate connection. Without the identification of truly homologous tissues, Smith and Hall (1990, p. 289) suggested 'conodont elements and hagfish keratinous toothlets may both be convergently derived structures relating to special modes of feeding and are certainly not in either case primitive examples of oral odontodes'. Elliott *et al.* (1991, p. 94) were of the same opinion when they stated that histological comparison meant 'that conodont-bearing animals...cannot be considered vertebrate'.

5.6 METHODOLOGY OF CONODONT HISTOLOGICAL STUDIES

A number of problems were encountered in preparing the conodont elements for histological study, and these have combined to result in the loss or damage of many specimens.

Preparation of orientated sections of conodont elements is very difficult due to their small size. To aid easy handling, it was necessary to embed specimens in resin, thus facilitating further preparation either as polished blocks or thin sections. Cool setting resin (Trylon EM 300 PA, names and addresses of suppliers included in Appendix 2), initially used as the embedding medium, was found to be too soft and smeared across the specimen during polishing. This was overcome using 'Crystic' resin, a bi-part resin requiring baking to cure, or Trylon EM 350 PA which achieves similar results but without the time penalities incurred by baking.

Specimens were placed on a cured base of resin, and highlighted by a ring of enamel paint. A subsequent layer of resin was then poured over the top and left in an oven to cure. The resultant 'conodont sandwich' enabled a degree of control over the orientation of the final preparation. On curing, the block was ground down in a series of stages to the desired level, initially using a grinding wheel, 1000 μm carborundum grit on a glass plate, and finally hand polished with 0.05 μm alumina powder on a soft-felt rotating lap. It should be noted that at this stage in the preparation many specimens were lost from overzealous polishing or by plucking of the element from the resin. Care must be taken to inspect the specimens at frequent intervals during grinding and polishing to prevent loss or damage to the specimen. Specimens were prepared as 60-80 μm thin sections, for transmitted light, phase contrast and Nomarski interference contrast examination.

Some sections were etched prior to study under the scanning electron microscope. Initial attempts at etching with dilute HCl (as employed by Barnes, Sass and Monroe 1970, 1973; Barnes, Sass and Poplawski 1973; Barnes and Slack 1975) proved unsatisfactory, even at 1%. This method of etching did not consistently resolve fine structures in the specimens (examples are illustrated on Plate 5) and alternative techniques were sought. After discussion with Dr. J. Dalingwater (University of Manchester), dilute $CrSO_4$ at 0.5wt% was employed as the etching medium (following the methodology of Sundström 1968). Etching times of approximately 15 minutes were found to be the most suitable for conodont studies, and a fresh solution was used on each batch of specimens. There can be some variation in the quality of etch over the surface of the specimen. Quite why this occurs is unclear.

Despite the many pitfalls, the application of the techniques described above, to conodont histology, especially the use of $CrSO_4$ as the etching medium, enables the consistent resolution of extremely fine scale structures.

5.7 HISTOLOGICAL DESCRIPTION AND INTERPRETATION OF CONODONT HARD TISSUES

This section deals with the general description and interpretation of the various histologies encountered during the course of this study. The distribution of these tissues in the genera examined is discussed in Section 5.8.

Conodont elements are divisible into three histologically distinct tissues; the lamellar crown, white matter, and the basal body often infilling the basal cavity (Text-fig. 5.3). The distribution of the tissues within the genera studied is given in Text-fig. 5.14.

	Panderodus	*Parapanderodus*	*Cordylodus*	*Eoconodontus*
Perpendicular Enamel			lamellar crown	lamellar crown
Parallel Enamel	lamellar crown	lamellar crown		
Cellular Bone	white matter	white matter	white matter	white matter
Dentine				
Globular Cartilage	basal filling	basal filling	basal filling	?

	Ozarkodina	*Dapsilodus*	*Pseudooneotodus*
Perpendicular Enamel	lamellar crown	lamellar crown	lamellar crown
Parallel Enamel			
Cellular Bone	white matter	white matter	
Dentine			basal filling
Globular Cartilage	?	?	

TEXT-FIG. 5.14. Distribution of tissue types within the studied conodont genera and *Pseudooneotodus*. Note the absence of cellular bone and the presence of dentine in *Pseudooneotodus*, this genus is thought to be histologically distinct from conodont elements.

5.7.1 Lamellar Crown Tissue

The lamellar crown is characterized by centrifugally deposited lamellae in a hypermineralised tissue. Each lamella is bounded by non-mineralised areas (Pl. 6, fig. 3; Pl. 7, fig. 3; Pl. 9, fig, 5; Pl. 10, fig. 2) which are thought to represent hiatuses of mineral growth. Two types of lamellar crown tissue have been recognised. The form most commonly encountered in this study has crystallites organized into rods or bundles oriented perpendicular to the growth lamellae. Individual increment lines are marked by slight steps and pinches in the crystallite rods, they are sub-parallel to each other and are regularly spaced between 0.5 - 1 μm (Pl. 8, fig. 2; Pl. 9, fig. 5; Pl. 10, figs 2 and 6). A second type of lamellar crown is typified by lamellae where the crystallites are oriented with their long axes sub-parallel to the growth surface, although the increment lines are again regularly spaced at around 0.5 - 1 μm (Pl. 6, fig. 3; Pl. 7, fig. 3). In both types the crystallites are 1 μm in maximum length and 0.1 μm in width. Most of the taxa studied exhibit centrifugal growth lamellae in the crown (Pl. 7, fig. 2; Pl. 10; fig. 2). In *Panderodus*, however, these growth lamellae show an asymptotic relationship to the external margin (Pl. 6, fig. 2; Text-fig. 5.15; see Sections 5.8.1 and 5.9).

There is a direct correspondence between the increment lines, crystallite orientation and crystallite size in the lamellar tissue seen in the majority of taxa studied and those of enamel, here this is termed 'perpendicular enamel' (Text-fig. 5.14). The second lamellar tissue, where the crystallites are oriented sub-parallel to the growth surface, is consistent with enamel in the presence of increment lines and crystallite size, but not in crystallite orientation. This tissue has been proposed as a new type of enamel by Sansom *et al.* (1992), and is here described as 'parallel enamel'. Parallel enamel appears to have been previously illustrated by Barnes, Sass and Monroe (1970) from *Drepanodus* Pander and *Curtognathus* Branson and Mehl, and by Müller (1981) from *Chirognathus* Branson and Mehl. Neither of these tissues are similar to enameloid which is devoid of lamellae and is formed of crystallites ten times larger than those seen here.

5.7.2 White Matter

Two types of white matter have been distinguished in the studied material. The first, here termed 'true white matter', is characterised by spherical spaces, between 3 and 10 μm in diameter, which are interconnected by a series of irregular, radiating tubules lying in a massive groundmass where no lamellae are present (Pl. 6, fig. 4; Pl. 7, fig. 4; Pl. 8, fig. 4; Pl. 9, figs 3 and 6; Pl. 10, fig. 5). The penetrating tubules and cavities give the tissue it s characteristic opaque appearance in incident light. In the specimens examined, there is a sharp junction between the white matter and surrounding enamel.

In other cases, 'white matter' is caused by variations in the lamellar enamel, and by the concentration of porous areas and microspheres between the individual crystallites (Pl. 10, fig. 3). This appears to correspond with the 'white matter' described by Barnes, Sass and Monroe (1970) and Barnes and Slack (1975). Such variations in the enamel crown are similar to those seen in human teeth which vary in colour from light yellow to greyish white depending upon the thickness of the enamel cap (Ten Cate 1989). Cross-cutting colour variations such as striae of Retzius are seen in ground sections of enamel (Shellis 1981; Ten Cate 1989). These are caused by variations and gaps in the enamel structure, similar structures in the enamel of conodont elements appear to have been illustrated by Müller and Nogami (1972; Text-Fig. 5.13).

The interconnecting spaces in true white matter *are* identical to the osteocyte lacunae and canaliculi of cellular bone (Text-fig. 5.11) and they are considered to be homologous (Sansom *et al.* 1992). The lacunae in conodont elements vary from 3-10 μm in diameter, a range which overlaps with those of the osteocytes in the cellular bone of the unnamed Harding Sandstone genus. The calibre of the canaliculi in conodont elements appears to be smaller than those seen in the Harding Sandstone material; it is suggested that this difference inhibits the permeability of the tissue and possibly explains the problems encountered by Lindström (1964) in impregnating this

tissue. True 'white matter' has been illustrated by Lindström (1964; figs 4, 5; from *Gnathodus* Pander, *Polygnathus* Hinde, *Idioprioniodus* Gunnell, and *Ozarkodina* Branson and Mehl), Barnes, Sass and Monroe (1973; figs 4 - 6; from *Oulodus* Branson and Mehl, and *Cordylodus* Pander), Krejsa (1990 b, fig. 7; from *Ozarkodina*) and Sansom *et al.* (1992, figs 1D, 2C and 3B,E from *Panderodus* Ethington, *Cordylodus*, *Ozarkodina* and *Parapanderodus* Stouge).

5.7.3 Basal Body

All the specimens examined with intact basal bodies show a clear structure in which discrete spherules are fused into continuous scalloped layers, the boundaries forming as Liesegang waves (Pl. 7, fig. 5; Pl. 8, figs 5 and 6). The individual spherules vary in size between 10-30 µm across, the layers show similar variations in width. In some specimens the spherulitic nature of the material is more pronounced away from the junction with the crown and towards the centre of the basal body where growth layers become less distinct.

Previously published illustrations of basal bodies show both spherulitic (Schwab 1965; Barnes, Sass and Poplawski 1973; Barskov *et al.* 1982; Szaniawski 1987) and laminated (Schwab 1965; Müller and Nogami 1972; Müller 1981) structures. Schwab (1965) divided these tissues into 'bone-like' and 'cartilage-like' respectively. The gradation between both forms in a single basal body (Pl. 8, figs 5 and 6) suggests that they represent the same tissue. The isolated nucleation sites required to produce a spherulitic texture towards the centre of the basal body suggests a relative shift in the rate of mineralisation as the tissue forms.

It is possible that the structures seen in the basal tissue of conodont elements could be produced by a variety of mineralisation processes. However, they bear a striking resemblance, both in scale and form, to globular calcified cartilage (Smith *et al.* 1987). This tissue is found in association with the Harding Sandstone vertebrates (Text-figs 5.12). The absence of tubules in this tissue precludes its identification as dentine (as suggested recently by Dzik 1986; and Andres 1988). Although a

spherulitic texture is the most common in the Harding Sandstone cartilage, where this tissue is seen in contact with 'bone' it shows a laminated structure (Text-figs 5.9 and 5.10).

5.8 THE DISTRIBUTION OF VERTEBRATE TISSUES IN CONODONT ELEMENTS

5.8.1 The Family Panderodontidae

This study was initiated in an attempt to resolve the growth pattern of *Panderodus*, consequently a greater number specimens of this genus have been studied than any other.

Panderodus (Ethington)

Seven species of *Panderodus* have been studied, namely *P. unicostatus* (Branson and Mehl), *P. gracilis* (Branson and Mehl), *P. equicostatus* (Rhodes), *P. feulneri* (Glenister), *P. intermedius* (Branson, Mehl and Branson), *P. panderi* (Stauffer) and *P. breviusculus* Barnes. These have been found to be histologically identical, varying only in the relative extent of white matter. **Pb** elements (falciform of other authors) form the majority of the specimens studied, as these are generally the largest in the *Panderodus* apparatus and thus comparatively easy to handle. Specimens of the other elements in the apparatus have been examined and these only show variations in the external morphology.

The lamellar tissue of *Panderodus* is formed of 'parallel enamel'. The individual increment lines (spaced at approximately 1 µm intervals) show an asymptotic relationship with the external margin of the elements (Pl. 6, fig. 2; Text-fig. 5.15). Each lamellar is defined by inter-lamellar areas which are notably more

open along the basal cavity than along the outer surface of the specimens (Pl. 6, figs 2 and 3).
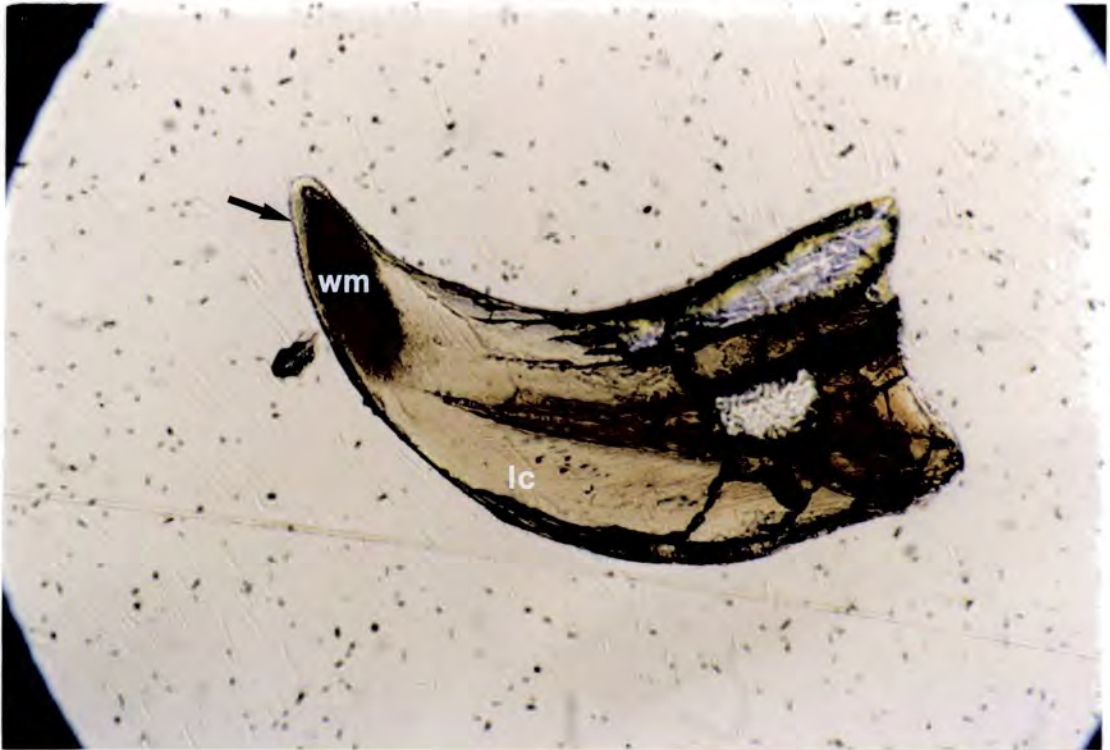
TEXT-FIG. 5.15. Longitudinal cross-section through a **Pb** element of *Panderodus breviusculus* Barnes viewed in plane-polarised light. A fine rim (arrowed) of lamellar crown (**lc**) extends around the block of white matter (**wm**) found at the cusp apex. Note also the clearly defined asymptotic growth lamellae of the lamellar crown (Slide no. 9/91/1: x100).

Barnes, Sass and Poplawski (1973) and Lindström and Ziegler (1981) felt that the internal structure of *Panderodus,* as seen in cross-section, was markedly affected by the invagination associated with the panderodontid furrow. This was suggested to be an abrupt change in lamellae orientation, from concentric to radial around the furrow (Text-fig. 5.16). This is not the case as the concentric lamellae continue into the furrow area, and are deflected around this feature (Pl. 6, figs 5 and 6). It is suggested that the 'radial lamellae' of previous workers represent artefacts of the wrinkle zone running parallel to the surface expression of the furrow.
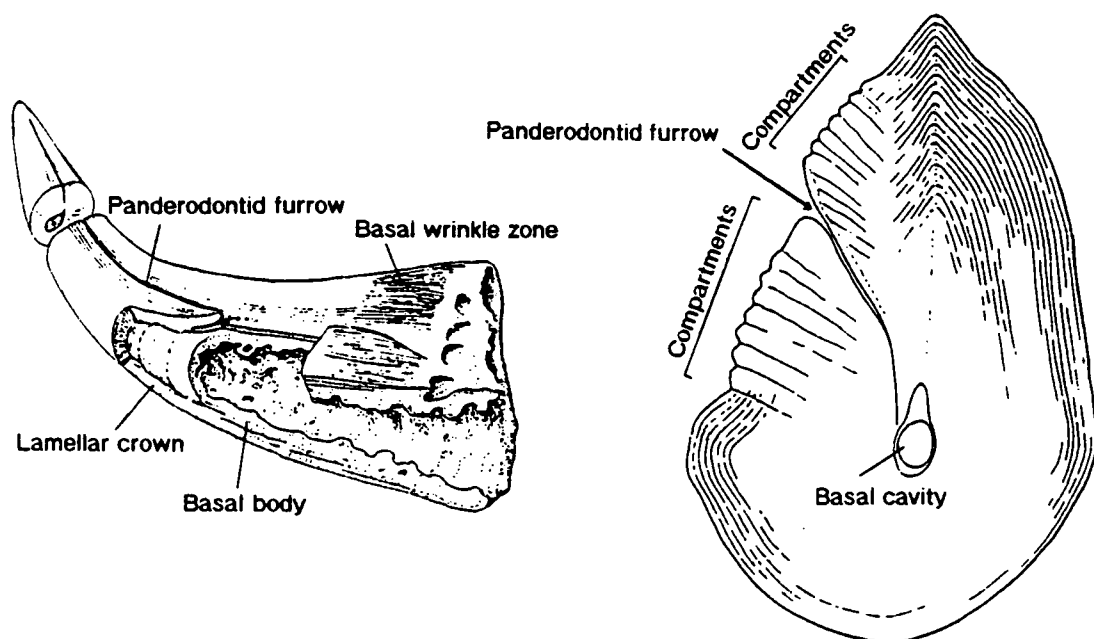
TEXT-FIG. 5.16. Diagrammatic sections through *Panderodus* elements based upon the work of Lindström and Ziegler (1971) and Barnes, Sass and Poplawski (1973). Note the inferred differentiation into concentric lamellae and radial 'compartments' around the panderodontid furrow. The presence of the radial 'compartments' is not substantiated by this study (Taken from Lindström and Ziegler 1981, fig. 41).

Cellular bone (as true white matter), has been found at the tip of all the studied specimens. The relative extent of this tissue varies between species (Text-fig. 5.17). The histology of this tissue can be seen in Plate 6, fig. 4 where well-developed canaliculi and lacunae (approximately 3 μm in diameter) lie in the acrystalline groundmass. Some sections suggest that a thin layer of enamel covers the cellular bone (Text-fig. 5.15). This has yet to be substantiated under the S.E.M. because the studied specimens appear to have been etched, possibly during acetic acid digestion of the host rock (Jeppsson *et al.* 1985).

Spherical mineralised cartilage has been seen in certain specimens (Pl. 7, fig. 5) and has also been illustrated by Barnes, Sass and Poplawski (1973; fig. 5E).

P. panderi

P. feulneri

P. staufferi

P. equicostatus

P. gracilis

P. unicostatus
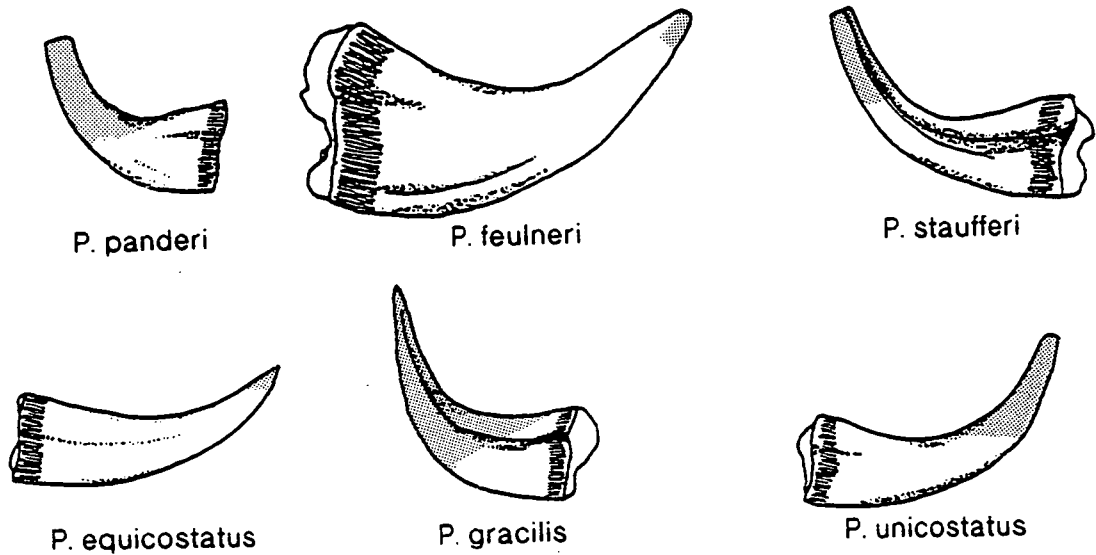
TEXT-FIG. 5.17. Variation in white matter distribution (stippled) between the **Pb** elements of six *Panderodus* species, approximately x 55.

Parapanderodus striatus (Graves and Ellison)

Smith (1991) has questioned the panderodontid affinities of *Parapanderodus* on the basis of external element morphology and apparatus architecture. However, this species is histologically similar to *Panderodus* due to the presence of parallel enamel which forms the lamellar tissue. The lamellae appear to be continuous around the element, as they run roughly parallel to the external margins (Pl. 7, fig. 2). Individual crystallites within the lamellae are of the same scale as those seen in *Panderodus* and are similarly orientated sub-parallel to the increment lines (Pl. 7, fig. 3).

Parapanderodus differs markedly from *Panderodus* in the distribution of cellular bone. This tissue forms a central core in the *Parapanderodus* element crown, approximately 20 μm in diameter (Pl. 7, fig. 4). It runs from close to the tip of the basal cavity up the cusp to somewhere close to the tip (Pl. 7, fig. 1). The exact termination points of the cellular bone stringer have not yet been determined due to sectioning damage and orientation. The presence of interconnecting cellular material

in this tissue is seen in Plate 7, fig. 4, although no measurement of the size of individual lacunae have been made.

No basal tissue has been found in the studied specimens.

5.8.2 Non-Panderodontids

Though this study has concentrated on *Panderodus*, a preliminary survey of the histology of a number of different conodont lineages has been undertaken. These include a variety of forms which may be placed in 3 or 4 of the Orders recognised by Sweet (1988), although there is some doubt about the suprageneric classification of certain of these forms.

Order Proconodontida Sweet, 1988

Cordylodus Pander

A single specimen of *Cordylodus* sp. has been examined in considerable detail using both optical and scanning electron microscopes. The section taken through this specimen is illustrated in Plate 8, fig. 1. The lamellar crown is formed of perpendicular enamel (Pl. 8, fig. 2). Lamellae run parallel to the external margin of the specimen, suggesting a concentric pattern; further specimens are needed to confirm this. The individual crystallites are not as regular in form as those seen in other genera (cf. Pl. 9, fig. 5), although this may be an artefact of section orientation. These crystallites are organised into a series of bundles, approximately 1 μm in width (Pl. 8, fig. 2). The structure of the enamel in this specimen is reminiscent of prismatic enamel described from higher vertebrates (Smith 1989). The cusp of *Cordylodus* shows increasing opacity; this appears to be formed by porosity in the enamel (Pl. 8, fig. 3).

Cellular bone forms the cores to the denticles of the specimen (Pl. 8, fig. 4). Interconnected cell lacunae and canaliculi are seen in transmitted light. As the plane of section in the studied specimen does not pass through the white matter, this tissue

has not been picked up on the S.E.M., and the boundary with the surrounding enamel has not been observed.

The basal body is dominated by globular cartilage. This tissue shows a gradual transition from essentially laminar (Pl. 8, fig. 5) to sphericular mineralisation (Pl. 8, fig. 6) from the crown-basal body junction towards the centre of this material. Similarly structured material has been illustrated by Pander (1856, pl. 3, fig. 10 a) and Szaniawski (1987; Text-fig. 5.18) from the basal bodies of other *Cordylodus* specimens.

A   B   C
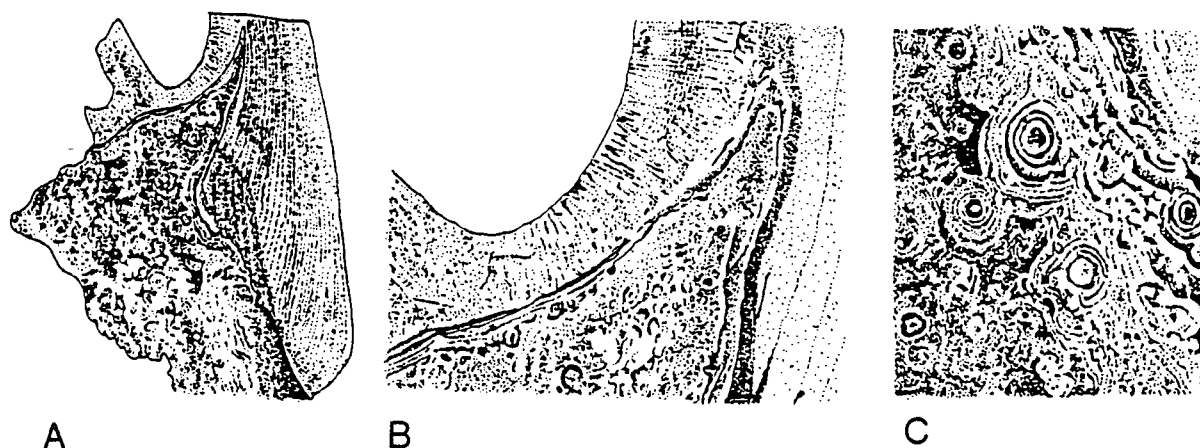
TEXT-FIG. 5.18. Structures in the basal areas of *Cordylodus* sp., as traced from Szaniawski (1987, pl. 2.3 fig. 1 a-c), showing spherulitic laminations in the basal body and the presence of lamellae cutting structures in the crown. These have been identified as globular calcified cartilage and enamel respectively (A x90; B x330; C x660).

Eoconodontus Miller

Two specimens of *Eoconodontus* have been examined. Although the studied material has not been particularly well prepared, they show a number of features which are particularly pertinent as they comprise the oldest material studied to date.

The lamellar crown of *Eoconodontus* is formed by crystallites that are organised into bundles (Pl. 10, fig. 6), similar to those seen in *Cordylodus* (Pl. 8, fig. 2). White matter in *Eoconodontus* is concentrated at the element tip. This appears to be formed of cellular bone, although the images seen with the S.E.M. do not clearly

resolve canaliculi and lacunae. The presence of interconnecting voids (over 2 μm in their maximum dimension) in an acrystalline matrix is apparent (Pl. 10, fig. 5). The longitudinal section does not pass through the median axis of the specimen, perhaps explaining the lack of clearly defined osteocytes, whilst a cross-section has been damaged by resin smearing.

Basal tissue has not been found in the studied specimens.

Order Ozarkodinida Dzik, 1976

Ozarkodina (Branson and Mehl)

Two specimens of *Ozarkodina confluens* have been examined. In these, the crystalline lamellar crown tissue is formed of perpendicular enamel, and the individual crystallites are organised into a series of discrete rods. They are orientated perpendicular to the growth surface and cut by growth lamellae (at 0.5 μm intervals) which are marked by pinches in these rods (Pl. 9, fig. 5).

Isolated denticles of true white matter are clearly seen in discrete specimens and in the specimens discussed here (Pl. 9, figs 1 and 4). Lacunae and canaliculi are clearly seen in transmitted light (Pl. 9, fig. 6). Neither of the sections studied under the S.E.M. are cut through the core of the white matter. As a result, cell lacunae have not been seen using this technique. The acrystalline groundmass of this material is penetrated by interconnecting canals, as is evident from sub-surface sampling using backscattered electron imaging (compare Pl. 9, fig. 3a with Pl. 9, fig. 3b).

Basal bodies have not been found in the studied specimens.

Order Belodellida Sweet, 1988

There appear to be a number of problems regarding the integrity of this Order, and the presence of *Dapsilodus* within it (See Chapter 2.7), although this classification is retained here for reference purposes.

Dapsilodus Cooper

The lamellar crown of *Dapsilodus obliquicostatus* (Branson and Mehl) is formed of enamel, where the individual crystallites are orientated perpendicular to the growth surface (Pl. 10, fig. 2). This tissue is similar to that seen in *Cordylodus* (Pl. 8, fig. 2) and *Ozarkodina* (Pl. 9, fig. 5). Opacity in the basal areas of the cusp appear to result from areas of enamel with spherical pores (Pl. 10, fig. 3; these are less than 0.5 μm in diameter).

In transmitted light, dense white matter is found towards the tip of the element (Pl. 10, fig. 1). This differs in texture from the translucent patches described above, and appears to be formed by much larger scale structures (approximately 5 μm in scale). I would tentatively suggest that this is cellular bone, although this has yet to be confirmed by S.E.M. studies.

No basal tissue is present in the studied material.

Order Unknown

Pseudooneotodus has been tentatively placed by Sweet (1988) in his Order Protopanderodontida and by Dzik (1991) in the Order Panderodontida. There seems to be little validity to either of these assignments as the apparatus of *Pseudooneotodus* is poorly known and appears to consist of simple squat conical elements (Armstrong 1990). In the light of this, and the histological information presented below, the suprageneric assignment of this genus is very questionable, as is the place of *Pseudooneotodus* within the conodonts.

Pseudooneotodus Drygant

A single specimen of *Pseudooneotodus* Drygant has been histologically examined. Utilising transmitted light, translucent patches seen in the element are not concurrent with a tissue differentiation, rather this 'white matter' results from a fibrous structure within the lamellar crown. Following etching and study under the S.E.M., this lamellar crown is seen to be formed of enamel (Pl. 12, fig. 2), which is

virtually indistinguishable from prismatic enamel seen in higher vertebrates (Pl. 7, fig. 6; Smith 1989). The individual crystallites are organised into a series of prisms, orientated perpendicular to the external margin; additionally, a dove-tailed structure, or decussation, is notable. The increment lines are spaced at approximately 0.5 μm intervals. On one side of the specimen, the enamel prisms pass down and laterally into an area where the increment lines are disrupted into a series of folds (Pl. 11, figs 6, 7 and 8; Pl. 12 fig. 1). These are thought to represent disruption during mineralisation of the organic matrix, as deformation of the crystallites appears to have occurred during a phase of plasticity.

The basal tissue is composed of a spherulitic tissue (Pl. 12, figs 5 and 6) similar in texture to the cartilage seen in other conodont elements, but this differs both in the size of the spherules which are ten times larger than seen in *Pseudooneotodus* (which are 5 μm in diameter at maximum), and the gradation into unlaminated material penetrated by a series of fine tubules (Pl. 12, fig. 4). The presence of tubules in an acrystalline groundmass, which has a well defined boundary with the overlying enamel (Pl. 12, fig. 3), is characteristic of dentine (Reif 1982). Scalloped laminations in dentine have been described from *Eriptychius* (Smith and Hall 1990) and other higher vertebrates.

If the basal tissue is dentine, then this marks a significant histological difference between *Pseudooneotodus* and the remainder of the conodonts investigated where dentine is absent.

5.9 DISCUSSION

The recognition of vertebrate hard tissues in conodont elements demonstrates unequivocally that the conodonts were of vertebrate stock. This is compatible with the conclusions of Aldridge *et al.* (1987) who have argued for the craniate affinities

of conodonts on the basis of the soft parts of the Granton specimens. Additionally, the presence of these tissues increases the number of character states which can be used in the cladistic analysis of conodonts and other primitive vertebrates (see Chapter 6).

Enamel, cellular bone and cartilage in Late Cambrian - earliest Ordovician conodonts (*viz Cordylodus* and *Eoconodontus*) predates the earliest previously recorded occurrence of vertebrate hard tissues by over 40 million years. Dentine has been proposed as one of the primitive hard tissues (Smith and Hall 1990). The oldest conodont elements examined contain cellular bone, enamel and cartilage but no dentine. This observation casts doubt on the presumed evolutionary and functional origin of dentine (see Chapter 6).

The presence of true phosphatised hard tissues in conodont elements is in conflict with the views of Krejsa *et al.* (1990 a, b) who have argued that the conodont elements are directly homologous with the keratin denticles of myxinoids. Cellular dermal bone and globular cartilage are formed within a collagen-based matrix (Ten Cate 1989), rather than keratin, indicating that the formation of conodont elements and myxinoid denticles is not a homologous process. Similarly, the sharp histological boundary between the basal cartilage and the crown enamel and cellular bone in conodont elements refutes suggestions that the basal body represents an incipient replacement element (Krejsa *et al.* 1990 b). This histological study provides no direct evidence as to whether conodonts periodically shed their elements (cf. Carls 1977; Krejsa *et al.* 1990 b).

The presence of cellular bone, enamel and cartilage in conodont elements suggests that they formed in an homologous style to other vertebrate odontodes. The different tissues in modern odontodes are derived from specific areas within the dental papillae (Reif 1982; Smith and Hall 1990), and it has been assumed that these processes have continued throughout the history of ossification of the vertebrate cranial and dermal skeleton (Smith and Hall 1990; M.M. Smith 1991). The widely accepted growth mechanism of Bengtson (1976; Text-fig. 5.4), where elements are

everted during function and retracted into an epithecal pocket surrounded by secreting cells, is, at best, oversimplified and must be systematically re-evaluated for each genus. Indeed, it is likely that this model might become redundant since it was invoked to explain the centrifugal growth of conodont elements. As enamel is delineated by centrifugal growth lamellae, and forms within the dental papillae without periodic eruptions of the odontode, the eversion model of Bengtson (1976) to explain conodont growth now becomes redundant.

The intimate association of cellular bone and enamel in conodont elements is not unique to conodonts, it has also been recorded from dipnoans by M.M. Smith (1979, 1992), although the developmental sequence in these forms has not been elucidated. These two tissues have distinct origins within the dental papillae; enamel is derived from the epidermis, whilst odontogenic bone forms from a population of mesenchymal cells which are derived from the neural crest (Smith and Hall 1990). The absence of dentine is a major problem in trying to identify a growth sequence in conodont elements, as this tissue develops before enamel and bone within the dental papillae (Shellis 1981; Smith and Hall 1990; Section 5.3) and forms the basis for the formation of the rest of the tooth germ. In order to develop any model of element growth, it has been assumed that cellular bone formed first, this assumption being substantiated by the occurrence of this tissue as internal within the denticles of the elements studied.

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TEXT-FIG. 5.19. Growth models for the development of *Panderodus* elements (a,b,c,d) and *Parapanderodus* elements (a,b,c',d') based upon the tissue identifications made in the text and the development of modern vertebrate odontodes (cf. Text-fig. 5.5). The arrows indicate relative expansion of the dental papillae. Cellular bone is thought to have formed in a single event in *Panderodus* and periodically in *Parapanderodus*, producing a 'cone-in-cone' structure in the latter. In *Parapanderodus* growth lamellae within the enamel are continuous around the tip of the cusp, whilst in *Panderodus* they are discontinuous, possibly representing the gradual eruption of the element during formation.

a — Epithelial cap

Mesenchymal cells

b

c

c'

d

d'

Enamel   Cellular bone   Cartilage
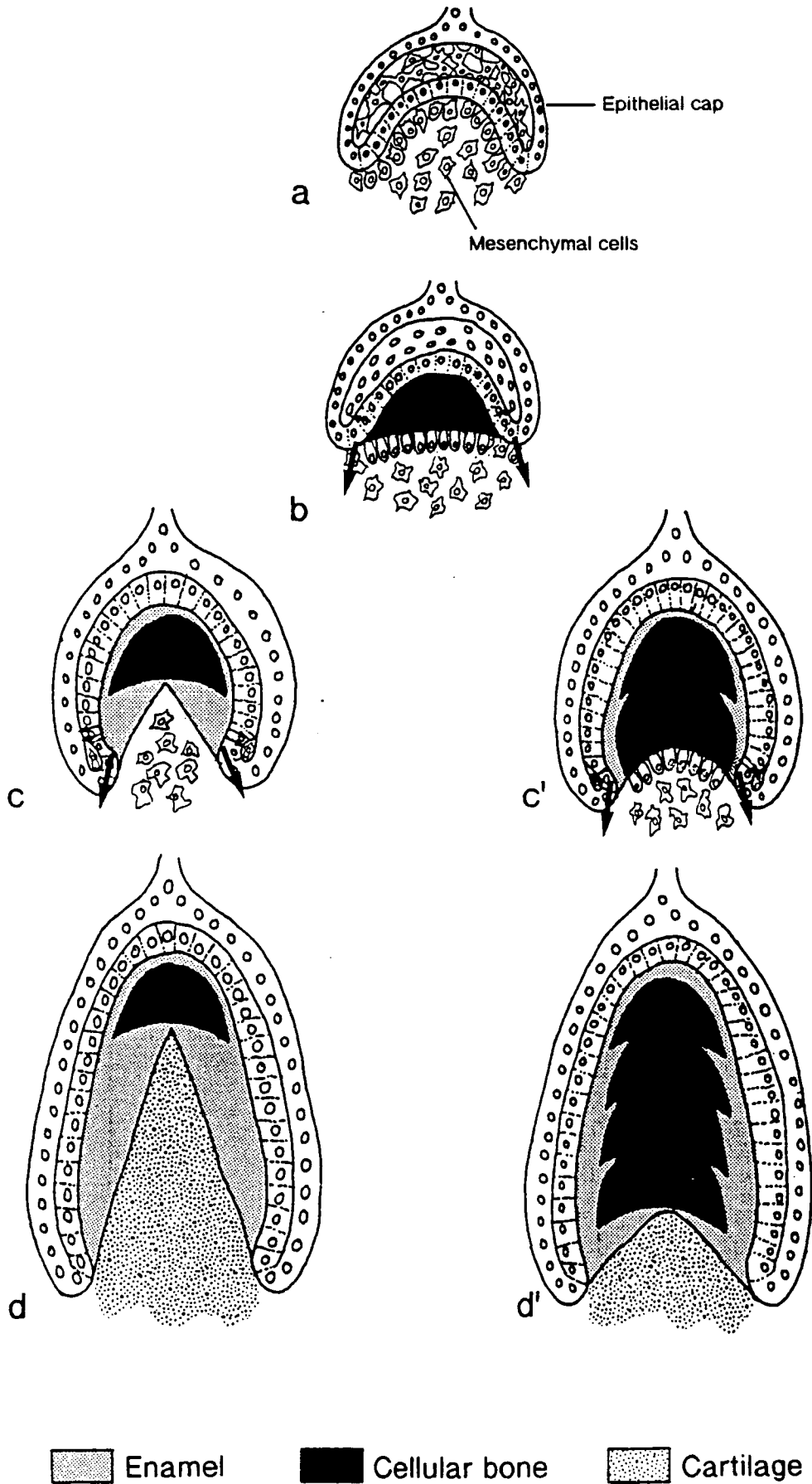
Variations in the relative distribution and extent of cellular bone and enamel in conodont elements indicate that the timing of formation of each tissue varied from genus to genus. One example highlighting this point is the difference in the occurrence of cellular bone in *Panderodus* and *Parapanderodus*. In the former, cellular bone appears to have formed, either from the ectomesenchyme or mesoderm, as the initial element bud (Text-fig. 5.19a, b). Subsequent development was dominated by the formation of parallel enamel from the epidermis, with cartilage forming as a ectomesenchymal/mesodermal component, keeping the basal cavity open (Text-fig. 5.19c, d). In *Parapanderodus,* cellular bone appears to have been formed throughout the genesis of the element, as is evident from the stringer of white matter running up the cusp (Text-fig. 5.19a, b, c', d'). This suggests that a heterochronic shift occurs in the formation of cellular bone in these two genera.

Damage and repair of conodont elements, as in the specimens illustrated by Müller and Nogami (1972) and Müller (1981), may result from defects or damage in the dental papilla, or shifts of the secreting cells during enamel secretion (Boyde *et al.* 1988). The deformation seen in the enamel crown of *Pseudooneotodus,* though probably not a conodont (see below), is clearly contemporaneous with growth, and not a result of damage during function. Further histological studies on 'damaged' conodonts are required to solve this problem.

It seems likely that *Pseudooneotodus* is not a true conodont, as it also lacks cellular bone. The association of enamel overlying dentine is common in non-conodont vertebrates, and it is suggested that *Pseudooneotodus* elements are dermal scutes of an unknown Late Ordovician-Lower Silurian vertebrate.

The techniques developed during the course of this study appear to represent a way forward in conodont studies. Enhanced resolution of histological structures in conodont elements has enabled, not only the recognition of vertebrate tissues, but also the generation of a growth model for two genera. Given more time and specimens, it seems likely that such study can be extended to provide a

comprehensive review of conodont histology, and perhaps use this information to enhance suprageneric classification.

Chapter 6.

CONODONT RELATIONSHIPS AND A
REINTERPRETATION OF CHORDATE PHYLOGENY

6.1 INTRODUCTION

The presence of vertebrate hard tissues in conodont elements (Sansom *et al.* 1992; Chapter 5) largely resolves the general debate on the relationships of conodonts. However, the position of conodonts within early vertebrate phylogeny remains to be established. Indeed, recent studies of conodont histology question a number of long held tenets of early vertebrate evolution (Sansom *et al.* 1992; Chapter 5). The inclusion of conodonts dramatically increases the generic diversity of Cambro-Ordovician vertebrates, from 5 to 149 genera (Aldridge and Smith *in press*). Histological features offer the potential to greatly expand the early vertebrate character set; this chapter employs a cladistic approach with this expanded database. Non-conodont data have been taken from previously published phylogenies (Janvier 1981; Halstead 1982; Forey 1984; Schaeffer 1987; Maisey 1988; Blieck 1992a) and this has been supplemented by information from Smith and Hall (1990), M.M. Smith (1991) and Sansom *et al.* (1992).

6.2 CLADISTIC TERMINOLOGY

Cairns (1985) provided an excellent introduction to the terminology and methodology of cladistics; what follows is essentially a *precis* of his section on this subject.
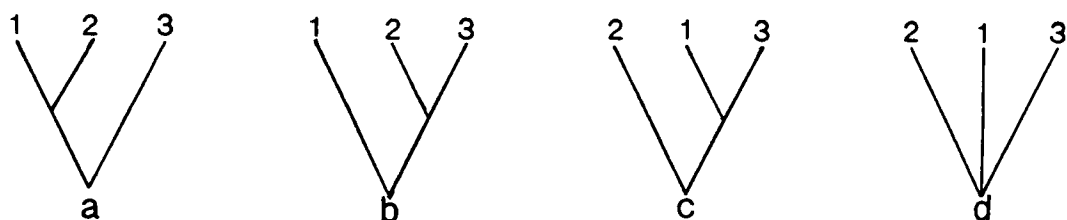
TEXT-FIG. 6.1. Possible solutions to a simple three taxon problem, including d) an indecisive expression (Modified from Forey 1984, figure 1).

Cladistics offers a rigorous approach to reconstructing phylogenies by identifying shared derived characters in groups of taxa. The simplest case of a three-taxon problem can be resolved in three possible ways (Text-fig. 6.1a-c); with a fourth indecisive expression (Text-fig. 6.1d), and the recognition of derived shared characters can be used to demonstrate their inter-relationships. Ancestral characters are termed *plesiomorphic* whilst those which are derived are termed *apomorphic*. Shared derived characters are termed *synapomorphies* and must be homologous. In Text-fig. 6.2 Character 1 is a uniting synapomorphy for the four taxa A - D, these form a *clade* which is *monophyletic*. Character 2 is a synapomorphy for A - C. Character 3 represents change from the primitive condition (g) to an advanced synapomorphy (h), the change occuring at the point illustrated on the cladogram. Character 4 is unique to Taxon A, and is thus not a synapomorphy but an *autapomorphy*. The point 'x' represents a hypothetical ancestor for Taxa A, B, C, and D, which exhibits Character 1, but not Characters 2, 3 or 4.

A large number of cladistic computer packages are now available, I have used MacClade Version 2.1 for the Macintosh PC (Maddison and Maddison 1987) and PAUP (Phylogenetic Analysis Using Parsimony) for the IBM PC (Swofford 1985). The characters have not been weighted and transformation states have not been imposed as this would involve the influence of my preconceptions. The resultant cladograms are thus selected purely on the basis of the degree of parsimony.
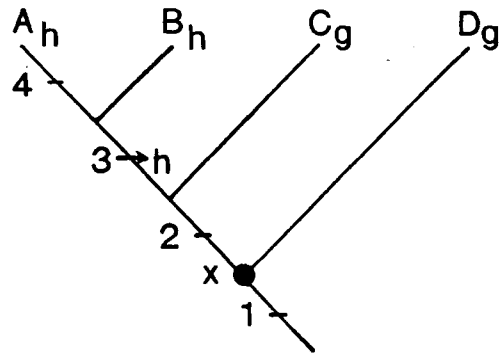
TEXT-FIG. 6.2. Hypothetical interrelationships between four taxa, expressed cladistically. Numbers 1-3 represent character state changes or *synapomorphies* for the taxa they define. Synapomorphy 3 represents the change from the primitive character g to the advanced character h, the change occurring at the point indicated on the diagram. Character 4 is an *autapomorphy* defining Taxon A. x represents a theoretical ancestor (Modified from Cairns 1985, text-figure 1).

6.3 TAXONOMIC UNITS

Conodonts (Late Cambrian - end Triassic)

A degree of uncertainty existed regarding the affinities of conodonts following the description of the first soft-bodied specimen. Briggs *et al.* (1983) discussed possible phylogenetic connections between conodonts and both chaetognaths and chordates. Bengtson (1983) argued in favour of the former view, whilst Janvier (1983) supported the chordate model. Tillier and Cuif (1986) proposed a link between conodonts and aplacophoran molluscs, but this was later considered untenable by Briggs *et al.* (1987). Additional soft-bodied specimens have yielded much more information about the conodont *bauplan*. Chordate features such as somites, a putative notochord and an asymmetric tail fin have now been recognised (Aldridge *et al.* 1986; Aldridge 1987; Smith *et al.* 1987; Conway-Morris 1989), although some authors consider alternative interpretations (Sweet 1988 for a review). Lobate lozenge-shaped features surrounding the head may represent eyes (Briggs

1992; Text-fig. 6.3). Conodont elements are located in the oral cavity, functioning as part of a bilateral multielement feeding apparatus (Aldridge *et al.* 1987; Smith *et al.* 1987; Chapters 2 and 4). Aldridge *et al.* (1987) and Smith *et al.* (1987) have argued that the ozarkodinid element battery functioned in a similar way to the myxinoid lingual apparatus. It is more likely that the operation of the petromyzontid longitudinal and transverse lamina provides a closer analogue for *Panderodus* and the ozarkodinids (Chapter 4). Histological studies have also established the presence of cellular bone, enamel and cartilage in conodont elements (Sansom *et al.* 1992; Chapter 5).
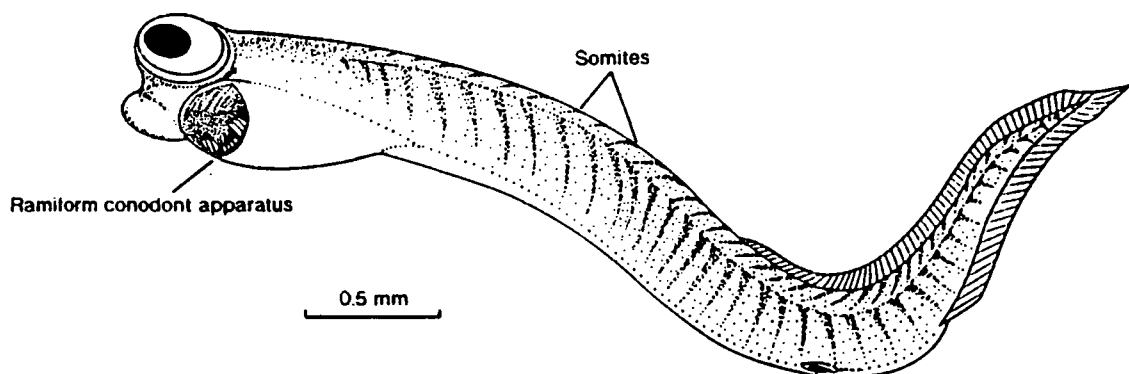
TEXT-FIG. 6.3. Reconstruction of a ramiform-bearing conodont based upon the Granton soft-bodied specimens described by Briggs *et al.* (1983) and Aldridge *et al.* (1986). The anterior lobes of these specimens have been interpreted as eyes by Briggs (1992), whilst the nature of the branchial openings has yet to be established.

Late Cambrian - Early Ordovician Problematica

Many authors have claimed to have discovered vertebrate remains in the Cambrian and Early Ordovician. However, most of these studies have been the subject of debate in the scientific literature, leading to expressions of doubt or reintepretation of the original authors' taxonomic assignment.

Hadimopanella and other members of the Utahphosphidae have figured in several discussions of early vertebrate biomineralisation (Bengtson 1977; Dzik 1986; Bendix-Almgreen and Peel 1988; Smith and Hall 1990). On the basis of

morphological comparison, Hinz *et al.* (1990) have reinterpreted *Hadimopanella*, *Kaimenella*, *Milaculum* and *Utahphospha* as sclerites of the "worm-like" Palaeoscolecida.

Anatolepis heintzi Bockelie and Fortey 1976 has been described from the Late Cambrian - Early Ordovician of North America, Greenland and northern Germany (Elliott *et al.* 1991), and is probably the most notable of the supposed 'oldest' vertebrate taxa. Despite the widespread occurrence of this form, the affinity of this material is unresolved. *Anatolepis* is characterised by rhombic tubercles tesselated over an extremely thin sheet of phosphate. Fragmentary remains of exoskeletal material are the most common; although Repetski (1978) described comparatively large plates, these are not whole animals with the scales *in situ* as stated by Smith and Hall (1990).

A

B
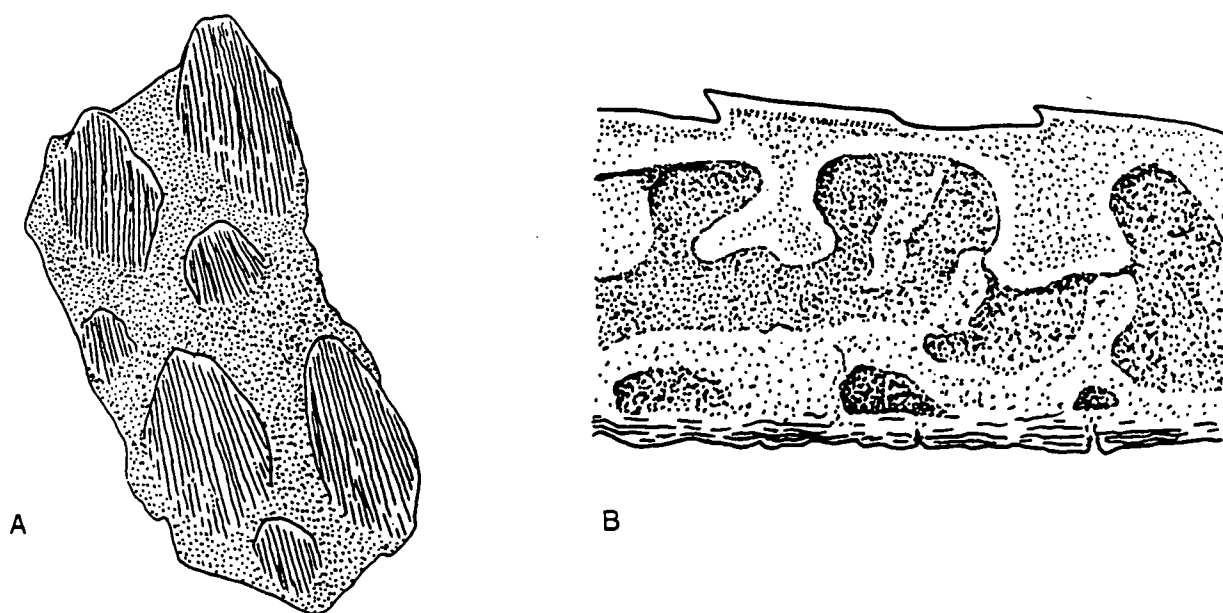
TEXT-FIG. 6.4. A) External morphology of *Anatolepis* sp. showing the sculpted surface (Traced from Nitecki *et al.* 1975 fig. 4; x 210). B) Section though a plate of *Anatolepis* showing the cavernous nature of the exoskeleton (Taken from Bockelie and Fortey 1976, fig. 3b; x 750).

Anatolepis was first illustrated by Nitecki *et al.* (1975; Text-fig. 6.4A), who suggested that their material resembled fragments of a merostome arthropod.

Bockelie and Fortey (1976) formally named this new taxon and considered that *Anatolepis* represented an early vertebrate, a view supported by Repetski (1978), Briggs and Fortey (1982) and Smith and Hall (1990). Peel and Higgins (1977) and Peel (1979) described additional specimens from North Greenland, and disputed the vertebrate nature of *Anatolepis*. They agreed with Nitecki *et al* (1975) that the material morphologically resembled fragments of the carapace of merostome arthropods. Janvier (1981) suggested that the material described by Repetski (1982) was probably vertebrate whilst Bockelie and Fortey's (1976) specimens were arthropods. Both Bockelie and Fortey (1976) and Repetski (1978) claim that the cavernous nature of the carapace of *Anatolepis* (Text-fig. 6.4B) supports their vertebrate interpretation, but Ørvig (1989) and Elliott *et al* (1991) were unconvinced by their histological arguements. The affinities of *Anatolepis* remain the subject of much controversy and have not been included in the phylogenetic discussion presented here. The potential importance of the genus, if conclusive evidence of vertebrate affinities is forthcoming, should not be underestimated.
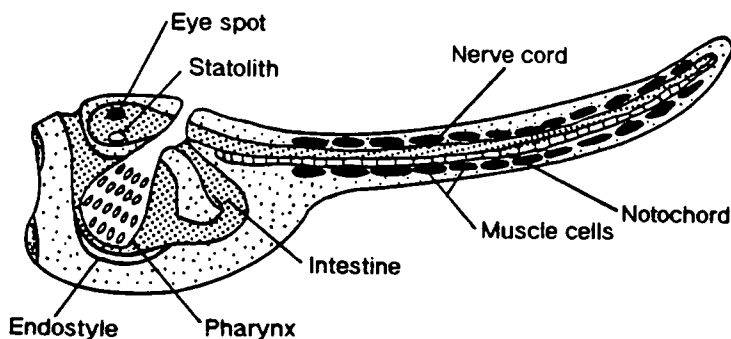
TEXT-FIG. 6.5. Structure of an ascidian (tunicate) tadpole larva (Taken from Walker 1987, fig. 2-5C).

Urochordates

The Urochordata (tunicates) are generally considered to be a sister group of the somitic chordates (Schaeffer 1987; Blieck 1992). They are divisible into forms

which are sedentary, for example the ascidians or sea squirts, and others which are pelagic, e.g. the thaliaceans and the larvacea (Walker 1987). The urochordates are surrounded by an aqueous/cellulose-based tunic (Jefferies 1986). The larval stage of all tunicates is motile, with a notochord, dorsal nerve and muscle cells (Text-fig. 6.5). The presence of a perforated pharynx and endostyle in the gut of both larval and adult forms (Text-fig. 6.6) warrant their inclusion in the chordates (Jefferies 1986).
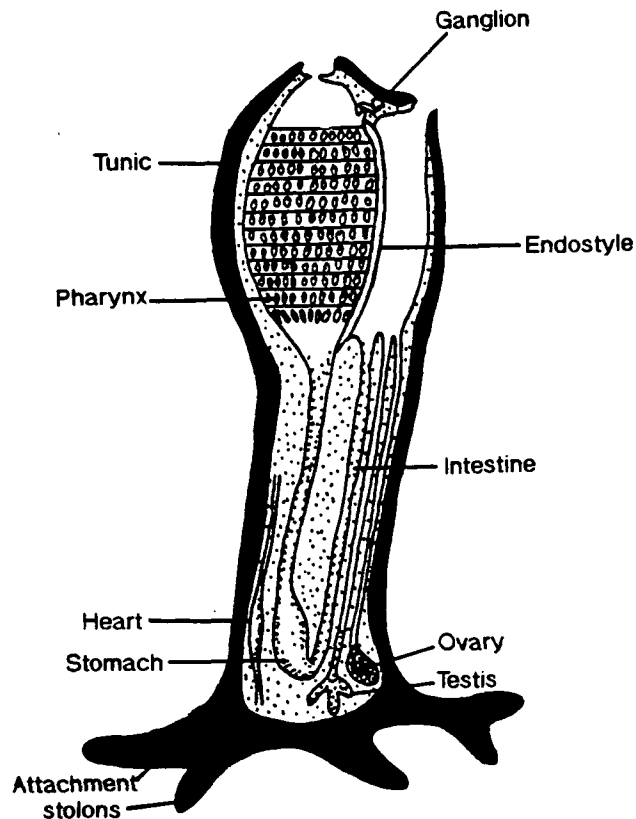
TEXT-FIG. 6.6. Structure of an adult ascidian (tunicate) *Clavelina* (Taken from Walker 1987, fig. 2-5B).

Fossil occurrences of urochordates are sparse, the trace fossil *Polycylindrichnus* Fournier *et al.* 1980, from the Silurian of Ontario, Canada, has been interpreted as a possible tunicate burrow, whilst the body fossil *Palaeobotryllus* Müller 1977 from the Upper Cambrian of Nevada has similarities with the modern ascidian *Botryllus*.

Cephalochordates

Cephalochordates have long been viewed as the living embodiment of a theoretical primitive chordate. Jefferies (1986) questioned this view, quoting the lack of symmetry in *Branchiostoma*, and considered the cephalochordates to be a sister group of the [urochordates + vertebrates]. However, Schaeffer (1987) reaffirmed the traditional position, placing urochordates as a sister group to the [cephalochordates + vertebrates] on the basis of five synapomorphies (characters 14 - 18 of Schaeffer 1987) including the presence of somites and a notochord. This interpretation remains the established orthodoxy (Blieck 1992) and has not been challenged in this study.
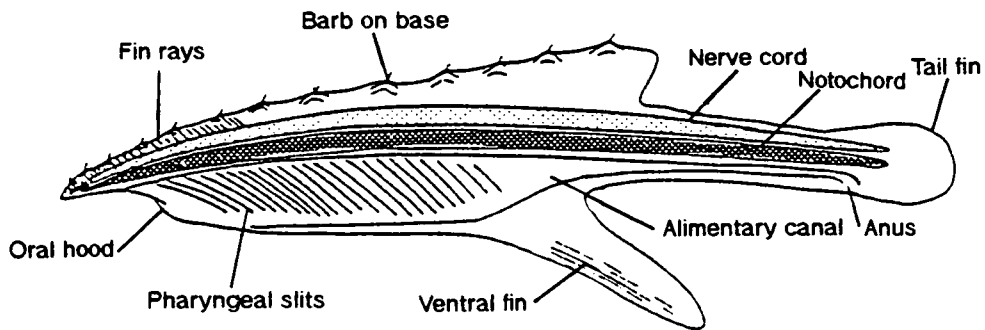
TEXT-FIG. 6.7. *Palaeobranchiostoma hamatotergum* in lateral view (Taken from Oelofsen and Loock 1981, fig. 3). The animal was some 11mm in total length and has been compared with the extant cephalochordate *Branchiostoma* (cf. Text-fig. 4.7.) by Oelofsen and Loock (1981) and Blieck (1992).

A fossil cephalochordate, *Palaeobranchiostoma hamatotergum* Oelofsen and Loock 1981, has been recorded from the Early Permian Whitehill Formation of South Africa . Longitudinal traces in the specimen have been attributed to a notochord and dorsal nerve chord. Pharyngeal slits have been identified in the anterior of the specimen (Text-fig. 6.7). These features allow comparison with the modern cephalochordate *Branchiostoma* (Oelofson and Loock 1981; Blieck 1992).

Palaeobranchiostoma differs from *Branchiostoma* in the presence of a dorsal fin which bears a series of fine barbs and a large posteriorly directed ventral fin.
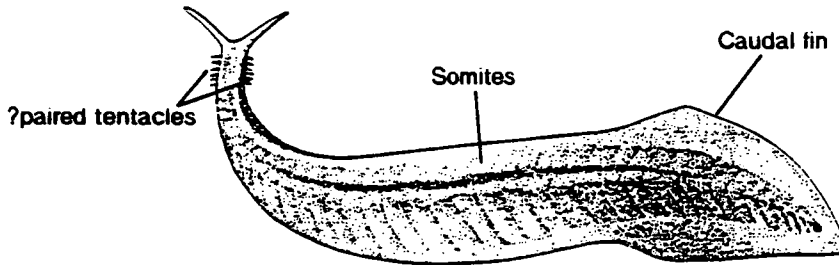
TEXT-FIG. 6.8. Reconstruction of the possible cephalochordate *Pikaia* from the Burgess Shale. The presence of somites, a caudal fin and possible paired oral tentacles invites comparison with similar structures in *Branchiostoma* (Text-fig. 4.7.) (Taken from Gould 1989, figure 5.8).

Pikaia gracilens Walcott 1911 (Text-fig. 6.8) from the Middle Cambrian Burgess Shale of British Columbia, Canada was originally described as a polychaete annelid. However, it has been reinterpreted as a primitive chordate (Conway-Morris 1982; Conway-Morris and Whittington 1985) despite the absence of a detailed redescription. Blieck (1992) drew a comparison with *Branchiostoma*, recognising gross morphological similarities in the lanceolated nature of *Pikaia*, a tapered anterior, putative notochord and 'v-shaped' myotomes. Anteriorly, *Pikaia* also bears paired tentacles which may correspond to the buccal cirri of *Branchiostoma* (Blieck 1992).

Myxinoids

Myxinoids are essentially eel-like in bodyplan, with an elongate trunk and asymmetric tail fin. The trunk in modern forms, such as *Myxine*, has many integumentary glands that secrete mucus, largely as a protective coating (Hardisty 1979; Text-fig. 6.9). Hagfish are in iso-osmotic equilibrium with the surrounding sea-water, a feature which they share with many marine invertebrates but not other

extant vertebrates, suggesting that the myxinoids have occupied a marine habit throughout their evolution (Walker 1987).
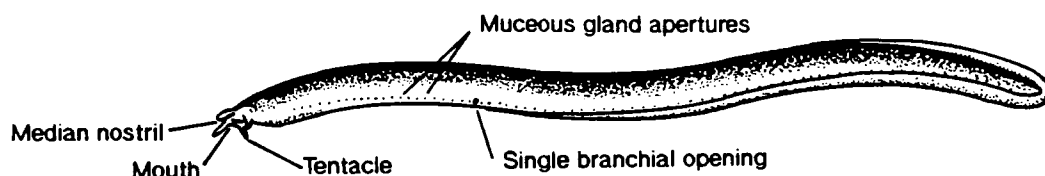
TEXT-FIG. 6.9. Lateral view of the hagfish *Myxine* (Taken from Walker 1987, figure 3-4C).

Only a single fossil myxinoid is known, a specimen of *Myxinikela siroka* from the Pennsylvanian Francis Creek Shale, Carbondale Formation of Illinois (Bardack 1991). This is probably due to the very low preservation potential of myxinoids due to the absence of mineralised skeletal components. The bilateral feeding apparatus of myxinoids is formed principally of keratin denticles (Krejsa *et al.* 1990, 1991) and the rigidity of internal skeletal components is provided by un-mineralised cartilage (Hardisty 1979). Biochemically, they may have the potential to secrete enamel, as proteins have been reported from hagfish denticles which are also found in mammalian enamel (Slavkin *et al.* 1983). Homology between the respective developmental sequences of hagfish denticles and vertebrate teeth has been questioned (Smith and Hall 1990). Extant myxinoids are little different from the fossil form, suggesting that they represent a very conservative clade (Bardack 1991).

Astraspis (Caradoc, Late Ordovician)

Since it s first description from the Harding Sandstone of Colorado (Walcott 1892), *Astraspis* has been reported from a number of localities in North America (see references in Elliott *et al.* 1991). *Astraspis desiderata* is most commonly found as isolated tesserae with a surface ornamentation of stellate tubercles. The two known articulated specimens have recently been reassessed by Elliott (1987; Text-fig. 6.10) who reconstructed *Astraspis* as a dorso-ventrally compacted animal, 130 mm in

length, with a robust caudal fin. The headshield is formed of sutured polygonal tesserae which pass posteriorly to form triangular imbricated scales. Eight branchial plates are found behind the lateral orbits.
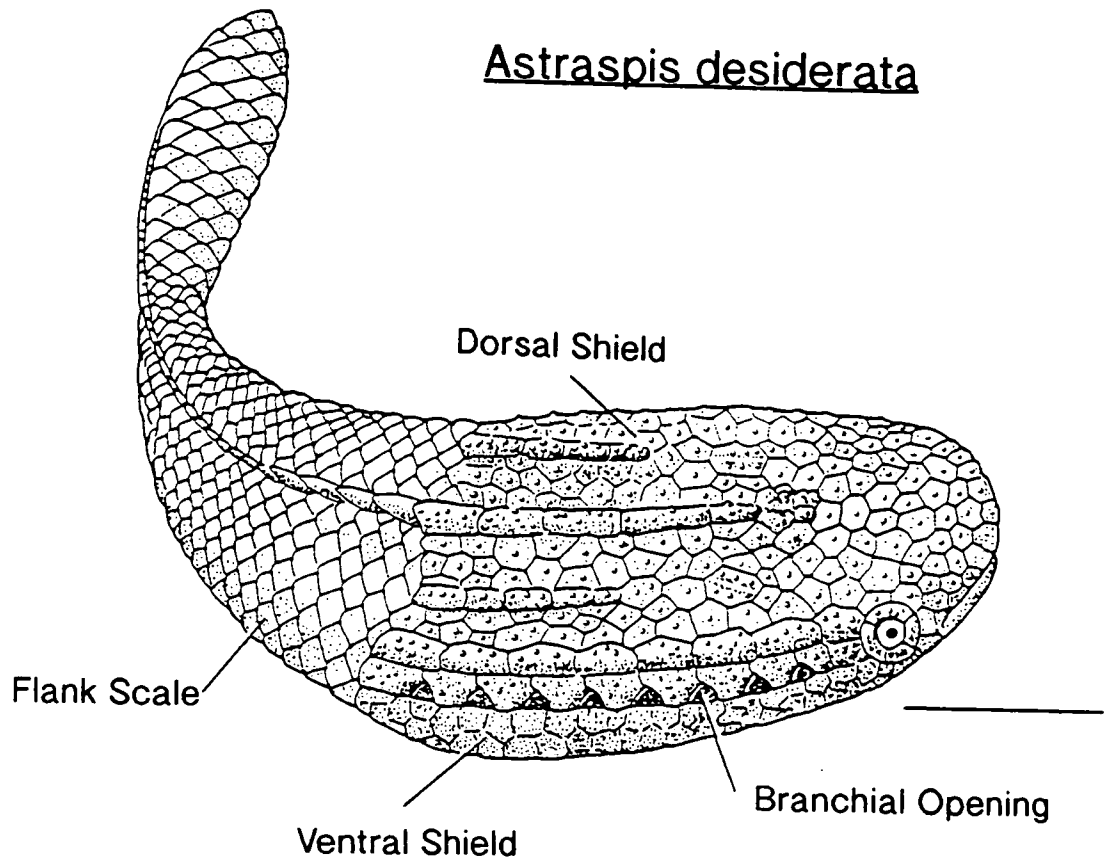
TEXT-FIG. 6.10. Reconstruction of *Astraspis desiderata.* Scale bar = 5cm (Taken from Elliott *et al.* 1991, figure 1B).

The histology of the tesserae is three-layered, consisting of basal laminated acellular bone (aspidin), a middle laminated layer penetrated by fine calibre tubules (astraspidin or fine calibre dentine, Halstead 1987; Elliott *et al.* 1991), and a glassy cap of enameloid (Smith and Hall 1990). The presence of a calcified cartilaginous endoskeleton has been suggested by Elliott *et al.* (1991). This is supported by the observation of globular calcified cartilage underlying dermal tesserae made during this study (Text-figs 5.8 and 5.9).

Ørvig (1958) described the closely related form, *Pycnaspis splendens,* from Wyoming. This genus differs from *Astraspis* in the presence of large mushroom-shaped tubercles on the tesserae of 'adult' specimens. Denison (1967) synonymised these genera, suggesting that this size difference was attributable to interspecific variability within *Astraspis.* Recently, Ørvig (1989) has reaffirmed the validity of *Pycnaspis* on the basis of its histological structure, as an extremely thin layer of dentine separates the enameloid cap from the underlying aspidin.

Eriptychius (Caradoc, Late Ordovician)

Eriptychius has also been recorded from the Harding Sandstone of Colorado and associated strata in North America (Ørvig 1989). Although it has been divided into two species (*E. americanus* Walcott 1892 and *E. orvigi* Denison 1967) on the basis of scale ornamentation; histologically these two species are identical (Ørvig 1989). The isolated tesserae and scales which form the vast majority of *Eriptychius* material are sculpted with elongate ridges. They are formed of a basal laminated layer of aspidin, overlain by laminated dentine which is penetrated by wide calibre tubules radiating from central pulp cavities (Ørvig 1989). Thin glassy coverings to these tubercles, thought to be formed of enamel, are generally missing due to abrasion (Smith and Hall 1990). Denison (1967) described a partially articulated specimen of *Eriptychius* and was able to demonstrate that patches of associated globular calcified cartilage formed endoskeletal components, possibly representing rostral and orbital cartilages (Elliott *et al.* 1991). Ørvig (1958) suggested that a single perforated plate of *Eriptychius* might represent a branchial plate, although additional specimens are required before definite statements can be made about the form of the branchial structure in *Eriptychius* (Elliott *et al.* 1991). Some authors have placed *Eriptychius* with the heterostracans (Janvier 1981; Halstead 1987) on the basis of histological comparison.

3rd unnamed vertebrate[1] from the Harding Sandstone (Caradoc, Late Ordovician)

The presence of further forms in the Harding Sandstone of Colorado has been known since Denison (1967) and Spjeldnaes (1967) figured and discussed a third taxon additional to *Astraspis* and *Eriptychius*. This species has recently been discussed by M.M. Smith (1991). It has yet to be recognised from discrete material, but has been only described from histologically distinct tubercles in thin sections. These are discrete, rather than linked as larger tesserae, and are composed of basal cellular bone and mesodentine, covered by a cap of enameloid (M.M. Smith 1991). Little else is known about the taxon, although the tubercles appear to be button-shaped. The histology of this taxon suggests that it may represent a stem group osteostracan (M.M. Smith 1991).
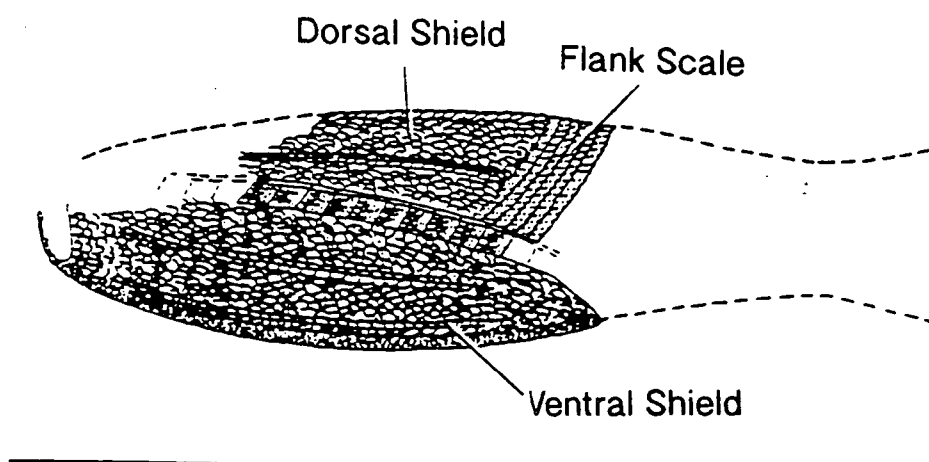
TEXT-FIG. 6.11. Reconstruction of *Arandaspis prionotolepis*. Scale bar = 5cm (Taken from Elliott *et al.* 1991, figure 1A).

Other Ordovician 'agnathans'

Two genera, *Arandaspis* and *Porophoraspis*, were described from the Llanvirn Stairway Formation of the Amadeus Basin, Northern Territory, Australia by

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[1] This term is employed here as, although three genera have already been described from the Harding Sandstone (*Astraspis*, *Pycnaspis* and *Eriptychius*), it follows the usage of M.M. Smith (1991).

Ritchie and Gilbert-Tomlinson (1977; Text-fig. 6.11). Both are known only from natural external moulds, so no histological inferences can be made, and *Porophoraspis* is too poorly preserved for any reconstruction to be possible. The branchial openings of *Arandaspis* differ from those seen in *Astraspis* in the presence of slanted branchial plates (Ritchie and Gilbert-Tomlinson 1977; Janvier 1981).

Sacabambaspis janvieri
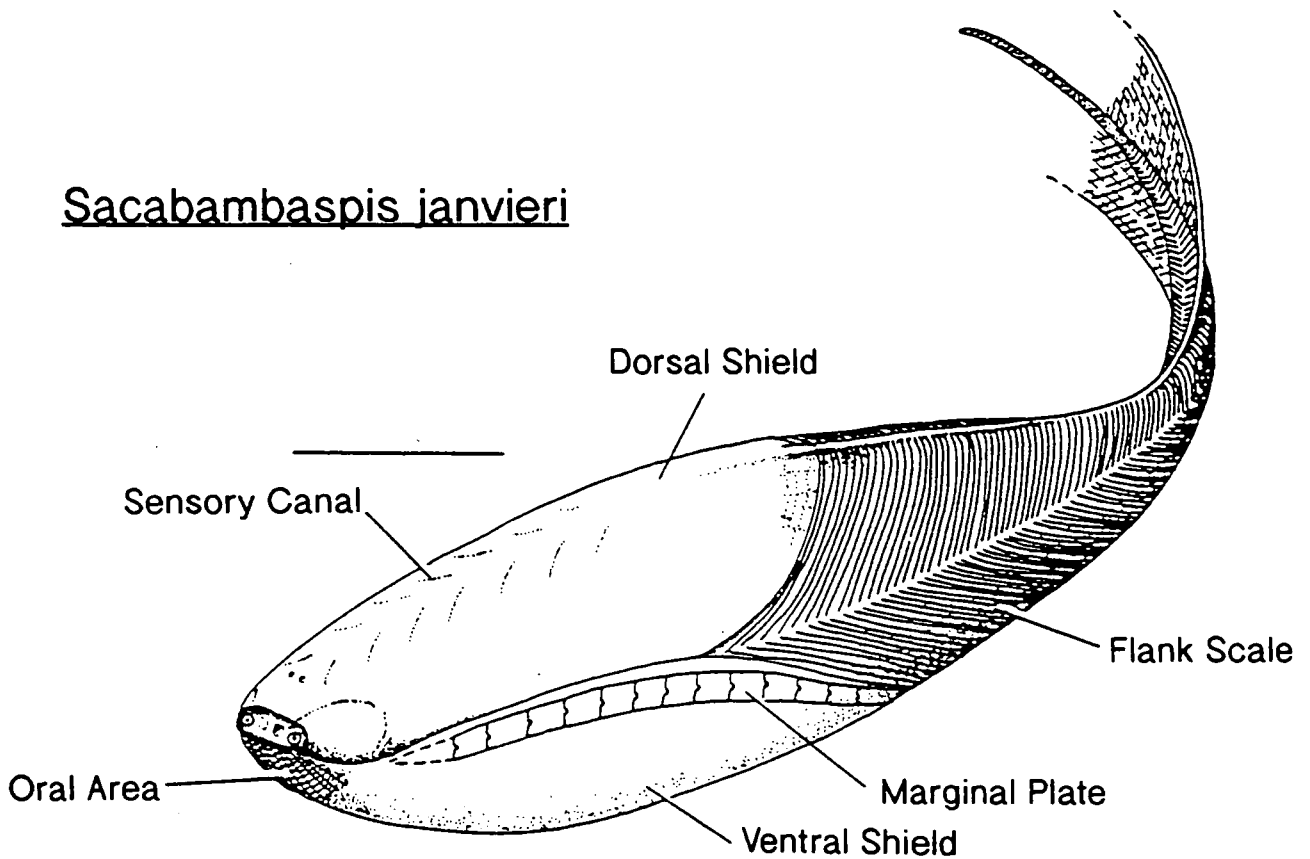
TEXT-FIG. 6.12. Reconstruction of *Sacabambaspis janvieri.* Scale bar = 5cm (Taken from Elliott *et al.* 1991, figure 1C).

An additional Ordovician form, *Sacabambaspis* has been recovered from the Caradoc Anzaldo Formation of Cochabamba Province, Bolivia (Gagnier *et al.* 1986: Gagnier 1989; Text-fig. 6.12). The histology of *Sacabambaspis* has yet to be described, although suitable material is now available for study (Blieck pers. comm.). *Sacabambaspis* is thought to be more closely related to *Arandaspis* than *Astraspis* as

it seems to bear numerous slanted branchial openings (Elliott *et al.* 1991; Blieck 1992).

As this study is focus ed on the development of chordate histology, and the place of conodonts in this phylogeny, the scant evidence available on the three forms described above has precluded their inclusion in the cladistic analysis. It is anticipated that they will be introduced into the data matrix when additional histological information is forthcoming.
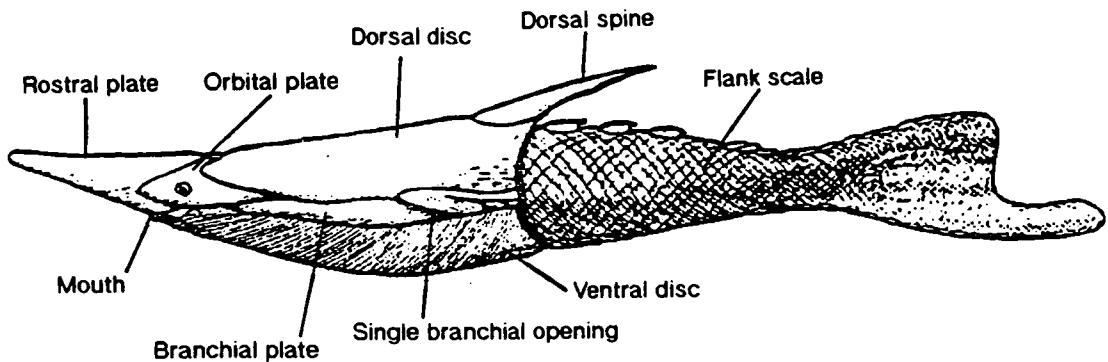
TEXT-FIG. 6.13. Reconstruction in lateral view of the Lower Devonian heterostracan *Pteraspis rostrata* (Taken from Jarvik 1980, fig. 370A).

Heterostracans (early Silurian - Late Devonian)

A wide variety of heterostracans has been described from the Silurian and Devonian. The dermal armour of heterostracans shows an evolutionary trend from isolated tubercles, through closely abutting tesserae, to fusion into large plates (Halstead 1967, 1982); other developments in the form of the exoskeleton have been discussed by Janvier (1984). Heterostracans are distinguished by the presence of a single branchial opening (Elliott 1987; Text-fig. 6.13) and the distinct histology found forming their dermal armour. A basal laminated layer of acellular bone or aspidin underlies a honeycombed layer of fibrous aspidin, and this is capped by tubercles formed of orthodentine (Smith and Hall 1990). Heterostracan tubercles do not possess a superficial enamel cap (Smith and Hall 1990), although if *Eriptychius*

does represent a stem heterostracan, the presence of enamel in this early form
suggests₍that₎the rest of the group subsequently lost this tissue.

Petromyzontids

The petromyzontids (Text-fig. 6.14) are represented at the present day by approximately 40 species of lamprey, and they are also know in fossil form from the Mississipian of Montana (*Hardistella montanensis* Janvier and Lund 1983) and the Pennsylvanian of Illinois (*Mayomyzon pleckoensis* Bardack and Zangerl 1968). Although the petromyzontids lack advanced craniate characteristics such as dermal ossificiation and paired fins, it is accepted that this is the result of the secondary loss of these characters (Janvier 1981).
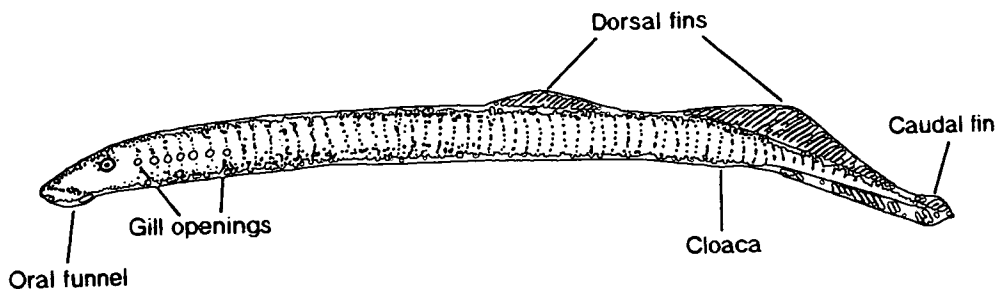
TEXT-FIG. 6.14. Lateral view of the lamprey *Petromyzon* (Taken from Walker 1987, figure 3-4A).

A large number of synapomorphies, principally based upon their soft tissue anatomy, have been used to demonstrate a close relationship between the petromyzontids and the osteostracans (Jarvik 1980; Janvier 1981; Forey 1984), as opposed to monophyly with the other order of extant naked agnathans, the myxinoids (Yalden 1985). *Jamoytius kerwoodi* White from the Silurian of Lanarkshire, Scotland (Ritchie 1968) has been placed with the petromyzontids by Janvier (1981; see below)
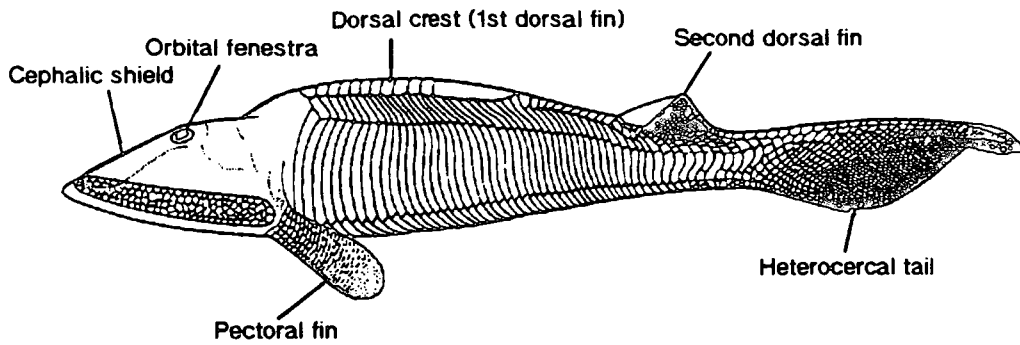
TEXT-FIG. 6.15. Reconstruction in lateral view of the Lower Devonian cephalaspid osteostracan *Hemicyclaspis murchinsoni* (Taken from Jarvik 1980, fig. 346).

Osteostracans (Early Silurian - Late Devonian)

The fossil record of the osteostracans is the most extensive of the 'agnathans' because of the comparatively increased ossification of the cranial area (Smith and Hall 1990; Text-fig. 6.15). The relationships of this group with other agnathans have been discussed by Janvier (1981, 1984). They are distinguished from the rest of the agnathan taxa dealt with here by the presence of perichondral bone, which is thought to line the inner cephalic shield (Janvier 1981; Smith and Hall 1990; Text-fig. 6.16). Endoskeletal calcified cartilage has been recorded from a Lower Devonian cephalaspid by Ørvig (1957). The exoskeleton of the trunk and cranium is formed on a base of cellular bone, although Ørvig (1965) recorded acellular bone in the highly derived form *Alaspis*. The bone is overlain by sculpted mesodentine tubercles. If the unnamed vertebrate from the Harding Sandstone does belong here as a stem group (M.M. Smith 1991), then enameloid has been recorded forming superficial caps to osteostracan denticles. The dermal armour is thought to be separated from the underlying perichondral bone by a layer of uncalcified cartilage (Smith and Hall 1990).

Osteostracan   Heterostracan
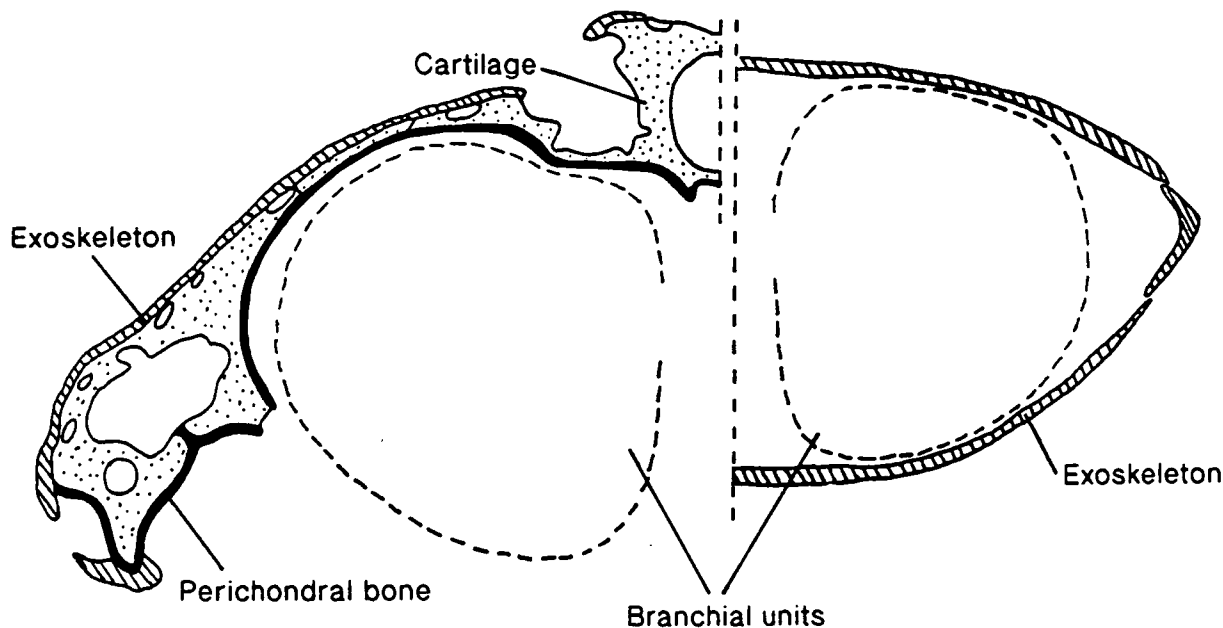
TEXT-FIG. 6.16. Transverse section through the branchial region of an osteostracan and a heterostracan showing the extent of the branchial units (dashed lines) and the relationship of perichondral bone to the osteostracan exoskeleton (Taken from Janvier 1981, figure 12 E_{1-2}).

Gnathostomes (Early Silurian - Present)

Four groups are included within the gnathostomes, two of these are extant, the Chondrichthyes (cartilage-dominated) and the Osteicthyes (bone-dominated) whilst the acanthodians and placoderms are known only as fossils. The evolutionary inter-relationships between these four groups has been discussed by Young (1986) and Maisey (1988), but there is little agreement on the phylogeny of the gnathostomes (Smith and Hall 1990). With this in mind, the following observations are generally based upon the gnathostomes as a whole.

The gnathostomes are histologically distinguished by the development of endochondral bone in three of the four groups. The absence of endochondral bone in the Chondrichthyes has been cited as evidence for their primitive position within the

gnathostomes (Maisey 1988), although it is possible that endochondral bone has been secondarily replaced by cartilage in these forms (Young 1986). The evolution of jaws in gnathostomes resulted from the modification of dermal denticles (odontodes) to form branchial arches which subsequently developed into specialised feeding and grasping structures (Reif 1982). These odontodes, homologous with dermal armour, are formed from basal bone of attachment (acellular and cellular), dentine (Smith and Hall 1990), and may be covered with a superficial cap of enamel or enameloid (Smith 1991). Calcified cartilage has been described from all forms of gnathostome (Smith and Hall 1990).

Post-Ordovician problematic vertebrates

Three major groups of post-Ordovician early vertebrates, thelodonts, anaspids and galeaspids, all of which belong to the 'agnathans', have been omitted from the cladogram presented here. This is largely a result of the relatively limited character states which are available from the conodonts and the problematic position of these taxa in vertebrate phylogeny.

Thelodonts are known mainly by isolated scales in residues from the Lower Silurian (possibly Upper Ordovician) into the Upper Devonian (Halstead and Turner 1973; Janvier 1981; Blieck 1992), although some articulated specimens are known (see Ritchie 1968, for example). The origin of this group is problematic in that monophyly (Moy-Thomas and Miles 1971) or paraphyly (Janvier 1981) can be argued for, as can their relationships with a disparate group of taxa including the heterostracans, galeaspids, osteostracans, anaspids and gnathostomes (Janvier 1981; Text-fig. 6.20). They have most recently been tentatively considered to be a primitive sister group to these taxa (Blieck 1992). Histologically, thelodonts are united by the presence of a single pulp chamber and a form of dentine which is either orthodentine or mesodentine (Smith and Hall 1990).

The anaspids (Lower Silurian-Lower Devonian) are thought to represent a paraphyletic group. Janvier (1981) proposed the exclusion of *Jamoytius* from the

anaspids as it lacks a dermal skeleton. Other anaspids have a thin covering of laminated acellular bone or dentine, although Smith and Hall (1990) pointed out that there is much confusion over the histological nature of these scales, and have developed branchial scales, postbranchial scales and pectorial plates (Forey 1984). As defined by Janvier (1981) the anaspids appear to be closely related to the petromyzontids, but are distinct in the replacement of the anterior dorsal fin by scutes (Janvier 1981)

The galeaspids are a little known group of Silurian to Upper Devonian 'agnathans' from North and South China. They possess a massive exo- and endoskeletal headshield, the latter being formed of perichondral bone (Smith and Hall 1990). Poor preservation has inhibited histological study; Forey (1984) claimed cellular bone was present without stating whether this was an exoskeletal or endoskeletal tissue. Halstead (1979) suggested that the galeaspids represent an isolated evolutionary radiation. Janvier (1981) and Forey (1984) have proposed a phylogenetic relationship with either the heterostracans or the osteostracans. The presence of perichondral bone and cranial nerves IX and X issuing from the braincase gives credence to the latter view. Maisey (1988) placed the galeaspids as a sister group to the gnathostomes, listing six morphological synapomorphies. Smith and Hall (1990) have stressed the importance of histological investigations of the galeaspids prior to any firm phylogenetic conclusions.

6.4 CHARACTERS

The characters used in the phylogenetic analysis are listed in Text-fig. 6.17. They are recorded on the basis of presence or absence within the data matrix presented in Text-fig. 6.18. Many of the "soft tissue" and biochemical characters employed by previous authors are not available for conodonts, and the data matrix is

thus based upon fewer characteristics than have been utilised by Janvier (1981), Halstead (1982), Forey (1984), Gans (1987), Maisey (1988) and Blieck (1992). However, this does not necessarily imply that the results are any less valid, as the characters below have played a central role in defining synapomorphies of the fossil taxa discussed in previous studies.

1. Somites
    0. absent
    1. present
2. Cartilagenous endoskeleton
    0. absent
    1. present
3. Dermal ossification
    0. absent
    1. present
4. Superficial cap
    0. absent
    1. enamel
    2. enameloid
    3. both
5. Dentine
    0. absent
    1. present
6. Cellular bone
    0. absent
    1. present
7. Acellular bone
    0. absent
    1. present
8. Aspidin
    0. absent
    1. present
9. Honeycombed middle layer
    0. absent
    1. present

10. Perichondral bone
    0. absent
    1. present
11. Endochondral bone
    0. absent
    1. present
12. Single branchial opening
    0. absent
    1. present
13. Slanted Gills
    0. absent
    1. present
14. Heterocercal Tail
    0. absent
    1. present
15. Nerves IX and X issuing from braincase
    0. absent
    1. present
16. Paired Fins
    0. absent
    1. present
17. Bite
    0. absent
    1. bilateral myxinoid
    2. bilateral petromyzontid
    3. jawed

TEXT-FIG. 6.17. Character states used in this cladistic study, all carry equal weighting.

6.4.1 Histological Characters

Assessments of the relative primacy of different vertebrate hard tissues have been hampered by ambiguous data. The presence of three taxa with distinct histological associations in the Ordovician Harding Sandstone of Colorado and

Wyoming, has provided the basis for a number of contradictory hypotheses of tissue development. The selection of the primitive tissue has largely coloured the scenarios developed by several authors (see discussion by Maisey 1988, p. 2). Halstead's final discussion of hard tissue evolution concluded that, on the basis of the information available to him, "any further discussion or debate on the relationships of the various vertebrate hard tissues to one another, in terms of which is the more advanced or primitive or advanced, is no longer worth pursuing" (Halstead 1987, p. 355). The addition of conodont data, extending the vertebrate fossil record back to the Late Cambrian, has an important role to play in the determination of the primacy of hard tissue character states.

Urochordates	00000000000000000
Cephalochordates	10000000000000000
Myxinoids	11000000000000001
Conodonts	11110100000??0002
Heterostracans	11101011100100001
Astraspis	11121011100000001
Eriptychius	11111011100?0000?
3rd unnamed vert.	11121100000??????
Osteostracans	11121100010001112
Gnathostomes	11131100011001113
Petromyzontids	11?????????????100?2

TEXT-FIG. 6.18. Data matrix for the taxonomic units examined in this study, based upon the character states of Text-fig. 6.17. Question marks indicate missing data, although the lack of dermal armour and paired fins in the petromyzontids is thought be a degenerative feature.

Cartilaginous endoskeleton:

The development of a cartilaginous endoskeleton in the myxinoids suggests that unmineralised cartilage formed within the body of 'protovertebrates' before phosphatised tissues (Janvier 1981; Forey 1984; Maisey 1988; Blieck 1992).

Cartilage is present in the endoskeleton of conodonts, the Harding Sandstone taxa, heterostracans, osteostracans and the gnathostomes.

Dermal ossification:

Combinations of phosphatised tissues such as enamel, enameloid, dentine dermal bone and mineralised cartilage have been described from the dermal skeleton of conodonts (Sansom *et al.* 1992; Chapter 5), *Astraspis, Eriptychius,* heterostracans, osteostracans and gnathostomes (Janvier 1981; Forey 1984; Maisey 1988; Smith and Hall 1990; Blieck 1992). The presence of such tissues has previously been used as a synapomorphy uniting the 'higher craniates' (but not conodonts as these authors have not yet accepted their vertebrate affinities), and separating them from the myxinoid outgroup. Maisey (1988) and Blieck (1992) have interpreted this character state as resulting from the induction of the neural crest, as these tissues in the dermal skeleton are thought to have been derived from this embryological feature (Halstead 1987; Gans 1987; Smith and Hall 1990); this is a point that will be addressed further on.

Superficial cap:

Three alternative hypotheses have been put forward to explain the histological development of superficial caps on dermal sclerites :

1) enameloid is primitive and enamel developed subsequently to replace enameloid (Poole 1967; Reif 1979).

2) enamel is primitive and enameloid developed subsequently in certain lineages (Smith 1992).

3) enamel and enameloid evolved independently (Rosen *et al.* 1981; Schultze 1986; Panchen and Smith 1987).

Prior to the recognition of enamel in conodont elements (Sansom *et al.* 1992; see Chapter 5), evidence from the fossil record could be cited in support of each of the above hypotheses. The Harding Sandstone vertebrates include taxa which possess both enamel (*Eriptychius*) and enameloid (*Astraspis* and the "3rd unnamed vertebrate).

However, the appearance of conodont elements with enamel lends support to the hypothesis that enamel represents the primitive tissue, although the third hypothesis cannot be discounted.

Dentine:

Dentine was proposed as the most primitive vertebrate hard tissue by Smith and Hall (1990) on the basis of the supposed occurrence of this tissue in the Late Cambrian - Early Ordovician genus *Anatolepis* (see discussion above). Janvier (1981) has also claimed that dentine is the primitive vertebrate hard tissue on the basis of his cladistic analysis of vertebrate phylogeny. However, neither of these proponents of dentine as a primitive tissue accept the inclusion of conodonts, which occur some 60 million years prior to dentine in the fossil record.

Cellular - acellular bone:

Evidence from the Harding Sandstone cannot be used to distinguish between the three hypotheses of the primacy of cellularity in bone (Smith and Hall 1990):

1) cellular bone is primitive, and acellular bone developed subsequently (Ørvig 1957, 1968; Maisey 1988).

2) acellular bone is primitive and cellular bone developed subsequently (Denison 1963; Janvier 1981; Maisey 1988).

3) that the two bone types developed independently (Ørvig 1965; Moss 1968)

Acellular bone (in *Astraspis* and *Eriptychius*) occurs in the Harding Sandstone contemporaneously with cellular bone (in the 3rd unnamed vertebrate). The formation of acellular bone occurs either by the retreat of the secreting osteoblasts or their reduction by pycnosis until the osteocytes disappear. Thus acellular bone would be considered as derived or secondary from the developmental point of view (Maisey 1988). With the recognition of cellular bone in conodont elements, the fossil record now supports the primacy of this tissue, which is in accordance with the developmental data.

Aspidin:

Aspidin was first described by Gross (1930) from psammosteid heterostracans and the nature of this tissue has subsequently been the subject of much debate (e.g. Halstead 1969, 1987; Maisey 1988; Smith and Hall 1990). The tissue itself is characterised by spindle shaped spaces and coarser fibrous cavities, and it has been recognised from all the heterostracans, *Eriptychius* and, more problematically, *Astraspis* (Halstead 1987; Smith and Hall 1990). Aspidin forms the trabeculae of the honeycombed middle layer in these taxa as well as the basal laminated material. It has been argued that aspidin is a form of acellular bone, but . the fine spaces seen in aspidin have frequently been described as the sites of the scleroblastic cells (see references in Halstead 1969). Ørvig (1965) has argued that these spindle shaped features represent the position of collagen bundles, a view finally accepted by Halstead (1987). The relationship of aspidin to dentine and bone is problematic, as there is evidence   to assign aspidin to either dentine or bone (Halstead 1969, 1987: Smith and Hall 1990). Perhaps there is a tendency to over-emphasize the distinction as there is an abundance of problematic fossil 'intermediate' tissues (Hall 1975; Maisey 1988). Despite these problems over the interpretation of aspidin, it has only thus far been recognised in the heterostracans, *Eriptychius* and *Astraspis,* and is a potentially useful character in phylogenetic reconstructions involving these forms.

Honeycombed middle layer:

The presence of a honeycombed middle layer, formed of aspidin, underlying the tubercles in the exoskeleton of *Astraspis, Eriptychius* and the heterostracans has been cited as a primitive condition in the vertebrates (Elliott *et al.* 1991; Blieck 1992). This has also been used to dispute the vertebrate affinities of conodonts as their elements do not possess a honeycombed layer (Elliott *et al.* 1991). However, these authors did not take into account the discrete denticles of the 3rd unnamed vertebrate which co-occurs with *Astraspis* and *Eriptychius* in the Harding Sandstone

and which clearly lacks a honeycombed middle layer. The presence of honeycombed middle layers in *Astraspis, Eriptychius* and the heterostracans may suggest a phylogenetic link between these forms, but is not indicative of the primitive vertebrate condition.

Perichondral Bone and Endochondral Bone:

The first skeletal tissue is thought to have been an uncalcified cartilage, and the subsequent formation of bone, both perichondral and endochondral, forms from the secondary replacement of this tissue (Smith and Hall 1990). Perichondral bone initially forms from the perichondrium, a connective tissue surrounding cartilage, and grows centripetally, whereas endochondral bone forms within the cartilage and grows centrifugally (Walker 1987). The development of perichondral bone in the cranium is encountered in the osteostracans; perichondral and endochondral bone is known from the gnathostomes (Smith and Hall 1990). The presence of these tissues has been used in phylogenetic analyses by Janvier (1981) and Blieck (1992).

6.4.2 Features relating to the bodyplan

Somites:

The presence or absence of somites has been used to define the somitic chordates, a group including the cephalochordates, myxinoids, euconodonts, the Harding Sandstone taxa, heterostracans, osteostracans and the gnathostomes.

Heterocercal Tail:

Caudal tails are described as 'normal heterocercal' or 'epicercal' when the vertebral axis is deflected upward into the enlarged dorsal lobe (Walker 1987). Forey (1984, p. 339) is more specific about this, referring to the "heterocercal tail with a change of scale orientation at the caudal peduncle". This condition has been described from osteostracans and gnathostomes (Janvier 1981; Forey 1984; Blieck

1992). Heterostracans possess a diphycercal tail (Denison 1971; Forey 1984), where the vertebral axis runs to the posterior tip, dividing the fin into symmetrical dorsal and ventral lobes (Walker 1987). The conodont tail appears to be a simple fin ray, although Briggs *et al.* (1983) and Aldridge *et al.* (1987) have discussed the possibility of two caudal fins in the Granton conodonts. If the orientation of the fin rays can be established from further study and additional specimens, this would suggest homology with the conodont tail and the petromyzontids, where two dorsal fins are recognised.

Paired fins:

True paired pectoral fins are present only in the gnathostomes, and homologous structures are thought to be present in osteostracans (Forey 1984). Internally supported pectoral fins are not found in myxinoids, conodonts, heterostracans and *Astraspis*, and are thought to also be absent in *Eriptychius* and the 3rd unnamed vertebrate from the Harding Sandstone.

Bite:

The 'bite' of vertebrates is divisible into that seen in the gnathostomes and that seen in the extant 'agnathans' (myxinoids and petromyzontids). Gnathostomes bite with an essentially dorso-ventral motion bringing the lower jaw into occlusion with the upper surface of the mouth (Text-fig. 6.19C). Jarvik (1980) divides 'agnathan' bites into the myxinoid and petromyzontid condition. In the former, the lingual apparatus functions with a bilateral closure, whilst in the latter the 'bite' is controlled by the longitudinal and transverse lamina which function in a lateral and ventro-dorsal sense (Text-fig. 6.19A and B). Jarvik (1980) has argued that osteostracans bit in a homologous way with the petromyzontids whilst the heterostracans functioned in the same way as the myxinoids. Janvier (1981) has also proposed homology between heterostracan and myxinoid bites. It seems that conodonts bit, in general terms, in a similar sense to the petromyzontids, although there is variation in the functional

models presented for ozarkodinid and panderodontid conodont apparatuses, and this may reflect ecological control (See Chapter 4).
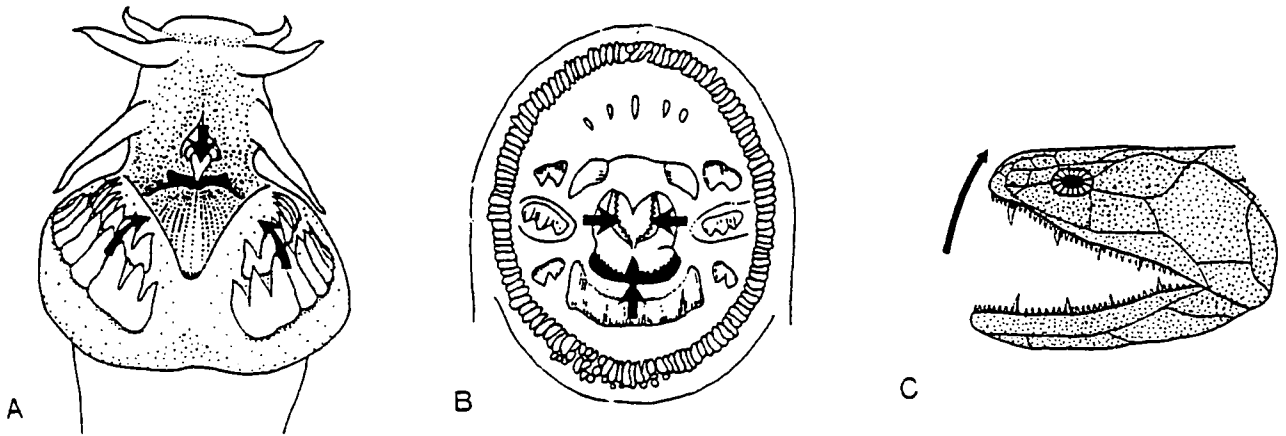
TEXT-FIG. 6.19. The bites of vertebrates: A) Bite style in the hagfish, a "prey's eye view" of the lingual apparatus of *Myxine* (Traced from Krejsa *et al.* 1991, figure 4); B) Bite style in the lampreys, an anterior view of the oral region of *Lampetra* (Modified from Jarvik 1980, fig. 341); C) Bite style in the gnathostomes, a lateral view of the skull of *Eusthenopteron* (Taken from Jarvik 1980, fig. 341). Arrows indicate biting, rasping and grabbing directions.

One paired Branchial opening:

The presence of a single paired branchial opening in heterostracans has been recognised as a diagnostic feature since their first description by Lankester (1869). Subsequent workers have included *Astraspis* and *Eriptychius* in this clade, despite the presence of eight branchial plates in the former (Elliott 1987) and the possibility of numerous openings in the latter (Elliott *et al.* 1991). These authors exclude *Astraspis* and *Eriptychius* from the heterostracans principally on the absence of a linked branchial opening. The nature of the branchial openings in conodonts has yet to be established.

Slanted Gill Openings:

Forey (1984) and Blieck (1992) have used the presence of slanted gill openings as a synapomorphy linking the petromyzontids, anaspids and the galeaspids.

Nerves IX and X issuing from braincase:

The cranial IX glossopharyngeal and X vagus nerves have functional components in somatic and visceral sense perception and the visceral motor (Walker 1987). They are only known to issue from the braincase in the osteostracans and the gnathostomes (Forey 1984).
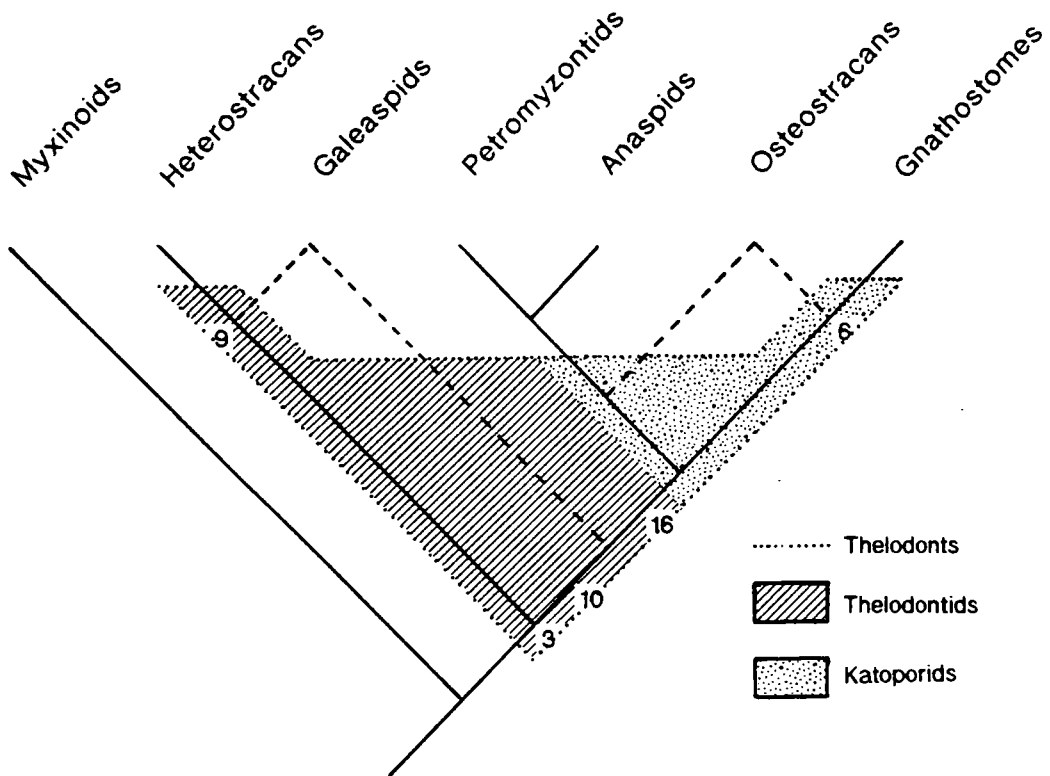
TEXT-FIG. 6.20. Cladogram showing the phylogenetic interrelationships of the craniates presented by Janvier (1981, figure 16). Numbers indicate the stated distribution of the character states utilitised in this study (Text-fig. 6.17).

6.5 RESULTS AND DISCUSSION

Few other vertebrate palaeontologists have accepted conodonts as true chordates or craniates, and they are absent from the cladograms presented by Janvier (1981, Text-fig. 6.20), Halstead (1982, Text-fig. 6.21), Forey (1984, Text-fig. 6.22)

and Maisey (1988, Text-fig. 6.23). However, the evidence furnished by the soft-bodied conodont specimens from Granton (see earlier) has merited their inclusion in more recent cladograms (Aldridge *et al.* 1986, Text-fig. 6.24; Gans 1987, Text-fig. 6.25; Blieck 1992, Text-fig. 6.26); these are compared with the new cladograms below. Although these have been produced on the basis of a limited data set, the relationships of the non-conodont taxa agree closely with those presented in previous studies, confirming the cogency of the methodology employed here.
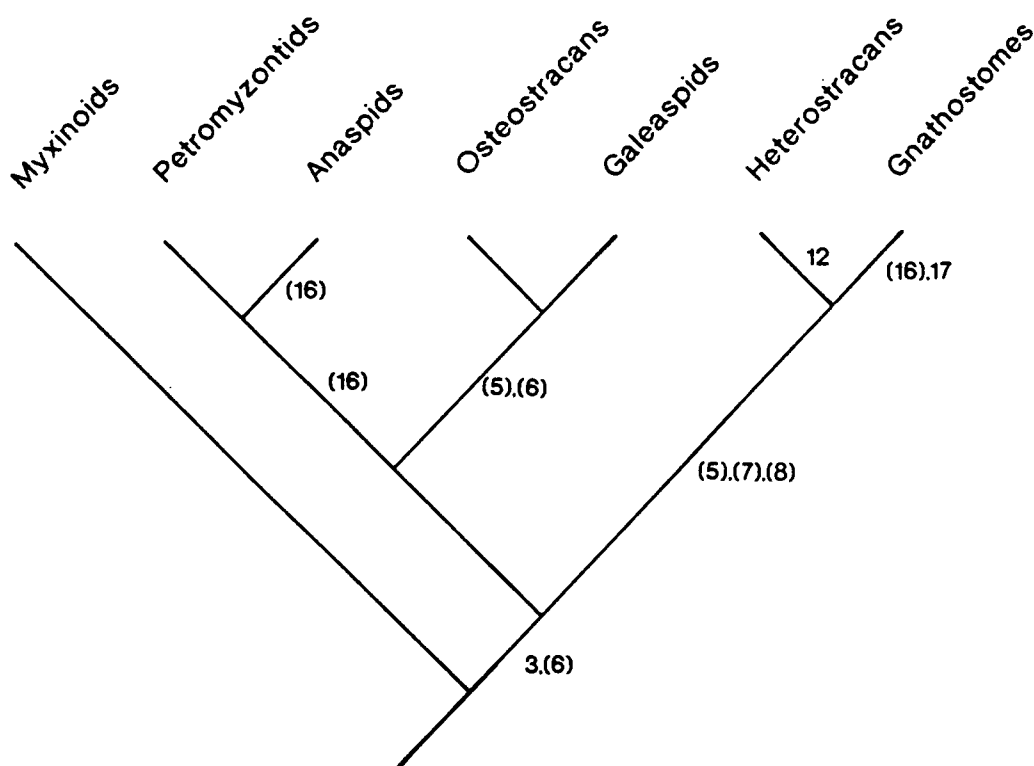
TEXT-FIG. 6.21. Cladogram showing the phylogenetic interrelationships of the craniates presented by Halstead (1982, fig. 3). Numbers indicate the stated distribution of the character states utilised in this study (Text-fig. 6.17), whilst those which are bracketed indicate multiple or ambiguous appearances and disappearances.
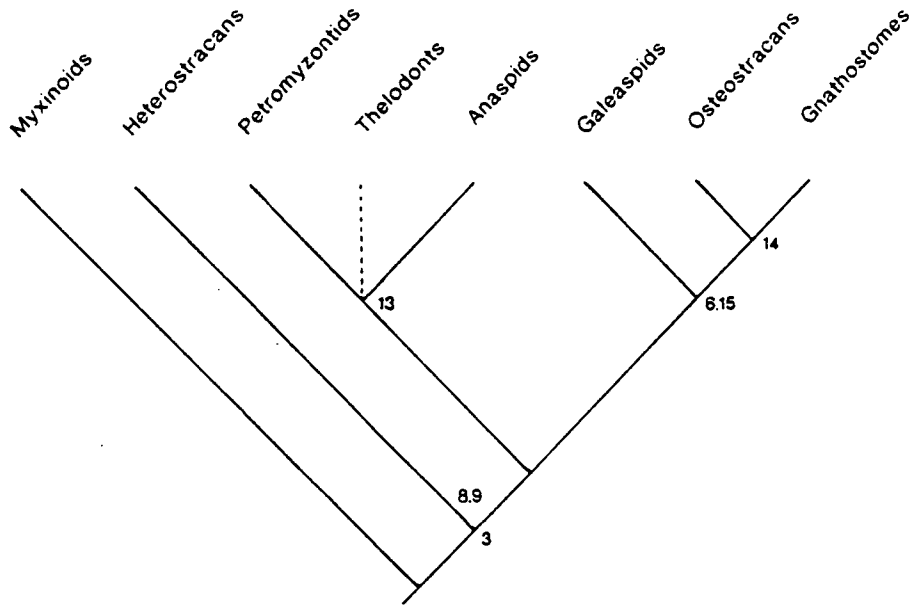
TEXT-FIG. 6.22. Cladogram showing the phylogenetic interrelationships of the craniates presented by Forey (1984, figure 5). Numbers indicate the stated distribution of the character states utilised in this study (Text-fig. 6.17).
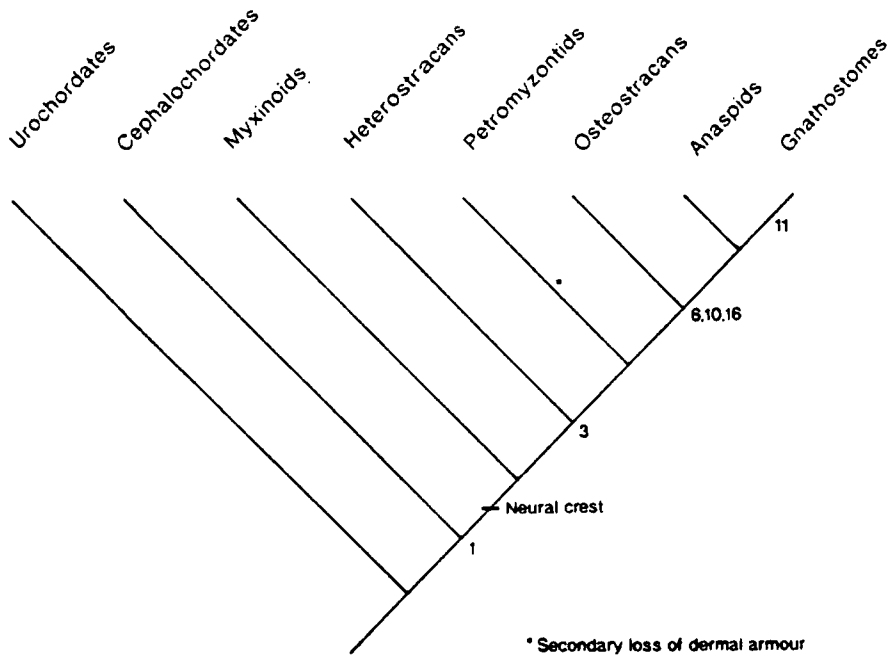
TEXT-FIG. 6.23. Cladogram showing the phylogenetic interrelationships of the chordates presented by Maisey (1988, figs 1-3). Numbers indicate the stated distribution of the character states utilised in this study (Text-fig. 6.17).
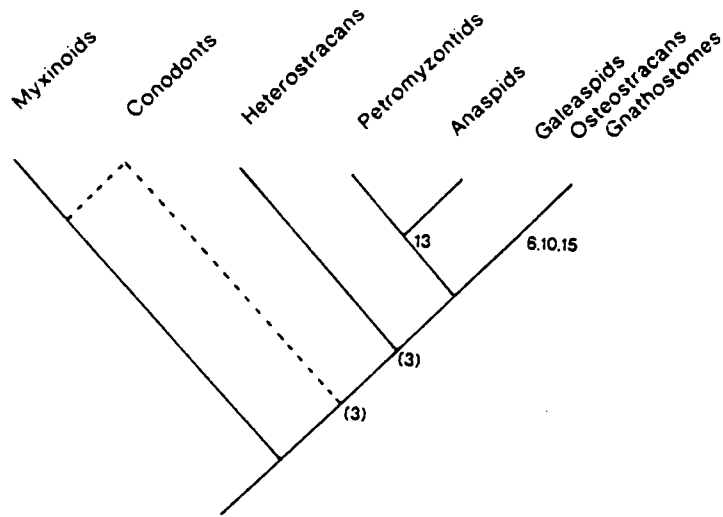
TEXT-FIG. 6.24. Cladogram showing the phylogenetic interrelationships of the craniates presented by Aldridge *et al.* (1986, fig. 9). The dashed lines indicate two possible positions for the conodonts based upon possible homology between conodont feeding apparatuses and the lingual apparatus of myxinoids, or homology between the dermal armour of heterostracans and conodont elements. Number indicate the stated distribution of the character states utilised in this study (Text-fig. 6.17), whilst those which are bracketed indicate ambiguous appearances and disappearances.
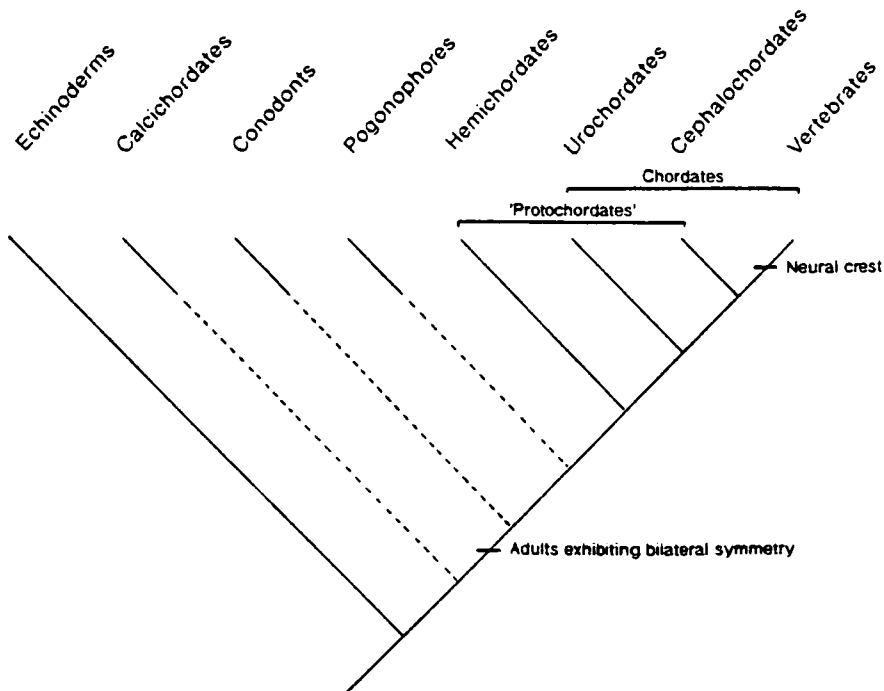
TEXT-FIG. 6.25. Cladogram showing the phylogenetic interrelationships of the deuterostomes presented by Gans (1989, fig. 1). Gans tentatively included conodonts within this cladogram between calcichordates and pogonophores with the acquisition of bilateral symmetry in adults.
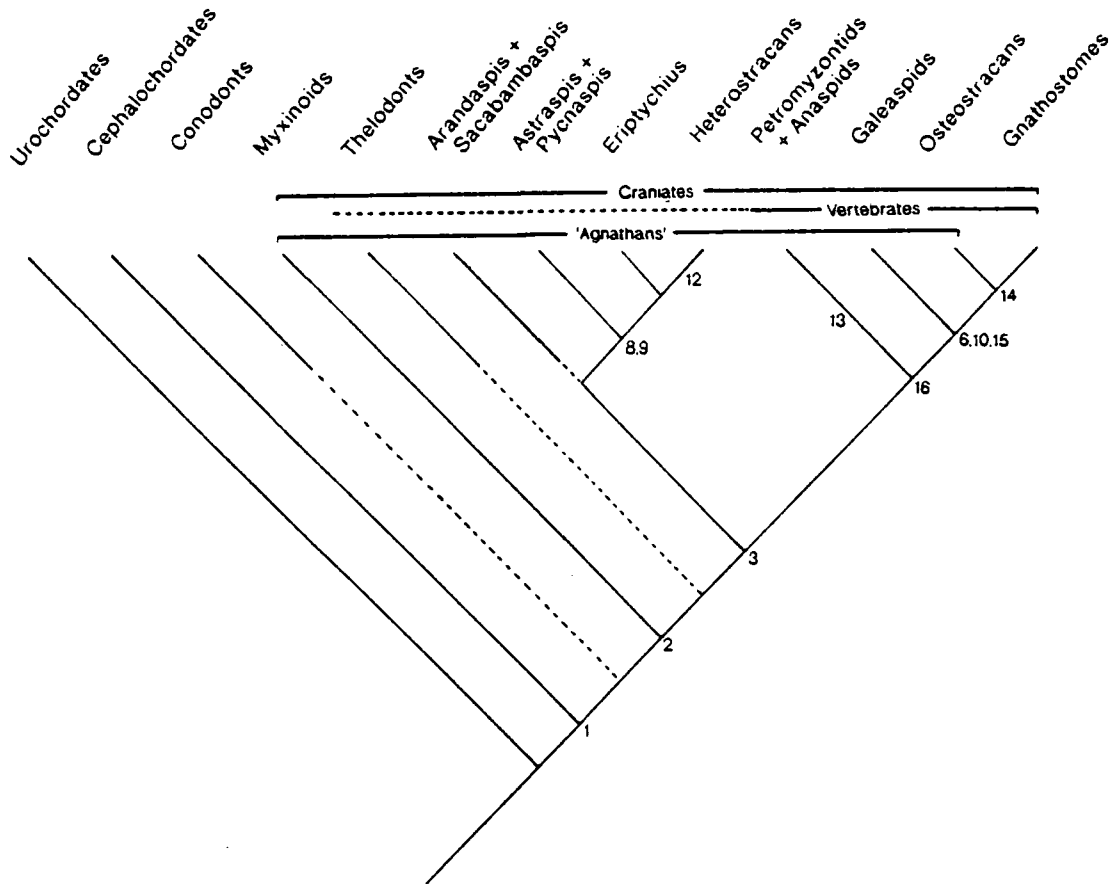
TEXT-FIG. 6.26. Cladogram showing the phylogenetic interrelationships of the chordates presented by Blieck (1992, figure 6). Blieck tentatively placed the conodonts between the cephalochordates and the myxinoids if the presence of somites in conodonts could be substantiated. Numbers indicate the states distribution of the character states utilised in this study (Text-fig. 6.17).

Cladogram A (Text-fig. 6.27), with a Consistency Index[2] (MacClade) of 0.88, places the urochordates and cephalochordates as sister groups to the craniates [myxinoids + conodonts + petromyzontids + 3rd unnamed vertebrate + osteostracans + gnathostomes + *Astraspis* + heterostracans + *Eriptychius*] which are united by the

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[2] The Consistency Index (C.I) is calculated as the minimum conceivable number of steps divided by the observed number of steps. If the characters in the data set are perfectly congruent with each other and the tree then the observed number of steps will equal the minimum, and the C.I. will be 1.00. As the data decreases in congruence the C.I. shrinks (Maddison and Maddison 1987).
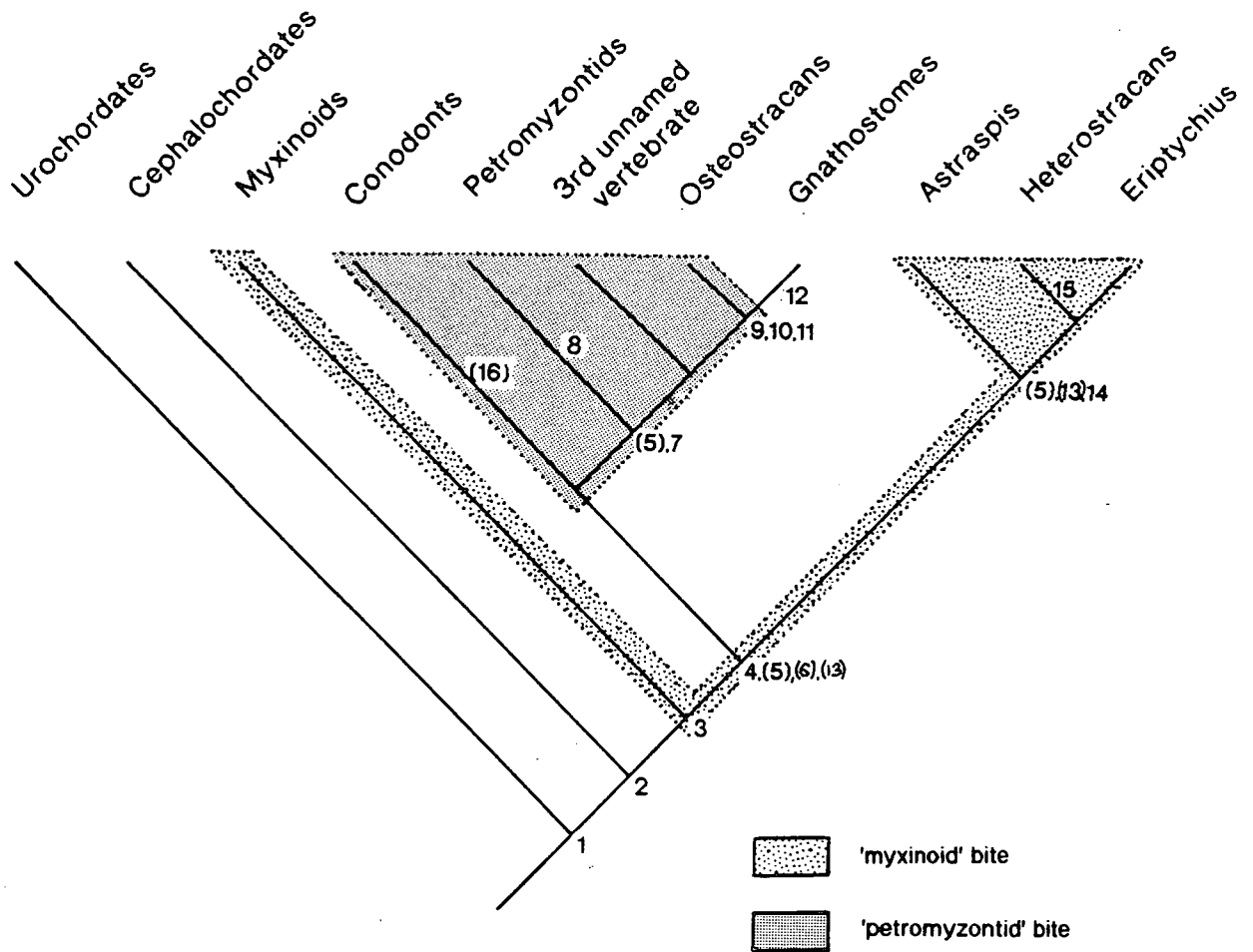
TEXT-FIG. 6.27. Cladogram A (MacClade Consistency Index 0.88) based upon the character states (Text-fig. 6.17) and data matrix (Text-fig. 6.18) utilised in this study. This cladogram has taken into account all of the characters, including the form of bilateral bite (shading). **1.** Basic chordate features such as notochord, mesoderm and neuroectoderm. **2.** Somites. **3.** Cartilaginous endoskeleton. **4.** Dermal ossification. **5.** Dentine. **6.** Cellular bone. **7.** Paired fins. **8.** Secondary loss of dermal skeleton and paired fins, acquisition of slanted gills. **9.** Heterocercal tail. **10.** Perichondral bone. **11.** Nerves IX and X issuing from braincase. **12.** Endochondral bone. **13.** Acellular bone and Aspidin. **14.** Honeycombed middle layer. **15.** Single branchial opening. **16.** Secondary loss of dentine. Numbers in brackets indicate ambiguous appearances and disappearances.

presence of a cartilaginous endoskeleton (Character 3). The myxinoids form a sister group to the ossified craniates as they lack dermal armour (Character 4). The ossified craniates are further divided into the 'heterostracomorphs' (*sensu* Blieck 1992, and

comprising [*Astraspis* + hetereostracans + *Eriptychius*]) and a crown group consisting of [conodonts + petromyzontids + 3rd unnamed vertebrate + osteostracans + gnathostomes] on the basis of the presence of a honeycombed middle layer (14), acellular bone and aspidin (13) in the former, and cellular bone (6) in the latter. The heterostracomorphs are further divided by the presence of a single branchial opening (15) in the heterostracans. The conodonts form a sister group to the 'myopterygians', a term introduced by Janvier (1981), encompassing the [petromyzontids + 3rd unnamed vertebrate + osteostracans + gnathostomes] and these are differentiated by the absence of paired fins (7) in conodonts. The genesis of dentine (5) in this cladogram is problematic, implying that either dentine formed independently in two lineages, the heterostracomorphs and the myopterygians, or was acquired at the initial point of dermal ossification (4) and subsequently lost in conodonts. However, evidence from the fossil record questions both of these hypotheses. Conodonts are the oldest vertebrates with hard tissues, and the absence of dentine in their elements suggests that the association of enamel, cellular bone and calcified cartilage is a closer approximation to the primitive state.

Cladogram B (Text-fig. 6.28), although slightly less parsimonious (C.I. 0.84), offers a potential solution to this problem. In this case, conodonts form a sister group to the 'dentineous craniates' [myopterygians + heterostracomorphs] with the acquisition of dentine (5) in the latter group. In this scenario, the association of enamel, cellular bone and cartilage represents primitive dermal ossification. This observation is consistent with the testament of the fossil record. In Cladogram B, a myxinoid bite is reverted to by the heterostracans following the development of a petromyzontid bite in conodonts and stem dentineous craniates.

Cladogram B represents the scenario favoured by the author as it correlates with the relative timing of first appearances of vertebrate hard tissues in the fossil record. This phylogeny is in marked contrast to that proposed by Gans (1987), who placed conodonts as a sister group to a crown group consisting of [pogonophores + hemichordates + urochordates + cephalochordates + vertebrates] (Text-fig. 6.25). He

placed them above the calcichordates with the acquisition of bilateral symmetry in the adult forms and the presence of a closed circulatory system. They also differ from the cladogram presented by Blieck (1992) who relegated the conodonts to a lower position within chordate phylogeny, placing them as a sister group to the craniate crown group (Text-fig. 6.26), and tentatively within the chordates, if the presence of somites could be substantiated.
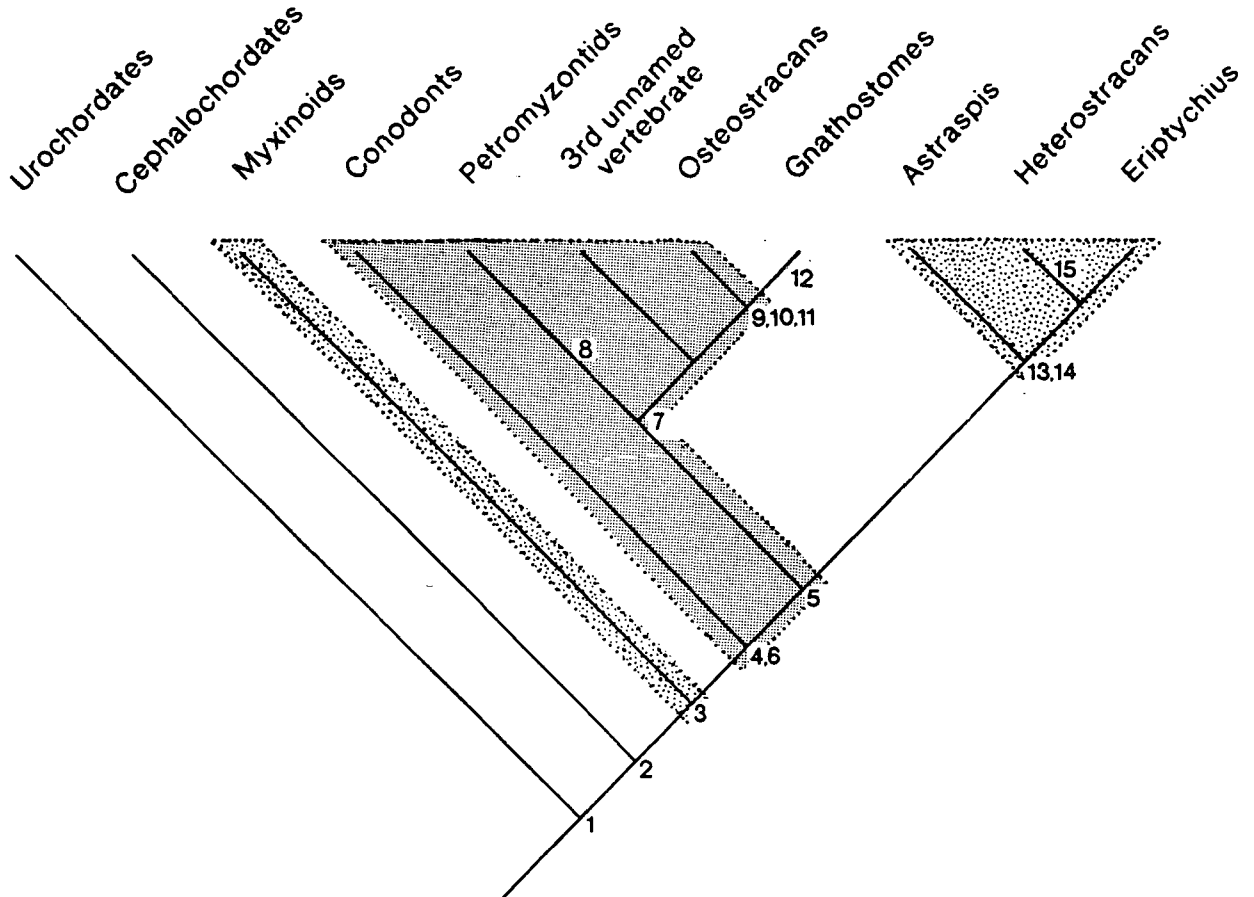
TEXT-FIG. 6.28. Cladogram B (MacClade Consistency Index 0.84) based upon the character states (Text-fig. 6.17) and data matrix (Text-fig. 6.18). This is the author's preferred solution as dentine (Character 5) has a single origination. This agrees with the data from the fossil record and avoids special pleading of the appearance of this tissue in different lineages. The shading refers to the distribution of inferred bite styles (see Text-fig. 6.27). 1. Basic chordate features such as notochord, mesoderm and neuroectoderm. 2. Somites. 3. Cartilaginous endoskeleton. 4. Dermal ossification. 5. Dentine. 6. Cellular bone. 7. Paired fins. 8. Secondary loss of dermal skeleton and paired fins, acquisition of slanted gills. 9. Heterocercal tail. 10. Perichondral bone. 11. Nerves IX and X issuing from braincase. 12. Endochondral bone. 13. Acellular bone and Aspidin. 14. Honeycombed middle layer. 15. Single branchial opening.

Cladogram B is topologically similar to that presented by Aldridge *et al.*
(1986) who linked the conodonts with either the myxinoids, on the basis of their
interpretation of the bite of the conodont apparatus, or as a sister group to what are
here termed the dentineous craniates on the basis of the development of
mineralisation potential in the dermal skeleton. In the cladogram of Aldridge *et al.*
(1986) cellular bone was identified as an advanced character state linking the
galeaspids, osteostracans and gnathostomes. As has been outlined above, conodont
elements are now known to possess cellular bone, a character which appears to be
primitive following this re-evaluation, and suggesting a closer evolutionary
relationship between conodonts and the myopterygians than the heterostracans.

The scenarios presented in Cladograms A and B have a number of important
implications for conodont palaeobiology and craniate development :

1) Since Horstadius (1950), the role of the neural crest has become
increasingly central to discussions of vertebrate development. The neural crest is
formed as a pair of ridges of ectodermal cells developed along the neural tube as the
surrounding folds (Walker 1987); the neural crest provides an area of interaction
between the ectoderm and mesoderm leading to a cascade of processes involving the
resultant ectomesenchymal cells. Gans (1987), a major advocate of the importance of
the neural crest, maintains that "*all* of the shared-derived characteristics of vertebrates
are induced by or otherwise associated with tissues derived from the neural crest and
epidermal neural placodes" (Gans 1987, p. 361). The question as to whether
conodonts possessed a neural crest now needs to be addressed.

Smith and Hall (1990) have postulated that many of the vertebrate hard
tissues are directly derived from a population of ectomesenchymal cells produced
from the neural crest. Cellular bone in the endoskeleton of the trunk is derived from
the mesoderm, but Smith and Hall (1990) have proposed that cellular *dermal* bone is
a neural crest derivative, and that it is homologous with the bone of attachment in

extant vertebrates. Smith (1991) claimed that the osteocytes in the dermal scutes of the 3rd unnamed vertebrate from the Harding Sandstone represent neural crest-derived cells. Enamel, although an ectodermal product, is only formed following induction caused by the secretion of an ectomesenchymal-derived tissue, in modern forms this sequence is initiated with the formation of dentine (Shellis 1981; Smith and Hall 1990; Smith 1992). Cartilage of the pharyngial and visceral arches, within the wall of the pharynx, also forms after dermal ossification in extant vertebrates and in association with bone of attachment, this too has been identified as a neural crest derivative (Smith and Hall 1990). Halstead (1987) has suggested that the neural crest may give rise to a variety of dermal hard tissues dependent upon the relative depth of the population of secreting ectomesenchymal cells.

Conodont elements are formed of cellular bone, enamel and cartilage (Sansom *et al.* 1992; Chapter 5), and it is clear that they occur in the oral cavity of the conodont as a feeding apparatus. The presence of these specific vertebrate tissues in conodont 'teeth' suggests that they are homologous with oral odontodes in other vertebrates. If this is the case, then it is extremely likely that conodont elements are a result of the same developmental processes, and are, in fact, the oldest record of neural crest-derived tissues.

2) Although the nature of the superficial caps in various taxa has been plotted, it is evident that this is of little use in cladistic analysis. Enamel and enameloid occur in cellular bone-based forms [3rd unnamed vertebrate + osteostracans + gnathostomes] and acellular bone-bearing forms [*Astraspis* + *Eriptychius*]. The presence of enamel in Late Cambrian conodonts suggests that this is the primitive superficial covering, supporting Smith (1992) who proposed that enameloid is a result of a subsequent heterochronic shift in later forms.

3) The pattern of mosaics of individual tesserae in *Eriptychius* and *Astraspis* has been cited as primitive among vertebrates (Ørvig 1958, 1967; Denison 1967;

Halstead 1969, 1973, 1974). Ritchie and Gilbert-Tomlinson (1977) proposed that the larger macromeric plates of *Arandaspis* represents the primitive condition, with subsequent breakdown producing the mesomeric armour seen in later forms. Ørvig (1989) has argued that both are primary. In contrast, the earliest vertebrate dermal elements are now known to occur in highly specialised feeding apparatuses within conodont oral cavities (Sansom *et al.* 1992; Chapter 5).
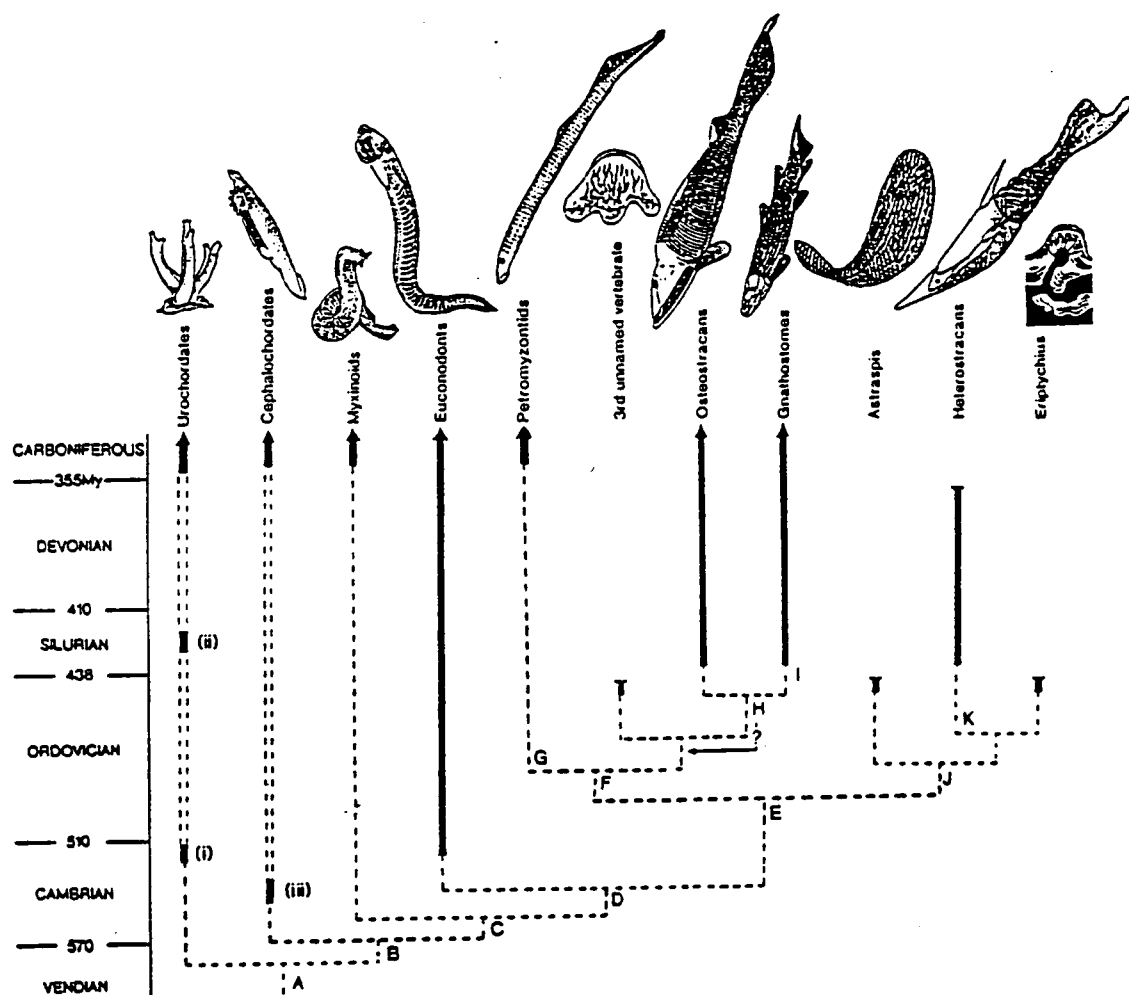
TEXT-FIG. 6.29. Revised phylogeny of the chordates, based upon Cladogram B, within a stratigraphic framework and showing appearances and disappearances during the Pre-Cambrian to Carboniferous. Capital letters refer to the nested hierachy presented in Table 6.1. i) *Palaeobotryllus* from Nevada, U.S.A.; ii) *Polycylindrichnus* from Ontario, Canada; iii) *Pikaia* from British Columbia, Canada. The 3rd unnamed vertebrate from the Harding Sandstone of Colorado may represent a stem group osteostracan. Radiochronologic ages taken from Cowie and Bassett (1989).

4) A resolution of hypotheses pertaining to morphological differentiation in the dermal skeleton is now close to hand. The main competing theories are the Lepidomorial Theory of Stensiö (1962), based upon increasing complexity of the unmineralised tissue; and the Odontode Regulation Theory of Reif (1982) which relies on dermal elements coalescing to produce more complex forms. It seems that the Lepidomorial Theory can offer no direct test in the fossil record (Reif 1982), as it relies upon changes in the secreting tissue which is unlikely to ever be detected. Odontode Regulation can, however, be tested in the fossil record. The recognition that conodont elements are probably homologous with odontodes provides the necessary database for such a test. If the fusion of simple cones to form more complex elements can be demonstrated in Late Cambrian conodonts then this would provide positive evidence for Odontode Regulation.

A revised phylogeny, with reference to the stratigraphic appearance of taxa dealt with here, is presented in Text-fig. 6.29, and based upon the nested hierachy presented in Table 6.1.

TABLE 6.1: Characters and the nested groups used in the postulated phylogenetic relationship in Text-fig. 6.29.

A: CHORDATES
- notochord
- perforated pharynx
- endostyle

B: SOMITIC CHORDATES
- somites

C: CRANIATES
- cartilagenous endoskeleton
- bilateral feeding apparatus

D: OSSIFIED CRANIATES
- dermal ossification
- cellular bone

E: DENTINEOUS CRANIATES
- dentine

F: 'MYOPTERYGIANS'
- paired fins

G: PETROMYZONTIDS
- slanted gills
- secondary loss of dermal armour
- secondary loss of paired fins

H: OSTEOSTRACANS AND GNATHOSTOMES
- perichondral bone
- heterocercal tail
- nerves IX and X issuing from braincase

I: GNATHOSTOMES
- endochondral bone
- jawed bite

J: 'HETEROSTRACOMORPHS'
- acellular bone
- aspidin
- honeycombed middle layer

K: HETEROSTRACANS
- single paired branchial opening

Chapter 7.

SYSTEMATIC PALAEONTOLOGY

7.1 GENERAL CONSIDERATIONS

This chapter represents an initial attempt at describing *Panderodus* species within the apparatus plan developed in Chapter 2. Gross element morphology and structure forms the basis of taxonomic division of conodont apparatuses, and this practice has also been followed in the definition of species in *Panderodus*. However, the rank of morphological variation which defines specific variation is entirely arbitrary. It can be foreseen that extended detailed studies of the subtle changes in morphology seen in these apparatuses may conclude that some of the 'species' described herein warrant only ecophenotypic status. Similarly, the question of dimorphism within conodonts has only been addressed by Jeppsson (1972), and such a process, either sexual or ontogenic, may be acting on the taxa discussed here.

Assessments of such problems can only be carried out with more data, probably beyond the scope of a single worker. To acquire these data, *Panderodus* needs to be considered within a stable taxonomic framework, and the preliminary observations made here represent a step towards this objective.

A major problem in the systematics of *Panderodus* is the inadequate nature of many previous authors descriptions and illustrations. There appears to have been a conscious or sub-conscious view of *Panderodus* as an unimportant part of conodont faunas, possibly stemming from it's 'poor' biostratigraphic utility. As a result, *Panderodus* apparatuses, if illustrated, are represented by a single view of one element, usually the **Pb**. This makes taxonomic assignment extremely problematic without reference to the original collections. With the recognition of seven distinct morphotypes, with the possibility of two further sub-divisions, it is hoped that the

genus will be more fully illustrated in future. This is especially relevant given the numerical abundance of *Panderodus* in many Late Ordovician - Silurian faunas and the pelagic mode of life adopted by this form (Barnes *et al.* 1973; Barnes and Fåhræus 1975; LeFèvre *et al.* 1976; Aldridge and Mabillard 1981).

The species range chart presented in Text-fig. 7.1. is based upon the synonymy lists compiled for each species. However, the reader is advised that this chart carries the *caveat* that many of these synonymies are questioned, and thus it may not reflect the true first and last appearances. Similarly the apparent radiations in the lower Caradoc and upper Ashgill may reflect taxonomic bias as these intervals have received concentrated attention from Barnes (1977), Sweet (1979), McCracken and Barnes (1981), Nowlan and Barnes (1981), and Nowlan *et al.* (1988).

As many of the holotype specimens that were unavailable during the period of research have not been studied, topotype material has been examined to supplement, and support taxonomic conclusions. Topotype material has also been selected to illustrate species where possible.

7.2 TERMINOLOGY

Many different notation schemes have been applied to *Panderodus* by previous authors. These are essentially divisible into those which are purely descriptive, such as that developed by Sweet (1979), and those which have implied homology between *Panderodus* elements and those borne by ramiform apparatuses (e.g. Barrick 1977) or other coniform apparatuses (e.g. Armstrong 1990). The revised scheme presented here is based upon Sweet and Schönlaub's (1975) notation, which is now widely applied to ramiform apparatuses (Sweet 1988). The graciliform elements in *Panderodus* are denoted by the new terms S_1 (asymmetrical graciliform), S_2 (sub-symmetrical graciliform), with an additional, abbreviated costate element
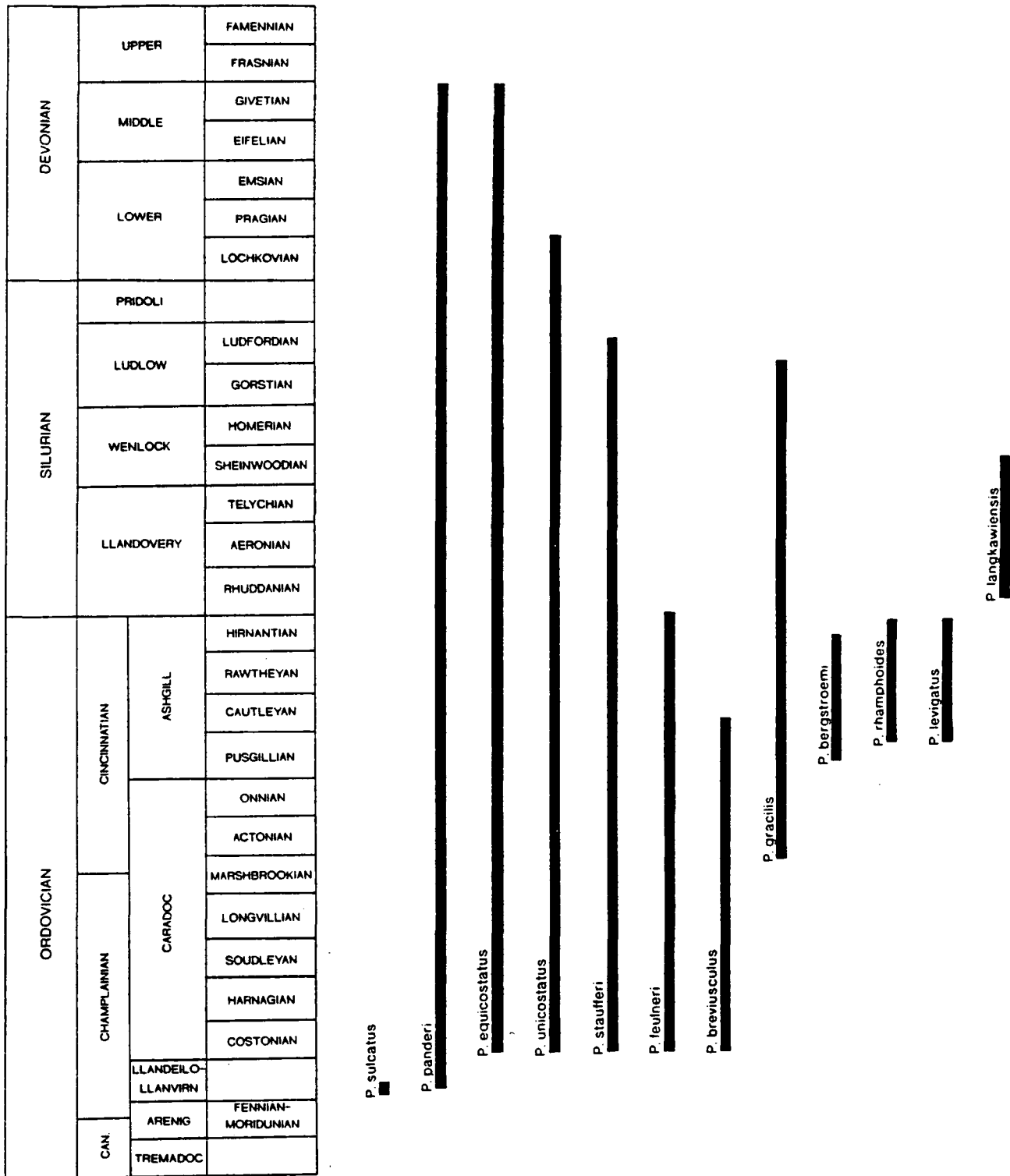
TEXT-FIG. 7.1. Range chart for the *Panderodus* species discussed in this work. This is based upon the synonymy lists complied herein. Stratigraphic divisions from Cowie and Bassett (1989).

described as **S₃**. I have used these terms as there is not yet sufficient evidence to apply the **Sb-Sd** notation of Sweet and Schönlaub (1975) in a notational sense, as it is

difficult to localised the graciliform elements within the clusters and bedding plane assemblage described in Chapter 2. These divisions may be somewhat artificial, as S_1 and S_2 elements with 'high' and 'low' basal margins occur in some apparatuses, and these differ only in the positioning of the lateral costae. The significance of costae distribution as against high and low bases needs to be assessed by dismembering clusters and deducing the relative position of these elements in an individual apparatus.

Descriptive terminology largely follows Clark (1981), and is illustrated in Text-fig. 7.2. One departure from Clark is the identification of the convex margin as dorsal and the concave margin as ventral, rather than anterior and posterior. This is based upon the orientation of paired elements within coniform apparatuses and the animal proposed in Chapters 2 and 4.
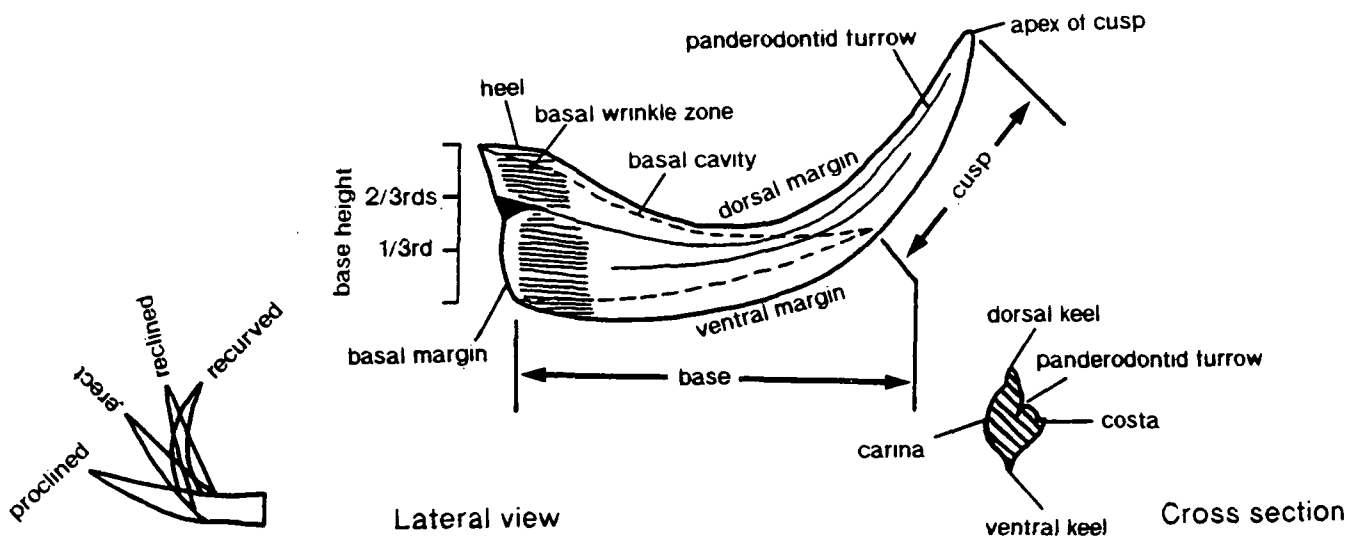
TEXT-FIG. 7.2. Orientation and terminology of *Panderodus* elements.

Synonymy lists have been annotated following Matthews (1973, after Richter 1948) and in the recommended style of the journal *Palaeontology* (see Instructions to authors, 1990, vol. 33, p. 993 - 1000).

Genus *Panderodus* Ethington, 1959

1959 *Panderodus* Ethington, p. 284.

1988 *Zanclodus* Nowlan and McCracken (in Nowlan *et al.*), p. 42-43.

Type species. Paltodus unicostatus Branson and Mehl, 1933, p. 42

Emended diagnosis. Septimembrate non-rastrate coniform apparatus consisting of paired **Pb, Pa, M, S₁, S₂, S₃** elements and a single **Sa** element. Deep furrow on the anterior lateral face of paired elements and both lateral faces of unpaired elements. The S_1 and S_2 elements can be further subdivided into two morphotypes within most apparatuses.

Remarks. The integrity of the genus *Panderodus* has been questioned by Nowlan and Barnes (1981) and Nowlan and McCracken (in Nowlan *et al.* 1988) on the basis of perceived differences in apparatus style. They divided *Panderodus* into three groups: Group I apparatuses being quinquemembrate; Group II panderodontids were trimembrate; and Group III apparatuses were bimembrate. However, the recognition of a septimembrate apparatus appears largely to unify the structure of *Panderodus* species, and I have been able to incorporate many of Nowlan and McCracken's 'species' within this revised species concept, thus avoiding their proposed division of the genus.

Nowlan and McCracken (in Nowlan *et al.* 1988) also introduced a new genus, *Zanclodus*. In the diagnosis of this genus the presence of elements which were bowed towards and away from the furrowed face was stressed. If this is accepted, then many populations of *P. panderi* would have to be transferred to *Zanclodus* on this basis alone. The known apparatus structure of *Zanclodus* is homologous with that seen in *Panderodus,* and it cannot be sustained as a separate genus.

Serrate M elements occur in two species, and these have previously been described as *Panderodus unicostatus serratus* Rexroad, 1967. Such elements appear to have sporadic and repeated occurrence, which seems to be temporally constrained. Unfortunately, the collections studied are not extensive enough to assess the palaeogeographic occurrence of serrate M elements, and as such I have been unable to determine as to whether their appearance is an example of iteration, or the sporadic expansion of refugia populations. It is also noted that serration appears in *Panderodus equicostatus* and *Panderodus unicostatus*, two species which appear to be closely related.

Species of *Panderodus* can now be recognised on the basis of element morphology, white matter distribution and the relative length of the cusp to the base. S_1 and S_2 elements are, generally, very difficult to differentiate as they appear to form a morphologically conservative group within many apparatuses. As a result their assignment has been questioned in the synonymy lists unless additional components of the apparatus are illustrated.

Range. Llanvirn: *E. suecicus* biozone (*P. sulcatus* subzone) - » Givetian: upper *varcus* biozone zone.

-»

TEXT-FIG. 7.3. Elements and apparatuses of the *Panderodus* species encountered during this study, showing the development of the basal cavity (dashed line) and white matter (shaded). Pa elements on the left, followed by Pb, Sa, S_3, S_2, S_1 and M elements, if present. The internal details of *P. sulcatus* are not known, and the *P. breviusculus* apparatus has not yet been fully reconstructed. All approximately x 30, except *P. sulcatus* x 60.
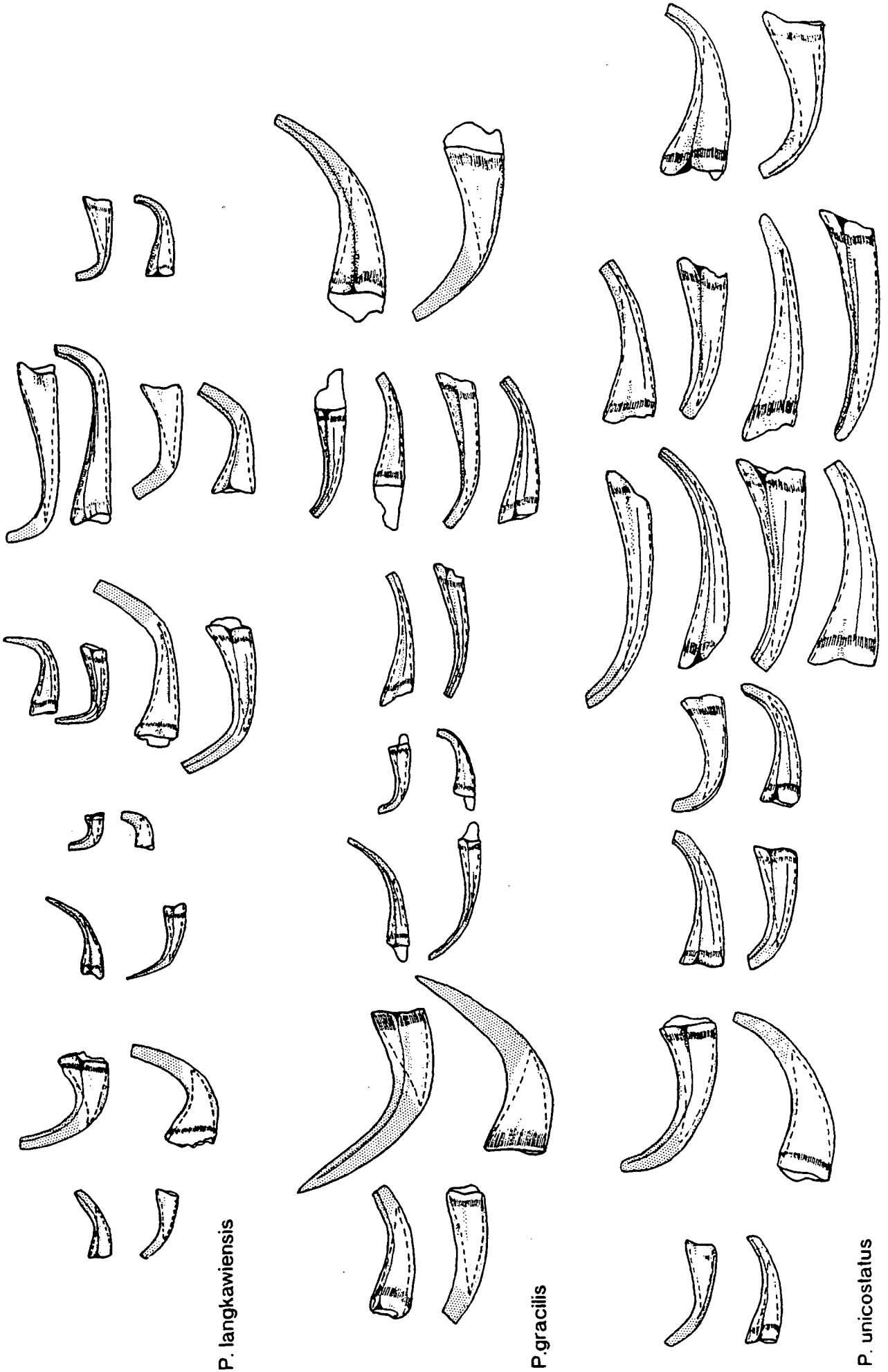
P. langkawiensis

P.gracilis

P. unicoslatus
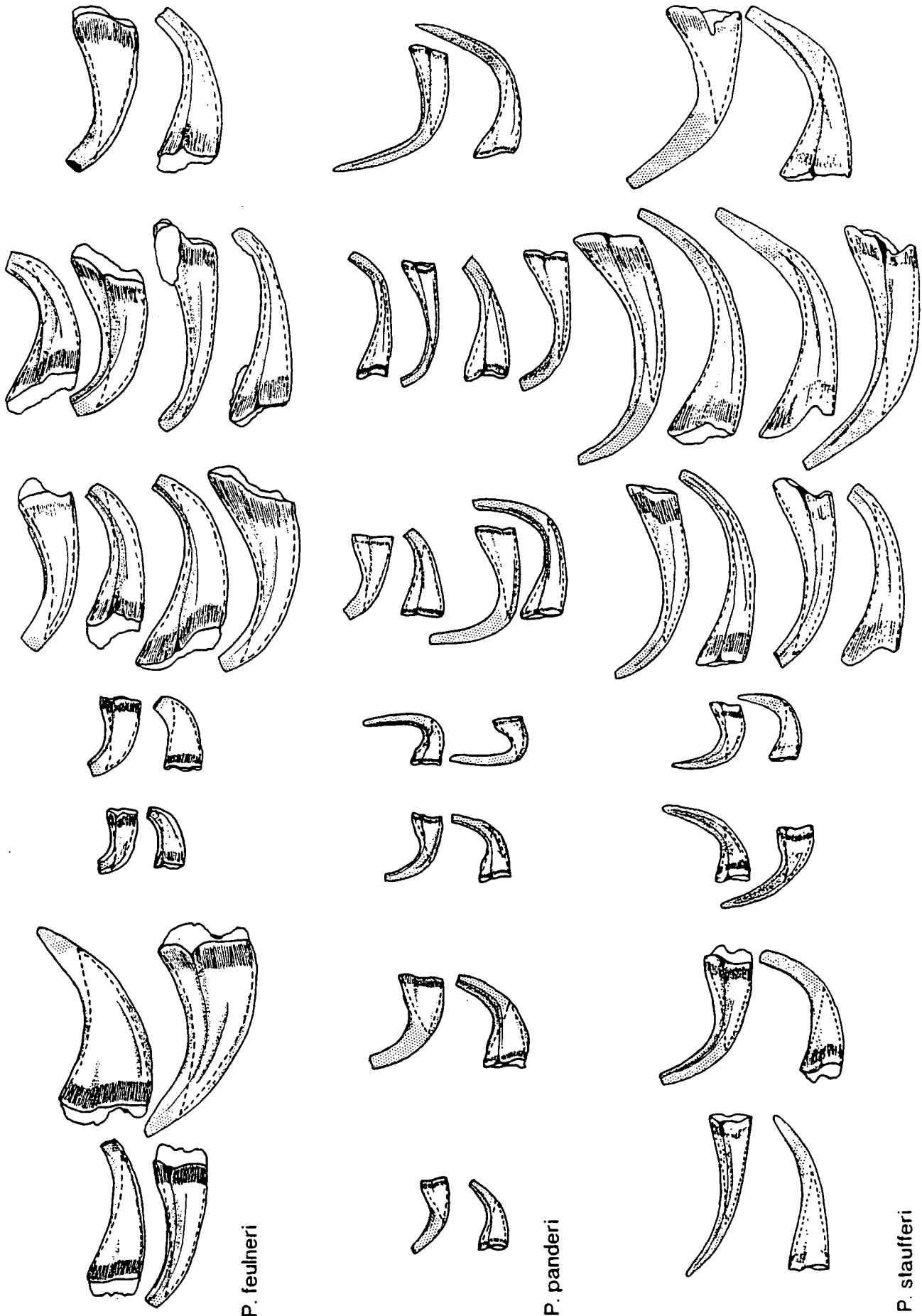
P. feulneri

P. panderi

P. staufferi
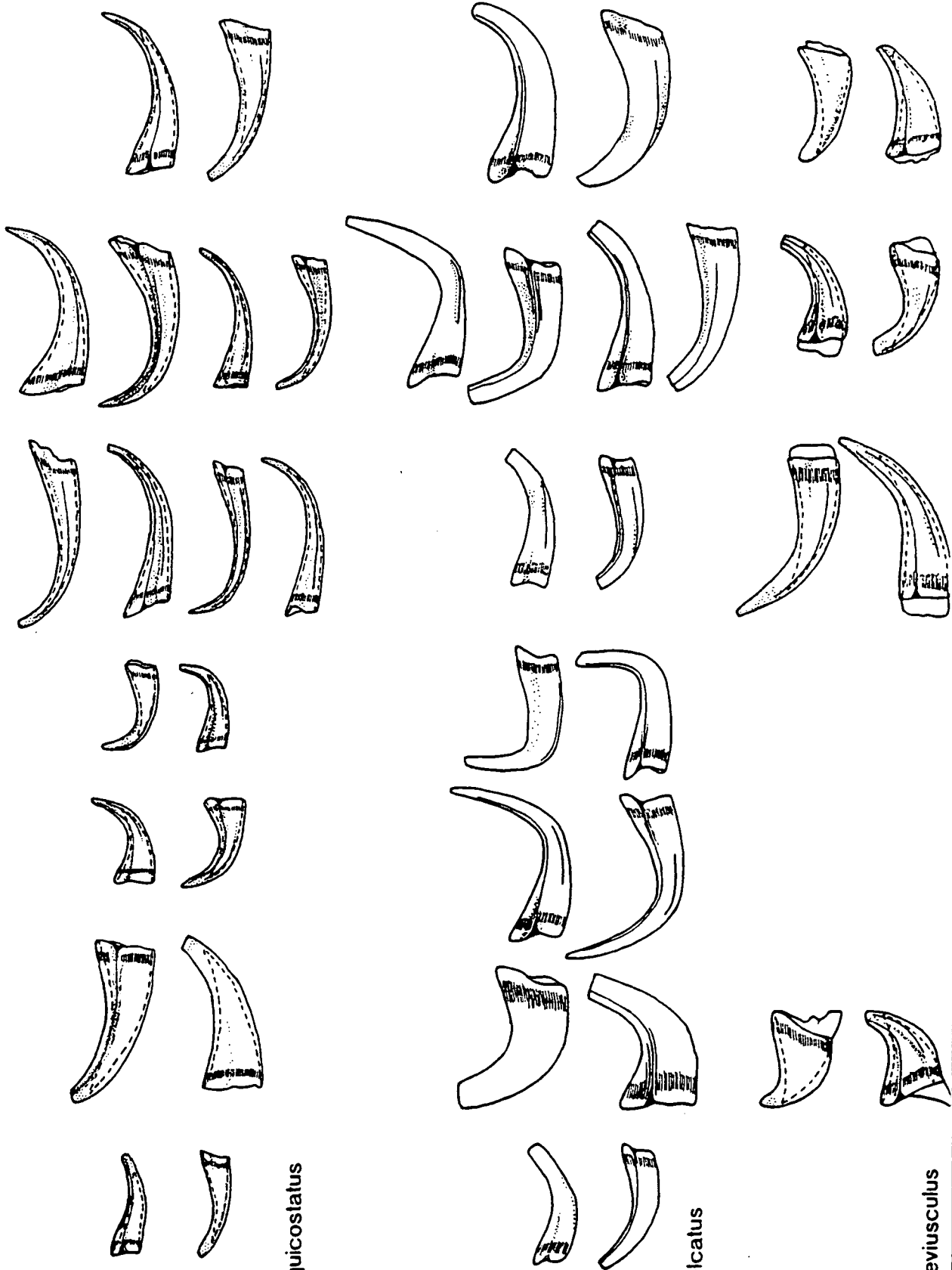
P. equicostatus

P. sulcatus

P. breviusculus

Panderodus bergstromi Sweet, 1979

* 1979   *Panderodus bergstromi* Sweet, p. 63, fig. 7 (7, 9, 15-16, 20).

?1988   *Panderodus* aff. *P. bergstromi* Sweet; Nowlan and McCracken (in Nowlan *et al.*), p. 20, pl. 6, figs 1-5.

Holotype. Panderodus bergstromi Sweet 1979, p. 63, fig. 7 (7, 9, 15-16, 20), five syntypes from the Bighorn Group, Florida Mountains, New Mexico, U.S.A..

Diagnosis. Refer to Sweet (1979, p. 63).

Description. Pa element. Described by Sweet's (1979, p. 63) as a tortiform element.

Pb element. Described by Sweet (1979, p. 63) as a falciform element.

M element. Described by Sweet (1979, p. 63) as an arcuatiform element.

S_1 *element.* Described by Sweet (1979, p. 63) as an asimiliform element.

S_2 *element.* Described by Sweet (1979, p. 63) as a similiform element

Remarks. As diagnosed by Sweet (1979) this apparatus was considered to consist of five element morphotypes, M, S_1, S_2, Pa, and Pb.

A shorter and more tightly recurved element was figured by Nowlan and McCracken (in Nowlan *et al.* 1988; pl. 6, figs 1-2) as a 'c' element of *Panderodus* aff. *P. bergstromi.* This element is homologous with S_3 elements in other apparatuses. The 'b' element figured by Nowlan and McCracken (in Nowlan *et al.* 1988; pl. 6, figs 3-5) is a costate Pb element. The robust nature of these elements (only seven are recorded) possibly represents geronitic or ecophenotypic variation within *P. bergstromi.*

Sweet (1988) mentions the presence of tru ly symmetrical elements "in the large collections [of *Panderodus*] on which [he] based [his] 1979 reconstructions" (p. 57). It seems likely that *P. bergstromi* is closely related to *Parabelodina*

denticulata (Sweet, 1979, p. 63), although the presence of well-developed denticles in the latter form places ᵢₜ‸outside the generic concept adopted here.

Range. lower-middle Pusgillian: lower *O. robustus* biozone - » lower Hirnantian: middle *A. divergens* biozone.

Panderodus breviusculus **Barnes, 1977**

Plate 17, figs 19-26; Text-fig. 7.3

* 1977   *Panderodus breviusculus* Barnes [*partim*], p. 106, pl. 3, figs 15-17.

non   1977   *Panderodus breviusculus* Barnes [*partim*], pl. 3, figs 13-14 [= ? *P. feulneri*].

          1979   *Panderodus breviusculus* Barnes; Sweet [*partim*], p. 63-64, fig. 7 (25, 36).

non   1979   *Panderodus breviusculus* Barnes; Sweet [*partim*], p. 63-64, fig.7 (24, 31, 35) [= ? *P. feulneri*].

Holotype. *Panderodus breviusculus* Barnes 1977, p. 106, pl. 3, fig. 16, from the Bad Cache Rapids Formation, Melville Peninsula, Southeastern District of Franklin, Canada.

Diagnosis. Refer to Barnes (1977, p. 106).

Description. **Pb element.** Refer to Barnes's (1977, p. 106) description of the type material.

    M element. Short squat cone with excavated unfurrowed face. Strong rounded carina on furrowed face and bold costa along convex margin of unfurrowed face. Extremely short proclined cusp.

    ? S₂ element. Transversely rounded cone with a comparatively elongate erect cusp. Costae run along both lateral faces at one-third base height, from the basal wrinkle zone and die out towards the apex of the cusp. Weak carinae are developed up to two-thirds base height on both lateral faces.

? S_1/S_3 element. Squat, transversely rounded cone with erect cusp. Unfurrowed face is excavated above a prominent costa which is located at one-quarter base height. Opposite face is prominently carinate up to the furrow at two-thirds base height, a weak costa is developed medially along this carina at one-third base height.

Remarks. Barnes (1977) figured additional elements in association with the **Pb** element of *P. breviusculus,* although he did not describe them (pl. 3, figs 13-14). Similar elements in the Ph.D. collections of Tull (1988) from the Morris Bugt Group of North Greenland, appear to be closer in form to the S_3 elements of *P. feulneri* than those of *P. breviusculus.* Sweet (1979) reconstructed *P. breviusculus* as a quinquemembrate apparatus, including elements which I have questionably placed in the *P. feulneri* apparatus (see synonymy lists).

P. breviusculus has not yet been reconstructed as a septimembrate apparatus, and the elements described above are only tentatively assigned to locations. The morphology of these elements is such that there is little doubt that this is a typical *Panderodus* species. It is predicted that the additional members of the apparatus will be identified when larger collections of this rare species are studied.

Range. Costonian: *A. tvaerensis* biozone (? *B. gerdae* subzone) -» Cautleyan: *O. robustus* biozone.

Panderodus equicostatus (Rhodes, 1953)

Plate 13, figs 1-18; Text-fig. 7.3

?1947 *Paltodus acostatus* Branson and Branson, p. 554, pl. 82, figs 1-5, 23-24.

?1947 *Paltodus unicostatus* Branson and Mehl; Branson and Branson [*partim*], p. 554, pl. 82, figs 7, 11-16.

v 1953 *Paltodus acostatus* Branson and Branson; Rhodes, p. 296-7, pl. 21, figs 111-112.

v*1953 *Paltodus equicostatus* Rhodes, p. 297, pl. 21, figs 106-109.

v 1953   *Paltodus unicostatus* Branson and Mehl; Rhodes, p. 298, pl. 21, figs 84-88.

non   v 1953   *Paltodus equicostatus* Rhodes, p. 297, pl. 22, figs 162, 165 [= *Panderodus unicostatus*]

1959   *Panderodus gracilis* (Branson and Mehl); Sweet, Turco, Warner and Wilkie, p. 1056, pl. 131, fig. 1.

1959   *Panderodus unicostatus* (Branson and Mehl); Sweet, Turco, Warner and Wilkie, p. 1057, pl. 131, fig. 3.

?1966 *Panderodus simplex* (Branson and Mehl); Clark and Ethington, p. 682 - 3, pl. 82, figs 10, 14.

?1966 *Panderodus unicostatus* (Branson and Mehl); Clark and Ethington [*partim*], p. 683, pl. 82, fig. 17.

1967   *Panderodus simplex* (Branson and Mehl); Rexroad, p. 45, pl. 4, figs 7-8.

1967   *Panderodus* cf. *P. unicostatus* (Branson and Mehl); Rexroad, p. 46, pl. 4, figs 5-6.

1967   *Panderodus unicostatus unicostatus* (Branson and Mehl); Rexroad, p. 46, pl. 4, figs 1-2.

1967   *Panderodus unicostatus serratus* Rexroad n. subsp., p. 47, pl. 4, figs 3-4.

1970   *Panderodus simplex* (Branson and Mehl); Pollock, Rexroad and Nicoll [*partim*], p. 758, pl. 114, figs 23-24.

1970   *Panderodus unicostatus unicostatus* (Branson and Mehl); Pollock, Rexroad and Nicoll [*partim*], p. 758, pl. 114, figs 26.

?1970 *Panderodus unicostatus unicostatus* (Branson and Mehl); Pollock, Rexroad and Nicoll [*partim*], p. 758, pl. 114, figs 27-28.

?1971 *Panderodus compressus* (Branson and Mehl); Fåhræus, p. 677, pl. 79, figs 19-20.

?1971 *Panderodus gracilis* (Branson and Mehl); Fåhræus, p. 677, pl. 79, figs 21-22.

?1971 *Panderodus simplex* (Branson and Mehl); Rexroad and Craig [*partim*], p. 696-7, pl. 81, figs 39-40.

?1972 *Panderodus serratus* Rexroad; Aldridge, p. 204, pl. 9 fig. 204.

?1972 *Panderodus simplex* (Branson and Mehl); Aldridge, p. 204-5, pl. 9, figs 8-9.

?1972 *Panderodus unicostatus* (Branson and Mehl); Aldridge, p. 205-6, pl. 9, figs 5-6.

?1972 *Panderodus unicostatus unicostatus* (Branson and Mehl); Rexroad and Nicoll, pl. 1, figs 46-47.

?1972 *Panderodus gracilis* (Branson and Mehl); Rexroad and Nicoll, pl. 1, figs 50-51.

?1972 *Panderodus simplex* (Branson and Mehl); Rexroad and Nicoll, pl. 1, figs 52-53.

?1972 *Panderodus unicostatus* n. subsp. (Branson and Mehl); Rexroad and Nicoll, p. 68, pl. 2, fig. 38.

?1972 *Panderodus unicostatus serratus* Rexroad; Rexroad and Nicoll, pl. 2, fig. 40.

?1974 *Panderodus gracilis* (Branson and Mehl); Uyeno, p. 15, pl. 3, figs 8-9, 11-14.

1975   *Panderodus* sp. cf. *P. serratus* Rexroad; Cooper, p. 994-5, pl. 1, figs 2-6.

1975 *Panderodus serratus* Rexroad; Cooper, p. 993-4, pl. 1, figs 3-5, 7-9, 13-14, 23.

1975 *Acodus unicostatus* Pander; Saladzhius [*partim*], pl. 1, fig. 3.

1975 *Panderodus simplex* (Branson and Mehl); Saladzhius, pl. 2, figs 3-4.

1975 *Panderodus unicostatus unicostatus* (Branson and Mehl); Saladzhius, pl. 2, figs 5-6.

?1976 *Panderodus unicostatus* (Branson and Mehl); Cooper, p. 213-4, pl. 1, figs 1-6.

1978 *Panderodus unicostatus* (Branson and Mehl); Miller, pl. 1, figs 1-3

1978 *Panderodus simplex* (Branson and Mehl); Miller, pl. 1, figs 4-5.

1978 *Panderodus gracilis* (Branson and Mehl); Miller [*partim*], pl. 1, fig. 7

?1980 *Panderodus serratus* Rexroad; Helfrich, pl. 2, figs 12-14.

?1980 *Panderodus gracilis* (Branson and Mehl); Orchard [*partim*], p. 23, pl. 3, figs 10-11, 14-15, 19, 22-23, 26.

?1983 *Panderodus* sp. Sparling, fig. 12 AR, AS.

v 1985 *Panderodus* cf. *P. gracilis* (Branson and Mehl); Savage and Bassett, p. 708, pl. 80, figs 42-47.

?1987 *Panderodus unicostatus* (Branson and Mehl); Mawson, pl. 41, figs 12-13.

?1987 *Panderodus recurvatus* (Rhodes); Mawson, pl. 41, figs 14-15.

1989 *Panderodus* cf. *unicostatus* (Branson and Mehl); Sorentino, pl. 7, figs 11, 14, 17-18, 22.

?1989 *Panderodus unicostatus* (Branson and Mehl); Sorentino, pl. 7, figs 12-13, 15-16, 20.

1989 *Panderodus* sp. Sorentino, pl. 7, figs 19, 21.

?1989 *Panderodus unicostatus* (Branson and Mehl); Wilson, pl. 1, figs 17-22.

?1989 *Panderodus* sp. Wilson, pl. 1, figs 23-24.

?1989 *Panderodus unicostatus* (Branson and Mehl); Mawson and Talent, pl. 8, fig. 17.

?1989 *Panderodus* sp. Mawson and Talent, pl. 8, fig. 18.

?1989 *Coelocerodontus reduncus* Telford; Mawson and Talent, pl. 8, fig. 20 [kop. Mawson 1987, pl. 41, fig. 13].

v 1990 *Panderodus* aff. *P. unicostatus* (Branson and Mehl); Armstrong, p. 110, pl. 17, figs 8-13.

Holotype. *Paltodus equicostatus* Rhodes 1953, p. 297, pl. 21, figs 107, 109 from the Pen-y-Garnedd Limestone of North Wales, U.K.

Emended diagnosis. A species of *Panderodus* where all the elements, apart from the proclined **Pb** and **Pa** elements, have extremely short erect cusps (5-10 percent of the

element length). The basal cavity is deep, and expands gradually from the cusp to occupy nearly all of the basal area. Surface ornament is confined to a shallow set of basal wrinkles which are developed in the lower tenth of the elements, and the lateral costae. The furrow is extremely narrow, and the surrounding area is free from ornamentation.

Description. Pa element. Slender proclined cone, which is laterally torted away from the furrowed face. A raised keel is found on the dorsal margin, extending from the basal wrinkle zone to the cusp. A prominent carina on the unfurrowed face is extended into a sharp edge along the dorsal margin.

Pb element. Elongate and broad proclined sub-symmetrical cone, ventral and dorsal edges converge along a long base to form an abbreviated cusp. Prominent carinae are developed on both lateral faces, and are traceable from the basal margin mid-height to the cusp. A prominent keel on the ventral margin runs from the basal wrinkle zone to the cusp.

M element. Broad, markedly asymmetrical cone, which narrows rapidly away from the basal margin, and is terminated by a short erect cusp. The unfurrowed lateral face is strongly excavated towards the dorsal margin, and the element is progressively bowed away from the furrowed face; the angle of deflection sharply increases at the cusp/base interface. A prominent lateral costa is developed on the unfurrowed face at approximately one third base height; this extends from the basal wrinkle zone to the cusp. The furrowed face possesses a rounded carina which developed along the element mid-height. Occasionally, anextremely thin serrated keel is developed on the dorsal margin of this element.

Sa element. Short and squat cone. Truly symmetrical as furrows are developed on both lateral faces at two-thirds base height. Lateral faces have prominent costa developed at one-third base height; these extend from the basal wrinkle zone to the cusp.

S₁ element. The two element sub-types that occupy this position in *P. equicostatus* are readily divisible. One has a relatively high base, the dorsal margin tapers sharply to form a triangular base. The cusp is sharply flexed towards the vertical. A lateral costa is developed on the unfurrowed face at one-third base height. A carina is developed at two-thirds base height on the furrowed face, a weakly developed costa commonly forms a dorsal shoulder to this feature.

The other S_1 element has a relatively low base, both margins of which gradually taper, producing an elongate base. This passes into the cusp, which is sub-erect. Prominent carinae are found on both lateral faces, each is drawn into a costa, on the furrowed face this is found at one-third base height, whilst on the unfurrowed face a costa is found at two-thirds base height.

Both of these elements are markedly asymmetrical in the distribution of the lateral costae. In 'mature' specimens the differences in base height are pronounced. However, it is possible that the two morphs are end members of an intra-specific transition series.

S₂ element. Elongate bilaterally subsymmetrical cone. The base gradually tapers towards the cusp, which gently curves into an erect posture. Both lateral faces are carinate and costate; the carinae are developed in the lower two-thirds of the base height, whilst costae are found on the carinae extending from the basal wrinkle zone to the base/cusp flexure, at about one-third base height. The furrow is narrow, and is mirrored on the unfurrowed face by an indentation of the basal area, above the lateral carinae.

Commonly, up to 50 percent of the S_2 elements have a high, triangular, base and these may represent a sub-division within this morphology.

S₃ element. Short cone with erect and twisted cusp. The cusp is deflected away from the furrowed face, the unfurrowed face being strongly excavated around the dorsal margin where the cusp meets the base. The anterior margin of the unfurrowed face is drawn into a poorly defined edge. A weak costa is occasionally developed on the furrowed lateral face at one-third base height.

Remarks. Element morphology in this species shows gross similarities to that of *P. unicostatus*, and this has led many previous authors to describe elements of the former as *P. unicostatus*. They are readily separated on the lower curvature of the **Pb** element and the shorter, squat base of the **Sa** element in *P. equicostatus*. The other elements of these apparatuses are superficially similar, but those of *P. equicostatus* can be recognised as they have abbreviated cusps, and restricted white matter distribution within these cusps.

Occasionally, large collections yield serrate **M** elements (e.g. Rexroad 1967; pl. 4, figs 3-4) which co-occur with non-serrate forms. The taxonomic significance of this is unknown.

Jeppsson (1984, 1987) has described a cyclical distribution pattern where *P. equicostatus* and *P. unicostatus* have an antagonistic relationship through the Silurian of Götland section. Jeppsson has yet to quantify these observations, neither has he illustrated elements of either apparatus. It is possible that *P. equicostatus* and *P. unicostatus* are ecophenotypic variants.

The type suite of specimens have a conodont ColourAlteration Index of 5, and the holotype specimen is missing. The selection of a neotype awaits recollection of the type locality.

Range. Costonian: *A. tvaerensis* biozone (? *B. variabilis* subzone) -» Givetian: upper *varcus* biozone.

Panderodus feulneri **(Glenister, 1957)**

Plate 15, figs 19-24; Plate 16, figs 1-12; Text-fig. 7.3

* 1957 *Paltodus feulneri* Glenister, p. 728, pl. 85, fig. 11.

? 1957 *Paltodus gracilis* Branson and Mehl; Glenister [*partim*], p. 728, pl. 85, fig. 4.

1957 *Paltodus intermedius* Branson, Mehl and Branson; Glenister, p. 728 , pl. 85, fig. 10.

1959   *Panderodus intermedius* (Branson, Mehl and Branson); Stone and Furnish, p. 225-226, pl. 31, fig. 1.

1959   *Panderodus feulneri* (Glenister); Stone and Furnish, p. 225, pl. 31, fig. 3.

1959   *Panderodus feulneri* (Glenister); Ethington, p. 284-285, pl. 39, fig. 2.

1959   *Panderodus intermedius* (Branson, Mehl and Branson); Ethington, p. 285, pl. 39, fig. 3.

1966   *Panderodus feulneri* (Glenister); Winder, pl. 9, fig. 19.

1966   *Panderodus arcuatus* (Stauffer); Winder, p. 58-59, pl. 9, fig. 23.

? 1974   *Panderodus gracilis* (Branson and Mehl); Uyeno [*partim*], p. 15 pl. 3, fig. 10.

? 1977   *Panderodus feulneri* (Glenister); Barnes, p. 105, pl. 3, figs 11-12.

? 1977   *Panderodus breviusculus* Barnes [*partim*], pl. 3, figs 13-14.

1979   *Panderodus breviusculus* Barnes; Sweet [*partim*], p. 63-4, fig. 7(24, 31, 35).

1979   *Panderodus feulneri* (Glenister); Sweet [*partim*], p. 64, fig. 7(1, 11-13, 17-18).

non   1979   *Panderodus feulneri* (Glenister); Sweet, p. 64, fig. 7(8, 14).

non   1981   *Panderodus feulneri* (Glenister); McCracken and Barnes, p. 85, pl. 1, fig. 16-21 [= *P. staufferi*].

non   v 1990   *Panderodus* cf. *P. feulneri* (Glenister); Armstrong, p. 100-2, pl. 15, figs 9-14 [= ? *Panderodus staufferi*].

Holotype. Paltodus feulneri Glenister 1957, p. 728, pl. 85, fig. 11 from the Brainard Member of the Maquoketa Formation, near Elgin, Iowa, U.S.A..

Emended diagnosis. A species of *Panderodus* in which all elements are extremely robust, with abbreviated cusps, and possess exaggerated ornament. White matter distribution is limited to a maximum of 10 percent of the total element length from the cusp apex.

Description. Pa element. Proclined spatulate element which is torted towards the excavated unfurrowed face. Ventral and dorsal margins of the unfurrowed face are drawn into a fine edge and keel respectively. Furrowed face is prominently carinate below the furrow, which is at two-thirds base height. An angular costa is often developed along the dorsal margin of this carina.

Pb -element. Refer to Glenister's (1957, p. 728) description of the type material.

M element. Squat erect element, strongly bowed towards the unfurrowed face. A single prominent costa is found along the ventral margin of the unfurrowed face, whilst the dorsal margin is drawn out as a fine keel. The furrowed face is rounded with a carina developed below the furrow at one-third base height, this often carries an angular costa.

Sa element. Short-based reclined element, markedly robust around the point of flexure. Prominent lateral costa are found at one third base height.

S_1 element. One of these elements is elongate with a gradually curving dorsal margin. This converges on the shallow convex margin to produce a high basal margin and an elongate triangular base. The unfurrowed face possesses a prominent costa which shifts apically from one-third to two-thirds base height at it's termination along the short and erect cusp. This face is excavated dorsal of the costa, and the cusp is torted away from the furrowed face. The furrowed face is largely unornamented, apart from the furrow which is found at two-thirds base height.

The other element referred to this location possesses an extremely high basal margin, and is markedly robust and rounded. The dorsal margin curves sharply to meet the reclined and squat cusp. The ventral margin also curves through the length of the base, although there is a gradual increase around the base of the cusp. The lateral faces have two, robust, carinae, the lowest up to two-thirds base height and the uppermost continuing up until the dorsal margin. On the furrowed face a sharp costa is developed apically of the basal wrinkle zone at one-half base height, and this shifts to a position at roughly two-thirds base height, and extremely close to the furrow, as it passes along the cusp. The unfurrowed face bears two rounded costae which are developed at one-third and two-thirds base height.

S_2 element. The high based S_2 element is similar to the high based S_1 element described above. It differs in the symmetrical placement costae on the lateral faces. In the former, a lower, sharp, costa is developed at one-third base height, apically of

the basal wrinkle zone, this transfers dorsally to two-thirds base height along the cusp. A second, but much weaker, costa is found running along the base at two-thirds base height. This converges on the lower costa and dies out at the cusp/base junction.

The low based S_2 element possesses a slight heel over the basal wrinkle zone on the dorsal margin. From this point it curves to form the proclined cusp. Along this margin of the base a narrow keel is developed, which is particularly prominent just in front of the dorsal heel. The ventral margin is also gently curved along the base and cusp. This element is transversely rounded by lateral carinae up to two-thirds base height, with a slight excavation of both lateral faces above these features. A single costa is borne on each lateral face at one-third base height until it dies out along the cusp.

S_3 *element*. Short reclined asymmetrical element. Unfurrowed face excavated with faint keel along dorsal margin, ventral margin is drawn into a faint edge. Furrowed face is rounded, with the furrow at two-thirds base height.

Remarks. Bergström and Sweet (1966) suggested that the *P. feulneri* and *P. gracilis* apparatuses could represent sub-specific variants. However, they show markedly different element morphologies, with the former possessing much more robust elements and abbreviated cusps.

Elements questionably synonymised with *P. feulneri* (Barnes, 1977; pl. 3, figs 13-14) have been previously placed in the *P. breviusculus* apparatus. They closely agree with the morphology of the S_3 elements that I have referred to *P. feulneri*, with which they co-occur in the collections of Barnes (1977).

Range. Costonian: *A. tvaerensis* biozone (possibly *B. variabilis* subzone) -» Hirnantian: *A. ordovicicus* biozone (*A shatzeri* subzone).

Panderodus gracilis (Branson and Mehl, 1933)

Plate 14, figs 1-18; Text-fig. 7.3

* 1933   *Paltodus gracilis* Branson and Mehl, p. 108, pl. 8, figs 20-21.

   1933   *Paltodus compressus* Branson and Mehl, p. 109, pl. 8, fig. 19.

   1943   *Paltodus compressus* Branson and Mehl; Branson and Mehl, p. 386, pl. 64, fig. 6.

   1943   *Paltodus gracilis* Branson and Mehl; Branson and Mehl [*partim*], p. 386, pl. 64, fig. 8.

non   1943   *Paltodus gracilis* Branson and Mehl; Branson and Mehl, p. 386, pl. 64, fig. 7 [= *Panderodus panderi*].

non   1951   *Paltodus gracilis* Branson and Mehl; Branson, Mehl and Branson, p. 6-7, pl. 1, figs 1-8 [= *Panderodus staufferi*].

non   1957   *Paltodus gracilis* Branson and Mehl; Glenister, p. 728, pl. 85, figs 2-3, 5 [= ? *Panderodus unicostatus*].

non   1957   *Paltodus gracilis* Branson and Mehl; Glenister, p. 728, pl. 85, fig. 4 [= ? *Panderodus feulneri*].

non   1959   *Panderodus gracilis* (Branson and Mehl); Sweet, Turco, Warner and Wilkie, p. 1056, pl. 131, fig. 1 [= *P. equicostatus*].

? 1959   *Panderodus gracilis* (Branson and Mehl); Stone and Furnish, p. 225, pl. 31, fig. 2.

non   1959   *Panderodus gracilis* (Branson and Mehl); Ethington, p. 285, pl. 39, fig. 1 [= *P. panderi*].

   1959   *Panderodus compressus* (Branson and Mehl); Ethington, p. 284, pl. 39, fig. 4.

   1959   *Panderodus compressus* (Branson and Mehl); Ethington and Furnish, pl. 75, fig. 8.

non   v 1966   *Paltodus gracilis* Branson and Mehl; Fåhræus, p. 26, pl. 3, fig. 14 [= *P. sulcatus*].

   1966   *Panderodus gracilis* (Branson and Mehl); Winder, pl. 9, fig. 25.

   1966   *Panderodus compressus* (Branson and Mehl); Winder, pl. 9, fig. 26.

non   1966   *Panderodus gracilis* (Branson and Mehl); Bergström and Sweet, p. 355-9, pl. 35, figs 1-6 [= *P. unicostatus*].

non   1966   *Panderodus gracilis* (Branson and Mehl); Oberg, p. 140, pl. 16, fig. 3 [= ? *P. unicostatus*].

   1968   *Panderodus gracilis* (Branson and Mehl); Kohut and Sweet [*partim*], p. 1469-70, pl. 185, figs 1, 6, 10, 13, 16.

non   1968   *Panderodus gracilis* (Branson and Mehl); Kohut and Sweet, p. 1469 - 70, pl. 185, fig. 9 [= *P. staufferi*].

? 1970   *Panderodus simplex* (Branson and Mehl); Pollock, Rexroad and Nicoll [*partim*], p. 758, pl. 114, fig. 25.

non   1971   *Panderodus gracilis* (Branson and Mehl); Rexroad and Craig, p. 695-6, pl. 81, figs 28-29 [= ? *P. unicostatus*].

non 1971 *Panderodus gracilis* (Branson and Mehl); Fåhræus, p. 677, pl. 79, figs 21-22 [= ? *P. equicostatus*].

non 1972 *Panderodus gracilis* (Branson and Mehl); Rexroad and Nicoll, pl. 1, figs 50-51 [= ? *P. equicostatus*].

1974 *Panderodus gracilis* (Branson and Mehl); Uyeno, p. 15, pl. 3, fig. 7.

non 1974 *Panderodus gracilis* (Branson and Mehl); Uyeno, p. 15, pl. 3, figs 9, 11-14 [= ? *P. equicostatus*].

non 1974 *Panderodus gracilis* (Branson and Mehl); Uyeno, p. 15, pl. 3, fig. 10 [= ? *P. feulneri*].

non 1977 *Panderodus gracilis* (Branson and Mehl); Liebe and Rexroad, pl. 2, fig. 23 [= ? *P. unicostatus*].

1977 *Panderodus* cf. *P. compressus* (Branson and Mehl); Liebe and Rexroad, pl. 2, fig. 26.

non 1977 *Panderodus gracilis* (Branson and Mehl); Barnes, p. 107, pl. 3, figs 6-7 [= ? *P. unicostatus*].

non 1978 *Panderodus gracilis* (Branson and Mehl); Miller, pl. 1, fig. 7 [= *P. equicostatus*].

non 1978 *Panderodus gracilis* (Branson and Mehl); Miller, pl. 1, figs 8-9 [= *P. staufferi*].

1979 *Panderodus gracilis* (Branson and Mehl); Stouge and Peel, fig. 2A.

v 1979 *Panderodus unicostatus* (Branson and Mehl); Aldridge, pl. 2, figs 17-22.

non 1980 *Panderodus gracilis* (Branson and Mehl); Orchard, p. 23, pl. 3, figs 10-11, 14-15, 19, 22-23, 26 [= ? *P. equicostatus*].

non 1980 *Panderodus gracilis* (Branson and Mehl); Orchard, p. 23, pl. 3, figs 1-2, 8, 32 [= *P. panderi*].

non 1981 *Panderodus gracilis* (Branson and Mehl); McCracken and Barnes, p. 85-86, pl. 1, figs 1-12, 15 [= *P. unicostatus*].

non 1981 *Panderodus gracilis* (Branson and Mehl); Nowlan, pl. II, figs 12, 19, pl. VI, figs 22-23 [= *P. unicostatus*].

? 1981 *Panderodus gibber* Nowlan and Barnes [*partim*], p. 16, pl. 6, figs 17-19.

? 1981 *Panderodus gracilis* (Branson and Mehl); Nowlan and Barnes, p. 16, pl. 6, figs 20, 23, 27.

1981 *Panderodus* aff. *P. gracilis* (Branson and Mehl); Nowlan and Barnes [*partim*], p. 16-17, pl. 6, figs 30, 33.

? 1981 *Panderodus* n. sp. A Nowlan and Barnes, p. 19, pl. 6, figs 5-6.

? 1981 *Panderodus* n. sp. B s.f. McCracken and Barnes, p. 87-88, pl. 1, fig. 14.

non 1982 *Panderodus gracilis* (Branson and Mehl); Lenz and McCracken, pl. 2, figs 2, 5-6, 8, 12, 15 [= *P. unicostatus*].

1983 *Panderodus gracilis* (Branson and Mehl); An *et al.*, p. 114-5, pl. 26, figs 1-9.

1984 *Panderodus gracilis* (Branson and Mehl); Chen and Zhang, pl. 3, figs 27-28.

non   v 1985   *Panderodus* cf. *P. gracilis* (Branson and Mehl); Savage and Bassett, p. 708, pl. 80, figs 42-47 [= *P. equicostatus*].

non   1987   *Panderodus gracilis* (Branson and Mehl); McCracken, pl. 2, figs 14, 17 [= *P. unicostatus*].

non   1988   *Panderodus gracilis* (Branson and Mehl); Nowlan and McCracken (in Nowlan *et al.*), p. 21, pl. 7, figs 1-10, 12-13, 19 [= *P. unicostatus*].

non   1990   *Panderodus gracilis* (Branson and Mehl); Uyeno, p. 69-70, pl. 1, figs 14, 19-20 [= *P. unicostatus*].

         1990   *Panderodus* cf. *P.* n.sp. A McCracken and Barnes; Uyeno, p. 71, pl. 1, fig. 31.

         v 1990   *Panderodus unicostatus* (Branson and Mehl); Armstrong, p. 108-110, pl. 17, figs 1-7 [kop. Aldridge 1979].

Syntypes. *Paltodus gracilis* Branson and Mehl 1933, p. 108, pl. 8, figs 20, 21, two 'co-types' from the Plattin Formation of New Hope, Missouri, U.S.A..

Emended diagnosis. Elements have a short base and elongate sub-erect to erect cusp, which comprises up to 50 percent of element length. Dense white matter is developed throughout the length of the cusp. Elements are triangular in cross-section. Surface ornamentation restricted to a shallow basal wrinkle zone which passes around the base of each element, and a smooth indentation in which the furrow lies. Furrow consistently found at two-thirds base height. The apex of the basal cavity is closer to the ventral margin than the dorsal, and fills the base as a sharp, triangular feature.

Description. *Pa element.* Proclined, slender, short based element, with an elongate cusp torted away from the furrowed face. Ventral margin of the unfurrowed face is extended into a pronounced edge; face strongly excavated. A prominent angular carina is found on the ventral third of the furrowed face.

Pb element. Short based, laterally compressed, erect element. Point of flexure at roughly 50 percent of element length. Cusp is elongate, with even curvature of both the dorsal and ventral margins. A prominent keel is developed along the ventral margin, extending from the basal wrinkle zone to the cusp.

M element. Proclined, short based element, similar to the **Pa**. Differs in the presence of a prominent costa at one-third base height on the unfurrowed face, rather than a marginal edge, and the more pronounced torsion of the cusp. The cusp/base flexure is also increased.

Sa element. Double-furrowed element with a sub-erect to proclined cusp comprising 50 percent of element length. Prominent costae developed on both lateral faces at one-third base height, producing a triangular cross-section.

S_1 *element.* One morphotype possesses a comparatively elongate and triangular base, making up 60 percent of the total element length. Cusp suberect to proclined and torted away from the furrowed face. Prominent lateral costa on the unfurrowed face at one-third base height; costa borne on the furrowed face at half base height, where an angular carina is developed between the convex margin and the furrow.

The second S_1 morphotype is slender with a proclined cusp. This element differs from the S_2 element in the asymmetrical distribution of the lateral costa.

S_2 *element.* Slender element where the ventral and dorsal edges converge to form an elongate, proclined cusp. Costae are borne on rounded carinae at one-third base height on both lateral faces.

S_3 *element.* Short, triangular based element. Prominent straight and erect cusp which comprises 50 percent of the element length. Prominent costa generated at one-quarter base height on the unfurrowed face. An angular carina on the unfurrowed face produces a sub-triangular cross-section.

Remarks. Many authors have used 'P. gracilis' as a taxonomic basket where they have placed elements of several species. This problem is also found with 'P. unicostatus' (see later remarks) and there appears to have been a stratigraphic division in the application of such 'catch all' names, as Ordovician workers have tended to use 'P. gracilis' whilst Silurian specimens are termed 'P. unicostatus'. P. gracilis is distinguishable from the similar P. equicostatus and P. unicostatus apparatuses on the

basis of the much greater cusp to base ratio, and the triangular cross-section of the elements.

Nowlan and Barnes (1981) suggested that *P. gracilis* may represent an ancestor of Silurian *P. unicostatus*. However, the phylogenetic relationship between the two forms is not as clear cut, and the age ranges appear to be largely parallel.

Range. Marshbrookian: *A. superbus* biozone -» Gorstian: uppermost *P. siluricus* biozone.

Panderodus langkawiensis (Igo and Koike, 1967)

Plate 14, figs 1-18; Text-fig. 7.3

* 1967   *Acodus langkawiensis* Igo and Koike, p. 12, pl. 1, figs 19-20.

   1967   *Panderodus unicostatus* (Branson and Mehl); Igo and Koike, p. 21-22, pl. 1, figs 12-14.

? 1972   *Panderodus* cf. *P. gracilis* (Branson and Mehl); Aldridge [partim], p. 203-4, pl. 9, fig. 12.

   1974   *Panderodus spasovi* Drygant, p. 66, pl. 1, figs 1-3.

   1977   *Panderodus spasovi* Drygant; Barrick, p. 56, pl. 3, figs 13-21.

   1984   *Panderodus spassovi* Drygant [*sic*]; Stouge and Stouge, pl. 2, figs 28-32.

   1984   *Panderodus barricki* Kozur [*partim*], p. 154-5, pl. 3, fig. 3, pl. 5, fig. 6.

? 1984   *Panderodus barricki* Kozur [*partim*], p. 154-5, pl. 5, fig. 1.

   1985   *Panderodus langkawiensis* (Igo and Koike); Mabillard and Aldridge, text-fig. 7h.

v?1990   *Panderodus* aff. *P. spasovi* Drygant; Armstrong, p. 107-8, pl. 17, figs 14-24.

Holotype. *Acodus langkawiensis* Igo and Koike 1967, p. 12, pl. 1, fig. 19, from the Setul Limestone of Langkawi Island, Malaysia.

Emended diagnosis. Species of *Panderodus* where the element cusps are elongate and reclined to recurved, with the exception of the proclined **Pa** element. The **Pb**, one S_1 and one S_2 elements show extreme lateral compression; the S_1 has a markedly elongate, rectangular base.

Description. Pa element. Small, proclined, spatulate element. Gradually tapers down from a low base into the elongate cusp. Unfurrowed face is excavated and the element is bowed towards this face, the ventral margin of which is drawn into a pronounced edge. Furrow _ ·. at two-thirds base height on the alternate face, . is underlain by a rounded carina.

Pb element. Refer to Igo and Koike's (1967, p. 12) description of the type material.

M element. Element with a high basal margin; the dorsal margin tapers at high angle to produce a short triangular base. Cusp is elongate, and is torted towards the unfurrowed face; torsion is initiated at the cusp/base interface. A single, sharp costa along the ventral margin of the unfurrowed face, at one-quarter base height produces a markedly triangular cross-section.

Sa element. Double furrowed element with a triangular base and an elongate erect cusp. Angular costa at one-third base height on the lateral faces produce a markedly triangular cross-section.

S_1 elements. One of these elements possesses an extremely elongate and laterally compressed base with a reclined cusp. The ventral margin of the base is straight; the dorsal margin is also straight but converges gradually with the venter, from a slight heel where it meets the basal margin. The dorsal margin also bears a slight keel which runs from the heel to the cusp. The lateral faces are very flat; the furrow is found at three-quarters base height and is surrounded by a single weak costa above and two faint costae below. On the unfurrowed face a single costa is developed where the keel expands into the lateral face.

The other S_1 element is markedly different, with a high triangular base with a faint keel, passing into a broad and rounded cusp which is twisted away from the furrowed face. The surface around the furrow is slightly raised to form a pair of ridges immediately adjacent to this feature.

S_2 *elements.* One of the S_2 elements is extremely laterally compressed, with two costae on both lateral faces at one-third and two-thirds base height. The lateral face above the second of these costae is angled to form a keeled dorsal surface which runs straight from the heeled basal margin into the reclined-recurved cusp.

The other S_2 element is rounded with costae at one-third base height on each face. The ventral margin of the base is straight with the dorsal margin slightly curved extending from a high heeled basal margin to meet the rounded and reclined broad cusp.

S_3 *element.* Extremely abbreviated element with a short, flattened base and comparatively elongate cusp. The lateral faces are unornamented apart from the basal wrinkle zone and a single furrow at two-thirds base height. The cusp is bowed towards the furrowed face.

Remarks. Specimens described as *P.* aff. *P. spasovi* Drygant by Armstrong (1990, pl. 17, figs 14 - 24) have accentuated costae and ventral keels. In collections from North Greenland (Armstrong 1990, GGU 216852) there is an apparent grad ation from weak to strongly keeled forms. Such variations in ornament may represent gerontic forms.

Kozur (1984) erroneously synonymised *P. spasovi* Drygant, as illustrated by Barrick (1977), with his new species *P. barricki.* A single, highly recurved element with a prominent keel (Kozur 1984, pl. 5, fig. 1), assigned to *P. barricki,* has only been questionably cited in this synonymy list, as such recurved elements are absent in the collections studied. This element may have been damaged, as a series of open fractures are seen along the ventral margin (Kozur 1984, pl. 5, figs 1b and 1c) accentuating the curvature.

P. langkawiensis is similar to *P. panderi* (Stauffer) in the laterally compressed nature of the elements, although this is much more extreme in *P. langkawiensis.* It seems likely that this species represents a Lower Silurian ancestor of *P. panderi.*

Range. lowest Rhuddanian: *I. discreta - I. deflecta* biozone -» Sheinwoodian: lower

P. amorphognathoides biozone.

Panderodus levigatus (Nowlan and McCracken, 1988)

1981   *? Panderodus* n. sp. B Nowlan and Barnes, p. 19, pl. 6, figs 8, 12-13, text-fig. 7E.

* 1988   *Zanclodus levigatus* Nowlan and McCracken (in Nowlan *et al.*), p. 43-44, pl. 20,

   figs 4, 9-24, pl. 21, figs 1-21, pl. 22, figs 1-2, 4-5.

Holotype. *Zanclodus levigatus* Nowlan and McCracken (in Nowlan *et al.*) 1988, p. 43-44, pl. 20, figs 11-12, from the Whittaker Formation, Mackenzie Mountains, Northwest Territories, Canada.

Diagnosis. Refer to Nowlan and McCracken (in Nowlan *et al.* 1988, p. 43).

Description. **Pa element.** Described by Nowlan and McCracken (in Nowlan *et al.* 1988, p. 43) as a low based Group 1 element.

Pb element. Described by Nowlan and McCracken (in Nowlan *et al.* 1988, p. 43-44) as a Group 3 element.

M element. Described by Nowlan and McCracken (in Nowlan *et al.* 1988, p. 43) as a Group 1 element with intermediate base height.

S_1 **elements.** Two morphotypes are referred to this location. The first has been described by Nowlan and McCracken (in Nowlan *et al.* 1988, p. 43) as a high based Group 1 element. The other morphotype has been described by Nowlan and McCracken (in Nowlan *et al.* 1988, p. 43) as a high based Group 2 element.

S_2 **elements.** Nowlan and McCracken (in Nowlan *et al.* 1988, p. 43) described two elements that fall into this category, the first termed a Group 2 element with an intermediate base height, the second described as a Group 2 low based element.

S₃ element. Described by Nowlan and McCracken (in Nowlan *et al.* 1988, p. 43-44) as an extremely low based Group 3 element.

Remarks. As a species *P. levigatus* appears to be closely allied to the *P. panderi* apparatus as they both possess heeled and laterally compressed elements, and the former may represent a Late Ordovician derivative of the latter. *P. levigatus* may be distinguished by the presence of pronounced keels on the dorsal margins of each element, and an exaggerated ventral keel on the base of the **Pb** element (Group 3 elements of Nowlan and McCracken). The **Sa** element illustrated by Nowlan and McCracken (in Nowlan *et al.* 1988, pl. 7, figs 23-24) as a b/c element of *Panderodus ? panderi* (Stauffer) also possesses a dorsal keel and a prounced heel, and may represent the symmetrical element of *P. levigatus* as they occur in a sample (AV1-20 m) where *P. levigatus* is the dominant form.

Range. Pusgillian: *O. robustus* biozone -» Hirnantian: *A. divergens* biozone.

Panderodus panderi (Stauffer, 1940)

Plate 17, figs 1-18; Text-fig. 7.3

* 1940 *Paltodus panderi* Stauffer, p. 427, pl. 60, figs 8-9.

  1943 *Paltodus gracilis* Branson and Mehl; Branson and Mehl [*partim*], p. 386, pl. 64, fig. 7.

v 1953 *Paltodus recurvatus* Rhodes, p. 297, pl. 23, figs 219-220.

  1957 *Paltodus panderi* Stauffer; Glenister, p. 728-9, pl. 85, figs 8-9.

? 1957 *Paltodus ? unicostatus* Branson and Mehl; Glenister, p. 729, pl. 85, fig. 1.

  1959 *Panderodus panderi* (Stauffer); Stone and Furnish, p. 226, pl. 31, fig. 4.

? 1959 *Panderodus gracilis* (Branson and Mehl); Ethington, p. 285, pl. 39, fig. 1.

  1959 *Panderodus panderi* (Stauffer); Ethington, p. 285, pl. 39, fig. 5.

  1959 *Panderodus panderi* (Stauffer); Ethington and Furnish, pl. 75, fig. 9.

  1966 *Panderodus striatus* (Stauffer); Winder, pl. 9, fig. 24.

  1966 *Panderodus panderi* (Stauffer); Winder, pl. 9, fig. 28.

1966   *Panderodus panderi* (Stauffer); Bergström and Sweet, p. 359-61, text-fig. 11, pl. 35, figs 14-15.

1966   *Panderodus panderi* (Stauffer); Oberg, p. 140, pl. 15, fig. 1.

1969   *Panderodus* sp. E Ethington and Schumacher, p. 470, pl. 69, fig. 1.

1969   *Panderodus* sp. F Ethington and Schumacher, p. 470, pl. 69, fig. 4.

1969   *Panderodus* sp. G Ethington and Schumacher, p. 471, pl. 69, fig. 2.

1969   *Panderodus panderi* (Stauffer); Ethington and Schumacher, p. 469, pl. 69, fig. 15.

1971   *Panderodus recurvatus* (Rhodes); Rexroad and Craig, p. 696-7, pl. 81, figs 23-25.

1972   *Panderodus* cf. *P. staufferi* (Branson, Mehl and Branson); Aldridge, p. 205, pl. 9, fig. 10.

1972   *Panderodus recurvatus* (Rhodes); Rexroad and Nicoll, pl. 2, fig 39.

1973   *Panderodus recurvatus* (Rhodes); Pollock and Rexroad, p. 83, pl. 1, figs 7-8.

1974   *Paltodus nudus* Drygant, p. 68, pl. 1, figs 21, 29.

1977   *Panderodus recurvatus* (Rhodes); Barrick, p. 54-5, pl. 3, figs 3-4, 7-12.

? 1977   *Panderodus recurvatus* (Rhodes); Liebe and Rexroad, pl. 2, fig. 22.

1977   *Panderodus arcuatus* (Stauffer); Barnes, p. 107, pl. 3, fig. 23-25.

1977   *Panderodus panderi* (Stauffer); Barnes, p. 107, pl. 3, figs 21-22.

? 1978   *Panderodus unicostatus* (Branson and Mehl); Helfrich [*partim*], pl. 1, fig. 1.

1978   *Panderodus* sp. Helfrich, pl. 2, fig. 13.

1978   *Panderodus recurvatus* (Rhodes); Miller, pl. 1, fig. 6.

1979   *Panderodus panderi* (Stauffer); Sweet, p. 64, fig. 7(2-6, 10).

1980   *Panderodus gracilis* (Branson and Mehl); Orchard [*partim*], p. 23, pl. 3, figs 1-2, 8, 32.

1980   *Panderodus panderi* (Stauffer); Orchard, p. 23, pl. 3, fig. 24.

? 1981   *Panderodus angularis* Branson, Mehl and Branson s.f.; Nowlan and Barnes, p. 15, pl. 5, figs 23-24.

1981   *Panderodus panderi* (Stauffer); Nowlan and Barnes, p. 17, pl. 6, figs 3-4,14.

? 1981   *Panderodus* n. sp. A Nowlan and Barnes [*partim*], p. 19, pl. 6, fig. 10.

1981   *Panderodus* n. sp. C Nowlan and Barnes, p. 20, pl. 5, figs 18-22.

1981   *Panderodus liratus* Nowlan and Barnes; McCracken and Barnes, p. 86, pl. 2, figs 19-21.

1981   *Panderodus* cf. *P. staufferi* (Branson, Mehl and Branson); McCracken and Barnes, p. 87, pl. 2, figs 14-18.

? 1981   *Panderodus* n. sp. C s.f. McCracken and Barnes, p. 88, pl. 2, fig. 29.

1981   *Panderodus panderi* (Stauffer); McCracken and Barnes, p. 86, pl. 2, figs 11-13.

1981   *Panderodus liratus* Nowlan and Barnes; Nowlan, pl. II, figs 12, 19.

1981   *Panderodus* n. sp. C Nowlan and Barnes; Nowlan, pl. II, figs 13-14.

1981   *Panderodus gibber* Nowlan and Barnes; Nowlan, pl. II, figs 18, 20, pl. VI, fig. 20.

1981 *Panderodus recurvatus* (Rhodes); Nowlan, pl. III, fig. 11.

1983 *Panderodus clinatus* McCracken and Barnes; Nowlan [*partim*], pl. 3, fig. 19.

1983 *Panderodus liratus* Nowlan and Barnes; Nowlan, pl. 3, figs 25-26.

1984 *Panderodus recurvatus densistriatus* Kozur, p. 156, pl. 2, figs 1-3.

1984 *Panderodus recurvatus recurvatus* (Rhodes); Kozur, pl. 4, figs 1, 3.

1985 *Panderodus* cf. *P. recurvatus* (Rhodes); Mabillard and Aldridge, text-fig. 7g.

1988 *Panderodus* ? *liratus* Nowlan and Barnes; Nowlan and McCracken (in Nowlan *et al.*), p. 21, pl. 7, figs 11, 15-18, 22.

1988 *Panderodus* ? *panderi* (Stauffer)?; Nowlan and McCracken (in Nowlan *et al.*) [*partim*], p. 21-22, pl. 7, figs 14, 20-21, 25.

non 1988 *Panderodus* ? *panderi* (Stauffer)?; Nowlan and McCracken (in Nowlan *et al.*) [*partim*], p. 21-22, pl. 7, figs 23-24.

1989 *Panderodus recurvatus* (Rhodes); Wilson [*partim*], pl. 1, fig. 12.

1989 *Panderodus recurvatus* (Rhodes); Mawson and Talent [*partim*], pl. 8, fig. 12.

1990 *Panderodus panderi* (Stauffer); Uyeno, p. 70, pl. 1, figs 23, 29.

v 1990 *Panderodus recurvatus* (Rhodes); Armstrong, p. 104-7, pl. 16, figs 1-11.

v 1990 *Panderodus* sp. A Armstrong, p. 110, pl. 16, figs 16-21.

v 1990 *Panderodus* sp. B Armstrong, p. 110, pl. 16, fig. 22.

v 1990 *Panderodus* sp. C Armstrong, p. 110, pl. 16, figs 23-24.

v 1990 *Panderodus* sp. D Armstrong, p. 111, pl. 18, figs 1-2.

Holotype. Paltodus panderi Stauffer, 1940, p. 427, pl. 60, fig. 8, from the shale above the Cedar Valley Limestone, Austin, Minnesota, U.S.A..

Emended diagnosis. A species of *Panderodus* in which the elements are laterally compressed and have triangular bases and elongate cusps forming 50 percent of the element length. Heels are developed, to some extent, over the basal wrinkle zone on the dorsal margin of all elements.

Description. Pa element. Short based element with elongate, proclined cusp which is torted away from the furrowed face. The ventral margin is drawn out as a sharp edge extending from the basal wrinkle zone up the cusp, where it gradually dies out.

Pb element. Laterally compressed element with broad base and elongate reclined cusp. The ventral margin curves apically from the basal wrinkle zone to the

termination of the cusp. At the junction of the dorsal and basal margin a heel is developed; the dorsal margin then curves apically to the cusp termination.

M element. High based element with gently curved dorsal and ventral margins converging apically towards the elongate, reclined to recurved cusp. The base and cusp are roughly the same length. A faint keel is borne on the dorsal margin of the base. The cusp is deflected away from the furrowed face, where the furrow is found at two-thirds base height with a rounded carina below this. The unfurrowed face possesses a sharp costa at one-third base height, extending apically from the basal wrinkle zone and fading out along the cusp, and is excavated above this feature.

Sa element. This element possesses a dorsal heel developed from the basal margin over the basal wrinkle zone. There is a slight step in profile onto a dorsal keel which is found along this margin of the base. The dorsal margin curves from this point to meet the elongate and reclined cusp. Single costae are borne on both lateral faces at one-third base height, and in some specimens the face below the costa is angled to produce a prominent ventral keel.

S_1 element. One of the S_1 elements possesses an elongate triangular base, more so than either of the S_2 elements, and an erect cusp. The furrowed face bears two costae at one-quarter and three-quarters base height with a single costa at one-third base height on the furrowed face. The dorsal margin over the basal wrinkle zone is flattened to produce a slight heel.

The other element referred to this position has an erect to reclined cusp and a shorter base than the morphotype described above. Asymmetry is denoted by a single faint costa just above the ventral margin of the unfurrowed face. The furrowed face possesses a flattened carina below the furrow at two-thirds base height and a series of ridges in close proximity and parallel to the furrow. This element has a similar profile to the M element but is distinguished by the absence of cusp torsion and the lower placement of the costa on the unfurrowed face.

S_2 element. Two morphotypes are identified. The first possesses a markedly triangular and laterally compressed base. The dorsal margin curves from the contact

with the high basal margin, and converges sharply with the straight ventral margin which flexes to form the erect to reclined cusp. Two weak costae are borne at one-quarter base height on both lateral faces. There is little other ornamentation apart from a weak furrow at two-thirds base height which is refelected by a slight indent on the alternate face, and a shallow basal wrinkle zone.

The second has a more elongate base, forming a lower triangular profile. This element also has compressed lateral faces, but they bear two costae on each lateral face, at one-quarter and three-quarters base height, and they follow the ventral and dorsal margins, respectively, from the basal wrinkle zone to the lower regions of the elongate recurved cusp.

S_3 *element.* Short, truncated element with an abbreviated base and an elongate, recurved cusp that forms over 50 percent of the element length. The dorsal margin possesses a short heel at the basal margin. Apical from this point the margin curves dramatically to form the upper margin of the cusp. The ventral margin of the base is slightly curved, with a strong point of flexure at the cusp/base junction. A short costa is borne on the excavated, unfurrowed face, whilst the cusp is torted towards the more rounded furrowed face.

Remarks. There appears to have been a stratigraphical preference for Ordovician workers to describe elements assigned to this apparatus as *P. panderi* whilst Silurian workers have called it *P. recurvatus* Rhodes. The holotype is Middle Devonian in age. I have studied Rhodes' (1953) type material and found little difference with collections from the Ordovician. As there appears to be little morphological difference through the range of these species, they have been synonymised.

The cusps of S_{1-2} may be torted towards or away from the furrowed face, or show no deflection at all. Such variability can be documented within the same element morphotype from a single sample, suggesting intra-specific variability.

Armstrong (1990; p. 106, pl. 16, figs 12-15) described a partial apparatus as *Panderodus* spp. aff. *P. recurvatus* Rhodes. The illustrated specimens appear to be

morphologically similar to those of *P. panderi.* They differ only in the presence of keeled dorsal and ventral margins of each element, and possibly represent a sub-specific variant. In the absence of additional material I am not yet confident of this taxonomic step.

Range. Llanvirn: *E. suecicus* biozone -» Givetian: Upper *varcus* biozone.

Panderodus rhamphoides Nowlan and McCracken (in Nowlan *et al.*), 1988

* 1988   *Panderodus rhamphoides* Nowlan and McCracken (in Nowlan *et al.*), p. 22-23, pl. 8, figs 1-4, 8-13.

? 1988   *Panderodus rhamphoides* Nowlan and McCracken (in Nowlan *et al.*), p. 22-23, pl. 8, figs 14-15, 20-21, 26.

Holotype. Panderodus rhamphoides Nowlan and McCracken (in Nowlan *et al.*), 1988, p. 22-23, pl. 8, figs 8-9, from the Whittaker Formation, Mackenzie Mountains, Northwest Territories, Canada.

Diagnosis. Refer to Nowlan and McCracken (in Nowlan *et al.* 1988, p. 22).

Description. *?Pb element.* Described by Nowlan and McCracken (in Nowlan *et al.* 1988, p. 22) as an e element.

M element. Described by Nowlan and McCracken (in Nowlan *et al.* 1988, p. 22) as an a element.

S_1 element. Described by Nowlan and McCracken (in Nowlan *et al.* 1988, p. 22) as a b element.

S_2 element. Described by Nowlan and McCracken (in Nowlan *et al.* 1988, p. 22) as a c element.

Remarks. Nowlan and McCracken (in Nowlan *et al.* 1988) described *P. rhamphoides* as having a transition series of **M, S₁** and **S₂** elements and the **?Pb.** The bulbous nature of the transition between the broad base and the abbreviated cusp in the costate suite is unlike any element I have come across elsewhere. However, the **?Pb** element (**e** in the terminology employed by Nowlan and McCracken) is very similar in appearance to those I have placed in the **S₃** category of other species, and I am uncertain as to the assignment of this element.

Elements illustrated as *Panderodus* ? n. sp. A by Nowlan and McCracken (in Nowlan *et al.* 1988; p. 23-24, pl. 8, figs 16-19, 22-25) have similarly broad bases and abbreviated cusps. It is possible, given their co-occurrence, that these elements represent marked sub-divisions within the **S₁** and **S₂** locations of *P. rhamphoides.*

Range. Pusgillian: *O. robustus* biozone -» Hirnantian: *A. divergens* biozone.

Panderodus staufferi (Branson, Mehl and Branson, 1951)

Plate 18, figs 1-18; Text-fig. 7.3

* 1951 *Paltodus staufferi* Branson, Mehl and Branson, p. 7-8, pl. 1, figs 23-27.

? 1951 *Paltodus gracilis* Branson and Mehl; Branson, Mehl and Branson, p. 6-7, pl. 1, figs 1-8.

? 1951 *Paltodus compressus* Branson and Mehl; Branson, Mehl and Branson, p. 7, pl. 1, figs 16-22.

  1951 *Paltodus robustus* Branson, Mehl and Branson, p. 8, pl. 1, figs 28-33.

  1951 *Paltodus angularis* Branson, Mehl and Branson, p. 8, pl. 1, figs 34-37.

  1968 *Panderodus angularis* (Branson, Mehl and Branson); Kohut and Sweet, p. 1469, pl. 185, figs 20,23,27.

  1968 *Panderodus gracilis* (Branson and Mehl); Kohut and Sweet [*partim*], p. 1469 - 70, pl. 185, fig. 9.

  1968 *Panderodus staufferi* (Branson, Mehl and Branson); Kohut and Sweet, p. 1470, pl. 186, figs 4-5.

  1972 *Panderodus* cf. *P. gracilis* (Branson, Mehl and Branson); Aldridge [*partim*], p. 203-4, pl. 9, fig. 13

1972   *Panderodus* sp. A Aldridge, p. 206-7, pl. 9, fig. 11.

1976   *Panderodus unicostatus* (Branson and Mehl); Cooper [*partim*], p. 213-4, pl. 1, fig. 7.

1977   *Panderodus staufferi* (Branson, Mehl and Branson); Barnes, p. 107, pl. 3, figs 8-10.

1978   *Panderodus gracilis* (Branson and Mehl); Miller [*partim*], pl. 1, figs 8-9.

v 1979 *Panderodus* spp. Aldridge, pl. 2, figs 23-30.

1981   *Panderodus feulneri* (Glenister); McCracken and Barnes, p. 85, pl. 1, fig. 16-21.

1983   *Panderodus* spp. Mabillard and Aldridge [*partim*], pl. 4, figs 16-17, 19-24.

1983   *Scolopodus euspinus* Jiang and Zhang F.; An *et al.*[*partim*], p. 140-1, pl. 14, figs 1-3.

v 1990 *Panderodus greenlandensis* Armstrong, p. 102-4, fig. 33.

v 1990 *Panderodus greenlandensis* Armstrong, p. 102-4, pl. 15, figs 1-8 [kop. Aldridge 1979].

v?1990 *Panderodus* cf. *P. feulneri* (Glenister); Armstrong, p. 100-2, pl. 15, figs 9-14.

Syntypes. *Paltodus staufferi* Branson, Mehl and Branson, p. 7-8, pl. 1, fig. 23-27, four syntypes from the Whitewater Formation, east of Versailles, Ripley County, Indiana, U.S.A.

Diagnosis. All elements of the apparatus are robust, with prominent costae borne on a rounded carina. The basal wrinkles are strongly developed as is a deep lateral furrow. White matter is concentrated around the base of the cusp, although in some populations it extends to the apex.

Description. **Pa element.** Proclined elongate cone. Spatulate cusp, torted away from the furrowed side. Short, rounded carina developed on the unfurrowed face from the basal margin to just beyond the basal wrinkle zone, where it passes into a sharply developed costa. The ventral margin of the unfurrowed face is drawn out into a sharp edge that extends along the element length; an indentation is found at mid-base height, mimicking the furrow on the alternate face.

Pb element. Robust, erect cone. Strong curvature of the dorsal and ventral margins produces an evenly curved element. A prominent, rounded carina is

developed below the furrow, extending from the basal wrinkle zone around the cusp. A weaker carina is developed on the unfurrowed face; additionally a shallow excavation of the dorsal margin results in a weak dorsal keel. A weak keel is also developed along the ventral margin.

M element. Extremely broad element, with a high basal margin forming a broad triangular base. The dorsal margin is extremely curved to meet the robust reclined to recurved cusp, whilst the ventral margin is more angular as it passes apically from base to cusp. The unfurrowed face is excavated in the upper two-thirds producing a asymmetric cross-section and resulting in the deflection of the cusp away from the furrowed face. The furrow is deeply developed, and underlain by a prominent sharp costa which passes from one-thirds to two-thirds base height from the basal wrinkle zone to it's termination along the cusp.

Sa element. Short reclined element, with an elongate cusp that comprises over 50 percent of the total length. Base is short and squat, with prominent carina developed around the basal wrinkle zone; these pass cuspward into costa developed at one-quarter base height. Furrows are developed at three-quarters base height.

S_1 elements. Two elements are referred to this location, one comparatively high based and the other low based.

The first of these has a high basal margin and a robust, elongate base formed by curved dorsal and ventral margins. Bold rounded carinae are found up to two-thirds base height on the unfurrowed face and one-half base height on the furrowed face. There is a transition into the proclined to erect cusp as the rate of curvature gradually steepens apically. A comparatively weak costa is borne on the carina at one-third base height on the unfurrowed face between the basal wrinkle zone and the base of this cusp where this feature quickly dies out. A sharp, prominent costa is found on the furrowed face, starting at the basal wrinkle zone at one-third base height. This shifts dorsally as it continues apically, reaching two-thirds base height as it dies out halfway up the cusp. The face dorsal of the costa, and surrounding the furrow, is flattened making the costa more prominent.

A lower based S_1 element is also found which shares many of the features described above, although ornamentation is less pronounced and a flattened heel is developed from the basal margin and over the basal wrinkle zone.

S_2 *elements*. Robust rounded element, with carinae developed to one-half base height on both lateral faces. These bear costae at one-third base height from initial development apically of the basal wrinkle zone to their termination at the base of the cusp.

The elements can be divided into high and low based forms, differing only in the rate of curvature of the dorsal margin as it converges with the ventral margin, to form the erect cusp.

S_3 *element*. Short, truncated element with an elongate and recurved cusp that accounts for some 50 percent of the total element length. The dorsal margin is slightly heeled over the basal wrinkle zone and then curves sharply to form the cusp. The ventral margin of the base is less rounded and there is a sharp change in orientation as it passes to the cusp. The unfurrowed face is excavated around the cusp/base junction and a costa is developed slightly above the ventral margin of the base. The base of the furrowed face possesses a rounded carina up to two-thirds base height until it meets the furrow, this feature is reflected on the unfurrowed face by a slight indentation close to the basal margin.

Remarks. Armstrong (1990, p. 100-2, fig. 33) described specimens from Götland and Greenland, which I consider to be con-specific with *Panderodus staufferi*, as a new species, *P. greenlandensis*. The type suite of elements illustrated as *P. greenlandensis* appear to be 'juveniles'. They are more slender than the mean size of *P. staufferi* elements I have found in collections from Armstrong's Götland locality (Nyhamn 1).

Range. Costonian: basal *A. tvaerensis* biozone -» Ludfordian: *P. dubius* biozone.

Panderodus sulcatus (Fåhræus, 1966)

Plate 19, figs 1-18; Text-fig. 7.3

1944   *Paltodus arcuatus* Stauffer; Mehl and Strothmann (in E.B. Branson), pl. 12, figs 27, 28.

v*1966   *Paltodus sulcatus* Fåhræus, p. 25, pl. 3, fig. 9.

v 1966   *Paltodus gracilis* Branson and Mehl; Fåhræus, p. 26, pl. 3, fig. 14.

v 1978   *Panderodus sulcatus* Fåhræus; Löfgren, p. 67, pl. 8, figs 7-9.

? 1990   *Panderodus* sp. Bergström [*partim*], pl. 1, figs 1-2, 4.

Holotype. *Paltodus sulcatus* Fåhræus 1966, p. 25, pl. 3, fig. 9, from the Skövde Limestone, Gullhögen quarry, Västergötland, central Sweden.

Emended diagnosis. A species of *Panderodus* where all element cusps are reclined, apart from in the erect **Pa** element, and characterised by a well developed basal wrinkle zone; this is drawn up along the furrow region as a series of longitudinal striations. Elongate cusps occupy up to 50 percent of the element length. The dorsal margin is drawn up basally to form a heel, which extends to the cuspward termination of the basal wrinkle zone.

Description. **Pa element.** Spatulate and torted element with an erect cusp. Dorsal margin curves gently from the basal heel along the element base, the degree of curvature increasing to form the dorsal magin of the cusp. This is torted away from the furrowed face. The ventral margin is gradually curved thoughout the element. A sharp edge is found along the venter of the unfurrowed face, which is excavated dorsally. The furrowed face is rounded along the base, as it has a carina developed up to the furrow at two-thirds base height.

Pb element. Refer to Fåhræus's (1966, p. 25) description of the type material.

M element. The dorsal margin curves apically from the basal heel into the erect cusp, which is strongly torted towards the unfurrowed face. This face is

dorsally excavated and possesses a sharp costa, apical of the basal wrinkle zone, which follows the curved ventral margin at one-fifth base height. A rounded carina is developed along the base of the furrowed face at up to two-thirds base height.

Sa element. Symmetrical, bi-furrowed element with a reclined cusp. The base of the element possesses a straight dorsal margin which converges on the curved ventral margin, until they meet the cusp/base junction where they are deflected sharply upward to form the margins of the elongate cusp. Costae are developed at one-third base height on both lateral faces, extending apically and basally from the cusp/base junction. The panderodontid furrows are found above weak carinae at two-thirds base height.

S_1 elements. Two elements are tentatively referred to this position, one high based, the other comparatively low based.

The first of these is similar to the M element described above, but differs in the higher placement of the costa on the unfurrowed face, at one-third base height. The cusp is less torted and a keel is developed along the dorsal margin of the base.

The lower based S_1 element has a longer base, which curves less dramatically into the reclined cusp. Prominent carinae are developed in the lower two-thirds of both lateral faces, and a sharp costa runs from the basal wrinkle zone to the basal part of the cusp on the unfurrowed face.

S_2 element. A single sub-symmetrical S_2 element has been identified. This has a comparatively elongate and rounded base. Both the lateral faces bear angular costa at one-third base height, at the point of maximum extension of the lateral carina, which are formed up to two-thirds base height. The dorsal margin curves apically of the basal wrinkle zone and converges on the flexed ventral margin.

? S_3 element. The possible S_3 element is similar in morphology to the lower based S_1 element, but has more compressed lateral faces and a shorter base. The cusp/base junction is extremely sharp.

Remarks. Unfortunately, the type specimen (Fahræus 1966, pl. 3, fig. 9) is damaged by the adhesion of glue to the unfurrowed lateral face. Löfgren's (1978) collections of *P. sulcatus* and prepared additional samples from two of her localities (J69-43 and J70-167) have specimens which are largely recrystallised (CAI 5+), obscuring much of the sub-surface detail and the white matter distribution.

P. sulcatus is the oldest *Panderodus* species. It shares features such as the generally elongate cusps, and laterally compressed **Pb** element, with *P. panderi.* However, the rounded nature of the other element bases is. shared with *P. equicostatus* and *P. unicostatus* type apparatuses. *P. sulcatus* would thus appear to form an ideal ancestor for the succeeding species which appeared in the lowest Caradoc.

Range. Llanvirn: *E. suecicus* biozone (*P. sulcatus* subzone) -» Llanvirn: *P. serra* biozone (*E. foliaceus* subzone).

Panderodus unicostatus (Branson and Mehl, 1933)

Plate 20, figs 1-18; Text-fig. 7.3

* 1933   *Paltodus unicostatus* Branson and Mehl, p. 42, pl. 3, fig. 3.

    1933   *Paltodus simplex* Branson and Mehl, p. 42-3, pl. 3, fig. 4.

non   1947   *Paltodus acostatus* Branson and Branson, p. 554, pl. 82, figs 1-5, 23-24 [= ? *P. equicostatus*].

non   1947   *Paltodus unicostatus* Branson and Mehl; Branson and Branson [*partim*], p. 554, pl. 82, figs 7, 11-16 [= ? *P. equicostatus*].

    v 1953   *Paltodus acostatus* Branson and Branson; Rhodes, p. 296-7, pl. 22, figs 163-164, pl. 23, figs 212-213.

    v 1953   *Paltodus equicostatus* Rhodes, p. 297, pl. 22, figs 162, 165.

    v 1953   *Paltodus unicostatus* Branson and Mehl; Rhodes, p. 298, pl. 22, figs 155-156, pl. 23, figs 214-216.

non   v 1953   *Paltodus unicostatus* Branson and Mehl; Rhodes, p. 298, pl. 21, figs 84-88 [= *Panderodus equicostatus*].

non 1957 *Paltodus ? unicostatus* Branson and Mehl; Glenister, p. 729, pl. 85, fig. 1 [=
Panderodus panderi].

1957 *Paltodus acostatus* Branson and Branson; Glenister, p. 727-8, pl. 85, fig. 7.

? 1957 *Paltodus gracilis* Branson and Mehl; Glenister [*partim*], p. 728, pl. 85, fig. 2-3, 5.

non 1959 *Panderodus unicostatus* (Branson and Mehl); Sweet, Turco, Warner and Wilkie, p.
1057, pl. 131, fig. 3 [= *P. equicostatus*].

? 1965 *Paltodus unicostatus* Branson and Mehl; Philip, p. 109, pl. 8, fig. 9.

? 1965 *Paltodus acostatus* Branson and Branson; Philip, p. 108, pl. 8, figs 10, 23, 43.

non 1966 *Panderodus unicostatus* (Branson and Mehl); Clark and Ethington [*partim*], p. 683,
pl. 82, fig. 17 [= ? *P. equicostatus*].

? 1966 *Panderodus* sp. Barnett, Kohut, Rust, and Sweet, pl. 58, fig. 3.

1966 *Panderodus gracilis* (Branson and Mehl); Bergström and Sweet, p. 355-9, pl. 35,
figs 1-6.

? 1966 *Panderodus compressus* (Branson and Mehl); Oberg, p. 140, pl. 15, fig. 8.

? 1966 *Panderodus intermedius* (Branson, Mehl and Branson); Oberg, p. 140, pl. 15, fig.
17.

? 1966 *Panderodus gracilis* (Branson and Mehl); Oberg, p. 140, pl. 16, fig. 3.

? 1966 *Panderodus* sp. D Ethington and Schumacher, p. 470, pl. 69, fig. 9.

non 1967 *Panderodus unicostatus unicostatus* (Branson and Mehl); Rexroad, p. 46, pl. 4, figs
1-2 [= *P. equicostatus*].

non 1967 *Panderodus unicostatus* (Branson and Mehl); Igo and Koike, p. 21-22, pl. 1, figs
12-14 [= *P. langkawiensis*].

1969 *Panderodus denticulatus* Schwab, p. 522-4, text-fig. 1 A-C.

non 1970 *Panderodus unicostatus unicostatus* (Branson and Mehl); Pollock, Rexroad and
Nicoll, p. 758, pl. 114, figs 26-28 [= *P. equicostatus*].

? 1971 *Panderodus* n. sp. Rexroad and Craig, p. 698, pl. 81, figs 26-27.

? 1971 *Panderodus gracilis* (Branson and Mehl); Rexroad and Craig, p. 695-6, pl. 81, figs
28-29.

* 1971 *Panderodus unicostatus* (Branson and Mehl); Rexroad and Craig, p. 697-8, pl. 81,
figs 30-33 [kop. Branson and Mehl 1933], 34.

1971 *Panderodus simplex* (Branson and Mehl); Rexroad and Craig [*partim*], p. 696-7, pl.
81, figs 35-37 [kop. Branson and Mehl 1933], 38.

non 1972 *Panderodus unicostatus* (Branson and Mehl); Aldridge, p. 205-6, pl. 9, figs. 5-6. [=
? *P. equicostatus*].

non 1972 *Panderodus unicostatus unicostatus* (Branson and Mehl); Rexroad and Nicoll, pl. 1,
figs 46-47 [= ? *P. equicostatus*].

non 1972 *Panderodus unicostatus* n. subsp. (Branson and Mehl); Rexroad and Nicoll, p. 68,
pl. 2, fig. 38 [= ? *P. equicostatus*].

non   1972 *Panderodus unicostatus serratus* Rexroad; Rexroad and Nicoll, pl. 2, fig. 40 [= ? *P. equicostatus*].

      1972 *Panderodus simplex* (Branson and Mehl); Miller, p. 562, pl. 1, figs 10-11.

      1972 *Panderodus unicostatus unicostatus* (Branson and Mehl); Miller, p. 563, pl. 1, figs 12-14.

  ? 1973 *Panderodus simplex* (Branson and Mehl); Pollock and Rexroad, pl. 1, fig. 1.

  ? 1973 *Panderodus gracilis* (Branson and Mehl); Pollock and Rexroad, pl. 1, figs 2-3.

  ? 1973 *Panderodus unicostatus* (Branson and Mehl); Pollock and Rexroad, pl. 1, figs 4-5.

  ? 1973 *Panderodus* n. sp. Pollock and Rexroad, p. 83, pl. 1, fig. 6.

non   1975 *Panderodus unicostatus unicostatus* (Branson and Mehl); Saladzhius, pl. 2, figs 5-6 [= *P. equicostatus*].

non   1976 *Panderodus unicostatus* (Branson and Mehl); Cooper [*partim*], p. 213-4, pl. 1, figs 1-6 [= ? *P. equicostatus*].

non   1976 *Panderodus unicostatus* (Branson and Mehl); Cooper, p. 213-4, pl. 1, fig. 7 [= *P. staufferi*].

      1977 *Panderodus* sp. nov. Barrick, p. 57, pl. 1, figs 7-8.

      1977 *Panderodus unicostatus* (Branson and Mehl); Barrick, p. 56-7, pl. 3, figs 1-2, 5-6.

  ? 1977 *Panderodus gracilis* (Branson and Mehl); Liebe and Rexroad, pl. 2, fig. 23.

  ? 1977 *Panderodus unicostatus* (Branson and Mehl); Liebe and Rexroad, pl. 2, fig. 24.

      1977 *Panderodus simplex* (Branson and Mehl); Liebe and Rexroad, pl. 2, fig. 25.

  ? 1977 *Panderodus gracilis* (Branson and Mehl); Barnes, p. 107, pl. 3, figs 6-7.

non   1978 *Panderodus unicostatus* (Branson and Mehl); Helfrich [*partim*], pl. 1, fig. 1. [= ? *P. panderi*].

  ? 1978 *Panderodus unicostatus* (Branson and Mehl); Helfrich [*partim*], pl. 1, fig. 2.

non   1978 *Panderodus unicostatus* (Branson and Mehl); Miller, pl. 1, figs 1-3 [= *P. equicostatus*].

      1978 *Panderodus gracilis* (Branson and Mehl); Miller, pl. 1, fig. 7.

      1978 *Panderodus unicostatus* (Branson and Mehl); Rexroad, Noland and Pollock, p. 11, pl. 1, figs 6-8.

non v 1979 *Panderodus unicostatus* (Branson and Mehl); Aldridge, pl. 2, figs 17-22 [= *P. gracilis*].

      1980 *Panderodus* sp.(p). Merrill, fig. 5 (16-20).

      1981 *Panderodus gracilis* (Branson and Mehl); McCracken and Barnes, p. 85-86, pl. 1, figs 1-12,15.

  ? 1981 *Panderodus serratus* Rexroad s.f.; McCracken and Barnes, p. 86-87, pl. 2, fig. 28.

  ? 1981 *Panderodus* n. sp. A s.f. McCracken and Barnes, p. 87, pl. 1, fig. 13.

      1981 *Panderodus gracilis* (Branson and Mehl); Nowlan, pl. II, figs 12, 19, pl. VI, figs 22-23.

1981 *Panderodus serratus* Rexroad; Nowlan, pl. III, fig. 21.

1982 *Panderodus unicostatus* (Branson and Mehl); McCracken and Barnes, pl. 2, fig. 1.

? 1982 *Panderodus gibber* Nowlan and Barnes; Lenz and McCracken, pl. 2, fig. 1.

1982 *Panderodus gracilis* (Branson and Mehl); Lenz and McCracken, pl. 2, figs 2, 5-6, 8, 12, 15.

1983 *Panderodus unicostatus* (Branson and Mehl); Mabillard and Aldridge, pl. 4, figs 9-14.

? 1983 *Panderodus* spp. Mabillard and Aldridge [*partim*], pl. 4, figs 15, 18.

? 1983 *Panderodus* cf. *P. serratus* Rexroad; Nowlan, pl. 3, fig. 11.

? 1983 *Panderodus gibber* Nowlan and Barnes; Nowlan, pl. 3, fig. 14.

? 1983 *Panderodus clinatus* McCracken and Barnes; Nowlan [*partim*], pl. 3, fig. 18, 28.

1984 *Panderodus serratus* Rexroad; Stouge and Stouge [*partim*], pl. 2, figs 23-26.

? 1987 *Panderodus gracilis* (Branson and Mehl); McCracken, pl. 2, figs 14, 17.

1987 *Panderodus unicostatus* (Branson and Mehl); Smith *et al.*, fig 6.5 A-I.

non   1987 *Panderodus unicostatus* (Branson and Mehl); Mawson, pl. 41, figs 12-13. [= ? *P. equicostatus*]

? 1988 *Panderodus gracilis* (Branson and Mehl); Nowlan and McCracken (in Nowlan *et al.*), p. 21, pl. 7, figs 1-10, 12-13, 19.

non   1989 *Panderodus unicostatus* (Branson and Mehl); Sorentino, pl. 7, figs 12-13, 15-16, 20. [= ? *P. equicostatus*].

non   1989 *Panderodus unicostatus* (Branson and Mehl); Wilson, pl. 1, figs 17-22. [= ? *P. equicostatus*].

non   1989 *Panderodus unicostatus* (Branson and Mehl); Mawson and Talent, pl. 8, fig. 17. [= ? *P. equicostatus*].

1990 *Panderodus gracilis* (Branson and Mehl); Uyeno, p. 69-70, pl. 1, figs 14, 19-20.

1990 *Panderodus unicostatus* (Branson and Mehl); Uyeno, p. 70-71, pl. 1, figs 27-28, 32, pl. 4, fig. 10.

non   v 1990 *Panderodus unicostatus* (Branson and Mehl); Armstrong, p. 108-110, pl. 17, figs 1-7 [kop. Aldridge 1979 = *P. gracilis*].

Syntypes. Paltodus unicostatus Branson and Mehl,1933, p. 42, pl. 3, fig. 3, two 'co-types' from the Bainbridge Formation near Lithium, Missouri, U.S.A..

Emended diagnosis. A species of *Panderodus* with gradually curved elements and elongate, transversely rounded bases, forming 75 percent of element length. White matter extends from the cusp apex over the dorsal margin of the deep basal cavity.

Descriptions. Pa element. Elongate, spatulate element where the dorsal margin gradually curves into the proclined cusp. The cusp is torted towards the unfurrowed face, which is excavated along the dorsal margin and rounded in it s lower two-thirds, with a sharp edge along the ventral margin between the basal wrinkle zone and the cusp. The furrowed face is rounded, with a broad carina below the furrow at two-thirds base height; the area above the furrow is more flattened.

Pb element. Dorsal and ventral margins of the base curved throughout the base, gradually converging and steepening to form an elongate, recurved cusp. A slight dorsal heel is developed from the basal margin over the basal wrinkle zone. Both lateral faces possess rounded carinae, with a slight ventral keel, that occupy the full element height. On the furrowed face this feature is depressed slightly by the furrow at two-thirds base height.

M element. Refer to Branson and Mehl's (1933, p. 42) description of the type material.

Sa element. Described by Barrick (1977, p. 57) as the Sa element of *Panderodus* sp. nov..

S_1 *element.* Two elements are referred to this position, one being high based and comparatively short, whilst the other is low based and extremely elongate.

The first of these elements is similar to the M, but is distinguished by a lack of torsion and the occasional presence of a weak costa on the furrowed face.

The second element has a gradually curving dorsal margin, which converges on the similarly curved ventral margin to form the proclined cusp. The unfurrowed face is largely flattened, although a weak costa is developed apically from the basal wrinkle zone and dies out along the cusp. The furrowed face is rounded with a carina up to one-half base height. A dorsally directed costa is found on the upper shoulder of this carina and passes from the basal wrinkle zone to the cusp. The furrow is developed at two-thirds base height.

S_2 *element.* One of the elements referred to this position is similar to the elongate S_1 element described above, but differs in the presence of rounded carinae on both lateral faces and costae developed at one-third base height.

The other S_2 element is comparatively high based and triangular. The dorsal margin is more curved than the ventral, forming a shorter base than in the element described above. Rounded carinae are developed at two-thirds base height, and bear costae at one-half base height apically from the basal wrinkle along the cusp.

S_3 *element.* Described by Barrick (1977, p. 57) as **Sb** element of *Panderodus* sp. nov..

Remarks. *P. unicostatus* is readily distinguished from *P. equicostatus* by the more recurved nature of the **Pb** element in the former, and the much abbreviated cusp and white matter in the latter. The *P. unicostatus* apparatus can similarly be differentiated from *P. gracilis* by the elongate and reclined cusp in the **Pb** of the latter (Text-fig. 7.4).

Uyeno (1990; pl. 4, fig. 10) figured a serrate **M** element which has been included in synonymy. Armstrong (1990) has suggested that such elements may be minor iterative variants.

Range. Costonian: *A. tvaerensis* biozone -» Lochkovian: *pesavis/sulcatus* biozone.

Chapter 8
CONCLUSIONS AND FUTURE RESEARCH

The principal focus of this thesis has been a discussion of the palaeobiology of *Panderodus*, a coniform-bearing conodont genus. This animal is thought to have possessed a dorso-ventrally compressed bodyplan, whilst the wide distribution of this genus suggests a pelagic mode of life. The *Panderodus* skeletal apparatus is septimembrate, divisible into paired and symmetrical components. A morphological division within the paired assemblage, into anterior costate and posterior compressed elements, is interpreted as a functional differentiation into grasping and processing components respectively. Functional modelling of this oral apparatus infers a bilateral motion for the paired elements, and a dorso-ventral motion for the medial, symmetrical element. The lateral panderodontid furrow may represent a muscle or ligament scar, the insertion of such a tissue would act to move elements with respect to each other. The elements themselves are histologically formed of a tip of cellular bone, surrounded by a newly described enamel homologue. A basal body of globular cartilage is occasionally preserved in the basal cavity, and this may extend into an unmineralised basal support to the element apparatus.

The work presented in this thesis has a number of important implications for the future study of *Panderodus* and other coniform genera :-

1) Coniforms must be considered within a multielement context if progress towards a biological supergeneric classification (Chapters 2 and 7) is to be made. To achieve this, workers must consider coniform apparatuses as an equally valid component of their collections as ramiform-pectiniform genera. Apparent differences in coniform apparatus architecture will provide the basis for supergeneric classification.

2) The establishment of architectural models for multielement coniform apparatuses provides the basis for locational homology with ramiform-pectiniform bearing apparatuses. This will enable the development and subsequent application of a universally applicable notation scheme (Chapter 3).

Additionally, wider implications of these studies in conodont palaeobiology have been identified :-

3) Functional modelling of the *Panderodus* apparatus, and comparison with ozarkodinid skeletal architecture, suggests that the petromyzontids may provide a close functional analogue (Chapter 4). This functional model needs to be tested against further architectural models for other conodont genera.

4) Studies of the ultrastructure of conodont elements has identified the presence of a number of vertebrate hard tissues. This work firmly establishes the vertebrate nature of conodonts. Future work in this field can now be focus ed on applying the techniques developed in Chapter 5 to confirm or reject problematic taxa from the conodonts.

5) Using a cladistic approach with this database, it is possible to place the conodonts within the phylogeny of the early vertebrates (Chapter 6). With the inclusion of the conodonts, the fossil record of early vertebrate development has been greatly expanded. Early vertebrates are now recognised from a much wider range of ecological habitats than had hitherto been realised.

It is now clear that *Panderodus* is anything but a 'simple cone'.

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Plate 1

Panderodus unicostatus (Branson and Mehl) animal from the Llandovery Brandon Bridge Formation of Waukesha County, Wisconsin.

FIGURE 1) *Panderodus* animal, anterior to the top. White arrow indicates the position of the conodont apparatus; UW 4001/7a Geology Museum, University of Wisconsin, Madison, x15. Specimen previously illustrated by Mikulic *et al.* (1985a, fig. 2G) and Smith *et al.* (1987, fig. 6.1).

FIGURE 2) Conodont assemblage from the Waukesha conodont animal; UW 4001/7b (counterpart). Directional back-scattered micrograph, taken at 5kV, of latex cast, x90. All paired elements display their furrowed faces, the anterior pair are **arcuatiform**, and the large element towards the posterior is a **falciform**. Specimen first illustrated by Smith *et al.* (1987, fig. 6.7).
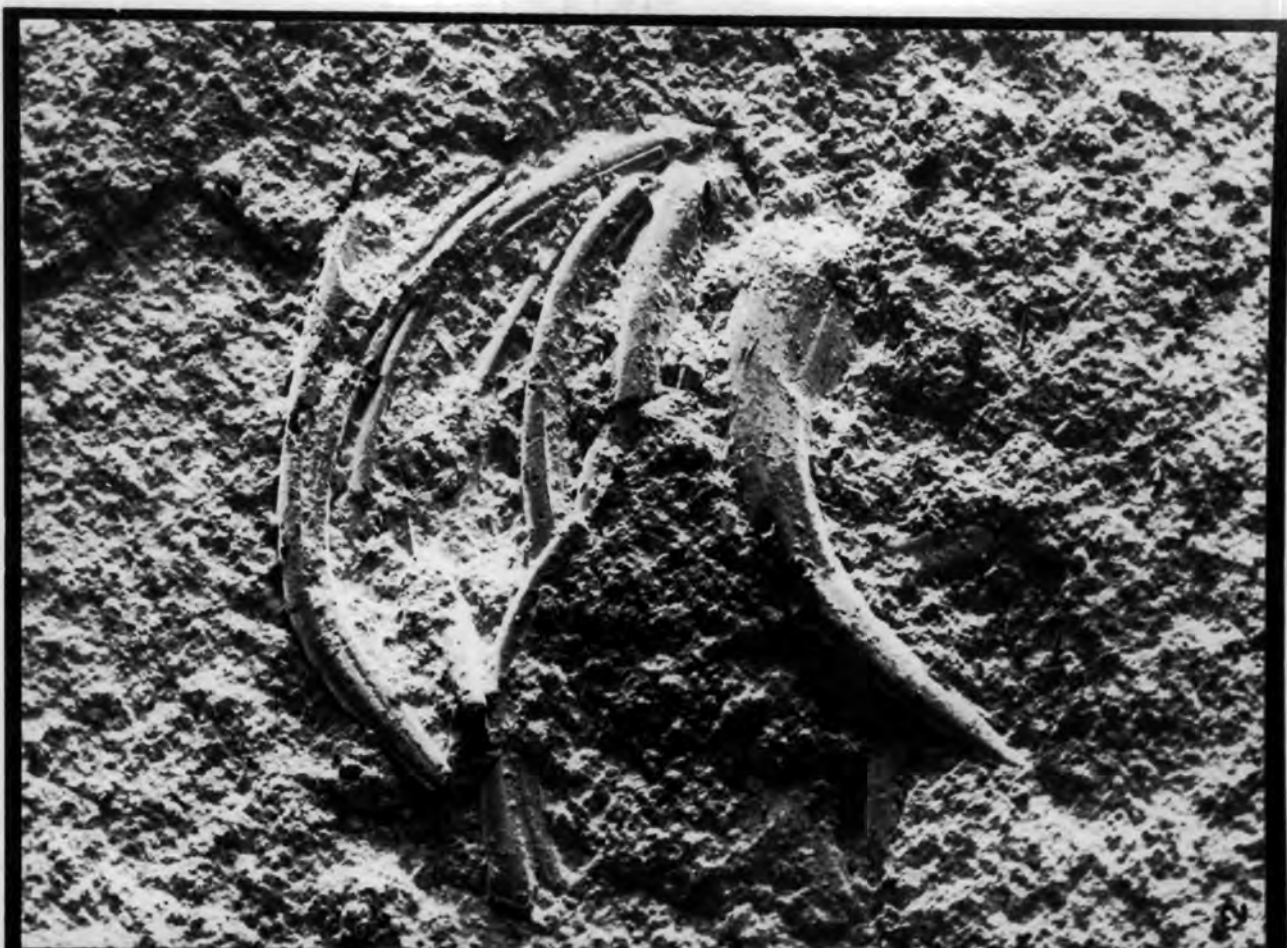
Plate 3

Panderodus clusters from the Llandovery Brandon Bridge Formation, Waukesha County, Wisconsin.

FIGURES 1 and 2) Alternate lateral views of a cluster consisting of at least eleven *P. langkawiensis* (Igo and Koike) elements. Opposed furrow orientations suggest that this is a deformed specimen. Specimen No. TG4/207; x 55.

FIGURES 3, 4 and 5) Alternate lateral views of a cluster of eight *P. langkawiensis* (Igo and Koike) elements. 3) is a lateral view of two **graciliform** elements which broke away from the main cluster during handling. Opposed furrow orientations suggest a deformed relationship. Specimen No. TG4/205; 3) x 110; 4 and 5) x 55.

FIGURES 6 and 7) Alternate lateral views of a fragmentary multielement cluster of *Panderodus unicostatus* (Branson and Mehl). Specimen No. TG4/195A; x 55.

FIGURE 8) Lateral view of a cluster consisting of two **graciliform** elements of *Panderodus unicostatus* (Branson and Mehl). Specimen No. TG4/203A; x 55.

Specimens are currently deposited in the Dept. of Geological Sciences, University of Durham.
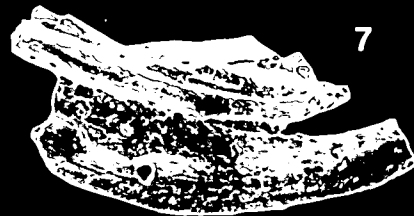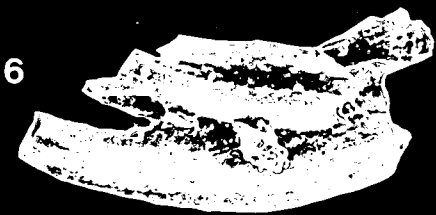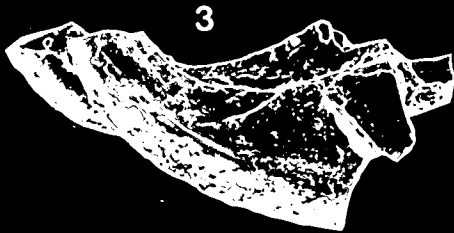
Plate 4

Panderodus clusters from the Llandovery Brandon Bridge Formation, Waukesha County, Wisconsin.

FIGURES 1 and 2) Alternate lateral views of a disrupted three element cluster of *Panderodus unicostatus* (Branson and Mehl) including a **falciform** element (largest component) and an **aequaliform** element (arrowed). Specimen No. IJSL/C/1; x 55.

FIGURES 3, 4, 5, 6, 8, 9, 10) Lateral views of disrupted multielement clusters of *Panderodus unicostatus* (Branson and Mehl). Specimen Nos IJSL/C/2, 3, 4, 5, 7, 8, 9 respectively; x 55.

FIGURE 7) *Panderodus langkawiensis* (Igo and Koike), lateral view of a disrupted three element cluster. Specimen No. IJSL/C/6; x 55.

Specimens currently deposited in the Dept. of Geology, University of Leicester.
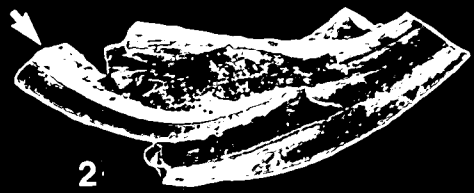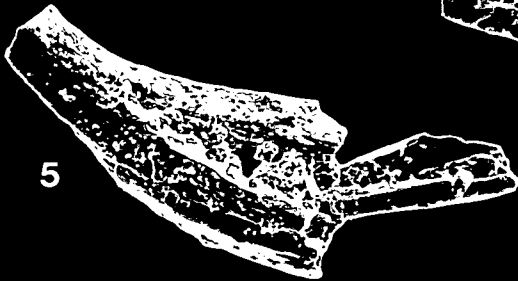
Plate 6

Histology of *Panderodus unicostatus* (Branson and Mehl) from the Ludlow of the tramway section, Netherton, West Midlands.

FIGURE 1) Scanning secondary electron micrograph of a longitudinal section through a **Pb** element showing the relationship between white matter, lamellar crown and basal cavity; there is no basal body occupying the basal cavity in this specimen (Specimen No. BU 2155; x 100).

FIGURE 2) Detail of one of the boxed areas in 1) showing the asymptotic growth lamellae of the lamellar crown (lc), and the basal cavity (bc). The form of the lamellae indicates that basal expansion dominated during the later stages of growth; x 800.

FIGURE 3) Subparallel orientation of individual crystallites within the lamellar tissue. This crystallite orientation is diagnostic of 'parallel enamel'. The porous interlamellar spaces are thought to result from hiatuses in the mineral phase of growth; x 7500.

FIGURE 4) Detail of white matter, boxed in 1), showing well-developed lacunae (l) and interconnecting canaliculi (c). The presence of cell spaces, interconnecting canaliculi, and the massive groundmass are indicative of cellular dermal bone; x 1100.

Specimen is deposited in the Lapworth Museum, School of Earth Sciences, University of Birmingham.

FIGURE 5) Transverse cross-section through a **Pb** element, Specimen No. 2/91/10; x 525.

FIGURE 6) Detail of the furrow region in this specimen. The deflection of the growth lamellae (black arrow) to accommodate this feature argues against the 'radial compartments' described by Barnes *et al.* (1973) and Lindström and Ziegler (1981: cf. Text-fig. 5.13); x 1850.

Specimen is currently deposited in the Dept. of Geological Sciences, University of Durham.

Figures 1-6. Labels visible: bc, lc (Figure 2); c, l, l (Figure 4); numbered panels 1, 2, 3, 4, 5, 6.
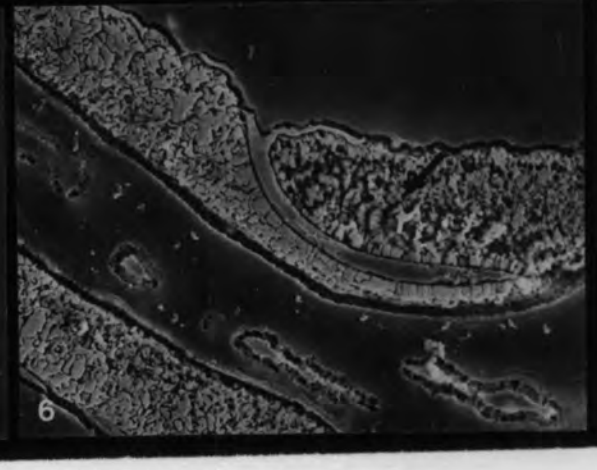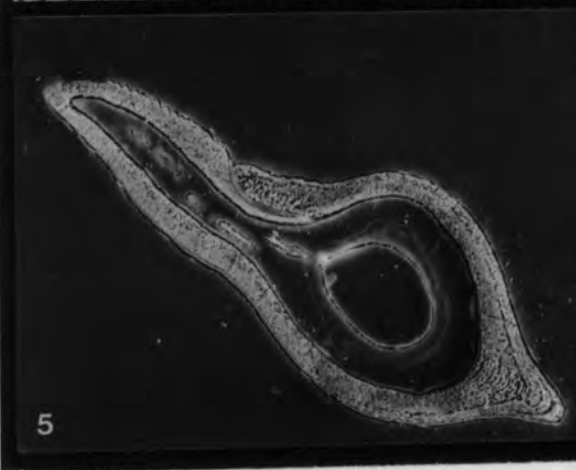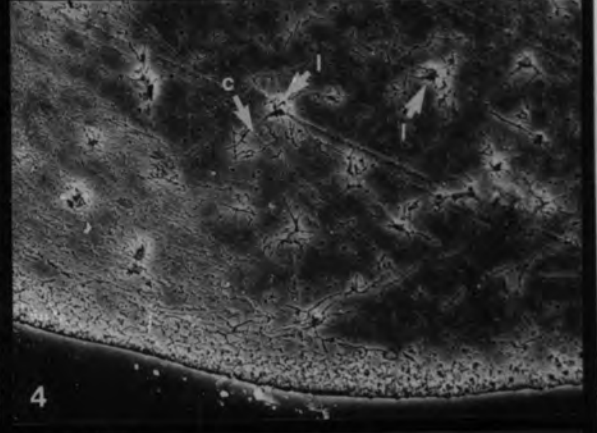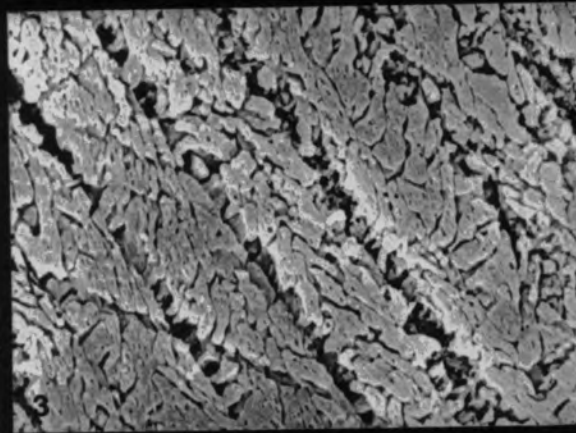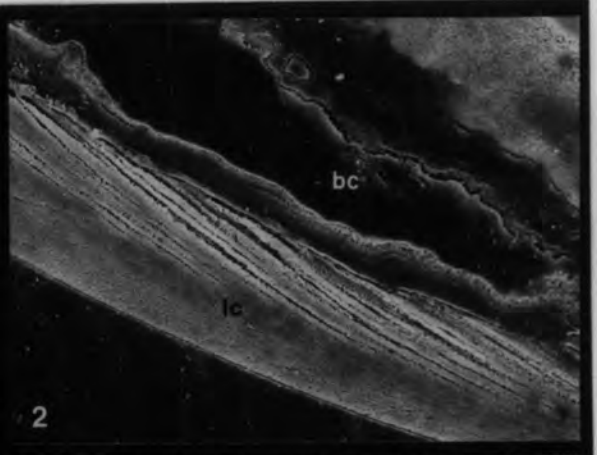
Plate 7

Histology of *Parapanderodus striatus* (Graves and Ellison) from the late Canadian (Early Ordovician) of Kronprins Christian Land, North Greenland (Figs 1-4); *Panderodus staufferi* (Branson, Mehl and Branson) from the Wenlock Upper Visby beds at Ireviken 3, Götland, Sweden (Fig. 5); and enamel from the amphibian *Mastodontosaurus giganteus* from the Middle Triassic of Germany.

FIGURE 1) Scanning secondary electron micrograph of a longitudinal section through an element of *Parapanderodus striatus*, showing the relationship between white matter (wm) and the lamellar crown (lc). Specimen No. MGUH 21142; x 100.

FIGURE 2) Detail of the relationship between the core of cellular white matter and the lamellar crown. The white matter shows a sharp contact with the surrounding tissue, and a cone-in-cone structure is developed; x 1125.

FIGURE 3) Subparallel orientation of the individual crystallites within the lamellar tissue (cf. Pl. 6, fig. 3); x 5850.

FIGURE 4) Transmitted light photomicrograph showing a 'string' of cellular white matter (wm) running through the element core. The lower black line represents the edge of the specimen; x 45.

Specimen is deposited in the Geological Museum, Copenhagen.

FIGURE 5) Reflected light photomicrograph of a polished section through an S_{1-2} element of *Panderodus staufferi*. The scalloped nature of the growth lamellae in the basal body (bb) is apparent. Specimen No. 2/91/2; x 77.

Specimen is currently deposited in the Dept. of Geological Sciences, University of Durham.

FIGURE 6) Scanning secondary electron micrograph of an etched section through the monotypic enamel of a tooth of *Mastodontosaurus giganteus*. Note the dove-tailed structure, or decussation, and the orientation of the crystallites perpendicular to the upper, external surface. Photomicrograph taken from Smith (1992; fig. 6D). Specimen No. BMNH 33091, x 9500.

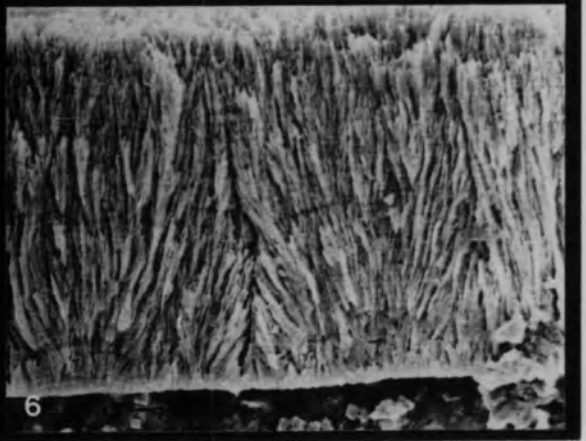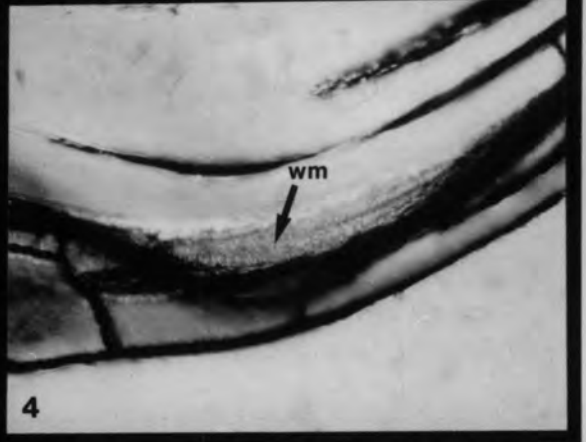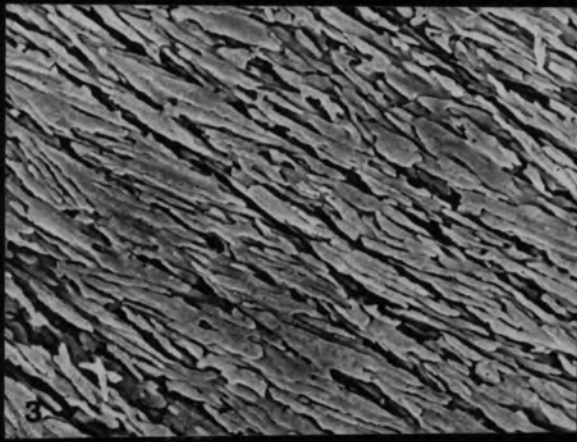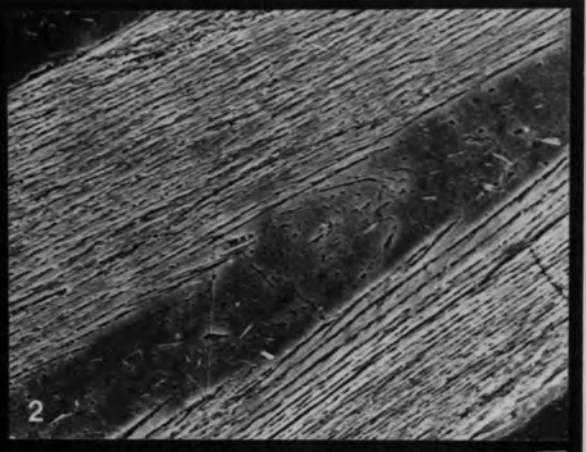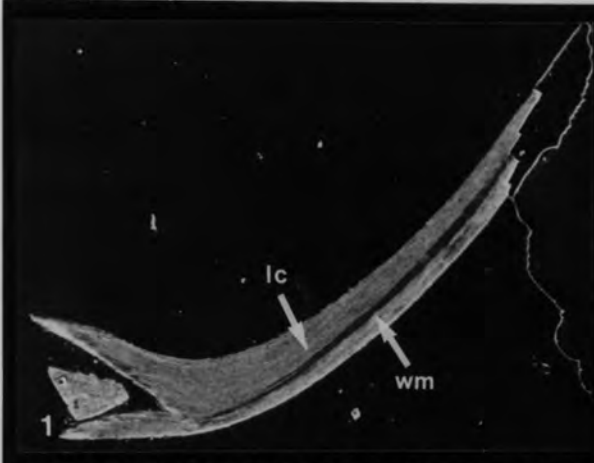Specimen is deposited in the Natural History Museum, London.

Plate 8

Histology of *Cordylodus* Pander, from the Tremadoc of Maardu, Estonia.

FIGURE 1) Scanning secondary electron micrograph showing differentiation into crown tissue (**ct**) and basal body (**bb**). Specimen No. BU 2156, x 65.

FIGURE 2) Boxed area in 1) at higher magnification, crystallites of the crown are seen to be organised into prisms perpendicular to the growth surface; x 4785.

FIGURE 3) Detail of cusp apex, boxed in 1), showing the open and porous nature of the lamellar crown in this area (cf. Fig. 2); x 4785.

FIGURE 4) Transmitted light micrograph (a), viewed under partial Nomarski optics, and drawing (b) of the boxed area in 1). Although 'white matter' is found throughout the cusp, it is only seen as a cellular tissue within the denticle cores, where lacunae and canaliculi are seen throughout; x 215.

FIGURE 5) Scanning secondary electron micrograph of the sharp junction between the lamellar crown (left) and the spherulitic basal body (right). Compare the development of Liesegang waves at the junction between the basal body and the crown ,with Fig. 6 taken in the core of the basal body; x 1195.

FIGURE 6) Detailed micrograph from the centre of the basal body showing the spherulitic appearance of this tissue. The internal appearance of this tissue is directly comparable with globular cartilage found in association with the Harding Sandstone vertebrates; x 1195.

Specimen is deposited in the Lapworth Museum, School of Earth Sciences, University of Birmingham.
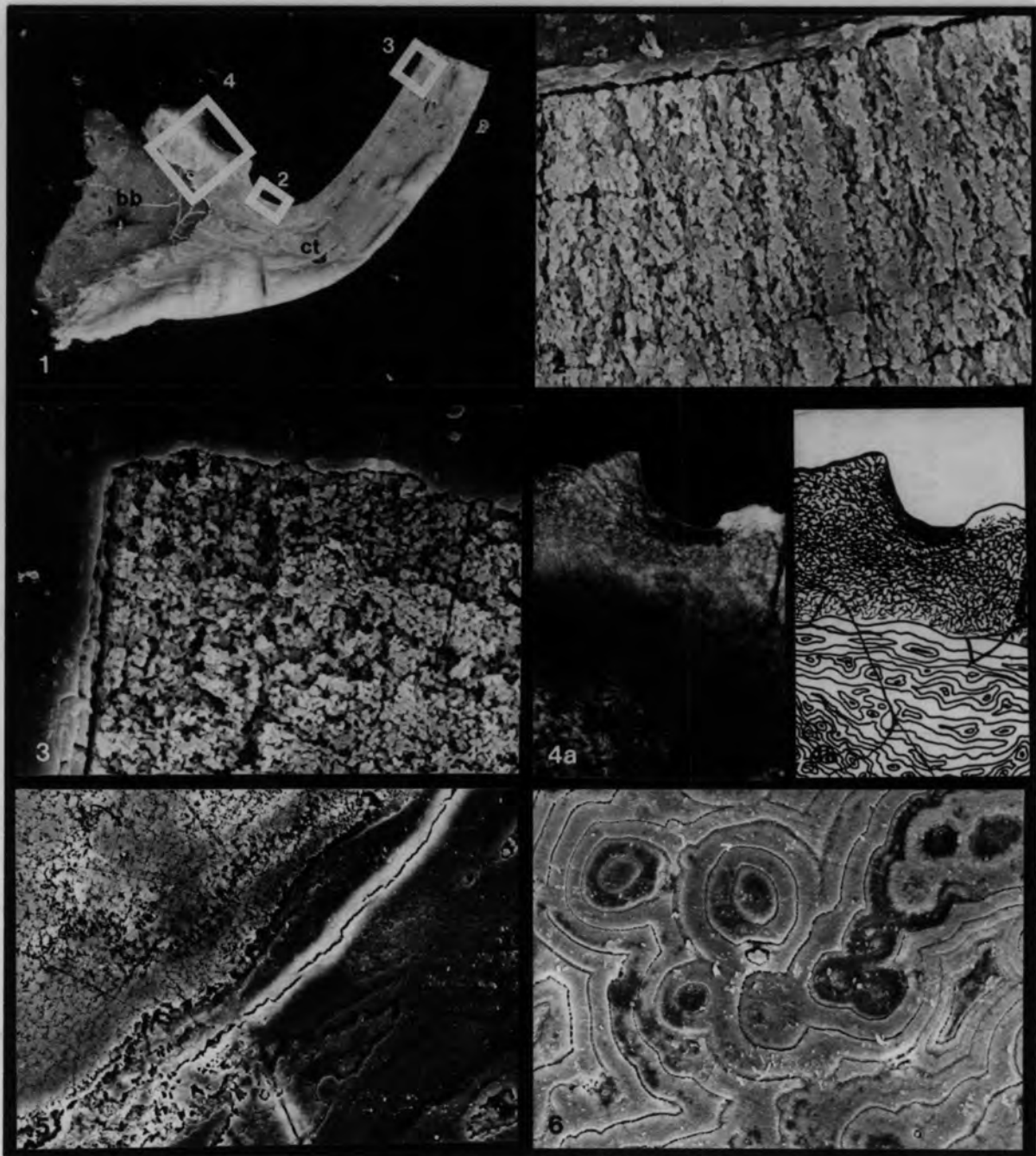
Plate 9

Histology of *Ozarkodina confluens* (Branson and Mehl) from the Llandovery of Själsö, Götland, Sweden.

FIGURE 1) Scanning secondary electron micrograph of a ramiform element of *Ozarkodina confluens*, showing isolated denticle cores of white matter (**wm**) surrounded by lamellar crown (**lc**). Specimen No. 4/91/19, x 110.

FIGURE 2) Detail of the area between two of the denticle cores, showing the crystalline lamellar crown (**lc**) and the sharp boundary with the massive, porous, white matter (**wm**); x 2190.

FIGURE 3) Core of white matter viewed with secondary electrons **a)** and backscattered electrons **b)**. Although the surface shows a series of isolated pores, sub-surface imaging with backscattered electrons shows the interconnecting nature of these canaliculi; x 2245.

Specimen is currently deposited in the Dept. of Geological Sciences, University of Durham.

FIGURE 4) Line drawing of an oblique section through a **Pa** element of *Ozarkodina confluens* showing the tissue distribution. Cellular white matter forms the denticle cores surrounded by lamellar crown tissue. Specimen No. BU 2157, x 120.

FIGURE 5) Scanning secondary electron micrograph of an etched surface of the lamellar crown tissue showing orientation of the individual crystallites perpendicular to the growth surface. Aligned steps in the crystallite rods represent the growth lamellae; x 5470.

FIGURE 6) Transmitted light micrograph, taken with partial Nomarski optics, of the area indicated in 1). A mass of lacunae interconnected with canaliculi form the denticle roots (arrowed). The superimposition of this cellular white matter onto the surrounding lamellar crown tissue is a cut artefact; x 600.

Specimen is deposited in the Lapworth Museum, School of Earth Sciences, University of Birmingham.
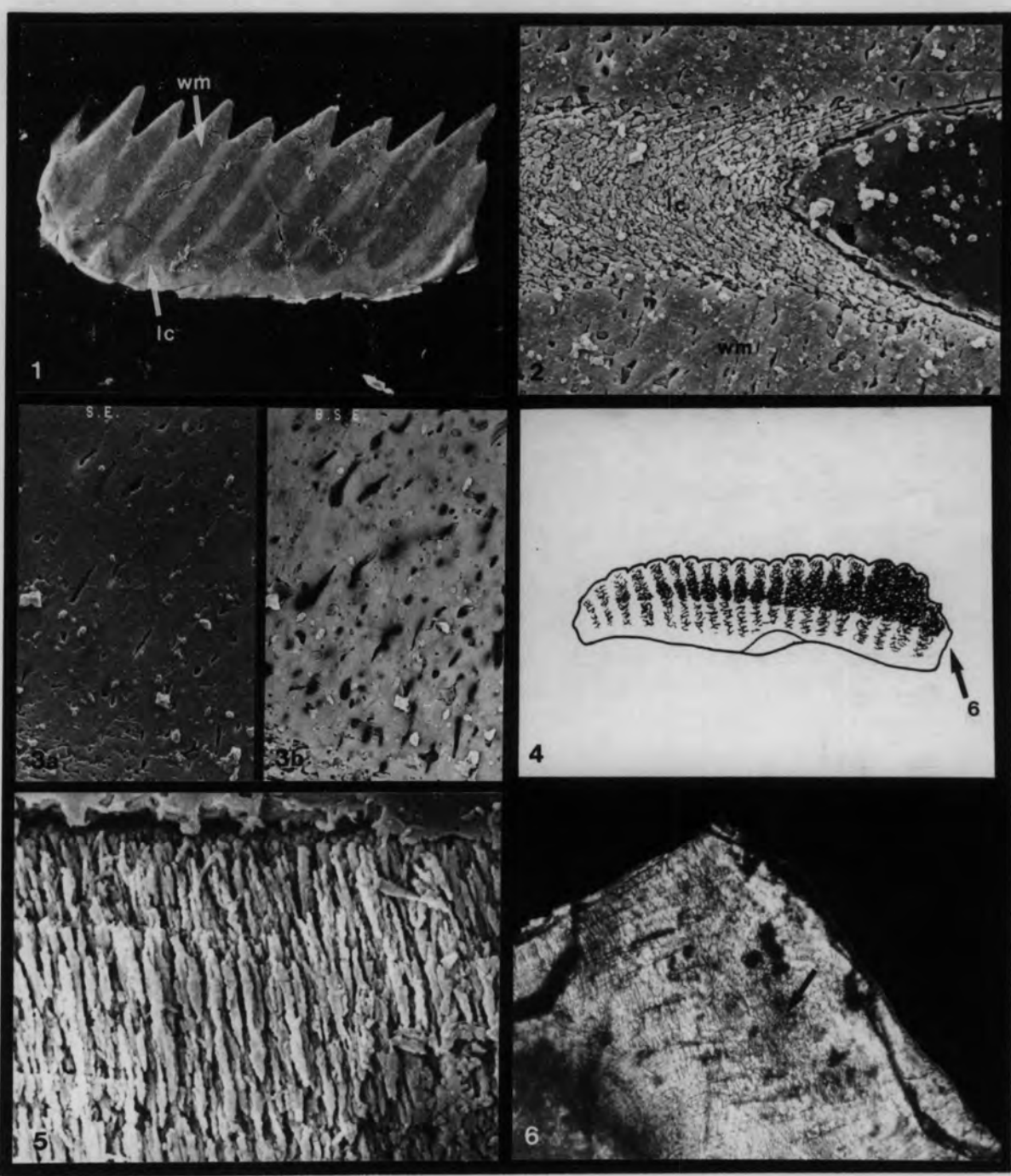
Plate 10

Histology of *Dapsilodus* Cooper from the Ludlow Bainbridge Formation of Lithium, Missouri, and *Eoconodontus notchpeakensis* from the Late Cambrian of the Ibex area, Texas.

FIGURE 1) Transmitted light micrograph of a longitudinal section through an S element of *Dapsilodus obliquicostatus*. Arrow indicates a region of dense white matter. Specimen No. 4/91/1, x 115.

FIGURE 2) Scanning secondary electron micrograph of area boxed in 1) following etching. Lamellar crown is formed of crystallites which are orientated perpendicular to the growth surface, and hence cross-cutting the growth lamellae; x 1840.

FIGURE 3) Detail of boxed area in 1) showing the lamellar crown surrounding the apex of the basal cavity. The tissue at the centre of the micrograph is dense, passing outward into more porous material, forming the less dense 'white matter' seen in Fig. 1); x 1840.

FIGURE 4) Scanning secondary electron micrograph of a longitudinal section through an element of *Eoconodontus notchpeakensis*. Specimen No. 6/91/6, x 165.

FIGURE 5) Detail of white matter found in the cusp of this specimen. The acrystalline nature of this tissue, penetrated by a series of interconnecting pores is indicative of the cellular bone illustrated in Pl. 6, fig. 4; Pl. 7, fig. 2; Pl. 8, fig. 4; Pl. 9, figs 3 and 6., although clearly developed lacunae are not apparent in this image; x 9050.

FIGURE 6) Fractured and etched section through the lamellar crown. Although the etch has not taken as well as in other specimens, an orientation of crystallites perpendicular to the growth surface (arrowed) is discernible; x 2655.

Specimens are currently deposited in the Dept. of Geological Sciences, University of Durham.
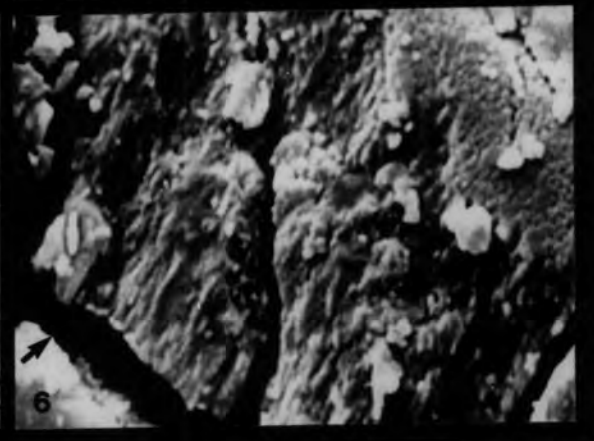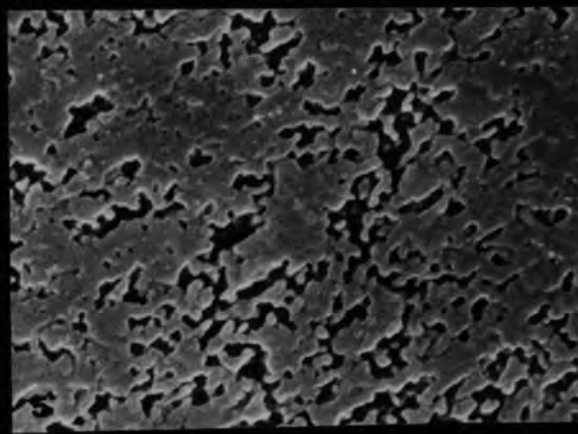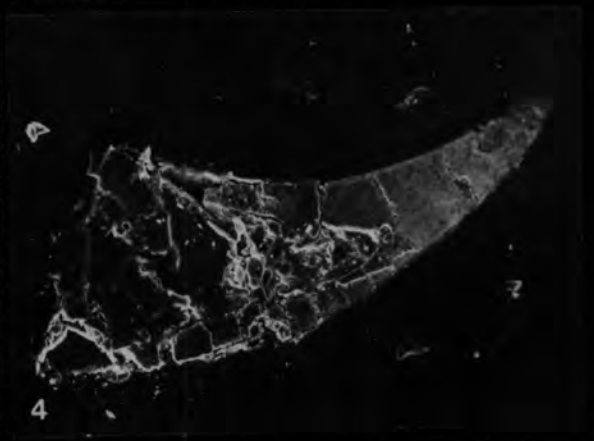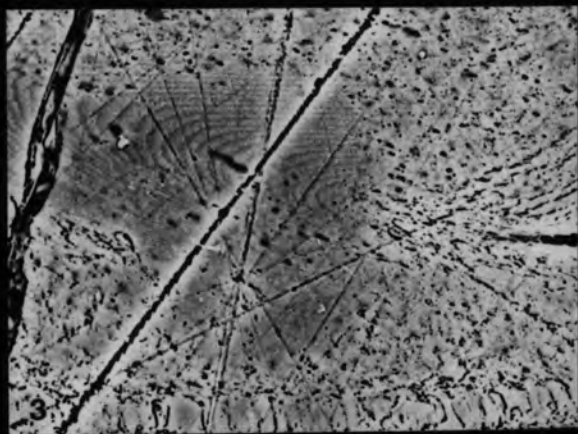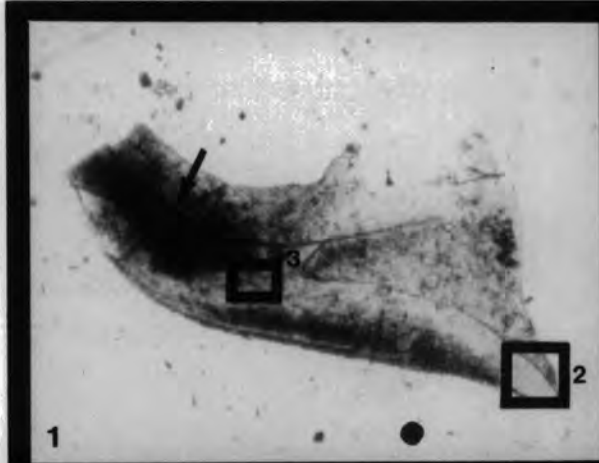
Plate 11

Histology of *Pseudooneotodus* Drygant from the Llandovery of Själsö, Götland.

FIGURES 1 and 2) Discrete element of *Pseudooneotodus* seen in dorsal and lateral views respectively. Specimen No. 23692/34-81; x 77.

FIGURE 3) Element viewed from the venter, showing the basal cavity and associated infilling; x 77.

FIGURE 4) Detail of arrowed area in 3) showing spherulitic texture of the basal infilling; x 500.

FIGURE 5) Scanning secondary electron micrograph of a transverse section through an element of *Pseudooneotodus* showing the differentiation into a lamellar crown and basal body. Specimen No. 2/91/5, x 107.

FIGURE 6) Detail of the boxed area in 5). Note the change in orientation of growth lamellae within this section of the lamellar crown; x 115.

FIGURE 7) Area of asymptotic growth lamellae seen at higher magnification. Note the folded nature of the lamellae in this section; x427.

FIGURE 8) Detail of the crystallites of the disrupted area seen in 7); x 9090.

Specimens are currently deposited in the Dept. of Geological Sciences, University of Durham.
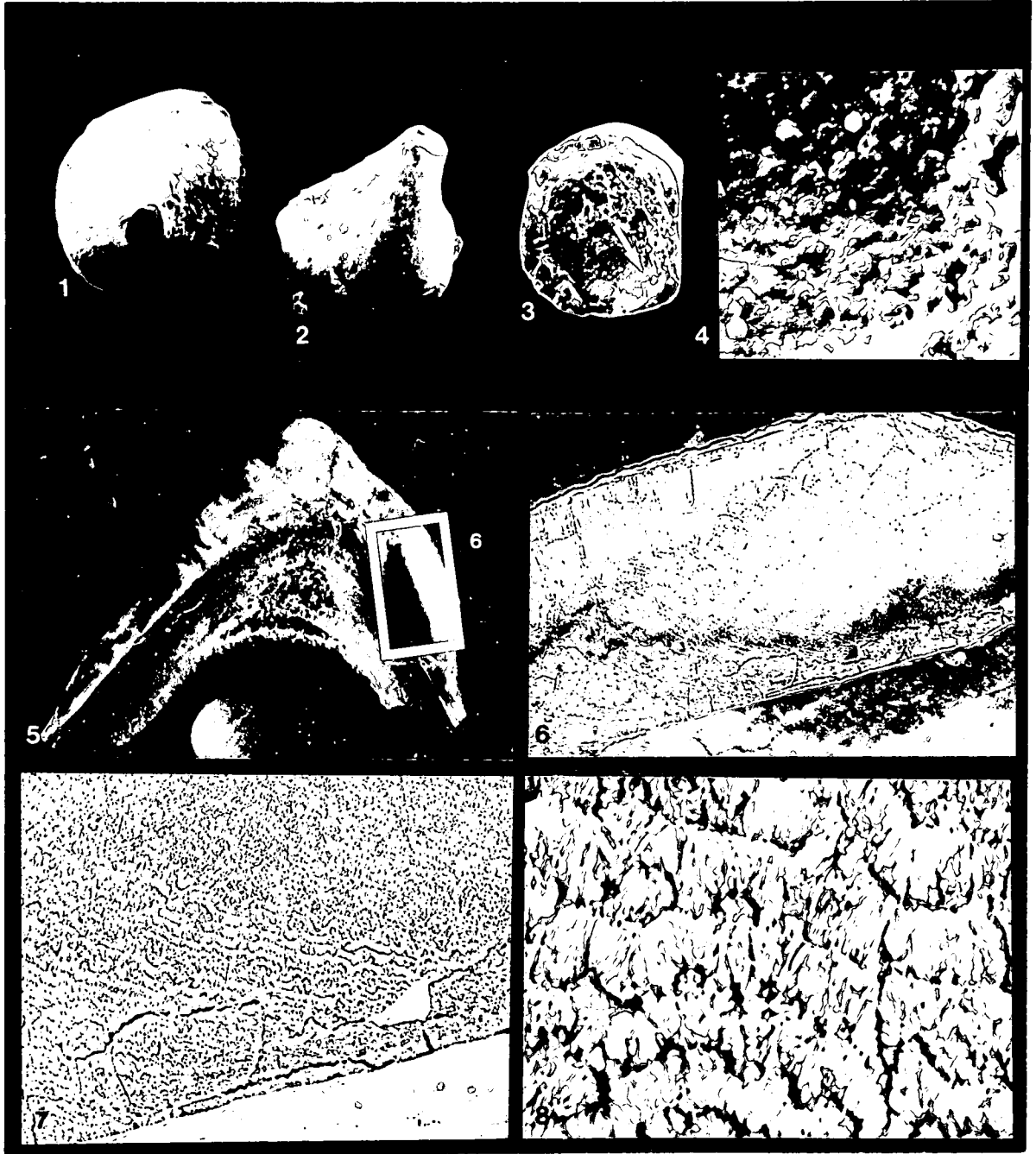
Plate 12

Histology of *Pseudooneotodus* Drygant from the Llandovery of Själsö, Götland (continued from Pl. 11).

FIGURE 1) Scanning secondary electron micrograph of the transition between the disrupted and 'normal' lamellar crown. The gradual nature of this transition suggests plastic deformation of the lower region; x 2275.

FIGURE 2) Detail of the lamellar crown showing the dove-tailed, or decussated, organisation of the crystallites perpendicular to the growth surface, and cross-cutting the growth lamellae; x 3594. Compare with the monotypic enamel of *Mastodontosaurus* illustrated in Pl. 7, fig. 6.

FIGURE 3) Junction between the lamellar crown (top) and the underlying basal body. The basal body is porous directly beneath the lamellar crown, and passes downward into a spherulitic tissue; x 1985.

FIGURE 4) Detail of the basal body directly below the lamellar crown. A series of isolated pores (arrowed) penetrate this tissue, and these may be sections through dentine tubuli; x 9885.

FIGURES 5 and 6) Areas of spherulitic basal body, showing the formation of Liesegang waves. A gradual transition from strongly mineralised 5) to weakly mineralised 6) tissue is seen away from the lamellar crown. These spherules are ten times smaller than those seen in the basal bodies of *Cordylodus* (Pl. 8, fig. 6) and *Panderodus* (Pl. 7, fig. 5); 5) x 1985, 6) x 1810.

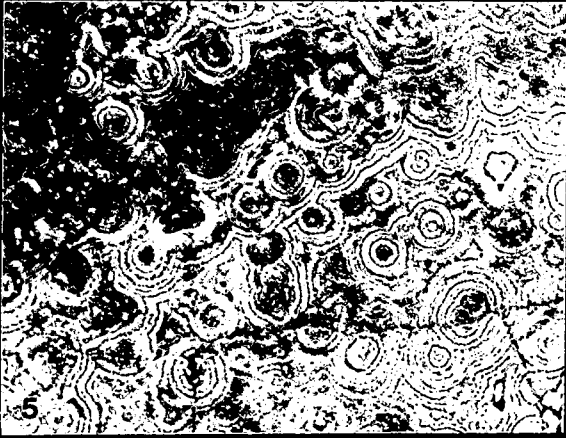Specimen is currently deposited in the Dept. of Geological Sciences, University of Durham.
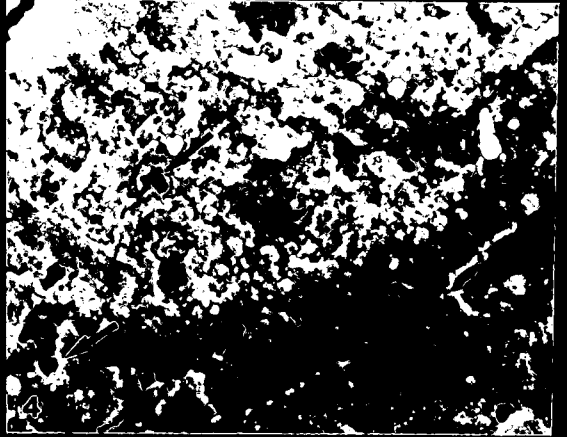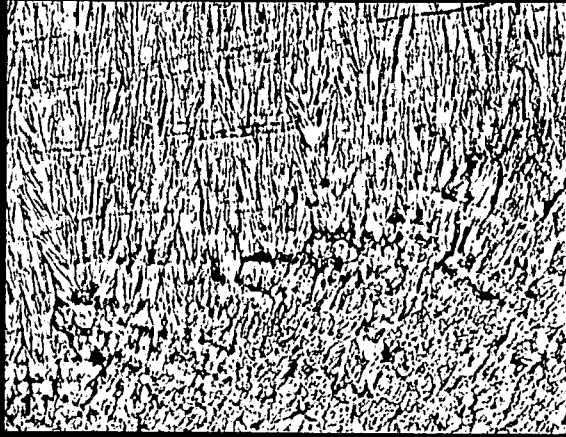
Plate 13

Panderodus equicostatus (Rhodes) from the Brassfield Formation (Brassfield Limestone) of the Cincinnati Arch Area (un-localised). All x 55.

FIGURES 1 and 2) anterior and posterior views of **Pb** element, 23692/25-28.

FIGURES 3 and 4) anterior and posterior views of 'high based' S_1 element, 23692/25-30.

FIGURES 5 and 6) anterior and posterior views of 'low based' S_1 element, 23692/26-32.

FIGURES 7 and 8) anterior and posterior views of 'low based' S_2 element, 23692/25-26A.

FIGURES 9 and 10) posterior and anterior views of 'high based' S_2 element, 23692/25-27.

FIGURES 11 and 12) posterior and anterior views of **M** element, TG4/360.

FIGURES 13 and 14) posterior and anterior views of **Pa** element, 23692/25-26B.

FIGURES 15 and 16) posterior and anterior views of S_3 element, 23692/25-25B.

FIGURES 17 and 18) lateral views of **Sa** element, 23692/25-25A.

Specimens are currently deposited in the Dept. of Geological Sciences, University of Durham.
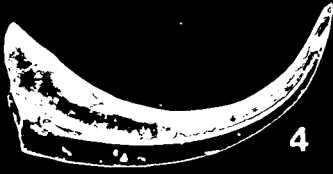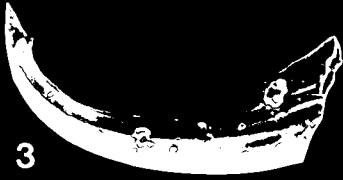
Plate 14

Panderodus gracilis (Branson and Mehl) from GGU 216773, Lafayette Bugt Formation, Washington Land, North Greenland (see Armstrong 1990). All x 55.

FIGURES 1 and 2) anterior and posterior views of Pb element, 23692/28-46.

FIGURES 3 and 4) posterior and anterior views of M element, 23692/27-37.

FIGURES 5 and 6) anterior and posterior views of S_2 element, 23692/8-4107.

FIGURES 7 and 8) posterior and anterior views of 'high based' S_1 element, 23692/27-40.

FIGURES 9 and 10) anterior and posterior views of 'low based' S_1 element, 23692/8-4110.

FIGURES 11 and 12) anterior and posterior views of 'low based' S_1 element, 23692/27-36.

FIGURES 13 and 14) anterior and posterior views of S_3 element, 23692/26-33.

FIGURES 15 and 16) lateral views of Sa element, 23692/8-4106.

FIGURES 17 and 18) posterior and anterior views of Pa element, 23692/9-4114.

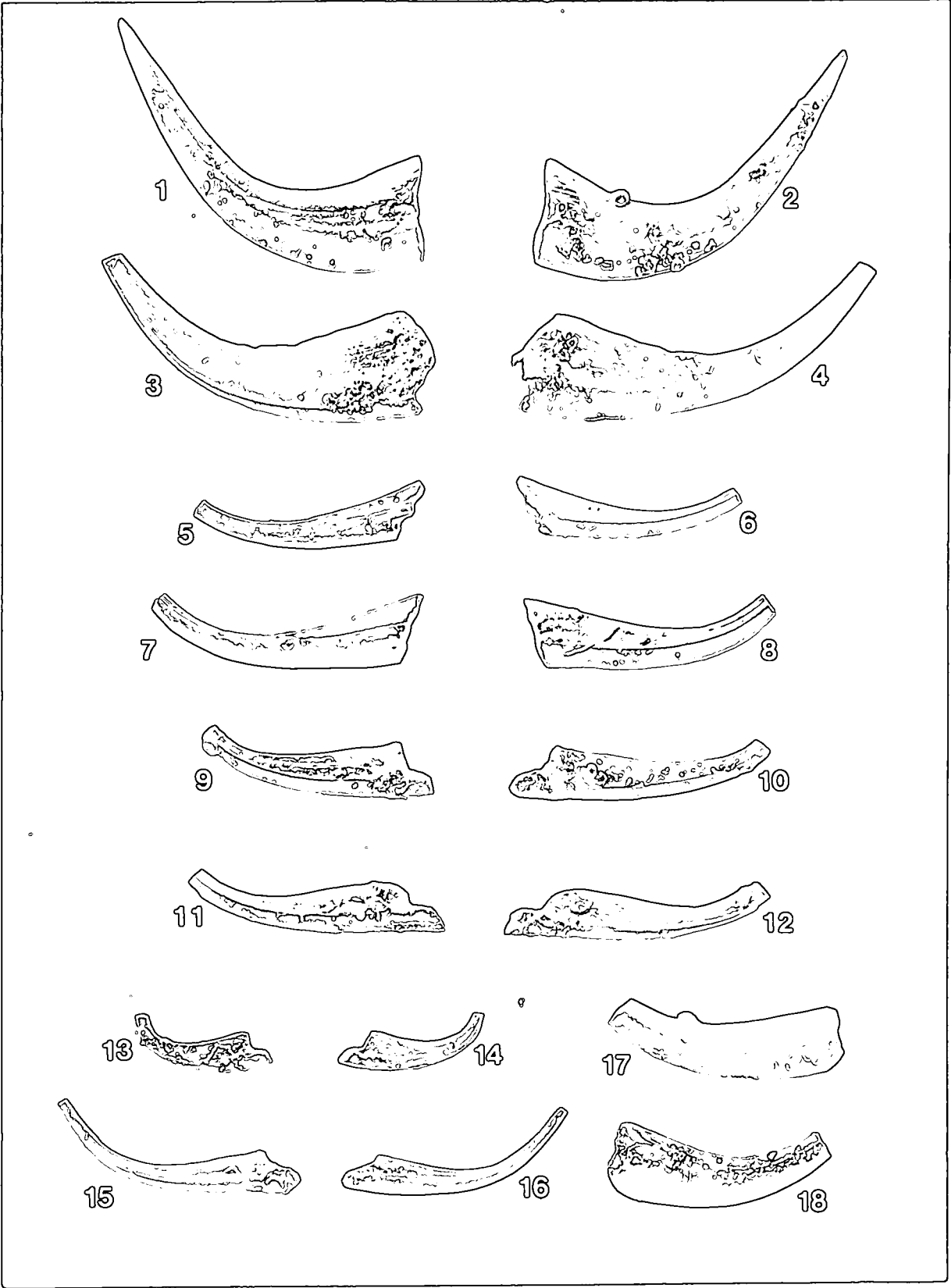Specimens are currently deposited in the Dept. of Geological Sciences, University of Durham.

Plate 15

Panderodus langkawiensis (Igo and Koike) from Nyhamn 1, Lower Visby Beds, Götland (see Laufeld 1974). All x 55.

FIGURES 1 and 2) anterior and posterior views of **Pb** element, TG4/77.

FIGURES 3 and 4) anterior and posterior views of 'low based' S_2 element, 23692/16-478.

FIGURES 5 and 6) posterior and anterior views of 'high based' S_1 element, 23692/16-476.

FIGURES 7 and 8) posterior and anterior views of **Pa** element, 23692/16-475.

FIGURES 9 and 10) lateral views of **Sa** element, 23692/16-482A.

FIGURES 11 and 12) posterior and anterior views of 'low based' S_1 element, TG4/80.

FIGURES 13 and 14) anterior and posterior views of 'high based' S_2 element, 23692/16-477.

FIGURES 15 and 16) posterior and anterior views of **M** element, 23692/21-5A.

FIGURES 17 and 18) anterior and posterior views of S_3 element, 23692/21-5B.

Panderodus feulneri (Glenister) from GGU 316839, Gonioceras Bay Member, Morris Bugt Group, North Greenland (see Tull 1988). All x 55.

FIGURES 19 and 20) anterior and posterior views of **Pb** element, 23692/29-51.

FIGURES 21 and 22) anterior and posterior views of S_3 element, 23692/30-58.

FIGURES 23 and 24) lateral views of **Sa** element, 23692/30-59.

Specimens are currently deposited in the Dept. of Geological Sciences, University of Durham.
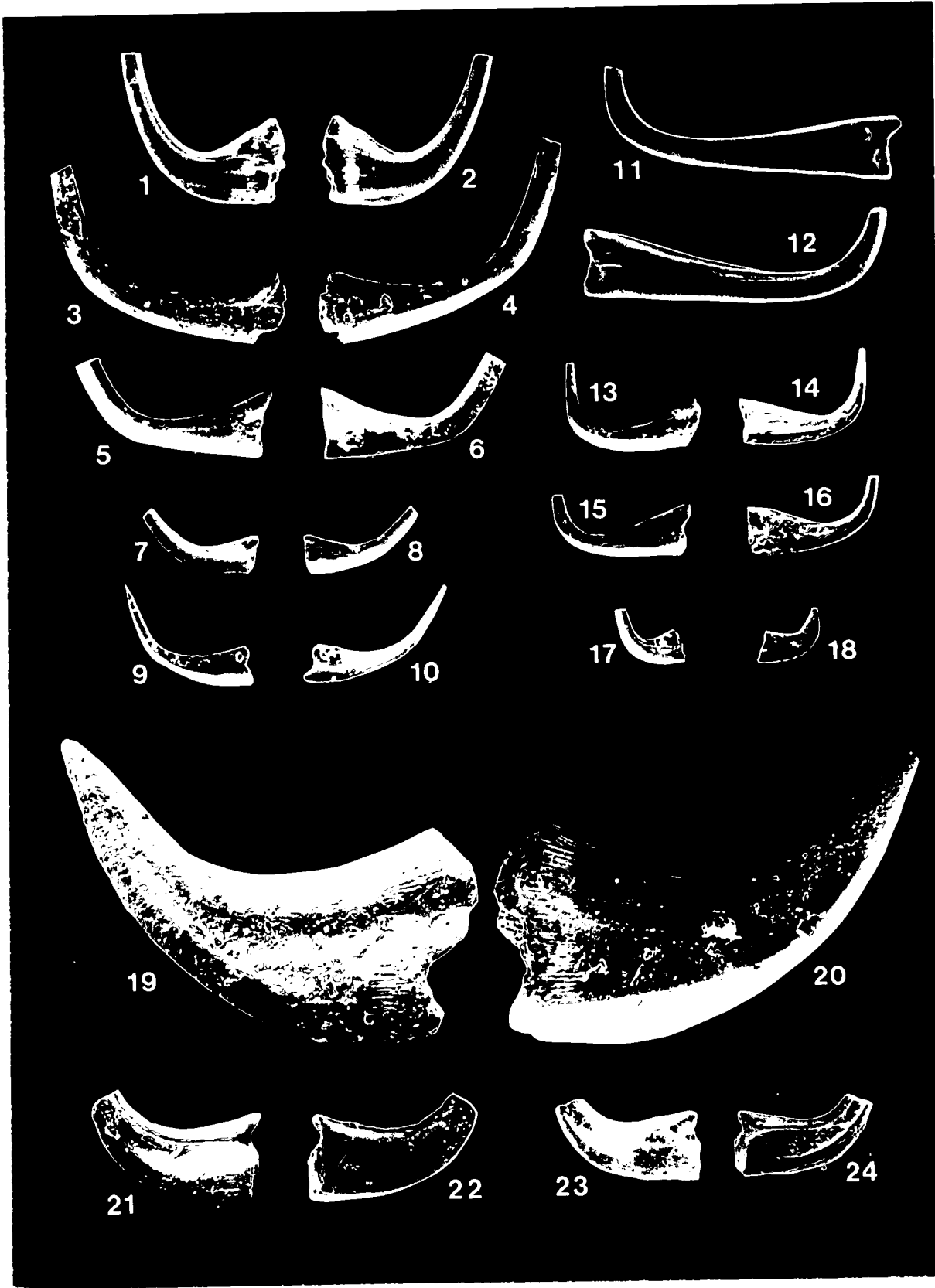
Plate 16

Panderodus feulneri (Glenister) from GGU 316839, Gonioceras Bay Member, Morris Bugt Group, North Greenland (see Tull 1988). All x 55 (continued from Plate 15).

FIGURES 1 and 2) anterior and posterior views of **Pa** element, 23692/29-52.

FIGURES 3 and 4) posterior and anterior views of 'low based' S_2 element, 23692/30-56.

FIGURES 5 and 6) posterior and anterior views of 'high based' S_2 element, 23692/30-57.

FIGURES 7 and 8) anterior and posterior views of 'high based' S_1 element, 23692/31-60.

FIGURES 9 and 10) posterior and anterior views of 'low based' S_1 element, 23692/31-53.

FIGURES 11 and 12) posterior and anterior views of M element, 23692/4-440.

Specimens are currently deposited in the Dept. of Geological Sciences, University of Durham.
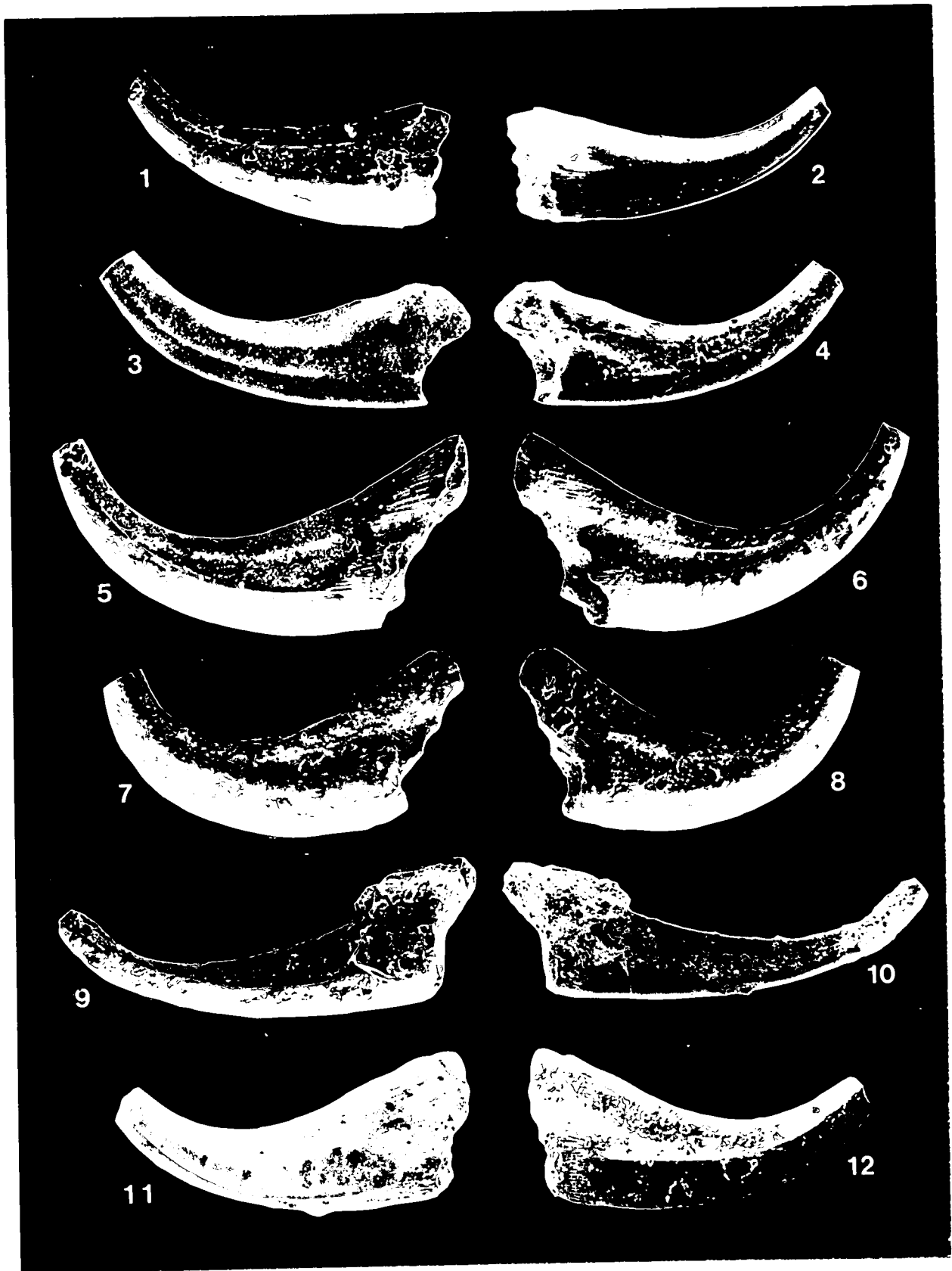
Plate 17

Panderodus panderi (Stauffer) from Shiqian 18, Leijiatun Section, Upper Member of Xiushan Formation, E. Guizhou Province, China (Aldridge, unpublished data). All x 55.

FIGURES 1 and 2) posterior and anterior views of **Pb** element, 23692/19-497.

FIGURES 3 and 4) posterior and anterior views of 'high based' S_2 element, 23692/19-493.

FIGURES 5 and 6) anterior and posterior views of elongate S_1 element, 23692/19-496.

FIGURES 7 and 8) posterior and anterior views of S_3 element, 23692/18-491.

FIGURES 9 and 10) lateral views of **Sa** element, 23692/19-498B.

FIGURES 11 and 12) posterior and anterior views of 'low based' S_2 element, 23692/19-492.

FIGURES 13 and 14) anterior and posterior views of **M** element, 23692/19-495.

FIGURES 15 and 16) posterior and anterior views of 'high based' S_1 element, 23692/16-478.

FIGURES 17 and 18) posterior and anterior views of **Pa** element, 23692/19-498A.

Panderodus breviusculus Barnes from GGU 316843, Gonioceras Bay Member, Morris Bugt Group, North Greenland (see Tull 1988). All x 55.

FIGURES 19 and 20) posterior and anterior views of **M** element, 23692/18-490.

FIGURES 21 and 22) posterior and anterior views of **Pb** element, 23692/23-14.

FIGURES 23 and 24) posterior and anterior views of $?S_1/S_3$ element, 23692/18-488.

FIGURES 25 and 26) posterior and anterior views of $?S_2$ element, 23692/18-489.

Specimens are currently deposited in the Dept. of Geological Sciences, University of Durham.
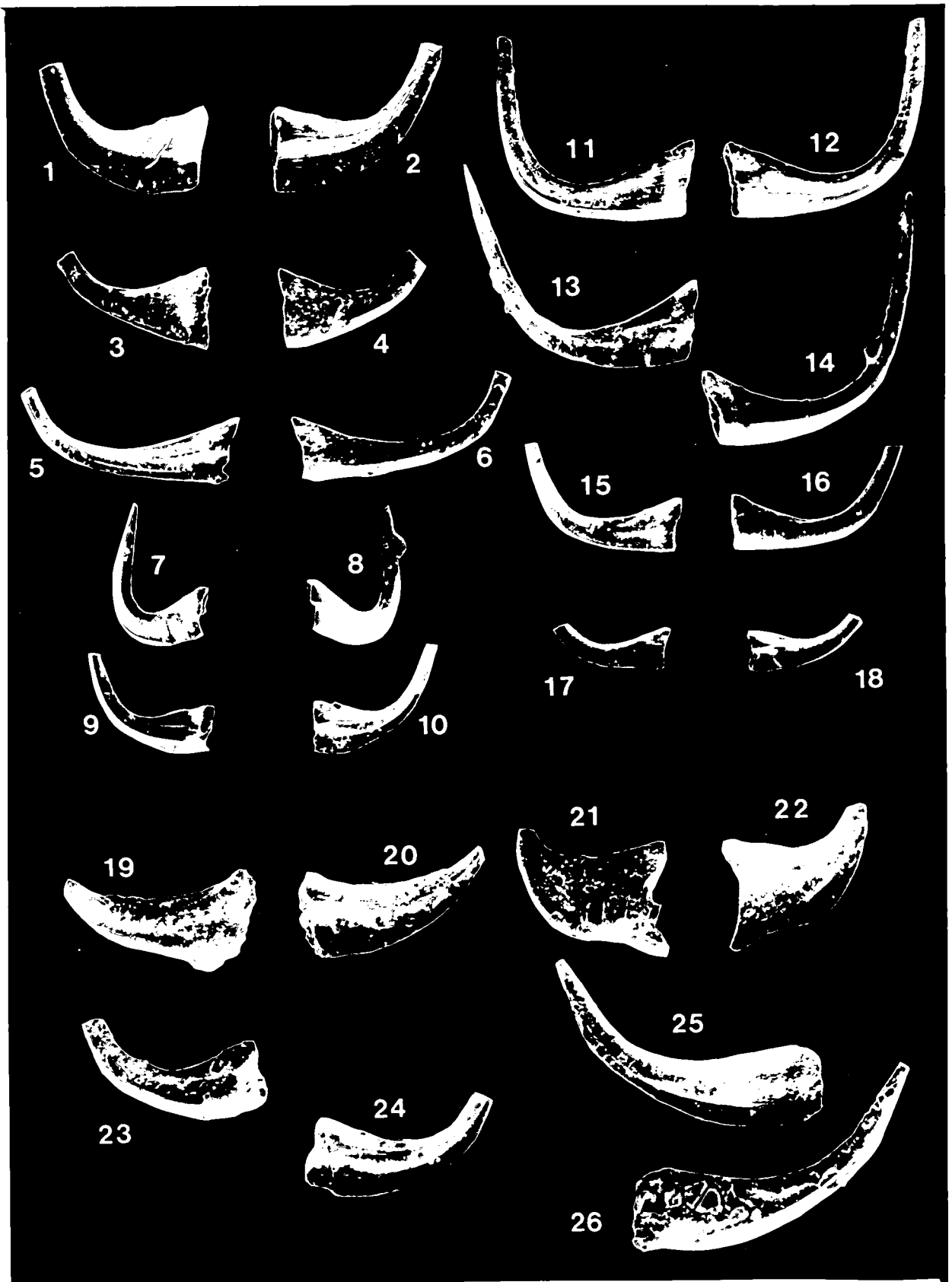
Plate 18

Panderodus staufferi (Branson, Mehl and Branson) from Ireviken 3, Upper Visby Beds, Götland (see Laufeld 1974). All x 55.

FIGURES 1 and 2) posterior and anterior views of M element, 23692/27-41.

FIGURES 3 and 4) anterior and posterior views of 'low based' S_1 element, 23692/17-486.

FIGURES 5 and 6) posterior and anterior views of 'high based' S_2 element, 23692/10-4116.

FIGURES 7 and 8) anterior and posterior views of 'high based' S_1 element, 23692/17-484.

FIGURES 9 and 10) posterior and anterior views of 'low based' S_2 element, 23692/17-485.

FIGURES 11 and 12) anterior and posterior views of Pb element, 23692/29-49.

FIGURES 13 and 14) anterior and posterior views of S_3 element, TG4/355.

FIGURES 15 and 16) lateral views of Sa element, TG4/407.

FIGURES 17 and 18) posterior and anterior views of Pa element, 23692/10-4117.

Specimens are currently deposited in the Dept. of Geological Sciences, University of Durham.
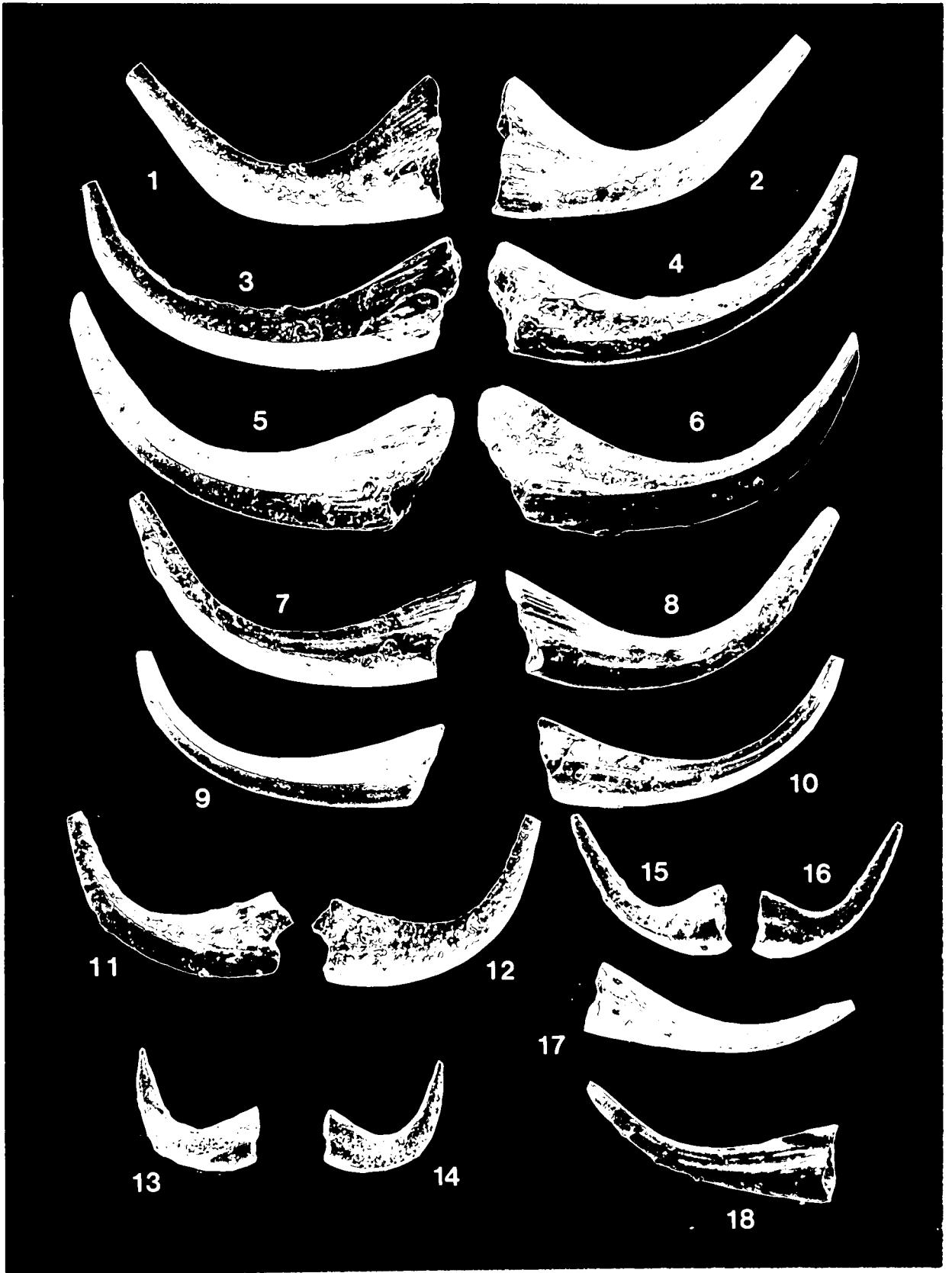
Plate 19

Panderodus sulcatus (Fåhræus) from J69-43, Flåsjö Formation, Gusta Quarry, Jämtland, Sweden (see Löfgren 1978). All x 110.

FIGURES 1 and 2) posterior and anterior views of **Pb** element, 23692/33-78.

FIGURES 3 and 4) posterior and anterior views of **M** element, 23692/33-75.

FIGURES 5 and 6) anterior and posterior views of 'high based' S_1 element, 23692/33-77.

FIGURES 7 and 8) posterior and anterior views of 'low based' S_1 element, 23692/33-73.

FIGURES 9 and 10) lateral views of **Sa** element, 23692/32-72.

FIGURES 11 and 12) anterior and posterior views of S_2 element, 23692/33-74.

FIGURES 13 and 14) posterior and anterior views of S_3 element, 23692/34-80.

FIGURES 15 and 16) lateral views of **Sa** element, 23692/6-451.

FIGURES 17 and 18) anterior and posterior views of **Pa** element, TG4/345.

Specimens are currently deposited in the Dept. of Geological Sciences, University of Durham.
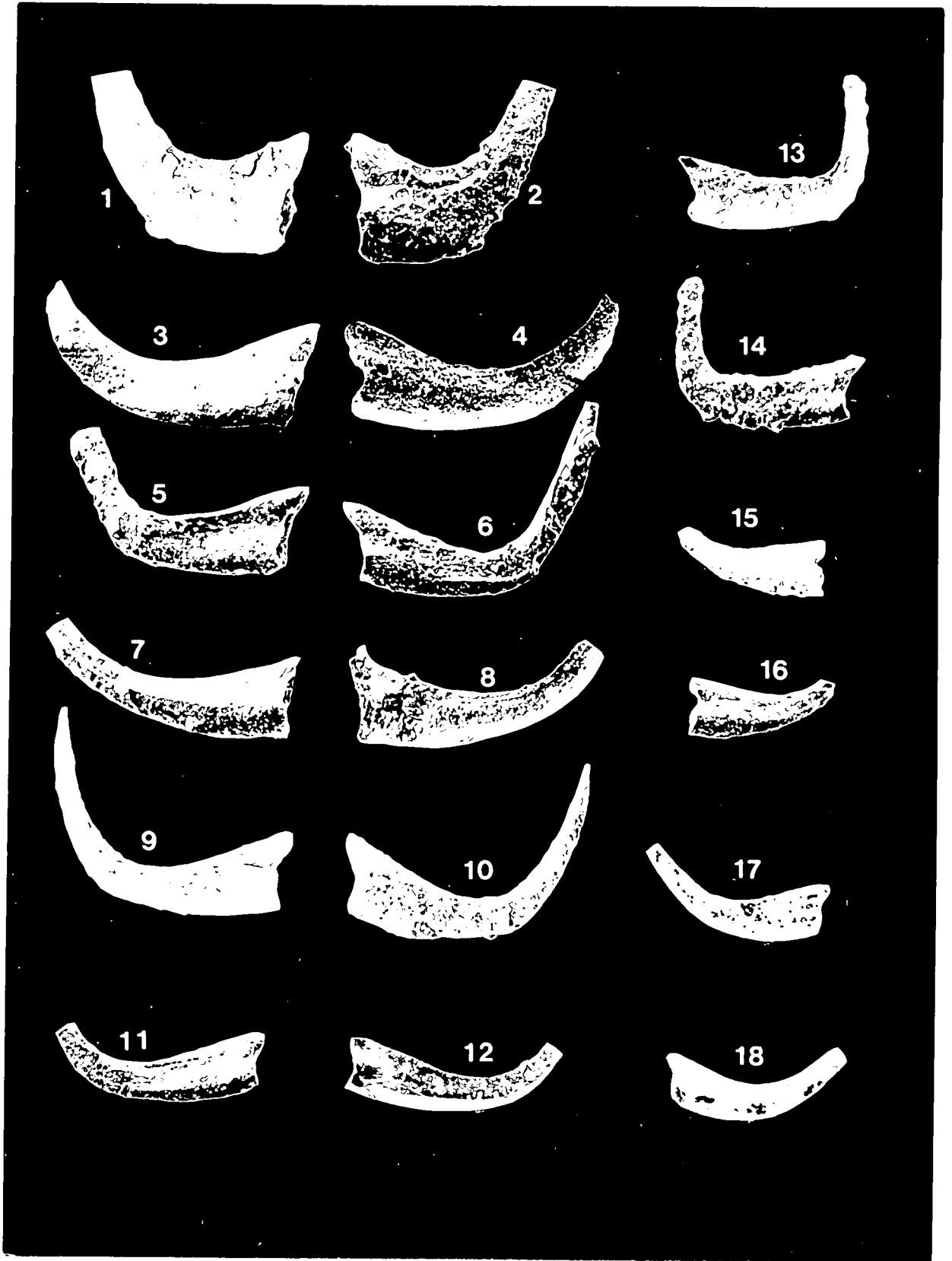
Plate 20

Panderodus unicostatus (Branson and Mehl) from the Bainbridge Formation, Lithium, Missouri (see Rexroad and Craig 1971). All x 55.

FIGURES 1 and 2) anterior and posterior views of Pb element, 23692/31-61.

FIGURES 3 and 4) anterior and posterior views of 'high based' S_1 element, 23692/32-67.

FIGURES 5 and 6) anterior and posterior views of 'low based' S_1 element, 23692/5-448.

FIGURES 7 and 8) posterior and anterior views of 'low based' S_2 element, 23692/32-66.

FIGURES 9 and 10) anterior and posterior views of 'high based' S_2 element, 23692/31-62.

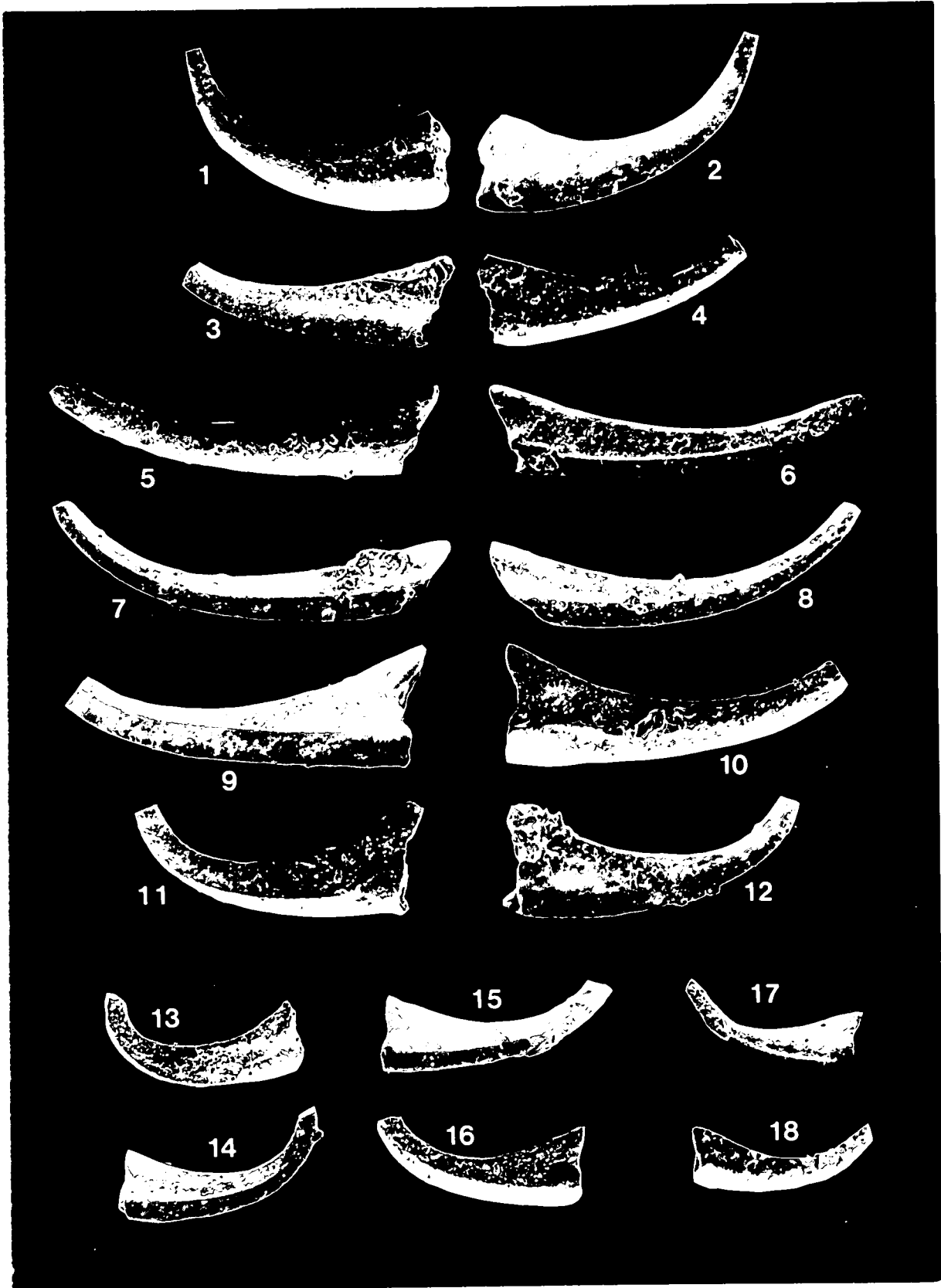**FIGURES 11 and 12)** posterior and anterior views of M element, 23692/32-68.

FIGURES 13 and 14) posterior and anterior views of S_3 element, 23692/5-447.

FIGURES 15 and 16) lateral views of Sa element, TG4/427.

FIGURES 17 and 18) posterior and anterior views of Pa element, 23692/31-65.

Specimens are currently deposited in the Dept. of Geological Sciences, University of Durham.

Appendix 1.
SAMPLE LOCATION AND PREPARATION

Sample preparation

Although this project has largely been laboratory based, a few limestone samples have been processed for conodonts. These were digested in acetic (ethanoic) acid solution. Jeppsson *et al.* (1985) have documented the detrimental effects of acetic acid on conodonts, and, following their recommendations, a buffered solution was used. Instead of spent acetic acid, 70 g of precipitated calcium carbonate was placed in a bucket containing up to 1.5 kg of sample, suspended in a plastic colander. Larger samples were split up into additional buckets. 875 cm^3 of 80% acetic (ethanoic) acid was then added, and the solution made up to 7L with hot tap water (i.e. 10% acetic acid solution). The digestion was allowed to proceed for 1 week, then the spent acid was decanted through a coarse top sieve (1 mm) with a 60 μm sieve below. The coarse fraction was returned to the bucket, fresh calcium carbonate and acid solution being added. This process was allowed to continue for 3 weeks, or until the rock had been totally digested, with the fine fraction being collected and dried after each sieving.

All dried fine residues were separated using a heavy liquid, bromoform (tribromomethane). The heavy residues were dried again, and allowed to run through a Cook isodynamic magnetic separator at 1 Amp with a 10° short axis tilt and a 16° long axis tilt. The magnetic fraction was run through twice to make sure that all the non-magnetic conodont elements were recovered.

The non-magnetic residue was then picked for conodont elements using a standard grid tray with a fine brush wetted with distilled water.

Samples

During the course of this project I have been allowed access to a large number of collections in the care of Dr. R.J. Aldridge (Leicester University). These include the thesis collections of Tull (1988) and the collections of Armstrong (1990), covering the Middle Ordovician to Early Silurian of the North Greenland carbonate platform. Dr. Aldridge has also allowed me access to material from Great Britain, Götland and China, as well as his collections of topotype material from the Bainbridge and Brassfield Formations of the U.S.A..

In addition, during visits to Lund University, Dr. L. Jeppsson has allowed me access to his collections from Götland (Jeppsson 1983a,b); and topotype collections from the Setul Limestone, Langkawi Islands, Malaysia. Dr. A. Löfgren has given me material yielding *Panderodus sulcatus* from Jämtland, Sweden, equivalent to J69-43 and J70-167 (Löfgren 1978).

Dr. G.A. Young (Manitoba) collected a number of samples from Götland, which he permitted me to process for conodonts, and I have also worked with a large number of specimens recovered from the tramway section, Netherton, W. Midlands (see Aldridge 1988).

Götland, Sweden

"Roda Lagret" (below Lower Visby Beds)

Själsö

Sample size: 1828 g

Själsö

	Pa	Pb	Sa	S3	S1	S2	M
P. unicostatus	3	28	5	2	30	25	20
P. gracilis		2				3	
P. langkawiensis		10		2	14	11	6

Lower Visby Beds

Nyhamn 1 (Laufeld 1974)

Sample size: 1155 g

Nyhamn 1

	Pa	Pb	Sa	S3	S1	S2	M
P. staufferi	1	3	2	1	6	1	1
P. unicostatus	3	67	2	1	36	44	38
P. langkawiensis	2	28	2	3	26	15	21

Ireviken 3 (Laufeld 1974)

Sample size: 3050 g

Ireviken 3

	Pa	Pb	Sa	S3	S1	S2	M
P. staufferi	9	37	7	14	19	26	23
P. langkawiensis	3	25	2	1	11	18	8
P. unicostatus	15	128	3	3	116	92	68

Mulde Beds (lower part)

Djupvik 1 (Laufeld 1974)

Sample size: 1151 g

Djupvik 1

	Pa	Pb	Sa	S3	S1	S2	M
P. equicostatus	5	4	1	1	4	6	2
P. unicostatus	1	6			2		1

Klinteberg Beds

Krasse 1 (Laufeld 1974)

Sample size: 786 g

Krasse 1

	Pa	Pb	Sa	S3	S1	S2	M
P. equicostatus		4		1	2	7	3

Jämtland, Sweden

J69/43 (see Löfgren 1978)

Sample size: 1954 g

J69/43

	Pa	Pb	Sa	S3	S1	S2	M
P. sulcatus	17	32	5	3	45	37	31

J70/167 (see Löfgren 1978)

Sample size: 499 g

J70/167

	Pa	Pb	Sa	S3	S1	S2	M
P. sulcatus	2	6	1		7	8	10

Brassfield Limestone, Cincinnati Arch, U.S.A.

(see Rexroad 1967)

Sample size: unknown

Brassfield

	Pa	Pb	Sa	S3	S1	S2	M
P. equicostatus	30	252	23	17	179	232	216
P. panderi	7	13	1	4	11	25	5

Bainbridge Limestone, Lithium, Missouri, U.S.A.

(see Rexroad and Craig 1971)

Sample size: unknown

Bainbridge

	Pa	Pb	Sa	S3	S1	S2	M
P. unicostatus	14	62	6	5	85	72	38
P. panderi	4	33		2	17	12	4

Upper Whitcliffe Beds, tramway section, Netherton, West Midlands.

(see Aldridge 1985)

Sample size: 1001 g

Tramway Netherton

	Pa	Pb	Sa	S3	S1	S2	M
P. unicostatus	85	359	29	14	259	209	261

Appendix 2

RESIN SUPPLIERS

Trylon Resins supplied by:

> Trylon Ltd.,
>
> Thrift Street,
>
> Wollaston,
>
> Northants NN9 7QJ.

'Crystic Resin' supplied by:

> B and K Resin,
>
> Unit 2, Ashgrove Estate,
>
> Ashgrove Road,
>
> Bromley,
>
> Kent.

Appendix 3.

SPECIMEN DEPOSITORIES

The material illustrated in this thesis from Waukesha, Wisconsin, U.S.A. (Plates 2, 3 and 4) is in the process of being transferred to the Geological Museum, University of Wisconsin, Madison.

Specimens illustrated from Greenland will be transferred to the Geological Museum, Copenhagen pending publication of these results.

Additional material described as 'currently deposited in the Dept. of Geological Sciences, University of Durham' is in the process of being transferred to the Lapworth Museum, University of Birmingham, where documentation detailing the transfer of the specimen numbers utilised herein into the Lapworth Museum system is kept with the collections.